School of Molecular and Life Sciences

## Urban native bee assemblages and the impact of the introduced European honeybee on plant-pollinator networks in the southwest Australian biodiversity hotspot

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This thesis is presented for the Degree of Doctor of Philosophy of Curtin University

July 2020

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## **Declarations**

My thesis contains no material previously published by any other person other than myself, except where due acknowledgment has been made.

I am primary author of all chapters and published manuscripts, and have included statements of the contributions of others of works included in my thesis. A summary table has been included stating the contributions of authors in terms of editing, however the study design, conceptualisation, field work, data collection, data analyses, drafting and writing of the manuscripts, creation of figures, were all performed solely by myself.

All content has been the product of work carried out since the commencement of my higher degree by research candidature. This thesis has not been submitted partially or in full to any other university or tertiary institution for the qualification of any other award or degree. I acknowledge that copyright of all my thesis content resides with the copyright holder, Curtin University, and will be made available immediately for research and study in the University Library.

This project received funding from my Forrest Research Scholarship award (2016); and my award as winner of the Australian Wildlife Society University Student Grants Scheme (2017).

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## Abstract

In a time of concerns over global pollinator declines, researching factors that influence the abundance and diversity of native bees has never been more pressing. Urbanisation and introduced species are both factors frequently cited as threatening processes, yet the ability of cities to host native bees, and the impact of the introduced European honeybee on native bees remain contested topics. In Chapter 1 I introduce these major issues surrounding native bee conservation, and the aims of my thesis.

In Chapter 2 I review research on bees in urban areas. I emphasise how urban areas are distinct landscapes compared with agricultural ones, and results on studies on the response of bees to anthropogenic landscapes that have been largely conducted in agricultural regions cannot be extrapolated to urban landscapes, which represent a major, increasing form of land-use where the majority of people live, work and play. I highlight that cities are not homogenous, and that the response of bees will vary according the historical land-use, habitat type within a city, and the ecological traits of the bee assemblage.

Any conclusions about bee assemblages are entirely dependent on the efficacy of the methods used to survey them. In Chapter 3 I empirically compare a number of standard entomological methods in sampling bees, as well as compare my findings with a review of the literature. I reveal that using passive methods alone is inadequate for sampling bee assemblages, and to accurately sample bees and draw valid conclusions, a variety of techniques should be deployed with sweep netting being indispensable.

As cities expand, native vegetation is cleared, whilst managed greenspaces in the form of residential gardens are created. In Chapter 4 I compare bushland remnants within urban areas with residential gardens in terms of the abundance, diversity and rarity of native bees, the abundance of honeybees, and whether the floral characteristics associated with these two habitat types explain the difference in their ability to host native bees. Bushland remnants were superior habitat for native bees

compared with residential gardens. In contrast, honeybees were unaffected by habitat type. A greater number of native flower species was, contrary to prediction, associated with fewer native bees, which may be explained by the specialised flower preferences of Australian bee biota.

There is an increasing recognition that species interactions are fundamental to the health and functioning of ecosystems. In Chapter 5 I construct plant-bee interaction networks, and reveal how bushland networks are healthier, but more vulnerable to species' losses, than are residential networks.

The European honeybee is an abundant, introduced species, and therefore has the potential to disrupt plant-pollinator networks and compete with indigenous bees. In Chapter 6 I reveal that honeybees occupy distinct positions in plant-pollinator networks, and abundance of honeybees is significantly associated with altering pollination network structure. In Chapter 7 I test the hypothesis that honeybees are outcompeting native bees. I found that the situation is nuanced, with the effect of honeybees varying between years, habitat type, and native bee guild; however, there was evidence that honeybees have negative impacts upon those bee taxa that had a higher niche overlap with honeybees in terms of body size and overlap in flora use.

In Chapter 8 I conclude my thesis by synthesising the chapters to discuss the state of the field of urban pollinator ecology and the issues facing pollinator conservation. This thesis breaks new ground by addressing both the issues of native bee habitat requirements as well as potential competition with introduced species, thereby advancing the state of knowledge about how to preserve our precious pollinators. Future directions are identified, and limitations are recognised. The first systematic study to be conducted on native bees in the southwest Western Australia biodiversity hotspot, my thesis underscores the incredible biodiversity of wild bees that exist in this urbanised region, and the results from my comprehensive surveys and investigation into the factors that influence native bee populations can offer evidence-based ways to contribute to conservation of pollinators in urban areas and ensure that native bees keep on buzzing in the 'burbs of this biodiversity hotspot.



Thyreus waroonensis © Kit Prendergast

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Photograph courtesy of Viva Photography

# Papers included in the thesis, and statement of contributions by others

Chapters 2 to 7 of this thesis have been prepared as manuscripts for peer-reviewed publications in the scientific literature, and are reproductions of submitted and published manuscripts. Signed author statements are provided in Appendix 10. I have obtained permission from the copyright owners to use any third-party copyright material reproduced in this thesis, and to use any of my own published work in which the copyright is held by another party. Permission for paper reproductions in this thesis can be found in Appendix 3.

The review that comprises Chapter 2 has been submitted to the peer-reviewed journal '*Insect Conservation & Diversity*' on 4 May 2021:

**Prendergast, K. S.,** Dixon, K. W., & Bateman, P. W. (2021). A global review of determinants of native bee assemblages in urbanised landscapes. *Insect Conservation & Diversity, under review*.

I conceived the ideas and conducted the literature search and review, analysed the data, wrote the manuscript, and created all figures and tables. All authors contributed to the revisions of the manuscript.

The study and review comprising Chapter 3 was published within the peer-reviewed journal, '*Ecosphere*' on May 20<sup>th</sup>, 2020:

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- Prendergast, K., Vanderstock, A., Neilly, H., Ross, C., Pirotta, V., & Tegart, P. (2021). Potential and pitfalls of citizen science with children: Reflections on Pollinators in the Playground project. *Austral Ecology*. (Online Early, Special Issue: Insect Traits/Ecology). DOI: 10.1111/aec.13031. Available: <u>https://doi.org/10.1111/aec.13031</u>
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Megachile sp., male. © Kit Prendergast

# Chapter 1

# **General Introduction**



Megachile speluncarum © Kit Prendergast

#### **1. General Introduction**

#### **1.1.** The stars of the show and the threats they face

Bees are a fascinating and diverse group of hymenopterans, and many species play crucial roles in ecosystems as pollinators (Brown & Paxton, 2009; Winfree, 2010). Recently, concerns that bees are declining across the globe have become prevalent (Potts et al., 2010). The exact causes differ according to the ecological traits of bees, but in general, common to biodiversity declines as a whole, loss of habitat is the leading cause of species declines and extinctions (Brown & Paxton, 2009; Pimm & Raven, 2000). For bees in particular, loss of flowering habitat, which bees require for food, is particularly egregious (Potts et al., 2010).

#### 1.1.1. The urban jungle

Today one of the most rapidly growing forms of habitat destruction is urbanisation (Güneralp et al., 2013). Urbanisation produces major changes to the environment, including loss of natural habitat, habitat fragmentation, increases in impervious surfaces, and altered plant community composition, with a preponderance of exotic flora (Faeth, Bang, & Saari, 2011). The impact of urbanisation on bees is, however, inconsistent, and varies according the city being surveyed, the habitat type(s) surveyed, and the ecological traits of bees (Hernandez, Frankie, & Thorp, 2009). Perth, the capital city of Western Australia, is a region of ongoing urban expansion (MacLachlan, Biggs, Roberts, & Boruff, 2017). Like many urban hubs however, it is located in a region that originally harboured high amounts of biodiversity (Ives et al., 2016). Notably, the Perth metropolitan region is situated in an internationally recognised biodiversity hotspot of the southwest Western Australian Floristic Region (Hopper & Gioia, 2004). With ongoing land-clearing for industrial, and especially residential, urban development, only a fraction of the original native vegetation remains, with patches of native remnant vegetation left interspersed throughout the metropolitan area (Gole, 2006; Hopper & Burbidge, 1989). Despite the high floristic diversity in the region, the native bee assemblages and their habitat associations has

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never been explicitly studied, and the response of native bees to urbanisation in this biodiversity hotspot has never been investigated.

#### 1.1.2. An introduced competitor

Another major factor that can pose a threat to native biodiversity is introduced species. Ironically, much of the attention by the public and the media has focussed on an introduced species, the European honeybee, Apis mellifera (Smith & Saunders, 2016). Although there have been colony losses in recent years, particularly in the United States and Europe, honeybees globally have in fact been on the rise (Aizen & Harder, 2009). In Australia, honeybees are by no means threatened with extinction, and being free of diseases that have impacted honeybees elsewhere on the globe, the honeybee population in Australia is thriving (Benecke & Rural Industries Research and Development Corporation, 2007). The success of this introduced species, however, may come at the expense of native bees. Both honeybees and native bees need flowers for food, and if these are in short supply, honeybees may compete with native bees (resource competition). Given the highly efficient search, communication and foraging behaviours of this eusocial species, its catholic diet, and high abundance, as well as aggressive tendencies, it can be expected that honeybees are superior competitors (Geslin et al., 2017). Australia has a high diversity of native bees (estimated at approximately 2,000 species, with many undescribed), the majority of which are endemic (Batley & Hogendoorn, 2009). Honeybees are a highly adaptable, successful, abundant species (Geslin et al., 2017), and there are concerns that this introduced species is a threat to native bee populations both overseas (Henry & Rodet, 2018), as well as in Australia (Sugden, Thorp, & Buchmann, 1996). However, actual empirical studies to date have found mixed evidence in support for the hypothesis that honeybees are outcompeting native bees (Mallinger, Gaines-Day, & Gratton, 2017). Given that Australia's native bees have evolved in isolation from this large, eusocial generalist species, the European honeybee, introduced just two centuries ago yet now a dominant component of insect assemblages across most of the country, may pose a major risk to the preservation of native bee biodiversity. It is important to provide a firm foundation on how honeybees affect native bee communities in the southwest Australian biodiversity

hotspot, given the economic importance of the honeybee industry, but also the potential for honeybees to cause declines or even extinctions of native pollinators.

#### **1.2.** Aims of this thesis

It is known that threatening processes do not act in isolation, and that when combined, can act synergistically to amplify negative impacts (Vanbergen, 2013); yet how honeybees interact with native bees in urban areas has been seldom studied, and has never been investigated explicitly in Australia. There is also an urgent need to document and describe the biodiversity of native bees, identify threatening processes, and identify what local and landscape factors influence the distribution, abundance and diversity of native bees in urban areas to inform management that preserves the integrity of native bee assemblages and the pollination networks in which they participate.

Based on a recognition of the crucial importance of native bees, concerns over pollinator declines, and key research gaps relating to how wild bees respond to urbanisation, and the impact of the introduced European honeybee, my thesis addressed the overarching question of what factors structure native bees and pollination networks in an urbanised landscape? (Fig. 1.1). The following chapters that comprise this thesis together produce a coherent narrative addressing these pressing research gaps (Fig. 1.1).

Chapters 2-7 comprise papers published, in review for publication, or prepared for publication in academic journals, and follow the formatting and referencing style of these journals. Due to being independent, yet connected, articles, there is therefore some redundancy when it comes to describing the study site, and sampling methodologies.

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Fig. 1. 1. Conceptual framework relating the background, key research questions, and aims of my thesis.

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## Chapter 2

# A global review of determinants of native bee assemblages in urbanised landscapes

This study presented in Chapter 2 has been submitted to the peer-reviewed journal *'Insect Conservation & Diversity,'* on May 4<sup>th</sup>, 2021:

Prendergast, K. S., Dixon, K. W., & Bateman, P. W. (2021). A global review of determinants of native bee assemblages in urbanised landscapes. *Insect Conservation & Diversity, under review.* 



Amegilla sp. © Kit Prendergast

# A global review of determinants of native bee assemblages in urbanised landscapes

### 2.1. ABSTRACT

- Loss of natural habitat through land-use change threatens bees. Urbanisation is a major, increasing form, of habitat loss, and a novel, pervasive form of disturbance.
- 2. Our comprehensive review, involving 215 studies, quantifies response of bees to urban landscapes, and local and landscape variables proposed to influence bee abundance and diversity.
- Urban areas tend to be favourable habitat for bees compared with agricultural ones, whereas compared with natural areas, urban areas often host more abundant populations yet fewer species.
- 4. Factors associated with urban landscapes, such as increases in non-native bees and plants, and changes in nesting substrate types and availability, contributes to changes in abundance, species richness, and composition of native bee assemblages. However, there is high variability in responses; arising from sampling methodology, ecological traits of bees, habitats surveyed, geographic region, and the very definition of what constitutes "urban" and "natural".
- 5. Identifying what biotic and abiotic features of cityscapes promote or threaten the persistence of diverse urban bee guilds is critical. This review provides a comprehensive evaluation of how bees (both in aggregate and according to their ecological guild) have responded to urbanisation, identifies gaps in knowledge in urban bee ecology, and proposes priorities for conserving and promoting diverse bee communities in urban habitats.

#### 2.2. INTRODUCTION

Bees are the most important pollinating group globally (Willmer et al. 2017) and the pollination services they perform are essential for stable, functioning ecosystems, both natural and anthropogenic (Potts et al. 2016). Although the domesticated European honeybee *Apis mellifera* is the most familiar and widely managed pollinator, wild bees, with an estimated global diversity of over 20,000 species, are critical to healthy ecosystems, and are an essential component of biodiversity (Garibaldi et al. 2013; Michener 2007).

There have been documented declines of bees across Europe and America, particularly over the last 50 years (Biesmeijer et al. 2006). Although monitored declines mainly focus on honeybees and bumblebees (*Bombus* spp.), there are concerns that bee declines are a global phenomenon (Potts et al. 2010). The conservation status of most bees, however, is unknown (Potts et al. 2016). The majority of investment directed towards addressing perceived declines in bees has been mainly confined to northern hemisphere agricultural contexts (Winfree 2010), and has predominantly involved agri-environmental schemes (AES), with varying outcomes (Kleijn et al. 2001; Wood et al. 2015). AES provide financial support for implementing measures such as setting aside grassy-field margins and sowing wildflower strips (Science for Environment Policy 2017); however, it is unclear whether such agricultural management strategies targeted at pollinator conservation is applicable to bees in urban settings.

Urbanisation is considered a leading form of ecologically-destructive global change (Elmqvist et al. 2016). Urbanised environments – landscapes of human settlement that are created specifically for human occupation (McIntyre et al. 2008) – are the most heavily-modified, and rapidly expanding forms of anthropogenic land-use modification (Seto et al. 2011). From 2000 to 2030 global urban expansion has been predicted to increase by 285% (Seto et al. 2012), and is occurring in regions known to harbour rare, endemic fauna (Ives et al. 2016; Phillips et al. 2010). Urbanisation is now a major driver of fragmentation and loss of natural habitat (Winfree et al. 2007), and a key cause of biodiversity loss worldwide (Brown and Paxton 2009), with bees

predicted to be especially susceptible (Winfree et al. 2011). However, depending on patch quality and connectivity, urban areas have the potential to support a high diversity and abundance of native bees (Hinners et al. 2012) (see Prendergast (2020): Dataset 1).

Compared with land-use change driven by agriculture, studies of bee communities in urban areas are underrepresented (De Palma et al. 2016). Evidence-based recommendations for bee-friendly management in cities are rare, yet there are promising opportunities to harmonise bee conservation with activities that promote ecosystem services and human welfare in cities.

Bee pollination maintains urban native and horticultural vegetation in reserves, parks, gardens, roadside verges and other green spaces (Cane et al. 2005; Lin et al. 2015). When urban bee communities are depleted, bee-pollinated plants may suffer poor fruit and seed set, inbreeding and loss of genetic diversity (Hobbs and Yates 2003). Because diversity of bee species with different functional traits underpins ecologically-resilient, thriving pollination services (Fontaine et al. 2005; Lowenstein et al. 2015), conserving a diverse assemblage of bees in urban areas is important for maintaining plant populations in urban greenspaces (Matteson and Langellotto 2009).

Here we review bee responses to urbanisation across the globe. Although there have been reviews on, or that include, bees in urban areas (Cane et al. 2005; De Palma et al. 2015; Hall et al. 2017; Hernandez et al. 2009; Wenzel et al. 2019; Winfree et al. 2009; Winfree et al. 2011; Wojcik 2009; Wojcik and Buchmann 2012), this review, considering 215 studies in total, is the most comprehensive to date. Moreover, previous reviews have not conducted semi-quantitative analyses for how either abundance or species richness vary according to landscape type, habitat type, and local and landscape variables, nor how responses vary by taxon and functional traits. We also provide a theoretical basis for developing hypotheses, and identify key knowledge gaps.

#### 2.3. METHODS

From August 2016 to Dec 2019 searches were performed in Google Scholar using terms: "bees, pollinators, insects, arthropods, urbanisation, cities, urban, land-use change, native bees, wild bees, suburban, metropolis" or combinations thereof. Google Scholar was most suitable for this review, give the greater coverage (Martín-Martín 2018, 2021). It is a search engine with less barriers than many other search engines, being not restricted to someone who is affiliated with a research institution, democratising the process; and does not suffer from constrained coverage, so as to ensure that publications that were still relevant - theses, books, reports, and conference proceedings, or which may not be in mainstream English science journals (e.g. especially those published in developing countries) - could be included. Cited literature was accessed and incorporated where appropriate. Papers were those conducted in urban landscapes, or considered the influence of surrounding urban land-use, on bees. This resulted in a total of 215 studies, comprising 198 texts (disparities in these numbers are because some studies were unpublished studies cited published studies, thesis chapters, or involved multiple studies published in one text). Texts were primarily peer-reviewed studies, but also reviews, books, theses, and field guides, were included (Prendergast 2020: Dataset 1). Landscape and habitat types were assigned according to categories provided by text authors. For single-species publications we excluded those on honeybees, as honeybee numbers are largely impacted by husbandry factors (Champetier et al. 2015). We could not attempt a meta-analysis due to the extreme variability in survey duration and frequency, sites surveyed, area surveyed, survey methods, sampling intensity, range of flora surveyed (single plant species, experimental plants, whole floral communities), and taxonomic resolution (Prendergast 2020: Dataset 1, Fig. 2.1). From these studies we conducted a semi-quantitative review, which nevertheless enables quantifying suggestive trends and patterns. To achieve this, for each study, we extracted the following information: the main findings; the type of study (whether it was a community study, on a subset of the bee community, or focused on just one or a few species); details about the study design, namely - the geographic region, city, and climatic zone in which the study was conducted; the number of sites surveyed, duration of the study (number of months per year, and number of years), the sampling area, the sampling intensity (effort), and the sampling method used; the

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landscape type it was conducted in (natural/rural/urban), and for urban studies, the habitat type(s) surveyed; and finally, whether it was a gradient study, looking at bee communities along a gradient of urbanization (Prendergast 2020: Dataset 1). This enabled us to summarise the biogeographic representation of urban bee studies and study design elements by tabulating the relative representation of studies by country, method and habitat. For studies providing data on bees in urban landscapes as well as those in agricultural and natural landscapes, we determined whether bees were more, less, or non-significantly different between these landscapes for both abundance and species richness. We also extracted information on environmental variables that can be considered to likely be influential in impacting bee communities that each study measured and how these related to bee abundance and/or diversity - these related to both food and nesting resources, and landscape composition, and we coded each study in terms of these variables having a positive, negative, or non-significant impact on bees (Prendergast 2020: Dataset 1). In addition, we investigated how ecological traits of bees influenced their response to these environmental variables, coding each study similarly when information was provided on bee responses according to ecological guilds based on nesting substrate, kleptoparasite/host guild, sociality, body-size, lecty (i.e. specialization), origin (native/exotic status), or bee taxonomic categories. We then tabulated for abundance and species richness the number of responses (positive, negative, non-significant) for each category (Prendergast 2020: Dataset 2; Prendergast 2020: Dataset 3). Finally, we also investigated the community composition of bees in urban areas, extracting information from each study in terms of the number of individuals recorded, the number of species, number of genera, dominant taxa, representation of rare species, and community composition. We also extracted information about the representation of exotic species, including the European honeybee, and the guild structure of bees in urban areas, in terms of the relative abundance and species richness of bees according to the aforementioned ecological guilds (Prendergast 2020: Dataset 1, Fig. 2.1).

#### 2.4. **RESULTS AND DISCUSSION**

#### 2.4.1. Overview of urban bee studies

Of the 215 studies reviewed (Prendergast 2021: Dataset 1) (Fig. 1a), 166 involved bee communities (Prendergast 2021: Dataset 1). Of studies looking at a subset of bees, 18 involved *Bombus*, two Meliponini, three Euglossini, and six involved cavity-nesting bees (Fig. 1b). Thirty-two studies focused on one (or a few species), covering a range of topics (Fig. 1d); despite this diversity of topics, there was a clear taxonomic bias: 76.3% were apids, and of these, 65.6% were *Bombus* (Fig. 1c). Therefore, both guild-based and species-level studies were over-represented by apids. Given that these are social, generalist bees, any conclusions on bees in general are restricted. More studies on specialist taxa are required, and on halictids and cavity-nesting megachilids, which are large components of bee fauna in urban areas (see Prendergast 2021: Dataset 1, and guild-based discussion below).

Methods to survey bees varied (Fig. 2.2a); most used only one method. This is concerning give that multiple methods are recommended to obtain a comprehensive and representative sample of bee communities (Prendergast et al. 2020). There was also a large variation in study duration and sampling intensity. Most studies were restricted to a single season or year (Fig. 1a), raising concerns over the reliability of conclusions given high variability in bee populations (Roubik 2001).



**Fig. 2. 1.** Summary of studies involved in this review, including a) the mean and range for the number of bee individuals, species and genera recorded; number of sites surveyed; and survey duration; b) break-down of taxonomic focus (communities, subset of bee communities, or species-focus); c) the single species taxonomic focus and d) single-species focus topics. *Bombus,* Meliponini and cavity-nesting bee images (b) by Kit Prendergast, Euglossini bee (b) by Alejandro Santillana, "Orchid bee (Apidae, Euglossa championi (Cheesman))CR, Heredia, 5 KM S.E. Pt. ViejoFinca La Selva, 350 ft.10°25'N 84°01'WVII.1975 L.E. Gilbert", created as part of the Insects Unlocked project at the University of Texas at Austin, based in the UT insect collection at Brackenridge Field Laboratory, part of the Department of Integrative Biology. Made available under the Creative Commons CC0 1.0 Universal Public Domain Dedication, available: https://flickr.com/photos/131104726@N02/36112353184



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**Fig. 2. 2.** Breakdown of urban bee studies in terms of a) survey methods; b) urban habitat types surveyed. Note that some studies included more than one topic/habitat type, or didn't include the habitat type and just classified it as "urban", hence total numbers may be greater or less than the total number of studies.

Categories of habitat types in which native bee surveys and studies have been conducted (f): residential garden: residential / home gardens; Industrial: industrial, commercial or business district; park: public green area, often recreational; urban ag: veggie garden, urban orchard; native remnant: native vegetation fragment or remnant vegetation within the urban matrix; green linear element: linear vegetation element including roadsides, rights-of-way, railways; Uni: university campus; cemetery: cemetery, churchyard or temple; wasteland: derelict site, landfill, vacant lot; greenspace: public lawn, sometimes ill-defined in papers.

There was an extreme geographic, and therefore associated climatic and phylogenetic bias in urban bee studies (Fig. 2.3): Approximately 40% were conducted each in Northern America and Europe; particularly under-represented was Africa and Asia, despite having a large proportion of the global population living in urban areas (Ritchie and Roser 2020). The fewest studies were conducted in the Middle East. There was a further bias considering countries – of the 26 countries were bee studies have been conducted, approximately 35% of studies were undertaken in the USA, 15% in the UK, 9% in Germany, and 7% in Brazil, indicating over two-thirds of studies occurred in just four countries. Across all types of studies there was a diversity of habitat types in which bee surveys were conducted; residential gardens were over-represented (Fig. 2.2b).



Source: Beck et al.: Present and future Köppen-Geiger climate classification maps at 1-km resolution, Scientific Data 5:180214, doi:10.1038/sdata.2018.214 (2018)

#### Fig. 2. 3. Geographic and thus climate locality of urban bee studies.

Map sourced from Beck et al. (2018) "Present and future Köppen-Geiger climate classification maps at 1-km resolution". Nature Scientific Data.

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#### 2.4.2. Bees in urban vs. natural and agricultural landscapes

Natural, urban and agricultural landscapes present different biotic and abiotic conditions which determine the assemblage of bees present (Table 2.1). Although urban and agricultural lands tend to be more similar to each other than to natural habitats in terms of both being anthropogenic habitats (Ellis et al. 2010), there are also distinct differences between them in abiotic and biotic conditions (Table 2.1), reflected in distinctive bee assemblages (De Palma et al. 2016; De Palma et al. 2015; Sattler et al. 2011). Generalisations from bee responses to agricultural landscape modification should not, therefore, be extrapolated to urban landscapes.

Urbanisation is associated with increased densities of humans and non-native species, urban heat island effects, environmental contaminants, and altered ecosystem dynamics, which may contribute to insect declines (Jones and Leather 2012) (Table 2.1, references therein). In many taxa, radical alterations of the environment through urbanisation leads to shifts in phenology, and changes in species richness, abundance and evenness (the relative abundance of all species in a community), translating into altered community composition and structure (Faeth et al. 2011).

Aspect	Urban	Agricultural	Natural	Potential effects on bees	Examples
Habitat	High	Low	Low-Intermediate	+: $\uparrow$ diversity of habitats = resources for $\uparrow$ species of	(Jha and Kremen 2013;
heterogeneity				bees	Kaluza et al. 2016)
				$-: \uparrow$ fragmentation & reduced patch size = $\downarrow$ patch	
				colonisation & $\downarrow$ area suitable for foraging/nesting	
Habitat	High	Intermediate	Low	+: ↑ range of habitat-types	(Cane 2001; Didham et al.
fragmentation				— : prevents (re)colonisation of suitable habitat	1996)
				patches;	
				$\downarrow$ demographic & genetic connectivity ; $\downarrow$ habitat size	
Patch size	Small	Large	Large	+: concentrate resources = $\uparrow$ bee density (but $\downarrow$	(Howell et al. 2017;
				abundance at landscape scales)	Steffan-Dewenter et al.
				— : smaller patches = $\downarrow$ bees & species	2006)
				Alter competitive dynamics: refuge from competition?	
				or intensify competition?	

<b>Table 2. 1.</b> Aspects of arban, agricultural, and that an arbitrary cupes, and then predicated encets for be	Table 2. 1. Aspe	ects of urban, a	agricultural/rural, ar	nd "natural"	landscape types	s, and their	predicated (	effects for bee
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Impervious	High	Low/absent	Absent	+: fences & buildings can provide nesting substrates for	(Eremeeva and Sushchev
surfaces				cavity-nesting bees	2005; Makinson et al.
				— : unsuitable for nesting, foraging	2016)
Roads	Numerous	Few	Few/none	+: linear landmarks = navigation and foraging efficiency;	(Baxter-Gilbert et al.
				vegetated roadsides = nesting and foraging resources	2015; Hopwood et al.
				$-: \uparrow$ isolation;	2015)
				vehicle collision mortality; impediments to movement	
				( $\downarrow$ foraging, nesting, population connectivity,	
				geneflow); pollutant exposure; adverse roadside	
				management practices; poor vegetation (weedy	
				grasses).	
Climate	Hotter, more	Natural	Natural	+: smaller, warm-adapted species in temperate areas	(Hamblin et al. 2017)
	stable			— : large-bodied, cool-adapted species in desert areas	
	Less water-stress			?: $\uparrow/\downarrow$ a species realised niche; alters species	
				composition	

	Alteration of bee				
	& plant				
	phenology				
Plant abundance	High depending	High during crop	Depends on	+: ↑ food = ↑ bee N & R	(Smith et al. 2006a; Smith
	on site type	bloom, low	natural habitat	?: alter species composition & competitive conditions	et al. 2006c)
		otherwise	type		
Plant species	High	Low	Depends on	+: $\uparrow$ resource diversity = +: $\uparrow$ nutrition (polyleges), $\uparrow$	(Ebeling et al. 2012;
richness			natural habitat	chance of host (oligoleges) = $\uparrow$ bee species richness.	Hennig and Ghazoul 2012;
			type		Steffan-Dewenter et al.
					2006)
Native flora	Low	Low	High	+: ↑ exotic pollinators	(Garbuzov and Ratnieks
				— : maladapted to local bees; $\downarrow$ oligoleges	2014b; Pardee and
				Alters assemblage composition	Philpott 2014)
Floral spatial	High (discrete	Low (large	Low (dispersed)	+: clumped, concentrated patches = $\downarrow$ time & energy	(Cresswell and Osborne
distribution	clumped patches)	monocultures)		costs; single-species of flora in clumps more attractive	2004)
				than dispersed	

Environmental	High (city centres	Low	Low	<ul> <li>— : direct and indirect mortality; exhaust fume</li> </ul>	(Lusebrink et al. 2015;
contaminants	&industrial areas)			chemicals interfere with bee foraging	Moroń et al. 2012)
	Intermediate				
	(suburbs)				
Weeds	High	Low	Low	+: abundance of flowers	(Bretagnolle and Gaba
				— : weeds = $\downarrow$ preferred forage plants;	2015)
				herbicides/pesticides applied to weeds = $\downarrow$ bees	
Herbicides	High	High	Low	+: eliminate competitively dominant unsuitable plants	(Hopwood et al. 2016; Le
				— : remove valuable foraging resources; can cause	Féon et al. 2010)
				harm/mortality	
Pesticides	Low –	High (conventional)	Low	— : direct & indirect mortality, reduced fitness	(Arena and Sgolastra
	Intermediate	Low (Integrated Pest			2014)
		Management or			
		Organic)			

Ground cover	Low to high	Low to high	Low to high	+: open sandy areas in vacant lots, landfills, construction	(Wesserling and
	depending on	depending on crop	depending on	sites & roadsides = $\uparrow$ ground-nesting bees	Tscharntke 1995)
	habitat type	and management	ecosystem	— : lawns = $\downarrow$ ground-nesting bees	
Canopy cover	Low	Low	Low to high	+: $\uparrow$ solar radiation = bee activity, & can $\uparrow$ herbaceous	(Jha and Vandermeer
			depending on	flowers	2009; Lowenstein et al.
			ecosystem type	— : $↓$ trees = $↓$ foraging & nesting resources	2014)
Tillage	Low	High	Low	$-: \downarrow$ food resources; destroys eggs, larvae, pupae &	(Hopwood 2008; Julier
				overwintering adults nesting in soil	and T'ai 2009; Roulston
					and Goodell 2011; Shuler
					et al. 2005)
Mowing/grazing	High (mowing)	High (mowing and	Low (mowing and	+: $\uparrow$ floral resources (at appropriate scales &	(Hatfield and LeBuhn
	Low (grazing)	grazing)	grazing)	frequencies)	2007; Hopwood et al.
		8	8		2016; Noordijk et al.
				$-:\downarrow$ flowering resources; altered vegetation	2009)
				structure; grazing animals compete with bees	

Exotic bees	Low – High	High	Low –	+: 个 pollination	(Prendergast 2018b;
(especially			Intermediate	— : outcompete native bees	Russo 2016)
honeybees)					

However, here we found mixed results (Fig. 2.4, Prendergast 2020: Dataset 1). There were 51 comparisons involving bee communities between urban with rural and/or "natural" landscapes, with remainder were conducted within the urban landscape in one or more landscapes. In five comparisons for both abundance, and six for speciesrichness, the results varied according to the type of urban, agricultural or natural habitat surveyed, guild or bee taxon involved. Comparing urban and agricultural landscapes, urban bee abundance was higher 38.1% of cases, lower in 19.0% of cases, but generally did not differ (42.9% of cases) (total n=21). Similarly, for comparisons with natural landscapes, 31.7% of cases showed abundance was higher, 22.0% abundance was lower, but in general abundance was similar (46.3%) (total n=41). With respect to species richness, urban areas tended to have higher numbers of species than agricultural landscapes (44.4%) or did not differ (33.3%), with 22.2% of cases having fewer species (total n=18). In contrast, for species richness comparisons with natural areas, for almost half of the comparisons (47.6%), urban landscapes hosted fewer species; in 26.2% they hosted more species compared with natural landscapes, and in 26.2% the difference was non-significant (total n=42). We also demonstrate the importance of assessing abundance and species richness separately: whilst abundance was often higher in urban than natural landscapes, urban landscapes had fewer species, suggesting that a subset of species are benefitting in urban areas (Fig. 2.4).

Urban areas tend to be more supportive for bees than agricultural landscapes. This may be attributed to higher pesticide and herbicide use, homogenisation of the landscape, cereal-dominated crops (wind pollinated), lack of suitable resources and floral monocultures in most agricultural contexts (Goulson et al. 2015; Roulston and Goodell 2011), which contrasts with the highly heterogeneous landscape and diversity of flora that can be found in some urban areas (Table 2.1).



**Fig. 2. 4** Studies involving comparisons between urban and natural habitat types that report no differences, a positive effect, or a negative effect on bee abundance and bee species richness for bees in urban compared with natural and agricultural/rural habitats (no. of studies assessed for abundance comparison: urban-agricultural = 21, urban-natural = 41; species richness comparison: urban-agricultural = 12,

#### 2.4.3. Determinants of native bee assemblages in urban areas

Urbanisation can be predicted to influence native bee populations by altering the amount, quality, diversity, native/exotic status, and distribution in space and time of flowering resources that native bees require for food, and the amount and distribution in space and time of nesting substrates – including bare ground for ground nesting bees, and premade cavities for above-ground nesting bees (Roulston and Goodell 2011). Both local and landscape factors are important determinants of wild bee abundance and diversity (Fig. 2.5). Proximity of nesting and foraging sites within a landscape influences bee assemblages, and as resources must be within flight range - typically <700m, but <150m for smaller-bodied species (Gathmann and Tscharntke 2002), surrounding land-use tends to be significant at distances up to 500m (Hennig and Ghazoul 2012; Steffan-Dewenter 2003).



**Fig. 2. 5** Response of bees (positive, negative or non-significant) to various local and landscape level factors measured in urban bee studies in terms of a) abundance, and b) species richness. Numbers above each column indicate the total number of studies involving that factor. Key: SITE SCALE: Flower N = flower abundance or density; Flower R = the species richness or diversity of flowering plant species; Native flora = the amount or proportion of native flowering plant species; Ground cover: the amount of ground cover, such as mulch, or grass at a site, or the reciprocal of open or bare ground; Openness: how open a site is, or the amount of solar radiation received, the reciprocal of canopy cover; Woody plants: the number of trees or woody plants, or tall plant forms; Habitat complexity: the diversity or complexity of habitats at the site scale; Area: the area or size of a habitat/patch; Mowing: the intensity of mowing or grazing at a site; Wildlife-friendly: whether a site has been intentionally managed for wildlife; Activity: the amount of human or management activity at a site; Pesticides: the amount or presence of pesticides; Temperature: temperature at a

site; Rainfall: amount of precipitation; LANDSCAPE SCALE: Built-space: a proxy of urbanisation, the proportion of built-space (impervious surfaces such as buildings, roads, pavement etc.) around a site, measured at varying degrees of resolution and radii; Greenspace: proportion of vegetated area of any description, measured at varying degrees of resolution and radii; Isolation: how fragmented a site is or isolated from natural areas; Distance to city centre: how far away a site is from the city of a centre, often in terms of a gradient approach; Landscape diversity: the diversity or heterogeneity of landscapes; Housing density: the density of houses measured at a landscape scale; Low housing density and High housing density: some studies differentiated levels of housing density; Human density: human population density around a site at the landscape scale; Socio-economics: socio-economic status of a neighbourhood; Traffic: traffic levels, distance to major roads. Note there is much variation in the number of studies that have investigated different explanatory variables

Reviewing studies that have investigated a range of local and landscape features in urban habitats, it is evident that no single factor emerges as being consistently associated with determining native bee abundance or species richness, however some general patterns are evident (Fig. 2.5).

Diversity, and especially abundance, of floral resources more often has a positive than negative effect on bee populations in terms of both bee abundance (Fig. 2.5a, Prendergast 2021). However, in an equal amount of cases, floral attributes had no effect. Floral abundance and richness likewise more often have positive than negative impacts on bee species richness (Fig. 2.5b); the relationship however between floral species richness and native bee species richness is dominated by nonsignificant associations, and in just under 15% of cases, even significant negative associations. Native flora also are generally beneficial, but may not necessarily boost bee abundance or species richness. With evidence in other landscape types that bees are more strongly correlated with the abundance of a few particularly attractive plant species than with plant diversity (Haaland et al. 2011; Lazaro and Totland 2010; Rundlöf et al. 2014), it is important that strategies in increasing flower abundance be targeted to plant species that are proven to be preferred by bees, and that maximise offspring production. Oligolectic bees (those that are specialised to forage for pollen on a restricted taxonomic range of plants) are inevitably tied to the limited plant taxa they forage on; even for generalists, fitness can be greatest on single-species pollen

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diets if these are high protein, sterol and essential amino acid content (Di Pasquale et al. 2016; Moerman et al. 2017).

Although floral resources appear to be of greater importance than nesting resources, availability of nesting resources can be significant in limiting bee populations (Fortel et al. 2016). Our review indicates that across urban bee studies less ground-cover (i.e. greater amounts of open, natural substrate) tends to increase bee abundance, and is especially important in promoting greater bee species richness (Fig. 2.5). This relates to how ground-nesting bees, which comprise the majority of species globally (Plant and Paulus 2016), require patches of bare or semi-bare ground to excavate nests. More trees, which represent nesting resources, but potentially foraging resources if they are angiosperms, is also more often beneficial than detrimental for bee abundance, and promotes bee species richness (Fig. 2.5). Greater openness also tends to promote bee abundance (Fig. 2.5a). Increasing site age also was found to support more bee individuals (Fig. 2.5a). Area tended to be associated with more bee species (Fig. 2.5b), as expected from the species-area relationship (Connor et al. 2000). In contrast, there were inconsistent effects on bee abundance (Fig. 2.5a). This may be due to the area-abundance relationship being in play in some cases (Taki et al. 2018), whereas in other cases a density effect was occurring whereby bees obtained higher densities in smaller areas (Andersson and Hambäck 2012). In the majority of cases mowing or grazing negatively impacted bee abundance, whereas there was no consistent association with species richness (Fig. 2.5). Despite evidence of pesticides harming bees (Goulson et al. 2015), no effect was found for abundance in two of three studies, and three of four studies for species richness (Fig. 2.5).

At landscape scales, although built-space was more often negatively than positively correlated with bee abundance and richness, in almost 50% of cases there was no impact (Fig. 2.5). Proportion of greenspace most frequently had no effect on bee abundance, and had variable associations with species richness (Fig. 2.5). Isolation from natural areas tended to negatively impact bee abundance and especially species richness (although non-significant results dominated for abundance), whereas distance from city centres tended to have a positive association with bees (Fig. 2.5). Landscape diversity was not associated with more bees or species (Fig. 2.5). Housing density had no effect on bee abundance, but for studies that categories housing density into low vs. high, low housing density tended to be positively

associated with bees, whereas high density negatively associated (Fig. 2.5). Interestingly, for human density, although limited to three studies, all found positive associations with bee abundance, whereas two found positive and one negative association with species richness (Fig. 2.5). Socio-economics had both positive and negative effects for abundance (two studies each), but high socio-economic parameters were more often negatively associated with richness (two out of three cases) (Fig. 5). Although roads are pervasive in urban areas, only three studies have investigated traffic flow or distances to major roads as a factor influencing abundance, and two for species richness, all finding no effect (Fig. 2.5).

Part of the variation in total abundance and diversity to these explanatory variables may arise from differences in the life-history strategies of different bee taxa. Whilst comparisons are limited by low sample size, some associations emerged (Prendergast 2021: Dataset 2, 3). Considering nesting guild, non-significant associations dominated for both ground and above-ground cavity nesters and responses were similar. Differences occurred for built-space where only groundnesting bee species richness was negatively affected; cavity-nester abundance was more negatively associated with area; ground-nesters were negatively associated with site age whereas the association with cavity-nesters was positive or neutral for both abundance and species richness; and for openness, counter-intuitively, positive associations were only found for abundance of above-ground cavity-nesters. There was some divergence in response to explanatory variables based on sociality: only social species abundances benefited from more abundant and diverse flora, which may relate to how social bees require more food and also are polylectic; only solitary bees were negatively associated with floral parameters and area. For body size, small bees exhibited more variation in their association with floral diversity, and only large-bodied bee species richness was negatively associated with built-space whereas only small bees were positively associated. Lecty had little influence, except for how only specialist abundances were positively associated with area, and negatively with built-space. The main difference regarding bee species' origin was that exotic species abundance was often negatively associated with native flora, and native bee abundance responded more favourably to built-space. Honeybees were strongly associated with flower abundance, more so than bees overall, which also raises the question of whether positive associations are largely driven by honeybees when

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analyses are performed with honeybees included as the total bee response. Honeybees also were often positively associated with built-space. *Bombus* abundance was also predominantly positively associated with flower abundance. Low sample sizes of other phylogenetic groupings limit comparisons.

#### 2.4.4. Urbanisation and non-native species

Urbanisation tends to favour non-native, often invasive, species (Gaertner et al. 2017). However, the impact of non-native plants and pollinators on their native counterparts regarding pollination, pollinator behaviour, and fitness consequences range from facilitative to competitive, and are dependent upon the bee and floral species, their traits, and environmental context (Fig. 2.6). Categorising species as "native/non-native" may hold little predictive power in their impact on native bees (Stout and Tiedeken 2017). There is a need to quantify the impact of exotic plants in order to make informed decisions rather than prescriptive assumptions that designate all natives as "good" and all introduced species as "bad" (Sagoff 2005). The extent to which invasive plants are incorporated into the diets of pollinators, and their effect on pollinator fitness, is likely to depend on their phylogenetic similarity to native flora used by resident pollinators, pollination syndrome, nectar/pollen chemistry and nutritional value, and the phenological and morphological match between exotic flora and resident pollinators (Memmott and Waser 2002; Stout and Tiedeken 2017).



**Fig. 2. 6.** Impacts that the proliferation of non-native/exotic flora such as ornamentals and weeds in urban areas have on native bee assemblages. The left-hand side details aspects associated with an increase in non-native taxa in urban areas and how these benefit bees, ultimately leading to a greater abundance and/or diversity of bees, whereas the right-hand side details aspects that are detrimental to bees and how this can lead to lower abundance or diversity of bees. Some facets interact with others, altering the valence of the impact on bees. \*K = carrying capacity. Refer to Online Resource 1 for references.

It has been hypothesised that invasive species promote the growth and spread of other invasive species (Simberloff 2000). The high abundance of alien flora in urban habitats may therefore favour the proliferation of non-native bees over native bees (Aizen et al. 2008). However, in contrast with patterns observed in non-bee taxa where non-native species dominate urban assemblages (McKinney 2002), there is little evidence that non-native bees are a major component of urban bee communities, comprising  $18.4 \pm 4.05\%$  of overall abundance (n= 27), and  $10.5 \pm 1.66\%$  of species (n studies = 36) (Prendergast 2020: Dataset 1).

European honeybees occur in hives managed by urban beekeepers (Lorenz and Stark 2015; Moore and Kosut 2013), as well as in feral colonies (Morse et al. 1990). As a hyper-abundant, eusocial, opportunistic floral generalist, concerns have been raised that honeybees compete with native bees (Moller 1996; Moritz et al. 2005; Pyke 1999). A non-native species across most of its range, honeybees might be expected to be favoured by urban habitats (Carre et al. 2009); however, honeybees were within the three most numerically-dominant species in less than half of urban bee studies (44 out of 102 surveys where data was presented) (Prendergast 2020: Dataset 1). Across 90 studies where data was presented on the percentage of all bees represented by honeybees, honeybees comprised  $25.2\% \pm 2.64\%$  (Prendergast 2020: Dataset 1). This contrasts markedly with studies in agricultural systems where honeybees often represent 80-92% of bees (Carre et al. 2009). However, this may be an artefact of sampling methods (Prendergast & Hogendoorn 2021) in over threequarters of studies using only passive methods honeybees were not dominant, whereas in approximately 60% of studies that used observations or sweepnetting, honeybees were dominant (Prendergast 2020: Dataset 1).

Few studies have considered how the introduced honeybee impacts native bee assemblages. In many studies, because honeybees are "managed", data on honeybees is excluded, thereby removing a potentially important explanatory variable (refer to Prendergast 2020: Dataset 1). Of the few studies where associations between honeybees and native bees could be assessed, three found a negative (Martins et al. 2017; Rollings and Goulson 2019; Ropars et al. 2019), six found positive correlations (Archer 2013; Blindbæk 2017; Fukase and Simons 2016; Gunnarsson and Federsel 2014; Kratschmer et al. 2018; Lomov et al. 2010), one found a negative association with species richness but not abundance (Plascencia and Philpott 2017), and four found no association (Fitch et al. 2019; Frankie et al. 2013; MacIvor and Packer 2016; Wilson and Jamieson 2019). Divergences in foraging preferences reported (Garbuzov et al. 2015a; Hennig and Ghazoul 2011; Plascencia and Philpott 2017) could be considered to indicate no competition due to resource partitioning, or alternatively that honeybees are excluding native bees. Negative associations based on habitat type (Hausmann et al. 2015; Threlfall et al. 2015) may indicate either competition, or different habitat preferences. Negative correlations may be due to divergent responses, rather than competition, given that honeybees are often favoured in more disturbed habitats, with more non-native plants, typical of cityscapes, whereas native bees suffer under these conditions (Aizen and Feinsinger 1994).

Observations of honeybee and native bee interactions from agricultural or natural habitats may not apply in urban contexts due to differences in native bee and plant community composition, honeybee densities and durations of hive presence. Although at densities lower than in cropping landscapes, the constant densities of urban hives (e.g. ~10 colonies/km<sup>2</sup> in London) (Alton and Ratnieks 2016; Barnes 2015), can exceed those estimated to be beyond which honeybees exert negative impacts on wild bees in "pristine" natural habitat (Torné-Noguera et al. 2016). However, the high abundance of honeybees, their ease of management, relative insensitivity to disturbed landscapes, generalized foraging behaviour, large flight distances promoting gene-flow in fragmented landscapes, and long season of activity, may make honeybees important pollinators of urban flora (Dick 2001; Lowenstein et al. 2014). With a rising interest in urban agricultural and urban beekeeping (Moore and Kosut 2013), it is important to identify opportunities for supporting both wild native bees and managed honeybees in urban environments.

A failure to consider honeybee competition may, however, give rise to counterintuitive findings. For example, although oligolectic bees are predicted to be vulnerable to urbanisation, honeybees have a greater floral niche overlap with polyleges; thus in areas of high honeybee densities, generalists may in fact be more vulnerable to declines or extirpation (Goodell 2000; Thorp et al. 2000). Studies aiming to identify optimal flora for attracting native bees in urban habitats should remove the potential for competition from honeybees, given that honeybees may exclude native bees from foraging on resources they otherwise prefer (Dupont et al. 2004; Gross 2001).

#### 2.4.5. Ecological traits of urban bee assemblages

Species do not respond uniformly to land-use change; a species' response to urbanised landscapes will depend on life history characters and ecological traits such as resource specialisation, flight season duration, sociality, nesting habits, and body size—which is highly correlated with both mobility/foraging range, energetic requirements and thermoregulatory abilities (Bates et al. 2011; Cariveau et al. 2013; De Palma et al. 2015) (Table 2. 2). Species with narrower niches, in terms of floral specialisation, flight season duration, volitism, thermal tolerances, and flight ranges, are more sensitive to environmental pressures than species with broad niches (De Palma et al. 2015).

Urbanisation acts as a selective force filtering out species that are maladapted to urban conditions, and selecting for "urbanophilic" species which may reach high abundances, at the expense of other species (McKinney 2006). Even if species richness and/or abundance is similar between habitat types, community composition and evenness is often altered (Faeth et al. 2011; Harrison et al. 2017). Specialised bees and those with a limited ability to move between dispersed resources are often depauperate in urbanised landscapes (Banaszak-Cibicka and Żmihorski 2012; Vanbergen 2013; Vanbergen 2014). In contrast species that can exploit anthropogenic structures for nesting, or the abundance of ornamental plants may increase in these "novel" environments (e.g. Banaszak-Cibicka and Żmihorski (2012); Bates et al. (2011); Deguines et al. (2012)). Shifts in community composition, functional diversity and taxonomic composition of bee assemblages can have implications for pollination, as functional trait diversity has been shown to maximise pollination (Burkle et al. 2013; Fründ et al. 2013). Elucidating what traits cause species to vary in their response to environmental and ecological variables in urban environments requires further research. Traits such as resource specialization, body size, sociality, nesting substrate, and kleptoparasitism can be expected to determine the success of bee taxa in urban landscapes (Table 2. 2).

In urban areas, polylectic foragers predominate, and even thrive, whereas some oligoleges are reduced or lost altogether (Jędrzejewska-Szmek and Zych 2013). Oligolectic bees appear to be underrepresented in urban bee assemblages, averaging 17.4 $\pm$ 3.23% of species (n=27) and 16.3 $\pm$ 8.07% of individuals (n=12) (refer to Prendergast 2020: Dataset 1), which compares with estimates of 26-33% species being oligolectic globally (Waser and Ollerton 2006). Disruptions of co-evolved symbioses through anthropogenic land-use modification places oligolectic species at greatest risk of extirpation (Didham et al. 1996). Specialist species may fail to develop when fed non-host pollen, and will not use other pollen available even when their host plants fail to flower (Praz et al. 2008; Strickler 1979). Lower effective population sizes of oligoleges also renders them at higher risk of extinction from stochastic and genetic events, reduce adaptability, and increase metapopulation extinction (Frankham et al. 2002; Zayed 2009). Nevertheless, there is evidence that some oligolectic species can persist in urban areas provided their specific floral hosts are available, and may even benefit if urbanisation increases the supply of their host plants (Cane et al. 2006). For example, a survey in Brazil assessing urbanisation impacts at a single site over forty years recorded a small increase in the proportion of oligolectic species, even as overall decline in bee richness and abundance overall declined (Martins et al. 2013).

Body size has also been predicted to influence the ability of a species to persist in urban habitats, but predictions vary regarding directionality of the response (Table 2. 2). Our review shows large-bodied bees tend to dominate (19 out of 35 cases). It should be noted that there is no standard for categorizing bees into body-size classes, making conclusions tentative.

Predictions about how sociality influences bees in relation to urbanisation also vary (Table 2. 2). Social bees numerically dominate urban bee communities, whereas for species richness there is no clear dominant social category. Solitary bees comprise  $29.4 \pm 4.54\%$  of individuals (n=30) and  $47.5 \pm 4.55\%$  of species (n=29) in urban environments, which however is much lower than the 75% of all species globally that are solitary (Plant and Paulus 2016). However, it should be noted that for halictids, which exhibit variation in sociality, even within a species (Yanega 1997),

author's varied regarding which sociality category they assigned this taxonomic group to.

Kleptoparasites are predicted to be vulnerable to urbanisation, with complex consequences on hosts (Table 2. 2), however urban environments can still represent supportive habitats for this guild (Tscharntke et al. 1998). Our review found that in urban areas kleptoparasites average  $9.71\% \pm 1.14$  of species (n=54), less than the approximately 15% of bee species worldwide that are kleptoparasites (Wcislo and Cane 1996). Only one study provided data on parasitism rates (32.35% (Archer 2013)), similar to the global average of 30% (Wcislo 1987). Kleptoparasites represent only 1.80%  $\pm$  0.54 of individuals (n=28) in cities, similar to relative kleptoparasite abundances in natural habitats (e.g. Minckley (2008)). Kleptoparasitic abundance and diversity are rarely associated with any explanatory variable (Prendergast 2020: Dataset 2, Prendergast 2020: Dataset 3), which may be due to their dynamics being more influenced by host populations.

Bees of different nesting guilds might be expected to show different responses to urbanisation, due to how urbanisation impacts substrates for ground-nesting vs. cavity-nesting taxa (Table 2. 1, 2) (Krombein 1967). Although it has been proposed that species nesting in small cavities predominate in urban areas (Cane et al. 2005), ground-nesting bees often represent the majority of urban bees in both abundance and species richness (Prendergast 2020: Dataset 1). On average, ground-nesting bees represent 63.2%  $\pm$  5.59 (no. studies = 28) of individuals, and 62.0%  $\pm$  4.17 (no. studies = 34) of species, somewhat lower than the global-level of 70% (Cornell University College: Department of Entomology 2017). However, in studies comparing nesting bee community composition across gradients of urbanisation, above-ground/cavity-nesting bees do tend to respond favourably (Fortel et al. 2014; Hernandez et al. 2009; Kennedy et al. 2013; Mazzeo and Torretta 2015). This contrasts with a review that found cavity-nesting bees were most vulnerable to "environmental disturbances" (Williams et al. 2010). This may relate to how cavitynesting bees can capitalise on the novel substrates present in urban areas (Gess and Roosenschoon 2017; MacIvor and Moore 2013; Prendergast 2019) (Fig. 2.7).

Urbanisation is often associated with a reduction in community evenness in various taxa, with assemblages being overwhelmingly dominated by just a few highly abundant species whilst the majority of species occur at relatively low abundances (Shochat et al. 2010). However how urbanisation affects bee community evenness is equivocal. Some studies find that urban bee communities exhibit high community evenness, maintained even when diverse species are abundant (Normandin et al. 2017), and that evenness is robust across land-use types (Leong 2016). In contrast, Cane et al. (2005) found bee genera that are numerous, abundant and widespread were those most commonly represented in cities, where 90% of native bee individuals belong to just a dozen genera.
Functional trait	Categories	Predictions		References	
		Advantaged	Disadvantaged		
Body-size	Larger	Greater mobility in fragmented	Higher energy demands	(Cane et al. 2006; Harrison and Winfree 2015; Martins et al. 2013; Müller et al. 2006; Wright et al. 2015)	
		landscapes			
	Smaller	Lower energy requirements	Limited mobility	(Banaszak-Cibicka and Żmihorski 2012; Harrison et al. 2017; Torné-Noguera et al. 2014; Tscharntke et al. 1998; Wray et al. 2014)	
Sociality	Social	Numerically dominant,	Found to be negative affected by	(Banaszak-Cibicka and Żmihorski 2012;	
		Highly efficient foraging, Polylectic	anthropogenic disturbance	Chapman and Bourke 2001; Roubik 2001; Williams et al. 2010; Winfree et al. 2009; Zanette et al. 2005)	
		Store food	bre food More susceptible to pesticide exposure		
	Solitary	Found to be more resilient to	Smaller population sizes	(Roubik 2001; Williams et al. 2010; Winfree	
		anthropogenic disturbances	Lower reproductive rates	et al. 2009)	
			Do not store food		
Host/	Host	If kleptoparasites are disadvantaged,	Depending on body size, search	(Archer 2013; Egerer et al. 2017; Holzschuh	
kleptoparasites		lowered rates of parasitism-induced mortality	capacities & host-specificity,	et al. 2010; Roland and Taylor 1997; Tylianakis et al. 2007)	
			kleptoparastic species may be less	, ,	
			sensitive than a host, exacerbating		
			pressures on host populations		

**Table 2. 2.** Predictions on how bee functional traits will influence how bees respond (at a relative advantage or disadvantage) to urbanisation.

	Kleptoparasite	Parasitoids increase with increasing	Specialisation & species occupying	(Albrecht et al. 2007; Cane et al. 2005; Fortel		
		landscape diversity	higher-trophic levels associated with	et al. 2014; Holzschuh et al. 2010; Loyola and Martins 2006: Steffan-Dewenter and Schiele		
			greater sensitivity to disturbance	2008; Tscharntke et al. 1998; Tscharntke et		
			Fate dependent upon hosts	al. 2002)		
			Low population sizes			
Nesting	Below-ground	More open habitat	Turf, pavement, fake grass unsuitable	(Benjamin et al. 2014; Cane 2015; Cane et al.		
substrate		Sand-pits, roadsides, vacant lots,	Regular mowing, weeding, irrigation,	2005; Linsley 1958; Matteson et al. 2008)		
		building sites provide nesting habitat	mulching, & weed-barrier fabrics			
		Soils are not tilled	prevent establishment & disturb			
			ground-nesting bees			
			High surface run-off & erosion from			
			storm drains & ditching			
	Above-ground	Installation of bee hotels	Removal of dead trees & wood	(Alves-dos-Santos 2003; Boyle and Pitts-		
		Cavities in brick mortar, adobe walls,	Few large, old trees	Singer 2017; Rolón and Cilla 2012; Roulston and Goodell 2011)		
		cavities & nail holes in wooden	Removal of lantana & blueberry weeds	,		
		telephone poles, fences & other				
		wooden man-made structures, bamboo				
		stakes in gardens				

#### 2.4.6. Are urbanised areas bee-friendly habitat?

Despite global bee declines (Tylianakis 2013), cities across the globe have been found to harbour remarkably intact, diverse and abundant bee assemblages (Fig. 2. 2a, Fig. 2. 5, Prendergast 2020: Dataset 1). Bumblebees, the most well-studied wild bee group (Fig. 2. 2b, c), and one of the most-globally threatened (Goulson et al. 2008; Williams and Osborne 2009), are frequently more diverse and abundant in urban habitats than in rural habitats and native forested habitats (Baldock et al. 2015; Gunnarsson and Federsel 2014; Osborne et al. 2008; Theodorou et al. 2016, 2020; Winfree et al. 2007).

Although some cities are deficient in rare bees (Harrison et al. 2017), other cities harbour rare endemic bees: a survey of four tree species in the urban region of Berlin, Germany, found that 17% of bee species were listed as endangered on the Red List of Threatened Species (Hausmann et al. 2015). In Northampton, UK, the urban core hosted a greater abundance and diversity of solitary and primitively eusocial native bees than did nearby meadows and even high-quality nature reserves (Sirohi et al. 2015).

Even though wild bees are adversely affected by some facets of urbanisation (Table 2. 1), some features of cities can be beneficial to bees (Fig. 2. 5). For example, in ecoregions where natural habitats comprised dominant natural vegetation types that are less favourable to bees, such as temperate forests (Grundel et al. 2010; Michener 2007), removal of native habitat of dense, floristically-poor wind-pollinated deciduous forest and replacement with flower-rich urban habitats (e.g. roadsides, waste-lands, and urban gardens) can be favourable for bees (Hall et al. 2017; Sirohi et al. 2015). By comparison, in regions with natural habitats that have a high, continuous supply of diverse bee-friendly flora, native bees may respond less favourably to replacement of natural vegetation by urbanised landscapes (e.g. South America) (Martins et al. 2013).



Fig. 2. 7. Aspects of the urban environment that can be beneficial for bees. Refer to Online Resource 2 for references.

Cities may boast a high abundance of bees if developed on originally highly biodiverse areas (e.g. southwest Australian biodiversity hotspot) (Kühn et al. 2004; Yates et al. 2005). That species richness is naturally high in areas undergoing rapid urban expansion underscores the importance of identifying how best to manage urban growth to preserve that local bee biodiversity (Luck 2007).

### 2.5. KNOWLEDGE GAPS AND FUTURE RESEARCH DIRECTIONS FOR BEES AND URBANISATION

A critical evaluation of these studies on urban bees has allowed identification of gaps in knowledge and shortcomings of studies, and factors to consider when evaluating urban bee studies. This includes: geographic biases, historical land-use, sampling methodologies, habitat classification, sampling methodology, and scale of analysis

Documenting patterns of urban bee biodiversity has been geographically biased (Fig. 2. 3). Caution is therefore needed when extrapolating findings globally, as bee taxa responses to land-use change are likely to differ greatly according to climate, biome, phylogeny, and types of human impacts (Faeth et al. 2011). Further studies underrepresented biomes and continents (Fig. 2. 3) are required to determine whether trends reported in this review are valid across other biogeographic regions. Divergent responses of bees to the same broad pressures are likely given variation in species composition, as well as the different nature of threats across different regions based on differences in land-use history, climate and phenology. Whilst part of the variation in responses of bees to environmental factors appeared to be due to differences in life-history traits of bees, there may also be interactions between geographic region and environmental factors on their effect on bee communities. Once more research is conducted in under-represented regions, this would be a fruitful topic to explore.

Historical land-use and the age of a city is likely to have a major influence on the composition of contemporary urban bee communities (Cusser et al. 2015), although there is also evidence that bees respond considerably rapidly to landscape alterations (Bommarco et al. 2014). Cities established for long periods may have bee fauna representing only those taxa that have tolerated or adapted to the city environment,

whereas in recently urbanized areas, bees have not had adequate time to adapt or develop adaptive behaviours, and sensitive species may not yet have been eliminated due to lag effects (Ramalho and Hobbs 2012; Ramalho et al. 2014). However such historical or legacy effects have not been specifically investigated when evaluating how bees respond to urbanisation. Only four studies (Archer, 2013; Frankie, Rizzardi, Vinson et al., 2009; Martins et al., 2013) have addressed long-term (>5 years) bee community changes under urbanisation, with no clear consistent findings (Online Resource 3). Moreover, these suffer from being comparisons in two points in time; ongoing systematic monitoring over time is required (Cane 2001). Historical land-use and eco-evolutionary history of the plant-pollinator community should influence responses to urbanisation: species that evolved in landscapes with spatially-contiguous flora may be most vulnerable to urbanisation, whereas species that evolved in landscapes characterised by naturally-fragmented plant populations may be more tolerant (Hopper and Gioia 2004; Menz et al. 2011). However, in areas that have only recently been subject to anthropocentric modification, the pool of species may be more likely to show losses and declines. In Western Europe, much of the land has been under intensive farming for most of recent human history, and little truly "natural" habitat remains; it can be predicted that species assemblages may show little response to land-use modification owing to "extinction filters" already eradicating disturbance-sensitive species (Balmford 1996). Future work requires addressing these predictions.

Inconsistencies between urban bee studies may arise due to methodological differences (Fig. 2. 2a); pan trapping is one of the most popular methods of bee sampling but is inferior to sweep-netting, creating differences in species capture rates between studies conducted in different regions (Prendergast et al. 2020). Moreover, pan traps cannot discriminate floral visitors vs. itinerant species, and captures fewer bees when resources are more abundant, resulting in misleading information about habitat quality (Popic et al. 2013; Prendergast et al. 2020). Taxonomic biases in captures between different methods means entire guilds of bees can be largely unrepresented, which may be particularly problematic in urban bee studies: Megachilidae are poorly represented in pan traps, yet as cavity-nesting bees, they are successful in urban habitats based on observations, trap-nest occupancy, and sweep-netting (Mazzeo and Torretta 2015; Prendergast et al. 2020). Trap-nesting studies have the power to determine the fitness of bees and whether bees are merely

transient visitors or are residing and/or colonising and reproducing in urban habitats, however they are limited to cavity-nesters.

Urban landscapes can differ markedly in impervious and "greenspace" cover, design and configuration (Fuller and Gaston 2009). A mechanistic understanding of factors determining urban bee assemblages is needed where studies measure variables (e.g. floral diversity and abundance, proportion of native flora, nesting substrate availability, patch size, connectivity), rather than provide merely categorical descriptions (e.g. "garden", "brownfield site"). Part of the variation reported here on the effect of urbanisation on bees likely stems from how there is no clear definition of what defines an urban landscape (McIntyre et al. 2008). Rural-to-urban approaches, which constituted 24 studies in our review, are oversimplified and cannot identify the mechanisms underlying patterns in bee assemblages: most regions do not exhibit clear gradients in the underlying drivers of bee diversity along the rural-urban gradient (Ramalho and Hobbs 2012). Very few studies defined explicitly what constituted an "urban area", and for those that did, definitions varied widely e.g. compare ""urban" areas, defined as those sites that are located within the bounds of private or public property dedicated to uses other than conservation. All the sites in this latter category were areas dominated by human urban or suburban development, such as railroad margins, ornamental gardens and the like" (Molumby and Przybylowicz 2018) with ">50% impervious cover" (Glaum et al. 2017). Under the latter definition, "village" habitats considered urban in Samuelson et al. (2018) based on clustering analysis would be considered to fall outside this category, having on average 13.8 (+3.7)% impervious cover, and the "urban" sites from the study by Nakamura and Kudo (2019) would fail to be considered urban, comprising 66.9% forest, 4.1% open grassland, 5.5% green-rich residential district, 9.7% pasture, 4.8% abandoned crop field, and 8.3% developed land, yet these urban sites were clearly distinct from their "natural" sites which had negligible (<0.2%) developed land, no agricultural/cropland, only 2.8% managed grassland, and was predominantly forest (95.2%).

For studies assessing the intensity of urbanization, some compared habitat types considered by the author's to be more urban than others; for other studies it was distance from the city centre; in other studies it was proportion of impervious surfaces or "development" or pre-defined land-use categories by management agencies, at varying distances, at various grain sizes in the surrounding landscape.

Variation also occurred in what constituted "natural" habitat: is some studies grazed grasslands were considered "natural", whereas in others natural landscapes referred to legally conserved areas with minimal anthropogenic influence. "Greenspace" also was vaguely defined (if defined at all) (Taylor and Hochuli 2017) (e.g. "any location where vegetation comprises at least 50% of the ground area" (Stewart et al. 2018). Our review emphasizes that not all greenspaces – be they natural greenspaces outside of urban areas, or various vegetated areas within urban areas – are equally suitable habitat for bees. Whereas in some regions 'greenspace' may comprise native vegetation (forest, heath, grassland), in others it may comprise lawns or managed gardens. This can also explain why there was such variation in bee responses to the proportion of "greenspace" in a landscape.

Many studies in urban landscapes categorise land-cover at coarse scales (≥30m), which fail to capture the fine-scale mosaics of greenspace in and around urban sites which provide important foraging and/or nesting habitats for urban bees (Koh et al. 2016; Zhao et al. 2019). Therefore, a grid-cell categorized as "intensive" urban habitat (highly developed) may actually host valuable plant species as road verge vegetation, which collectively may ameliorate negative effects of landscape intensification. It is likely that bees - small, yet mobile animals - perceive their environment at scales that satellite imagery cannot detect. Future studies should focus on mapping at finer resolutions (e.g. Zhao et al. 2019) or use alternative methods to capture the nuances of cityscapes such as emerging drone-based high resolution images.

Although there is a global push to "green" cities, few city planners consider creating landscapes that are pollinator friendly. Research is required to determine the optimal floral selection for native bees in urban habitats. Rather than floral abundance or diversity, floral composition may be of overriding importance (Picanço et al. 2017). Of urban bee studies that examined whether floral community composition explained variation in urban bee communities (n=27), 25 reported significant effects (SuppInfo1). There is no shortage of lists of "pollinator-friendly" plants, but few are

supported by empirical data (Garbuzov and Ratnieks 2014a). Many anecdotal lists of "bee-friendly" flowers focus on generalists (honeybees and bumblebees), and are of little value to solitary bees (Garbuzov and Ratnieks 2014a). Preference tests need to be conducted in urban environments because plant species can vary in attractiveness to pollinators depending on the landscape type (Frankie et al. 2013; O'Neill et al. 2004). Importantly, weeds may act as potential resources for urban bees, but this topic is understudied.

Because standard practices of weed removal, pesticide application, and mowing in most managed gardens reduce bees (Rundlöf et al. 2015; Wastian et al. 2016), it can be predicted that wild bees within urban regions may depend on retention of "unmanaged" natural areas in the urban matrix (Batista Matos et al. 2013; McFrederick and LeBuhn 2006). Native vegetation in urban landscapes is the overriding factor in determining the persistence of unique and rare urban bee species (Geslin et al. 2016).

Native vegetation remnants may also represent important refugia, being the only sites where specialist bees that are dependent upon particular native plant species can persist in an otherwise hostile urban matrix (Letourneau et al. 2012; Venturini et al. 2016). As source habitats with spill-over effects, they are a source of pollinators in more modified greenspace sinks (Hunter 2002; Öckinger and Smith 2007). Establishing or maintaining ecological connectivity between native remnant source populations will be important for enabling native bees to move throughout urbanised landscapes (Banaszak-Cibicka et al. 2016). "Hotspots" where native bees are particularly abundant can be used to guide restoration of other sites, or even seed sites with pollinators; such sites must be prioritised for protection against urban development. However, identifying practices that maximise the value of anthropogenic greenspaces is also important because native vegetation remnants may be of insufficient size and connectivity (Allen-Wardell et al. 1998; Rosenzweig 2003). Greater investigation into the importance of large, old trees as nesting resources for bees in urban areas is required to prevent potentially important nesting habitats from being removed. Research into how well artificial "bee hotels" can compensate for losses of natural nesting resources for cavity-nesting bees and identifying of optimal bee hotel design holds promise for increasing reproductive

output of cavity-nesting bees (agricultural examples: Bosch et al. (2000); Boyle and Pitts-Singer (2017)).

Our ability to restore fully functional natural habitats and reintroduce bees in urban landscapes is a major knowledge gap. Fischer et al. (2016) evaluated bee responses to restoration, and found limited positive outcomes: bee community composition did not differ between wastelands restored by planting native grassland flora compared with unrestored wastelands and other greenspaces, and of nine bee species contributing the most to assemblage patterns, only three responded significantly (positively) to restoration. Restoration projects in other landscapes suggest removing exotic shrubs can increase pollinator species richness, floral visitation, and interaction richness and diversity (Kaiser-Bunbury et al. 2017), but this may not be true in urban contexts. Modelling based on empirical data may guide restoration to increase chances of success; for example, using a systems approach surveying 360 sites comprising nine major land-uses across four UK cities, Baldock et al. (2019) found improved management of public greenspaces represented the greatest potential for increasing pollinator habitat quality. Modelling the effect of increasing three abundant, frequently visited plant species, this was found to increase pollinator network robustness.

It is unknown if bees can recolonise patches unaided from which they have been extirpated. Given the limited flight ranges of many bees (Zurbuchen et al. 2010), it cannot be assumed that "plant it and they will come" (Tasker et al. 2019); proximity to healthy source populations may be the only practical means to reinstate native bees in restored/designer landscapes. Because many bees are philopatric (Cane et al. 2006; Michener 2007; Morato and Martins 2006), in some cases it may be necessary to translocate native bees (Seddon 2010), for the benefit of both bees and plants. Mark-recapture studies and population genetic analyses are needed to understand how bees use the landscape for foraging and nesting, both at individual and metapopulation levels, and whether green corridors provide connectivity between patches in urban landscapes.

As cities expand, how to best develop cities in harmony with biodiversity is a challenge. In the context of urban design, land sharing involves extensive urban

sprawl with an interspersion of built land and greenspaces, whereas land sparing involves intensive, compact built spaces leaving aside larger contiguous greenspaces (Lin and Fuller 2013). There is some evidence that to optimise ecosystem services, land sparing is superior to land sharing in urban ecosystems (Stott et al. 2015), and recent research indicates urban native vegetation remnants are crucial for conserving native bees (Prendergast 2018a).

### 2.6. CONCLUSIONS

Here we show that responses of bees to urbanisation differ considerably compared to what occurs in response to agriculture, despite both causing fragmentation and destruction of natural habitat. Moreover, in some cases urbanisation can represent a bee-beneficial landscape compared with natural landscapes. Strategies to conserve urban areas therefore cannot be extrapolated from agricultural schemes. We furthermore found that responses of bees to urbanisation differ widely according to life-history strategy of the bee taxa involved. Our identification of short-comings from the literature so far provide meaningful recommendations for where to focus future research efforts on how to progress the field of urban ecology and conservation of bees in cities. If we are to mitigate the global decline in bees, a greater understanding of how bees respond to urbanisation is required so that effective management strategies and restoration/landscaping strategies are designed and implemented. Most importantly, it is evident that urban areas have the potential to successfully harbour native bees, with their attendant pollination services, provided the ecological needs of species are understood.

### 2.7. REFERENCES

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### Chapter 3

# The relative performance of sampling methods for native bees: an empirical test and review of the literature

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Megachile aurifrons. © Kit Prendergast

## The relative performance of sampling methods for native bees: an empirical test and review of the literature

### 3.1. Abstract.

Many bee species are declining globally, but to detect trends and monitor bee assemblages, robust sampling methods are required. Numerous sampling methods are used, but a critical review of their relative effectiveness is lacking. Moreover, evidence suggests the relative effectiveness of sampling methods depends on habitat, yet efficacy in urban areas has yet to be evaluated. This study compared the bee community documented using observational records, targeted netting, mobile gardens, pan traps (blue and yellow), vane traps (blue and yellow), and trap-nests. The comparative surveys of native bees and honeybees were undertaken in an urbanized region of the southwest Australian biodiversity hot spot. The outcomes of the study were then compared to a synthesis based on a comprehensive literature review of studies where two or more bee sampling methods were conducted. Observational records far exceeded all other methods in terms of abundance of bees recorded, but were unable to distinguish finer taxonomic levels. Of methods that captured individuals, thereby permitting taxonomic identification, targeted sweep netting vastly outperformed the passive sampling methods, yielding a total of 1324 individuals, representing 131 taxonomic units-even when deployed over a shorter duration. The relative effectiveness of each method differed according to taxon. From the analysis of the literature, there was high variability in relative effectiveness of methods, but targeted sweep netting and blue vane traps tended to be most effective, in accordance with results from this study. However, results from the present study differed from most previous studies in the extremely low catch rates in pan traps. Species using trap-nests represented only a subset of all potential cavitynesters, and their relative abundances in the trap-nests differed from those in the field. Mobile gardens were relatively ineffective at attracting bees. For urbanized habitat within this biodiversity hot spot, targeted sweep netting is indispensable for obtaining a comprehensive indication of native bee assemblages; passive sampling methods alone recorded only a small fraction of the native bee community. Overall, a combination of methods should be used for sampling bee communities, as each has

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their own biases, and certain taxa were well represented in some methods, but poorly represented in others

### 3.2. Introduction

In many regions, bees are important pollinators of a large number of native and agricultural plant species (Tepedino 1979, Klein et al. 2007, Potts et al. 2016). However, bees are declining across the globe due to a number of often interacting threats, including habitat loss, degradation, and fragmentation due to agricultural and urban expansion, disease, pesticides, and climate change (Goulson et al. 2015, Potts et al. 2016). Indeed, declines in pollinator populations are among the most pressing environmental issues of the 21st century due to the threat to food security and ecosystem functioning (Brown et al. 2016).

A reliable, robust methodology for surveying bees is required to make valid assessments of the status of bee populations, understand the ecology of species, and to track whether management actions have had their desired out-comes (Cane 2001, Cane and Tepedino 2001). A number of methods for sampling bees have been developed, each with their own benefits and limitations, including sampling effort, skill required, taxonomic and functional group biases, and cost of implementation (Table 3.1). However, as yet, there is no consensus on which method is superior, with the optimal method likely to differ depending on the study system and research aim. Using a range of methods has been previously recommended to reduce biases in any one method and because methods often are complementary in the bee fauna they collect (Krug and Alves-dos-Santos 2008, Wilson et al. 2008). There is growing evidence that phylogenetic group and bee functional traits (e.g., body size, lecty, and sociality) influence various variables of interest, such as response to land-use change (Williams et al. 2010, Banaszak-Cibicka and Zmihorski 2012, Rader et al. 2014) and pollination services (Brittain and Potts 2011, Munyuli 2014). However, the sampling method used may be biased toward bees of a particular lineage or functional group, meaning that the appropriate sampling method varies depending on the taxonomic group or question at hand (Gonzalez et al. 2016, Sircom et al. 2018, McCravy et al. 2019).

	Sweep net	Pan traps/bowl traps/bee bowls/ Moericke traps	Vane traps	Baits	Vacuum/ Aspirator	Malaise	Trap-nests
Advantages	<ul> <li>Can match bees with floral hosts</li> <li>Can identify diel activity patterns</li> <li>Active search- and-net collecting can target specialist bees</li> <li>Low cost</li> <li>Easily transportable</li> <li>No set-up time</li> <li>Opportunity for catch-and- release</li> <li>Specimens collected in good condition</li> </ul>	<ul> <li>Easy to deploy</li> <li>Cost-effective</li> <li>No experience required</li> <li>Can sample from hours to days</li> <li>Samples bees active over entire day (and night)</li> </ul>	<ul> <li>Can sample for extended durations</li> <li>Easy to deploy</li> <li>Samples bees active over entire day (and night)</li> </ul>	<ul> <li>Target specific taxa of interest (mainly orchid bees, (Tribe: Euglossini)), including those that have rapid flight</li> <li>Targets males so that females are not depleted, limiting potential to reduce population reproductive capacity</li> <li>Samples bees active over entire day (and night)</li> </ul>	<ul> <li>Can match bees with floral hosts</li> <li>Can collect bees from flowers without damaging vegetation</li> <li>Can identify diel activity patterns</li> <li>Easily transportable</li> <li>No set-up time</li> <li>Opportunity for catch-and- release</li> </ul>	<ul> <li>Can sample for extended durations</li> <li>Easy to deploy</li> <li>Samples bees active over entire day (and night)</li> <li>Can be hoisted into canopies</li> <li>No experience required</li> </ul>	<ul> <li>Can sample for extended durations</li> <li>Measures demographic parameters: sex ratios, reproductive output, individual fitness</li> <li>Assesses mortality from predators and parasites/parasitoids of brood</li> <li>Can target particular species based on hole diameter</li> <li>Can uniquely associate males with females</li> <li>Can match bees with floral hosts (by analysis of food provisions)</li> <li>Easy to replicate</li> </ul>

 Table 3. 1 Advantages and disadvantages of common methods used for sampling bee communities.
- - by handle length High bycatch
  - Requires skill
  - Limited duration Limited height
  - No standard protocol/difficult ٠ to standardise

audibly

conditions

temperature,

time of day)

(wind.

type

bees

- deplete • Biased towards populations of slower-flying, some species visually or
  - Success can vary with colour conspicuous
    - Success can
- Catch rates vary vary with bowl with size environmental
  - Bias against large bees

Only catch

sampled

Potential to

- Contents can evaporate if left out for
- Catch rates vary long durations with vegetation Contents can
- spill over if • Labour-intensive rain occurs
  - Subject to disturbance from
  - wind/animals Cannot match bees with host
  - flowers<sup>a</sup>
  - Specimens can be degraded<sup>‡</sup>

- High bycatch
- low-flying bees Potential to deplete
  - populations of some species
  - Success varies with colour
  - Cannot match bees with host
  - flowers<sup>a</sup>
  - be degraded

- Targets only limited range of taxa
- Dependent

flowers<sup>†</sup>

- No
- Specimens can
- on bait used
- standardised method for
- comparison
  - Cannot match bees with host

- Limited to slow. lowflying,
- conspicuous, smaller bees
  - Requires skill
- Limited height sampled Limited
- duration Catch rates
- vary with environmental conditions (wind, temperature,
- time of day) Catch rates vary with vegetation type
- Labourintensive

- High bycatch
  - Success
  - varies with colour

placement

- Success highly
- depended on
- - i.e. within flight path such as
    - corridors Cannot
    - match bees with host flowers<sup>†</sup>
    - Specimens can be degraded
    - Can be vulnerable to damage from vandalism, animals, wind
    - Limited height sampled

- Limited to cavity-nesting bees, and of those, a subset that use trap-nests
- Success varies with hole diameter, trap nest material, orientation
- Requires facilities to rear offspring
- Utilisation in relation to natural nesting resources in the landscape unknown
- Mortality in trapnests compared with natural nests unknown
- Labour-intensive: requires obtaining material to construct trap-nests, making the nests
  - (potentially drilling through hardwood), installing nests, periodically checking them, and then rearing offspring

Suitable habitat	Flowering shrubs in open habitat	Open habitat	All	All	Flowering shrubs in open habitat	Most (preferred method in tropical habitat)	Most
Non-suitable habitat	Dense vegetation Thorny vegetation	Sites with rich and abundant flora Shaded habitat High vegetation			Dense vegetation, plants flowering in inaccessible locations	Exposed, windy habitats	Limited colonisation in closed- canopy forest

Note: Specific examples are presented in Kit, P., Menz, M. H. M., Dixon, K., & Bateman, P. W. (2020). *Publications used to review the relative effectiveness of different methods for sampling bees in "The relative performance of sampling methods for native bees: an empirical test and review of the literature"*. Retrieved from: <a href="https://doi.org/10.25917/5ee848123cdae">https://doi.org/10.25917/5ee848123cdae</a>, <a href="https://doi.org/10.25917/5ee848123cdae">https://researchdata.edu.au/publications-used-review-review-literatureguot</a>

<sup>+</sup> Analyses of pollen on body or in gut can aid matching bees to foraging resources but requires time, money, skill and equipment.

<sup>+</sup> Although traps can be filled with preservative (e.g. propylene glycol), specimens can nevertheless degrade, and whilst protocols for washing specimens to retain quality exist, this is time-consuming and specimens can nevertheless be damaged, compromising species-level identification.

A recent review of the efficacy of different sampling methods was focused on tropical forest agroecosystems (Prado et al. 2017), and almost all other empirical studies explicitly comparing sampling methods have been restricted to natural or agricultural ecosystems in the Northern Hemisphere (Wilson et al. 2008, Grundel et al. 2011; see also Appendix S1: Table S1). No reviews that explicitly compare bee monitoring or surveying methods have so far considered urban habitats. Urban habitats may differ from natural and agricultural ones in having higher plant species richness and habitat complexity (McKinney 2008, Faeth et al. 2011), which may alter the relative efficacy of different sampling methods (Templ et al. 2019). Urban areas often have a high diversity of plant associations across the region, which contrasts with often large monocultural fields in agricultural areas, and fairly uniform habitat types even in natural areas, which, however, differ from urban areas in having large, contiguous patches of native vegetation (Kaluza et al. 2017).

Urbanization is a significant form of land-use change and is set to increase (United Nations 2015), with the potential for adverse consequences to bee abundance and diversity and through the associated loss of natural habitat and other aspects of the built environment (Mar-tins et al. 2013, Potts et al. 2016). Alternatively, urbanization may provide benefits to bees, depending on type of urban habitat, the regional context, and local and landscape conditions (Hall et al. 2017). For example, in cold, temperate regions with low floral diversity, and dominated by closed-canopy conifer forests, the urban heat island effect and preponderance of flowering plant species may allow a longer foraging season with a greater abundance and diversity of flowering resources (Baldock et al. 2015, Luder et al. 2018). Similarly, in arid regions, management of urban flora can extend plant bloom, with benefits to pollinators (Neil et al. 2014).

The urbanized region on the Swan Coastal Plain of Perth, southwest Western Australia (SWWA), is within a globally recognized biodiversity hot spot that has been severely affected by historical and ongoing land-clearing for urbanization (Hopper and Gioia 2004, Lambers 2014). With a high diversity of endemic flora, this region has the potential to harbor a high diversity of native bees. Indeed, Western Australia is known to host a diversity of bees (estimated at 800 species; Houston 2011), yet no systematic surveys of native bees in the urbanized parts of this region have been conducted. Consequently, there has been little research into the response of native bee communities in this region to land-use change. Many bee species remain undescribed, and only two of the estimated 800 species in the state have been adequately assessed to be given legislative protection and recognized as threatened (Department of Sustainability 2016)

We used a range of methods to characterize the bee community in an urbanized area of SWWA: observations (randomized bee walks); targeted sweep netting; baiting in the form of mobile gardens; blue and yellow pan traps; blue and yellow vane traps; and trap-nests (bee hotels). The first two methods are active sampling methods, and the latter four are passive. Furthermore, we compared their relative efficiency to determine the most effective method(s) for sampling the community and identified any biases in monitoring of native bee assemblages, as well as providing comparative data on the advantages and disadvantages of each method. Finally, to place the results in the context of the wider literature, a review was conducted to identify articles that compare sampling methods or were surveys of bee communities that included two or more sampling methodologies. Articles were sourced through Google Scholar using the search terms "sampling bees method\* technique pan bowl trap\* sweep net\* pollinator bait vane" and through references in the articles thus found. Articles included were those published prior to 28 November 2019.

# **3.3.** Methods

### 3.3.1 Study region and sites

Perth is Australia's fourth largest city, with a population of 2.14 million people and a density of 317.7 people/km2, and is also Australia's fastest-growing city (Population Australia 2017). The region has a Mediterranean climate and is characterized by a high incidence of nutrient-deficient landscapes with highly weathered sur-face soils (Hopper and Gioia 2004). The metropolitan region on the Swan Coastal Plain is renowned for a high concentration of endemic flora (Hopper and Gioia 2004). The region has also undergone extensive clearing, with over 80% of the original vegetation being removed, and ongoing clearing for development being a continuing threat (Hopper and Burbidge 1989, Witham 2012).

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Bees were surveyed at seven sites each of bush-land remnants and residential gardens within the same geographic, geological, and climatic region (Newman et al. 2013; Fig. 3.1). To ensure independence and minimize spatial autocorrelation, sites were greater than 2 km apart, which exceeds the average flight range of most bee species (Gathmann and Tscharntke 2002, Greenleaf et al. 2007, Zurbuchen et al. 2010). Site area ranged from 835 to 4,370,000 m<sup>2</sup>, but the area surveyed was standardized to a 100 x 100 m area.



Fig. 3. 1 Map of the 14 sites surveyed for native bees in the urbanized region of the southwest Western Australian biodiversity hotspot. Bushland sites (green): Star Swamp, Bold Park, Kings Park, Maniana Reserve, Wireless Hill, and Piney Lakes; and residential sites (red): Osborne Park, Wembley, Nedlands, Wilson, Jandakot, Bibra Lake, and Gosnells.

# 3.3.2. Sampling methods

Each site was surveyed once per month over the Southern Hemisphere spring/summer period (November–February) in 2016/2017. Surveys were conducted during conditions conducive to bee activity (clear skies, wind speed <30 km/h, and temperatures >17°C). All specimens collected were identified by KSP to the lowest taxonomic resolution possible using published keys, the Australian Pests and Diseases Image Library (PaDIL) website (http://www.padil.gov.au/), and with reference to the collection at the Western Australian Museum. Separate taxonomic units were used for each male and female of a species due to limitations in the taxonomy of Australian bee fauna (Batley and Hogendoorn 2009) and because there can be sex-specific differences in catch rates (Leong and Thorp 1999).

*Observations and targeted sweep netting*: Targeted sweep netting and observations (randomized bee walks) were conducted for three hours, from 10:45 until 13:45 hours, the time of peak bee activity (Yates et al. 2005). Targeted sweep netting was performed using an entomological net (119 cm aluminum handle, 38 cm diameter hoop, and 74 cm long white net with 0.9 x 0.3 mm mesh). Targeted sweep netting and timed observations were conducted by a sin-gle collector (KSP) using an active search-and-net approach, walking randomly around a 100 x 100 m area of the site observing flowering plants. Areas with flowering resources were observed for 5 min before moving on to another if no bees were observed. Each bee captured was transferred into an individual labeled vial for later identification. The European honeybee (*Apis mellifera*) was counted but was not captured. For bushland remnants, the 100 x 100 m area was at least 100 m away from roads to avoid edge effects. As residential gardens were mostly <100 m<sup>2</sup>, surrounding vegetation on the verge and adjacent front yards was also surveyed.

*Mobile gardens:* A mobile garden of potted plants was taken to each site to measure bee visitation. A number of studies have conducted observations and/or targeted sweep netting of bees at mobile gardens—standardized arrays of bee-attractive potted plants that are placed at each site (Lowenstein et al. 2015). These gardens allow patch size and floral species to be standardized, and control for edaphic and genetic variables that can alter attractiveness of flora between sites. Four Australian plant species—*Eutaxia myrtifolia* (syn. *obovata*; Fabaceae, flowers in November, plant size 0.4 x 0.5 m), *Dianella revoluta* (Hemerocallidaceae, flowers in November–December, 0.4 x 0.4 m), *Leptospermum* "Pink Cascade" (Myrtaceae, flowers in November, 0.4 x 0.2 m)—were selected for use in the mobile garden experiment. These species were selected as the genera represent common elements of the Australian flora, and they are also commercially available and often planted in garden beds. Five plants per species were purchased from a commercial native flower nursery and kept in a shade house. During

each survey, two to four plants were placed in an open location approximately 10 m apart from each other for the duration of the survey (3 h) of each site, and monitored for 5 min/h, as well as opportunistically observed for bee visitation when in view. Plant species visited, and the species of the bee visiting, were recorded.

*Pan traps:* Prior to commencing targeted sweep netting surveys, nine large (350 mL) yellow pan traps and 20 small (96 mL) pan traps painted UV-fluorescent yellow and UV-fluorescent blue (New Horizons Support Services, Upper Marlboro, Maryland, USA) were deployed. These were two-thirds filled with water and surfactant (Tween-80). Size and color of the pan traps were selected based on pilot trials published in Droege (2006). The large pan traps were placed on the ground. The smaller pan traps were mounted 20 cm above the ground on bamboo stakes, as elevating pan traps has been reported to increase capture success (Tuell and Isaacs 2009, McCravy and Ruholl 2017). Pan traps were placed randomly around the site away from vegetation in open, sunny areas, and spaced 5 m apart as this has been found to maximize capture success (Carboni and LeBuhn 2003). Pan traps were collected at the end of each targeted sweep netting survey (after 3 h). Captured bees were transferred into vials containing 75% ethanol.

*Vane traps:* At each site, two blue vane and two yellow vane traps (Springstar, Woodinville, Washington, USA) were installed at 1–2 m above the ground on branches, or, in residential areas, under eaves, and half-filled with water and propylene glycol (Droege and Guldin 2011). Vane traps were installed the month prior to the start of the survey period and remained there until the survey season ended. Captured specimens were transferred to vials containing 75% ethanol during each monthly visit. Rainfall was low during the sampling period, and at no point did the vane traps overflow.

*Trap-nests:* Trap-nests were used to sample cavity-nesting bees. Trap-nests were made from untreated jarrah (*Eucalyptus marginata*, a local Myrtaceae endemic to SWWA) blocks 100 mm tall x 100 mm wide x 150 mm deep. Fifteen 120 mm deep holes were drilled into each block, and five cardboard bee tubes (Jonesville Paper Tube) of each size, 4, 7, and 10 mm diameters, were inserted into the holes. Trap-nests were installed on tree branches, or, in residential areas, under eaves or on

fences and windowsills 1–2 m above the ground in locations that were minimally obscured and received sunlight. A total of eight trap-nests were installed at each site, representing a total of 120 potential nesting cavities (40 per diameter) across all trapnests at each site. Trap-nests were installed during the first survey in November 2016 and removed after the last survey in February 2017. During each monthly survey, completed tubes (nests capped with material) were collected and replaced with new tubes. The capped tubes were stored individually in plastic containers with perforated lids and kept in the laboratory at ambient temperatures to complete development. At the end of October, bee tubes were moved from the laboratory into a greenhouse. Tubes were checked every two days for emergence.

# 3.3.3. Data analysis

Linear mixed-effects models were used to compare the relative effectiveness of sampling methods in terms of individuals and taxonomic units collected, using the package lme4 (Bates et al. 2015) in R (R Core Team 2014). The non-native A. mellifera was analyzed separately. A generalized linear mixed-effects model with a Poisson error distribution was used to model the effect of method and a method x habitat interaction on the number of taxonomic units recorded, and a glmer with a binomial error distribution was used to investigate the effect of habitat type (urban and bushland) on the proportion of native bee individuals observed or collected by sweep net. Site was included as a random factor in all models. Models were tested for overdispersion using the dispersion\_glmer function in the package blemco (Korner-Nievergelt et al. 2015); response variables were transformed in order to improve model fit with the particular transformation (e.g.,  $\ln$ ,  $\ln + 0.1$ ,  $\log_{10}$ ) depending on the fit of residuals. Significance of the explanatory variable (sampling method) or interactions (sampling method x habitat, and sampling method x sex) was obtained by comparing models with and without the variable/ interaction using ANOVA. Differences between levels were analyzed using Tukey's post hoc tests in the package lsmeans (Lenth 2016).

Due to differences in duration in which the blue vane traps were deployed compared to the other sampling methods, we also performed analyses by standardizing the sampling time to 3 h, which involved dividing the results for vane traps by 90 (assuming that the traps could potentially collect bee for a period of 9 h, which encompasses the activity period of bees from 08:00 to 17:00 hours, hence approximately 270 h per monthly survey). However, due to the overall difficulty in determining comparative sampling effort, we retained the actual capture data in our presentation of the results, but also discuss the standardized results. Model outputs using the standardized vane trap data are presented in Appendix S5.

Variation in the composition of bee communities (taxonomic units) between sampling methods (excluding trap-nests) was analyzed using Primer/Permanova 7 (http://www.primer-e.com/). Data were log<sub>10</sub>-transformed to remove the influence of extremes, given that the data were non-normal and included many zeros, singletons, and doubletons, as well as some species having >100 individuals. A Bray–Curtis similarity matrix was then calculated to quantify the percentage similarity between sampling methods. Results were visualized using non-metric multidimensional scaling (NMDS).

An estimate of the completeness of each sampling method was assessed by creating rarefaction curves and calculating Chao 1 estimates in EstimateS (Colwell 2013). Biased correction was applied when calculating the Chao 1 estimates. However, for yellow pans, yellow vanes, and blue vanes, the Chao 1 classic estimate was calculated as recommended for when the coefficient of variation in the abundance distribution is >0.5, under which the bias-corrected formula becomes imprecise (Colwell 2013).

# 3.4. Results

### 3.4.1. Comparison of collection methods for native bees

Both the number of specimens collected and their taxonomic richness differed among the collection methods (Table 3.2). Targeted sweep netting was by far the most effective method for sampling bees with respect to both abundance and taxonomic unit richness, and blue vane traps were the next most effective in terms of absolute numbers (Table 3.2; Appendix S2: Table S1). However, when standardized to approximate an equal sampling duration to the other methods (3 h), blue vane traps caught a comparable number of bees to pan (Table 3.2). Blue vane traps caught more individuals and taxonomic units than yellow vane traps, whereas yellow pan traps were more effective than blue pan traps. Large (non-UV) yellow pan traps were the least effective (Table 3.2

There were significant differences in number of individual native bees caught between the different methods (P < 0.0001; Appendix S2: Table S1). All pairwise comparisons between targeted sweep net-ting and all passive methods were significantly different (P < 0.0001). All pairwise comparisons between blue vane traps and other methods were significantly different (P < 0.0001; Appendix S2: Table S2), but were not once vane trap data were standardized (P > 0.05; Appendix S5: Table S2). There was a significant method x habitat interaction (P < 0.0001; Appendix S2: Table S1), but the main findings of the superiority of targeted sweep netting were consistent across habitats (Fig. 3.2).

Taxonomic unit richness also differed between sampling methods (P < 0.0001, Appendix S2: Table S3, Appendix S3: Table S1), following a similar pattern to that for abundances (Appendix S2: Table S4). Targeted sweep netting caught over 90% of all taxonomic units (Table 3.2). Blue pan traps caught slightly more taxonomic units than yellow pan traps, but the difference was non-significant (Table 2; Appendix S2: Table S4). As with abundance, blue vane traps caught more taxonomic units overall than the other passive methods (Table 3.2; Appendix S2: Table S4), but not when catch rates were standardized to three hours (Table 2; Appendix S5: Table S4). There was no method x habitat interaction (P = 0.376; Appendix S2: Table S3).

Of the 145 taxonomic units (separate for each sex), of those with  $n \ge 10$ , all 43 were collected at higher frequencies by targeted sweep netting except for four: *Amegilla chlorocyanea* (female; 196 blue vane, 17 targeted sweep netting, 2 yellow vane, and 1 blue pan trap); *A. chlorocyanea* (male; 68 blue vane and 9 targeted sweep netting); the kleptoparasite of *Amegilla*, *Thyreus waroonensis* (female; 11 blue vane and 2 targeted sweep net-ting); and *Lasioglossum* (*Chilalictus*) *castor* (female; 14 blue vane, 12 targeted sweep netting, 9 yellow pan trap, 4 yellow vane, and 2 blue pan trap; Appendix S3: Table S1).

Method	Targeted sweep netting	Blue vane	Yellow vane	Blue pan trap	Yellow pan trap	Large yellow pan trap
Individuals caught	1324	347 (3.86)‡	15 (0.17) ‡	8	15	6
Taxonomic units caught $^{\dagger}$	134	31 (0.34) ‡	10 (0.11) ‡	7	6	5
Genera caught	20	11	7	4	3	2
Families caught	4	4	4	3	3	2

Table 3. 2. Total number of native bee individuals and taxonomic diversity caught by the different collection methods

<sup>+</sup> Given variation in body size between sexes (Prendergast, unpublished), and known differences in colour preferences between sexes (Heneberg & Bogusch, 2014), for species where both sexes were collected, these were treated as distinct "taxonomic units".

‡ Numbers in parentheses are divided by 90 to standardise results to 3 hrs in order to quantitatively compare results with the other methods



**Fig. 3. 2** Abundance (± s.e.) of native bees (a) and honeybees (b) sampled by all collection methods in bushland remnants and residential gardens. Circles represent outliers.

No species were exclusive to large yellow pan traps or UV-blue or UV-yellow pan traps. Only two species, *Lasioglossum (Chilalictus) sp.12* [female] and *Braunsapis nitida* [female], both singletons, were exclusive to yellow vane traps. Five taxonomic units were exclusive to blue vane traps (*Lasioglossum (Chilalictus) lanarium* [male], *Lasioglossum (Chilalictus) inflatum* [female], *Homalictus (Homalictus) sphecodoides* [female], all singletons, *Euryglossula fultoni* [male, n = 3], and *L. (Chilalictus) lanarium* [female, n = 4]). By contrast, 98 taxonomic units were captured exclusively by targeted sweep netting (Appendix S3: Table S1). There was a significant sex x method interaction (P = 0.0002), indicating that the sexes were sampled differently depending on the method used (Appendix S2: Table S5).

Rarefaction curves and Chao estimates followed the same general pattern based on the observed numbers of taxonomic units by sampling method (Table 3.3; Appendix S4: Fig. S1). While the passive sampling methods followed a shallow incline with increasing sampling effort (Appendix S4: Fig. S1), the netting followed a curvilinear pattern and had still yet to plateau (Appendix S4: Fig. S1), indicating that despite high sampling effort, more taxonomic units were likely with increased sampling effort. Considering the taxonomic units captured as a percentage of the Chao 1 estimate, netting, large yellow pans, and blue pans had values above 70%, whereas the number collected in the blue vanes was only 55.6% of the estimated value, and for the yellow vane and yellow pan traps, taxonomic unit richness was only 46.7% and 44.5%, respectively, of the estimated value (Table 3.3). It should be noted that the confidence intervals of the Chao 1 estimates were relatively wide (Table 3.3).

A Bray–Curtis similarity matrix of species composition revealed that of the five collection methods, pan traps of different colors were the most similar. Both blue and yellow vanes were more similar to blue pan traps than yellow pan traps. The most successful method—targeted sweep netting—had a species composition most similar to blue vane traps, but low similarity to the other methods (Table 3.4). An NMDS analysis comparing taxonomic composition between the methods had low stress (0.01), indicating a good fit to the data, and depicted that the two small UV-reflective pan traps were most similar to each other (Fig. 3.3). Taxonomic composition of the bees caught in large yellow pan traps was most dissimilar to all other methods. Targeted sweep netting was also dissimilar to all other methods, but most similar to blue vanes. Conclusions regarding similarity are, however, hampered by large disparities in numbers of species caught between some methods.

**Table 3. 3** Chao 1 estimates of the number of taxonomic units collected by the different sampling methods, compared with the number observed to have been collected.

Method	Observed	Chao 1 mean	95% CI lowerbound	95% Cl upperbound	Chao 1 sd	%obs of Chao 1
Large yellow pans	4	5.2	4.12	16.5	2.14	76.9
Yellow pans	6	13.5	6.92	66.7	10.9	44.5
Blue pans	9	12.4	9.58	29.4	3.9	72.3
Yellow vanes	10	21.4	12.1	73.8	12.3	46.7
Blue vanes	32	57.5	39.4	119.9	17.9	55.6
Targeted sweep netting	134	181.5	154.6	243.5	21.2	73.8

*Notes:* CI = confidence intervals. sd = standard deviation. %obs = percentage the observed number of taxonomic units is of that calculated by the Chao 1 analysis.

	Targeted sweep netting	Blue vane	Yellow vane	Blue pan trap	Yellow pan trap	Large yellow pan trap
Targeted sweep netting	<b>B</b>					
Blue vane	23.75					
Yellow vane	5.68	15.77				
Blue pan trap	4.15	21.36	24.53			
Yellow pan trap	4.01	15.04	22.31	30.58		
Large yellow pan trap	2.53	5.88	0.00	14.11	0.00	

**Table 3.4**. Percentage similarity in species composition of native bees collected by different sampling methods.

*Note:* The species x method Bray-Curtis matrix was log+1 transformed for the analysis.



**Fig. 3. 3.** Non-metric multi-dimensional scaling (NMDS) plot showing the similarity in species composition of native bee assemblages in 2D space according to (a) habitat type and (b) method collection. Greater distance between points corresponds to greater dissimilarity.

### 3.4.2. Native bees observed vs. targeted sweep netting

Due to being inaccessible (out of reach of the entomological sweep net) or to the difficulty in catching rapid-flying taxa, not all bees that were observed were netted. Out of a total 5299 native bees recorded by active sampling, 1324 were netted and 4366 were observed: a ratio of observed to netted bees of 1:3. Across all surveys, a mean of  $6.32 \pm 1.07$  (standard error) bees were netted vs.  $17.16 \pm 4.01$  observed. The proportion of net-ted bees to observed bees did not differ according to habitat (P = 0.147; Appendix S2: Table S2). There were, however, significant differences between taxa in the proportion of bees netted relative to that of bees observed (<0.001; Table 5; Appendix S2: Table S6), with differences in most pairwise comparisons between taxa (Tukey's post hoc test; Appendix S2: Table S7). The greatest differences in netted: observed catch rates were for the genus Amegilla, which included only a single, large-bodied species (A. chlorocynea), and for Exoneura, a genus of small social bee. For Amegilla, the larger numbers observed relative to net-ted related to their extremely fast, erratic flight and short duration alighting at flower. For *Exoneura*, the high observed:netted ratio was likely due to the large numbers that often forage simultaneously on bushes, making netting some individuals easy yet impossible to catch all that were foraging. Excluding the rarely encountered taxa, most taxa were observed more frequently than netted, except for Meroglossa, represented by a single species (M. rubricata) that was often observed in trap-nests but seldom foraging, and Lipotriches, mainly represented by L. *flavoviridis*, a common species present at most sites and foraging on a wide range of flora.

Taxon	Total netted	Total observed	Netted:observed	Body-size	Flight characteristics
Amegilla	26	214	1:8.23	Large	Very rapid, zipping flight, seldom alights long on flowers In reach of sweep nets, often foraging on vegetation that can be sweep netted
Coelioxys	2	0	2:0	Large	Rapid, rare bee
Euryglossinae	162	423	1 : 2.6	Small	Seldom encountered singly Flying rapidly around inflorescences often in a "cloud" Never on ground-level flora; prefer branches of flowering trees but if within reach are relatively easy to capture by sweeping through 'cloud'
Exoneura	46	373	1:8.1	Small	Intermediate flight speed Seldom encountered singly Prefer shrubs and trees to forage on, never at ground-level
Homalictus	31	54	1:1.7	Small	Intermediate flight speed Prefer shrubs and trees to forage on, never at ground-level
Hylaeus	136	234	1:1.7	Predominantly small	Seldom encountered singly Flying rapidly around inflorescences often in a "cloud" Never on ground-level flora; prefer branches of flowering trees but if within reach are relatively easy to capture by sweeping through 'cloud'.

**Table 3. 5.** Total number of individuals netted and observed, and the ratio of netted to observed individuals for each major bee taxon, and body size and flight characteristics that could influence catchability.

					Males may be territorial around flowers
Lasioglossum	46	65	1:1.4	Small – medium	Intermediate flight speed Forage at multiple heights, including low-lying flora
Leioproctus	70	153	1:2.2	Medium	Intermediate flight speed Often forage on low-lying flora
Lipotriches	88	77	1:0.88	Predominantly medium	Intermediate flight speed Buzz-pollinators – stay on flowers for a longer period of time Forage at various heights, including ground-level
Megachile	586	1648	1 : 2.8	Small - medium	Fast flight Alight only briefly on flowers Forage at various heights, including ground-level
Meroglossa	18	15	1:0.83	Medium	Intermediate flight speed Longer foraging duration Frequently observed just resting inside entrances of trap-nests
Thyreus	3	1	1:0.33	Large	Rarely encountered
Trichocolletes	1	3	1:3	Large	Intermediate flight speed Prefer shrubs and trees to forage on, never at ground-level

Notes: Body size categories small: 0.48-1.78 mm ITD, medium: 1.79-3.10 mm, large 3.11-4.41 mm. Categories were based on subtracting the minimum body size, as measured by intertegular distance (ITD), from the maximum and dividing by three.

# 3.4.3. Observed vs. passive collections

Both native bees and honeybees were surveyed using observational recording and passive collections. For both, observational counts vastly exceeded numbers recorded by all passive sampling methods combined. A total of 572 honeybees were collected across all passive sampling methods, whereas 19,825 were observed, amounting to numbers observed being 34.7 times greater than numbers caught by the passive traps. Numbers of native bees observed were 11-fold greater than those caught passively (391 native bee individuals caught by passive traps, compared with 4366 being observed), despite there being more passive than active methods employed.

# 3.4.4. Trap-nests

Only a small subset of the potential cavity-nesting bee species used the trap-nests. Of the 34 cavity-nesting megachilids (including the kleptoparasitic *Coelioxys*) caught, only 10 species used the trap-nests, and of the 17 hylaeine bees, only four species used the trap-nests (Table 3.6). However, the value of the trap-nests was in being able to confirm males and females belonging to the same species; namely, no males of *Megachile (Eutricharaea) chrysopyga, Megachile (Mitchellapis) fabricator*, and *Hylaeus (Euprosopis) violaceus* were collected in the field, but they emerged from bee tubes. Not only did the composition of trap-nesting species represent only a fraction of the diversity of cavity-nest species, but also the relative abundances did not mirror those caught in the field (Table 3.6).

Taxon	Species	No. of tubes	No. emerged	Proportion of tubes	Proportion of bees emerged	No. collected during surveys	Proportion of cavity- nesting bees collected during surveys
Hylaeinae	Hylaeus (Euprosopis) violaceaus	15	68	0.093	0.133	3	0.004
	Hylaeus (Gnathoprosopis) amiculus	1	1	0.006	0.002	7	0.009
	Hylaeus (Gnathoprosopis) euxanthus	1	1	0.006	0.002	14	0.018
	Meroglossa rubricata	4	8	0.025	0.016	19	0.024
Megachilidae	Megachile (Eutricharaeae) obtusa	3	14	0.019	0.028	27	0.035
	Megachile (Mitchellapis) fabricator	39	145	0.24	0.285	3	0.004
	- Megachile apicata	1	1	0.006	0.002	10	0.013

# Table 3. 6. Species utilising trap-nests.

Megachile aurifrons	6	37	0.037	0.070	25	0.032
Megachile erythropyga	85	227	0.525	0.446	6	0.008
Megachile fultoni	1	1	0.006	0.002	24	0.031
Megachile "houstoni' M306/F367 <sup>+</sup>	' 1	1	0.006	0.002	151	0.195
Megachile ignita	3	3	0.019	0.006	20	0.026
Megachile (Hackeriapis) tosticauda	2	2	0.012	0.004	6	0.008
	162	509				

*Notes:* Number of tubes occupied, the number of bees to emerge, proportion of all tubes occupied by a given species, proportion of all cavity-nesting bees are presented.

To compare with survey results, number of a given species collected during the bee surveys and the proportion of all cavity-nesting bees collected during surveys (i.e. no. of

sp. collected / no. of all cavity-nesting bees collected) is provided.

Totals

<sup>+</sup> Undescribed species, lodged in the WA Museum as M306/F367.

### 3.4.5. Mobile gardens

The mobile gardens were unsuccessful, despite the plants having a high density of blooms. Throughout the four months (56 sampling days), only *Scaevola aemula* was visited, and on only five days at three sites. It should be noted that *S. aemula* was the only plant that flowered throughout the survey season; the other three were restricted to the first month (only *D. revoluta* had some flowers still present in December). A total of 15 bees visited the mobile garden plants, but only one of these was native (*L. (Chilalictus) castor*, female) - the remainder were honeybees.

# 3.4.6. Comparison of different passive sampling methods for honeybees and native bees and the influence of habitat type

There was a significant difference in catch rates of native bee individuals by different methods (P < 0.001; Appendix S2: Table S8). Significantly more individuals were caught in blue vane traps than all other methods (P < 0.001); no other comparisons were significantly different (P > 0.05). There was no significant interaction between method and habitat (P = 0.115; Appendix S2: Table S8), although vane traps caught more bees in bushland than residential areas, where the other methods were comparable between habitats, but the sample size was too small for any valid conclusions (Fig. 3.2a).

Honeybee catch rates differed significantly by method (P < 0.001; Appendix S2: Table S6). Pairwise comparisons between both colored vane traps and all pan traps were highly significant (P < 0.001). Blue vanes also caught significantly higher numbers of honeybees than yellow vanes (P = 0.001). Comparisons between the pan traps were non-significant. There was also a significant method x habitat interaction (P < 0.001; Appendix S2: Table S8), where vane traps, which caught more bees overall, had higher catch rates in bushland remnants than residential habitats, whereas for the other methods, these caught no honeybees in most cases except for a few outliers, in both habitat types (Fig. 3.2b)

Assessing each method regarding whether there were differences in abundance of native bees and honeybees, it was found that the relative differences in abundance of honeybees vs. native bees differed between methods (Appendix S2: Table S9). Abundances of native bees and honeybees were similar for blue vane traps (mean native bees  $8.26 \pm 1.45$  vs. mean honeybees  $9.14 \pm 1.27$ , P= 0.171), whereas there was a trend for honeybees to be recorded at higher abundances based on observational counts (mean native bees  $94.3 \pm 11.0$  vs. mean honeybees  $360.3 \pm 97.1$ , P = 0.077, Appendix S2: Table S7). Both types of yellow pan traps caught significantly more native bees than honeybees  $0 \pm 0$ , P < 0.001; and large yellow pan traps, mean native bees  $0.392 \pm 0.116$  vs. mean honeybees  $0 \pm 0$ , P < 0.001; and large yellow pan traps, mean native bees  $0.303 \pm 0.119$  vs. mean honeybees  $0.024 \pm 0.024$ , P = 0.001), but the trend was reversed for yellow vanes, which caught sixfold more honeybees than native bees  $0.722 \pm 0.172$  vs. mean honeybees  $9.14 \pm 2.17$ , P < 0.001; Appendix S2: Table S9).

### 3.4.7. Literature review

The literature review yielded 70 articles, of which 12 were conducted in urban areas (Appendix S1: Table S1). Sixty studies involved two or more methods; the remaining studies com-pared variables within a method, for example, pan or vane traps differing in color, height, or size. There was high variability in the number of studies comparing different methods, and so conclusions are tentative, but targeted sweep netting emerged as both one of the most common methods and the method that is relatively more effective than alternative methods (Fig. 4a; Appendix S1: Table S1). Vane traps, only if they are blue, are also relatively effective, but have been less commonly employed (Fig. 4a). Compared with pan traps-the second most frequently used method and often used in conjunction with targeted sweep nettingit appears that targeted sweep netting tends to be more effective (Fig. 4a; Appendix S1: Table S1). However, there was considerable variation in the relative effectiveness of methods between studies (Fig. 4a). This may be explained by the different duration a method is used; for example, targeted sweep netting has been used for anywhere between 10 min per sampling period and a number of hours throughout the day, whereas pan traps are typically deployed for 24–48 h, leading to unequal sampling effort (Appendix S1: Table S1). The effect of sampling effort on relative performance between methods in species capture rates can be seen in analyses that used rarified species richness (Nardone 2013). The pattern of relative

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effectiveness was similar when including studies conducted in urban landscapes only (Fig. 4b). Vane traps had yet to be used prior to this study.



**Fig. 3. 4.** Number of studies where a given method was reported to be relatively more effective than other methods employed to sample bees: (a) all studies (n = 71) and (b) subset of studies in urban landscapes (n = 12). See also Appendix S1: Table S1.

Almost all studies found that trap color influenced catch rates, as well as species composition (Appendix S1: Table S1). In all vane trap studies, blue vanes outperformed yellow vanes (Fig. 4a). Of studies comparing pan traps of different colors, most studies compared blue, yellow, and white (Appendix S1: Table S1). Of these, no color emerged as consistently being superior, but white pan traps were the least frequent in having the highest catch rates: Blue and yellow pan traps had the highest catch rates in 13 studies each, white in five studies, and no significant differences between colors in seven studies (Appendix S1: Table S1).

# 3.5. Discussion

### 3.5.1. Active vs. passive sampling methods

Observational counts yielded the highest numbers of individual bees. However, this method must be supplemented with those that catch specimens to provide finer taxonomic level classification. Of the methods where bees were captured, targeted sweep netting was by far superior, which is in agreement with the literature (Appendix S1: Table S1). Blue vane traps were the next most effective method in catching bees, especially large-bodied species (i.e. *Amegilla*), when deployed for their standard month-long duration, whereas yellow vanes performed poorly, consistent with results of our literature review (Rhoades et al. 2017, Hall 2018).

Although targeted sweep netting was the most effective method of bee collection in terms of both individuals and taxonomic units, it still only caught about one-quarter of all bees in terms of abundance. The relative number of individuals observed-to-netted differed significantly among the higher taxonomic categories. This finding strongly suggests that although species-level identification cannot be obtained via observations, including observational counts is important for recording abundances. While it is often believed that smaller-bodied taxa are more likely to be missed from targeted sweep netting (Prado et al. 2017, Templ et al. 2019), this was not the case in the present study. In fact, the largest-bodied taxon had the lowest number of bees netted relative to that of bees observed. The discrepancy may relate to the behavior of particular taxa, whereas large-bodied *Bombus* are generally both easy to detect visually and are slow fliers, making them relatively easy to catch. In contrast, *Amegilla* are rapid flyers (K. S. Prendergast, personal observation), and their large body size likely contributes to these bees being relatively harder to catch.

In this study, sweep netting caught more taxonomic units and individuals than pan traps. The two previous Australian studies that compared targeted sweep netting with pan traps found that targeted sweep netting outperformed pan traps (Popic et al. 2013, Threlfall et al. 2015). Studies outside of Australia have had mixed results: 20 studies comparing sweep netting with pan trapping found targeted sweep netting was more effective, 14 found pan trapping was more effective, and three found that while targeted sweep netting caught more species, pan trapping caught more individuals (Appendix S1: Table S1). In the present study, pan traps were deployed for the same duration as the active sampling methods (3 h). While this was shorter than the typical duration over which pan traps are deployed (24–48 h; see Appendix S1: Table S1), it ensured an equal duration of time employed as sweep netting—something other studies have often not controlled for. However, even if catch rates in pan traps are multiplied 16 times to extrapolate to 48 h, numbers still fall short of those caught by targeted sweep netting. This further underscores the utility of targeted sweep netting as an effective sampling method for native bees, a finding that not only was clear from our study, but also emerged from our review of the literature (Appendix S1: Table S1). One caveat is that people may vary in their collection efficiency in using an entomological net.

# 3.5.2. Pan and vane traps

A benefit of passive methods is that they can be employed for large-scale monitoring, and circumvent inter-observer variability (Westphal et al. 2008). However, there remains bias in attracting an unrepresentative subset of bee taxa and guilds, and bias in detection methods according to habitat type – in particular, in floral rich habitats pan traps may be relatively unattractive to real flowers, whereas in areas of low floral abundance or diversity, the bright traps may attract insects, including those that may not be typical visitors to an area, resulting in high type-I error rates (Prendergast & Hogendoorn 2021).

No previous published studies using pan traps to study native bee communities have been conducted in SWWA, but of those conducted in Australia, Threlfall et al. (2015) found yellow and white pans traps had higher catches than blue, whereas Gollan et al. (2011) found yellow pan traps had higher catch rates than white, and Saunders and Luck (2013) found that yellow pans traps had higher catch rates of both native bees and honeybees compared with white pans traps, with blue pans traps having the lowest catch rates.

In the present study, there were no differences in the mean number of individuals or taxonomic units captured among the colors of pan traps. Based on the literature

review, it was apparent that no single color emerged as being superior, with the relative effect of colors in capturing bees being highly variable to non-existent. We also found no significant differences between the UV-fluorescent and non-UV-fluorescent pan traps, and the blue vane traps caught more bees than the UV-fluorescent pan traps. The importance of UV fluorescence in attracting bees has recently been challenged, with bees having no significant difference in their preference for fluorescent or non-fluorescent pan traps (Shrestha et al. 2019).

The relatively low success of pan traps in the present study may be due to the flight characteristics of native bees in the region. Even elevated, the traps were only ~25 cm above ground level. If most bees have flight trajectories higher up, and typically forage in canopies, pan traps may not attract these species due to their behavioral patterns. Indeed, the preferred foraging height of bees in Western Australia is poorly known and could result in underestimation of bee abundance and diversity. Although various species were netted in abundance on low-lying vegeta-tion such as Jacksonia, Scholtzia, and Scaevola, many species, in particular the species-rich but tiny hylaeine and euryglossine bees, were also observed to be highly attracted to mass-flowering Myrtaceae such as E. marginata and Corymbia calophylla-large trees that produce masses of blossom in the canopy, out of reach of sweep nets and even visual observation. There is evidence from some habitats in other countries that bees are more frequent in canopies than near the ground (Ramalho 2004, Ulyshen et al. 2010). Future studies investigating the vertical stratification of bees foraging on such flora (e.g., using a cherry picker at different heights) would be very informative and allow future surveys to ensure that surveys take into account foraging preferences of bees and are not biased toward lower-flying species.

This urban bee study corroborates results from studies conducted in non-urban habitats that blue vane traps tended to have higher catch rates compared with yellow vane traps (Appendix S1: Table S1). The comparatively high catch rates of *A*. *chlorocyanea* in blue vane traps corroborate other studies that have found that blue vane traps are highly attractive to larger-bodied bees (often represented by *Bombus* in the Northern Hemisphere), whereas such bees are often under-represented in pan traps (Stephen and Rao 2007, Wilson et al. 2008, Geroff et al. 2014, Buchanan et al. 2017, Rhoades et al. 2017). The relatively high catch rates of large-bodied bees

found here (up to 45 *A. chlorocyanea* in one month), as well as reported in several other studies, caution against leaving these traps out for extended durations due to concerns over over-sampling (Tepedino et al. 2015).

The differences in captures in blue vane traps compared to yellow vane traps as found in our study, as well as in the broader literature (refer to Appendix S1: Table S1), compared with no clear color preference when it comes to pan traps remain to be elucidated. Future studies could measure the spectral properties of the blue vanes and replicate their spectral properties with pan traps, as well as place the blue vane traps at ground level, to test whether the difference is due to the spectral properties of the blue vanes, or a combination of the blue color and the relatively more elevated trap placement.

Blue vane traps had higher absolute catch rates compared to the pan traps, whereas yellow vane traps were comparable to the pan traps. However, the vane traps were deployed for a longer duration, and when standardized to three hours, the vane traps had the lowest catch rates (Table 2; see also Appendix S5). Attempting to standardize sampling of different methods is a challenge; however, we presented our results here based on the standard entomological practice whereby vane traps are typically deployed for longer durations. This is one of the practical advantages of vane traps as a sampling method whereby they can be left to sample for insects in the field for a month or more. In contrast, pan traps can often only be deployed for a more limited duration: In hot weather (as occurred in the present study), the water evaporates, and in rainy weather, they soon fill up and overflow (Prado et al. 2017). Pan traps can also be knocked over by wind or animals, or vandalized (Droege et al. 2017; K. S. Prendergast, personal observation). There are also animal welfare concerns: In hot weather, vertebrate animals may drink out of the pan traps and potentially fall ill from ingesting soapy water. Consequently, when considering how these passive methods are deployed in practice, we recommend including blue vane traps when sampling bee communities, based on their detection of large-bodied bees that were seldom caught by the other methods. From our own surveys, and considering the literature, it is evident that it is hard to achieve a level playing field when comparing different sampling methods, given that each has their own standard usage.

### 3.5.3. Trap-nests

Trap-nests have advantages over other monitoring methods in that they enable studying trophic relations (bee–pollen relationships and bee–parasitoid relationships; e.g., Roubik and Villanueva-Gutierrez 2009) and enable bee demographic and fitness parameters to be quantified (Paini 2004, Hudewenz and Klein 2013). However, occupancy of nests may be influenced not only by the abundance of bees in the environment but also by nesting resources already present in the wider environment, and the design of the trap-nests themselves (MacIvor 2016). And while trap-nests enable monitoring of bee populations, this is limited to aboveground cavity-nesting bees, which may comprise only a minor component of the overall bee assemblage (Twerd and Banaszak-Cibicka 2019) and may differ in their response to environmental variables (Neame et al. 2013).

A key finding of our research, which to our knowledge has yet to be explicitly investigated in previous trap-nesting studies, was our comparison of the representation of cavity-nesting bees collected during surveys vs. those using the trap-nests. Trap-nests were only occupied by a subset of the potential diversity of cavity-nesting species present at a site, and even for species both observed in the field and utilizing the bee hotels, the relative representation of species differed markedly. We nevertheless recorded a substantial diversity of cavity-nesting bees using a trap-nests, and in some cases, species, or individuals of both sexes, that were not observed in the field. A previous study in urban community gardens in Australia found only an exotic bee species occupied the trap-nests (Makinson et al. 2016); the reasons for this are unclear but it may have been poor trap-nest design or location, or that better nesting resources were present in the wider environment. Other Australian studies outside of urban areas (Murphy 2015), as well as urban bee studies overseas, have, however, had more success (Fortel et al. 2016). We conclude that trap-nests provide a complimentary means of monitoring native bee populations, with a number of advantages over other methods, but are inadequate for evaluating the composition of native bee assemblages.

### 3.5.4. Mobile gardens for surveying bees

Of all methods, the mobile gardens were the least effective. Few bees were attracted to the mobile gardens, despite selecting flora known to be visited by bees in the region. This may be due to foraging behavior of bees in a known environment, in that they previously learned where the flora hot spots are at a site and so avoid these new plants. Studies on Bombus and euglossine bees have often reported site constancy (at least temporarily) where individuals establish home ranges or foraging routes (e.g., trap-lines) such that they remember, and repeatedly return to, rewarding resource patches (Amaya-Marquez 2009). Three other studies have used mobile gardens in urban areas with far greater success (Williams and Winfree 2013, Lowenstein et al. 2014, 2015). Observations per survey went for a longer duration than the current study, yet the greater visitation success was disproportionately higher (Table 7). The reason for the discrepancy can only be speculated, but may be due to different foraging strategies of bees in Australia compared to other countries or the relatively high proportion of specialized pollination systems that occur in Australia (Phillips et al. 2010). Due to the uncertainty of bees actually visiting mobile gardens, recording visitation to plants in situ is more effective for monitoring native bee communities.

# 3.5.5. The effect of habitat

Habitat can impact the suitability and success of different sampling methods (Rhoades et al. 2017, O'Connor et al. 2019; Table 1), and this was supported by our data. As with Saunders and Luck (2013), we found evidence that relative attractiveness of pan trap colors varies according to habitat type. While vane traps caught a higher number of individuals in bushland sites, pan traps had higher relative percentages of bees of the total catch when placed in residential areas despite native bees being more abundant in bushland remnants (pooled across all sampling methods). Relatively lower catch rates of native bees in pan traps located in bushland habitat may be due to bushland having more bee suit-able flowers, whereas in residential areas, the wide array of unsuitable flowers may mean that bees are more likely to be attracted to colored pan traps, akin to suggestions that pan traps are more effective in resource-poor habitats (Potts et al. 2005, Roulston et al. 2007, Baum and Wallen 2011). Furthermore, bee communities in residential areas tend to be dominated by generalist species (Cane et al. 2005), which may make them more likely to respond to pan traps.

Publication	Plant species used	Plants/site	Flowers (n)	Bees visiting (n)	Average visits/ survey (range)	Average R per survey (range)	Sites (n)	No. times visited/ site	Duration	Country, City	Habitat
This study	Scaevola aemula	2	approx. 10 - 40	15	0.286 (range 0 - 8)	0.036 (range 0 - 1)	14	4	15 min	Australia, Perth	Urban (bushland remnants and residential gardens)
	<i>Leptospermum</i> 'Pink Cascade'	1	approx. 5 - 20	0	0	0	14	4	15 min		
	Dianella revoluta	1	approx. 2 - 6	0	0	0	14	4	15 min		
	Eutaxia myrtifolia	1	approx. 5 - 20	0	0	0	14	4	15 min		
Lowenstein et al. (2014)	purple coneflower ( <i>Echinacea purpurea,</i> var. 'Magnus')	-	20 - 30	-	7.8 (range 0–31)	4 (range 0 –11)	25	3	60 min	USA, Chicago	Urban (residential gardens)

 Table 3. 7. Comparison of results from surveys recording bee visitation to mobile gardens

Lowenstein et al. (2015)	cucumber ( <i>Cucumis sativus,</i> var. 'Picklebush')	3	6 - 9 female flowers (2:1 ratio)	-	9 (median, all visitors, not restricted to bees)	1.5 (median, all visitors, not restricted to bees)	30	2	30 min		
	eggplant plants ( <i>Solanum melongena,</i> var. 'Black Beauty')	3	5- 9 flowers		1 (median, all visitors, not restricted to bees)	1.0 (median, all visitors, not restricted to bees)	30	2	30 min		
	purple coneflower plants ( <i>Echinacea purpurea</i> , var. 'Magnus')	3	6 - 9 flowers	-	10 (median, all visitors, not restricted to bees)	3.0 (median, all visitors, not restricted to bees)	30	2	30 min		
Williams & Winfree (2013)	Claytonia virginica	5 - 7 per pot (10 x 8L pots)	40 - 70	<0.001–1.6 visits/flower/hr	1 - 5 spp/hr		21	1	60 min	USA, Chicago	Urban (residential gardens)

Polemonium reptans	1 per pot (10 x 8L pots)	160 - 200	0.05–1.8 visits/flower/hr	1 - 8 spp/hr	19	1	60min	USA, Philadelphia	Urban (forest remnants)
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# 3.6. Conclusions

Although pan traps are widely used, are easy to deploy, and can collect large numbers of specimens in certain habitats in the Northern Hemi-sphere, they were found to be insufficient at sampling native bee communities in this study in an urbanized region of the southwest Western Australian biodiversity hot spot. Targeted sweep netting was shown to be the most effective method for collecting a representative, comprehensive sample of native bee assemblages. Blue vane traps are recommended to accompany targeted sweep netting, as they can be effective at collecting a subset of taxa that may be underrepresented in other methods.

Although there have been a number of studies employing different sampling methods to survey bees, no synthesis of these methods across landscapes, countries, and habitat types has been undertaken. Our literature review therefore contributes to the global goal of monitoring native bee populations and emphasizes that a number of methods should be employed in order to sample the bee community as well as possible.

### **3.7.** References

Every reasonable effort has been made to acknowledge the owners of the copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

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### Chapter 4

# Residential gardens are a poor alternative to urban native vegetation remnants in supporting native bee communities

The study presented in Chapter 4 is in preparation for submission for publication within the peer-reviewed journal '*Biological Conservation*':

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Megachile oblonga © Kit Prendergast

## Residential gardens are a poor alternative to urban native vegetation remnants in supporting native bee communities

#### 4.1. Abstract

Native bees are declining in many regions, associated with loss of natural habitat. Urbanisation replaces natural vegetation with a highly-modified landscape, where residential gardens are a major component of urban greenspace. Whilst many cities retain native vegetation remnants within the urban matrix, these are often small, isolated and degraded compared to natural habitat. However, there is little empirical information on whether residential gardens can serve as equivalent or beneficial habitat for native bees, and which local and landscape factors influence bee assemblages. We surveyed bee assemblages in the southwest Australian biodiversity hotspot at seven residential gardens and seven bushland remnants over two years, in the austral spring and summer. Native bees were more abundant in bushland remnants than residential gardens, whilst abundance of the introduced honeybee Apis mellifera was generally high, but did not differ between habitats. Bushland remnants hosted more species and more rare and unique native bee species than residential gardens. Native bee body-size and nesting guilds varied in their response to habitat type. Native bee abundance and richness increased with abundance of native plant species, but decreased with total flower species richness. In addition, native bee species richness was negatively impacted by urbanisation (built space and isolation from bushland reserves). In contrast, we found no significant relationships between local and landscape factors and honeybee abundance. Our study demonstrates that whilst residential gardens can host native bees, urban bushland remnants harbour a more comprehensive suite of species and are key for the conservation of native bee populations.

#### 4.2. Introduction

Urbanisation involves loss, fragmentation, degradation and alteration of natural landscapes (Elmqvist et al. 2016), where natural or near-natural vegetation is replaced by infrastructure including impervious surfaces such as roads and buildings (McKinney 2008). However, urbanisation also involves the creation of greenspaces, where residential gardens comprise a large proportion of the urban footprint [for example, Sheffield, UK: 23%, Dunedin, New Zealand: 36% (Gaston et al. 2005; Mathieu et al. 2007)], and contribute substantially to urban greenspace [e.g. 35% in Edinburgh to 47% in Leicester, UK (Loram et al. 2007)]. In many cities, fragments of the original natural vegetation remain within the urban matrix (Muller et al. 2010). Such remnant native vegetation may, however, be isolated and degraded (Fisher et al. 2009; Faeth et al. 2011), and threatened by further land clearing (McDonald et al. 2008). Nevertheless, urban areas may harbour substantial biodiversity (Baldock et al., 2015; Ives et al. 2016; Hall et al. 2017), with implications for how urban areas are managed for biodiversity conservation.

Bees are key pollinators in many ecosystems (Danforth, 2007). There are, however, concerns that bee populations are declining across the globe (Potts et al. 2016), caused in part by habitat loss and fragmentation resulting from human-induced landscape alteration (Brown and Paxton 2009), and changes in land management practices (Goulson et al. 2015). The majority of land-use change in the past century has been due to the spread of urban landscapes (Dearborn and Kark 2010). However, there is variation in how bee communities respond to urbanisation (Hernandez, Frankie & Thorpe 2009), likely due to differences in the habitat types and floral communities sampled, and the diverse ecology of bees in different ecosystems. Some groups of bees will be more resilient to changes wrought by urbanisation ("urbanophiles") than others, especially in ecosystems where urban greenspaces are not host to substantially different vegetation communities to the native habitat.

Native flora in non-urban managed landscapes are important for supporting native bee communities (Morandin and Kremen 2013; Williams et al. 2015). Reliance of bees on remnant native vegetation has been less well-studied in urban areas than for agricultural and rural landscapes (Kremen et al. 2004). However, there is evidence

that urban habitats dominated by diverse, yet exotic, plants reduce native bee diversity, instead favouring exotic bee species, primarily the European honeybee (*Apis mellifera*) (Hernandez et al. 2009; Head and Muir 2006; Loram et al. 2008). Furthermore, standard management practices in most residential gardens such as weed removal, pesticide application, and mowing, have negative effects on wild bees (Wastian et al. 2016; Lerman et al. 2018). As such, biodiversity of native bee species could decline in residential gardens due to loss of rare and specialised species, leaving primarily generalist species that can utilise exotic flora (Hernandez et al. 2009). Native vegetation remnants may therefore represent refugia for oligolectic bees and species that are negatively affected by landscape modification (Venturini et al. 2016). In contrast, honeybees may benefit from residential gardens, as they are polylectic and can exploit the diverse, mainly exotic, floral resources in urban landscapes (McKinney 2008; Requier et al. 2015). Consequently, in these domestic greenspaces, a few, common species dominate (Threlfall et al. 2015), adversely affecting the evenness of the bee assemblages.

There is growing awareness that greenspaces in urban landscapes can be important for the conservation of bee diversity, if properly managed (Hall et al. 2017), but comparison of native bee assemblages between managed residential gardens or greenspaces and original native vegetation remnants has been largely unexplored (Dylewski et al. 2019). Many studies investigating urban bee communities have compared urban gardens with natural habitat outside the urban matrix (eg. Fortel et al., 2014; Gotlieb, Hollender, & Mandelik, 2011; Verboven et al., 2014), which can confound habitat type with landscape context. Whether residential gardens serve as analogous, complimentary, superior or inferior habitat to support species-rich native bee communities compared with urban remnant native vegetation is relatively unknown. Moreover, the majority of studies on bees in urban areas have been conducted in the Northern Hemisphere (Wenzel et al. 2019), with very few occurring in Australia (but see Prendergast & Ollerton 2020; Prendergast et al. 2021; Threlfall et al. 2015; Kaluza et al. 2016; Makinson et al. 2016), a country with a diverse wild bee fauna (Batley and Hogendoorn 2009).

We compared bee communities in urban native vegetation (bushland) remnants with those of residential gardens. We hypothesised that bushland remnants would host a

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greater abundance and species richness of native bees than residential gardens, and a greater number of numerically rare native bee species. In contrast, we hypothesised that honeybees would be more abundant in residential gardens. In addition, we investigated the influence of local and landscape level environmental factors, such as the abundance, diversity and origin of flower resources, nesting substrate availability, and proxies for fragmentation and urbanisation, on the abundance and species richness of native bees, and the abundance of honeybees. We also investigated how key life-history traits – body-size and nesting substrate guild – influenced the responses of native bees to urbanisation. We avoided the confounding effect of different landscape context by surveying both gardens and bushland within the same urbanised landscape.

#### 4.3. Methods

#### 4.3.1. Study sites

Bee communities were studied at fourteen sites (seven native vegetation remnants, hereafter referred to as bushland remnants and seven residential gardens) around the city of Perth (Fig. 4.1a, Appendix Table A1), which is situated within the southwest Australian biodiversity hotspot (Hopper and Gioia 2004). The Perth metropolitan area covers 641,786 ha, with an average density of six houses per ha (Australian Bureau of Statistics 2011; Ramalho et al. 2014). Interspersed within the urban matrix are bushland remnants, most of which are <50 ha in size (Dixon et al. 1995). Urban development is the main threat to native vegetation in the region (Ramalho et al. 2014), with 48-84% of native vegetation communities in the urbanised Swan Coastal Plain lost to clearing (Department of the Environment 2015). Land clearing for urban development is an intensifying threat, given projections that the population of Perth will grow between 200-300% by 2061 (Australian Bureau of Statistics 2018).

Bushland remnants were selected at random with the only constraint that they were dispersed across the Perth metropolitan region and retained native understorey species. The residential gardens were selected out of a pool of citizens who responded to social media requests for permission to survey their garden. To maintain objectivity and sampling independence, the only criteria for selection were

that sites were interspersed with the bushland remnants and separated by greater than 1 km to ensure that we were not sampling bee communities from adjacent sites, given that 1 km is greater than the flight range of most wild bees (Gathmann and Tscharntke 2002; Greenleaf et al. 2007; Zurbuchen et al. 2010).



**Fig. 4. 1.** (a) Layout of study locations within the Perth metropolitan area (N = 14), located within the southwest Western Australian Floristic Region biodiversity hotspot. Black points indicate native bushland remnants, white points indicate residential gardens. The green areas indicate the current land areas included in Australia's protected areas network of conservation reserves. (b) Schematic of survey design for each habitat type.

#### 4.3.2. Bee surveys

Bee communities were surveyed monthly in the austral spring and summer between November 2016-February 2017 (year one) and October 2017-March 2018 (year two). The sites were surveyed in random order with a given habitat type (bushland or residential) never surveyed for more than three consecutive days. One site was surveyed each day, and each site was surveyed a total of 10 times over the two seasons. Each survey lasted for three hours during peak bee activity between 10:45am and 1:45pm. As the total area of sites differed, survey area was standardised to cover 100 m x 100 m. For residential sites, the area surveyed included the front and back yard, and adjacent road verges (Fig. 1b).

To overcome inherent biases in survey techniques, we used several methods to quantify bee communities (Packer & Darla-West 2021; Portman, Bruninga-Socolar & Cariveau 2020; Prendergast et al. 2020). At each site, a single researcher (K.S.P) observed patches of flowering vegetation and recorded the number of honeybees and native bees present. Observed bees were assigned to the lowest taxonomic level possible in the field. Native bees were also collected with an entomological sweep net, allowing for these specimens to be identified to species or morphospecies (Prendergast et al. 2020). Each flowering patch was observed for 5 mins before moving to another patch. Due to differences in the number of flower patches between surveys, some patches were visited multiple times per survey.

At each site 10 UV-fluorescent yellow and 10 UV-fluorescent blue 96 mL pan traps (New Horizons Support Services Inc., Upper Marlboro, Maryland) and nine 350 mL yellow pan traps were deployed randomly throughout each study site. Pan traps contained water and a few drops of unscented detergent and were left out for the duration of each survey (3 hrs) (Prendergast et al. 2020).

Two blue and two yellow UV-reflective vane traps (64 oz., SpringStar, Woodinville, Washington) were placed at each site, approximately 1 m above the ground. Vane traps contained approximately 1400 mL of 50% propylene glycol preservative and remained in place for the duration of the survey period for each season. Vane traps

were cleared monthly and the samples washed and stored in 90% ethanol (Prendergast et al. 2020).

Bee specimens were identified using published keys where available (Houston (2018) and references therein), and with reference to the Western Australian Museum (WAM) collection. Where no formal description could be determined, specimens were assigned to unique morphospecies. Representative specimens are to be lodged with the WAM. The number of observed and collected bees from all methods each month were pooled for analysis.

#### 4.3.3. Local and landscape factors

Within the 100 x 100 m survey area, we counted the number of flowering plant species and the total number of flowers. We then calculated the number and proportion of flowers and flowering plants that were native to Australia. The number of woody plants in the 100 x 100 m area was counted as a proxy for the availability of nesting resources for cavity-nesting bees. Nesting resources for ground-nesting bees were estimated as the proportion of bare ground (open dirt or sandy substrate with minimal vegetative litter) every 5 m along two 50 m x 4 m transects. Local environmental variables were recorded for each survey period.

As a representative for the level of urbanisation and connectivity, we measured the amount of built space surrounding the site and the linear distance to the nearest bushland remnant (km), respectively, using Google Earth Pro v7.3.3.7699 (https://www.google.com/earth). The level of urbanisation was measured as the proportion of 10 x 10 m grid cells comprising impervious surfaces within a 500 m radius around each site.

#### 4.3.4. Data analyses

Honeybee abundance, native bee abundance, and native bee species richness were calculated for each survey. Since species richness does not take into account the differences in relative abundances of species, we calculated species evenness using Pielou's index (J', Pielou 1966):

$$J' = \frac{H'}{\ln(S)} \tag{1}$$

where S is species richness, and H' is the Shannon-Weiner diversity index, which is calculated as:

$$H' = -\sum_{i=1}^{S} p_i (\ln p_i)$$
(2)

where  $p_i$  is the proportional abundance of species. Species evenness (*J'*) is a ratio of the maximum diversity of a community given the number of species it contains. An assemblage with a high evenness score is one where individuals are apportioned equitably among species, whereas an assemblage with a low evenness score is dominated by a small number of species. Species evenness was calculated for each survey from the abundances of each native species collected.

Species collected in only one habitat type (residential gardens or bushland remnants) across all 140 surveys were considered to be exclusive to that habitat. Singletons and doubletons – species that were only represented by one or two individuals across all surveys - were considered to be "rare" species following Perillo et al. (2017) and Ramírez et al. (2016).

Functional composition regarding nesting substrate and body-size of bee assemblages was compared between habitat types for abundance and species richness from collected specimens. Species were classified as above-ground (cavitynesting in wood, resin pot nests, pithy stems) or below-ground nesters (burrows in substrate) based on the literature (Houston 2018) and field observations (K.S. Prendergast); species for which the nesting habits remain unknown were classified according to related species. Body-size (inter-tegular distance; ITD) of an individual of each sex per native bee species/morphospecies was measured from macrophotographs (Canon DLSR, 100mm lens, 1:1 magnification, f-stop 8) imported into Adobe Photoshop using the "Set measurement scale" and "ruler" features. Bee species were subsequently categorised as small (0.48-1.78 mm), medium (1.79-3.10 mm) and large (3.11-4.41 mm). When sexes differed in their body-size category (eight out of 68 species with both sexes) they were treated as separate taxonomic units.

Analyses were conducted in R v3.6.2 using generalised linear mixed effects models with a Poisson error distribution for count data and a binomial error distribution for proportion data (GLMM; package *lme4*; Bates et al., 2015). Site was included as a random factor to account for repeated sampling and sampling year was included as a categorical variable in all models. Model fit and the presence of overdispersion in the data were checked using the package DHARMa (Hartig 2017). If overdispersion was present (dispersion factor > 1.4; Korner-Nievergelt et al. 2015), we included an observation-level random effect (OLRE) in the model (Harrison 2014). Significance of the OLRE was tested by comparing the models with and without the OLRE using ANOVA. In the case of honeybee abundance, the OLRE did not fully account for overdispersion, so we applied a negative binomial model (Lindén and Mäntyniemi 2011). As species evenness was bounded (0-1), we employed a beta model with a logit link (package *glmmTMB*) (Brooks et al. 2017). Marginal  $R^2$  (the variance explained by the fixed factors,  $R^2_{\rm m}$ ) and conditional  $R^2$  (the variance explained by the fixed and random factors,  $R^2_{\rm c}$ ) were calculated for each model using r.squaredGLMM (package MuMIn; Burnham and Anderson 2003).

We compared native bee abundance, richness and evenness, honeybee abundance, proportional abundance of native bees, and abundance and richness of bees of different body-size and nesting guilds between the habitat types (bushland remnant and residential garden). Significance (p < 0.05) of habitat type and year were tested by removing the variable of interest and comparing the models using ANOVA.

We additionally investigated the influence of local and landscape variables on native bee abundance and richness, and honeybee abundance. Pairwise correlation between the explanatory variables was tested using Spearman's rank correlation tests. If variables were correlated (r > 0.7; Dormann et al. 2013), the most biologically meaningful variable was retained for the analysis (Appendix Table A2). Consequently, we excluded the variables 'site area', 'total flower abundance', 'total flower richness', and 'woody plant'. While 'proportion of native flowers' and

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'richness of native flowers' were correlated, we retained both in the analyses as these were of particular interest in the study. These variables did not appear together in any of the final models. The global models used to investigate the influence of environmental variables on bees therefore involved: the number of native flowers, species richness of native plants, proportion of native flowers, proportion of native plant species, proportion of bare ground, proportion of built space, and distance to bushland (km). All continuous explanatory variables were scaled before modelling by subtracting the mean and dividing by the standard deviation, using the scale function in R. Model selection was conducted using backwards stepwise regression, starting with a model that included all explanatory variables (Zuur et al. 2009). We systematically excluded each explanatory variable and compared the models using ANOVA. Non-significant variables (p > 0.05) were excluded from subsequent models until only significant predictors remained. Multicollinearity between the predictor variables in the final models was investigated with variance inflation factors using the package *car* (Fox and Weisberg 2019). Predictions from the models were made using the *ggeffects* package (Lüdecke 2018).

#### 4.4. Results

#### 4.4.1. Bee communities in urban landscapes

A total of 27 664 native bees, representing 153 species and morphospecies, and 55 324 honeybees were recorded across all sites over the two study years. Species from 24 genera (21 in the first year, and 23 in the second year) from all families in Australia except for Stenotritidae (Houston 2018) were collected. The families Colletidae and Megachilidae were the most species rich and abundant, and *Megachile* spp. were more abundant and represented by more species than all other genera (Appendix Tables A3 & A4). In total, 137 species were recorded from bushland remnants and 93 species from residential gardens.

Sixty species were found exclusively in bushland remnants, whereas only 16 species were recorded solely from residential gardens. Seventy-seven species (50.3%) were collected from both habitats. Fifty-four (35.3%) were rare (41 species represented by one individual, 13 represented by two individuals). There were more rare species in

bushland remnants than residential gardens: 73% of singletons were recorded in bushland remnants. Of the doubletons, eight were exclusive to bushland remnants, five had an individual collected in each habitat, and one was exclusive to residential gardens.

#### 4.4.2. Influence of habitat type on urban bee communities

Native bee abundance was higher in bushland remnants (mean  $\pm$  SE = 279  $\pm$  65.0 individuals) than in gardens (116  $\pm$  16.3, Fig. 4.2a). Native bee abundance was higher in the second year of the study (Table 4.1, Fig. 4.2a).

Honeybee abundance did not differ between habitat types (bushland =  $463 \pm 121$ , gardens =  $328 \pm 36.3$ , Fig. 4.2b), nor was there a difference between years (Table 4.1). Native bee species richness was higher in bushland remnants ( $13.1 \pm 0.70$  species) than in residential gardens ( $7.7 \pm 0.40$  species, Table 4.1, Fig. 4.2c). Native bee richness was higher in the second year of the study (Table 4.1, Fig. 4.2c). In all cases, there was no significant interaction between habitat and year (Table 4.1).

Evenness of native bee communities was generally high  $(0.79 \pm 0.01)$  and did not differ between habitats (bushland mean=  $0.78 \pm 0.02$  vs. residential garden mean= $0.80 \pm 0.02$ ,  $X^2 = 0.776$ , p=0.378). There was also no main effect of year, or a year x habitat interaction (both p>0.05; Table 4.1).

Native bees comprised a greater proportion of total bee abundance in bushland remnants (0.54  $\pm$  0.037) than in gardens (0.34  $\pm$  0.03,  $X^2$ = 4.25, p=0.039). There was a significant effect of year ( $X^2$ = 1321.0, p<0.001), as well as a year x habitat interaction ( $X^2$ = 3.85, p=0.050) (Table 4.1), such that native bees comprised a greater proportion of bees in the second year, but this was only observed in residential gardens.

**Table 4. 1.** Results of generalised linear mixed effects models for the influence of habitat type on native bee abundance, honeybee abundance, and native bee species richness. Significant factors (p < 0.05) based on likelihood ratio tests ( $X^2$ ) are presented in bold. # indicates models that included an observation-level random effect. Habitat\*Year denotes an interaction. Estimates, SE and R<sup>2</sup> are provided for significant models;  $R^2_m$  is the variance explained by only the fixed factors and  $R^2_c$  is the variance explained by the fixed and random factors. † Estimates refer to residential gardens, compared with bushland habitat, and year two, compared with year one.

Response variable	Explanatory variables	Estimate <sup>+</sup>	SE	R <sup>2</sup> m	R <sup>2</sup> <sub>c</sub>	df	<i>X</i> <sup>2</sup>	р
Native bee abundance <sup>#</sup>	Habitat	-0.701	0.017	0.12	0.99	1	11.3	0.001
	Year	0.685	0.152	0.11	0.99	1	18.8	<0.001
	Habitat*Year					1	0.038	0.846
Honeybee abundance <sup>#</sup>	Habitat					1	0.905	0.342
	Year					1	2.06	0.152
	Habitat*Year					1	0.040	0.841
Native bee richness <sup>#</sup>	Habitat	-0.534	0.116	0.250	0.348	1	12.2	<0.001
	Year	0.177	0.074	0.027	0.377	1	5.95	0.015
	Habitat*Year					1	0.101	0.750

Evenness (J')	Habitat					1	0.776	0.378
	Year					1	0.401	0.527
	Habitat*Year					1	0.068	0.794
Proportion of native bee	Habitat	-1.055	0.486	0.065	0.252	1	4.25	0.039
individuals	Year	0.687	0.020	0.025	0.268	1	1231	<0.001
	Habitat*Year	-0.080	0.041	0.088	0.267	1	3.85	0.050
Below-ground nesting	Habitat	-0.051	0.175	0.002	0.857	1	175	<0.001
abundance	Year					1	<0.001	0.991
	Habitat*Year	-0.250	0.087	0.157	0.872	1	8.13	0.004
Above-ground nesting	Habitat	-0.744	0.173	0.141	0.955	1	12.5	<0.001
abundance <sup>#</sup>	Year	0.561	0.156	0.076	0.955	1	11.5	<0.001
	Habitat*Year					1	0.228	0.663
						1		
	Habitat					1	1.06	0.303

Below-ground nesting	Year					1	3.03	0.081
species richness	Habitat*Year					1	0.077	0.782
Above-ground nesting	Habitat	-0.562	0.116	0.200	0.596	1	7.79	0.005
species richness <sup>#</sup>	Year	0.269	0.095	0.043	0.600	1	13.6	<0.001
	Habitat*Year					1	0.016	0.883
Small bee abundance	Habitat	-0.889	0.199	0.342	0.899	1	19.5	<0.001
	Year	0.461	0.045	0.122	0.860	1	106	<0.001
	Habitat*Year	0.205	0.094	0.391	0.902	1	4.750	0.003
Medium bee abundance	Habitat					1	0.028	0.868
	Year	0.529	0.051	0.127	0.860	1	115	<0.001
	Habitat*Year					1	0.405	0.525
Large bee abundance	Habitat					1	3.05	0.065
	Year					1	78.4	<0.001
	Habitat*Year	-0.620	0.120	0.057	0.937	1	26.3	<0.001

Small bee species richness	Habitat					1	2.18	0.140
	Year	0.360	0.088	0.066	0.494	1	16.8	<0.001
	Habitat*Year					1	0.902	0.342
Medium bee species	Habitat	-0.595	0.121	0.238	0.303	1	14.2	<0.001
richness	Year					1	2.18	0.193
	Habitat*Year					1	0.010	0.919
Large bee species richness	Habitat	-0.582	0.204	0.153	0.351	1	4.81	0.028
	Year					1	<0.001	0.999
	Habitat*Year					1	1.434	0.231



Fig. 4. 2. Comparison of bee assemblages in bushland remnants and residential gardens in year one (white) and year two (grey) for (a) native bee abundance; (b) honeybee abundance; and (c) native bee species richness. Outliers have been removed for visualisation purposes. Images of bees created by Kit Prendergast.

#### 4.3.3. Influence of habitat type according to life-history traits

Native bees of different nesting habits and body-sizes varied in their response to habitat type (Fig. 4.3, 4.4). Mean abundance and species richness of below-ground nesting bees was  $22.1 \pm 1.92$  and  $4.09 \pm 0.21$ , and that of above-ground nesting bees was  $20.6 \pm 1.55$  and  $6.21 \pm 0.34$ , respectively. Compared with residential gardens, bushland remnants hosted a greater abundance of both above-ground ( $27.1 \pm 2.44$  vs.  $14.2 \pm 1.59$ ,  $X^2$ =12.5, p<0.001) and below-ground nesting bees ( $31.4 \pm 3.33$  vs.  $12.8 \pm 1.10$ ,  $X^2$ =175, p<0.001) (Fig. 4.3a, c); there was only an interaction with year for below-ground nesting bees, where there was a greater difference between habitat types in the second year (Table 4.1). Species richness of above-ground nesting bees was greater in bushland remnants than residential gardens ( $7.94 \pm 0.52$  vs.  $4.47 \pm 0.32$ ,  $X^2$ =7.79, p=0.05), whereas there was no difference for below-ground nesting bee species richness ( $4.94 \pm 0.33$  vs.  $3.24 \pm 0.23$ ,  $X^2$ =1.06, p=0.303) (Fig. 3b, d). There was no interaction with year (Fig. 4.3, Table 4.1).

Mean abundance of small, medium and large bees across all surveys was  $16.8 \pm$ 1.54, 13.5  $\pm$  1.24 and 12.5  $\pm$  1.34 individuals per site, and mean species richness was  $4.19 \pm 0.33$ ,  $3.82 \pm 0.20$  and  $2.72 \pm 0.18$  species per site, respectively. There were no differences in abundance of medium or large bees between bushland remnants and residential gardens (medium bees:  $18.7 \pm 2.12$  vs.  $8.31 \pm 0.97$ ,  $X^2=0.03$ , p=0.883; large bees:  $19.1 \pm 2.31$  vs.  $5.97 \pm 0.80$ ,  $X^2 = 3.05$ , p=0.07), whereas small bees were more abundant in bushland remnants (20.8  $\pm$  2.43 vs. 12.8  $\pm$  1.79,  $X^2$ =19.5, p<0.001) (Fig. 4.4a, c, e,) (Table 4.1). There was an interaction between body size and year on the abundance of small and large bees (Table 4.1): the difference in abundance of small bees between habitat types was significant in year one ( $X^2=20.5$ , p<0.001), but not year two ( $X^2$ =20.5, p<0.001). When analysed by year, abundance of large bees was significantly different in bushland remnants compared to residential gardens in year one ( $X^2$ =6.29, p=0.01), and significantly different in year two ( $X^2$ =11.7, p<0.001) (Fig. 4.4). Species richness of medium and large bees was greater in bushland remnants than residential gardens (medium bees:  $4.94 \pm 0.29$  vs.  $2.70 \pm$ 0.20,  $X^2$ =14.2, p<0.001; large bees: 3.62 ± 0.27 vs. 1.81 ± 0.19,  $X^2$ =4.81, p=0.03), whereas there was no significant difference for small bees ( $5.0 \pm 0.53$  vs.  $3.37 \pm$  $0.35, X^2 = 2.18, p = 0.14$ ) (Fig. 4.4b, d, e; Table 4.1); this did not vary with year.



**Fig. 4. 3.** Comparison of native bee nesting guilds in bushland remnants and residential gardens in year one (white) and year two (grey) for: (a) above-ground native bee abundance; (b) below-ground native bee abundance: (c) above-ground native bee species richness; (d) below-ground native bee species richness.



**Fig. 4. 4.** Comparison of native body-size guilds in bushland remnants and residential gardens in year one (white) and year two (grey) for: (a) small body-size native bee abundance; (b) medium body-size native bee abundance; (c) large body-size native bee abundance; (d) small body-size native bee species richness; (e) medium body-size native bee species richness; (f) large body-size native bee species richness.

#### 4.4.4. Environmental determinants of native bees in urban areas

Native bee abundance was negatively correlated with richness of native flower species (Fig. 4.5a), but positively influenced by the proportion of native flower species at a site (Table 4.2, Fig. 4.5b). There was a positive trend between native bee abundance and the amount of bare ground at a site ( $X^2 = 3.277$ , df = 1, p = 0.070, Table 4.2), but this was not retained in the final model. Year was retained in the final model.

Native bee species richness decreased with increasing proportion of built space in a 500 m radius around the site (Fig 4.5c) and with increasing distance to the nearest bushland remnant (Fig 4.5d). Similar to native bee abundance, species richness of bees was negatively associated with species richness of native flower species at a site (Fig. 4.5c). However, native bee species richness increased with an increasing proportion of native flowers (out of total flower abundance) at a site (Fig. 4.5e). There was also a positive trend with increasing proportions of native flower species) ( $X^2 = 3.73$ , df = 1, p = 0.054, Fig. 4.5f, Table 4.2), but this was not retained in the final model due to proportion of native flowers and proportion of native flower species being correlated. Year was retained in the final model (Fig. 4.5, Table 4.2).

We found no significant relationships between honeybee abundance and any of the local or landscape predictors (Appendix Table A5).



**Fig. 4. 5.** Native bee community responses of (a) abundance in relation to the number of native flower species, (b) abundance in relation to the proportion of native flower species, (c) species richness in relation to the proportion of built area in the surrounding 500 m radius, (d) species richness in relation to distance to the nearest bushland reserve, (e) species richness in relation to native flowers, and (f) species richness in relation to the proportion of native flowers. Values for year one are in red and year two are in blue. Solid lines represent the fitted estimates of Poisson GLMM models, and shaded areas indicate 95% confidence intervals.

Table 4. 2. Results of generalised linear mixed effects models for the influence of environmental variables on native bee abundance and native bee species richness. Significant factors (p < 0.05) based on likelihood ratio tests ( $X^2$ ) are presented in bold; trends towards significance (p < 0.10) are presented in italics. # indicates modes that included an observation-level random effect. Estimates are based on the final model for each explanatory variable.  $R_m^2$  is the variance explained by only the fixed factors and  $R^2_{c}$  is the variance explained by the fixed and random factors, calculated for the final model.

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Response variable	Explanatory variables	Estimate	SE	R <sup>2</sup> m	R <sup>2</sup> <sub>c</sub>	df	<i>X</i> <sup>2</sup>	р
Native bee abundance <sup>#</sup>	Intercept	4.12	0.113	0.23	0.99			
	Proportion of built space					1	0.271	0.602
	Distance to bushland (km)					1	0.851	0.356
	Number of native flowers					1	0.263	0.608
	Richness of native plants	-0.366	0.073			1	23.3	<0.001
	Proportion of native flowers					1	0.232	0.630
	Proportion of native plants	0.461	0.072			1	27.6	<0.001
	Proportion of bare ground					1	3.28	0.070
	Year	0.949	0.145			1	40.6	<0.001

Native bee richness <sup>#</sup>	Intercept	2.40	0.122	0.27	0.65			
	Proportion of built space	-0.643	0.129			1	15.6	<0.001
	Distance to bushland (km)	-0.099	0.038			1	5.47	0.019
	Number of native flowers					1	0.338	0.561
	Richness of native plants	-0.026	0.006			1	15.9	<0.001
	Proportion of native flowers	0.526	0.111			1	16.2	<0.001
	Proportion of native plants					1	3.73	0.054
	Proportion of bare ground					1	0.399	0.527
	Year	0.298	0.058			1	15.7	<0.001

#### 4.5. Discussion

Our results show that residential gardens and natural vegetation remnants did not support equally species-rich and abundant native bee assemblages. Instead, we found that even remnant patches of native vegetation supported more species-rich and abundant bee communities than gardens. This is consistent with findings that residential gardens do not have equivalent plant-bee visitation networks to bushland remnants (Prendergast & Ollerton 2021).

Native bee abundance and species richness were greater in the second year of surveys, whereas honeybee abundance did not differ. The higher abundance and species richness of native bees, however, corresponded with a greater sampling effort in the second year, and potential inter-annual variation typical of wild bee assemblages (Williams et al. 2001).

#### 4.5.1. Remnant natural vs. managed home greenspaces

The higher abundance and species richness of native bees in bushland remnants than residential gardens are consistent with some studies comparing native vegetation and managed gardens (e.g. Tonietto et al. 2011), but not others (e.g. Winfree et al. 2007), suggesting that responses of bees to these contrasting habitat types are sensitive to ecological and evolutionary context. Differences in the response of wild bees to urban landscapes between studies may be due to the type of greenspaces being compared. Furthermore, historical land-use may have a significant influence on bee community structure with the loss of "urbanophobic" species that require continuous large tracts of natural areas and the growth of populations of "urbanophilic" bee species (Faeth et al. 2011). Most European cities have a long heritage of human management, and it is difficult to identify unmodified 'native vegetation' for comparative purposes (Wells 1984). In the southwest Australian biodiversity hotspot, remnant bushland is renowned for consisting of floristically diverse, open canopied systems (Beard et al. 2013; Lambers 2014). In contrast, relatively speciespoor, closed canopy forest dominated by anemophilous gymnosperms - the dominant native vegetation cover in higher latitude northern hemisphere regions can be of lesser value for bees when compared with floristically-diverse, open

greenspaces with a high diversity of insect-friendly plants in residential gardens (Grundel et al. 2010; Michener 2007).

Consistent with predictions that exotic species are more likely to benefit from urbanisation than native species (Gaertner et al. 2017), honeybee abundance did not differ between residential gardens and bushland remnants. Honeybees had the highest density of all bee species, especially in residential gardens, which may be attributed to their broad diets and their ability to exploit exotic food sources (Geslin et al. 2017), and hobby apiarists maintaining hives across the study region. Abundance of this introduced species was higher than reported in other parts of the world (Bates et al. 2011; Cane et al. 2006), but consistent with other studies in Australia (Cane et al. 2005; Yates et al. 2005), where honeybees thrive in residential gardens (Threlfall et al. 2015). The lack of observed differences in honeybee abundance between years may be due to local populations consisting of a mix of feral and managed bees. As managed bees are tended by beekeepers, it is likely that their numbers are more stable since they can be buffered against environmental variation through beekeeping husbandry (Geldmann and González-Varo 2018). Honeybees are also highly adaptable, as evidenced by their successful introduction across many climatic and biogeographic regions (Geslin et al. 2017). This also suggests that campaigns for honeybee conservation may not benefit native bees (Geldmann and González-Varo 2018; Wood et al. 2020). While there are concerns that honeybees can displace native bees through competition for food resources (Cane and Tepedino 2016; Shavit et al. 2009), the data from Australia are equivocal (Paini 2004). With evidence that native bee species that have high niche overlap with honeybees may be adversely impacted by this introduced species in urban areas (Prendergast et al. 2021), more research is required.

Urbanised habitats tend to be associated with decreased community evenness (Shochat et al. 2010). However, we did not observe differences in bee community evenness between residential gardens and bushland remnants. Although residential gardens were dominated to a greater extent by a few common species, bushland remnants hosted a greater number of numerically rare species, resulting in similar values of evenness. High community evenness of the native bee assemblages observed in this urban bee study was similar to that observed in a large-scale urban

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study across two Canadian cities (Normandin et al. 2017), suggesting that urbanised habitats have the potential to support even bee assemblages.

The introduced European honeybee was recorded based on observational counts alone and not included in our calculations of evenness. The much greater numbers of bees when observational records are included (Prendergast et al. 2020) implies a methodological inequivalence with our estimates of native bee abundance that would inappropriately bias the calculation of evenness in this study were honeybee counts included. The inclusion of honeybees in an evenness calculation may produce differences in community evenness between habitats, and, like many introduced species, an overall decrease in evenness (Shochat et al. 2010).

#### 4.5.2. Responses of habitat type according to life-history traits

Small and large-bodied native bees were less abundant in residential gardens, and residential gardens supported fewer species of medium and large bees. There have been mixed findings regarding how bees of different body sizes respond to urbanisation; our findings, however, align with those of Banaszak-Cibicka et al. (2018), with richness of larger-bodied bees being reduced with greater urbanisation, and results of Hamblin, Youngstead & Frank (2018), where it was also found that small bee abundance, and large bee species richness, were reduced with increasing urbanisation. The effects on species richness of larger bees may be due to how due to preferred foraging resources being fewer in residential gardens, there is greater resource overlap between species with similar foraging niches, and reduced resource partitioning opportunities (Prendergast & Ollerton 2021). In addition, the largebodied European honeybee may be a major resource aggressor for the same resources as larger bodied native bees (Paini 2004), which may exacerbate energetic stress in larger-bodied bee species, particularly late in the foraging season (Tomlinson et al. 2015), amplifying their susceptibility to resource competition (Prendergast, Dixon & Bateman 2021). Richness of small native bee species was equivalent in both habitats, potentially because the resources required to support a population of smaller-bodied bees are less than those required by larger-bodied species (Darveau et al. 2005), allowing more species to co-exist. However, smallbodied bees were less abundances in the residential gardens; which may be due the

inability of small-bodied species to forage as far to find resources that may be more sparsely dispersed in residential areas (Zurbuchen et al. 2010). Whilst there were fewer medium-sized bee species in residential gardens, hypothesised to be due to the mechanisms of resource partitioning and carrying capacity described above, medium sized bee abundance may have been least affected compared with the small and large sized bees due to lower resource requirements than large bees, but greater mobility than small bees.

# 4.5.3. Environmental drivers of bees in the urbanised southwest Western Australian biodiversity hotspot

We found positive associations of native bee abundance and species richness with proportions of native plant species and native flowers, respectively. This is consistent with positive correlations of resource patch size and density with increased bee abundance and richness, and optimised foraging by bees reported by Wojcik and McBride (2012). Contrasting with other studies (Pardee & Philpott, 2014), the negative association between native bee species richness and native plant species richness may be due to many native bees specialising on certain plant species (Houston 2000; Phillips et al. 2010; Prendergast & Ollerton 2021). Hence, many native flowering plants may not be within the foraging niche of native bees, constraining the array of flowers that bees can utilise (Wood et al. 2016). This negative relationship may also result from reduced foraging efficiency of bees targeting specific resources (Goulson 2000). There is also the possibility this reflected a reduced chance of observing bees on specific resources in areas of high flower diversity.

We found some evidence that proportion of bare ground positively influenced native bee abundance, as frequently reported in other studies of bee communities in urban landscapes (Marín et al. 2019; Ballare et al. 2019). We interpreted bare ground as a proxy for nesting habitat for ground-nesting bees, which comprise the majority of species globally (Michener 2007). Insofar as nesting habitat limits recruitment, this explains these associations (Naeme et al. 2013; Roulston and Goodell 2011). Bees of different nesting guilds responded similarly in abundance to habitat type, however above-ground nesting bee species were more sensitive to conversion of natural habitat to residential gardens. Our results contrast with previous studies that have found cavity-nesting bees to be less-sensitive to urbanisation than ground-nesting bees (e.g. Pereira, Carneiro & Goncalves, 2020). However, our results may be due to associations between nesting guild and pollen specialisation: ground-nesters in our study were primarily generalists (Amegilla, Halictidae), which would be better able to exploit the diversity of flowers in gardens, whereas the cavity-nesting bees primarily Hylaeinae and Megachilidae - include more specialised taxa (Houston, 2018). Thus, the patterns reported here may arise from covariation between cavitynesting bees with specialisation on native flora, and ground-nesting bees being pollen generalists. Indeed, it appears that in some habitats, bees are more strongly limited by reduced foraging opportunities than by reduced nesting opportunities (Torné-Noguera et al., 2014). Additionally, despite urbanisation, there may be adequate substrates for ground-nesting bees in gardens (Frankie et al., 2005; Prendergast, 2021), whereas the specific substrates for cavity-nesting species (holes of suitable diameters, wood type, other nesting materials like resin and plant materials (da Rocha-Filho et al., 2020; Prendergast, 2018) may be more limiting in the residential gardens.

We found fewer native bee species at greater distances from the nearest bushland remnant. Similarly, we also found fewer native bee species in areas with greater proportions of built space surrounding the sites. This is consistent with the role of habitat connectivity and isolation from natural vegetation in influencing bee assemblages (Braaker et al., 2014; Krimmer et al. 2019; Steffan-Dewenter and Tscharntke 1999). Although distance to the nearest bushland was a simple proxy for habitat connectivity (and conversely, isolation from native vegetation), especially in heterogeneous urban landscapes, it does emphasise the importance of maintaining native vegetation for urban biodiversity (Taylor and Ives 2009). Connectivity between bushland remnants should enable some native bee species to move throughout the cityscape, including gardens and other public green areas (Banaszak-Cibicka et al. 2016).

#### 4.5.4. Australian bee communities and management insights

The higher abundance and species richness of native bees in bushland remnants compared to floristically-diverse gardens in our study may reflect the long evolutionary history between plant-pollinator communities in south-west Australia, such that they do not respond positively to the diversity of exotic plant species in gardens (Hopper 2009; Phillips et al. 2010). We speculate that residential gardens may represent "sink" habitats, colonised by native bees from bushland remnant "sources" (Hunter 2002; Öckinger and Smith 2007), but this requires further investigation. While habitat improvement and connectivity may be facilitated by planting "bee-friendly" native flora (Hülsmann et al. 2015; Phillips et al. 2010), our results indicate that urban bushland remnants represent important habitat for conserving urban bee biodiversity (Hall et al. 2017).

We found that urban habitats in the Southwest Australian Floristic Region hosted a remarkably high biodiversity of native bees, far exceeding that reported for other urban areas in Australia (Makinson et al. 2016; Threlfall et al. 2015). Our findings comparing urban habitat types support literature from other parts of the world (e.g. Normandin et al., 2017; Twerd & Banaszak-Cibicka 2019), demonstrating that urban greenspaces are not of comparable conservation value, and ecological and evolutionary context is important in understanding this (Buchholz & Egerer, 2020; Prendergast, Dixon & Bateman, Chapter 2 of this thesis). In ecosystems with high diversity of both native plants and native bees, such as southwest Australia, even fragments of native bushland may be of substantial importance to the conservation of native bee assemblages in urban areas and should be preserved and restored. In addition, encouraging the planting of a greater diversity of native species, particularly those plant species that are required by specialist foraging native bees, will provide opportunities to conserve and enhance diversity of native bees.
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Every reasonable effort has been made to acknowledge the owners of the copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

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### Chapter 5

## Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens

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Leioproctus sp. © Kit Prendergast

## Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens

#### 5.1. Abstract

Urbanisation is a prominent and increasing form of land-use change, with the potential to disrupt the interactions between pollinators such as bees and the flowering plants that they visit. This in turn may cause cascading local extinctions and have consequences for pollination services. Network approaches go beyond simple metrics of abundance and species richness, enabling understanding of how the structure of plant-pollinator communities are affected by urbanisation. Here we compared pollination networks between native vegetation (bushland) remnants and residential gardens in the urbanised region of the southwest Australian biodiversity hotspot. Across fourteen sites, seven per habitat, plant-bee visitor networks were created from surveys conducted monthly during the spring-summer period over two years. Extinction slope (a measure of how extinctions cascade through the network), and network robustness and nestedness were higher for bushland remnants, suggesting that networks in bushland remnants had greater functional integrity, but if disrupted, more cascading extinctions could occur. In contrast, niche overlap between pollinators was higher in residential gardens, suggesting greater competition for resources. Most species-level properties did not differ between habitats, except for normalised degree, which was higher in bushland remnants. In conclusion, it appears that pollination networks in managed residential gardens are not structurally equivalent with those in bushland remnants. This has implications for conservation of wild bee assemblages in this biodiversity hotspot, and suggests removal of remnant native vegetation for residential development could disrupt the integrity of plant-pollinator assemblages.

#### 5.2. Introduction

Ecosystems that function well involve robust mutualistic networks. However, if there are losses of key interactions, this can cause declines in network functioning (Kearns et al. 1998). Conserving networks of species interactions is vital for conservation and maintenance of ecosystem functions such as animal-mediated pollination (Tylianakis et al. 2010). Analyses of plant-pollinator communities using interaction networks have enhanced understandings of ecological patterns and processes, and the structure and functioning of these ecological assemblages (Burkle and Alarcón 2011; Thébault and Fontaine 2010; Vázquez et al. 2009). Wild bees are integral to many ecosystems due to their roles as pollinators (Garibaldi et al. 2013; Ollerton 2017), however there are recorded declines and extinctions of bees across the globe, with concomitant declines in pollination services (Biesmeijer et al. 2006), jeopardising plant populations (Pauw 2007). Pollinators appear to be particularly susceptible to habitat loss (Taki and Kevan 2007), suggesting that habitat loss can lead to declines in flower-visitor network integrity.

Urbanisation is a major and ongoing cause of habitat loss (Güneralp et al. 2013). The effect of urbanisation on wild bees and pollination services however is inconsistent, varying according to the habitat type being surveyed (Dylewski et al. 2019), and ecological traits such as specialisation (Hernandez et al. 2009). Despite the importance of looking at bees and plants using a network-level approach (Ings et al. 2009), and the increased sophistication of analytical tools to do so, plant-pollinator networks have rarely been analysed in urban areas. This is a major knowledge gap, given that urbanisation is an increasing and significant form of land-use modification (Faeth et al. 2011), causing changes in the composition of both plants and pollinators (Bartomeus et al. 2017; Harrison and Winfree 2015).

Urbanisation results in loss, degradation and fragmentation of the original native vegetation, to be replaced by builtspace and managed greenspaces, such as residential gardens (Niinemets & Peñuelas 2008). These vegetation changes often result in increased numbers of flowering plant species, most of which are exotic, often horticulturally-modified, varieties (Niinemets & Peñuelas 2008). Such changes

are expected to disrupt co-evolved plant-pollinator networks (Kearns, Inouye & Waser 1998). Namely, it can be expected that in more modified urban greenspaces, networks will involve a greater number of nodes due to the increased plant species richness, but a loss of specialisation, which may be observed in terms of greater generalisation of the network and interacting taxa. Depending on the foraging flexibility of pollinators, they may expand their niche breadth, and increase overlap, dividing up the resources, resulting in greater functional complementarity. Conversely, if pollinator taxa are restricted in their foraging preferences, the loss of native flora may mean they must concentrate their foraging on a narrower subset of native flora that persist. Urbanisation, by causing loss of specialised mutualisms, could lead to loss in the robustness of pollination networks, and cascading extinctions (Kaiser-Bunbury et al. 2010).

Previous studies in urban habitats have looked at number of interactions (essentially visitation frequency) rather than networks *per se* (Buchholz and Kowarik 2019; Geslin et al. 2013) or compared urban habitats with those outside the urban context (Theodorou et al. 2017). Likewise, in the recent large-scale study by Baldock et al. (2019), the properties and structure of pollinator networks was not compared among habitat types. Our knowledge of the effects of urbanisation on plant-pollinator networks is still limited, particularly in the context of how different habitat types within urban areas such as remnant natural areas compare with managed greenspaces, and the influence of exotic species on the structure of these networks. Few studies have compared plant-pollinator networks between natural vegetated habitats and anthropogenic garden habitats in the same urban setting, and thus this study is a major advance in understanding how plant-pollinator networks are structured in different habitat types within urban areas.

This study assessed the structure of urban flower-visitor networks, with the aim of investigating how flower-visitor networks in bushland remnants of natural vegetation embedded within the urban matrix compare with those of residential gardens, in terms of network- and species-level properties. We hypothesised that bushland remnants were not comparable habitats to residential gardens, and due to divergent plant and pollinator assemblages and ecological conditions in these two urban greenspaces, plant-pollinator networks would differ in both network- and species-level properties.

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#### 5.3. Methods

Flower visitation networks were constructed from data on visits by both native Australian bees and the introduced European honeybee to flowers during surveys of fourteen sites in the region of Perth, Western Australia, located in the southwest Western Australian (SWWA) biodiversity hotspot (Myers et al. 2000). Seven of these were bushland remnants – fragments of the original native vegetation that persisted on the Swan Coastal Plain (Hopper & Burbidge 1989); the other seven sites were residential gardens. To prevent selection bias, and with the aim of sampling a representative sample of residential gardens in the region, residential gardens were not visited prior to selection, and were chosen blindly from a pool of citizens offering to allow their property to be surveyed on a first to offer basis. The only constraint was that they were interspersed among bushland sites, and that each site was at least 2 km away from the closest site to ensure independence, as this is beyond the flight range of the majority of bee species (Greenleaf et al. 2007). A map of the sites and the surrounding landscape can be found in Prendergast et al. (2020), Fig. 1. The two urban habitats differed significantly in plant community, with bushland remnants having fewer total plant species, but a higher proportion of native flora (Prendergast 2020b).

#### **5.3.1.** Flower visitor surveys

Sites were surveyed once a month between 1045h-1345h over the austral spring/summer from November to February 2016/2017 and October to March 2017/2018. Surveys were conducted over an approximately 100 m x 100 m area of greenspace. As bushland remnants were larger than 100 x 100 m, this encompassed part of a bushland remnant, such that bushland remnant sites surveyed consisted only of the remnant native vegetation ecosystem. For residential gardens, only one property was surveyed, however as the 100 x 100 m often was larger than the garden of property, the area surveyed comprised the front and backyard, and often road verges. For the entire three-hour duration a single researcher (KSP) walked haphazardly between flowering patches, with a minimum of 5 min spent at each patch, recording the visitations of all native bees and honeybees to flowers. Plant species were photographed and identified using Barrett and Tay (2016) and in consultation with botanists for native flora; Hussey et al. (1997) for weeds; and webbased searches and garden community forums for exotic species. Patterns of

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visitation were constructed from visual observations, as well as from specimens collected by targeted sweep-net collection to confirm the taxonomic identity. Networks were not constructed from collected specimens alone due to the bias in collecting specimens by sweep-netting, whereby some taxa are relatively more difficult to capture due to their body size and flight characteristics, and how abundant taxa foraging in trees were outside the reach of the sweep-net (Prendergast et al. 2020). Due to difficulties in species-level classification from observations of bees on the wing, they were assigned into the following meaningful taxonomic groups which correspond to both level of identification possible in the field, and similarities in body-size, flight behaviour, nesting, and often flower preferences: honeybees, Amegilla, Coelyoxis, Euryglossinae, Exoneura, Homalictus, Hylaeinae, Lasioglossum, Leioproctus, Lipotriches, Megachile, Trichocolletes, Thyreus (Online Resource 1). Such classifications into phylogenetic and (assuming phylogenetic conservatism) similar functional groups represent "functional taxonomic groups of flower visitors" (sensu Fenster et al. 2004; Ollerton et al. 2007). We also felt this was also a more appropriate level due to the many singletons and doubletons, and species occurring only in one survey (Prendergast 2020a), limiting our ability to make generalisations. The use of higher-level categorisations such as generic level like in the present study, as well as coarser levels, are often used in pollination network studies (e.g. Ballantyne et al. 2017; Watts et al. 2016). Specimens were also collected with an entomological sweep net (Prendergast 2020a), which verified these assignments. Although we acknowledge there are biases in all methods, we did not constrain our analyses to only specimens that were collected due to disparities in the ease of collecting different taxa (Prendergast et al. 2020).

#### 5.3.2. Construction of flower-visitation networks

Flower-visitor networks were constructed using the package *bipartite* (Dormann et al. 2008) in R (version 3.6.2) (R Core Team 2014). Individual flower-visitor networks were constructed for each survey (N = 140). Network and species-level indices commonly used in plant-pollinator networks, and which are considered to provide ecologically-relevant information about the structure and functioning of these networks, were calculated using *bipartite*. The following network-level indices were calculated for each plant-pollinator network (for more comprehensive descriptions, refer to Online Resource 2):

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- H<sub>2</sub>': network generalisation
- weighted connectance: realised proportion of possible links weighted by network size
- nestedness based on overlap and decreasing fill (NODF): the extent to which specialists interact with a subset of species that also interact with generalists
- niche overlap of bees: mean similarity in interaction patterns between flower visitors
- extinction slope at both the bee and plant level: simulated secondary loss of species with extinctions of species in the other level
- robustness at both the bee and plant level: the "fragility" of a level to losses in the other level
- functional complementarity of bees: the extent of sharing of interactions between bees

At the level of the participants – the bee taxa and plants visited - in the interaction networks ("species-level", following the terminology for describing theses metrics in bipartite analyses (Dormann et al. 2008)), the following parameters were calculated, using the function 'specieslevel' in *bipartite* (for more comprehensive descriptions, refer to Online Resource 1):

- normalised degree: links per species, scaled by the number of possible partners
- species strength: sum of the dependencies for each plants species for a given visitor, and is co-determined by the specialisation of other pollinators in the network
- interaction push-pull (IPP): asymmetry in dependencies between flower visitors and the flowers they visit
- species specificity: coefficient of variability in interactions
- pollination service index (PSI): an index measuring the importance of a flower-visitor taxon for all plant species in the network
- Bluthgen's d (d'): a measure of specialisation of a flower visitor taxon in terms of its discrimination from a random sampling of plant partners

Modularity is an important feature of plant-pollinator networks (Olesen et al. 2007). Above a given size, networks often exhibit modularity, whereby within the network there are link-dense regions and link-sparse regions. These link-dense regions are known as modules, and species within a module are more tightly linked to each other than to species in other modules (Olesen et al. 2007). The number of modules was calculated using the "computemodules" function in *bipartite*. Modularity was calculated using the function DIRT\_LPA\_wb\_plus, which is based on Beckett (2016)'s DIRTLPAwb+ algorithm, which aggregates modules until no further improvement of modularity can be achieved. Modularity calculations used combined networks including all surveys per habitat type for each month of surveys, since networks conducted from each survey were too small for modularity to be calculated.

#### 5.3.3. Statistical analysis

Comparison of flower-visitor network metrics and species-level metrics between urban gardens and bushland remnants were made using mixed effects models (lme4, lmer function) in R (Bates et al. 2015). Site was included as a random factor in the models to account for multiple surveys per site. The significance of habitat-type was determined by performing an ANOVA between a model with and without habitat type (Kuznetsova et al. 2017); a significant difference between habitat types was considered when the ANOVA produced a value of p<0.05, and lower AICc of greater than two for the model containing habitat. Differences in modularity between habitat types was tested with linear models (Im function) as data were pooled across sites for each habitat type. Model fit was checked visually using diagnostic plots (quantile plots) and the data natural log-transformed if model assumptions were violated. Analyses were performed for each year separately due to the different number of months over which surveys were conducted in each year, and how pollination networks can vary inter-annually (Alarcón et al. 2008; Dupont et al. 2009; Santamaría et al. 2018). Critically, combining networks between years could create an unrealistic network (e.g. when plants are only present, or visited by a given bee taxon, in one year) (see also Chacoff, Resasco & Vázquez 2018), and lead to misleading results comparing the two habitat types, where differences occur in only one year, or are in different directions between one year and the next. Results of

network metrics are presented as the means across the seven sites per habitat  $\pm$  standard error.

#### 5.3.4. Pollinator and plant community structure

In addition to analysing the plant-pollinator networks between habitat types, we visually depicted the species composition between the bushland remnants and residential gardens for both the pollinators and flowering plants by constructing NMDS (non-metric multi-dimensional scaling) plots for each year of surveys. For the plant NMDS plots, only flowering plants visited during a survey were included. NMDS plots were constructed using the multivariate statistical software PRIMER v7 and the PERMANOVA+ add-on package (PRIMER-E Ltd, Plymouth, UK). NMDS plots (100 restarts) were based on Bray-Curtis species x site matrices. Abundances were fourth-root transformed and log+1 transformed for the bee assemblage and plant matrixes, respectively, to reduce the influence of dominant taxa. Each point in the plot represents the taxonomic composition (taxa and their relative abundances) of each survey, with distances between points representing the similarity/dissimilarity between surveys, and surveys in each habitat type being assigned a different colour and symbol. In addition, for the bee assemblages, we performed a DISTLM (distance-based redundancy analysis, dbRDA and DISTLM, routines, available in the suite of programs for multivariate ecological data in the PERMANOVA+ addons to PRIMER v7 (Anderson et al., 2008)). DISTLM analysis used an AICc (Akaike Information Criterion adjusted for small sample size) selection procedure run with 9999 permutations (Anderson et al. 2008). Here, vectors of each bee taxon were overlaid on the plot of the sites, with the length of the vector representing the strength of the association. A PERMANOVA (9999 permutations, unrestricted permutation of raw data), with habitat type and month as factors, was performed for the bee and plant assemblage in each year to determine if community composition differed between bushland remnants and residential gardens.

#### 5.4. **RESULTS**

# 5.4.1. Bee and plant communities in urban bushland remnant and residential gardens

In both years of surveys the bee and plant community composition differed significantly between habitat type (p=0.0001, Table 5.1), with assemblages clearing clustering in NMDS space (Fig. 5.1a-d), with differences being particularly pronounced for the plant communities (Fig. 5.1c-d). Average similarity of assemblages within each habitat were similar for both bushland remnants and residential gardens (Table 5.1). Honeybees and to a lesser extent, the native bee taxa *Amegilla, Exoneura, Lasioglossum,* and *Homalictus,* were associated with residential gardens. In contrast, the native bee taxa Euryglossinae, *Leioproctus,* and especially *Megachile,* were associated with bushland remnants (Fig. 5.1a, b). These differences in the association of bee taxa to bushland remnants and residential gardens were reflected in variation in the relative proportion of each taxonomic group (Fig. 5.2a, b).



**Fig. 5.1**. NMDS plots of the bee taxonomic composition in year one (a) and year two (b) and plant community composition in year one (c) and year two (d). Each point represents a survey, with surveys in bushland remnants and residential gardens symbolised by different colours and symbols. Vectors of each bee taxon are overlain on a and b, with the length of the vector approximating the strength of the association.



Fig.

**Table 5. 1.** Percentage similarity between bushland remnants and residential gardens in the bee and floral taxonomic community composition, and the test statistics associated with a PERMANOVA comparing community composition between habitat types.

Year	Assemblage		Average similar	ity (%)	df	t	р	unique perms
		Bushland	Residential garden	Bushland				
		- Bushland	- Residential garden	- Residential Garden				
One	Bees	51.8	51	45.3	48	3.08	0.0001	9950
	Plants	14.1	12	4.4	48	2.57	0.0001	9896
Two	Bees	55.6	55	52.2	72	2.81	0.0001	9948
	Plants	17.5	17	4.7	72	3.85	0.0001	9893

#### 5.4.2. Network summary

Across all surveys network size ranged from 3 - 27 (where network size = bee taxa + plant taxa), with the number of interactions ranging from 10 - 6165 (Online Resource 3). Mean network size in the first year was  $9.6 \pm 0.4$ , with a mean number of interactions of  $339.8 \pm 66.9$ , whereas in year two mean network size was  $13.8 \pm 0.5$ , with an average of  $633.1 \pm 93.9$  interactions. Across all surveys residential gardens had larger network sizes than bushland remnants on average (residential gardens:  $13.8 \pm 0.9$ , bushland remnants:  $10.4 \pm 0.5$ ), as well as a greater number of interactions (residential gardens:  $651.5 \pm 109.1$ , bushland remnants:  $380.1 \pm 61.2$ ) (Table 5.2). Differences in network size by habitat were significant in the second year, and trending towards significance in the first year; however, there was no significant difference between habitats in number of interactions for either year (Table 5.2). Examples of a network in each habitat type in each year are visualised in Fig. 5.3 a-d.



**Fig. 5. 3.** . Illustrative examples of bipartite plant-pollinator networks: a) bushland remnant (Wireless Hill, January 2017), year one; b) residential garden (Gosnells, January 2017), year one; c) bushland remnant (Piney Lakes, January 2018), year two; d) residential garden (Bibra Lake, January 2018), year two. Pollinators are the upper level, plants the lower level. Honeybees are depicted in red, native bees in gold, exotic flora in dark green, and native flora in light green. The width of bars indicate the number of visits to a plant species by a bee taxon.

**Table 5. 2.** Network-level properties of urban plant-pollinator networks constructed from bushland remnants (7 sites) and residential gardens (7 sites). For each year of surveys, average values are provided for each metric across all surveys, as well as that for each habitat type. Generalised linear mixed effect model outputs comparing metrics between habitats are presented; significant differences (p<0.05) are in bold, and trends towards significance (p=0.05-0.1) are italicised.

	Year one						Year two					
Network property	Overall (n=56)	Bushland (n=28)	Residenti al (n=28)	Δ AICc	X²	p	Overall (n=56)	Bushland (n=28)	Residenti al (n=28)	Δ AICc	X²	р
Network size	9.61 ± 0.44	8.36 ± 0.42	10.86 ± 0.71	1.1	3.60	0.080	13.76 ± 0.511	11.76 ± 0.62	15.76 ± 0.694	18.3	20.27	<0.001
No. of interactions	339.8 ± 66.8	220.40 ± 48.5	513.1 ± 65.6	0.1	2.05	0.152	633.1 ± 93.9	486.5 ± 93.6	743.8 ± 175.9	1.4	0.60	0.435
H₂'	0.63 ± 0.04	0.67 ± 0.06	0.59 ± 0.06	0.4	1.58	0.209	0.593 ± 0.032	0.65 ± 0.04	0.53 ± 0.04	1.6	3.62	0.057
weighted connectance	0.20± 0.01	0.21 ± 0.01	0.19 ± 0.01	1.0	1.01	0.316	0.150 ± 0.005	0.16 ± 0.01	0.14 ± 0.001	1.5	3.57	0.059
nestedness (NODF)	35.73 ± 3.45	38.32 ± 5.77	33.14 ± 3.82	1.4	0.57	0.449	42.36 ± 1.69	42.38 ± 2.34	42.33 ± 2.46	1.9	0.13	0.723
extinction slope bee visitors	1.74 ±	2.07 ±	1.42 ±	4.5	7.47	0.006	2.03 ±	1.97 ±	2.11 ±	1.4	0.60	0.440
(higher level)	0.01	0.15	0.09				0.08	0.12	0.11			
extinction slope plants visited (lower level)	1.80 ± 0.09	1.73 ± 0.10	1.88 ± 0.14	1.2	0.82	0.367	1.65 ± 0.07	1.89 ± 0.12	1.43 ± 0.05	8.8	10.80	0.001
robustness bee visitors	0.61 ±	0.65 ±	0.58 ±	6.8	8.87	0.003	0.67 ±	0.68 ±	0.66 ±	1.7	0.29	0.593
(higher level)	0.01	0.01	0.01				0.01	0.12	0.01			

robustness plants visited	0.63 ± 0.01	0.63 ± 0.01	0.63 ± 0.01	2.0	0.03	0.858	0.61 ± 0.01	0.65 ± 0.01	0.60 ± 0.01	8.9	10.90	0.001
niche overlap	0.38 ±	0.42 ±	0.33 ±	1.1	0.90	0.344	0.50 ±	0.39 ±	0.60 ±	4.5	6.51	0.011
functional complementarity	0.03 505.31 ±	0.04 595.49 ±	0.04 415.13 ±	0.6	2.55	0.110	0.03 992.19 ±	<b>0.03</b> 1404.09	<b>0.04</b> 570.23 ±	0.3	1.68	0.194
	119.35	221.73	90.02				204.06	± 389.75	67.18			

#### 5.4.3. Network-level properties

#### *H*<sub>2</sub>': network generalisation

Across all surveys in year one, average  $H_2$ ' was  $0.7 \pm 0.04$ . No difference between bushland vs. residential habitats in the generalisation of their plant-pollinator networks was observed (p=0.210, Table 5.2). In year two, average  $H_2$ ' score across all surveys was  $0.6 \pm 0.03$ . There was a trend for plant-pollinator networks in bushland remnants to be more generalised (based on their  $H_2$ ' score) than those in residential gardens (p=0.057, Table 5.2).

#### Weighted connectance

Average weighted connectedness of plant-pollinator networks was  $0.2 \pm 0.01$  in year one and  $0.2 \pm 0.005$  in year two. There was no significant difference in plantpollinator networks between urban and residential sites with respect to weighted connectance in year one (p=0.320), whereas in year two here was a trend (p=0.059) for connectance to be higher in bushland remnants than residential gardens (p=0.059) (Table 5.2)

#### Nestedness (NODF)

Average NODF in year one was  $35.7 \pm 3.5$ , and was  $42.4 \pm 1.7$  in year two. NODF did not differ by habitat in year one (p=0.489, Table 5.2), but trended towards being high in in bushland remnants than residential gardens (p=0.067, Table 5.2).

#### Extinction slope (pollinators)

Extinction slope for pollinators was significantly higher in bushland sites in year one (p=0.006, Table 5.2), suggesting that pollinators were more prone to secondary extinctions if plant taxa are eliminated from bushlands sites. Extinction slopes of the pollinators, however, did not differ between habitats in year two (p=0.44),

#### Extinction slope (plants)

There was no significant difference in extinction slopes for the plant network on which bees were recorded foraging in year one (p=0.411, Table 5.2), whereas extinction slope at the plant level was significantly higher in bushland remnants than residential gardens in year two (p=0.001, Table 5.2).

#### Robustness to extinction

In the first year of surveys pollinator-level network robustness was significantly higher in bushland sites than residential (p=0.003), whereas robustness at the level of the visited plants did not differ between habitats (p=0.594, Table 5.2). Robustness of plant-pollinator networks in both habitats in the first year was >0.5, with a mean robustness value of  $0.6 \pm 0.01$ , indicating that few secondary extinctions of native bees will occur if some plants are lost from the network (Table 2). Plant networks were also robust to secondary extinctions, with a mean robustness of  $0.6 \pm 0.01$ . In the second year, robustness at the level of pollinators did not differ between habitats (p=0.593), whereas robustness was significantly higher for the plant level in bushland remnants (p=0.001, Table 5.2).

#### Niche overlap

Overall niche overlap between all bees across all sites and months was  $0.4 \pm 0.03$  in year one and  $0.5 \pm 0.03$  in year two. Niche overlap did not vary by habitat type in year one (p=0.34), however niche overlap was significantly higher in residential areas in year two (p=0.011, Table 5.2).

#### Functional complementarity

Functional complementarity between pollinators did not differ between habitat types (year one: p=0.410, year two; p=0.194, Table 5.2).

#### Normalised degree

Normalised degree was the only index to differ significantly between habitats, where species in networks in bushland remnants had a significantly higher normalised degree than those in residential garden networks in both year one (mean bushland remnants:  $0.5 \pm 0.02$  vs. mean residential:  $0.4 \pm 0.03$ , p=0.005, Table 5.2), and in year two (mean bushland:  $0.4 \pm 0.02$  vs. mean residential:  $0.3 \pm 0.02$ , p=0.0003).

#### Species strength

There was no difference in strength bewteen habitats in year one or year two (Table 5.2).

#### Species specificity

Specificity did not differ between bushland remnants and residential gardens in both year one and year two (Table 5.2).

#### Pollination Service Index (PSI)

There was a trend for PSI to differ between habitats in year one (p=0.077), being higher in residential areas, suggesting bees are more reliant on plants than vice versa in residential gardens, but in both habitat types on average bees were more reliant on the plant level than plants on the pollinator level (bushland:  $-0.3 \pm 0.05$ , residential:  $-0.1 \pm 0.06$ , Table 5.2).

#### Blüthgen's d'

The degree of interaction specialisation at the species level, d', did not vary between habitats in either year (Table 5.2). d' did not differ between habitats (Table 5.2).

#### 5.4.3. Species-level properties

#### Year one

In year one, species-level indices of strength, specificity, PSI, and d' did not differ between habitats (Table 5.3). The only index to differ was normalised degree, where species in networks in bushland remnants had a significanlty higher normalised degree than those in residential garden networks (mean bushland remnants:  $0.5 \pm$ 0.02 vs. mean residential:  $0.4 \pm 0.03$ , p=0.005, Table 5.3). There was however a trend for IPP to differ between habitats (p=0.077), being higher in residential areas, suggesting bees are more reliant on plants than vice versa in residential gardens, but in both habitat types on average bees were more reliant on the plant level than plants on the pollinator level (bushland:  $-0.3 \pm 0.05$ , residential:  $-0.1 \pm 0.06$ , Table 5.3).

#### Year two

In year two, species had on average a higher normalised degree in bushland remnants than in residential areas (mean bushland:  $0.4 \pm 0.02$  vs. mean residential:  $0.3 \pm 0.02$ , p=0.0003), as occurred in year one (Table 5.3). There was no difference between habitat in species-level indices of strength, specificity, IPP, PSI or d' (Table 5.3).

#### 5.4.4. Modularity

In year one all networks had 4 or 5 modules, with an average of  $4.3 \pm 0.2$ , and modularity was low, averaging  $0.3 \pm 03$ . In year two, networks contained 3-5 modules, with an average of  $4.2 \pm 0.2$ , and mean modularity was  $0.3 \pm 0.02$ . Modularity and number of modules did not differ between habitats in either year (Table 5.4).

**Table 5. 3.** Species-level properties of urban plant-pollinator networks constructed from bushland remnants (7 sites) and residential gardens (7 sites). For each year of surveys, average values are provided for each metric across all surveys, as well as that for each habitat type. Generalised linear mixed effect model outputs comparing metrics between habitats are presented; significant differences (p<0.05) are in bold, and trends towards significance (1<p>0.05) are italicised.

Species-level network	Year one						Year two					
property	Overall (n=219)	Bushland (n=114)	Residenti al (n=105)	ΔAICc	X²	р	Overall (n=389)	Bushland (n=209)	Residenti al (n=180)	ΔAICc	X²	р
normalised degree	0.430 ± 0.018	0.468 ± 0.022	0.389 ± 0.030	6.06	8.0	; 0.005	0.361 ± 0.014	0.391 ± 0.017	0.325 ± 0.015	10.9	12.9	0.0003
species strength	1.29 ± 0.126	0.872 ± 0.091	1.74 ± 0.236	0.15	1.8	5 0.17	1.81 ± 0.143	1.33 ± 0.135	2.36 ± 0.181	0.2	1.86	0.172
interaction push-pull	-0.212 ± 0.040	-0.273 ± 0.049	-0.146 ± 0.063	1.12	3.1.	2 0.08	-0.134 ± 0.030	-0.166 ± 0.038	-0.095 ± 0.032	0.58	1.42	0.234
species specificity index	0.848 ± 0.014	0.852 ± 0.019	0.843 ± 0.020	1.9	0.1	L 0.755	1.89 ± 1.06	2.81 ± 1.97	0.820 ± 0.012	290.63	292.6	<0.001
PSI	0.701 ± 0.026	0.686 ± 0.036	0.718 ± 0.037	1.79	0.2	0.649	0.484 ± 0.018	0.459 ± 0.023	0.509 ± 0.019	0.08	1.921	0.166
d'	0.444 ± 0.023	0.417 ± 0.031	0.474 ± 0.036	0.55	1.4	0.23	0.456 ± 0.017	0.443 ± 0.022	0.468 ± 0.017	1.37	0.633	0.426

**Table 5. 4.** Modularity and number of modules of urban plant-pollinator networks in bushland remnant and residential gardens, calculated from networks constructed pooling all surveys conducted in each habitat in a given month.

Modularity	ty Year one						Year two						
	Overall (n=8)	Bushland (n=4)	Residential (n=4)	SS	F	р	Overall (n=12)	Bushland (n=6)	Residential (n=6)	SS	F	р	
Modularity	0.253 ± 0.027	0.287 ± 0.031	$0.219 \pm 0.041$	-0.002	0.27	0.621	0.300 ± 0.028	0.335 ± 0.050	$0.266 \pm 0.021$	-0.014	1.66	0.227	
Module N	4.25 ± 0.164	4.25 ± 0.25	4.25 ± 0.25	-1	0	1	4.167 ± 0.207	3.83 ± 0.167	4.5 ± 0.342	-1.333	3.08	0.110	

#### 5.5. DISCUSSION

Consistent with our hypothesis of how plant-pollinator networks would differ in their structure between managed residential gardens and natural remnant native vegetation, we found that there were significant differences for a number of properties between these two urban habitat types. Extinction slopes, robustness and nestedness were often higher for bushland remnants, whereas niche overlap was higher in residential gardens (Fig. 5.4a). Species-level properties did not differ between habitat types, except normalised degree, which was higher in residential gardens, and in year two species specificity index was higher in bushland remnants, whilst there was a trend for interaction push-pull to be higher in residential gardens in year one (Fig. 5.4b). Modularity and number of modules was unaffected by habitat type (Fig. 5.4c). These differences in network structure likely were due to differences in the assemblage composition of bees and plants in these habitat types, which exhibited clear difference at both the bee (Fig. 5.1a,b, Fig. 5.2) and plant levels in both years (Fig. 5.1c, d).

#### Network-level indices

а

		Urban h	abitat type
Parameter	Year	Bushland remnant	Residential garden
	one	₽	1
Network size	two	Ŷ	1
	one		
No. of interactions	two	=	
Network specialisation	one	1	₽
(H <sub>2</sub> )	two		
Weighted connectance	one		
	two	1	Ŷ
Nestedness (NODE)	one		
	two		
Extinction slope - hees	one	1	÷
	two	=	
Extinction slope - plants	one		
	two	1	4
Robustness - bees	one	1	Ŷ
	two	=	
Robustness - nlants	one		
nobustness - plants	two	1	Ŷ
Niche overlan - bees	one		
intene overlap - bees	two	Ŷ	1
Functional	one		
complementarity	two	=	

Species-level i	ndices
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b

С

		Urban habitat type			
Parameter	Year	Bushland remnant	Residential garden		
	one	1	₽		
Normalised degree	two	1	Ŷ		
Spaciac strangth	one				
Species strength	two				
Interaction nuch-null	one	1	Ŷ		
	two				
Spacias spacificity index	one				
	two	1	<b>•</b>		
Pollination service index	one				
	two	=	-		
Specialisation (d')	one				
Specialisation (d')	two	=	=		

Network modularity

		Urban habitat type				
Parameter	Year	Bushland remnant	Residential garden			
and deather	one					
Niodularity	two		=			
No of modulos	one					
No. of modules	two					

**Fig. 5. 4.** Summary of how network parameters compare between plant-pollinator networks in bushland remnants and residential gardens. Up arrows indicate higher in that habitat and conversely down arrows indicate that parameter is lower in that habitat; equal sign means that parameter does not differ significantly between habitat types.

A previous network analysis was performed comparing ornamental garden networks with networks in a natural habitat outside of urban settlements (Gotlieb et al. 2011). Unlike in our study where H<sub>2</sub>' (generalisation) did not differ between garden and natural network, Gotlieb et al. (2011) found that network-level generalisation was significantly higher in gardens. The difference may stem from how Gotlieb et al. (2011)'s study was undertaken in a desert where differences between the habitat types are more extreme and there was almost no overlap in plant species. Another non-mutually-exclusive explanation is that, because in our study plots of the differences were dampened out. However, as with our study, Gotlieb et al. (2011) also did not find differences in community or species-level generalisation. It thus appears the difference in network-level generalisation is largely due to the plant species in the gardens.

A recent study compared network complexity, specialisation, and flower visitor generality of plant-pollinator networks across an agricultural to urban gradient (Theodorou et al. 2017), where it was found that the degree of urbanisation was positively associated with network and flower-visitor specialisation. These findings align with the present study where the more urbanised residential sites had lower network generalisation than the urban bushland sites (at least in year two). This pattern can be considered to arise from how in more urbanised areas the majority of flowering plants are exotic and are not preferred by native bees, such that the native bees concentrate their foraging efforts on the few native, preferred plants available.

#### 5.5.1. Network properties

The average value of  $H_2$ ' across all networks in both years revealed that that plantpollinator networks in the urbanised SWWA biodiversity hotspot are composed of specialised species. Moreover, it should be emphasised that this value considerably underestimates the true selectivity given that bee taxa were not resolved to specieslevel for these analyses.

H<sub>2</sub>' was higher in bushland remnant networks than in networks in residential gardens, which reflects how bushland remnants provided habitat for more specialised species, with a greater number of oligolectic bee species being dependent upon such habitats (Prendergast 2020a). In particular, there was a greater representation of Euryglossinae – an Australian endemic subfamily that are almost all oligoleges

(Houston 2018), in the bushland remnants, whereas the social polylectic *Exoneura* (Allodapini) (Houston 2018), were associated with residential gardens. This pattern therefore reveals how bushland remnants are important for the preservation of specialised species' interactions. The average level of H<sub>2</sub>' across all surveys in both habitats however indicated that plant-pollinator networks observed here are highly specialised. The reason for this high degree of specialisation remains to be elucidated, but it may reflect the long period of isolation and relative climate stability in the southwest Western Australian biodiversity hotspot, allowing co-evolution between native bees and flora (Hopper 2009). Further studies in similar habitat types in other countries, and studies in different habitat types in the southwest Western Australian biodiversity hotspot (i.e. agricultural and natural landscapes) may help identify an explanation. Further studies looking at the fidelity of bee-plant associations across years will shed light on the extent of specialisation (Alarcón et al. 2008; Prendergast & Ollerton, in prep.).

Nestedness is proposed to enhance community stability (Bastolla et al. 2009; Saavedra et al. 2013), and therefore it appears that our bushland networks, with generally higher nestedness values than residential networks, have greater stability. Analyses outside of urban areas have found most plant-visitor networks are highly nested in structure (Bastolla et al. 2009). The levels of nestedness (as NODF) reported here are comparatively high for plant-visitor networks, compared with a dataset of 54 community-wide pollination networks (4.0-63.6, mean 20.9, median 28.8) (Trøjelsgaard and Olesen 2013). Comparing NODF values of other urban flower visitor networks, the NODF values here are exceptionally higher than those of (Jędrzejewska-Szmek and Zych 2013), however making direct comparisons is difficult since they included non-bee taxa at the pollinator-level, whilst limiting observation to ruderal communities at the plant-level. In contrast, those reported by Zotarelli et al. (2014) were higher than those of the NODF values reported here, but again direct comparisons are difficult to make since only corbiculate bees were included in their study. Further studies are required to determine whether these differences reflect differences in the assemblage, environment, taxonomic resolution, or taxonomic range of pollinators.

Values of weighted connectance averaged across sites were comparatively high compared with those typically reported across networks in the literature (Traveset et al. 2016), which don't exceed values of about 0.16; this contrasts with values reported here of  $0.205 \pm 0.012$  for the bushland remnant networks, and  $0.189 \pm 0.010$ for the residential garden networks. Therefore, a high number of links were realised, and networks were highly connected. This high level of connectance can also be taken to indicate a high level of stability in these networks (Thébault and Fontaine 2010), which counters the assumption that urbanised habitats, as 'disturbed' habitats, are unstable (Ferreira et al. 2013; Garibaldi et al. 2011). It should be noted however that, in comparison to networks resolved at the species-level, those resolved at lower taxonomic resolution tend to have higher absolute values of connectance (Renaud et al. 2020). Additionally, the interpretation of connectance as being an indicator of stability has been called into question (Heleno et al. 2012). Moreover, it should be noted that, as is typical for most bipartite networks, only realised interactions were included – plants that were not visited were not included in the construction of the networks. Field observations revealed that, especially for the residential gardens, the majority of plants were in fact not visited (Prendergast2020b). Thus, common to bipartite networks as a whole, our results only apply to the subset of flora that were involved in interactions with bees in the system.

The lower niche overlap of plant-pollinator networks in bushland sites in year two can be considered to reflect how bee taxa were better able to partition resources, and there was lower competition among pollinators in this habitat. This result may at first seem counter-intuitive, given that residential gardens tend to be characterised by a high floral diversity (McKinney 2008). However, they are in accordance of the higher network specialisation values in bushland, such that specialised species could partition resources in bushlands that hosted high number and proportions of native flora (Prendergast2020b), whereas the relatively lower proportion of native flowers of the total flower diversity in residential gardens meant that native bees were constrained to forage on the same restricted set of resources in residential gardens. As niche overlap is often considered to be a proxy for competition (Pianka 1974), this suggests competition for resources may be more intense in residential gardens, and is in accordance with greater potential for competition in more disturbed habitats (Aizen & Feinsinger 1994). These patterns do not reflect differences in relative abundance of flora, since we previously found that not only did floral abundance not influence pollinator visitation patterns (Prendergast & Mason, in review), but a greater number of plants were visited in bushland remnants than residential gardens, despite the lower species diversity (Prendergast & Mason, in review). Measures of niche overlap were unusually high compared with the 52 networks analysed by Traveset et al. (2016), despite urban areas having an exceptionally high diversity of flowering plants. It may be that the native bee fauna of Australia has coevolved to forage on a restricted range of endemic flora, resulting in high overlap in the resources used. Due to many singletons in the system (Prendergast 2020a), this limited calculating niche overlap between bees at species-level, however it may be that values of niche overlap would be reduced if they were calculated at a specieslevel taxonomic resolution.

We found opposite patterns between habitats comparing extinction slope and robustness: extinction slope of bushlands was higher than that of residential gardens for pollinators (year one) and plants (year two), whereas robustness was of bushlands was higher than that of residential gardens for pollinators (year one) and plants (year two). This suggests that although bushland remnants are less fragile to losses of one level causing losses at another level, if losses do occur, the severity of cascading extinctions is greater.

#### 5.5.2. Species-level properties

In year one and two, normalised degree at the species level across taxa was significantly higher in bushland remnants than in residential gardens. This finding is unexpected, given that residential gardens had a significantly higher number of plant taxa potentially available for bees to interact with (Prendergast2020b), and studies in other systems have found plant species richness tends to promote bee species richness and visitation frequency (Ebeling et al. 2008). Our results suggests that there are larger number of *preferred* plant species in bushland remnants, providing a greater range of plants that bees will visit, and shows the value of using a network approach to reveal unexpected patterns that are not apparent when considering observed numbers of flowering plants present. A previous pollinator network approach likewise found that increases in the number of plant species available to pollinators does not necessarily translate into increased numbers of flora visited for
specialists – which represented the majority of bees in our system, who are "choosy" in the flowers they visit (Vamosi et al. 2014). In year two, species specificity index was higher in bushland remnants, again emphasising the greater number of specialised species in this habitat type.

Values of interaction push-pull revealed that in both habitats, bees tended to be more reliant on plants than vice versa. This dependence asymmetry of pollinators being more reliant on plants may be a reflection of the urbanised environment, whereby only native flora that are visited by many pollinators can persist, and exotic flora are necessarily visited by generalist bees. It may also relate to our study system, as Myrtaceae, which represents the dominant plant family in Australia, relies on a generalist pollination strategy, and is visited by a great many native bees, including a large number of specialists (Brown 1997; Houston 2000). Our results underscore the importance of planting native flowering species that cater to native bees in urban areas, especially in light of a recent study revealing the vulnerability of pollinators to habitat disturbance, exotic species, and loss of host plants (Mathiassen & Rehan 2020). Average values of d' fall within that measured from other habitat types (Weiner et al. 2011) suggesting that bees as a taxonomic group have a general range of d' values across habitat and landscape types.

#### 5.5.3. Modularity of networks

The modularity scores calculated here were comparatively low compared with those calculated for 23 plant-pollinator networks by Beckett (2016). This may be influenced by the pollinator-level networks being resolved at genus, rather than species-level (Renaud et al. 2020); alternatively, the low modularity scores may be a positive sign of the intactness of plant-flower visitor networks in this biodiversity hotspot. This is despite habitat loss due to urbanisation, since increased modularity has been associated with habitat loss and a corresponding potential to result in extinction debts for assemblages already suffering from habitat loss (Spiesman and Inouye 2013). Increases in network modularity have also been proposed to reflect the loss of many links across modules when core nodes are lost (such as when generalist connector species are lost and disconnected from modules), rendering networks less cohesive and more vulnerable (Olesen et al. 2007; Thébault and Fontaine 2010). On the other hand, low modularity has been proposed to be an indicator of disruptions of

specialised co-evolutionary plant-pollinator units, as can be expected to occur under recent disturbance (Dalsgaard et al. 2013). It should be noted that modularity could only be calculated from networks at the larger scales, created from surveys across multiple sites. As such, whether these modularity results (as well as modules calculated from other studies that have likewise pooled networks across sites or months), are "real" modules is questionable: they may be an artefact of lumping.

#### 5.5.4. Biological implications for urban plant-pollinator networks

Our results suggest that replacement of natural vegetation with home gardens, despite both being "urban greenspaces" causes major alterations of plant-pollinator interactions. Even with a greater number of interactions occuring in residential gardens, these interactions were less robust, and nesteded, whereas bushland remnants appears to be more vulnerbale to cascading extinctions, and contain more specialised interactions. Together these differences suggest that residential networks that are of lower conservation value. We can see that this altered structural appears to arise from the greater dominance of the introduced European honeybee, which can monopolise interactions, and occupy interactions with exotic plants that are unsuitable for native bees (Aizen, Morales & Morales, 2008). Our study has also suggests that differences assemblage composition in terms of relative abundances of different taxa translate to differences in the emergent structure of networks. Consequently, to preserve biodiversity as a whole across urban environments (Tylianakis et al. 2020), preservation of native bushland remnants is required to prevent loss of mutual interactions and co-evolved relationships (Pauw 2007).

#### 5.5.5. Caveats and considerations

This study involved constructing and comparing network properties across two years. By doing so it was revealed that values of network and species-level properties, as well as the significance or lack thereof of differences between habitats or species, at times differed between the networks constructed in the first and second years. This raises questions about the interpretation of conclusions of previous studies where networks are created by merging data gathered over multiple years, or just based on a single year of data collection. Indeed, in this study, and in plantpollinator networks in general, it is known that plants and bees both display strong

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temporal dynamics (Alarcón et al. 2008; Burkle and Irwin 2009; Lázaro et al. 2010; Olesen et al. 2008; Trøjelsgaard and Olesen 2016).

In our analyses, the pollinator-level was represented by bee genera (or in the case of Euryglossinae, subfamily). It remains to be determined whether taxonomic resolution would alter the qualitative conlusions observed here (Renaud et al. 2020). Whilst networks could be constructed at the species-level, the ease at which different taxa can be collected, and their observed:sweepnetted ratio varies, resulting in taxonomic biases (Prendergast et al. 2020). The ability to calculate various metrics would also be hampered by the numerous singletons in this system. Moreover, by using functional taxonomic groupings, this provides an eco-evolutionary context. Differences between the current study and some studies cited above which involved finer (or coarser) levels of taxonomic resolution however may limit such cross-study comparisons, in terms of absolute values of network properties except for network robustness (Renaud et al. 2020); nevertheless, relative values of indices appear to be robust to taxonomic resolution (Renaud et al. 2020).

#### 5.6. Conclusion

For the first time comparing urban plant-pollinator networks between patches of remnant native vegetation with residential garden greenspaces, we have revealed that plant-flower-visitor networks differ in numerous network-level properties. Bushland remnants had lower niche overlap, higher robustness and nestedness, but higher extinction slopes. This suggests that they had greater environmental integrity, and represented higher environmental quality, than pollination networks in residential gardens (Ferriera, Boscolo & Viana 2013); however, if disrupted, they would be more prone to cascading extinctions. We conclude that conversion of native vegetation remnants to residential gardens under urbanisation has major impacts on plant-pollinator network properties.

#### 5.7. References

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### **Chapter 6**

## Impacts of the introduced European honeybee on Australian bee-flower network properties in urban bushland remnants and residential gardens

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Apis mellifera and Megachile aurifrons © Kit Prendergast

## Impacts of the introduced European honeybee on Australian bee-flower network properties in urban bushland remnants and residential gardens

#### 6.1. Abstract

The European honeybee Apis mellifera is a highly successful, abundant species, and has been introduced into habitats across the globe. As a super-generalist species, the European honeybee has the potential to disrupt pollination networks, especially in Australia, whose flora and fauna have co-evolved for millions of years. The role of honeybees in pollination networks in Australia has been little explored, and has never been characterised in urban areas, which may favour this exotic species due to the proliferation of similarly exotic plant species which this hyper-generalist can utilise, unlike many native bee taxa. Here, we use a bipartite network approach to compare the roles, in terms of species-level properties, of honeybees with native bee taxa in bee-flower ("pollination") networks in an urbanised biodiversity hotspot. We also assessed whether the abundance of honeybees influences overall network structure. Pollination networks were created from surveys across seven residential gardens and seven urban native vegetation remnants, conducted monthly during the spring-summer period over two years. There were consistently differences in species-level properties between bee taxa, with honeybees often differing from all other native bees. Honeybees had significant impacts on network properties, being associated with higher nestedness, extinction slopes of plants, functional complementarity, and niche overlap (year two), as well as lower weighted connectance and generalisation. These associations all are indicative that competition is occurring between the introduced honeybee and the native bee taxa in bee-flower networks. In conclusion, the introduced honeybee occupies a dominant, distinct position in bee-flower networks in urban habitats in the southwest Western Australian biodiversity hotspot and has a major, potentially disruptive, influence on plant-pollinator network properties in these areas.

#### 6.2. INTRODUCTION

Interactions between flowering plants and their bees, which constitute a significant fraction of plant-pollinator networks in most habitats, are important for the functioning of healthy ecosystems (Kearns, Inouye & Waser 1998). Analysing patterns of visitation between bees and their floral host using a bipartite network approach has enhanced our understandings of the structure, dynamics and potential function of these networks, their vulnerability to disruptions, and the positions and influence different taxa in these networks play, and their contribution to network properties (Vázquez *et al.* 2009; Thébault & Fontaine 2010; Burkle & Alarcón 2011).

Recent studies on the relative contributions of different taxa have revealed that native bees are integral to many ecosystems, often exceeding honeybees in their contribution to pollination services (Garibaldi *et al.* 2013). The important contributions of wild bees to pollination services has also been demonstrated in urban areas (Hausmann, Petermann & Rolff 2015; Lowenstein, Matteson & Minor 2015; Potter & LeBuhn 2015). Wild bees may, however, also be at a relative disadvantage compared with honeybees in urban areas due to loss of natural habitat. The super-generalist honeybees, with colonies maintained in hives, does not rely on native vegetation for foraging or nesting, whereas native bees are less versatile in their foraging preferences – some of which are specialised on a narrow range of flora (e.g. Norfolk, Gilbert & Eichhorn 2018), and can suffer from loss of trees (e.g. Prendergast 2018) and bare ground that occur with urbanisation (Geslin *et al.* 2016). Declines of native bees under urbanisation can cause declines in pollination services (Biesmeijer *et al.* 2006), jeopardising plant populations (Pauw 2007), and flowervisitor network integrity (Valdovinos *et al.* 2009; Lance *et al.* 2009).

The European honeybee *Apis mellifera* has been introduced across the globe, and as an abundant, super-generalist species, there is reason to believe this species may have significant impacts on native plant-pollinator networks (Geslin *et al.* 2017). Honeybees can readily integrated into pollination networks, and there is evidence that they can be detrimental to bee-flower mutualisms (Russo 2016). Yet there is limited empirical evidence on how this alien pollinator influences network structure of plant-pollinator communities. In natural ecosystems in Brazil the Africanized honeybee alters the structure of plant-flower visitor networks, monopolizing interactions, and has been found to increase nestedness, plant niche overlap, and bind together modules (Santos *et al.* 2012; Giannini *et al.* 2015). A recent experiment in a natural ecosystem revealed the practice of beekeeping reduced wild pollinator diversity and interaction links in pollination networks, disrupting the hierarchical network structure by causing a loss of interactions by generalist species as well as impairing reproductive success of plant species that were highly-visited by honeybees (Valido, Rodríguez-Rodríguez & Jordano 2019). Yet calls for the eradication or exclusion of honeybees from areas may have unintended consequences if honeybees now occupy major roles in mutualistic networks (Burkle & Alarcón 2011; Watts *et al.* 2016), and the socio-economic importance of this managed species (Gill 1991)

In Australia *Apis mellifera* occurs in both managed and feral colonies (Paini 2004), and is a common, abundant component of most flower visitor assemblages (Yates, Hopper & Taplin 2005). Colonies of *A. mellifera*, both managed and feral, in Australia are some of the healthiest in the world, being free of *Varroa destructor* mites and associated diseases which have caused losses of colonies elsewhere on the globe (Roberts, Anderson & Durr 2017). Although there are suggestions that, under some conditions, honeybees can negatively impact Australian native bee populations or pollination services to some plants, the evidence is inconsistent (Paini 2004). The influence of honeybees on pollination network structure has never been investigated in Australia.

Whether this introduced species can perform a similar role to native pollinators, with a facilitative influence, or alternatively occupies a distinct role, with a disruptive influence, on urban pollination networks, is unknown. It has been suggested that honeybees may negatively impact bee-flower networks through monopolising resources or causing declines in native flower-visitors; alternatively, by virtue of being resilient to land-use change and highly polylectic, may also be important for plant-pollinator networks through rescuing plants if their wild pollinators are scarce, thereby buffering networks from cascading extinctions (Harrison & Winfree 2015). Given the logistic challenges of measuring pollination effectiveness of hundreds of

different bee taxa to hundreds of different flower taxa to determine the pollination services across multiple sites and seasons, bipartite interaction networks, and an analysis of their structural properties and species-level, can be fruitful for informing conservation (Alarcón 2010; Elle, Elwell & Gieldens, 2012).

Bee-flower networks that are resilient to local extinctions and maintain mutual interactions in urban areas are important for conservation of flora in natural vegetation remnants (Pauw 2007), many of which also support threatened taxa (Lambers 2014; Ives *et al.* 2016), as well as for pollination services in urban greenspaces, including urban agriculture (Frankie *et al.* 2009; Zhao, Sander & Hendrix 2019). With urban beekeeping on the rise, and the increased recognition of the importance of wild bees as targets for conservation under increasing urbanisation (Cane, Johnson & Klemens 2005), it is important to understand the role of the European honeybee on bee-flower networks.

Urban greenspace habitats are not homogenous, and include both managed, artificial greenspaces of which domestic/residential gardens are a large component (Smith, 2006) as well as patches of the original native vegetation interspersed within the urban matrix (Newman et al., 2015). Our previous research has revealed that urban native vegetation remnants and residential gardens are not equivalent in their network properties, and that the species-level property of normalised degree, and network-level properties of robustness, nestedness, and extinction slope (an index of how extinctions cascade through networks), were higher in bushland remnants than residential gardens, whereas niche overlap was higher in residential gardens (Prendergast & Ollerton, 2021). All this suggests that residential gardens are of lower quality habitat for native bees; whether the exotic honeybee influenced such properties we now focus on in the present paper. Given that habitat type can influence competition (Herbertsson et al., 2016); exotic species can facilitate each other (Goodell, 2008); and network properties can vary by habitat type (Gotlieb, Hollender & Mandelik, 2011), it is conceivable that the influence of honeybees on network properties will vary between more managed, anthropogenic greenspaces and "wild" vegetation greenspaces.

This study assessed the role of native and introduced bees in bee-flower networks in urban native vegetation remnants and residential gardens in an urbanised biodiversity hotspot, with the aims of determining:

- 1. The species-level role of the European honeybee and how this compares with native bee taxa.
- The influence of European honeybee abundance on plant-pollinator network--level properties.

#### 6.3. METHODS

#### 6.3.1. Surveys of bee visitors to flowers

Bee-plant networks were constructed from surveys of native bee and honeybee visits to flowers at fourteen sites in the region of Perth, southwest Western Australia, comprising seven bushland remnants and seven residential gardens. Each site was at least two km away from the closest site, and so beyond the flight range of the majority of bee species, to ensure independence (Greenleaf et al. 2007; Zurbuchen et al, 2010). Both habitat types were located within in the same region of the urbanised southwest Western Australian biodiversity hotspot on the Swan Coastal Plain, and sites of each habitat type were interspersed (refer to Fig. 1 in Prendergast et al., 2020). A novel feature of our study was including natural vegetation patches within the same region as the residential sites, such that any differences were not due to geographic or landscape type differences. These two urban habitats were selected as they each comprise substantial proportions of the urban greenspace (New 2018), and have numerous values for urban biodiversity and citizens. Sites were selected without observing the site prior so as to not bias selection. Bushland sites were selected by viewing a map of the region and selection sites that were distributed over the Perth metropolitan region. Residential sites were selected based on requesting via social media for residents to offer to enable K.S. Prendergast to conduct surveys, with the only selection criteria being that they were adequately interspersed among the bushland sites. Urban bushland remnants and residential gardens differed significantly in plant community composition, with bushland remnants having fewer total plant species, but a higher proportion of native flora (Prendergast & Ollerton, 2021; refer also to the dataset Prendergast, 2020). Prior to the surveys by K.S. Prendergast, the native bee fauna of the region and their habitat associations was

unknown. Regarding honeybees, the urbanised region of southwest Western Australian biodiversity hotspot on the Swan Coastal Plain hosts a large number of honeybees, both domestic (kept in hives by urban beekeepers) (DPIRD, 2018), and in feral colonies which occupy tree hollows in parks and bushland remnants (Manning et al., 2006; Yates, Hopper & Taplin, 2005). Due to lack of beekeepers registering their hives, and the difficulty of locating feral honeybee colonies, we were unable to quantify the density of honeybee colonies around our sites. Sites were surveyed once a month for three hours between 1045h-1345h over the austral spring/summer from November to February 2016/2017 and October to March 2017/2018, equating to a total of 30 hrs per site. Surveys were conducted over an 100 x 100 m area of greenspace which encompassed part of a bushland remnant, and for residential gardens, the front and backyard, and often road verges. A single researcher, KSP, walked between flowering patches, with a minimum of 5 minutes spent at each patch. Networks of plant-pollinator interactions were then constructed from each survey per site (n=140), with the number of interactions (visits) made by honeybees and native bee taxa for each flowering plant that received visits. Plant species were identified using Barrett and Tay (2016) and in consultation with botanists (see Acknowledgements) for native flora; Hussey et al. (1997) for weeds; and web-based searches and garden community forums for exotic species. Although a variety of taxa other than bees can visit flowers (either as pollinators, or nectar thieves or florivores), we focused on bees as due to their reliance on nectar and pollen throughout their entire lifecycle and associated adaptations. Based on niche overlap theory, the phylogenetic similarity between bees, and exclusive reliance on nectar and pollen, means that measures of niche overlap will be most valid here (as opposed to, for example, flies and wasps, whose offspring are not nectivorous/pollenivorous, or birds, that often include insects in their diets and forage over a much larger scale than the plots surveyed). Additionally, bees tends to be the most important from a pollination perspective (Willmer, Cunnold & Ballantyne 2015; Ballantyne et al. 2017).

Due to difficulties in species-level classification from observations of bees on the wing, they were assigned into the following meaningful taxonomic groups: honeybees, *Amegilla, Coelioxys*, Euryglossinae, Allodapini, *Homalictus*, Hylaeinae, *Lasioglossum, Leioproctus, Lipotriches, Megachile, Trichocolletes, Thyreus* (Appendix S1). These taxonomic groupings correspond to both level of identification

possible in the field and similarities in body-size and flight behaviour, tongue-length, nesting, and often flower preferences. Due to phylogenetic conservation, species in the same genus share life-history traits, which influence flight distance, energy demands, and ability to access flowers of different sizes (body size); ability to access flowers of different corolla shapes (tongue length), nesting substrate preferences (nesting behaviour), and floral preferences (e.g. Pacheco Filho *et al.* 2015). Moreover, from an eco-evolutionary pollination network perspective, there are very few cases of one-on-one species specialisation, and therefore these represent appropriate units for this analysis, as well as enabling adequate sample sizes in order to perform statistical analyses, and enable generalisation from the results of this study regarding predictions of what species in a given genera may be more vulnerable to honey bee competition. It remains to be determined whether taxonomic resolution would alter the qualitative conlusions observed here (Renaud, Baudry & Bessa-Gomes 2020).

Specimens of native bees were also collected by targeted sweep-net collection to confirm the taxonomic identity where possible. We did not construct plant-pollinator networks from collected specimens alone, as this would vastly under-estimate the native bee component; moreover, native bee taxa differ in their ease of capture (Prendergast *et al.* 2020).

#### 6.3.2. Construction of flower-visitation networks

Plant-pollinator networks were constructed using the package *bipartite* (Dormann, Gruber & Fründ 2008) in R (version 3.6.2) (R Core Team 2014). Bipartite networks have traditionally been constructed by pooling across sites and sampling times, however recent analyses have questioned this due to the high spatio-temporal variation in pollination networks (Alarcón, Waser & Ollerton, 2008; Dupont et al., 2009; Simanonok & Burkle, 2014), which is obscured when pooling. Moreover, due to turnover in plants and pollinators across space and time, pooling creates "forbidden links", for example suggesting a greater plant pool that a taxon can forage on which is otherwise unavailable at certain sites or sampling durations, and can erroneously suggest overlap between pollinators yet when they co-occur in space and time they may partition resources. There is also evidence that competition can vary in space and time. In light of these considerations, we conducted analyses from pollination networks conducted during a standardised 100 x 100 m survey over three

200

hours, which also meant there was an adequate sample size so as to conduct statistical analyses. To account for interannual-variability, as bees and flowers can exhibit substantial variation in visitation associations (Nakano & Washitani 2003; Cirtwill *et al.* 2018; Rabeling *et al.* 2019; Vitt *et al.* 2020)., differences in the duration (Nov-Feb in 2016/17 and Oct-March in 2017/18), and thus phenology of plants and bees, analyses were conducted separately for each year. Bee-flower networks for each habitat and the proportion and diversity of links honeybees and native bee taxa were involved in were visualised by constructing a bipartite network pooling all visitations across all surveys for each habitat type in year one and year two.

To explore the role of honeybees compared with native bees, and their influence on network properties, a number of species-level and network-level properties of bipartite networks were calculated, using each individual survey as a replicate (year one: N=56, year two: N=84).

Network and species-level indices commonly used in pollination networks, and which provided information about the structure and functioning of the networks, and the roles of flower visitors, were calculated using the package *bipartite* (Dormann, Gruber & Fründ 2008).

The following network-level indices were calculated for each bee-flower network (for more comprehensive descriptions, refer to Appendix S2):

- H<sub>2</sub>': network generalisation
- weighted connectance: realised proportion of possible links weighted by network size
- nestedness based on overlap and decreasing fill (NODF): the extent to which specialists interact with a subset of species that also interact with generalists
- niche overlap of bees: mean similarity in interaction patterns between flower visitors
- extinction slope at both the bee and plant level: simulated secondary loss of species with extinctions of species in the other level
- robustness at both the bee and plant level: the "fragility" of a level to losses in the other level

• functional complementarity of bees: extent of sharing of interactions between bees

We would expect increases in the supergeneralist honeybee would increase network generalism, result in greater overall niche overlap with other taxa, lower functional complementarity, and increase connectance and NODF. We also wanted to investigate if honeybees influenced the extinction slopes and robustness of plants and pollinator levels in networks.

We then investigated the roles of honeybees and native bee taxa in pollination networks, following the definition of roles in the context of bipartite networks. Here "role" refers to the position of the flower visitor in the network in terms of the number of different species of plant that it visits, how it overlaps with other flower visitors, its position within modules of bees with similar ecologies etc. To assess the roles of honeybees and native bee taxa in bee-flower networks, the following species-level parameters were calculated, using the function 'specieslevel' in *bipartite* (for more comprehensive descriptions, refer to Appendix S2):

- normalised degree: links per species, scaled by the number of possible partners
- species strength: sum of the dependencies for each plants species for a given visitor, and is co-determined by the specialisation of other pollinators in the network
- interaction push-pull (IPP): asymmetry in dependencies between flower visitors and flowers they visit
- species specificity: co-efficient of variability in interactions
- pollination service index (PSI): an index measuring the importance of a flower-visitor taxon for all plant species in the network
- Bluthgen's d (d'): a measure of specialisation of a flower visitor taxon in terms of its discrimination from a random sampling of plant partners

We were interested in determining if the species-level properties of honeybees were notably distinctive compared with native bees, given their different co-evolutionary history, and different life-history characteristics and behaviours with Australian bee taxa. We expected that honeybees would visit relatively more flowers (higher normalised degree), be less dependent upon flowers ("pullers"), have high variability in interactions (low specificity), have a high PSI due to being the sole visitor of many exotic plants, and a low d' score due to having limited discrimination of plant partners.

Above a given size, networks often exhibit modularity, with link-dense regions known as modules, and species within a module are more tightly linked to each other than with species in other modules (Olesen *et al.* 2007). In these modules species can be assigned roles as network hubs, module hubs, connectors, or peripherals (Appendix S2). Networks were constructed for each habitat for each month which enabled the "role" of bee taxa in network modules to be computed using the function 'czvalues' within *bipartite*, which calculates the standardized among-module connectivity (c-values) and within-module degree (z-values). C-values measure the contribution of a species in connecting other modules, and z-values measure the contribution of a species in connecting members within the same module. Identification of the roles of taxa followed (Olesen *et al.* 2007), where taxa were assigned as: (1) network hubs, c>0.62 and z>2.4; (2) module hubs, c< 0.62 and z<2.5.

#### 6.3.3. Statistical analysis

Comparison of species-level metrics between bee taxa were evaluated with mixed effects models (package *lme4*, 'lmer' function) in R (Bates *et al.* 2015). Site was included as a random factor in the models to account for multiple surveys per site. Whether each species-level property varied significantly between bee taxa was determined using a model comparison approach whereby a model containing bee taxon (fixed factor, with each bee taxon present as a level) was compared with a null model without bee taxon as an explanatory factor, using an ANOVA between the two models (Kuznetsova, Brockhoff & Christensen 2017). A significant effect of bee taxon was indicated if the ANOVA between models had a p value of <0.05. The effect of bee taxon in explaining variation among c- and z-values involved the same model comparison approach for assessing significance, however linear models were used as cz-values were calculated from networks constructed at the habitat-level, pooled across sites.

Pairwise differences between taxa in species-level properties and c- and z- values were made using Tukey's post-hoc tests in the *lsmeans* package (Lenth 2016), to account for multiple pairwise comparisons.

The influence of honeybees on network-level metrics was modelled using linear mixed-effects models and comparing models of network-level metrics as a function of honeybee abundance (ln+1 transformed due to extreme values) with a null model lacking honeybee abundance as an explanatory variable, using the ANOVA approach described above (Kuznetsova, Brockhoff & Christensen 2017). Proportion of variance explained by honeybee abundance (R<sup>2</sup> values) were calculated from the models using the 'r.squaredGLMM' function from the R package *MuMIn* (Burnham & Anderson 2003). To investigate whether the influence of honeybees on network metrics varied between habitat types (residential gardens and bushland remnants), we used an ANOVA comparing models for each network metric with and without a habitat x honeybee abundance interaction effect.

Model fit was checked visually using diagnostic plots (q-q plots to check for normality of residuals) and the data ln or ln+1 transformed if model assumptions were violated.

#### 6.4. **RESULTS**

# **6.4.1.** Whole network summary of honeybee and native bee taxa – flower interactions

Across all 140 surveys, network size ranged from 3 - 27 (where network size = bee taxa + plant taxa), with the number of interactions ranging from 10 - 6165 per survey (Prendergast & Ollerton, 2021). Honeybees dominated interactions in both habitat types, and in both years; this is despite each native bee taxonomic category comprising multiple species. In the first year of surveys, of the 10421 bee-flower interactions in bushland remnants, honeybees were involved in 69.7% of these (Fig. 6.1a), and of the 8263 interactions in residential gardens, honeybees were involved in 81.9% (Fig. 6.1b). In the second year, of the 32520 interactions in bushland remnants, 60.2% of these involved honeybees (Fig. 6.1c), and of the 14045 bee-

flower interactions in residential gardens, honeybees were involved in 75.2% (Fig. 6.1d).

Moreover, honeybees visited a substantially greater number of plant species than native bees across both habitats and years (Table 6.1).

**Table 6. 1**. Number of flowering plant species visited by European honeybees Apis mellifera and

 Australian native bee taxa in bushland remnants and residential gardens.

Survey year	Habitat type	Total plants visited	Honeybees	Native bee taxa		
				median	min	max
one	bushland remnants	41	32	7	1	17
	residential gardens	102	91	7	2	25
two	bushland remnants	85	68	10	2	38
	residential gardens	177	165	9	1	42





а



206



**Fig. 6. 1.** Weighted bipartite urbanbee-flower visitor networks constructed from plant-bee taxa visitation summed across all months for the first year of surveys in: a) bushland remnants, b) residential gardens, and for the second year of surveys in c) bushland remnants, d) residential gardens. Top bars are bee visitors, bottom bars are plant taxa, grey bars are plant-bee visits, with the width of the bars corresponding to the number of visits. Introduced honeybees *Apis mellifera* = red bar, native bee taxa = gold bars, dark green bars = introduced plants, light green bars = Australian native plants. Refer to Appendix S8 for names of bee taxa and flowering plant species visited corresponding to code names in bee-plant bipartite network diagram.

#### 6.4.2. Variation between bee taxa in species-level indices

#### Year one

There were differences between taxa in normalised degree (p<0.0001), with honeybees having significantly higher normalised degree than all other taxa (p<0.0001) (Fig. 6.2a; Appendix S3). The only significant pairwise difference between native bee taxa was that *Megachile* had a higher normalised degree than *Amegilla* (p=0.0062; Appendix S4).

Species strength differed between taxa (p<0.0001; Appendix S3) (Fig. 6.2b), with honeybees having a higher species strength than all other taxa (p<0.05; Appendix S4). There were also significant differences between *Amegilla*-Hylaeinae, *Amegilla*-*Lasioglossum*, and *Amegilla*-Thyreus, and between *Megachile*-Euryglossinae, *Megachile*-Lipotriches, and *Megachile*-Thyreus (Fig. 6.2b; Appendix S4).

Taxa differed significantly in interaction push-pull (p<0.0001; Appendix S3) (Fig. 6.2c). The IPP value for honeybees far exceeded that of all native bee taxa, and was the only taxon whose lower quartile range was positive (Fig. 6.2c; Appendix S4). Thus honeybees were clearly different from native bees in being "pullers"; for all other native bees, they were "pushers" (see Appendix S1 for description of roles). Significant pair-wise differences occurred in IPP between honeybees and all taxa, as well as between *Amegilla*-Euryglossinae, *Homalictus* and Hylainae; and *Megachile*-Euryglossinae, Allodapini, *Homalictus*, Hylaeinae, *Lasioglossum, Leioproctus* and *Lipotriches* (Appendix S4).

Species specificity index differed significantly according to taxon (p<0.0001; Appendix S3) (Fig. 6.2d). However, pairwise tests found the only significant difference was between honeybees and Euryglossinae (p<0.0001), honeybees and *Amegilla* (p=0.0019), honeybees and Hylaeinae (p=0.0001) and honeybees and *Lasioglossum* (p=0.0002) (Appendix S4). No pairwise differences between native bee taxa were significant (p>0.05) (Appendix S4). Pollination Service Index differed between taxa (p<0.0001; Appendix S3) (Fig. 6.2e). Relatively high PSI indexes were observed for honeybees and megachilids (Fig. 6.2e). Significant paiwise differences occurred between *Megachile-Lipotriches* (p=0.022), Hylaeinae-*Thyreus* (p=0.0029), honeybees-*Lasioglossum* (p=0.0001), honeybees-Euryglossinae (p<0.0001), and *Megachile*-Euryglossinae (p=0.0012) (Appendix S4).

Pollinator specialisation, as measured by d', differed between taxa (p<0.0001; Appendix S3) (Fig. 6.2f). The d' score for all taxa exhibited high variation, however *Amegilla*, honeybees, and *Megachile* had relatively high d' score, whereas Euryglossinae, *Homalictus*, and Hylaeinae had relatively low d' scores (Fig. 6.2f). Significant pairwise differences occurred between *Amegilla*-Euryglossinae, *Amegilla-Homalictus*, *Amegilla*-Hylainae, *Amegilla-Leioproctus*, and *Amegilla-Lipotriches*; Euryglossinae-honeybees and Euryglossinae-*Megachile*; honeybees-Hylaeinae, and *Megachile*-Hylaeinae (Appendix S4).



Fig. 6. 2. Differences between taxa in year one in species-level properties of: a) normalised degree;b) species strength; c) interaction push-pull; d) species specificity; e) Pollination Service Index (PSI); f)d'

#### Year two

Taxa differed significantly in normalised degree (p<0.0001; Appendix S3) (Fig. 6.3a). Honeybees had by far the highest normalised degree, sigbificantly higher than all other taxa in all pairwise tests (p<0.0001). Significant pairwise differences also occurred between *Amegilla-Megachile*, *Amegilla*-Euryglossinae, Euryglossinae-*Megachile*, Euryglossinae-*Lipotriches*, *Homalictus-Megachile*, Hylaeinae-*Lipotriches*, Hylaeinae-*Megachile*, *Lasioglossum-Megachile*, and *Lasioglossum-Lipotriches* (Appendix S4).

Bee taxa differed in species strength (p<0.0001; Appendix S3) (Fig. 6.3b), with honeybees again exceeding all native bees (p<0.0001). Pairwise comparisons among native bees revealed *Amegilla* had significantly higher species strength than *Homalictus*, Hylaeinae, and *Lasioglossum*; *Megachile* had significantly higher species strength than Euryglossinae, Allodapini, *Homalictus*, Hylaeinae, *Lasioglossum* and *Lipotriches*; and Hylaeinae had greater species strength than *Homalictus*, wheras *Lipotriches* had higher species strength than Hylaineae (Appendix S4).

IPP differed significantly between taxa (p<0.0001; Appendix S3) (Fig. 6.3c). As with Year one, honeybees had on average positive IPP values, indicating the plants they visited were more reliant upon them than vice versa. Honeybee IPP values exceeded all other taxa, with only megachilid bees have on average positive IPP values (Fig. 6.3c). All pairwise comparisions with honeybees were significant (Appendix S4). Significant pairwise comparisions between native bees included *Amegilla* and Euryglossinae, Hylainae, and *Lasioglossum*; and *Megachile* with *Amegilla*, Allodapini, *Homalictus*, Hylaeinae, *Lasioglossum*, *Leioproctus*, *Lipotriches*, and *Thyreus*; and between *Lipotriches* and *Homalictus* (Appendix S4).

Species-specificity differed according to taxon (p<0.0001; Appendix S3) (Fig. 6.3d), but the only significant paiwise difference was between honeybees-Hylaeinae and *Lipotriches*-Hylaeinae, and Euryglossinae-honeybees and Euryglossinae-*Lipotriches*, whereby honeybees and *Lipotriches* had a lower SSI than these colletids (Fig. 6.3d; Appendix S4). PSI differed significantly among taxa (p<0.0001; Appendix S3) (Fig. 6.3e). Honeybees, *Megachile* and *Amegilla* had relatively high PSI values (Fig. 6.3e). Pairwise difference were significant between *Amegilla* and *Homalictus*, honeybees, Hylaeinae, *Lasioglossum*, *Leioproctus*, and *Lipotriches*; between honeybees and all taxa except *Megachile*; and between *Megachile* and Euryglossinae, Allodapini, *Homalictus*, *Lasioglossum* and *Leioproctus* (Appendix S4).

Specialisation as measured by d' differed significantly among taxa (p<0.0001; Appendix S3) (Fig. 6.3f). *Megachile* and *Amegilla* had relatively high d', whereas *Homalictus* and Hylaeinae had relatively low d' (Fig. 6.3f). Most taxa however had a wide range of d' values, especially honeybees (Fig. 6.3f). There were significant pairwise differences between *Amegilla*-Euryglossinae, *Homalictus*, Honeybees, Hylaeinae, *Leioproctus* and *Lipotriches*; between *Megachile* and Euryglossinae, honeybees, *Homalictus* and *Lipotriches* (Appendix S4)



Fig. 6. 3. Differences between taxa in year two in species-level properties of: a) normalised degree;b) species strength; c) interaction push-pull; d) species specificity; e) Pollination Service Index (PSI); f)d'

#### 6.4.3. The role of honeybees in determining network-level characteristics

#### Year one

Honeybee abundance had no effect on H<sub>2</sub>', NODF, overall niche overlap among plant visitors, pollinator extinction slope, plant extinction slope, pollinator-level robustness, or plant-level robustness (Appendix S5). There was a significant negative effect of honeybee abundance on network weighted connectance (estimate=-0.01, se=0.004, df=53, t-value=-3.45, p=0.001), suggesting that with more honeybees, networks become less connected (Fig. 6.4a, Appendix S5). Honeybee abundance was highly significantly positively correlated with functional complementarity (estimate = 0.183, se=0.090, df=54, t-value=2.04, p=0.043, Fig. 4b) (Appendix S5). These relationships were consistent across habitats, except for pollinator-level robustness (habitat x honeybee interaction effect: p=0.048), and a trend for the effect of honeybee abundance on a network's pollinator extinction slope to vary between habitats (p=0.060). For both metrics, whilst there was no relationship in bushland remnants, in residential gardens honeybee abundance was significantly positively correlated with pollinator-level extinction slope (p=0.03), and there was a trend for honeybee abundance to be positively correlated with pollinator-level robustness (p=0.06) (Fig. 6.5a, b) (Appendix S5 Table 3).



**Fig. 6. 4.** Significant relationships between honeybee abundance on plant-bee network properties, site-scale analyses: a) weighted connectance, year one; b) functional complementarity, year one; c) H2, Year two; d) weighted connectance, year two; e) functional complementarity, year two; f) niche overlap, year two





#### Year two

In Year two, honeybee abundance was again unrelated to pollination network nestedness, extinction slope of both bees and plants, or network robustness at the level of both bees and plants (Appendix S5). Unlike in Year one, network generalisation (H<sub>2</sub>') was significantly related to honeybee abundance, whereby higher honeybee abundance had a significant negative effect on H<sub>2</sub>' (estimate=-0.079, se=0.020, t=-3.85, p=0.0002) (Fig. 6.4c) (Appendix S5). Honeybee abundance also had a significantly negative relationship with weighted connectance (estimate=-0.01, se=0.004, t-vaue=-2.64, df=81, p=0.011) (Fig. 6.5d), and a significantly positive relationship with niche overlap (estimate=0.077, se=0.016, t-value=4.91,

df=80, p<0.0001) (Fig. 6.5e), as well as with functional complementarity (estimate=0.381, se=0.071, t-value=5.361, df=65, p<0.0001, Fig. 6.4f) (Appendix S5).

These impacts of honeybee abundance on network metrics did not vary between bushland remnants and residential gardens for weighted connectance, NODF, robustness and extinction slopes, however there was a significant habitat x honeybee interaction effect for H<sub>2</sub>' (p=0.035) and niche overlap (p=0.017) (Appendix S5 Table 2). Network specialisation was only weakly related to honeybee abundance in bushland remnants, where the relationship was below significance (p=0.06), whereas there was a stronger negative relationship in residential gardens (Fig. 6.5c). For niche overlap, although honeybee abundance was significantly positively correlated with niche overlap in both habitats, the strength and slope of the relationship was greater in residential gardens (bushland remnants: p=0.022, residential gardens: p<0.001) (Fig. 6.5d) (Appendix S5 Table 3).

#### 6.4.4. Modularity and species' roles

Modularity of the networks and number of modules were calculated from networks at the habitat level for each month was low, with 3 - 5 modules per network (Prendergast & Ollerton, 2021).

In Year one, there was only a single example where a taxon was identified as a connector species (i.e. had a c-score>0.62): megachilids in the December 2016 bushland network, with a c-score of 0.65 (Appendix S6). Taxa did not vary significantly in c-scores (p=0.322, Appendix S3 and S7), but higher average c-scores were found for *Lipotriches*, Hylaeinae and honeybees (Fig. 6.6a). No taxon fulfilled the role of a hub species (i.e. had a z-score>2.5) (Appendix S6). The highest z-score was 1.66, for *Megachile* in the Nov 2016 bushland network. Nevertheless, there was significant difference between taxa in z-score (p=0.003, Appendix S3) (Fig. 6.6b). Significant pair-wise differences occurred between Euryglossinae-*Megachile* (p=0.032), *Lasioglossum-Megachile* (p=0.003), and *Lipotriches-Megachile* (p=0.021), with *Megachile* having higher z-scores (a higher within module degree) (Fig. 6.6b; Appendix S7). Honeybees had the highest average z-scores after megachilids (Fig. 6.6b).

In Year two, there was only a single instance of a taxon serving as a connector species: *Amegilla*, in the February 2018 bushland network, with a c-value of 0.656 (Appendix S6). There were no significant differences among taxa in c-scores, but honeybees tended to have higher c-scores than the native bee taxa, and *Leioproctus* among the lowest (Fig. 6.6c; Appendix S3). No taxa were identified as a hub species (Appendix S6). The highest z-score recorded was 0.177, by honeybees in the February 2018 bushland network. Z-scores differed significantly among taxa (p<0.0001, Appendix S3), with honeybees and megachilids having particularly high z-scores (Fig. 6.6d). Significant pair-wise differences occurred between honeybees and all native bee taxa except for *Megachile*; and between *Megachile* and Allodapini, *Amegilla*, *Homalictus*, *Lasioglossum*, *Leioproctus*, *Thyreus*, and *Trichocolletes*; and Hylaeinae and *Homalictus* (Appendix S7).



**Fig. 6. 6.** Differences between bee taxa calculated from habitat-scale networks in average c-scores and z-scores: a) c-scores, Year one; b) z-scores, Year one; c) c-scores, Year two; d) z-scores, Year two.

#### 6.5. DISCUSSION

Our network analysis revealed honeybees not only monopolize interactions in floral networks across urban native vegetation remnants and home gardens, in both visitation frequency and diversity of flowering plant species visited, but also differ significantly in species-level indices in plant-pollinator networks compared with native bee taxa. Moreover, greater abundances of honeybees had significant influences on network structure, being associated with less connected and therefore potentially more unstable networks; networks that exhibited lower specialisation; and networks with higher functional complementarity and niche overlap. All these are indicators of competition occurring between the introduced honeybees and native bee taxa.

Honey bees have been present in Australia for 200 years, and we have no baseline data. Whilst native bees may have become extinct since their introduction, we nevertheless show that honeybees still have an influence on network structure, and differed from native bees in their species-level properties. Although it is coneivable that native bee taxa present today are those that can co-exist with honey bees, with ongoing pressures on bushland remnants, and increased interest in urban beekeeping, our study does suggest that native bees may still be vulnerable.

It should be acknowleged that the present study is correlative: it is difficult in practice to manipulate honeybee densities in urban areas due to the unknown number of backyard beekeepers and feral colonies, and artificially increasing honeybee densities also represents a public and environmental hazard. Future studies attempting feral colony removal experiments, or simulation studies (e.g. Santos et al., 2012) may be insightful. Our results however are in accordance with studies artificially increasing honeybee densities in agricultural landscapes that suggest honeybees have disruptive impacts on pollination networks (Valido et al., 2019).

#### 6.5.1. Species-level properties

Introduced honeybees appear to be fully integrated into the visitation networks, with key roles, including being major visitors and thus potential pollinators to a wide

range of plant taxa. They are also "pullers", with plants being more dependent upon honeybee visitation than vice versa. The success of honeybees in invading habitats can be explained by their positive interaction push-pull values. In contrast, native bees were more dependent on plants than vice versa, underscoring the vulnerability of native bees to the loss of their host plants.

Most comparisons in species-level properties found that honeybees differed significantly from all the native bee taxa. High values in species strength can indicate such taxa play important roles in the entire interaction network. This included the European honeybees; of the native bee taxa, key players were Amegilla and *Megachile* – both including relatively large-bodied species that were highly polylectic (Amegilla) or at least included some polylectic species (Megachile). The PSI values also indicated that honeybees and megachilids had the potential to be important pollinators across networks, however studies measuring actual pollen loads and deposition to conspecific plants are required. The high PSI value of the honeybee in these networks is consistent with the role of non-native species in general, where non-natives have been found to significantly exceed native species in PSI, largely due to the large number of plant partners in a network that generalist, exotic species tend to have (Aslan 2019). The high PSI of honeybees compared with native bees is especially to be expected in urbanised regions where the suite of plants in the network includes many of exotics that are not visited by native bees. Common to most plant-"pollinator" network studies, our networks were based on floral visitation, with the assumption that floral visitors are acting as pollinators. As such, the pollinator service index (PSI) therefore should be interpreted as hypothesis of pollination service, rather than a quantification of pollination. Future studies are required to quantify pollinator effectiveness (Ballantyne, Baldock & Willmer 2015).

When comparing bee taxa in terms of specialisation, the results differed according to the network index used. Results of IPP revealed that honeybees had values that exceeded the other native bee taxa. The high positive IPP values for honeybees also suggested honeybees were less dependent upon flowers than native bee taxa, whereas the converse was true for most native bee taxa, where native bees were more dependent upon the flowers than vice versa.Bluthgen's d' produced counterintuitive results, whereby polylectic taxa (refer to Supplementary Information, Table
1) had high d' and oligolectic taxa had low d'. This discrepancy can be explained how the polylectic species visited relatively rare plant taxa, whereas the oligolectic bees visited plants species that were common and visited by numerous species.Compared with honeybees, the SSI of small colletids (Euryglossinae and Hylaeinae) was relatively high, reflecting their oligolectic foraging. These taxa may therefore be highly vulnerable to the loss of taxa on which they foraged on, which were almost exclusively native flowering plants (Fig. 6.1a-d), as well as vulnerable to competition with honeybees if such resources are limiting.

Normalised degree, species strength, species specificity, and d' all can be considered to provide information on the specialisation of a species, however they convey very different concepts of specialisation (Dormann 2011). For normalised degree, specialists have fewer links than generalists, hence a lower degree. Normalised degree is purely a property of how many species the bee taxon visits. The other indices however consider specialisation within a particular community context (Dormann 2011). Species strength and PSI takes into account the proportion of visits to other plants, and so specialists are those that have little overlap with preferences of other flower visitors in the network. If a bee taxon has minimal overlap with other taxa, it can be considered to be more specialised and less redundant than generalists (Dormann 2011). Although specialists can have a high PSI, this index is also determined by how specialised the plant is, and hence a generalist can also have a high PSI. The d' metric is an index that corrects for differences in abundances between plants and pollinators and thus considers a pollinator's discrimination, such that a pollinator which visits a single plant species that dominates the plant community would not be considered a specialist.

The comparisons reported here between normalised degree and d' indicates the vlaue of using multiple indices of "specialisation." Based on normalised degree, honeybees for example, and to a lesser extent megachilids, visit many plant taxa, having a comparatively high normalised degree score, whereas Euryglossinae and Hylaeinae have low normalised degrees. However, the roles are reversed when looking at d' scores, because although Euryglossinae and Hylaeinae only visit a limited number of taxa (mainly Myrtaceae), these taxa are often dominant.

### 6.5.2. The influence of honeybees on plant-pollinator network properties

Measures of niche overlap (Prendergast & Ollerton, 2021) were unusually high compared with the 52 networks analysed by Traveset et al. (2016), and it may be that honeybees contributed to this. In year two it was found that honeybee abundance was significantly positively associated with niche overlap, suggesting that with more honeybees, the overall niche overlap of the pollinator guild increases. This may provide greater reliability and stability in pollination services (Rogers, Tarpy & Burrack 2014), but can also lead to greater competition (Pianka 1974). Despite higher niche overlap, honeybee abundance was also significantly correlated with functional complementarity, suggesting that even though pollinators in the network had higher overlap (greater similarity in interactions patterns) when there were more honeybees, they also displayed greater functional complementarity. Thus honeybees appeared to exert changes in network structure through competition with native bees. Whether this has adverse impacts on the native bees is yet to be determined, however finding that honeybee abundance was positively correlated with functional complementary in both years suggests that when there were more honeybees, bee taxa as a group visit different plants and reduce overlap. This is expected to result in positive effects on total pollination services (Fründ et al. 2013). However, the consequences for native bee fitness are yet to be determined: if niche partitioning means that native bees are forced to forage on suboptimal resources, this could reduce their populations.

Our finding of honeybees increasing overall niche overlap in the pollination network contrasts with that of Giannini *et al.* (2015) where *Apis mellifera* was found to be negatively and weakly related to niche overlap. This difference may stem from how, in the study by (Giannini *et al.* 2015), *A. mellifera* was a recent invader in a bee community that comprised other competitive eusocial native bee species. In our study, none of the native bee taxa are eusocial or aggressive, therefore leaving an unfilled role for *A. mellifera* to occupy (Daehler 2001).

We found honeybees had a significant effect on connectance; this contrasts with Santos *et al.* (2012) who found honeybees were unrelated to connectance; moreover, the negative relationship we observed is in the oppositve direction predicted by Santos *et al.* (2012). Our study also reported a significant postive relationship

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between honeybees and network nestedness, which contrasts with that reported by Santos *et al.* (2012), but is in line with their prediction. As with Santos *et al.* (2012), honeybees did not influence the robustness of networks to extinctions of plants or other insect visitors. Differences in the influence of honeybees between the networks in the current study and that of Santos *et al.* (2012) could be due to the different land-use and ecosystem types in which the studies were conducted i.e. Brazilian Caatinga vs. urbanised kwongan heathland.

The finding that honeybees reduced network connectance actually runs counter to predictions considering how this supergeneralist species is expected to increase generalisations of interactions at the community level (Santos *et al.* 2012). However, our results of honeybees being associated with reduced connectance of plant-flower visitation networks is in line with a recent analysis on the role of non-native species in networks, where networks containing non-natives exhibited lower connectance (Aslan 2019). Given that more connected networks are proposed as being more resilient and robust to biodiversity loss (Dunne, Williams & Martinez 2002), our results suggest honeybees could have a destabilising effect on pollination networks.

The R<sup>2</sup> values for these relationships between honeybee abundance and network properties are typical of ecological studies (Møller & Jennions, 2002). Whilst the variation explained by honeybee abundance for weighted connectance were relatively low (Fig. 4), those that can be considered proxies for competition - niche overlap and functionaly complementarity - in year two were considerable, considering the multitude of factors that can influence competition (Krebs, 2009).

We additionally revealed that for some network properties, the impact of honeybees varied by habitat. In particular, honeybee impacts were more pronounced in residential gardens. This adds to the recognition that native remnant vegetation and managed home gardens are not equivalent greenspace habitats for native bees; rather, pollinator betworks in urban bushland are healthier and superior in supporting native bee assemblages (Prendergast 2018; Prendergast & Ollerton, 2021). Here we furthermore show that the impact of honeybees on pollinator networks is more pronounced in residential gardens.

#### 6.5.3. Hubs and connectors in network modules

Few bee taxa were considered network hubs or connectors, in that they did not exceed the z-score thresholds to be considered a hub. It therefore appears that plant-insect visitation networks in this region are not overly dominated by a given species. This may be interpreted as indicating that all taxa are equally important in playing a role in the cohesiveness of the network; an alternative interpretation is that there are no major key players. Nevertheless, there were significant differences among the taxa in c and z-scores, indicating that all species do not contribute equally to the pollination network, and as with the other species-level indices, honeybees often had c- and z-scores exceeding that of other taxa. The lack of taxa with c and z-scores assigning them to roles as key hubs or connectors may be due to using a weighted network: the citical thresholds for classification of taxa as connectors and hubs of 0.62 and 2.6, respectively, were based on a non-weighted network, and thus may not apply for a quantitative one (Dormann, Gruber & Fründ 2008).

This is not the first study to find that no insect visitors meet the participation thresholds to be assigned as hubs. An Australian study comparing forested habitats and three disturbed agricultural habitat types also found no insect visitors met the criteria for network hubs, but did identify *Homalictus* and *Apis mellifera* as between-module connectors (Saunders & Rader 2019). In our study *Megachile* was identified as an important connector species. Whether these differences in the roles of taxa relate to differences in the types of landscapes studied, or the species composition of the bees present, remains to be elucidated.

# **6.5.4.** *Apis mellifera* as an influential species in pollination networks: conservation implications

The results that we have found in this study, indicating introduced honeybees may have a disruptive influence on native bees and the plant visitation networks they participate in, are similar to those found across a range of environments and geographical areas. For example, Aizen *et al.* (2008) and Valido *et al.* (2019) found that honeybees disrupt the structure and functionality of plant-pollinator networks in natural areas. Our results therefore add weight to suggestions that beekeeping is not a benign activity for the wider native ecosystem. Similarly, Henry & Rodet (2018) found apiaries had adverse impacts on native bees in a protected area in France; our results may likewise support placing limits on the density and distribution of apiary operations not only in natural areas (Henry & Rodet 2018), but also within urbanised landscapes that contain a high diversity of endemic bee fauna, such as the southwest Australian biodiversity hotspot.

### 6.6. CONCLUSION

We have demonstrated that the European honeybee has a major influence on plantpollinator networks in an urbanised biodiversity hotspot. The European honeybee monopolized interactions, and occupied distinct roles in these networks, having a higher normalised degree, species strength, interaction push-pull, Pollination Service Index, higher d', and lower species specificity than most native bee taxa. Moreover, honeybees were found to alter network structure, where at higher abundances, honeybees caused networks to become more unstable, have greater overall generalisation, and have higher functional complementarity and niche overlap, which may reflect competitive effects this species has on native bees. The impact of honeybees was more pronounced in residential garden networks than bushland remnants, indicating the importance of conserving these remnant native vegetation patches for native bee assemblages. We conclude that European honeybees have the potential to disrupt plant-pollinator networks, and this introduced species occupies distinct positions in these networks.

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### Chapter 7

## Interactions between the introduced European honey bee and native bees in urban areas varies by year, habitat type and native bee guild.

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Apis mellifera and Megachile aurifrons © Kit Prendergast

### The impact of the introduced European honeybee on native bees in urban areas varies according to native bee guild

### 7.1. Abstract

European honey bees have been introduced across the globe and may compete with native bees for floral resources. Compounding effects of urbanisation and introduced species on native bees is, however, unclear. Here, we investigated how honey bee abundance and foraging patterns related to that of native bee abundance and diversity in residential gardens and native vegetation remnants for two years in urbanised areas of the southwest Australian biodiversity hotspot, and assessed how niche overlap influenced these relationships. Honey bees did not overtly suppress native bee abundance, however complex relationships emerged when analysing these relationships according to body-size, time of day, and floral resource levels. Native bee richness was positively correlated with overall honeybee abundance in year one, but negatively correlated in year two, and varied with body-size. Native bees that had higher resource overlap with honey bees were negatively associated with honey bee abundance, and resource overlap between honey bees and native bees was higher in residential gardens. Relationships with honey bees varied between native bee taxa, reflecting adaptations to different flora, and specialisation. Thus, competition with introduced bees varies by species and location, mediated by diet breadth and overlap, and other life-history traits of individual bee species.

### 7.2. INTRODUCTION

Invasive species are a key threatening process and act as a driver of pollinator declines (Aizen, Morales & Morales, 2008; Clavero & Garcia-Berthou, 2005; González-Varo et al., 2013). The European honey bee *Apis mellifera* occupies every inhabited continent through intentional introductions for honey production and pollination services, especially for agricultural and horticultural crops (Geslin et al., 2017; Moritz, Härtel & Neumann, 2005). Honey bees occur as a domesticated species in managed hives, operating at scales from small local hobby beekeeping ventures to commercial ventures involving hundreds to thousands of hives.

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Additionally, there are wild populations, which represent established feral populations in regions where it has been introduced (Moritz et al., 2005).

First introduced into Australia in the early 1820s, managed honey bees can be found in high densities due to apicultural deployment of managed colonies in crop fields and in natural areas during peak flowering periods of plants used in honey production (Pyke, 1999). Feral colonies are also well-established over much of Australia's temperate and sub-tropical regions (Geslin et al., 2017). Honey bees in Australia are free from most parasites and diseases limiting honey bee populations elsewhere across the globe (Staveley et al., 2014). Australia's honey bee industry has an estimated gross value of AUS\$90M *per annum* from hive products, with an additional AUS\$4-6B per annum value to the Australian economy through pollination services (BeeAware, 2014). Australia has approximately 2000 species of native bees, many of which are undescribed, with a unique phylogenetic composition (Batley & Hogendoorn, 2009). TheSouthwest Australian biodiversity hotspot hosts a diversity of native bees, many of which are endemic (Houston, 2018; Phillips, Hopper & Dixon, 2010), yet there are few areas where honey bees are absent, and feral colonies occur over the entire southwest hotspot region (Manning, 1997).

Both native bees and honey bees depend upon pollen and nectar for nutrition, and when multiple species utilize a common resource that is in short supply, interspecific competition will reduce fitness (survival and reproduction) of the weaker competitor (Tilman, 2004). At the population level, this may ultimately cause declines, local extirpation, and even extinction. Honey bees are highly successful organisms, as evidence by their establishment across the globe, and their tendency to dominate bee assemblages (Geslin et al., 2017). They can forage at relatively low temperatures, enabling them to usurp resources (Goulson, 2003). Unlike most Australian native bees, honey bees are highly eusocial, and are able to effectively locate and exploit the most productive floral resources through social recruitment (Dornhaus et al. 2006). In addition, they have high nectar and pollen requirements to sustain colonies (Cane & Tepedino, 2016), store nectar and pollen to allow for survival in adverse periods, and have a catholic diet, enabling exploitation of a wide range of flowering species (Goulson, 2003). Moreover, Australian native bees have experienced a long history of isolation and may not have evolved mechanisms enabling co-existence

with this super-generalist, adaptable, large-bodied bees. We can, therefore, hypothesise that honey bees are superior competitors (Cane & Tepedino, 2016). Despite this, studies conducted in Australia, as well as various regions globally, have reported inconsistent impacts of honey bees on native bees: while there have been studies reporting negative effects of honey bees (Goulson, 2004; Paini, 2004; Thomson, 2004), others have found no effect of honey bees on native bee diversity or abundance (Paini, Williams & Roberts, 2005; Pedro & De Camargo, 1991; Steffan-Dewenter & Tscharntke, 2000), or even positive associations (Evans et al., 2018; Spessa, 1999)

Co-existence of honey bees and native bees can occur through resource partitioning of floral types used, optimal times and weather conditions for foraging, foraging height, reversals in competitive superiority, habitat selection, and size-related spatial scaling of resource utilisation patterns (Eickwort & Ginsberg, 1980; Rogers, Tarpy & Burrack, 2014; Walther-Hellwig et al., 2006; Westphal, Steffan-Dewenter & Tscharntke, 2006; Wilson & Thomson, 1991). Introduced honey bees often forage on introduced plants, while native bee species have a preference for native plant species (Hanley & Goulson, 2003; Iwasaki et al., 2018; Morandin & Kremen, 2013). In Australia many native bees have co-evolved with native plant lineages (Houston, 2018).

Co-existence of multiple species occupying similar niches however may be enabled through stochastic variability in bee populations, and high spatio-temporal variability in distribution, abundance and foraging patterns of pollinator assemblages, from daily partitioning to annual shifts, allows co-existence of multiple species occupying similar niches (Adler et al., 2013; Davila & Wardle, 2008; Frankie, Rizzardi, Vinson & Griswold, 2009; Gezon et al., 2015; Herrera, 1988; Minckley, Cane, Kervin & Roulston, 1999). Honey bees can also exhibit preferences for certain plant species or patches (Ginsberg, 1983; Westerkamp & Gottsberger, 2000), allowing co-existence by leaving high-quality floral resources unexploited for native bees to use, and patches or flower species that native bees can visit without being contested for resources.

The strength of competition varies according to species' traits (Hrncir & Maia-Silva, 2013). Body size likely influences competitive outcomes (Smith & Brown, 1986): larger bees have higher energy requirements and thus may suffer more from limited resources under competition than smaller species (Müller et al., 2006); alternatively, because they have larger flight ranges, larger bees can escape competition by spatial partitioning (Heinrich, 1976). Specialisation may also influence vulnerability to competition: specialist species that overlap with honey bees in resource use may be more susceptible to declines under honey bee competition because they cannot switch to other resources if their preferred food source is depleted (Büchi & Vuilleumier, 2014). Alternatively, specialisation may provide an advantage in being superior in harvesting the resource (Larsson, 2005), or reduce resource overlap if it involves a resource that few generalist bees use (Weiner et al., 2010). Other factors influencing the intensity of competition are niche overlap, such as the degree of resource overlap (Sale, 1974). Phylogenetic similarity is also predicted to increase the intensity of competition (Violle et al., 2011).

Research into the impact of honey bees on native bee communities has been conducted in natural landscapes and agricultural settings, yet the impact of honey bees in urban areas is rarely explicitly studied (Lindström et al., 2016; Pyke & Balzer, 1985). Importantly, it is unlikely that results can be extrapolated across landscapes (i.e. agricultural vs. natural vs. urban), given the distinctive environmental features associated with each landscape (Shochat, Warren, Faeth, McIntyre & Hope, 2006). Unlike agricultural settings where hundreds of hives may be placed for crop-pollination, the number and density of urban beekeepers' hives is comparatively low. Yet, the constant presence of urban honey bees may represent a greater level of chronic competition, since in natural and agricultural areas, seasonal agistment to capitalise on honey flow or crop pollination needs means that managed honey bee-native bee competition is transient (Schwarz & Hurst, 1997). With a growing interest in urban beekeeping (Lorenz & Stark, 2015), and urban agriculture (Mok et al., 2014), as well as a growing importance of urban areas to support biodiversity (Baldock et al., 2015; Threlfall et al., 2017), we need to identify opportunities for supporting both wild native bees and managed honey bees in urban contexts, and ensure that native bee communities are protected from potential

negative impacts of honey bees (Dick, 2001; Hausmann, Petermann & Rolff, 2015; MacIvor, 2016).

Even within an urban landscape, the effect of honey bee competition may vary depending on habitat type, such as residential gardens or remnants of native vegetation. Honey bees tend to thrive in more disturbed environments (Aizen & Feinsinger, 1994), and so they may be at a competitive advantage in residential gardens compared with native vegetation remnants, which may represent a refuge for native bees. Alternatively, the potential for competition may be reduced in residential gardens due to the high diversity of flowering plant species (McKinney, 2008), enabling niche partitioning. These possibilities have not been investigated for Australia, where feral honey bees can reach particularly high densities in native bushland (Hinson et al., 2015)

In this study, we investigated the correlation between honey bee density and native bee abundance, species assemblage, and floral preferences to identify potential competitive interactions. We made the following predictions:

- As a result of exploitative competition from honey bees usurping floral resources, native bee abundance and species richness will be negatively correlated with honey bee abundance
- Bee taxa with higher overlap in resource use with honey bees will be associated with lower abundances.
- 3) Larger-bodied native bees, having higher resource requirements, will be more vulnerable to exploitative competition with honey bees, and therefore with increasing honey bee densities, the abundance and species richness of large bees will decrease more than of small bees
- Competition will vary diurnally, with more intense competition during the latter part of the day when food resources are diminished
- 5) By preventing resources from being limiting, greater abundance and diversity of floral resources will reduce competition through enabling a higher carrying capacity when there are more flowers and facilitating niche partitioning when there is a greater diversity of flowers. We therefore expect that the relationship between honey bees and native bees will interact with floral resource levels, such that under low flower resources there will be a negative

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correlation between honey bees and native bees, but under higher floral resources there will be no association between honey bees and native bees.

6) Interspecific competition will vary between natural remnant vegetation (bushland remnants) and residential gardens, being reduced in residential gardens because a higher diversity of flowering plant species will enable resource partitioning. We therefore predict that niche overlap will be lower in residential gardens, and that the relationship between honey bees and native bees will be less negatively correlated (or even non-significant or positive) in residential gardens compared with bushland remnants.

### 7.3. MATERIALS AND METHODS

Fourteen sites in Perth, the capital city in Western Australia, in the southwest Western Australian biodiversity hotspot (Myers, Mittermeier, Mittermeier, Da Fonseca & Kent, 2000) were surveyed, with seven residential gardens sites, and seven remnant native vegetation (bushland) sites (refer to Fig. 1 in Prendergast, Menz, Bateman & Dixon (2020) for a map of the sites and study region). Perth has a very large and contemporary urban sprawl predicted to stretch over 270 km by 2050 (Weller, 2009), with urban development mostly replacing natural woodlands. Sites were interspersed and separated by >1 km, beyond the flight range of most wild bees (Gathmann & Tscharntke, 2002). Each site was surveyed monthly in Nov-Feb 2016/17 and Oct-March 2017/18, for a total of 140 surveys. Each survey lasted three hours and took place from 10:45h - 13:45h, totalling 420 hrs of surveys. Due to variation among sites in area (mean  $0.808 \pm 0.399$  km<sup>2</sup>, range 0.0008 - 4.37 km<sup>2</sup>), the area surveyed was standardised to 100 x 100 m. This represented a portion of bushland within the bushland remnants, and comprised the front yard, backyard, and verges around a residential site. Analyses were performed separately for the two years of surveys due to the different number of months that surveys were conducted over the two years, and because of potential high inter-year variation in bee abundance, as well as inter-annual variation in potential for competition (Roubik, 2001).

### **Bee surveys**

During each survey, numbers of honey bees and native bees and the floral resources they visited were recorded. Native bees were classified to genus, or in the case of the diminutive Euryglossinae, to subfamily, in the field. In addition, native bees were collected and identified to species-level, or to morphospecies. A range of sampling methods was used due to biases in any given method (Prendergast et al., 2020). During the three-hour bee observation period, native bees were collected with a sweep net. In addition, bee bowls (also known as pan traps) - nine 350 mL yellow bowls placed at ground level and ten UV-fluorescent yellow and 10 UV-fluorescent blue 96 mL cups placed at 15 cm height on bamboo stakes, filled with water and unscented surfactant (Tween 80) - were randomly placed around the site in exposed locations for the duration of the survey. Bees were also collected passively over each month with two blue and two yellow vane traps (SpringStar Inc.) filled with propylene glycol and water were suspended from branches at 1-1.5 m from the ground for the duration of each study year (Nov-Feb 2016/17 and Oct-March 2017/18), with their contents collected monthly during each survey. Specimens were identified to species, or morphospecies, by K.S. Prendergast, using Michener (2007), published keys of genera where available (references in Houston (2018), PaDil (PaDIL), and by consulting the Western Australian Museum's Entomology collection.

### Prediction (1): Correlations between honey bee density and native bee abundance and species richness

Analyses involving native bee abundance and species richness in comparison to honey bee abundance used mixed effect models (package 'lme4' (Bates, Maechler, Bolker, & Walker, 2015)) in R (R Core Team, 2014), with site included as a random factor. Honey bee abundance was ln or ln+1 transformed to improve model fit. Generalised linear mixed effect models (function "glmer") with a Poisson distribution were constructed and model assumptions were evaluated with diagnostic plots (QQ-plots, and fitted vs. predicted plots of the residuals), and the package "blemco", function "dispersion\_glmer" was used to check for overdispersion (Korner-Nievergelt, Roth, Felten, Guelat, Almasi & Korner-Nievergelt, 2015), where a dispersion value is >1.4 indicates significant overdispersion (Korner-Nievergelt et al., 2015). If overdispersion was exhibited, linear mixed effect models (function "lmer") with a Gaussian distribution were used, and the response variable lntransformed or ln+1-transformed which resolved the issues of non-normality and overdispersion.

### Carry-over effects

If honey bees exert negative impacts on native bees through resource competition, and if effects on reproductive output occur, it can be predicted that offspring production would be reduced. Due to the seasonal nature of native bee species in Australia where the majority of species are active for only a few months during the warmer months of each year (Houston, 2018), any effects of honey bees on native bee reproductive output would be observed in the following year. To test this hypothesis, the abundance and diversity of native bees in the second year of study was analysed in relation to honey bee abundance the year prior. Due to the different number of months sampled over the two years of surveys, only the months which were sampled in both years (Nov, Dec, Jan, Feb) were included.

### **Prediction (2): Interaction with floral resources**

Because resource competition only occurs if species compete over a common resource that is in short supply (Krebs, 2009), the relationship between honey bees and native bees was modelled with floral abundance and species richness. A significant interaction would indicate that floral resource levels affect the strength of competition. Total abundance, total species richness, as well as proportion of native Australian flowers and proportion of native Australian flowering plant species were scored during each survey in the 100 x 100 m area surveyed. All plants in bloom were counted, and number of flowers was estimated in terms of the number of flowering heads (Prendergast, 2020a). For large trees or flower patches, the number of flowers in a 1 x 1 m area was counted and subsequently extrapolated to the total flowering area.

# **Prediction (3): Honey bee-native bee associations in relation to body-size categories of native bees**

Body size was measured using inter-tegular distance (ITD), which is the best predictor of dry weight and therefore investment in floral resources (Cane, 1987). A

high-resolution photograph (Canon DLSR, 100mm lens, 1:1 magnification, f-stop 8, or 65mm MPE lens 2x magnification f-stop 5.6) was taken of each species/morphospecies, imported into Adobe Photoshop, and ITD measured using the set measurement scale and ruler features. Bees were classed into small (ITD 0.48-1.78 mm), medium (ITD 1.79-3.10 mm), and large-bodied (ITD 3.11-4.41 mm) categories of equal bandwidth. These categories were created by subtracting the morphospecies with the smallest ITD from that with the largest ITD and dividing by three. Honey bees have an ITD of 3.31 (Greenleaf et al., 2007), and therefore were considered large-bodied bees in this system. Due to sexual dimorphism, for species where both sexes were collected, they were treated in terms of the analysis as separate taxonomic units.

### **Prediction (4): Temporal patterns over the day**

The period of sampling occurred during observed peak activity times for honey bees and native bees whilst encompassing a morning, midday, and afternoon sampling period. This allowed investigation of whether honey bees and native bees display temporal partitioning over the day, and if competition varies over the day, such that abundance of native bees, abundance of honey bees, and relationship between honey bees and native bees, was compared between the first (morning), second (midday) and final (afternoon) hours of surveys. Linear mixed effect models of native bee and honey bee abundance (In-transformed) were constructed with time period as the independent variable and sites as a random factor to determine if native bees and honey bees exhibited variation in activity among time periods. The relationship between honey bee and native bee abundance was modelled for each time period to investigate if time period influenced these associations

# **Prediction (5): Relationship between potential for apparent competition and abundance of native bees**

At each site, visits of honey bees and native bee taxa (Supporting Information 1 Table S1) to flowering plant species were recorded, and from these bee-visitation networks, resource overlap was assessed by calculating the "Potential for Apparent Competition" (PAC) using the package 'bipartite' in R (Dormann, Gruber & Fründ, 2008). At each site, the abundance of native bees (ln+1 transformed) as the response variable was regressed against their PAC score as the explanatory variable using linear mixed effect models (lmer function) with site as a random factor, and native bee abundance ln-transformed following check of the residual fit, using qqPlot(resid(model)) in R (Fox & Weisberg, 2018).

To compare PAC between habitat types and native bee taxonomic categories, because data were bounded (PAC values range from 0.0 - 1.0), this was modelled using the package "glmmTMB" (Generalized Linear Mixed Models using Template Model Builder) (Brooks, Kristensen, van Benthem, Magnusson, Berg, Nielsen, Skaug, Machler & Bolker, 2017). As some y values assumed the extremes 0 and 1, data were transformed (y \* (n-1) + 0.5) / n, where n is the sample size) (Internicola et al, 2006).

### **Prediction 6: Interaction with habitat type**

Relationships between honey bee density and native bee abundance and species richness, as well as resource overlap, were evaluated to determine whether they varied with habitat type (bushland remnant or residential garden). This was determined by an ANOVA between models with habitat type + honey bee abundance vs. habitat type \* honey bee abundance, and with an ANOVA between a model with and without habitat type as the explanatory variable.

### Statistical tests

Statistical models were all checked to ensure that assumptions of the distribution of residuals were met prior to evaluating the significance of explanatory variables as described above with diagnostic plots and tests. Significance of explanatory factors in all analyses was determined by an ANOVA between a model with and without the explanatory factor, where a  $X^2$  value associated with a p<0.05 indicated that factor was significant, and the model with the explanatory factor or interaction had an Akaike information criterion corrected for small sample size (AICc) value lower than that without (Burnham & Anderson, 2003). This likelihood ratio  $X^2$  approach was used to determine the significance of interaction effects. The direction and estimate of the effect of honey bees on the response variable was determined from a summary output of the model. The proportion of variation in the response variable explained by honey bee abundance was estimated from the marginal R<sup>2</sup> value calculated using the r.squaredGLMM function (package 'MuMIn' (Barton 20093)).

We follow standard statistical approaches whereby a p<0.05 indicated a significant effect, and a p<0.1 indicated a trend towards significance, suggesting that the result was not evidence against the hypothesis being tested (Stanton-Geddes, de Freitas & de Sales Dambros 2014). Statistical results from the likelihood ratio chi-squared approach were interpreted together with consideration of the effect size (estimate) and  $R^2$  value.

### 7.4. RESULTS

A diverse assemblage of native bees was recorded, with 97 species and 135 species collected in the first and second years respectively (Prendergast, 2020b). Honey bees numerically dominated these urban bee assemblages in both years. In year one 20,397 honey bees (mean  $\pm$  SE per survey: 364.2  $\pm$  97.3) were record compared with 5,690 native bees (101.6  $\pm$  11.6), and in year two 34, 927 honey bees were recorded (415.8  $\pm$  83.7) compared with 21,954 native bees (261.4  $\pm$  55.3). In year one, the proportion of native bees of the total number of bees observed varied widely between surveys, from a minimum of 0.011 to a maximum of 0.957, and from 0.017 to 1.00 in year two. Overall, native bees tended to comprise less than the majority, with a median of 0.321 in year one, and 0.366 in year two. Therefore, the introduced honey bee was a dominant component of the bee assemblages across both years.

# **Prediction (1): Correlations between honey bees and native bee abundance and species richness**

In the first year of surveys there was no correlation between overall native bee abundance with honey bee abundance (estimate: 0.07;  $R^2$ = 0.014; p=0.40). There was however a honey bee x habitat interaction effect (p=0.05), indicating that the relationship between honey bees and native bee abundance differed according to habitat type. In bushland remnants, honey bee abundance was not correlated with the abundance of native bees (estimate: -0.06;  $R^2$ = 0.015, p=0.53). In residential areas, there was a non-significant positive correlation between honey bee and native bee abundance (estimate: 0.24;  $R^2$ = 0.119, p=0.06) (Fig. 7.1A). In the second year of surveys no relationship between honey bee abundance and native bee abundance was found (estimate: -0.12;  $R^2$ = 0.034, p=0.10), and there was no interaction with habitat (p=0.61) (Fig. 7.1C). In the first year, honey bee abundance had a significant positive relationship with native bee species richness (estimate: 0.14;  $R^2$ = 0.19; p<0.001) (Fig. 7.1B). There was also a significant interaction with habitat (p=0.01). Although the relationship remained significant and positive in both bushland remnants and residential gardens, the association was stronger in residential gardens (estimate: 0.22;  $R^2$ = 0.43, p<0.001) compared with bushland remnants (estimate: 0.08;  $R^2$ = 0.16, p=0.05) (Fig. 7.1B).

In contrast, in the second year, there was a significant negative, albeit weak, relationship between native bee species richness and honey bee abundance (estimate: -0.06; R<sup>2</sup>= 0.05, p=0.01) (Fig. 7.1D). There was no interaction with habitat type (p=0.95). Model outputs for the interaction variables and the relationship between honey bee abundance and native bee abundance and species richness can be found in Supporting Information 2, Table S1 and S2 respectively.

No carry-over effects were observed: abundance and species richness of native bees were unrelated to honey bee abundance the year prior (abundance: estimate: 0.67;  $R^2$ = 0.03, p=0.25; species richness: estimate= -0.01,  $R^2$ = 0.0001, p=0.88) (Supporting Information 2 Table S3).



**Fig. 7.1** Relationship between honeybee abundance and native bee abundance and species richness: A) relationship between native bee abundance (In-transformed) and honeybee abundance (In-transformed) according to habitat type in year one; B) relationship between native bee species richness and honeybee abundance (In-transformed) according to habitat type in year one; C) relationship between native bee abundance (In-transformed) and honeybee abundance (In-transformed) and honeybee abundance (In-transformed) in year two; D) relationship between native bee species richness and honeybee abundance (In-transformed) in year two.

#### **Prediction (2): Interaction with flower resources**

The relationship between honey bee abundance and native bee abundance varied with flower resource levels where at low levels, there was no relationship between honey bees and native bee abundance, whereas at increasing levels, there was a negative relationship between honey bees and native bee abundance (Fig. 7.2A, B). However this was statistically significant for flower abundance (p=0.05), whereas the interaction effect with flower species richness was non-significant (0=0.08). The effect of honey bees on native bee species richness varied according to flower abundance, with a significant honey bee x flower abundance interaction in the second year (p=0.02), but not the first (p=0.08) (Fig. 7.2C, D). In the second year the negative association between honey bees and native bee species richness became more pronounced as levels of total numbers of flowers increased (Fig. 7.2D). All other honey bee\*flower interactions in relation to native bee abundance and species richness were non-significant (p>0.05). Refer to Supporting Information 2 Table S1 for model outputs.





### **Prediction (3): Honeybee impact according to body size categories of native bees** Abundance of bees for all three body-size categories was unrelated to honey bee abundance in both years, with the exception of abundance of small-bodied bees in year one, with a weak positive correlation (estimate: 0.22, $R^2$ =0.04, p=0.05) (Fig. 7.3A). For species richness, honeybee abundance was positively correlated with species richness of small-bodied native bees in the first year of surveys (estimate: 0.21; $R^2$ = 0.14, p=0.004), whilst large-bodied bee richness was weakly positively related (estimate: 0.10; $R^2$ = 0.07, p=0.05 (Fig. 7.3C) (Supporting Information 2 Table S4). In contrast, species richness of medium-sized bees exhibited a significant negative relationship with honey bee abundance in year two (estimate: -0.15; $R^2$ = 0.15, p<0.001) (Fig. 3D). All other relationships between honey bee abundance and native bees of the different size classes were non-significant (Fig. 7.3A-D). Refer to Supporting Information 2 Table S4 for model outputs.



Fig. 7.3. Relationship between native bees of different body-size categories with honeybee abundance for A) abundance in year one; B) species richness in year one; C) abundance in year two; D) species richness in year two.

#### **Prediction (4): Temporal patterns over the day**

No difference in abundance in foraging activity between the morning, midday and afternoon periods was observed in both years of survey for both native bees (year one: p=0.16, year two: p=0.43) and honey bees (year one: p=0.85, year two: p=0.81). However, the relationship between honey bees and native bees varied according to time period in year one, indicated by a significant honey bee\*time period interaction (year one: p=0.02, year two: p=0.05). See Supporting Information 2 Table S5 for model outputs.

Here, there was a significant negative relationship between native bees and honey bees in the earliest time period (morning, estimate: -0.19;  $R^2$ = 0.109, p=0.012), whereas in the latter two survey periods native bee foraging activity was unrelated to honey bee abundance (second period, midday: estimate: -0.04;  $R^2$ = 0.005, p=0.588; third period, afternoon: estimate: 0.11;  $R^2$ = 0.023, p=0.254). Refer to Supporting Information 2 Table S5 and S6 for model outputs.

### **Prediction (5): Greater resource overlap (Potential for Apparent Competition)** with honey bees is associated with reduced abundances of native bees

There was evidence that honey bees were negatively affecting the abundance of native bee taxa when there was higher resource overlap (as measured by Potential for Apparent Competition, PAC (see Methods)). In the second year of surveys, there was a negative relationship between honey bee abundance and the abundance of native bee taxa that had high resource overlap with honey bees (estimate: -0.88;  $R^2$ = 0.04, p<0.001) (Fig. 7.4C), whereas this relationship was non-significant in the first year (estimate: -0.05;  $R^2$ = 0.02, p=0.06) (Fig. 7.4A). There was no interaction with habitat type in year two (p>0.05), however in year one there was a significant negative relationship between native bee abundance and PAC with honey bees in bushland remnants, but not residential gardens (Fig. 7.4B) (habitat interaction: p=0.05). Average PAC varied between habitat types in year one (p=0.01; Fig. 7.5A), being higher in residential gardens, but there was no significant effect of habitat type on average PAC in year two (p=0.06; Fig. 7.5B).



**Fig. 7.4.** Relationship between abundance of native bees according to their resource overlap (measured as Potential for Apparent Competition) with honeybees in A) year one, and B) year one in bushland remnants and residential garden, and C) year two. PAC was calculated for each native bee taxonomic category (refer to Supporting Information 1).



**Fig. 7.5.** Potential for Apparent Competition according to habitat type in year one (A) and year two (B)

Despite each native bee taxon varying widely in extent of resource overlap with honey bees across surveys (Fig. 7.6A, B), average PAC varied significantly between native bee taxonomic categories (both years p<0.001) (Fig. 7.6A, B). In the first year PAC with honey bees was significantly higher for *Hylaeus* compared with *Amegilla*, *Leioproctus*, *Lipotriches*, *Megachile*, and trending towards significance with Euryglossinae (Fig. 7.6A). In the second year, PAC with honey bees was significantly lower for *Amegilla* compared with *Homalictus*, *Lasioglossum*, *Leioproctus*, and trending towards significance with *Exoneura*. *Hylaeus* had a significantly higher PAC compared with *Megachile* and *Amegilla*. In addition, *Megachile* had a significantly lower PAC compared with *Homalictus*, *Lasioglossum*, *Leioproctus*, and trending towards significance with *Exoneura* (Fig. 7.6B).

Model output for relationships between abundance of native bee taxa and resource overlap with honey bees (measured as Potential for Apparent Competition with honey bees) is provided in Supporting Information 2 Table S7, an interaction effect with habitat type in Supporting Information 2 Table S8, for testing if PAC varies by habitat and taxon is provided in Supporting Information 2 Table S9, and pairwise differences between taxa in PAC in year one and year two are provided in Supporting Information 2 Table S11.



**Fig. 7.6.** Potential for Apparent Competition and according to native bee taxonomic category in year one (A) and year two (B).

### 7.5. DISCUSSION

We found mixed evidence in support of the hypothesis that the introduced European honey bee exerts a negative impact on native bee assemblages. Rather, impact

seemed to be dependent on spatial and temporal scale, habitat type, and bee taxa. Our predictions of (1) negative relationships between native bee abundance and species richness with honey bee abundance were either not supported, or supported only in one year; and our data did not support the predictions that competition would be most severe (2) when there was fewer floral resources and (4) in the latter part of the day. In addition, while we did find some support for our prediction that (6) competition would vary between habitat types, we found, contrary to expectations, that at times competition was exacerbated in residential gardens and reduced in bushland remnants. Our predictions similarly had mixed support regarding (3) that larger bees would be negatively correlated with honey bees. We did find support for a predicted negative relationship between resource overlap with honey bees and abundance of native bees (5). This data indicate that such species with higher resource overlap with honey bees would be more susceptible to negative impacts from honey bees.

# **Prediction (1): Correlations between honey bees and native bee abundance and species richness**

Honey bee density was not significantly correlated with native bees in terms of overall abundances, and in residential areas in the first year of surveys there was a non-significant positive association between honey bee and native bee abundance. This may be due to residential habitats acting as a "filter", such that urban-sensitive species are reduced or eliminated, but for synanthropic species, such as honey bees and generalist native bees, there is a positive response to the same environmental variables (Banaszak-Cibicka & Żmihorski, 2012). The relationship between honey bees and native bee species richness was complex, exhibiting opposing patterns between the first and second year of surveys. This dynamic nature of competition has been observed in other studies investigating competition between the invasive African honey bee and native stingless bee species (Roubik & Wolda, 2001).

#### **Prediction (2): Interaction with flower resources**

We found no evidence that lower levels of resources in terms of total numbers of flowers or flower species increased the intensity of competition. Given that only a subset of flowers present were visited (Prendergast, 2020a; Prendergast & Ollerton, 2021), it may be that specific floral resources required by native bees and utilised by honey bees were limiting. Contrary to predictions, we found that in the second year of surveys, higher flower resource levels, in terms of both the number of flowers and of flower species, appeared to exacerbate potential for competitive interactions by honey bees, such that a negative relationship between honey bee abundance and native bee abundance and richness became apparent, and more pronounced. This may be due to how honey bees, being highly effective foragers, can locate and exploit dense flower patches, and how, being highly polylectic, they benefit from a high diversity of flowers, which, in this study, often occurred in residential gardens where much of the increase in floral resources was due to greater numbers of nonnative plant species (Prendergast, 2020a). It may be that under higher flower resource levels, honey bees benefit disproportionately, or are better able to exclude native bees from patches that are highly rewarding to honey bees. This has been observed in previous studies where dominant competitor bee species dominated the resource-rich patches, whereas subordinate bees dominated sparsely-distributed patches (Johnson & Hubbell, 1975). Future studies are required to determine whether these reflect evolved (adaptive) strategies, or competitive displacement with potential fitness consequences.

## **Prediction (3): Honey bee-native bee associations in relation to body-size categories of native bees**

Body-size mediates traits that influence competition such as resource requirements, foraging range, physical competitive ability (Bosch & Vicens, 2002; Greenleaf et al., 2007; Peters, 1986; Torné-Noguera, Rodrigo, Arnan, Osorio, Barril-Graells, da Rocha-Filho & Bosch, 2014; Wray, Neame & Elle, 2014). We found some support for body size to influence relationships between honey bees and native bees, whereby small-bodied bees were the least affected by honey bees, and in some cases, there was a positive association. In year one, the positive correlation between small-bodied native bees responding similarly to the same environmental factors (e.g. flowering *Eucalyptus*). Another explanation may be that this represents a release of competition exerted on small native bees by larger native bees.

Although not affected in terms of abundance, in year two, medium-sized native bee species richness was significantly negatively correlated with honey bee abundance.

This could mean that some medium-sized species are excluded under high honey bee abundances, whereas those that are not can compensate numerically. The exclusion of medium-sized bees may relate to how they are vulnerable to competition, for they have higher food requirements than small bees, but cannot forage as far compared with large bees on alternative resource patches particularly if honey bees are excluding them from a resource patch. Medium-sized bees may also be the most vulnerable to competition from honey bees, as based on theory and modelling, moderately similar species are the most likely to be excluded by honey bees (Carmel, Suprunenko, Kunin, Kent, Belmaker, Bar-Massada & Cornell, 2017; Mayfield & Levine, 2010).

The inconsistency in the significance of correlations between honey bee density and native bee abundance between the years suggests that these relationships may be mediated by other factors, such as abundant flowering of a strongly preferred food source for native bees of a body size category, or of honey bees, during part of the observational period in one year and not in the other. Other explanations include compensatory effects, or variation in limiting factors like predation (McGrady-Steed & Morin, 2000).

#### **Prediction (4): Temporal patterns over the day**

There was no evidence for niche partitioning over the day, but we did find that the relationship between honey bee abundance and native bee abundance varied according to time period. However, the relationships observed derive from that predicted under competition. Given that resources are most abundant in the morning (Real, 1981), this is expected to be the time of least competition, and the greatest level of competition is expected to occur later in the day when resources have been depleted by earlier foragers. Thus the negative relationship between honey bee abundance and native bee abundance in the morning in the first year may be a result of the fact that honey bees, as larger-bodied species with hive-related thermoregulation (Fahrenholz, Lamprecht & Schricker, 1989), commence foraging earlier in the morning, whereas on colder days native bees have yet to achieve a temperature where they are at a metabolic capacity to support foraging forays.

### Prediction (5): Greater resource overlap (Potential for Apparent Competition) with honey bees is associated with reduced abundances of native bees

Importantly, although not apparent in terms of overall abundances, a negative association was observed between the abundance of a bee guild and the extent to which it overlapped in resource use with honey bees. This is in line with competition theory (Stachowicz & Tilman, 2005), and is a far more realistic approach when assessing competition, given that not all species share resources with honey bees. A species-level study involving two American megachilid species also found that resource overlap was a good predictor of the effect of honey bees on the fitness of native bees (Goodell, 2000). Our results however cannot be extrapolated and it remains unknown whether honey bees will outcompete and cause the local extirpation of native bee taxa with high niche overlap. Longer-term monitoring is required, as the dynamics of competition and extent of niche overlap will vary with resource levels, with negative impacts often being temporary (Roubik, 1983; Schaffer et al., 1983). Honey bees have been present in the Australian environment for nearly two centuries, and unfortunately we lack data on the abundance, distribution, and diversity of native bees prior to their introduction. There is the possibility that vulnerable taxa have already been eliminated, and those present today are exapted, or are able to co-exist with honey bees. However, competition clearly varies according to a multitude of factors, and there may also be lag-effects at play: land-clearing, climate change, replacement of key plant resources required by native bees with those that honey bees thrive on, or any other factor that favours honey bees over native bees could tip the scales and result in extirpations/extinctions of those taxa identified as being vulnerable in the present study (Bommarco et al., 2014; Urban, Tewksbury & Sheldon, 2012).

Resource overlap varied between native bee taxa. Many *Hylaeus* species are oligolectic on the widespread and common family, Myrtaceae (Hopper 2021; Houston, 1975; Houston, 1981), and thus have limited ability to forage on alternative resources. Honey bees also are known to forage prolifically on Myrtaceae, and many of these species represent dominant nectar and pollen sources, and form the basis of Australia's honey industry (Sniderman et al., 2018). The relatively lower resource overlap of *Amegilla* relates to the fact that they are highly polylectic, and unlike honey bees, are capable of sonication, which allows them to collect pollen on
flowers with poricidal anthers (Switzer, Hogendoorn, Ravi & Combes, 2016), which allows niche partitioning. The relatively low resource overlap between honey bees with *Megachile* can be explained by divergent foraging preferences. Many Australian *Megachile* are oligolectic on, or prefer, Australian pea flowers (Fabaceae) (Houston, 2000; Prendergast, 2020a). Honey bees however tend to avoid pea flowers, which may relate to the restrictive nature of the flower's keeled morphology and internal pollen and nectar resources, requiring evolved foraging behaviours (Cerceau et al., 2020; Córdoba & Cocucci, 2011; Córdoba & Cocucci, 2017). In addition, such legumes may also have toxic compounds in the pollen and or nectar that require adaptations (possessed by co-evolved native bees) to process in large quantities (Arnold et al., 2014; Cane, Gardner & Weber, 2020; de Carvalho, 2004; Detzel & Wink, 1993).

#### **Prediction (6): Interaction with habitat type**

Resource overlap with honey bees was higher in residential gardens, suggesting that competition may be most likely to occur in these more anthropogenic habitats. Compared with bushland remnants, greater potential for apparent competition in residential gardens may be due to fewer native plant species that native bees have evolved to forage on. This would restrict native bees to a narrower realised niche, and concomitant higher resource overlap with honey bees.

#### **Inter-annual variation in competition**

The correlations between honey bees and native bees often varied between the two years of surveys, indicating that relationships between honey bees and native bees varies temporally, ranging from negative, to neutral, to positive, depending on the native bee parameter being measured. This indicates that potential for competition between honey bees and native bees is not consistent or chronic, but variable, as has been found in other systems (Roubik, 1983; Schaffer et al., 1983). It is likely that competition and its intensity varies across time as environmental variables such as resource levels fluctuate, as found in one of the few long term studies on the relationship between honey bees and native bee assemblages by Roubik and Wolda (2001), as well as a study on the effect of honey bees on bumblebees in relation to drought (Thomson, 2016). Conditions in the previous generation may also be influential.

Importantly, this study demonstrates that single-year investigations of bee interactions are likely to be misleading if management outcomes (e.g. exclusion of bee-keeping in protected areas; control of feral colonies; planting of supplemental resources for native bees) are the goal of the study. In the absence of rigorous experimental evidence, negative correlations between honey bees and native bees have been interpreted alternatively as evidence both *for* competition i.e. competitive displacement, but also *against* competition i.e. as a means of avoiding competition through spatial or temporal resource partitioning (Kronfeld-Schor & Dayan, 2003; Morse, 1977; Ranta & Vepsäläinen, 1981; Sowig, 1989; Tommasi et al., 2004). Experimental studies and studies over longer timespans are required to assess if assemblages in this system exhibit a negative association over inter-annual timescales.

#### Considerations and recommendations for further research

The patterns reported here may have implications for the eco-evolutionary trajectory of bee assemblage composition when honey bees are a selection factor. If this selection pressure of honey bee competition is consistent, we may see a shift towards smaller-bodied bees, from selective extirpation of larger bees, and/or (if intraspecific variation exists) evolution of towards smaller body sizes (Bowers 1985; Sota et al., 2000). We also identified taxa that were at reduced abundances under higher resource overlap with honey bees. Whether such species go locally extinct or are able to adaptively modify their phenotype to reduce overlap is unknown, but may induce rapid evolutionary changes (Pujol-Buxó et al., 2020; Závorka et al., 2019), with potential implications for pollination networks (Prendergast & Ollerton, 2021). Yet the fluctuating associations reported here reveal extrapolating from short-term associations is complicated.

The lack of a clear negative relationship honey bees with native bee abundance and species richness found in this study is supported by how strong evidence for competition is seldom found in Australia (Paini 2004). This may be due to how differences in floral preferences enable niche partitioning, and when floral communities differ according to habitat, this allows spatial partitioning (Franklin, Carroll, Blake, Rickard & Diaz, 2018; Steffan-Dewenter et al., 2002). Differential responses to heterogeneous habitats, rather than competition, may explain negative

correlations reported in other studies on bee assemblages in urban areas (Makinson, Threlfall & Latty, 2016).

A caveat of our study was that it was a mensurative study, and did not involve experimental manipulations, due to the difficulty of executing experimental manipulations *in situ* (Hurlbert 1984). Consequently, findings are correlative (Morin 1998). The many interacting and various factors that can mediate competition in ecological communities also means that large variation such as that observed here is to be expected. Despite that, we were able to detect significant associations between honeybees and native bees, and parse out how ecological conditions and ecological traits can mediate these relationships in an eco-evolutionary framework. It should also be acknowledged that against this variation, based on visualisation of the data there appeared to be suggestions of associations that did not meet statistical significance.

The pervasiveness and unknown locations of urban beekeepers, large flight ranges of honey bees, and logistic difficulties in locating and removing feral colonies meant we were unable to have control sites lacking honey bees. The potential harm caused by high honeybee densities (e.g. Thompson 2016) also meant from a conservation perspective we adopted the precautionary principle (Pyke, 1999) and believed it inadvisable to artificially experimentally increase honeybee colonies such as has been performed in Iwasaki *et al.* (2018). Conducting competition experiments in controlled conditions in enclosures can complement field-based studies by minimising environmental vagaries. This approach was adopted in one study which demonstrated that honey bees significantly depressed fitness of the native European megachilid *Osmia bicornis* (Hudewenz & Klein 2015). However such an approach has major logistical difficulties, limits multispecies interactions, and may not extrapolate to real communities in the field (Eglund & Cooper 2003; Morin 1998).

A more thorough understanding of fitness impacts of honey bees on native bees would involve investigating reproductive output. Although difficult for groundnesting bees, the reproductive output of cavity-nesting species could be assessed using "trap-nests" also known as "bee hotels" (Prendergast, 2020c). The draw-back however is that not only do trap-nests cover only a subset of bee nesting guilds, but within cavity-nesting species, only a subset of species use these, and the species composition (relative representation) does not match that seen in the field (Prendergast et al., 2020).

Longer-term studies are also required, in order to determine true trends from "noise", which is all-the-more important for insects like bees whose populations fluctuate spatially and temporally (Cane, 2001; Roubik, 2001). Even within the two years of survey, we found at times contrasting patterns, in particular, the highly significant positive correlation between honey bee abundance and native bee species richness in the first year of surveys, yet a highly significant negative correlation the second year. Longitudinal studies are especially important when investigating the effect of competition, as evidenced by the 30 year study on competition between Africanized honey bees on native stingless bees in South America (Roubik, 2001; Roubik & Wolda, 2001). Yet such long-term studies however are hampered by short-term funding and doctorate or employment timespans (Kuebbing et al., 2018). Variation in the intensity of competition is especially likely in urban areas, which are highly heterogeneous spatially and temporally (e.g. planting of annual species in gardens can vary year to year).

There have been no studies in Australia that have explicitly investigated honey bee competition with native bees in urban areas. With the ongoing expansion of both cities (Seto, Güneralp & Hutyra, 2012), and urban beekeeping (Lorenz & Stark, 2015; Moore & Kosut, 2013), this represents a major knowledge gap. Our study provides an important contribution to evaluating the relationships between honey bees and native bees, for it cannot be assumed that such relationships are consistent across all landscapes, and the distinctive environmental features of urban areas are likely to influence how competition plays out (Prendergast et al., under review (Chapter 2 of this thesis)). As we found here, even within urban areas, different habitat types represent different levels of competition, as was observed comparing residential gardens and native vegetation remnants. There has only been a single study that specifically investigated relationships between honey bees and wild bees in an urban area. Conducted in Paris (France), honey bee colony densities at both 500m and 1000m in the surrounding landscape were found to be negatively correlated with wild pollinator visitation rates (Ropars et al., 2019). In our study, the

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outcomes were less clear. Differences may be due to how the variable measured to represent honey bee competition differed: honey bee colony density is relatively permanent, whereas the numbers of honey bees observed foraging at a given site can vary according to where honey bees are recruiting foragers (Waddington et al., 1994).

#### 7.6. CONCLUSION

A complex picture of honey bee–native bee interactions emerges from this study in urban gardens and native vegetation remnants. Our research shows that niche overlap in floral resource use and body size are indications of vulnerability to competition with honey bees. Longer-tern monitoring of taxa with high niche overlap with honey bees is necessary to derive robust long-term trends, for as shown in this study, interannual variation in interactions can be considerable. Native bees are a diverse group ecologically, and differences in their life-history traits will influence how they interact with honey bees, yet the approach adopted in the majority of other published studies of solely investigating native bee numbers can overlook more nuanced dynamics, as found in this study. Given that the impact of competition is the result of both overlap in resource use, and limitations in those shared resources, competition with honey bees by such taxa could be ameliorated by increasing the availability of shared resources in the environment, such as focused planting with flowering species that provide abundant resources preferred by vulnerable native bee taxa.

#### 7.7. REFERENCES

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## Chapter 8

### **General Discussion**



Megachile erythropyga © Kit Prendergast

#### **General Discussion**

#### 8.1 Thesis synthesis

This study on native bees is the first to systematically study native bees in the urbanised region of the southwest Western Australian hotspot. My results shed light on how bee abundance, diversity, and species composition, is influenced by local and landscape processes, and can be informed through the understanding of ecological traits of bees and ecological processes, including niche overlap, co-evolution with native flora, competitive interactions, niche breadth, and plant-pollinator networks (Fig. 8.1).

In Chapter 2, my comprehensive review of the literature on bees in urban studies revealed that, in general, bee abundance tends to be higher in urban landscapes compared with natural and agricultural ones, but whereas species richness tends to be higher in urban than agricultural landscapes, urban areas have fewer species than do natural areas. I also found that impervious surfaces tend to negatively affect bees, whereas floral resources positively affect bees. Yet within these trends, looking at the response of bees of different life-history traits in terms of sociality, dietary specialisation, body size and nesting habitat revealed that ecological traits were influential in how bees responded to urbanisation. With an extreme biogeographic bias in studies being centred in Europe (especially the UK) and northern America (mainly USA), it was unclear whether these patterns could even be transferred to cities in Australia, such as Perth – a comparatively young, yet rapidly expanding, urban area – in the southwest Western Australian biodiversity hotspot, on an old, climatically-buffered, isolated landscape. Moreover, cities tend to be associated with a large number of exotic species, however the influence of the exotic European honeybee on native bees in urban areas had been seldom considered.

To be able to make valid conclusions about how bees respond to urbanisation, this requires a robust sampling methodology. In Chapter 3 I put a number of entomological sampling methods to the test. I found that observational counts often exceeded methods that involved collecting specimens, yet the ratio of bees observed

to be collected varied by bee taxon. To identify bees to species however collecting specimens is irreplaceable. Of these methods, sweep netting was by far superior to all other passive collection methods. A review of the literature also found that sweep netting was often more effective than were passive collection methods, and there was inconsistent evidence of bee bowl colours that are most attractive to native bees. Overall, a comprehensive sampling regime requires multiple collection methods, but cannot forgo sweep-net collections. I was therefore able to validate my use of multiple sampling methods for the collection of data that comprised my empirical studies.

Part of the variation in bee assemblages in urban areas could be influenced by the type of habitat being considered, and in Chapter 4, I found that, indeed, not all greenspaces are created equal for supporting native bees. I found that whilst residential gardens can host native bees, native vegetation remnants host a far greater diversity and abundance of native bees, as well as a greater number of rare bees, with many bees being recorded solely from this habitat type.

Not only do bushland remnants and residential gardens differ in the abundance and species richness of bees, but they also differ in the structure of the plant-bee networks as I discovered in Chapter 5. Bushland remnants were characterised by network features that suggested such networks were healthier than those in residential gardens, being more connected and robust, and with less competition between bees for resources.

In Chapter 6 introduced European honeybees were found to contribute to competitive interactions in plant-pollinator networks, and their influence on network structure was more pronounced in residential gardens. I found that honeybee abundance not only influenced network structure, with higher abundances being associated with networks features indicating greater competition occurring between pollinators, that honeybees were often distinct from other native bee taxa in the species-level role they occupied.

Honeybees clearly had a major influence on plant-pollinator networks in urban areas, and their influence on native bee population was addressed in Chapter 7. The

hypothesis that this introduced species was outcompeting native bees was only partly supported, and my results revealed that the situation is complex, nuanced and dynamic. At the aggregate level of native bee abundance honeybees had no association. However, parsing this into different time periods, years, habitat types, body sizes, and foraging guilds, the picture became more complex: in the first year, in residential gardens, there was a positive relationship with overall bee abundance; in the early, but not latter parts of the day, native bee abundance was negatively associated with honeybees; small bee abundance was positively associated with honeybees, whereas large-bodied bees tended to be negatively associated with honeybees; finally, when native bee taxa had higher overlap with honeybees in the flower species they foraged on, this was associated with lower abundances. Moreover, the potential for competition was greater in residential gardens, and varied according to native bee taxon, with Hylaeinae being particularly vulnerable to apparent competition, whereas *Amegilla* and *Megachile* were less vulnerable. In terms of the impact of honeybees on species richness, again the picture that emerged was complex: honeybee abundance was positively correlated with the number of native bee species in the first year of surveys, yet negatively correlated in the second, and body-size again influenced the direction and extent of competition, with smallbodied species richness exhibiting positive relationships, whereas large-bodied bees were positively associated with honeybees in year one yet negatively associated in year two. Overturning conventional ideas that more flowers would reduce competition, this in fact exacerbated competition, which can be explained by the specialised, restricted foraging behaviours of native bees, leaving the supergeneralist honeybee to exploit and benefit disproportionately from greater total floral resources.

#### 8.2. Limitations and considerations

A key short-coming of the studies in this thesis, common to many ecological studies, but especially those involving a thesis, is the constraints on the duration over which the surveys could be conducted. Insects are characterised by inter-annual variation, in part reflecting variation in weather and climatic conditions, the bloom of their host flora, predators and parasitoids, as well as stochastic variation (Cane & Payne, 1993; Cane & Tepedino, 2001; Roubik, 2001). Indeed, a strength of my studies was analysing my data for each season rather than lumping it together as many authors tend to do; this reflected the biological reality of the annual lifecycles of bees, as well as revealing how responses to explanatory variables could vary not only in strength but even in direction between years. To be able to determine whether the patterns here hold across time, long-term annual monitoring is required. Indeed, this limitation in the duration of studies was highlighted in my review of studies in urban bees. This is pertinent in the context of "extinction debts." Similarly, given the many factors that can influence the intensity of competition, as noted in my chapter addressing the impact of honeybees on native bees, ongoing monitoring of native bee populations in relation to honeybee abundance is needed.

The chapters in this thesis involved observational counts, but true measures of native bee fitness involve looking at reproduction. As noted in my methods paper (Chapter 3), trap nests (bee hotels) can uniquely provide this data, with the caveat that they are used by only a subset of bees in an assemblage, and the relative representation of species using bee hotels was found to differ from their relative representation in the field. Limitations in the length of this thesis meant I was unable to include chapters on looking at how bee hotel use, and reproductive output parameters of native bees, varies between habitats and in relation to environmental variables, including how honeybee abundance influences nesting success and reproductive output. This data will form the basis of future publications and preliminary results have been presented as a conference poster (Prendergast, 2019). The utility of bee hotels in being able to provide insights into native bee biology and ecology was identified in Chapter 3, and is demonstrated in other publications that arose throughout my PhD studies (refer to Appendix 2) (Prendergast, 2017; Prendergast, 2017; Prendergast, 2018; Prendergast & Yeates, 2018).

The studies that comprise this thesis all involved mensurative experiments, making use of already-present variation in potential explanatory variables. The results here could be strengthened by performing manipulate experiments. This could form the basis of an adaptive management approach (e.g. Duru et al., 2015), for example, by manipulating the floral composition of gardens to include fewer exotic species and instead by dominated by preferred native flora, which, based on results in Chapter 3 and Chapter 5, can be predicted to enhance native bees and reduce the competitive advantage of honeybees. An experimental assessment of flower species composition

could follow a similar experimental design by Salisbury et al. (2015) involving replicated field experiments evaluating the relative attractiveness of native, nearnative and exotic flowering plants to bees. Similarly for addressing the impact of honeybees on native bees, a manipulative experimental approach (Prendergast, unpublished) would complement the correlational approach presented in this thesis. I have performed manipulations of honeybee abundances, both in the field involving removing feral colonies, and in a greenhouse experiment, with publications forthcoming. However both these experimental approaches were found to be beset by logistical challenges. Locating and removing feral honeybee colonies requires cooperation from local governments and can be challenging and costly. Artificially increasing honeybee densities by adding colonies - an approach used in previous studies (e.g. Sugden & Pyke, 1991; Walther-Hellwig et al., 2006) - is ill-advised given the suggestive evidence that greater honeybee densities can depress certain native bee taxa. Whilst previous greenhouse experiments have found honeybees depress native bee fitness (Hudewenz & Klein, 2015), my results suggest the impacts will be highly dependent upon the species involved and resource levels, and whether these caged experiments are applicable in the field is uncertain. Moreover, when performing such experiments myself (Prendergast, in prep.) I found that the bees behaved erratically, and being confined, would not forage but instead clustered on the roof of the cages. Nevertheless, such investigations should be conducted if there are concerns over a particular native bee species, or if native bee species are to be used alongside honeybees specifically for greenhouse pollination (e.g. dos Santos et al., 2009).

Native vegetation remnants were found to host a far greater abundance and species richness of native bees compared with residential gardens. Whilst this may be true of many cities, in my review of bees in urban areas, I also raised to the point that whether urbanisation is relatively beneficial or detrimental to native bees will depend on the form of the "natural habitat" that is being replaced. This study took place in city located in a biodiversity hotspot, renowned for a high diversity of native flora, and where the natural structure of the vegetation is relatively open. It can be predicted that when the original habitat comprises floristically-depauperate, closed-canopy conifer forests with little flowering understory, residential gardens may represent comparatively superior habitat for native bees.

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#### 8.3. Take-away messages for urban bee conservation

Synthesising the results from the studies that comprise my thesis, my results have broken new ground, and have overturned traditional ideas about bee conservation. Against the notion that cities are inhospitable habitat for wildlife, I have revealed that, at least in Perth, this city still harbours a remarkable high abundance and diversity of native bee species. A large proportion of this bee biodiversity however resides in patches of native vegetation that remain in the suburbs. It is therefore evident that if this level of biodiversity is to be preserved, these remnant native vegetation patches need to be protected from further urban development. Despite residential gardens representing inferior habitat, they nevertheless still hosted a sizeable number of native bee individuals and species. Many of these bees were collected on native flowering plants that line verges, representing a key way to augment native bees in residential areas. Emphasis should be made on retaining and planting local mass-blossoming trees like Marri, as opposed to exotic trees like beech trees or conifers. This strategy can also serve to connect remnant vegetation patches and reduce habitat fragmentation.

A revolutionary finding was that the mantra of "more flowers means more bees" needs to be reconsidered, and simply planting more flowers, without regards to their identity or origin, may not enhance native bees in urban areas. Pollination networks revealed most bee taxa were relatively specialised; additionally, a greater number of flowering plant species at a site was negatively correlated with fewer native bee species, and a greater intensity of competition from the introduced honeybee. Promoting native bees and reducing the potential for honeybee competition therefore requires selecting flowers that have been empirically demonstrated to be attractive to native bees, and planting these in large patches, as opposed to a garden scattered with many different, and often exotic, species. My results also reveal how guidelines for enhancing native bees cannot be extrapolated between landscapes: in agricultural landscapes, it is unsurprising that augmenting a crop monoculture with a diversity of flowers will have largely beneficial effects on bees. Moreover, in such landscapes, the bees present are often adaptable generalists (Wood, Holland & Goulson, 2017). In contrast, in urban areas such as the southwest Western Australian biodiversity hotspot, the "baseline" consists of a relatively floristically-diverse habitat with

numerous native bees that are specialised on these flora (Houston, 2000). Increasing the number of flowers that are not within the foraging repertoire of many of the bees present, with a concomitant decrease in the relative proportion of these flora, therefore reduces the attractiveness of the habitat.

#### 8.4. Conclusion – keeping the bees buzzing in the 'burbs

My thesis is the first to systematically evaluate how to sample bees, as well as explore the interactions between habitat type, floral features, niche characteristics, and interactions between introduced and native species in an urban setting (Fig. 7.1). With a rapidly expanding urban population, it is crucial that we do not diminish this habitat where we live, work and play in supporting the precious pollinators that provide both crucial ecosystem services, but are also a rich source of biological diversity, beauty and intrigue. My thesis has revealed a number of counter-intuitive yet theoretically explicable associations between factors of urban environments with indigenous bee abundance and diversity, which provide an evidence-base for harmonising urban management with conservation of native bees. I have shown there is clearly a rich biota of bees in this biodiversity hotspot, and I have gotten a real buzz out of discovering and documenting this incredible biodiversity, and understanding the complex interactions that influence these creatures. The insights gleaned from my research presented here I hope will be used to improve the conservation of bees in the burbs so that they can keep on buzzing.

### What factors structure native bees and pollination networks in an urbanised landscape?

	Chapter 2: Global review on the effect of urbanisation on bees	Chapter 3: Evaluation of methods to survey bees	Chapter 4: Bushland remnants vs. residential gardens	Chapter 5 & 6: Bee-plant networks – habitat & honeybee influences	Chapter 7: Honeybee competition
Outcomes	<ul> <li>215 studies globally</li> <li>UK &amp; USA bias</li> <li>Bee N often highest in urban landscapes; R lower in urban compared w natural, but higher compared w agricultural</li> <li>Variation in response to factors associated w urbanisation; skew in studies investigating each factor</li> <li>↑ floral resources often = ↑ bees; ↑ impervious surfaces = ↓ bees</li> <li>Species traits influenced response to urbanisation</li> </ul>	<ul> <li>Observations exceed almost all captures</li> <li>Taxonomic identification requires collection</li> <li>Sweep-netting caught more individuals and species than all passive methods</li> <li>Blue-vane traps were effective at sampling large- bodied <i>Amegilla</i></li> <li>Honeybees vastly under- sampled in passive traps</li> <li>Trap-nest bee communities differed to those in the field</li> </ul>	<ul> <li>Bushland remnants = ↑ individuals, species, rare species, and species exclusive to that habitat type compared w residential gardens</li> <li>Honeybee abundance did not differ between habitat types</li> <li>↑ proportion native flower species &amp; ↓ native flower species = ↑ native bee N</li> <li>↑ proportion of native flower species, ↓ builtspace, ↓ isolation &amp; ↓ native flower species = ↑ native bee species</li> <li>Honeybees unaffected by local or landscape variables</li> </ul>	<ul> <li>Habitat type influences on pollination networks:</li> <li>Extinction slopes, robustness and nestedness higher for bushland remnants</li> <li>Niche overlap higher in residential gardens</li> <li>Species-level properties did not differ between habitats, except for normalised degree (higher in bushland remnants)</li> <li>Effect of honeybees:</li> <li>Honeybee abundance correlated w lower connectance, higher functional complementarity, generalisation, &amp; higher niche overlap</li> </ul>	<ul> <li>No association w aggregate native bee abundance, but -v associations in earliest parts of the day</li> <li>+v relationship w native bee species richness in yr1, but -v in yr2</li> <li>+v association w smaller bees, but -v association w larger bees</li> <li>Higher resource overlap with honeybees = ↓ abundances</li> <li>Resource overlap higher in residential gardens</li> <li>Resource overlap varied by bee taxon</li> </ul>
Implications	<ul> <li>Need to conduct urban bee studies in S. Hemisphere in non-temperate regions</li> <li>Important to look at both abundance &amp; species richness - can show different responses</li> <li>Ecological traits of bees important in influencing responses</li> <li>Urban areas are heterogeneous -&gt; response of bees will depend on urban habitat type</li> </ul>	<ul> <li>No collection method is perfect</li> <li>Taxonomic identification requires collection</li> <li>Passive sampling insufficient</li> <li>Sweep-netting indispensable</li> <li>Relying on passive traps underestimates levels of honeybee competition</li> <li>A range of methods should be used: strengths and weaknesses of each</li> </ul>	<ul> <li>Residential gardens cannot replace bushland as habitat</li> <li>Strategies to promote honeybees do not help native bees</li> <li>Common recommendation of planting flower-rich gardens will not conserve Aus solitary bees; bee-friendly gardens need high proportions of native plant species</li> <li>Enhancing habitat requires conserving &amp; restoring native bushland</li> </ul>	Habitat type influences on pollination networks:         Bushland networks "healthier", but if disrupted, more cascading extinctions         Greater competition for resources in residential gardens         Effect of honeybees:         Honeybees have distinct roles in pollination networks         Honeybees may cause networks to be more unstable, generalised, and alter structure due to their competitive interactions	<ul> <li>Looking at only abundance without considering ecological traits can overlook competitive effects</li> <li>Larger-bodied bees, &amp; native bee taxa w high resource overlap vulnerable to competitive effects</li> <li>Effect of the introduced honeybee on native bees is nuanced, varies temporally, &amp; depends on floral resources, resource overlap, &amp; ecological traits of native bee taxa</li> </ul>

Fig. 8. 1. Conceptual framework relating the background, key research questions, and aims of my thesis.

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Lipotriches (Austronomia) australica © Kit Prendergast

## 9. Appendices



Amegilla (Asarapoda) dawsoni © Kit Prendergast

## 9.1. Appendix 1: Published thesis chapters



Megachile aurifrons, male © Kit Prendergast 9.1.1. Prendergast, K.S., Menz, M.H.M., Dixon, K.W., and Bateman, P.W.
(2020) The relative performance of sampling methods for native bees: an empirical test and review of the literature. *Ecosphere* 11:e03076 doi:10.1002/ecs2.3076

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#### The relative performance of sampling methods for native bees: an empirical test and review of the literature

KIT S. PRENDERGAST, '' MYLES H. M. MENZ, 2,3,4 KINGSLEY W. DIXON, AND PHILIP W. BATEMAN

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Abstract. Many bee species are declining globally, but to detect trends and monitor bee assemblages, robust sampling methods are required. Numerous sampling methods are used, but a critical review of their relative effectiveness is lacking. Moreover, evidence suggests the relative effectiveness of sampling methods depends on habitat, yet efficacy in urban areas has yet to be evaluated. This study compared the bee community documented using observational records, targeted netting, mobile gardens, pan traps (blue and yellow), vane traps (blue and yellow), and trap-nests. The comparative surveys of native bees and honeybees were undertaken in an urbanized region of the southwest Australian biodiversity hot spot. The outcomes of the study were then compared to a synthesis based on a comprehensive literature review of studies where two or more bee sampling methods were conducted. Observational records far exceeded all other methods in terms of abundance of bees recorded, but were unable to distinguish finer taxonomic levels. Of methods that captured individuals, thereby permitting taxonomic identification, targeted sweep netting vastly outperformed the passive sampling methods, yielding a total of 1324 individuals, representing 131 taxonomic units-even when deployed over a shorter duration. The relative effectiveness of each method differed according to taxon. From the analysis of the literature, there was high variability in relative effectiveness of methods, but targeted sweep netting and blue vane traps tended to be most effective, in accordance with results from this study. However, results from the present study differed from most previous studies in the extremely low catch rates in pan traps. Species using trap-nests represented only a subset of all potential cavity-nesters, and their relative abundances in the trap-nests differed from those in the field. Mobile gardens were relatively ineffective at attracting bees. For urbanized habitat within this biodiversity hot spot, targeted sweep netting is indispensable for obtaining a comprehensive indication of native bee assemblages; passive sampling methods alone recorded only a small fraction of the native bee community. Overall, a combination of methods should be used for sampling bee communities, as each has their own biases, and certain taxa were well represented in some methods, but poorly represented in others.

Key words: bee assemblages; biodiversity; honeybees; monitoring; native bees; sampling; surveys; urbanization.

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May 2020 🛠 Volume 11(5) 🛠 Article e03076

9.1.2. Prendergast, K.S. & Ollerton, J. (2021). Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens. *Urban Ecosystems*. doi:10.1007/s11252-020-01089-w

> Urban Ecosystems https://doi.org/10.1007/s11252-020-01089-w



#### Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens

Kit S. Prendergast<sup>1</sup> · Jeff Ollerton<sup>2</sup>

#### Accepted: 27 December 2020

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#### Abstract

Urbanisation is a prominent and increasing form of land-use change, with the potential to disrupt the interactions between pollinators such as bees and the flowering plants that they visit. This in turn may cause cascading local extinctions and have consequences for pollination services. Network approaches go beyond simple metrics of abundance and species richness, enabling understanding of how the structure of plant-pollinator communities are affected by urbanisation. Here we compared pollination networks between native vegetation (bushland) remnants and residential gardens in the urbanised region of the southwest Australian biodiversity hotspot. Across fourteen sites, seven per habitat, plant-bee visitor networks were created from surveys conducted monthly during the spring-summer period over two years. Extinction slope (a measure of how extinctions cascade through the network), and network robustness and nestedness were higher for bushland remnants, suggesting that networks in bushland remnants had greater functional integrity, but if disrupted, more cascading extinctions for resources. Most species-level properties did not differ between habitats, except for normalised degree, which was higher in bushland remnants. In conclusion, it appears that pollination networks in managed residential gardens are not structurally equivalent with those in bushland remnants. This has implications for conservation of wild bee assemblages in this biodiversity hotspot, and suggests removal of remnant native vegetation for residential development could disrupt the integrity of plant-pollinator assemblages.

 $\textbf{Keywords} \hspace{0.1 cm} Bees \cdot Bipartite \cdot Honeybees \cdot Plant-pollinator networks \cdot Flower-visitors \cdot Urbanisation$ 

#### Introduction

Ecosystems that function well involve robust mutualistic networks. However, if there are losses of key interactions, this can cause declines in network functioning (Kearns et al. 1998). Conserving networks of species interactions is vital for conservation and maintenance of ecosystem functions such as animal-mediated pollination (Tylianakis et al. 2010). Analyses of plant-pollinator communities using interaction networks have enhanced understandings of ecological patterns and processes, and the structure and functioning of these ecological assemblages (Burkle and Alarcón 2011; Thébault and Fontaine 2010; Vázquez et al. 2009). Wild bees are

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integral to many ecosystems due to their roles as pollinators (Garibaldi et al. 2013; Ollerton 2017), however there are recorded declines and extinctions of bees across the globe, with concomitant declines in pollination services (Biesmeijer et al. 2006), jcopardising plant populations (Pauw 2007). Pollinators appear to be particularly susceptible to habitat loss (Taki and Kevan 2007), suggesting that habitat loss can lead to declines in flower-visitor network integrity.

Urbanisation is a major and ongoing cause of habitat loss (Güneralp et al. 2013). The effect of urbanisation on wild bees and pollination services however is inconsistent, varying according to the habitat type being surveyed (Dylewski et al. 2019), and ecological traits such as specialisation (Hernandez et al. 2009). Despite the importance of looking at bees and plants using a network-level approach (Ings et al. 2009), and the increased sophistication of analytical tools to do so, plantpollinator networks have rarely been analysed in urban areas. This is a major knowledge gap, given that urbanisation is an increasing and significant form of land-use modification (Faeth et al. 2011), causing changes in the composition of both plants and pollinators (Bartomeus et al. 2017; Harrison and Winfree 2015).

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# 9.1.3. Prendergast, K.S. & Ollerton, J. (2021). Impacts of the introduced European honeybee on Australian bee-flower network properties in urban bushland remnants and residential gardens. *Austral Ecology*. doi:10.1111/aec.13040



#### Impacts of the introduced European honeybee on Australian bee-flower network properties in urban bushland remnants and residential gardens

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Abstract The European honeybee Apis mellifera is a highly successful, abundant species and has been introduced into habitats across the globe. As a supergeneralist species, the European honeybee has the potential to disrupt pollination networks, especially in Australia, whose flora and fauna have co-evolved for millions of years. The role of honeybees in pollination networks in Australia has been little explored and has never been characterised in urban areas, which may favour this exotic species due to the proliferation of similarly exotic plant species which this hyper-generalist can utilise, unlike many native bee taxa. Here, we use a bipartite network approach to compare the roles, in terms of species-level properties, of honeybees with native bee taxa in beeflower ('pollination') networks in an urbanised biodiversity hotspot. We also assessed whether the abundance of honevbees influences overall network structure. Pollination networks were created from surveys across seven residential gardens and seven urban native vegetation remnants conducted monthly during the spring-summer period over two years. There were consistent differences in species-level properties between bee taxa, with honeybees often differing from all other native bees. Honeybees had significant impacts on network properties, being associated with higher nestedness, extinction slopes of plants, functional complementarity and niche overlap (year two), as well as lower weighted connectance and generalisation. These associations all are indicative that competition is occurring between the introduced honeybee and the native bee taxa in bee-flower networks. In conclusion, the introduced honeybee occupies a dominant, distinct position in bee-flower networks in urban habitats in the southwest Western Australian biodiversity hotspot and has a major, potentially disruptive, influence on plant-pollinator network properties in these areas

Key words: bees, bipartite, competition, honeybees, introduced species, urbanisation.

#### INTRODUCTION

Interactions between flowering plants and their bees, which constitute a significant fraction of plantpollinator networks in most habitats, are important for the functioning of healthy ecosystems (Kearns *et al.* 1998). Analysing patterns of visitation between bees and their floral host using a bipartite network approach has enhanced our understandings of the structure, dynamics and potential functions, and the positions and influence different taxa in these networks play, and their contribution to network properties (Vázquez *et al.* 2009; Thébault & Fontaine 2010; Burkle & Alarcón 2011).

Recent studies on the relative contributions of different taxa have revealed that native bees are integral to many ecosystems, often exceeding honeybees in their contribution to pollination services (Garibaldi

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et al. 2013). The important contributions of wild bees to pollination services has also been demonstrated in urban areas (Hausmann et al. 2015; Lowenstein et al. 2015; Potter & LeBuhn 2015). Wild bees may, however, also be at a relative disadvantage compared with honevbees in urban areas due to loss of natural habitat. The supergeneralist honeybees, with colonies maintained in hives, do not rely on native vegetation for foraging or nesting, whereas native bees are less versatile in their foraging preferences some of which are specialised on a narrow range of flora (e.g. Norfolk et al. 2018), and can suffer from loss of trees (e.g. Prendergast 2018) and bare ground that occur with urbanisation (Geslin et al. 2016). Declines of native bees under urbanisation can cause declines in pollination services (Biesmeijer et al. 2006), jeopardising plant populations (Pauw 2007), and flower-visitor network integrity (Valdovinos et al. 2009).

The European honeybee *Apis mellifera* has been introduced across the globe, and as an abundant, supergeneralist species, there is reason to believe this

Prendergast, K.S., Dixon, K. W., & Bateman, P. W. (2021).
Interactions between the introduced European honey bee and native bees in urban areas varies by year, habitat type and native bee guild. *Biological Journal of the Linnean Society*.
doi:10.1093/biolinnean/blab024

Biological Journal of the Linnean Society, 2021, XX, 1-19. With 6 figures.

9.1.4.

#### Interactions between the introduced European honey bee and native bees in urban areas varies by year, habitat type and native bee guild

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European honey bees have been introduced across the globe and may compete with native bees for floral resources. Compounding effects of urbanization and introduced species on native bees are, however, unclear. Here, we investigated how honey bee abundance and foraging patterns related to those of native bees abundance and diversity in residential gardens and native vegetation remnants for 2 years in urbanized areas of the Southwest Australian biodiversity hotspot and assessed how niche overlap influenced these relationships. Honey bees did not overtly suppress native bee abundance; however, complex relationships emerged when analysing these relationships according to body size, time of day and floral resource levels. Native bee richness was positively correlated with overall honeybee abundance in the first year, but negatively correlated in the second year, and varied with body size. Native bees that had higher resource overlap with honey bees were negatively associated with honey bee abundance, and resource overlap between honey bees and native bees was higher in residential gardens. Relationships with honey bees varied between native bee taxa, reflecting adaptations to different flora, plus specialization. Thus, competition with introduced bees varies by species and location, mediated by dietary breadth and overlap and by other life-history traits of individual bee species.

#### INTRODUCTION

Invasive species are a key threatening process and act as a driver of pollinator declines (Clavero & Garcia-Berthou, 2005; Aizen et al., 2008; González-Varo et al., 2013). The European honey bee, Apis mellifera, occupies every inhabited continent through intentional introductions for honey production and pollination services, especially for agricultural and horticultural crops (Moritz et al., 2005; Geslin et al., 2017). Honey bees occur as a domesticated species in managed hives, operating at scales from small local hobby beekeeping ventures to commercial ventures involving hundreds to thousands of hives. Additionally, there are wild populations, which represent established feral populations in regions where it has been introduced (Moritz et al., 2005).

First introduced into Australia in the early 1820s, managed honey bees can be found in high densities owing to apicultural deployment of managed colonies in crop fields and in natural areas during peak flowering periods of plants used in honey production (Pyke, 1999). Feral colonies are also well established over most of the temperate and sub-tropical regions of Australia (Geslin *et al.*, 2017). Honey bees in Australia are free from most parasites and diseases that limit honey bee populations elsewhere across the globe (Staveley *et al.*, 2014). The honey bee industry in Australia has an estimated gross value of AUS\$90M per annum from hive products, with an additional AUS\$4-6B per annum value to the Australian economy through pollination services (BeeAware, 2014).

Australia has ~2000 species of native bees, many of which are undescribed, with a unique phylogenetic composition (Batley & Hogendoorn, 2009). The Southwest Australia biodiversity hotspot hosts a diversity of native bees, many of which are endemic (Phillips *et al.*, 2010; Houston, 2018), yet there are few areas where honey bees are absent, and feral colonies occur over the entire Southwest hotspot region (Manning, 1997).

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April

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## **9.2.** Appendix 2: Publications arising from this research not included in the thesis

The first page of each publication, and key figures if relevant, are reproduced below

9.2.1 Andrew, N.R., Evans, M.J., Svejcar, L., Prendegast, K., Mata, L., Gibb, H., Stone, M.J., & Barton, P.S. (2021). What's hot and what's not – Identifying publication trends in insect ecology. *Austral Ecology*. (Online Early). DOI: 10.1111/aec.13052. Available:

https://onlinelibrary.wiley.com/doi/abs/10.1111/aec.13052

Austral Ecology (2021) ••, ••-••

What's hot and what's not – Identifying publication trends in insect ecology

NIGEL R. ANDREW,\*<sup>1</sup> () MALDWYN J. EVANS,<sup>2,3</sup> LAUREN SVEJCAR,<sup>4</sup> KIT PRENDEGAST,<sup>5</sup> LUIS MATA,<sup>6</sup> HELOISE GIBB,<sup>7</sup> () MARISA J. STONE<sup>8</sup> AND PHILIP S. BARTON<sup>9</sup> ()

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Abstract Research disciplines in science have historically developed in silos but are increasingly multidisciplinary. Here, we assessed how the insect ecology literature published in ecological and entomological journals has developed over the last 20 years and which topics have crossed discipline boundaries. We used structural topic modelling to assess research trends from 34 304 articles published in six ecology journals and six entomology journals between 2000 and 2020. We then identified and compared topics that memreged from the entire body of literature, or corpus, with topics that emerged from a subsection of articles that focused only on insects (insect corpus). We found that, within the entire corpus, topics on 'Community ecology', 'Traits, life history & physiology' and 'Ecological methods & theory' became more prevalent over time (hot topics), whereas 'Population modelling', 'Insect development', 'Reproduction & ontogeny' and 'Plant growth' declined in prevalence over the 20 years we surveyed (cold topics). In the insect corpus, we found that hot topics included 'Thermat tolerance' and 'Disease vectors', whereas cold topics included 'Herbivore phenology', 'Insect-plant interactions' and 'Parastitoids and parasites'. 'Landscape ecology' was a growth topic area for both corpora. Our findings suggest that insect-related research is a major component of the broader ecological discipline, and there are topics in ecology where insect research aligns with general ecologiat trends, However, specific topics unique to the insect corpora – such as insect taxonomy – are fundamental to both insect and ecology research. Abstract in Spanish and Portugese is available with online material.

Key words: entomology, insects, publication trends, review, structural topic modelling, taxonomy.

#### INTRODUCTION

Like all scientific disciplines, ecology changes and evolves (Carmel et al. 2013; Borrett et al. 2014; Westgate et al. 2015). For example, in Austral Ecology, several research topics have emerged and changed in importance over the past four decades (Westgate et al. 2020): most dramatically, research related to 'communities' and 'landscapes', which were ranked 30 and 29, respectively, in the 1970s (according to the prevalence of keywords among articles) were ranked second and fourth, respectively, in

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the 2010s. It is intriguing to know where research trends are heading and how foci change as new theories arise, techniques develop and problems emerge. Assessing broad research trends enables researchers to identify gaps and opportunities (e.g. Andrew et al. 2013) and to target key research areas (Morton et al. 2009; Sutherland et al. 2013). Historically, studies identifying trends and openal

Historically, studies identifying trends and overall scientific literature patterns have relied on classic systematic reviews and meta-analyses (Culina et al. 2018; Gurevitch et al. 2018). These approaches generally provide an overall assessment of the literature or examine a set of defined questions deemed important by the authors. However, a major shortcoming of systematic literature reviews is that they can be

9.2.2 Prendergast, K., Vanderstock, A., Neilly, H., Ross, C., Pirotta, V., & Tegart, P. (2021). Potential and pitfalls of citizen science with children: Reflections on Pollinators in the Playground project. Austral Ecology. (Online Early, Special Issue: Insect Traits/Ecology). DOI: 10.1111/aec.13031. Available: https://doi.org/10.1111/aec.13031



#### Austral Ecology (2021) ••, ••-••

#### Potential and pitfalls of citizen science with children: Reflections on Pollinators in the Playground project

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Abstract Engaging school-age children in activities involving 'real-world' science and interacting with scientific researchers can promote an interest in appreciating and understanding the natural world and the scientific method. Here, we describe a project involving five female early-career and PhD researchers who facilitated a citi-zen science project with school-age children. Under the guidance of the researchers, across five schools, children created artificial flowers and installed them on school ovals. Over repeated 10-min observations, students recorded how colour (vellow vs. blue) and configuration (isolated, clumped adjacent, clumped mixed colour and clumped single colour) influenced how many and what taxa of insects visited. Here, we reflect on what we were able to achieve including creating a simple, fun, cost-effective project; anecdotal student interest in insects, and positive female STEM role models. We also acknowledge constraints and shortcomings, including set curricula resulting in suboptimal season for pollinator studies; confounding of results due to children's observations; and being unable to verify the data. We offer recommendations for more robust projects in future, which include col-lecting specimens to verify results, and measuring learning outcomes. If these recommendations are met, researcher-student projects can engage children in conducting scientific experiments with applications for home and school garden management.

Key words: artificial flowers, citizen science, flies, pollinators, science education, urban ecology.

#### INTRODUCTION

Raising awareness about insects and how to bolster their populations is important in light of global insect declines (Sánchez-Bayo & Wyckhuys 2019). Insects are an ideal group of organisms through which to engage children in understanding and contributing to scientific observations (Kim 1993). Learning about ecology through experiential (Bauerle & Park 2012) and authentic (Rahm et al. 2003) research partnering students with scientists (e.g. Barab & Hay 2001) is increasingly recognised as means to boost Science, Technology, Engineering and Maths (STEM) educa-tion outcomes. Conducting ecology-focused field activities in schools benefits society, as children are the next generation of citizens, policy-makers and stakeholders, and encourages children to transfer environmental messages to their families (Monroe 2019).

Citizen science is a collaborative way of data collection which can improve community scientific

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knowledge (Kobori et al. 2016) and is increasingly used as a tool to engage children in learning experiences (Bonney et al. 2009; Pirotta et al. 2019). Here, we report on a citizen science project conducted in schools testing the effect of colour and configuration of artificial flowers to attract insects. The overarching objective was to use a citizen science project to engage primary school students in data collection and create opportunities to learn about pollination and insects. The aims of the experiment were to test the abundance and diversity of insect taxa to artificial flowers. Specifically;

- 1. compare the relative attractiveness of blue versus vellow flowers, controlling for other signal variables (e.g. scent, nectar and pollen nutritional values, flower shape)
- test the effect of spatial arrangement of flowers on insect visitation by comparing the relative attractiveness of 'clumped' versus 'isolated' flow ers
- compare the relative attractiveness of isolated vs. 3. interspersed flowers of different colours when in clumps (i.e. configuration)

## 9.2.3 Prendergast, K. & Hogendoorn, K. (2021). Flawed methods beleaguer bee studies. *Austral Ecology*. (Online Early, Special Issue: Insect Traits/Ecology). DOI: 10.1111/aec.12998. Available:

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#### FORUM: Methodological shortcomings and lack of taxonomic effort beleaguer Australian bee studies

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Bees are a diverse insect group (Michener 2007). Their variation in sociality, nesting and foraging behaviour, and close association with angiosperms have made bees a topic of interest from ethological, ecological (Gross 1992; Hingston & Potts 2005; Magrach et al. 2012), agricultural (Hogendoorn 2004; Hogendoorn et al. 2006; Cunningham 2017) and conservation perspectives (Bischoff et al. 2013; Glatz et al. 2015). Reported declines of insects, including bees, across the globe (e.g. Goulson & Nicholls 2016; Mathiasson & Rehan 2020) has increased research attention for pollinators. While this is welcome, we are concerned about some persistent methodological shortcomings in native bee research. This critique focusses on two issues: biased sampling and taxonomic neglect.

#### PASSIVE TRAPPING ALONE IS POOR PRACTICE

In the past three decades, evidence of the shortcomings of passive trapping methods has been accumulating (e.g. Cane et al. 2000; Roulston et al. 2007; Prendergast et al. 2020; Fig. 1). Despite this, some studies still solely rely on passive methods such as pan or vane traps to document and monitor bee diversity (e.g. Saunders & Luck 2014; Saunders et al. 2018) and vane traps (e.g. Lentini et al. 2012; Neave et al. 2020). Passive methods are attractive from an effort-saving perspective, and may present a form of standardised sampling (Hall 2018). However, when only passive traps are used, this leads to a poor faunal representation, for four main reasons.

Firstly, adherence to a single sampling method is an issue for entomological studies (Yi et al. 2012), as a single method often does not allow capturing a representative sample of the group of interest. For bees, comparisons of methods shows that passive trapping favours capture of some taxonomic groups over others. For example, in Australia, the introduced European honey bee and native euryglossine and megachilid bees are vastly underrepresented in vane

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traps, while larger generalist bees – Lasioglossum and Amegilla – are overrepresented (Prendergast et al. 2020, and references therein). Such sampling bias can lead to erroneous interpretations of the relative and absolute abundance of bee species. It is therefore important to realise that bees caught in blue vane or pan traps are not 'indicative of real-world populations' (Hall 2018).

Secondly, the numbers of bees caught in traps depend on the availability and quality of floral resources: visual traps can be more attractive when floral resources are lower in abundance (Baum & Wallen 2011; K. Hogendoorn pers. obs., 2015; K. Prendergast pers. obs., 2019). This potentially leads to erroneous interpretations concerning the abundance of bees in areas of high and low floral resource availability. For example, this bias might explain why higher abundances of bees were found in wheat fields (Lentini et al. 2012), and in weedy orchards (Saunders et al. 2013), than in native vegetation.

Thirdly, the numbers of bees caught in vane and pan traps depend on their visibility. These traps are attractive over a distance, by reflecting light of certain wavelengths. Compared to forested areas, traps in open locations are visible from further away and more attractive as they reflect more sunlight. Therefore, they would attract more bees over longer distances. Any difference between forested and open sites in numbers of bees caught in vane or pan traps should therefore not lead to conclusions such as 'species richness and abundance of bees was greater at sites containing little or no tree cover' (Hall *et al.* 2019), as asserted from a study solely using blue vane traps.

Fourthly, when used for longer periods, for example to monitor changes in bee composition over time, it should be recognised that bees are central place foragers, and that keeping traps in the same position for a longer time is therefore likely to reduce the local population density (Gibbs *et al.* 2017). This could lead to erroneous interpretations regarding population fluctuations (e.g. Brown *et al.* 2020; Neave *et al.* 2020).

While studies using passive trapping can be useful to compare captures between sites (e.g. between equally sized paddocks, or at distances from an edge), it is important to avoid erroneous





#### PROBLEM:



SOLUTIONS: To resolve these serious issues affecting publication of bee research, we propose:

#### For those conducting field research on bees and pollinators

- 1. Specimens should be collected by skilled entomologists when possible
- 2. Passive methods should only be used to complement active
- methods 3. Specimens should be identified by the lowest taxonomic level possible by those with experience in bee identification
- 4. Lists of the specimens, who identified them, how, and where they are kept should be made available

#### For those researching or making management decisions based on previous studies

- 1. Treat any conclusions based on data collected with passive methods alone with caution
- 2. Include caveats when citing studies using only passive methods
- 3. Recognise methods using active collections as holding greater strength, all else being equal, in the validity of their findings

#### For reviewers and editors

- 1. Question any studies that use only passive collection methods
- Request that specimens are 2. collected, species lists accompany publications (either in the manuscript or as data in online data repositories), and that the method of identification is clear (who identified them, how, and where specimens are kept for verification if required)
9.2.4 Prendergast, K. S. (2021). Natural History Note: Urban domestic gardens support nesting populations of the native bee *Leioproctus (Leioproctus)* plumosus. Austral Ecology. (Online Early, Special Issue: Insect Traits/Ecology). DOI: 10.1111/AEC.13016. Available: https://onlinelibrary.wiley.com/doi/10.1111/aec.13016



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### Natural history note: Urban domestic gardens support nesting populations of the native bee *Leioproctus* (*Leioproctus*) plumosus

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**Abstract** The nesting habits of many Australian native bees are poorly known, with observations of nests being few and far in between. Here, I report three independent nesting aggregations of a native colletid bee *Leioproctus* (*Leioproctus*) plumosus, accompanied by videos of its nesting behaviour and photographs of its nesting substrate. These discoveries were made possible through the citizen science group 'Bees in the burbs'. Despite extensive surveys in the region, the only nesting occurrences of *L. plumosus* have been found in domestic gardens, all in highly urbanised areas. With this species more frequently encountered in residential gardens, this suggests that despite evidence of ground-nesting bees being relatively disadvantaged by urban development due to replacement of bare ground with impervious surfaces, this species is able to still use residential areas for nesting. I propose potential explanations for this phenomenon, which includes new observations of commonly foraging on *Callistemon* – a popular tree in gardens and on nature strips. That this native bee's nests appear to be associated with residential gardens, provides both opportunities to engage citizen scientists in documenting and preserving native bee populations, but also indicates the threat ongoing urban development may pose.

Key words: citizen science, Colletidae, Leioproctus, native bees, nesting, urbanisation, urban ecology.

#### INTRODUCTION

Urban areas are often considered inferior habitat for wildlife (McDonald et al. 2008); however, there is an increasing recognition that they can still harbour a considerable diversity of native bees (Theodorou et al. 2020). Although urban areas can provide a high abundance, and diversity of flowers for bees (Hülsmann et al. 2015), flowers represents only half of the equation: bees also need nesting resources. This is where urban areas may be unfavourable, especially for ground-nesting bees, as by replacing natural substrate with impervious surfaces, this destroys nesting substrates (Xie et al. 2013; Geslin et al. 2016; Quistberg et al. 2016; Pereira et al. 2020).

Despite this, here I report three nesting aggregations of a ground-nesting bee *Leioproctus (Leioproctus) plumosus* (Colletidae), all in residential gardens, in highly urbanised areas of Western Australia (Fig. 1). I was informed of these through my citizen science Facebook group 'Bees in the burbs' (Prendergast 2016), which underscores the benefits of citizen science for making observations of 'backyard biodiversity', which would otherwise be inaccessible to researchers.

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The first nest was discovered in the backvard of C. Wood on 29th September, 2019, in Perth. Following images posted on 'Bees in the burbs', I visited the property, where numerous bees were observed. Males flitted close to the substrate (Prendergast (2020a): Appendix S1), females were actively using burrows (Prendergast (2020a): Appendix S2; Fig. 2a,b), and parasitic wasps (Labium pettitorium: Ichneumonidae, Fig. 2c) were flying over the nesting area (Prender-gast (2020a): Appendix S2), and one entered a burrow. The nesting area was on open, grey and white sandy substrate ('Vasse complex') with small rubble. Nests were made in the coarse white sandy substrate with some organic matter, and were noticeable as slightly raised mounds of dirt located on bare sand with scattered vegetative litter, and in between the rubble (Fig. 2a, see also Prendergast (2020a): Appendices S1 and S2). Approximately, 15 active nests were observed over an area of approximately  $5 \times 5$  m. A female specimen was collected, and its identity as Leioproctus (Leioproctus) plumosus was confirmed (Maynard 2014).

The second nests were in the yard of F. Shaw, observed on 27th September, 2020, at Tapper Lane, Claremont. Bees were first observed by F. Shaw on 19th September and posted on 'Bees in the burbs' to confirm if they were native bees. Nests occurred between a brick pathway running down the side of the house and in soil between the pavement and

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Fig. 3. Nesting observations of *Leioproctus plumosus* nesting along a garden side path at a residential house at Tapper Lane, Claremont, 27 September, 2020: (a) three nests dug between the bricks; (b) an active nest located against the house wall (left) and a female exiting a nesting burrow (right); and (c) a female resting on a ivy leaf that bordered the fence adjacent to the nesting burrows. Photographs by Kit Prendergast.



Fig. 4. Nests of *Leioproctus plumosus* located in a front yard at Alfred Road, Mt Claremont: (a) nests were located around the base of a ceramic pot plant; and (b) close-up of two nests that were surrounded by leaf litter and had small turrets. A female *Leioproctus plumosus* with pollen on her scopae was observed entering one on 1st October, 2020. Photographs by Kit Prendergast.



**Fig. 5.** Leioproctus plumosus nesting aggregation in Kensington: (a) burrow located between bricks; and (b) a male *L. plumo*sus – hundreds were observed flying around near the nests and surrounding bushes on 12th November, 2020. Photographs by Kit Prendergast.

Prendergast & Yeates 2018), nest architecture (Houston 1970), substrate preferences (Yasmineantonini & Martins 2000), and identifying important nesting habitat to conserve populations (Batley & Hogendoorn 2009). Although impervious surfaces like

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pavement, roads and buildings eliminate nesting substrate, at the Tapper Lane site, some nests were located between brick paving, suggesting that if there are gaps between impervious surfaces, bees may still be capable of nesting. It may even be that by nesting

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9.2.5 Prendergast, K. S. Leclercq, N. & Vereecken, N. (2021). Honey bees (Hymenoptera: Apidae) outnumber native bees in Tasmanian apple orchards: perspectives for balancing crop production and native bee conservation. *Austral Entomology*. (Online Early). DOI: 10.1111/aen.12521. Available:

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Honey bees (Hymenoptera: Apidae) outnumber native bees in Tasmanian apple orchards: Perspectives for balancing crop production and native bee conservation

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Abstract

Apples are a major crop globally, including in Tasmania (Australia) - known as 'the Apple Isle' owing to the key role of apples in Tasmania's history and economy. Most apple cultivars are obligate entomophilous species, and fruit quantity, quality and economic value are enhanced under insect pollination. Whilst the introduced European honey bee (Apis mellifera) is often assumed to be the main pollinator of apple in most regions of the world, including Australia, there is an increasing interest in alternative pollinators. The pollinator community of Tasmanian apple crops, however, has never been assessed. In this study, we surveyed four apple orchards for 3 days each during peak bloom in the Huon Valley region to characterise bee assemblages visiting blooming apple trees and the native bee fauna associated with surrounding flowering vegetation. Our results show that honey bees were the predominant visitors to apple blossoms (90.7% of visits), followed by the introduced bumble bee Bombus terrestris (5.9% of visits), with only a minor contribution by native bees (3.3% of visits). Twenty-six species of native bees were collected in total, of which only 10 species (five Exoneura (Apidae), four Lasioglossum (Halictidae) and one Euryglossa (Colletidae) species) were collected from apple blossoms, with Exoneura being the most abundant visitors. Few native bees were captured on apple blossoms, however co-blooming surrounding native vegetation, as well exotic flowers, hosted a high diversity and abundance of native bees. Site conditions influenced community composition, including abundance and representation of introduced bees compared to native bees visiting apples. Additionally, warmer temperatures favoured native bees. Collectively, our results suggest that Tasmania's apple production in its current state is unlikely to rely exclusively on native pollinators. Native bees nevertheless warrant conservation in such an insular crop production system. This can be achievable through retaining native flowering plants and even exotic non-crop flowers in and around orchards. Promoting the diversity and abundance of native bees through habitat enhancement may have additional benefits, such as filling current and future pollination demands and gaps, a key strategy under scenarios of climate chang

Key words apple, bee, bumblebee, honey bee, native bee, Tasmania, weather, weed, wild bee, wildflower.

#### INTRODUCTION

Apples (Malus domestica varieties: Rosaccae) are a major food crop across the world, including in Australia where it has been introduced by colonists and cultivated since the late 17th century (Luby 2003; Kcogh et al. 2010a). The majority of apple cultivars are self-incompatible (Dulta & Verma 1987), produce seeds through obligate entomophily, and insect pollination is reported to enhance yield, fruit quality and overall crop economic value (Kkin et al. 2007; Garratt et al. 2014; Miñarro & García 2018; Pardo & Borges 2020). Honcy bees (Apis spp., predominantly Apis mellifera, but also Apis cerana in southern, south-eastern and eastern Asia) are traditionally used as the main pollinators of apples (Pardo & Borges 2020), yet there is increasing interest in alternative pollinators, including in Australia, owing to the similar or higher per-visit performance in pollen transfer by native or other managed species (Hogendoorn et al. 2006; Rader et al. 2009; Mader et al. 2010; Christmann & Aw-Hassan 2012).

Although honey bees are usually considered to be the most important pollinator of apple flowers, there is evidence to suggest that solitary native bees have proven as effective, if not more effective, than honey bees as pollinators of apple flowers (Vicens & Bosch 2000; Bosch & Kemp 2002; Mallinger & Gratton 2015; Park et al. 2016). This is due to comparatively low pollination efficiency at the individual level in honey bees because they move between flowers on the same plant or because the pollen they collect is no longer available for plant sexual reproduction, making them poor pollinators for plants such as self-incompatible apple varieties (Free 1966). Honey bees may even be detrimental to successful pollination as they have been observed to primarily visit petal-less or even wilted flowers with dehiscing anthers (Williams & Brain 1985). In addition, pollinator diversity has been found to positively affect apple yield (Martins et al. 2015; Blitzer et al. 2016; Földesi et al. 2016), and more generally, reports indicate that diverse wild bee communities are of overarching importance for effective pollination and inter-annual yield stability for many crops (Garibaldi et al. 2011; Garibaldi et al. 2013), particularly in a context of global change

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# **9.2.6** Prendergast, K. S. (2021) Critiquing the notion of a species natural range

in an era of unprecedented change. Austral Ecology, 45(6), 672-674.

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#### Forum

# Critiquing the notion of a species natural range in an era of unprecedented change

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In recent years, much progress has been made in building up populations of threatened animals (mainly vertebrates) in Australia (Moseby et al. 2009), often in semi-captive conditions in fenced reserves (Moseby *et al.* 2009). The next step for suc-cessful recovery is reintroduction (van Oosten 2015). Translocations (moving individuals between populations, or establishing new sub-populations) are also being increasingly used to boost populations and increase the genetic health of populations, and relocation activities (relocating populations) are con-ducted for species in areas of risk, for example due to their original habitat being converted for mining, agriculture or urban development (van Oosten 2015). Reintroductions are a hot topic, with a search using the terms 'reintroduction' OR 'translocation' OR 'relocation', yielding 186 publication in Austral *Ecology*, 56 of which were published in the last 5 years as of 16 April 2020. Yet to date, the vast majority of reintroductions and translocations involve selecting locations in the species 'natural' or 'histori-cal' range. But is this a viable strategy? By neglecting to consider areas outside this 'natural range', is this a missed opportunity? And despite good intentions and theory to support reintroducing species to areas where they historically occurred, could this even be dooming them to become extirpated once again? In this Forum piece, I will explore the pros and cons of this focus on species' natural ranges, and the opportunities and risks of introducing species outside their natural range.

How to even define a species natural or historical range is vague. 'Historical range' is often taken to be the range present at the time of European colonisation. Making this a time-point to define what is deemed a historical range however could be argued to be more a vagary of European history, rather than based on any biological reasoning (Jørgensen 2011). Our knowledge of a species historical range just prior to European colonisation moreover can be scant or unreliable (Bilney 2014).

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Species ranges are not static, and how long a species has to be established in a region before it can be considered part of its natural range is contentious. This is evident in the debate over whether dingos Canis lupus dingo are native (introduced to Australia 5000 ya; Greenville et al. 2019), and over reintroducing/introducing Tasmanian Devils Sarcophilus harrisii to the mainland (a species that was historically pre-sent but became extinct from the mainland approximately 3000 ya; Westaway et al. 2019). The case for the Tasmanian Devil is particularly poignant: having experienced drastic population declines on Tasmania due to a transmissible contagious cancer, restoring Tasmanian Devils to the mainland may be the only viable way to prevent this species extinction, with corollary benefits to native ecosystems through this predator exerting top-down control of invasive species (Hunter et al. 2015; Westaway et al. 2019).

Importantly, the historical range may no longer be suitable due to factors such as changing soil conditions as a result of erosion, livestock grazing or salinity; changes in vegetation structure due to introduced herbivores or drought; and changes in the biotic assemblages of predators, parasites, mutualistic species and food and shelter resources. A major reason for a species former range to be unsuitable both now and also in the future is climate change; which can alter all the factors mentioned above. Under climate change, translocations within a species natural range may be unable to rescue populations (Schiffers et al. 2013) and instead assisted migration/colonisation into areas that are predicted to be suitable may be necessary to prevent extinction (Vitt et al. 2009; Gallagher et al. 2015). The fact that species are already naturally shifting their ranges to keep within their cli-matic envelope (Schiffers *et al.* 2013) suggests that adhering to keeping species within their historical distribution is not in line with ecological reality.

In Australia, there are proven benefits for ecological communities following reintroductions of extirpated keystone species such as ecosystem engineers (Fleming *et al.* 2014). However, Australia has also suffered mass extinctions both from Aboriginal hunting and burning of the landscape which led to the

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# 9.2.7 Prendergast, K. S. (2020). First records of the introduced African Carder Bee *Pseudoanthidium (Immanthidium) repetitum* (Hymenoptera: Megachilidae) in Western Australia. *Pacific Conservation Biology*, 27(1), 39-46. <u>https://doi.org/10.1071/PC20041</u>. Available: https://www.publish.csiro.au/pc/CrossrefCites/PC20041

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Pacific Conservation Biology, 2021, 27, 39–46 https://doi.org/10.1071/PC20041

#### First records of the introduced African carder bee, *Pseudoanthidium (Immanthidium) repetitum* (Hymenoptera: Megachilidae), in Western Australia



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Abstract. Globalisation has increased the occurrence of species being introduced outside of their natural range. The African carder bee, *Pseudoanthidium (Immanthidium) repetitum* (Hymenoptera: Megachilidae), is one such species. *P. repetitum* was first recorded in Australia in 2000 in Queensland (north-east Australia), and rapidly spread down the east coast of Australia, and by 2015 was reported to be a common component of bee assemblages in urban community gardens in Victoria (southern Australia). Here, I report the first occurrences of this species. Thus far there are three other side of the continent, representing a major expansion of the distribution of the species. Thus far there are three confirmed and one unconfirmed localities where this species has been seen, all localised to the Mandurah region in residential areas of Western Australia. Female specimens were collected from a garden in Halls Head, where it was observed to be abundant. Other bees, both native and the introduced European honeybee, were foraging alongside it. The occurrence of *P. repetitum* represents a major expansion in its distribution. It remains rare and localised; however, given known negative impacts of introduced species on native fauna and flora, especially in Australia, vigilance is required to monitor this species.

Additional keywords: alien species, citizen science, introduced species.

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#### Introduction

Pseudoanthidium (Immanthidium) repetitum (Schulz, 1906) (Hymenoptera: Megachilidae) (previously Afranthidium (Immanthidium) repetitum: Litman et al. 2016) (Fig. 1), commonly known as the African carder bee, is one of the few non-Apis introduced bee species in Australia. Native to South Africa, *P. repetitum* was first documented in Australia in Brisbane, south-east Queensland, in 2000 (Burwell and King 2000). Since then, *P. repetitum* has undergone an extensive, rapid range expansion. By 2008 it was established in Sydney, and was recorded in Rockhampton, Queensland, in 2014, Albury, New South Wales, in 2014, Clermont, Queensland, in 2015, Melbourne, Victoria, in 2014 (Baumann et al. 2016), and Whyalla, South Australia, in 2015 (Atlas of Living Australia 2020b). As of 22 February 2020, 85 observations had been recorded on the website Atlas of Living Australia (Atlas of Living Australia 2020b) (Fig. 22); however, until now there have been no known recorded observations in Western Australia.

Nesting behaviour of *P. repetitum* differs from that of Australian megachilids in its easily distinguished nests, which are made from hair-like plant fibres that females scrape (or carder) from leaves and stems with the mandibles, and roll into balls, with the nest resembling a mass of cotton wool, described as 'felted cotton' (Litman *et al.* 2016) (Fig. 3). Unlike Australian megachilids, which all are solitary nesters (Houston 2018),

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P. repetitum nests communally, where masses of brood cells from multiple females are commonly found in the one place (Litman 2012) (Fig. 3b).

#### Methods

Taxonomic validation

Identifications were made by K. Prendergast with reference to Litman et al. (2016). As the only species in its genus known to be found in Australia, this species is highly distinctive. Identification involved observing the specimens under a light microscope to confirm diagnostic characters. Five specimens (one specimen for Dover Street, Halls Head, and four from Janis Street, Halls Head) were deposited in the entomology collection of the Western Australian Museum, voucher numbers WAM E105936 to WAM E105940.

#### Results

There have been four recent confirmed records of *P. repetitum* in Western Australia (Fig. 2b). The first record of *P. repetitum* in Western Australia was from Greenfields on 1 April 2019, where a pest control operator from Pest Guard WA reported a 'furry substance with little black insects' to the Department of Primary Industries and Regional Development of Western Australia (DPIRD) Pest and Disease Information Service (PaDIS).

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Fig. 6. Megachile (Eutricharaea) serricauda and M. oblusa – native Australian megachilid species that are often mistaken for Pseudoanthidium (Immanthidium) repetitum. Megachile (Eutricharaea) serricauda (a) female, (b) male, (c) male on exotic Asteraceae; Megachile (Eutricharaea) obtusa (d) female, (e) male, (f) female using a bee hotel. Note the metasoma bands being formed by hairs, and how the female is nesting solitarily. Images by Kit Prendergast.



No impact

- Potential negative impacts: Potential negative impacts: - competition with native bees for nesting sites - competition with native bees tor floral resources - pollination of invasive weeds - spread of pathogens and parasites - damage to buildings - daftecting the pollination of native plant species - changing the structure of pollination networks

Fig. 7. Potential impacts of Pseudoanthidium (Immanthidium) repetitum.

Principle, effort and funding going into eliminating this intro-duced species may not be worth the costs (Hoffmann and Broadhurst 2016). At present, it appears that *P. repetitum* is at such low abundances that its impact, if any, will be negligible.

While there are concerns that introduced species may also be the main benefactors of efforts to enhance nesting resources for cavity-nesting bees (MacIvor and Packer 2015), it also does not appear to be the case in Western Australia, or in Australia

Potential positive impacts:

species

+ enhanced pollination of native flora
 + enhanced pollination of
 horticultural species
 + enhanced pollination of crop

# 9.2.8 Prendergast, K. S. (2020). Defending biodiversity through our diets. *Austral Ecology*, 45(5), 520-522. doi:10.1111/aec.12893. Available:

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#### Defending biodiversity through our diets

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Earth is currently undergoing a mass extinction, and for the first time in Earth's history, this one is driven by anthropogenic factors (Ellis 2011). There is abundant evidence that a diet with a high prevalence of animal-derived products is implicated in biodiversity loss and endangement (Steinfeld et al. 2006; Bailey, Froggatt & Wellesley 2014; Machovina et al. 2015). Such diets are an overlooked issue (Bailey et al. 2014), especially in Australia, where the meat industry has negative impacts on biodiversity, which plays out in numerous ways.

Habitat destruction (loss and fragmentation) is the overriding cause of species endangerment and extinction in many countries, including Australia (Evans *et al.* 2011). In Australia, cattle grazing is the primary driver of land clearing (Australian Government 2009). Livestock has a disproportionally sizeable land-use footprint (Poore & Nemecek 2018). Due to the inefficiency of energy conversion up food chains (Eshel & Martin 2006), meat production requires larger areas of land by orders of magnitude than plant-based foods, on a per kilogram, per 1000 calories and per 100 g of protein consumed (Poore & Nemecek 2018).

Climate change is a current and ongoing threat to biodiversity, including in Australia (IPCC 2019). Australia is one of the global leaders in per capita greenhouse gas emissions, of which land clearing for livestock production and meat consumption plays a substantive role (Poore & Nemecek 2018; OECD 2020; Ritchie & Roser 2020). Moreover, the Australian livestock industry is contributing to meatheavy, and therefore high-carbon, diets worldwide, being the leading exporter worldwide in sheep, and the world's third-largest beef and veal exporter in 2017 (MLA 2020). As of June 2017, there was 26.2 million head of cattle involved in beef and veal production, and 72.1 million head of sheep for lamb and mutton production (MLA 2020). These introduced ruminants emit more substantial amounts of greenhouse gases than native herbivores (Wilson & Edwards 2008). The sheer scale of livestock on the land results in extremely high greenhouse gas emissions, with enteric fermentation alone comprising an estimated 70.6% of agricultural emissions (Australian Government 2017).

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In addition to land clearing, livestock also contributes to land degradation (Yates et al. 2000; Pettit & Froend 2001; Pringle & Landsberg 2004; Tasker & Bradstock 2006). Livestock grazing is a threat to native flora (Yates *et al.* 2000; Hunt 2010), and their grazing activities can also favour the proliferation of weeds (Gentle & Duggin 1997; Sims et al. 2019), and by altering (simplifying) habitat structure, can reduce biodiversity (Eyre et al. 2009). Australia has never had hoofed animals, and these heavy, hoofed animals wreak havoc upon soils, causing soil erosion and compaction (Yates et al. 2000; Sims et al. 2019). Livestock grazing has shown to seriously negatively affect unique endemic flora and fauna through graz-ing, trampling, and habitat degradation (Yates et al. 2000; Davies et al. 2010). The large densities of livestock and their wastes also lead to nutrient imbal-ances (Sims et al. 2019), and eutrophication of waterways (Burger et al. 2010), with flow-on effects for aquatic biota and marine ecosystems such as the Great Barrier Reef that receive agricultural run-off (Haynes 2001). The catastrophic vegetation and soil changes wrought by livestock grazing may be irrecov erable (Sims et al. 2019).

Introduced animals are cited as a leading cause of species declines and extinctions in Australia (Kearney et al. 2019). Whilst the focus is on cats and foxes (Moseby et al. 2009), in biomass cattle and sheep dwarf, these introduced species by orders of magnitude. Rabbits and deer, as introduced herbivores, are also as a leading threat to biodiversity (Moseby et al. 2009), yet sheep and cattle – also introduced, abundant, grazing herbivores – are seldom mentioned. However, livestock is indirectly involved in facilitating introduced species, due to livestock farmers reducing numbers of apex predators that control cats and foxes and predate upon introduced herbivores: dingos have been demonstrated to be effective at controlling introduced predators and grazing herbivores (Letnic & Koch 2010; Forsyth et al. 2018; Greville et al. 2019; however, their numbers have drastically declined, primarily due to persecution from farmers over (largely unfounded) fears that dingos will kill their livestock (Greville et al. 2019).

There are few large grazing herbivores in Australia, as the megafauna were wiped out historically, again from human activities, namely from indigenous people burning the landscape, as well as through hunting (Johnson & Prideaux 2004). Today, only large

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9.2.9 Prendergast, K. S. (2020). Beyond ecosystem services as justification for biodiversity conservation. *Austral Ecology*, 45(2), 141-143. doi:10.1111. Available: https://onlinelibrary.wiley.com/doi/abs/10.1111/aec.12882



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#### Forum

# Beyond ecosystem services as justification for biodiversity conservation

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The earth is currently facing its sixth mass extinction event and, unlike previous events, is anthropogenic in origin (Cafaro 2015). Against the backdrop of this extinction crisis, and the apparent lack of concern of our world leaders, many conservationists feel they need to justify conservation efforts by stating that biodiversity, or a particular organism(s), are important for provision of ecosystem services most commonly defined as "the benefits provided to humans through the transformations of resources (or environmental assets, including land, water, vegetation and atmosphere) into a flow of essential goods and services, for example clean air, water and food" (Costanza et al. 1997). For recent examples, 'preserving species diversity is critical to ensure ecosystem functioning' (Coulin et al. 2019); 'critical weight range mammals could provide considerable ecosystem services to a range of industries, including farming, which highlights the value of maintaining these species and assisting their recovery within the landscape' (Halstead et al. 2020); and 'it is important to have native species around novel, disturbed ecosystems as they provide a range of ecosystem services for native pollinators' (Everingham et al. 2019). However, is this the best way to encourage conservation, be it of a single species or a diversity of species? Is it true? And can this approach have unintended consequences? Below, I critique the focus on ecosystem services and highlight how a more nuanced perspective is required.

If the focus is on 'ecosystem services', often defined in what services nature can provide just one species – humans, of course – this can mean compromising species richness. For example, in some agricultural contexts, especially in Australia where many crops are exotic, and many pollinators have evolved to forage only on native plants (Murray *et al.* 2009), the European honeybee, *Apis mellifera*, is the sole, or most effective pollinator (Hermansen *et al.* 2014). Honeybees can also be more effective pollinators of native flora compared with native bees (Schmidt-Adam *et al.* 2009). Many Australian bee species are

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arguably rather poor pollinators: euryglossines and hylacines comprise over 50% of native bee species (Batley & Hogendoorn 2009), yet these taxa swallow pollen and lack scopae (Michener 2007), suggesting they are relatively ineffective pollinators (Beardsell *et al.* 1993). Additionally, most are specialists on native flora and hence are underrepresented as crop pollinators (Michener 2007). At the same time, there are numerous where wild native bees have proven to be more effective pollinators than honeybees, both overseas (Garibaldi *et al.* 2013) and in Australia (Hogendoorn *et al.* 2006). This variation makes it evident that ecosystem services cannot always serve as a justification for biodiversity conservation (Kleijn *et al.* 2015; Winfree *et al.* 2015).

While there are numerous examples of positive correlations between ecosystem services and species richness (Weyland et al. 2019), this is not ubiquitous (Ridder 2008). Taxonomic diversity can be lost without impacting functional diversity (Doupé et al. 2006), and not all components of biodiversity or ecosystem services respond similarly to a given management regime, for example Coulin et al. (2019). Moreover, the mechanism underlying the biodiversity-ecosystem service provisioning (BD-ESP) relationship is a topic of ongoing debate but appears to vary depending on the ecosystem service, community, scale and context (Norgaard 2010; Harrison et al. 2014). In some cases, the positive BD-ESP is due to a 'sampling effect' (Wardle 1999), in which case most of the species could be lost without consequence to the ecosystem service in question.

Trying to advocate that one particular species is important to conserve for its ecosystem services is even less tenable. This is especially so when that species is rare and at low abundance, yet therefore most in need of conservation efforts (Winfree *et al.* 2015). Ecosystems naturally have redundancy, and losing one species may be inconsequential (the 'portfolio effect'; Ehrlich & Walker 1998; Figge 2004; Hooper *et al.* 2005). Consider the iconic koala: at high densities, it can even cause an ecosystem 'disservice' by defoliating keystone eucalypt trees; however, few people would be comfortable with trading the survival of

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9.2.10 Prendergast, K.S. (2019). Scientific note: mass-nesting of a native bee *Hylaeus (Euprosopoides) ruficeps kalamundae* (Cockerell, 1915) (Hymenoptera: Colletidae: Hylaeinae) in polystyrene. *Apidologie*, *51*, 107–111. doi:10.1007/s13592-019-00722-8. Available:

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#### Scientific note: mass-nesting of a native bee *Hylaeus* (*Euprosopoides*) *ruficeps kalamundae* (Cockerell, 1915) (Hymenoptera: Colletidae: Hylaeinae) in polystyrene

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Abstract – Plastic is pervasive across ecosystems, with polystyrene being a common plastic synthetic material used in buildings. Although polystyrene is used in hive construction for European honeybees and managed megachilds, cavity-nesting colletids have never been documented to nest in such materials. Here, observations of the solitary native bee *Hylaeus (Euprosopoides) ruficeps kalamundae* mass-nesting in polystyrene insultation boards in a house in Darlington, Western Australia, are reported. This represents the first instance of a *Hylaeus* species nesting in polystyrene. The abundance of individuals nesting in this material over successive years suggests this behaviour is not detrimental to the fitness of this species; however, experimental studies comparing fitness between polystyrene and natural materials are required. These observations contribute to the recognition that anthropogenic materials are increasingly being used by wild animals.

#### bees / plastic / hylacine / adaptive flexibility / nesting

Synthetic materials are globally becoming a ubiquitous component of cosystems, accompanied with a loss of natural materials. Plastics in particular are recognised as an omnipresent part of the Anthropocene (Zalasiewicz et al. 2016). There have been increasing observations of wild animals utilising anthropogenically sourced materials (Hartwig et al. 2007; Pickrell 2012).

Bees have also been observed to make use of anthropogenic resources as nesting habitat. Nesting in mortar appears to be a common phenomenon (Dollin 2019a; Prendergast, personal observation), even with "pest control" services offering eradication (e.g. Koelewyn 2019). Two species of *Megachile* in the northern hemisphere have been observed to incorporate plastic materials into their nests (MacIvor and Moore 2013): *M. rotunda*, which typically uses cut plant leaves, has been observed to construct brood cells out of pieces cut from polyethylene-based plastic bags, and *M. campanulae*, which typically uses plant resins in construction of brood cells, has been observed constructing brood cells out of polyurethane-based exterior building sealant. Recently, a nest produced by a megachilid, postulated to be *M. rotunda*, was found to contain three cells constructed entirely out of two types of plastic (Allasino et al. 2019).

The majority of cases of anthropogenic materials being used by native bees has involved megachilids and, to a lesser extent, apids. There have never been observations of hylacine bees utilising anthropogenic materials as nesting resources. The majority of hylacine bees nest in premade cavities in wood created by woodboring beetles and, unlike Megachilidae, but characteristic of colletids, line and seal their nests with "cellophane-like" secretions consisting of a mixture of liquid polyesters and silk protein (Almeida 2008).

On 10 January 2019, the author investigated an infestation of native *Hylaeus (Euprosopoides) ruficeps kalamundae* (Houston 1981) nesting in the polystyrene insulation of a house located in Darlington, Western Australia. Polystyrene insulation panels had been

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K. S. Prendergast



**Figures 1–5 1** Polystyrene insulation board. **2** *Hylaeus ruficeps kalamundae* often entered the house and became trapped and attempted to escape by flying and crawling along the glass door, leaving excrement, with many being unable to escape and perishing. **3** *Hylaeus ruficeps kalamundae* were entering and exiting to nest in the polystyrene insulation panels through cracks in the boards; entrances sealed over by the owner of the house resulted in an accumulation of dead Hylaeus ruficeps kalamundae that attempted to encer. **4** Female *Hylaeus ruficeps kalamundae* on the polystyrene block that had been put out to attempt to encourage them to vacate the insulation boards in the house. **5** A female *Gasteruption*—a predator-inquiline parasitoid wasp—investigating the polystyrene insulation panel where *Hylaeus ruficeps kalamundae* were ensting. Photos: Kit Prendergast.

installed between the upper and lower levels of the twostory house built by the homeowner (Figures 1, 3, and 5). These insulation panels had been left exposed for about a year before being covered, and during this time, native bees had begun nesting in them. Hundreds of hylaeine bees were observed flying in and out of gaps in the outer boards of the house to access the polystyrene insulation. Bees had also taken to nesting in hardened

9.2.11 Prendergast, K. S. (2018) Euryglossina (Euryglossina) perpusilla (Hymenoptera: Colletidae: Euryglossinae) nesting in pre-formed cavities in Banksia attenuata (Proteaceae), Journal of Melittology, 28, 1-5. Available: https://journals.ku.edu/melittology/issue/view/1114

# Journal *of* Melittolog The latest buzz in bee biology

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#### BRIEF COMMUNICATION

Euryglossina (Euryglossina) perpusilla (Hymenoptera: Colletidae: Euryglossinae) nesting in pre-formed cavities in Bankisa attenuata (Proteaceae)

#### Kit S. Prendergast<sup>1</sup>

Abstract. This article reports observations of nesting by Euryglossina (Euryglossina) perpusilla Cockerell in preformed cavities in a Banksia attenuala Brown tree in an urban bushland remnant.

#### INTRODUCTION

The natural history of biological organisms - what they are, and how they live and interact with their biotic and abiotic environment, e.g., habitat preferences and their reproductive behaviours, are vital for advancing science (Boero, 2013). Moreover, effective conservation requires knowledge of a species' niche and interactions with its environment. Consequently, the task of increasing knowledge and understanding of the natural history of Australian native bees is one of urgency given the rapid transformation of natural habitats to urbanization, as well as reports of bee declines across the globe (IPBES, 2016). Australia's native bee assemblages include a great diversity of species, many endemic, but there are large gaps in our knowledge about their taxonomy, ecology, and habitat requirements (Batley & Hogendoorn, 2009).

The subfamily Euryglossinae is the most speciose of bee subfamilies in Australia, with 404 named species comprising minute to small-bodied bees endemic to Australia (Kayaalp, 2011; Michener, 2007; Randall, 2017). Their nesting habits are poorly known, and observations of the reproductive behaviors of Euryglossinae are rare. Within this taxon, nesting behaviors and nesting substrates are not conserved. From a hypothesized plesiomorphic condition of ground-nesting for colletids, followed by a shift to wood-nesting in the common ancestor of the clade comprising Colletinae, Euryglossinae, Hylaeinae, Scrapterinae, and Xeromelissinae, and Callomelitta Smith, there have

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9.2.12 Prendergast, K.S. (2018). Nesting biology of *Megachile ignita* Smith 1853 (Hymenoptera: Megachilidae) in artificial nesting blocks in urbanised Western Australia. *Australian Entomologist*, 45 (2), 139-148. Available: <a href="https://search.informit.com.au/documentSummary;dn=714753535034353;res=IELHSS;type=pdf">https://search.informit.com.au/documentSummary;dn=714753535034353;res=IELHSS;type=pdf</a>

Australian Entomologist, 2018, 45 (2): 139-148

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#### NESTING BIOLOGY OF *MEGACHILE IGNITA* SMITH, 1853 (HYMENOPTERA: MEGACHILIDAE) IN ARTIFICIAL NESTING BLOCKS IN URBANISED SOUTHWESTERN AUSTRALIA

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#### Abstract

Bees require floral resources in the form of pollen and nectar for food but, in addition, many cavity-nesting species require other plant resources for nesting materials, which might come from plants on which they do not forage for food. This paper records the habitual use of dry flowers and indumentum from tomentose floral bracts of *Banksia* as nesting material by the Australian megachilid bee *Megachile ignita* Smith, which appears to be characteristic of this species. Additional aspects of its nesting biology are discussed, including phenology, number of brood cells per nest, mortality rate, sex ratio, body size and infestation of nests by parasitoid wasps.

#### Introduction

Artificial nesting blocks, known as bee blocks or trap nests in the literature, are recognised as useful for boosting populations of cavity-nesting Hymenoptera, for monitoring these taxa and for engaging the public in native bee conservation (MacIvor 2016, Dainese *et al.* 2017, Krombein 1967, Tscharntke *et al.* 1998). Monitoring them can provide insights into the nesting behaviour of native bees. Here, I describe nesting behaviour of the megachilid bee *Megachile ignita* Smith, 1853 in artificial nesting blocks installed around Perth, an urbanised region in south-west Western Australia.

*Megachile ignita* belongs in the Megachilidae, a large family with numerous subgenera. It was placed in the subgenus *Hackeriapis* Cockerell by Michener (1965) but was left unplaced when King (1994) restricted the concept of that taxon. The presence of a large medial apical spine on S1 suggests that this species should be placed in subgenus *Austrochile* Michener (Michener 2007).

The Megachilidae comprises species that are predominantly above-ground cavity nesters, utilising preformed holes – mainly abandoned tunnels made by wood-boring beetles in trees – but also appropriately-sized cavities in anthropogenic materials (Halcroft and Batley 2014). The materials used to build partitions between cells (if present) and cap the completed nest are diverse and include resin, mud, pebbles, sand, leaves, petals and even plastic particles (Horne 1995, Paini 2004, MacIvor and Moore 2013, Gess and Roosenschoon 2017). Documenting the materials used by bees in nest construction can aid in ensuring suitable nesting materials are available to support bee populations. Although much attention has focused on food provisions, nesting substrates are just as critical to the reproductive success of bees (Potts *et al.* 2005). Here, the nesting biology of *M. ignita* is described, including the use of *Banksia* flowers and indumentum from the tomentose floral bracts (the compressed downy material that covers the central spindle



**9.2.13 Prendergast, K (A).** (2018). Intra and interspecific interactions involving *Mergolossa rubricata* at bee blocks in urbanised south-western Australia. *The Western Australian Naturalist, 31*(2), 82-87.

#### INTRA AND INTERSPECIFIC INTERACTIONS INVOLVING MEROGLOSSA RUBRICATA AT BEE BLOCKS IN URBANISED SOUTH-WESTERN AUSTRALIA

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#### ABSTRACT

Behaviours of the Western Australian endemic bee, *Meroglossa rubricata* Smith 1879 (Colletidae: Hylaeinae) at bee blocks in the urbanised region of southwest Western Australia are documented. Observations of co-habitation between individuals are described, and antagonistic interactions between a female *M. rubricata* with a female megachilid at bee blocks is documented. In addition to increasing knowledge about the natural history and behaviour of *M. rubricata*, this paper indicates the value of artificial nesting blocks, not only for the potential to provide nesting substrate for native bees, but also for providing opportunities to observe nesting behaviours of cavity-nesting bees.

#### INTRODUCTION

Artificial nesting blocks, known in the literature as trap-nests, or among the general public as bee hotels, bee blocks or bee condos are recognised as having utility in boosting populations of cavity-nesting Hymenoptera; for monitoring these taxa; and for engaging the public in native bee activities (MacIvor 2016, Dainese et al., Krombein 1967, Tscharntke et al. 1998). Monitoring them can provide insights into the nesting behaviour of native bees, interactions between native bees, their fitness in relation to various local and landscape variables, and their nesting and developmental biology. Here, I describe behaviour of the cavity-nesting native hylaeine bee *Meroglossa rubricata* (Smith 1879) which were utilising bee blocks installed around Perth, urbanised southwest Western Australia.

Meroglossa rubricata (Smith, 1879) is a strikingly-coloured native bee in the family Colletidae, subfamily Hylaeinae, endemic to the western areas of the Australian continent. Like the majority of hylaeine bees, *Meroglossa rubricata* is a cavity-nesting species



**Figure 2.** Female Meroglossa rubricata head-butting the behind of a native megachilid bee in an adjacent bee tube within a bee block located at Jandakot, WA.

 9.2.14. Prendergast, K. S. & Yeates, D. K. (2018). New records of bee fly (Diptera: Bombyliidae) and mite (Acari: Pyemotidae) parasites of Australian *Megachile* bees (Hymenoptera: Megachilidae) in Western Australia, *Australian Entomologist*, 45(1), 51-56. Available: <u>https://search.informit.com.au/documentSummary;dn=479791767934112;re</u> s=IELHSS

Australian Entomologist, 2018, 45 (1): 51-56

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#### NEW RECORDS OF BEE FLY (DIPTERA: BOMBYLIIDAE) AND MITE (ACARI: PYEMOTIDAE) PARASITES OF AUSTRALIAN *MEGACHILE* BEES (HYMENOPTERA: MEGACHILIDAE) IN WESTERN AUSTRALIA

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#### Abstract

We report three new host-parasite relationships observed during an extensive trap-nest survey of native bees in Perth, Western Australia during 2016-2017. The brood of *Megachile apicata* Smith was parasitised by a native ectoparasitic bee fly, *Anthrax incomptus* Walker and the bee offspring that developed to adulthood from the same nest being host to *Pyemotes* sp. mites. In addition, we also provide the first record of *Megachile (Mitchellapis) fabricator* Smith being host to *Anthrax incomptus*. Given that of the 691 bee tubes occupied, only seven instances of parasitism by bombylids and one case of parasitism by *Pyemotes* involving two bee species occurred, rates of parasitism by both the fly and the mite are low, suggesting that these are not important natural enemies of native bees in the Perth metropolitan area. These new observations highlight the value of utilising bee hotels for documenting not only patterns of bee occupancy and species diversity of cavity-nesting bees, but also for discovering parasites.

#### Introduction

Australia has approximately 1600 described species of native bees (Hymenoptera: Apoidea), with hundreds more awaiting formal scientific description (Dollin 2016). Despite their ecological importance for pollination, there is little published information on the biology and ecology of most species. Here, we contribute to an understanding of the natural history of cavity-nesting native bees and their fly and mite parasites in southwestern Western Australia.

The Bombyliidae (bee flies) contains over 4,500 described species worldwide, with hundreds of described and undescribed species in Australia. With only one exception they are parasitoids, attacking seven different orders of insects with Hymenoptera the most commonly reported (Yeates and Greathead 1997). The majority of bombyliid species are ectoparasitoids, except for two distantly related subfamilies (Toxophorinae and Anthracinae) that are endoparasitoids (Yeates and Greathead 1997). Bombyliids are known to attack bees in the families Megachilidae, Colletidae, Apidae (*Xylocopa* Latreille) and Halictidae (Yeates and Greathead 1997).

There are approximately 250 described *Anthrax* Scopoli species globally (Evenhuis and Greathead 1999); the 14 Australian species were revised by Yeates and Lambkin (1998). *Anthrax* has been reported parasitising various species in the family Megachilidae globally but has a diverse host range, including various wasps, tiger beetles (Coleoptera: Cicindelinae) and even a lepidopteran (Yeates and Greathead 1997). *Anthrax incomptus* Walker is a common and widespread species found throughout Australia except

# 9.2.15 Prendergast, K. (A) & Bateman, B. (2017). Natural History Notes: *Cryptoblepharus buchananii* (Fence Skink). Bee hotels as resources,

Herpetological Review, 48(5), 20-21.

#### NATURAL HISTORY NOTES 845

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BUNOPUS BLANFORDH (Blanford's Rock Gecko). REPRODUCTION. Bunopus blanfordii occurs in Israel and Jordan (Uetz et al. 2017. The Reptile Database. http://www. reptile-database.org, accessed 4 April 2017). The status of B. blanfordii remains unclear and it may be conspecific with Bunopus tuberculatus, However, until further study, B. blanfordii is considered valid (Bauer et. al. 2013. Zootaxa 3599:301–324). Bar and Haimovitch (2011. A Field Guide to Reptiles and Amphibians of Israel. Pazbar Ltd, Herzliya, Israel. 245 pp.) reported multiple clutches of two eggs were laid each year by B. blanfordii (as B. tuberculatus) in Israel. In this note we present additional information on the reproductive cycle of B. blanfordii from Israel based on a histological examination of museum specimens.

The gonads of 16 adults of *B. blanfordii* consisting of nine males (mean SVL = 40.3 mm ± 5.9 SD, range = 28–47 mm) and seven females (mean SVL = 46.6 mm ± 5.9 SD, range = 38–53 mm) from Israel deposited in the Steinhardt Museum of Natural History (TAUM), Tel Aviv University were histologically examined. These were all from the Arava Valley Region: TAUM 573, 1278, 1802, 1803, 1809, 1810, 2189, 2190, 2225, 2233, 3345, 5089, 5090, 10021, 10929, 13002. *Bunopus blanfordii* were collected 1950 to 1985. The lower part of the body cavity was opened and the left testis or ovary was removed. Histological sections were cut at 5  $\mu$ m and stained by Harris hematoxylin followed by eosin counterstain. Histology slides were deposited at TAUM.

Two stages were present in the  $\vec{B}$  blanfordii testis cycle: 1) Spermiogenesis, in which the seminiferous tubules are bordered by sperm or clusters of metamorphosing spermatids; 2) Regressed, germinal epithelium within the seminiferous tubules is reduced to a few layers of spermatogonia and interspersed Sertoli cells. Males in spermiogenesis were by month: March (N = 1), April (N = 5), May (N = 1), July (N = 1). The one October male had a regressed testis. The smallest reproductively active male (TAUM 3345) measured only 28 mm SVL and was collected in April. The rate of sperm production in this small male was not as high as seen in testes of larger males in which the inner border of each seminiferous tubule was lined by sperm or metamorphosing spermatids. Nevertheless, there was at least one cluster of sperm in virtually all seminiferous tubules of TAUM 3345.

Two stages were present in the ovarian cycle of *B. blanfordii*: 1) Quiescent, no yolk deposition was present: April (N = 2), May (N = 1), October (N = 1), November (N = 2); 2) Oviductal eggs, two were present in TAUM 1810 (SVL = 52 mm), collected in April. In view of our small female sample (N = 7) we did not report a minimum size for female reproductive activity.

We thank Shai Meiri (TAUM) for permission to examine *B. blanfordii* and the National Collections of Natural History at Tel Aviv University for providing the *B. blanfordii* to examine. **STEPHEN R. GOLDBERG**, Whittier College, Department of Biology,

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CRYPTOBLEPHARUS BUCHANANH (Fence Skink), BEE 110-TELS AS RESOURCES. Bee or insect hotels, also known as bee condos or, in the scientific literature, "trap nests," are installed as a resource to encourage cavity-nesting hymenopterans to nest. Not only are bee hotels useful for scientific purposes for monitoring species diversity, abundance, and reproductive output of native bees and their natural enemies, but the installation of these hotels can boost bee numbers given that nest sites are often limiting (e.g., Torné-Noguera et al. 2014. PLOS ONF 9: e97255). Adult female bees gather food provisions for the offspring, deposit the provisions in the cavity, and then lay eggs. Typically a number of cells, each containing one food provision with an egg, are laid, the number being dependent on the species and the depth of the tube.

Despite good intentions, many bee hotels are not designed by bee scientists, and the proliferation of bee hotels being sold in various gardening venues have questionable value for supporting their intended occupants. For example, given that most cavity-nesting bees are smaller than honeybees, holes of diameters larger than 10 mm are unlikely to be occupied by bees (Prendergast, unpubl. data). This does not mean, however, that they are useless and will remain barren, as we describe below.

These observations occurred at a commercially manufactured bee hotel located on a tree at about 1 m high in the corner of a vegetable garden near the outdoor eating area of the Kings Park Biodiversity and Conservation Centre in Kings Park Botanic Gardens, Western Australia (31.57210°S, 115.59345°E). *Cryptoblepharus buchananii* (SVL 45 mm) are common

Cryptoblepharus buchananii (SVL 45 mm) are common lizards endemic to Western Australia, with a distribution concentrated in the southwest region. On 26 May 2017 at about midday, two *C. buchananii* were observed, one occupying a large (approx. 2-cm diameter) bamboo tube, the other occupying a crevice between bamboo tubes that were part of a bee hotel. Both had partly emerged, and appeared to be basking, apparently taking advantage of the safety the crevices provided. A second observation occurred on 20 June 2017. One *C. buchananii* was observed basking, with almost half of its body protruding from one of the largest bamboo tubes. When approached, rather than flee, it retreated back into the end of the tube and curled up, suggesting that *C. buchananii* was using the bamboo tube as a refuge. A few hours later, the bee hotel was checked again and a *C. buchananii*, presumably the same one, was still present, but had moved into a crack at the bottom of the hotel between two bamboo tubes. A third observation on 26 June 2017 revealed three *C. buchananii* at the bee hotel (Fig 1.)

The recorded daily temperature extremes at the time of the first observation were 19°C/8°C and 22°C/8°C for the two following observations. Under cooler winter temperatures the



Fig. 1. Cryptoblepharus buchananii using a bee hotel for shelter (left); three C. buchananii using both bamboo tubes and cracks between them at the same bec hotel (right).

Herpetological Review 48(4), 2017

 9.2.16 Prendergast, A. (K). (2017) Establishment of the east Australian Masked Bee Hylaeus nubilosus (Smith) (Hymenoptera: Colletidae: Hylaeinae) in Western Australia. Australian Entomologist, 44(4), 213-218. Available: <u>https://search.informit.com.au/documentSummary;dn=299890430436191;re</u> s=IELHSS;type=pdf

Australian Entomologist, 2017, 44 (4): 213-218

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#### ESTABLISHMENT OF THE EAST AUSTRALIAN MASKED BEE HYLAEUS NUBILOSUS (SMITH) (HYMENOPTERA: COLLETIDAE: HYLAEINAE) IN WESTERN AUSTRALIA

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#### Abstract

*Hylaeus (Hylaeorhiza) nubilosus* (Smith) is a common, widespread, native bee endemic to the eastern States of Australia. It is recorded from several, mostly suburban, sites in the Perth region of southwestern Western Australia and appears to be well established. The species nests in abandoncd mud wasp nests in synathropic situations and might have been transported across Australia by human traffic.

#### Introduction

*Hylaeus (Hylaeorhiza) nubilosus* (Smith, 1853) (Figs 1-4) is a common species of masked bee (subfamily Hylaeinae) endemic to eastern Australia (Halcroft and Batley 2014). This species has a broad range, encompassing Victoria all the way up the east coast to Cairns in northern Queensland, as well as occurring in Tasmania (Atlas of Living Australia 2017, Houston 1981). This paper reports recent records from south-west Western Australia.

*Hylaeus nubilosus* is one of the most common of the hylaeinae bees, most of which nest in pre-made cavities (Almeida 2008, Halcroft and Batley 2014, Houston 2011), such as those created by wood-boring beetles, or in hollow pithy stems and will readily occupy 'bee hotels' made out of wooden blocks with holes drilled in them or bundles of bamboo of appropriate diameter (Halcroft and Batley 2014, Fortel *et al.* 2016). However, *H. nubilosus* prefers to nest in abandoned nests of mud-dauber wasps (Sphecidae) and potter wasps (Vespidae: Eumeninae) (T.F. Houston pers. comm.).

Hylaeus nubilosus, the sole species in subgenus Hylaeorhiza Michener, 1965 (Houston 1981), is a medium-sized (6-9 mm) masked bee with a conspicuous yellow thoracic 'badge' in the middle of the scutellum and metanotum (Fig. 1). Other diagnostic features include the mesosternum with a prominent transverse ridge anterior to each mid coxa, the propodeum almost wholly vertical with a steeply sloping dorsal surface that is smooth and rounding onto the posterior surface and, unlike other genera and subgenera, the lack of outer apical spines on the hind tibia (Houston 1981). The body of both sexes is black, with a yellow spot in front of the wings on the mesosoma (Figs 2-4). Like many Hylaeinae, the sexes are dimorphic, the female having cream markings on the lateral margins of the paraocular area as well as a medial cream stripe on the clypeus (Fig. 2), whereas in the male the cream facial markings encompass the entire paraocular area and clypeus. Males also have some yellow on the scape of the antennae. As with all hylaeines, females lack scopae and, rather than having specialised pollen-carrying hairs, ingest pollen and carry it in the crop - a derived condition (Plant and Paulus 2016).

**9.2.17** Prendergast, K. (A). (2017). The first nesting observations of a potter wasp *Rhynchium superbum* (Vespidae, Eumenidae) – a recent eastern invader inhabiting the suburbs of Perth Western Australia, *The Western Australian Naturalist*, *31*(1), 1-6.

# THE WESTERN AUSTRALIAN NATURALIST

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#### THE FIRST NESTING OBSERVATIONS OF A POTTER WASP RHYNCHIUM SUPERBUM (VESPIDAE, EUMENIDAE) – A RECENT EASTERN INVADER INHABITING THE SUBURBS OF PERTH WESTERN AUSTRALIA

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Rhynchium superbum Saussure, 1852 is an attractive potter wasp (family Vespidae, subfamily Eumenidae) native to the eastern states of Australia (Photo 1, Photo 3). In recent years observations of this wasp have been reported Western from Australia (Houston, 2016). The first record of a specimen to the WA Museum was from a suburban garden in the south-eastern suburb of Kelmscott, in 2010. Reports, accompanied by photos, followed, from Waikiki (south of Rockingham) in 2014, and from Swan View (on the Darling Escarpment) in 2015 (Houston, 2016). The next observation was reported by me, where in 2016 I photographed an individual resting on the wall above a door in the suburb of Wembley at

around 10pm. Although Perth has a number of native potter wasps, none are in the genus Rhynchium, nor are any so large, or, it can be argued, so "superb" (hence the species epithet). Following this observation of a large, beautiful wasp, I reported it to Dr Terry Houston, expert in hymenopteran taxonomy and ex-curator of entomology at the WA Museum. Terry was very interested, and informed me I'd found a Rhynchium superbum. He kindly provided me with 10 pine batons with approx. 10mm diameter holes drilled in them to place around the garden of the Wembley property to encourage a female R. superbum to nest in them, and thus obtain specimens. In particular, the WA Museum male lacked a specimen.

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# **9.4. Appendix 4:** A global review of determinants of native bee assemblages in urbanised landscapes Supplementary Material

Supporting Information 1: References for citations in Fig. 6 Impacts that the proliferation of non-native/exotic flora such as ornamentals and weeds in urban areas have on native bee assemblages

1 (Lowenstein et al. 2014), 2 (Rogers et al. 2014), 3 (Gonzalez et al. 2017), 4 (Carvalheiro et al. 2011), 5 (Requier et al. 2015), 6 (Traveset and Richardson 2014), 7 (Larson et al. 2014), 8 (Grimm et al. 2008), 9 (Loram et al. 2007), 10 (Loram et al. 2007), 11 (McKinney 2008), 12 (Smith et al. 2006), 13 (Carper et al. 2014), 14 (Baldock et al. 2015), 15 (Hall et al. 2017), 16 (Tepedino et al. 2008), 17 (MacIvor et al. 2014), 18 (Carvell et al. 2004), 19 (Levy 2011), 20 (Matteson and Langellotto 2011), 21 (Comba et al. 1999), 22 (Garbuzov and Ratnieks 2014), 23 (Tommasi et al. 2004), 24 (MacIvor et al. 2014), 25 (Geslin et al. 2017), 26 (Hanley and Goulson 2003), 27 (Krend and Murphy 2003), 28 (Lopezaraiza–Mikel et al. 2007), 29 (Robbins et al. 2001), 30 (Williams et al. 2011), 31 (Abe et al. 2011), 32 (MacIvor et al. 2015), 33 (Stouffer et al. 2014), 34 (Cariveau and Winfree 2015), 35 (Vanbergen 2013), 36 (Lazaro and Totland 2010), 37 (Montero-Castaño and Vilà 2017), 38 (Petanidou et al. 2008), 39 (Vilà et al. 2009), 40 (Cane et al. 2005), 41 (da Silva Mouga et al. 2015), 42 (Frankie et al. 2005), 43 (Frankie et al. 2009), 44 (Harrison and Winfree 2015), 45 (Matteson et al. 2008), 46 (Nielsen et al. 2008), 47 (Stout and Morales 2009), 48 (Hanley and Goulson 2003), 49 (Aleixo et al. 2014), 50 (McFrederick and LeBuhn 2006), 51 (Frankie et al. 2013), 52 (Everaars et al. 2011), 53 (Fetridge et al. 2008), 54 (Schweiger et al. 2010), 55 (Leong 2016), 56 (Stelzer et al. 2010), 57 (Loreau et al. 2001), 58 (Inchausti and Halley 2003), 59 (Hinners et al. 2012); 60 (Eickwort and Ginsberg 1980), 61 (Müller et al. 2006), 62 (Vanderplanck et al. 2016), 63 (Aronne et al. 2012), 64 (Harmon-Threatt and Kremen 2015), 65 (Bretagnolle and Gaba 2015), 66 (Rathcke 1993), 67 (Ballantyne et al. 2015), 68 (Vázquez and Aizen 2006), 69 (Bowers 1985), 70 (Kowarik 2011), 71 (Sax and Gaines 2003), 72 (Hahs et al. 2009), 73 (McKinney 2006), 74 (Moroń et al. 2009), 75 (Pawelek et al. 2009), 76 (Hopwood 2008), 77 (Pardee and Philpott 2014), 78

(Garbuzov et al. 2015), 79 (Corbet et al. 2001), 80 (Naug 2009), 81 (Deguines et al. 2016), 82 (Knapp et al. 2008), 83 (Knop 2016), 84 (Bosch et al. 1997), 85 (Waser et al. 1996), 86 (Herrera 1988), 87 (Hoeksema and Bruna 2000), 88 (Petanidou et al. 2008), 89 (Hanula and Horn 2011), 90 (Hanula et al. 2015)

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# Supporting Information 2: References for Fig. 7 Aspects of the urban environment that can be beneficial for bees

1 (Holzschuh et al., 2007), 2 (Kaluza et al., 2016), 3 (Mallinger et al., 2016), 4 (Fründ et al., 2010); 5 (Ebeling et al., 2011); 6 (Iwasaki et al., 2018), 7 (Burkle and Irwin, 2009), 8 (Banaszak-Cibicka et al., 2019), 9 (Vaudo et al., 2015), 10 (Gotlieb et al., 2011), 11 (Petanidou et al., 1999), 12 (Wuellner, 1999), 13 (Carper et al., 2014), 14 (Rubene et al., 2015), 15 (Silva and Ramalho, 2016), 16 (Zhao et al., 2016), 17 (Banaszak-Cibicka, 2014), 18 (Shochat et al., 2006), 19 (Klein et al., 2017), 20 (Glatz et al., 2015), 21 (Leong et al., 2016), 22 (Faeth et al., 2011)

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# **Supporting Information 3:**

**Table 1.** Long-term (> 5 year) studies in changes in bee communities under urbanisation (Archer 2013; Frankie *et al.* 2009; Martins *et al.* 2013; Vieira *et al.*2016)

Study	Region	Habitat type	Duration	Species Richness	Species Abundances	Species composition	Other observations
Archer (2013) The solitary wasps and bees (Hymenoptera: Aculeata) of a suburban garden in Leicester, England, over 27 years	England, UK	Suburban garden	27 years	Stable then increased since 1992	Variable – no clear trend, but some suggestion of a slight decrease. Of thirteen species whose abundances exceeded 100 individuals, 4 exhibited a decreasing trend, 2 an increasing trend, and 7 no trend.		
Frankie et al. (2009) Decline in bee diversity and abundance from 1972-2004 on a flowering leguminous tree, <i>Andira inermis</i> in Costa Rica at the interface of disturbed dry forest and the urban environment.	Costa Rica, South America	Andira inermis in and around the city.	32 years	Initially species richness declines from 70 to 28 species between 1972 to 1996, but then slightly increased to 32 species by 2004.	Despite initial large declines from 1972 to 1996, total number of bees did not continue to decline with increasing human populations, but rather increased from 659 and 631 in 1996 and 1999 to 1057 in 2004.	Patterns of changes in abundance were similar in all major bee taxa save Africanized honeybees (which in 2004 comprised just under 20% of bees)	Declines then partial recovery of bee abundances, attributed to how after the major loss of natural habitat due to agricultural land conversion, in more recent years urban growth has provided areas with a large diversity of ornamental flowering plants, many native. A non-mutually exclusive explanation is that the few remaining <i>Andira</i> trees represent "magnets", drawing in a higher density of bees that remain after much of their natural habitat was lost.
Martins et al. (2013) Changes in wild bee fauna of a grassland in Brazil reveal negative effects associated with growing	Brazil, South America	Grassland	40 years	Decreased by 22%. No taxonomic bias.	Overall declines. A few species had increased in abundance (three halicitds: Augochlora iphigenis, A.	Proportion of species within each functional group (nesting location, sociality, lecty, body size) were maintained, except for a slight increase in oligolectic relative to polylectic species. Large-bodied bees	Even previously abundant species were lost. Although (unquantified) confounding factors of crop cultivation, honeybee competition and climate change were proposed to have been potential

urbanization during the last 40 years.					amphrite, Augochloropsis iris, and Bombus morio).	decreaed in abundance, but increased in richness. <i>Apis mellifera</i> , was by far the most abundant (59% of individuals) but were also more abundant than native bees 40 years ago.	contributions, the authors concluded that urban expansion (5-56% land are) and the paucity of natural preserved areas was the primary cause of declines. There was a 3- fold increase in ruderal native and exotic flora visited.
Vieira et al. (2016) Nesting stingless bees in urban areas: a re-evaluation after eight years.	Brazil, South America	University campus	8 years	Increase from 4spp to 7spp	Increase in total number of colonies by 150% and nest density by 140%. All species found in both surveys were more abundant	Diversity index (H') and Evenness Index (J') both increased. Species nesting in artificial substrates were most abundant however this was no different from the previous survey.	Use of natural substrates decreased, while the use of artificial substrates increased, suggesting that increased provision of man- made structures on the university campus provided favourable sites for establishment of some of the stingless bee species. However, whilst the two most abundant species preferred artificial substrates (94% and 86% of nests), four of the seven species only nested in natural substrates (trees).

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# **9.5. Appendix 5:** *The relative performance of sampling methods for native bees: an empirical test and review of the literature* **Supplementary Material**

Appendix S1: Publications used to review the relative effectiveness of different methods for sampling bees (in "The relative performance of sampling methods for native bees: an empirical test and review of the literature". DOI: 10.1002/ecs2.3076). Available online at: Prendergast, Kit; Menz, Myles H.M.; Bateman, Philip; Dixon, Kingsley (2020): Publications used to review the relative effectiveness of different methods for sampling bees in "The relative performance of sampling methods for native bees: an empirical test and review of the literature". Curtin University. http://dx.doi.org/10.25917/5ee848123cdae

#### **Appendix S2: Generalised Linear Mixed Effect Models**

**Table S1.** Results of ANOVAs comparing lmer models of the effect of all collection sampling method (targeted sweep netting, blue vanes, yellow vanes, large yellow pan traps, and UV-reflective blue and yellow pan traps) on native bee abundance (ln+1 transformed), and an interaction between method and habitat (bushland remnants vs. residential garden). Site was a random factor.  $\Delta$ AIC is the difference between the model with and without the predictor or interaction of interest. Significant results (p<0.05) are in bold.

Model	AIC	ΔΑΙC	Х <sup>2</sup>	df	р
Method	639.3	342.72	352.9	5	<0.0001
Habitat	969.5	6.53	8.35	1	0.003
Method*Habitat	600.20	26.58	36.38	5	<0.0001

**Table S2.** Results of pairwise comparisons using Tukey's post hoc tests between all collection

 methods in abundance of native bees collected. Native bee abundance was ln+1 transformed.

	Targeted	Blue	Yellow	Blue	Yellow	Large
	sweep	vane	vane	pan	pan	yellow
	netting			trap	trap	pan
						trap
Targeted sweep netting						
Blue vane	<0.0001					
Yellow vane	<0.0001	<0.0001				
Blue pan trap	<0.0001	<0.0001	0.80			
Yellow pan trap	<0.0001	<0.0001	0.91	1.00		
Large yellow pan trap	<0.0001	<0.0001	0.69	1.00	0.99	

**Table S3.** Results of ANOVAs comparing glmer models (poisson error distribution) of the effect of all collection sampling method (targeted sweep netting, blue vanes, yellow vanes, large yellow pan traps, and UV-reflective blue and yellow pan traps) on the number of taxonomic units captured, and an interaction between method and habitat (bushland remnants vs. residential garden). Site was a random factor.  $\Delta$ AIC is the difference between the model with and without the predictor or interaction of interest. Significant results (p<0.05) are in bold.

Model	AIC	ΔΑΙϹ	<b>X</b> <sup>2</sup>	df	р
Method	855.4	1391.6	1401.6	5	<0.0001
Method*Habitat	851.06	4.66	5.34	5	0.376

**Table S4.** Results of pairwise comparisons using Tukey's post hoc tests between all collectionmethods in number of taxonomic units of native bees collected.

	Targeted	Blue	Yellow	Blue	Yellow	Large
	sweep	vane	vane	pan	pan	yellow
	netting			trap	trap	pan
						trap
Targeted sweep netting						
Blue vane	<0.0001					
Yellow vane	<0.0001	<0.0001				
Blue pan trap	<0.0001	<0.0001	1.00			
Yellow pan trap	<0.0001	<0.0001	0.99	0.99		
Large yellow pan trap	<0.0001	<0.0001	0.80	0.80	0.45	

**Table S5.** Results of ANOVAs comparing lmer models of the effect of all collection sampling method (targeted sweep netting, blue vanes, yellow vanes, large yellow pan traps, and UV-reflective blue and yellow pan traps) and sex on native bee abundance ( $log_{10}+1$  transformed) with a model of an interaction between method and sex. Site was a random factor. Significant results (p<0.05) are in bold.

Model	AIC	ΔΑΙϹ	Х <sup>2</sup>	df	р
Method	1072.8	59.5	609.5	5	<0.0001
Sex	1072.8	32.7	34.7	1	<0.0001
Method*Sex	1058.0	7.1	24.7	5	0.0002
**Table S6.** Results of ANOVAs between a null model and a binomial glmer models with the response variable of interest to determine whether the proportion of native bees observed vs. netted differed by habitat (bushland remnant vs. residential garden) or by taxon (*Amegilla, Coelioxys, Colletinae, Exoneura,* Euryglossinae, *Homalictus, Lasioglossum, Lipotriches, Megachilidae, Thyreus*). Site was a random factor.  $\Delta$ AIC is the difference between the model with and without the predictor of interest. Significant results (p<0.05) are in bold.

Model	AIC	ΔΑΙC	Х <sup>2</sup>	df	р
Habitat	1067.1	0.1	2.10	1	0.147
Taxon	917.57	149.64	173.64	12	<0.0001

Table S7. p-values associated with post hoc Tukey's pairwise comparison tests between native bee taxa in the proportion of netted:observed

	Amegilla	Coelioxys	Euryglossinae	Exoneura	Homalictus	Hylaeus	Lasioglossum	Leioproctus	Liopotriches	Megachile	Meroglossa	Thyreus	Trichocolletes
Amegilla													
Coelioxys	1.00												
Euryglossinae	<0.0001	1.00											
Exoneura	0.593	1.00	0.00										
Homalictus	<0.0001	1.00	0.997	0.00									
Hylaeus	<0.0001	1.00	0.836	<0.0001	1.00								
Lasioglossum	<0.0001	1.00	0.934	0.001	1.00	1.00							
Leioproctus	<0.0001	1.00	1.00	<0.0001	0.961	0.598	0.771						
Liopotriches	<0.0001	1.00	0.00	0.005	0.631	0.106	0.574	0.0001					
Megachile	<0.0001	1.00	0.86	<0.0001	0.748	0.012	0.246	1.00	<0.0001				
Meroglossa	<0.0001	1.00	0.234	0.001	0.887	0.783	0.924	0.136	1.00	0.042			
Thyreus	0.054	1.00	0.923	0.274	0.981	0.979	0.986	0.881	1.00	0.850	1.00		
Trichocolletes	0.976	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.996	1.00	0.995	0.976	

**Table S8.** Results of ANOVAs comparing lmer models of the effect of passive sampling methods (blue vanes, yellow vanes, large yellow pan traps, and UV-reflective blue and yellow pan traps) on native bee abundance (ln+0.1 transformed) and honeybee abundance (ln+1 transformed), and an interaction between method and habitat (bushland remnants vs. residential garden). Site was a random factor. ΔAIC is the difference between the model with and without the predictor or interaction of interest. Significant results (p<0.05) are in bold.

	Native bee abundance (In+0.1 transformed)				Honeybee abundance (In+1 transformed)					
	AIC	ΔΑΙΟ	Х <sup>2</sup>	df	р	AIC	ΔΑΙΟ	<i>X</i> <sup>2</sup>	df	р
Method	754.1	113.82		4	<0.0001	486.5	163.53	172.2	4	<0.0001
Method*Habitat	753.7	0.58	7.42	4	0.115	471.8	13.54	21.5	4	0.0002

**Table S9.** Mean numbers of individuals of native bees vs. honeybees caught by methods that were employed to record both (observational, and passive sampling methods), and model results of ANOVAs for observational counts and each passive sampling method to test for significant differences in abundances recorded for native bees vs. honeybees.  $\Delta$ AIC is the difference between the model with bee identity (native vs. honeybee) and a null model (abundance not distinguishing between native bees and honeybees). Significant results (p<0.05) are in bold. Trends towards significance are indicated by \*.

Methods	Native bees Hon		Honeybees		AIC	ΔΑΙϹ	<b>Х</b> <sup>2</sup>	df	р
	mean	se	mean	se					
Observations	94.304	11.007	360.250	97.119	405.0	1.13	3.14	1	0.077 *
Blue vane	8.262	1.451	9.143	2.174	790.63	0.13	1.87	1	0.171
Yellow vane	0.722	0.172	4.357	1.079	320.3	126.6	128.6	1	<0.0001
Blue bowl	0.333	0.116	0.073	0.073	126.8	8.47	10.5	1	0.001
Yellow bowl	0.392	0.116	0.000	0.000	95.0	27.5	29.5	1	<0.0001
Large yellow bowl	0.303	0.119	0.024	0.024	57.6	9.04	11.0	1	0.0009

#### Appendix S3

#### Table S1. Taxonomic units by sampling method

Taxonomic unit code	Species	Targeted aerial netting	Blue vane	Yellow vane	Blue pan trap	Yellow pan trap	Large yellow pan trap	Trap- nest
Amegilla 1 F	Amegilla (Notomegilla) chlorocyanea	17	196	2	1	0	0	У
Amegilla 1 M	Amegilla (Notomegilla) chlorocyanea	9	68	0	0	0	0	
Braunsapis nitida	Braunsapis nitida	0	0	1	0	0	0	
Coelioxys 1 F	Coelioxys (Coelioxys) froggatti	2	0	0	0	0	0	
Euryglossinae 1 F	Euhesma sp.	1	0	0	0	0	0	у
Euryglossinae 10 F	Euryglossina sp.	2	0	0	0	0	0	
Euryglossinae 10 M	Euryglossina sp.	1	0	0	0	0	0	
Euryglossinae 11 F	Euryglossina (Microdontura) mellea	9	0	0	0	0	0	
Euryglossinae 11 M	Euryglossina (Microdontura) mellea	1	0	0	0	0	0	у
Euryglossinae 13 F	Euryglossina (Euryglossina) perpusilla	7	0	0	0	0	0	
Euryglossinae 15 F	Euhesma sp.	14	1	0	0	0	0	
Euryglossinae 15 M	Euhesma sp.	14	0	0	0	0	0	
Euryglossinae 16 F	Xanthesma (Xenohesma) perpulchra	3	1	0	0	0	2	
Euryglossinae 16 M	Xanthesma (Xenohesma) perpulchra	16	0	0	0	0	0	

Euryglossinae 17 F	Euryglossina (Turnerella) argocephala	5	0	0	0	0	0	
Euryglossinae 19 F	Euryglossa jucunda	2	0	0	0	0	0	
Euryglossinae 2 F	Euhesma sp.	28	0	1	0	0	0	
Euryglossinae 2 M	Euhesma sp.	18	0	0	0	0	0	
Euryglossinae 22 F	Euryglossina (Euryglossina) cf. lynettae	39	0	0	0	0	0	
Euryglossinae 3 F	Euhesma (from Kelleberrin loan 12806 Museum collection Euryglossa (Euhesma?))	6	0	0	0	0	0	
Euryglossinae 5 F	Hyphesma atromicans	3	0	0	0	0	0	
Euryglossinae 5 M	Hyphesma atromicans	3	0	0	0	0	0	
Euryglossinae 6 F	Euryglossula fultoni	13	0	0	0	0	0	
Euryglossinae 6 M	Euryglossula fultoni	0	3	0	0	0	0	
Euryglossinae 7 F	Euryglossina (Euryglossina) hypochroma	14	0	0	0	0	0	
Euryglossinae 7 M	Euryglossina (Euryglossina) hypochroma	27	0	0	0	0	0	
Euryglossinae 9 F	Pachyprosopis (Pachyprosopula) purnongensis	1	0	0	0	0	0	у
Euryglossinae 9 M	Pachyprosopis (Pachyprosopula) purnongensis	2	0	0	0	0	0	
Exoneura 1 F	Exoneura (Exoneura) pictifrons	44	0	0	0	0	0	
Exoneura 2 F	Exoneura robusta	2	0	0	0	0	0	
Exoneura 4 F	Exoneura (Exoneura) laeta	1	0	0	0	0	0	
Exoneura 5 F	Exoneura (Brevineura) sp.	1	1	0	0	0	0	у
Homalictus 1 F	Homalictus (Homalictus) urbanus	7	0	2	0	0	0	

Homalictus 2 F	Homalictus (Homalictus) sphecodoides	0	1	0	0	0	0	
Homalictus 3 F	Homalictus (Homalictus) megastigmus?	1	0	0	0	0	0	
Homalictus 4 F	Homalictus (Homalictus) dotatus	47	0	0	0	0	0	
Homalictus 4 M	Homalictus (Homalictus) dotatus	1	0	0	0	0	0	у
Hylaeus (Rhodohylaeus) lateralis F	Hylaeus (Rhodohylaeus) lateralis	1	0	0	0	0	0	
Hylaeus 1 M	Hylaeus sp.	1	0	0	0	0	0	у
Hylaeus 11 F	Hylaeus (Gnathoprosopis) euxanthus	10	0	0	0	0	0	
Hylaeus 11 M	Hylaeus (Gnathoprosopis) euxanthus	4	0	0	0	0	0	
Hylaeus 12 F	Hylaeus (Euprosopis) violaceus	3	0	0	0	0	0	
Hylaeus 12 M	Hylaeus (Euprosopis) violaceus	0	0	0	0	0	0	
Hylaeus 13 M	Hylaeus (Prosopisteron) chlorosomus	1	0	0	0	0	0	
Hylaeus 15 F	Hylaeus (Euprosopoides) ruficeps kalamundae	7	0	0	0	0	0	
Hylaeus 15 M	Hylaeus (Euprosopoides) ruficeps kalamundae	3	0	0	0	0	0	
Hylaeus 16 F	Hylaeus (Gnathoprosopis) amiculus	5	0	0	0	0	0	
Hylaeus 16 M	Hylaeus (Gnathoprosopis) amiculus	1	0	0	0	1	0	
Hylaeus 2 F	Hylaeus (Prosopisteron) sp. Hylaeinae code: A216	3	3	1	0	0	0	
Hylaeus 22 M	Hylaeus (Prosopisteron) perhumilis	1	0	0	0	0	0	

Hylaeus 24 F	Hylaeus (Prosopisteron) "bicurvatus" TFH Hylaeinae code FemaleA: 157	1	0	0	0	0	0
Hylaeus 24 M	Hylaeus (Prosopisteron) "bicurvatus" TFH Hylaeinae code MaleB: 7	4	0	0	0	0	0
Hylaeus 3 F	Hylaeus (Prosopisteron) aralis	22	0	1	0	0	0
Hylaeus 3 M	Hylaeus (Prosopisteron) aralis	32	0	0	0	0	0
Hylaeus 4 F	Hylaeus (Prosperisteron) "curviscapatus" TFH Hylaeinae code: 29	5	0	0	0	0	0
Hylaeus 4 M	Hylaeus (Prosperisteron) "curviscapatus" TFH Hylaeinae code: 39	19	0	0	0	0	0
Hylaeus 5 F	Hylaeus (Macrohylaeus) alcyoneus	1	0	0	0	0	0
Hylaeus 5 M	Hylaeus (Macrohylaeus) alcyoneus	3	0	0	0	0	0
Hylaeus 6 F	Hylaeus (Rhodohylaeus) proximus	2	0	0	0	0	0
Hylaeus 7 F	Hylaeus (Euprosopoides) obtusatus	1	0	0	0	0	0
Hylaeus 7 M	Hylaeus (Euprosopoides) obtusatus	3	0	0	0	0	0
Hylaeus 8 F	Hylaeus (Hylaeorhiza) nubilosus	1	0	0	0	0	0
Hylaeus 9 F	Hylaeus (Rhodohylaeus) rufipes	3	0	0	0	0	0
Hylaeus 9 M	Hylaeus (Rhodohylaeus) rufipes	1	0	0	0	0	0
Lasioglossum (Chilalictus) mirandum F	Lasioglossum (Chilalictus) mirandum	2	0	0	0	0	0
Lasioglossum 1 F	Lasioglossum (Chilalictus) castor	12	14	4	2	9	0

Lasioglossum 11 F	Lasioglossum (Chilalictus) erythrurum-group	4	0	0	0	0	0	
Lasioglossum 12 F	Lasioglossum (Chilalictus) sp.	0	0	1	0	0	0	
Lasioglossum 13 F	Lasioglossum (Chilalictus) sp.	1	0	0	0	0	0	
Lasioglossum 15 F	Lasioglossum (Chilalictus) inflatum	0	1	0	0	0	0	
Lasioglossum 2 F	Lasioglossum (Chilalictus) hemichalceum	19	2	0	1	2	0	
Lasioglossum 2 M	Lasioglossum (Chilalictus) hemichalceum	2	0	0	0	0	0	
Lasioglossum 6 F	Lasioglossum (Chilalictus) bicolor	1	0	0	0	0	0	
Lasioglossum 8 F	Lasioglossum (Chilalictus) lanarium	0	4	0	0	0	0	
Lasioglossum 8 M	Lasioglossum (Chilalictus) lanarium	0	1	0	0	0	0	
Leioproctus 1 F	Leioproctus (Leioproctus) sp.	1	0	0	0	0	0	
Leioproctus 2 F	Leioproctus (Leioproctus) sp.	2	0	0	0	0	0	
Leioproctus 3 F	Leioproctus (Leioproctus) plumosus	3	0	0	0	0	0	
Leioproctus 3 M	Leioproctus (Leioproctus) plumosus	1	0	0	0	0	0	
Leioproctus 5 F	Leioproctus (Euryglossidia) sp. F480 'knob- nosed'	8	0	0	0	0	0	
Leioproctus 7 F	Leioproctus "zephyrus" sp. nov. F188/M173	14	0	0	0	0	0	
Leioproctus 7 M	Leioproctus "zephyrus" sp. nov. F188/M173	34	0	0	0	0	0	
Leioproctus 8 F	Leioproctus (Cladocerapis) ignicolor	1	0	0	0	0	0	
Lipotriches 1 F	Lipotriches (Austronomia) moerens	1	0	0	0	0	0	
Lipotriches 2 F	Lipotriches (Austronomia) flavoviridis	100	7	0	1	0	0	

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Lipotriches 2 M	Lipotriches (Austronomia) flavoviridis	16	0	0	0	0	0
Lipotriches australica F	Lipotriches (Austronomia) australica	2	1	0	0	0	0
Lipotriches australica M	Lipotriches (Austronomia) australica	1	0	0	0	0	0
Megachile 1 F	Megachile (Hackeriapis) speluncarum	41	0	0	0	0	0
Megachile 1 M	Megachile (Hackeriapis) speluncarum	39	0	0	0	0	0
Megachile 10 F	Megachile (Eutricharaea) sequior	7	0	0	0	1	0
Megachile 10 M	Megachile (Eutricharaea) sequior	8	1	0	0	0	0
Megachile 11 M	Megachile (Hackeriapis) tosticauda	5	1	0	0	0	0
Megachile 12 F	Megachile "houstoni" M306/F367	82	7	0	1	0	0
Megachile 12 M	Megachile "houstoni" M306/F367	54	5	0	1	0	1
Megachile 13 F	Megachile (Hackeriapis) apicata	4	1	0	0	0	0
Megachile 13 M	Megachile (Hackeriapis) apicata	5	0	0	0	0	0
Megachile 15 M	Megachile atrella	1	0	0	0	0	0
Megachile 16 F	Megachile (Eutricharaea) captionis	5	0	1	0	0	0
Megachile 16 M	Megachile (Eutricharaea) captionis	4	0	0	0	0	0
Megachile 17 F	Megachile leeuwinenesis	25	0	0	0	0	0
Megachile 17 M	Megachile leeuwinenesis	15	0	0	0	0	0
Megachile 18 F	Megachile preissi	5	1	0	0	0	0

Megachile 19 M	Megachile nigrovittata	5	0	0	0	0	0	У
Megachile 2 F	Megachile (Eutricharaea) chrysopyga	52	0	0	0	0	0	
Megachile 2 M	Megachile (Eutricharaea) chrysopyga	36	2	0	0	0	0	
Megachile 20 M	Megachile sp.	3	0	0	0	0	0	
Megachile 22 F	Megachile ferox	2	0	0	0	0	0	
Megachile 23 F	Megachile (Eutricharaea) obtusa	13	0	0	0	0	1	
Megachile 23 M	Megachile (Eutricharaea) obtusa	13	0	0	0	0	0	
Megachile 24 F	Megachile (Eutricharaea) serricauda	7	2	0	0	1	0	
Megachile 24 M	Megachile (Eutricharaea) serricauda	17	0	0	1	0	0	
Megachile 25 F	Megachile canifrons	3	2	0	0	0	0	У
Megachile 26 F	Megachile fultoni	9	4	0	0	0	0	
Megachile 26 M	Megachile fultoni	11	0	0	0	0	0	
Megachile 27 M	Megachile sp.	1	0	0	0	0	0	
Megachile 28 F	Megachile (Austrochile) sp.	5	0	0	0	0	1	
Megachile 29 M	Megachile sp.	7	0	0	0	0	0	
Megachile 3 F	Megachile aurifrons	11	2	0	0	0	0	
Megachile 3 M	Megachile aurifrons	12	0	0	0	0	0	У
Megachile 31 F	Megachile (Hackeriapis) oblonga	6	1	0	0	0	0	
Megachile 31 M	Megachile (Hackeriapis) oblonga	4	0	0	0	0	0	
Megachile 32 F	Megachile (Mitchellapis) fabricator	3	0	0	0	0	0	У

Megachile 32 M	Megachile (Mitchellapis) fabricator	0	0	0	0	0	0	
Megachile 33 F	Megachile Austrochile Perth Resin-pot Bee	3	0	0	0	0	0	у
Megachile 34 F	Austrothurgus sp. (tribe Lithurgini)	0	0	0	0	0	1	
Megachile 39 M	Megachile (Eutricharaea) sp	1	0	0	0	0	0	
Megachile 4 F	Megachile horatii	8	1	1	0	0	0	
Megachile 4 M	Megachile horatii	5	0	0	0	0	0	
Megachile 41 M	Megachile Hackeriapis s. lato tosticauda-group	1	0	0	0	0	0	
Megachile 5 F	Megachile (Schizomegachile) monstrosa	1	1	0	0	0	0	
Megachile 5 M	Megachile (Schizomegachile) monstrosa	2	0	0	0	0	0	
Megachile 6 F	Megachile ignita	11	0	0	0	0	0	
Megachile 6 M	Megachile ignita	8	0	0	0	0	0	
Megachile 7 F	Megachile erythropyga	6	0	0	0	0	0	у
Megachile 7 M	Megachile erythropyga	0	0	0	0	0	0	У
Megachile 9 M	Megachile (Autrochile) remotula	4	0	0	0	0	0	у
Megachile 9 F	Megachile (Autrochile) remotula	2	0	0	0	1	0	
Megachile simplex F	Megachile (Eutricharaea) simplex	2	0	0	0	0	0	
Megachile simplex M	Megachile (Eutricharaea) simplex	2	0	0	0	0	0	
Meroglossa rubricata	Meroglossa rubricata	18	0	0	0	0	0	

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Meroglossa rubricata M	Meroglossa rubricata	1	0	0	0	0	0
Thyreus 1 F	Thyreus waroonensis	2	11	0	0	0	0
Thyreus 1 M	Thyreus waroonensis	2	1	0	0	0	0
Trichocolletes 1 M	Trichocolletes cf. platyprosopis	1	0	0	0	0	0

#### **Appendix S4**



**Figure S1.** Species accumulation curves of taxonomic units for each of the sampling methods: large yellow pan traps, blue pan traps, yellow pan traps, yellow vane traps, blue vane traps, and targeted nettings. Dashed lines indicate the 95% confidence intervals.

## Appendix S5: Generalised Linear Mixed Effect Models with vane traps standardised to 3 hrs

**Table S1.** Results of ANOVAs comparing Imer models of the effect of all collection sampling method (targeted sweep netting, blue vanes, yellow vanes, large yellow pan traps, and UV-reflective blue and yellow pan traps) on native bee abundance ( $log_{10}+1$  transformed), and an interaction between method and habitat (bushland remnants vs. residential garden). Site was a random factor.  $\Delta$ AIC is the difference between the model with and without the predictor or interaction of interest. Significant results (p<0.05) are in bold.

Model	ΔΑΙϹ	<b>Х</b> <sup>2</sup>	df	р
Method	443.1	430.2	5	<0.0001
Habitat	2.03	4.04	1	0.045
Method*Habitat	47.0	57.0	5	<0.0001

**Table S2.** Results of pairwise comparisons using Tukey's post hoc tests between allcollection methods in abundance of native bees collected. Native bee abundance was ln+1transformed.

	Targeted	Blue	Yellow	Blue	Yellow	Large
	sweep	vane	vane	pan	pan	yellow
	netting			trap	trap	pan
						trap
Targeted sweep netting						
Blue vane	<0.0001					
Yellow vane	<0.0001	0.99				
Blue pan trap	<0.0001	0.95	0.61			
Yellow pan trap	<0.0001	0.85	0.42	1.00		
Large yellow pan trap	<0.0001	1.00	0.86	1.00	0.99	

**Table S3.** Results of ANOVAs comparing glmer models (poisson error distribution) of the effect of all collection sampling method (targeted sweep netting, blue vanes, yellow vanes, large yellow pan traps, and UV-reflective blue and yellow pan traps) on the number of taxonomic units captured, and an interaction between method and habitat (bushland remnants vs. residential garden). Site was a random factor. Data were log<sub>10</sub>+1 transformed to meet model assumptions.  $\Delta$ AIC is the difference between the model with and without the predictor or interaction of interest. Significant results (p<0.05) are in bold.

Model	AIC	ΔΑΙC	X <sup>2</sup>	df	р
Method	-301.87	580.42	590.4	5	<0.001
Method*Habitat	-347.93	35.46	45.46	5	<0.001

**Table S4.** Results of pairwise comparisons using Tukey's post hoc tests between allcollection methods in number of taxonomic units of native bees collected.

	Targeted	Blue	Yellow	Blue	Yellow	Large
	sweep	vane	vane	pan	pan	yellow
	netting			trap	trap	pan
						trap
Targeted sweep netting						
Blue vane	<0.0001					
Yellow vane	<0.0001	1.00				
Blue pan trap	<0.0001	0.68	0.48			
Yellow pan trap	<0.0001	0.32	0.18	0.99		
Large yellow pan trap	<0.0001	0.99	0.94	0.96	0.71	

**Table S5.** Results of ANOVAs comparing Imer models of the effect of all collection sampling method (targeted sweep netting, blue vanes, yellow vanes, large yellow pan traps, and UV-reflective blue and yellow pan traps) and sex on native bee abundance ( $log_{10}+1$  transformed) with a model of an interaction between method and sex. Site was a random factor. Significant results (p<0.05) are in bold.

Model	ΔΑΙC	<i>X</i> <sup>2</sup>	df	р
Method	902.57	922.57	10	<0.0001
Sex	51.54	63.40	6	<0.0001
Method*Sex	32.88	42.89	5	<0.0001

**Table S6.** Results of ANOVAs comparing lmer models of the effect of passive sampling methods (blue vanes, yellow vanes, large yellow pan traps, and UV-reflective blue and yellow pan traps) on native bee abundance (ln+0.1 transformed) and honeybee abundance (ln+1 transformed), and an interaction between method and habitat (bushland remnants vs. residential garden). Site was a random factor.  $\Delta$ AIC is the difference between the model with and without the predictor or interaction of interest. Significant results (p<0.05) are in bold.

	Native l	pee abund	ln+0.1	Honeybee abundance (In+1					
	transfo	rmed)		transformed)					
	ΔAIC	<i>X</i> <sup>2</sup>	df	р	ΔΑΙϹ	Х <sup>2</sup>	df	р	
Method	2.30	10.30	4	0.036	584.3	592.3	4	<0.0001	
Method*Habitat	4.98	3.02	4	0.554	536.3	544.3	4	<0.0001	

**Table S7.** Mean numbers of individuals of native bees vs. honeybees caught by methods that were employed to record both (observational, and passive sampling methods), and model results of ANOVAs for observational counts and each passive sampling method to test for significant differences in abundances recorded for native bees vs. honeybees for the blue and yellow vane traps standardised to 3 hrs per month (n/90).  $\Delta$ AIC is the difference between the model with bee identity (native vs. honeybee) and a null model (abundance not distinguishing between native bees and honeybees). Significant results (p<0.05) are in bold. Trends towards significance are indicated by \*.

Methods	AIC	$\Delta AIC \qquad X^2$		df	р
Dive vere	200.25	1.00	0.07	1	0.745
Blue vane	-290.25 - <b>377 14</b>	1.93 12 78	0.07 14 78	1	0.745 <b>0.0001</b>
	-377.14	12.70	14.70	-	0.0001

# **9.6. Appendix 6:** *Residential gardens are a poor alternative to urban native vegetation remnants in supporting native bee communities* **Supplementary Material**

Site	Latitude	Longitude	Habitat type	Area (ha)
Bibra Lake	-32.090789°	115.811681°	Residential garden	1.99
Bold Park	-31.956153°	115.771194°	Bushland remnant	437.00
Gosnells	-32.075489°	116.004589°	Residential garden	0.10
Jandakot	-32.098131°	115.861100°	Residential garden	1.49
Kings Park	-31.962312°	115.831514°	Bushland remnant	406.00
Maniana Reserve	-32.001501°	115.956265°	Bushland remnant	7.00
Nedlands	-31.987193°	115.803525°	Residential garden	0.16
Osborne Park	-31.895031°	115.821761°	Residential garden	0.10
Piney Lakes Reserve	-32.048236°	115.837416°	Bushland remnant	50.00
Shenton Park Bushland	-31.948018	115.79479°	Bushland remnant	51.31
Star Swamp	-31.857472°	115.760179°	Bushland remnant	136.02
Wembley	-31.940000°	115.822780°	Residential garden	0.10
Wilson	-32.021461°	115.924081°	Residential garden	0.08
Wireless Hill Park	-32.031054°	115.826448°	Bushland remnant	40.00

 Table A1. Details of sites surveyed.

	Area	Built	Dist.Bush	FloralN	FloralR	NatFIN	NatFIR	PrNnatFl	PrRnatFl	Bare.gr	Woody.pl
Area	1	-0.70	0.27	0.02	-0.68	0.39	0.20	0.65	0.80	0.39	0.81
Built	-0.70	1	0.05	0.03	0.57	-0.29	-0.03	-0.60	-0.65	-0.37	-0.59
Dist.Bush	0.27	0.05	1	0.14	-0.10	0.10	0.04	0.02	0.12	-0.16	0.04
FloralN	0.02	0.03	0.14	1	0.20	0.74	0.30	0	-0.02	0.01	0.09
FloralR	-0.68	0.57	-0.10	0.20	1	-0.23	0.35	-0.73	-0.80	-0.31	-0.61
NatFIN	0.39	-0.29	0.10	0.74	-0.23	1	0.34	0.56	0.43	0.19	0.43
NatFIR	0.20	-0.03	0.04	0.30	0.35	0.34	1	0.06	0.17	-0.06	0.18
PrNnatFl	0.65	-0.60	0.02	0	-0.73	0.56	0.06	1	0.87	0.37	0.64
PrRnatFl	0.80	-0.65	0.12	-0.02	-0.80	0.43	0.17	0.87	1	0.36	0.71
Bare.gr	0.39	-0.37	-0.16	0.01	-0.31	0.19	-0.06	0.37	0.36	1	0.39
Woody.pl	0.81	-0.59	0.04	0.09	-0.61	0.43	0.18	0.64	0.71	0.39	1

**Table A2.** Pairwise Spearman's rank correlations between explanatory variables. Correlations > 0.07 are indicated in bold.

**Table A3.** Summary of bee taxa collected in the first sampling year (November 2016 - February 2017). Full details of number of bees recorded at each site during each survey are available in the supplementary data (Prendergast K (2020) Species of native bees in the urbanised region of the southwest Western Australian biodiversity hotspot. Curtin University. doi:10.25917/5ee09df795b7c).

Family	Species	Abundance	Subfamily	Species		Abundance	Genus	Species	Abundance
Apidae		7 352	Apinae		2	302	Amegilla	1	286
							Thyreus	1	16
			Xylocopinae		5	50	Braunsapis	1	1
							Exoneura	4	49
Colletidae		37 407	Hylaeinae		17	125	Hylaeus	18	144
							Meroglossa	1	19
			Euryglossinae		13	217	Euhesma	4	83
							Euryglossa	1	2
							Euryglossina	2	105
							Euryglossula	2	16
							Hyphesma	1	6
							Pachyprosopis	1	3
							Xanthesma	1	22
			Colletinae		7	65	Leioproctus	6	64
							Trichocolletes	1	1

Halictidae	16	318	Halictinae	16	318	Homalictus	4	168
						Lasioglossum	9	26
						Lipotriches	3	124
Megachilidae	35	607	Megachilinae	35	607	Coelioxys	1	2
						Rozenapis	1	19
						Megachile	34	601

**Table A4**. Summary of bee taxa collected in the second sampling year (October 2017 - March 2018). Full details of number of bees recorded at each siteduring each survey are available in the supplementary data (Prendergast K (2020) Species of native bees in the urbanised region of the southwest WesternAustralian biodiversity hotspot. Curtin University. doi:10.25917/5ee09df795b7c).

Family	Species	Abundance	Subfamily	Species		Abundance	Genus	Species	Abundance
Apidae	7	844	Apinae		3	772	Amegilla	2	759
							Thyreus	1	13
			Xylocopinae		4	72	Exoneura	4	72
Colletidae	73	1348	Hylaeinae		26	607	Hylaeus	23	573
							Meroglossa	1	34
			Euryglossinae		32	567	Callohesma	1	11
							Dasyhesma	1	9
							Euhesma	6	78
							Euryglossa	2	2
							Euryglossina	14	320
							Euryglossula	3	76
							Hyphesma	2	9
							Pachyprosopis	2	26
							Xanthesma	1	36

			Colletinae	14	174	Callomelitta	1	1
						Leioproctus	10	146
						Trichocolletes	3	27
Halictidae	16	858	Halictinae	15	858	Homalictus	2	160
						Lasioglossum	10	257
						Lipotriches	3	441
Megachilidae	43	1179	Megachilinae	43	1179	Coelioxys	1	4
						Rozenapis	1	126
						Megachile	41	1149

**Table A5**. Results of generalised linear mixed effects models (negative binomial) for the influence of environmental variables on honeybee. Significant factors (p < 0.05) based on likelihood ratio tests ( $X^2$ ) are presented in bold.

Response variable	Explanatory variable	df	Х <sup>2</sup>	р
Honeybee abundance	Intercept			
	Proportion of built space	1	0.919	0.338
	Distance to bushland (km)	1	0.518	0.472
	Number of native flowers	1	0.133	0.716
	Richness of native plants	1	0.031	0.860
	Proportion of native flowers	1	1.561	0.212
	Proportion of native plants	1	1.559	0.212
	Proportion of bare ground	1	2.682	0.102
	Year	1	0.219	0.640

### 9.7. Appendix 7: Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens Supplementary Material

#### **Online Resource 1 Table S1 Taxonomic categories**

Taxonomic	Includes	Traits
category		
Honeybee	European honeybee, Apis	Introduced species
(Apidae)	mellifera	Eusocial
		Polylectic
		Large body-size
		Feral and managed
		colonies
Amegilla	Amegilla (mainly A.	Solitary
(Apidae)	chlorocyanea)	Polylectic
		Large body-size
		Ground nesting
Exoneura	Exoneura (mainly E. pictifrons)	Semi-social
(Apidae)	and Braunsapis	Polylectic
		Small body-size
		Pithy-stem nesting
Euryglossinae	Callohesma	Solitary
(Colletidae)	Euhesma	Mostly oligolectic
	Euryglossa	Small body-size
	Euryglossina	Ground and pre-made
	Euryglossula	cavity nesting
	Hyphesma	
	Pachyprosopis	
	Xanthesma	

#### Table S1. Bee taxonomic categories and ecological traits

Hylaeinae	Hylaeus, Meroglossa rubricata	Solitary
(Colletidae)		Mostly oligolectic
		Small to medium body-
		size
		Mostly pre-made cavity-
		nesting
Homalictus	Homalictus (mainly H. dotatus)	Communal
(Halictidae)		Mostly polylectic
		Small body-size
		Ground nesting
Lasioglossum	Lasioglossum	Communal
(Halictidae)		Mostly polylectic
		Small to medium body-
		size
		Ground nesting
Lipotriches	Lipotriches (mainly L.	Solitary
(Halictidae)	flavoviridis)	Polylectic
		Medium body-size
		Ground nesting
Leioproctus	Leioproctus	Solitary
(Colletidae)		Mostly polylectic
		Medium to large body-
		size
		Ground nesting
Trichocolletes	Trichocolletes	Solitary
(Colletidae)		Mostly oligolectic
		Large body-size
		Ground nesting
Megachile	Megachile (and Rozenapis	Solitary
(Megachilidae)	ignita, recently reclassified)	Oligolectic and
		polylectic
		Small to large body-size

		Mostly pre-made cavity
		nesting
Thyreus	Thyreus waroonensis	Solitary
(Apidae)		Kleptoparasitic (host:
		Amegilla)
		Large body-size
Coelioxys	Coelioxys froggatti	Solitary
(Megachilidae)		Kleptoparasitic (host:
		Megachile)
		Large body-size

#### **Online Resource 2 Definitions of network and species-level indices**

#### **Network-level:**

- H<sub>2</sub>' is a specialisation index calculated for a pollination network, independent of network size, and ranges from 0 (highly generalised) to 1 (highly specialised), where a highly specialised network corresponds to containing many species with high species-level specialisation indices (i.e. d'). It is calculated on weighted interactions that measure how much a species discriminates in choice of interaction partners compared with the total number of interaction partners in the network (Blüthgen et al. 2006). This index describes the level of "complementarity specialisation", or "selectiveness" of an entire bipartite network (Dormann et al. 2008). Higher generalisation is often considered to indicate higher functional redundancy and thus a more resilient pollination network (Kaiser-Bunbury et al. 2017) (but see (Hoiss et al. 2015) for a study finding that higher generalisation was associated with less stable networks).
- Nestedness refers to the architecture of a network where specialists interact with a subset of species that also interact with generalists. A number of metrics measuring nestedness exist. NODF (nestedness based on overlap and decreasing fill) was selected as this appears to be the most common metric used in the recent literature, therefore enabling comparisons between our results and the literature, and NODF has a number of benefits over other nestedness metrics, including being less prone to type 1 statistical errors (Almeida-Neto et al. 2008), corrects for matrix dimensionality (Almeida-Neto et al. 2008), and is less sensitive to sample size (Rivera-Hutinel et al. 2012).

NODF ranges from 0 to 100, with increasing values representing an increase in nestedness.

Connectance is the realised proportion of possible links, with weighted connectance being linkage density divided by number of species in the network (Dormann et al. 2008). Connectance is also proposed to contribute to stability (Thébault and Fontaine 2010) (but see (Heleno et al. 2012)). Weighted connectance was used due to how connectance is largely a function of network size (Dormann et al. 2009).

- Extinction slopes are hyperbolic fits for each level (pollinator and plant) to a simulated sequence of extinctions which cause secondary extinctions in the other trophic level (Dormann et al. 2008).
- Robustness is related to extinction slopes and calculates the area below the extinction curve as a measure of the robustness of the system to the loss (removal) of species: R = 1 indicates a robust network whereby the extinction curve only decreases mildly until almost all species of a given level are lost, whereas in contrast as R approaches 0, this indicates a fragile system, with the area under the extinction curve declining sharply as soon as any species is lost (Dormann et al. 2008). Robustness calculated for the "higher-level" therefore provides an indication of whether, if many plant species are lost, most of the pollinators will still survive (high R), or if many secondary extinctions of pollinators will occur if even a small fraction of the plants in the network are eliminated (low R).
- Functional complementarity is a measure of community-level niche complementarity, where "functional" refers to the function of sharing interactions (Devoto et al. 2012; Dormann et al. 2008)
- Niche overlap calculated in bipartite is based on Horn's index and is an index of the mean similarity in interaction patterns between species of the same level (Dormann et al. 2008).

#### **Species-level:**

- Normalised degree is the sum of the links per species, scaled by the number of possible partners. Computed as degree/number of species in the network (Dormann 2011).
- Species strength is the sum of the dependencies for each plants species for a given visitor species. It involves calculating the observed number of interactions by the total number of interactions for each plant, and then the proportion of visits a plant receives from the pollinator are summed across all plants, to give the strength of the pollinator to all plants in the network. A specie's strength is a network property, co-determined by the specialisation of other pollinators in the network (Dormann 2011).
- Interaction push-pull is a metric measuring dependence asymmetry, ranging from -1 to +1. Positive values indicates plants have a higher dependence on

the pollinator (such pollinator species would be described as "pushers"); negative values indicates that a pollinator is on average, more dependent upon the plants (such species are "being pulled"). Values are correlated with species strengths, but are standardised to fall between -1 and +1, and quantifies to net balance rather than the average effect.

- Species specificity is the coefficient of variation of interactions, normalised to take on the values between 0 and 1, where 0 indicates low variability, and 1 indicates high variability, in turn suggesting low and high specificity. However, the drawback of this value is that it does not correct for the number of observations, so species with low numbers will be assigned a higher specificity.
- PSI (pollination service index) is an index measuring the importance of a flower-visitor for all plant species, attempting to quantify the pollination services of a flower-visitor to all plants in the network. For a given plant, a flower-visitor will have a high pollination service to the plant if the flowervisitor is a) common and b) a specialist on this plant. PSI uses three steps in the calculation: For a given flower-visitor 1) the proportion of visits to each plant species; 2) the proportion of visits to the plant that are by that flowervisitor; 3) these are then multiplied, which gives an estimate of the proportion of conspecific pollen delivered to each plant species (which depends on the flower-visitor's specialisation (1) and the plant's specificity in flower-visitors that visit it (2)). PSI ranges from a maximum of 1, which indicates all pollen is delivered to only one plant species that is completely dependent on a flower-visitor that visits only that plant species, to 0, which indicates a pollinator is irrelevant to all plant species. In formula, PSI can be expressed as: 'dependence'\_i\_on\_j \* per.visit.efficiency\_i\_visitedby\_j, where per.visit.efficiency i visited by i = (average proportion visits to i by i in allvisits by j)^beta. The default value for beta is 1, which controls for "pollen purity." This index considers how if a flower-visitor visits many different plant species, it delivers diluted pollen to the target species (Dormann 2011) (as assumption that may not hold true for species that show floral constancy, even if they are polylectic). PSI recognises that even if a pollinator is highly specialised on a plant, if the pollinator is rare, it will still only rarely pollinate

a flower, and also considers that a pollinator which is a generalist may deliver a large proportion of non-target pollen.

d (Bluthgen's d') is a measure of specialisation of a species in terms of its discrimination from a random sampling of plant partners, ranging from 0 (no specialisation, or perfect opportunist) to 1 (perfect, or disproportionate, specialist). d' takes into account the relative abundance of partners: for example, if a pollinator only occurs on one plant species, but this plant species is highly abundant and dominant in a community, the pollinator cannot be considered specialised, and d' will be low. In contrast, if a pollinator interacts with a greater number (say three) plant species, but these plant species are the rarest in the community, the pollinator's d' value will be high. It should be noted that d' is sensitive to rare species (Dormann 2011).

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#### Online Resource 3

Table S1. Network sizes. Network size was calculated as animals + plants (following Albrecht et al. 2010; Chacoff et al. 2012; Santamaría and Rodríguez-Gironés 2007).

Year	Month	Site	Habitat	Bee taxa R	Plant species R	Network size	No. of interactions
one	Nov	Bold Park	Bushland	3	5	8	125
one	Nov	Piney Lakes	Bushland	7	4	11	41
one	Nov	Wireless Hill	Bushland	4	2	6	160
one	Nov	Star Swamp	Bushland	5	5	10	145
one	Nov	Kings Park	Bushland	5	2	7	141
one	Nov	Maniana	Bushland	6	3	9	173
one	Nov	Shenton Park	Bushland	5	6	11	770
one	Dec	Bold Park	Bushland	2	3	5	182
one	Dec	Piney Lakes	Bushland	7	4	11	418
one	Dec	Wireless Hill	Bushland	5	5	10	550
one	Dec	Star Swamp	Bushland	6	5	11	23
one	Dec	Kings Park	Bushland	4	3	7	1223
one	Dec	Maniana	Bushland	2	4	6	158
one	Dec	Shenton Park	Bushland	4	5	9	192
one	Jan	Bold Park	Bushland	2	3	5	305
one	Jan	Piney Lakes	Bushland	2	3	5	129
one	Jan	Wireless Hill	Bushland	3	3	6	58
one	Jan	Star Swamp	Bushland	5	3	8	138
one	Jan	Kings Park	Bushland	2	2	4	137
one	Jan	Maniana	Bushland	5	3	8	95
one	Jan	Shenton Park	Bushland	6	4	10	218
one	Feb	Bold Park	Bushland	6	4	10	113

one	Feb	Piney Lakes	Bushland	5	3	8	10
one	Feb	Wireless Hill	Bushland	7	3	10	318
one	Feb	Star Swamp	Bushland	5	6	11	10
one	Feb	Kings Park	Bushland	8	3	11	108
one	Feb	Maniana	Bushland	4	6	10	161
one	Feb	Shenton Park	Bushland	4	3	7	71
two	Oct	Star Swamp	Bushland	6	6	12	304
two	Oct	Wireless Hill	Bushland	5	5	10	196
two	Oct	Shenton Park	Bushland	6	8	14	163
two	Oct	Kings Park	Bushland	5	8	13	171
two	Oct	Maniana	Bushland	5	12	17	115
two	Oct	Bold Park	Bushland	5	15	20	269
two	Oct	Piney Lakes	Bushland	7	7	14	3271
two	Nov	Maniana	Bushland	6	10	16	59
two	Nov	Shenton Park	Bushland	7	8	15	14
two	Nov	Kings Park	Bushland	7	10	17	271
two	Nov	Bold Park	Bushland	3	11	14	1144
two	Nov	Wireless Hill	Bushland	6	9	15	123
two	Nov	Star Swamp	Bushland	6	9	15	62
two	Nov	Piney Lakes	Bushland	10	7	17	186
two	Dec	Maniana	Bushland	6	9	15	1375
two	Dec	Shenton Park	Bushland	8	3	11	383
two	Dec	Wireless Hill	Bushland	8	6	14	197
two	Dec	Kings Park	Bushland	3	3	6	194
two	Dec	Piney Lakes	Bushland	4	3	7	1005
two	Dec	Star Swamp	Bushland	4	4	8	231
two	Dec	Bold Park	Bushland	3	5	8	143
two	Jan	Maniana	Bushland	7	6	13	408

two	Jan	Kings Park	Bushland	4	3	7	151
two	Jan	Star Swamp	Bushland	2	4	6	662
two	Jan	Wireless Hill	Bushland	8	6	14	361
two	Jan	Piney Lakes	Bushland	7	3	10	254
two	Jan	Shenton Park	Bushland	3	3	6	523
two	Jan	Bold Park	Bushland	3	7	10	621
two	Feb	Maniana	Bushland	4	6	10	234
two	Feb	Piney Lakes	Bushland	8	6	14	380
two	Feb	Wireless Hill	Bushland	7	7	14	615
two	Feb	Kings Park	Bushland	4	7	11	255
two	Feb	Star Swamp	Bushland	2	3	5	2184
two	Feb	Bold Park	Bushland	6	6	12	79
two	Feb	Shenton Park	Bushland	8	11	19	385
two	March	Maniana	Bushland	4	3	7	378
two	March	Kings Park	Bushland	5	4	9	662
two	March	Piney Lakes	Bushland	6	3	9	97
two	March	Star Swamp	Bushland	1	2	3	368
two	March	Wireless Hill	Bushland	7	4	11	1154
two	March	Shenton Park	Bushland	6	8	14	318
two	March	Bold Park	Bushland	5	7	12	467
one	Nov	Gosnells	Residential	3	10	13	588
one	Nov	Wembley	Residential	3	11	14	1379
one	Nov	Jandakot	Residential	5	9	14	886
one	Nov	Osborne Park	Residential	2	2	4	177
one	Nov	Nedlands	Residential	5	10	15	527
one	Nov	Bibra Lake	Residential	3	3	6	707
one	Nov	Wilson	Residential	3	8	11	1037
one	Dec	Gosnells	Residential	2	6	8	826

one	Dec	Wembley	Pecidential	2	7	٥	16
one	Dec	landakot	Residential	2	13	19	280
one	Dec		Desidential	0	10	15	200
one	Dec	Osborne Park	Residential	2	3	5	280
one	Dec	Nedlands	Residential	5	10	15	1160
one	Dec	Bibra Lake	Residential	4	8	12	263
one	Dec	Wilson	Residential	3	8	11	569
one	Jan	Gosnells	Residential	2	6	8	325
one	Jan	Wembley	Residential	3	8	11	351
one	Jan	Jandakot	Residential	6	6	12	138
one	Jan	Osborne Park	Residential	6	3	9	368
one	Jan	Nedlands	Residential	2	5	7	947
one	Jan	Bibra Lake	Residential	3	3	6	777
one	Jan	Wilson	Residential	4	6	10	154
one	Feb	Gosnells	Residential	6	7	13	116
one	Feb	Wembley	Residential	8	10	18	244
one	Feb	Jandakot	Residential	6	4	10	160
one	Feb	Osborne Park	Residential	4	5	9	493
one	Feb	Nedlands	Residential	3	8	11	395
one	Feb	Bibra Lake	Residential	4	5	9	653
one	Feb	Wilson	Residential	9	6	15	545
two	Oct	Nedlands	Residential	4	17	21	4459
two	Oct	Bibra Lake	Residential	3	11	14	237
two	Oct	Osborne Park	Residential	4	5	9	143
two	Oct	Gosnells	Residential	7	14	21	206
two	Oct	Wembley	Residential	5	9	14	800
two	Oct	Jandakot	Residential	4	10	14	355
two	Oct	Wilson	Residential	6	11	17	259
two	Nov	Nedlands	Residential	4	5	9	564
two	Nov	Jandakot	Residential	4	13	17	467
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two	Nov	Gosnells	Residential	5	11	16	632
two	Nov	Osborne Park	Residential	4	6	10	281
two	Nov	Bibra Lake	Residential	5	11	16	327
two	Nov	Wilson	Residential	5	11	16	6165
two	Nov	Wembley	Residential	5	3	8	387
two	Dec	Jandakot	Residential	4	14	18	725
two	Dec	Nedlands	Residential	5	7	12	790
two	Dec	Gosnells	Residential	3	9	12	448
two	Dec	Osborne Park	Residential	3	7	10	262
two	Dec	Bibra Lake	Residential	3	7	10	624
two	Dec	Wilson	Residential	4	9	13	446
two	Dec	Wembley	Residential	5	15	20	696
two	Jan	Nedlands	Residential	4	13	17	1296
two	Jan	Jandakot	Residential	4	17	21	169
two	Jan	Gosnells	Residential	4	17	21	632
two	Jan	Osborne Park	Residential	5	8	13	632
two	Jan	Bibra Lake	Residential	6	5	11	85
two	Jan	Wembley	Residential	4	21	25	858
two	Jan	Wilson	Residential	5	5	10	1114
two	Feb	Jandakot	Residential	5	11	16	233
two	Feb	Nedlands	Residential	5	17	22	416
two	Feb	Gosnells	Residential	7	11	18	870
two	Feb	Osborne Park	Residential	6	10	16	84
two	Feb	Bibra Lake	Residential	7	6	13	88
two	Feb	Wembley	Residential	6	21	27	261
two	Feb	Wilson	Residential	6	10	16	430
two	March	Nedlands	Residential	6	12	18	219

two	March	Jandakot	Residential	5	10	15	604
two	March	Gosnells	Residential	7	6	13	173
two	March	Osborne Park	Residential	6	11	17	421
two	March	Wembley	Residential	5	18	23	2705
two	March	Bibra Lake	Residential	5	12	17	458
two	March	Wilson	Residential	6	10	16	218

### **9.8. Appendix 8:** *Impacts of the introduced European honeybee on plant-pollinator network properties in Australian urban environments* **Supplementary Material**

#### **Appendix S1 Taxonomic categories**

Taxonomic category	Includes	Traits
Honeybee (Apidae)	European honeybee, Apis mellifera	Introduced species
		Eusocial
		Polylectic
		Large body-size
Amegilla	Amegilla (mainly A. chlorocyanea)	Solitary
(Apidae)		Polylectic
		Large body-size
Allodapini (Apidae)	Exoneura (mainly E. pictifrons) and	Semi-social
	Braunsapis	Polylectic
		Small body-size
Euryglossinae	Callohesma	Solitary
(Colletidae)	Dasyhesma	Mostly oligolectic
	Euhesma	Small body-size
	Euryglossa	
	Euryglossina	
	Euryglossula	
	Hyphesma	
	Pachyprosopis	
	Xanthesma	
Hylaeinae	Hylaeus, Meroglossa rubricata	Solitary
(Colletidae)		Mostly oligolectic
		Small to medium body-
		size
Homalictus	Homalictus (mainly H. dotatus)	Communal
(Halictidae)		Mostly polylectic

Table S1. Bee taxonomic categories and ecological traits

		Small body-size
Lasioglossum	Lasioglossum	Communal
(Halictidae)		Mostly polylectic
		Small to medium body-
		size
Lipotriches	Lipotriches (mainly L. flavoviridis)	Solitary
(Halictidae)		Polylectic
		Medium body-size
Leioproctus	Leioproctus	Solitary
(Colletidae)		Mostly polylectic
		Medium to large body-
		size
Trichocolletes	Trichocolletes	Solitary
(Colletidae)		Mostly oligolectic
		Large body-size
Megachile	Megachile (and Rozenapis ignita,	Solitary
(Megachilidae)	recently reclassified)	Oligolectic and polylectic
		Small to large body-size
Thyreus	Thyreus waroonensis	Solitary
(Apidae)		Kleptoparasitic (host:
		Amegilla)
		Large body-size
Coelioxys	Coelioxys froggatti	Solitary
(Megachilidae)		Kleptoparasitic (host:
		Megachile)
		Large body-size

#### Appendix S2 Definitions of network- and species-level indices

#### **Network-level:**

- H<sub>2</sub>': specialisation index calculated for a pollination network, independent of network size, and ranges from 0 (highly generalised) to 1 (highly specialised). A highly specialised network corresponds to containing many species with high species-level specialisation indices (d'). H<sub>2</sub>' is calculated from weighted interactions that measure the extent a species discriminates in choice of interaction partners compared with the total number of interaction partners in the network (Blüthgen, Menzel, & Blüthgen, 2006). H<sub>2</sub>' describes the level of "complementarity specialisation", or "selectiveness" of an entire bipartite network (Dormann, Gruber, & Fründ, 2008). Higher generalisation may be considered to indicate higher functional redundancy, and therefore a more resilient pollination network (Kaiser-Bunbury et al., 2017) (but see Hoiss, Krauss, and Steffan-Dewenter (2015) for a study finding that higher generalisation was associated with less stable networks).
- Nestedness (NODF): a description of network architecture. Nested networks involve specialists interacting with a subset of species that also interact with generalists. A number of metrics measuring nestedness exist, but we selected NODF (nestedness based on overlap and decreasing fill) because this appears to be the most common metric used in the recent literature, enabling comparisons. NODF also has a number of benefits over other nestedness metrics, including being less prone to type 1 statistical errors (Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008), corrects for matrix dimensionality (Almeida-Neto et al., 2008), and is less sensitive to sample size (Rivera-Hutinel, Bustamante, Marín, & Medel, 2012).NODF ranges from 0 to 100, with increasing values representing an increase in nestedness.
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- Species strength: sum of the dependencies for each plants species for a given visitor species. It involves calculating the observed number of interactions by the total number of interactions for each plant, and then the proportion of visits a plant receives from the pollinator are summed across all plants, to give the strength of the pollinator to all plants in the network. A specie's

strength is a network property, co-determined by the specialisation of other pollinators in the network (Dormann, 2011).

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plant species, it delivers diluted pollen to the target species (Dormann, 2011) (as assumption that may not hold true for species that show floral constancy, even if they are polylectic). PSI recognises that even if a pollinator is highly specialised on a plant, if the pollinator is rare, it will still only rarely pollinate a flower, and also considers that a pollinator which is a generalist may deliver a large proportion of non-target pollen.

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#### Appendix S3

**Table S1** Statistical test output of models evaluating the significance of bee taxon in explaining variation among species-level network indices and c- and z-values.

	Year one	:					Year two		
Species-level network property	Δ AICc	X²	р	df		Δ AICc	X²	р	df
normalised degree	145.3	167.3	<0.0001		11	303.72	326.72	<0.0001	11
species strength	117.48	176.8	<0.0001		11	360.4	262.39	< 0.0001	11
interaction push-pull	194.2	226.2	<0.0001		11	289.59	311.59	< 0.0001	11
species specificity index	154	176.8	<0.0001		11	112.82	134.82	<0.0001	11
PSI	41.6	63.6	<0.0001		11	201.03	223.07	<0.0001	11
d'	38.5	60.5	<0.0001		11	76.78	98.38	<0.0001	11
Module roles	SS	F	р	df		SS	F	р	df
c-score	-0.5	1.16	0.332		12	-0.43	1.23	0.27	12
z-score	- 15.13	3.05	0.003		12	-33.9	8.08	<0.0001	12

#### **Appendix S4: Table S1 Pairwise differences between taxa in species-level network indices (Tukey's tests)**

(refer to 9.8 *AppendixS4 pairwise differences.xls*)

#### Appendix S5

#### **Table S1** Statistical test output on the relation between honeybee abundance with network-level properties

	Year one									Year two								
Network property	Δ AICc	X²	р	df	Est.	se	df	R²m	R²c	Δ AICc	X²	р	df	Est.	se	df	R²m	R²c
H2	0.49	1.51	0.219	1	0.029	0.023	53	0.027	0.027	11.90	13.9	0.002	1	-0.07	0.02	81	0.153	0.153
weighted connectance	9.12	11.1	0.001	1	-0.014	0.004	53	0.18	0.18	4.44	6.45	0.011	1	-0.01	0.004	54	0.08	0.11
NODF	1.8	0.29	0.652	1	0.81	1.97	48	0.003	0.013	0.09	2.09	0.148		2.18	1.21	58	0.041	0.106
extinction slope bees	1.99	0.02	0.914	1	0.179	1.22	54	0.0004	0.264	0.29	1.72	0.191	1	2.34	1.8	81	0.02	0.02
extinction slope plants	0.19	1.82	0.178	1	0.033	0.02	54	0.031	0.031	0.96	1.04	0.307	1	0.003	0.003	81	0.01	0.38
robustness bees	1.91	0.08	0.767	1	-0.002	0.007	54	0.001	0.254	1.99	0.01	0.93	1	-0.15	1.7	81	<0.001	<0.001
robustness plants	1.09	0.01	0.924	1	0.0005	0.005	54	<0.001	<0.001	2	0.001	0.975	1	<0.001	<0.001	81	<0.001	0.4
niche overlap	0.24	1.76	0.185	1	-0.111	0.08	50	0.034	0.071	19.5	21.50	<0.0001	1	0.08	0.02	80	0.21	0.54
functional complementarity	2.11	4.11	0.043	1	0.183	0.09	54	0.07	0.07	21.82	23.8	<0.0001	1	0.38	0.07	65	0.27	0.33

**Table S2** Statistical test output on interaction effects between honeybee

	Year o	one						
Network metric	ΔΑΙϹ	<b>X</b> <sup>2</sup>	р	df	ΔΑΙϹ	<b>X</b> <sup>2</sup>	р	df
H2	1.4	0.58	0.446	1	2.4	4.4	0.035	1
Weighted connectance	1.5	0.54	0.463	1	1.1	0.3	0.559	1
NODF	1.4	0.58	0.448	1	1.2	0.8	0.345	1
Extinction slope (bees)	1.5	3.54	0.06	1	1.7	0.4	0.549	1
Extinction slope (plants)	0.7	1.32	0.25	1	0.7	1.3	0.255	1
Robustness (bees)	1.9	4.92	0.048	1	1	0.9	0.339	1
Robustness (plants)	1.9	0.14	0.708	1	1.9	0.03	0.863	1
Niche overlap	1.9	0.045	0.832	1	3.8	5.8	0.017	1
Functional complementarity	1.2	0.79	0.374	1	1.3	0.7	0.405	1

abundance and habitat type on network-level properties

Table S3 Statistical test output on the relationship between honeybee abundance in each habitat type for those network metrics where the

effect of honeybees varied by habitat type (as per SuppInfo S5 Table 2).

Year	Network metric	Habitat type	ΔΑΙΟ	<b>X</b> <sup>2</sup>	р	df	Estimate	SE	R <sup>2</sup> m	R <sup>2</sup> <sub>c</sub>
Year one	Extinction slope	bushland remnant	1.4	0.6	0.456	1	-1.04	1.56	0.016	0.102
	Extinction slope (In-transformed)	residential garden	2.7	4.7	0.03	1	0.21	0.1	0.148	0.178
	Robustness (bees)	bushland remnant	0.9	1.1	0.294	1	-0.008	0.008	0.035	0.111
	Robustness (plants)	residential garden	1.2	3.3	0.071	1	0.02	0.009	0.106	0.106
Year two	H2'	bushland remnant	0.7	2.7	0.1	1	-0.04	0.03	0.061	0.061
	H2'	residential garden	11.9	13.9	0.0002	1	-0.13	0.03	0.282	0.282
	Niche overlap (bees)	bushland remnant	3.2	5.23	0.022	1	0.04	0.02	0.101	0.576
	Niche overlap (bees)	residential garden	15.9	17.9	<0.001	1	0.11	0.02	0.352	0.368

Appendix S6 : Table S1 C-scores and z-scores of bee taxa (refer to 9.8 AppendixS6 cz values.xls)

**Appendix S7 : Table S1 Pairwise differences between taxa in c- and z-values (Tukey's tests)** (refer to 9.8 *AppendixS7 pairwise differences cz values.xls*)

Appendix S8. Names of bee taxa and flowering plant species visited corresponding to code names in bee-plant bipartite network diagrams (Fig. 1 and Fig. 2)

Network	Bee taxon	Network Code	Flowering plant species	Network code
Urban bushland	Allodapini	Allo	Corynotheca micrantha	FP1
remnant year 1	Amegilla	Ameg	Jacksonia furcellata	FP2
	Euryglossinae	Eury	Banksia attenuata	FP3
	Homalictus	Hom	Jacksonia sternbergiana	FP4
	Hylaeinae	Hyl	Jacksonia sericea	FP5
	Lasioglossum	Las	Daviesia divaricata	FP6
	Lipotriches	Lipo	Hibbertia cuneiformis	FP7
	Leioproctus	Leio	Arnocrinum preissii	FP8
	Megachile	Meg	Eucalyptus marginata	FP9
	Coelioxys	Coe	Banksia sessilis	FP10
	Thyreus	Thy	Calothamnus quadrifidus	FP11
	Trichocolletes	Tri HB	Tricoryne elatior	FP12
	Honeybee		Hemiandra pungens	FP13
			Scaevola albida	FP14
			Grevillea whitea	FP15
			Rhagodia baccata	FP16
			Melaleuca lanceolata	FP17
			Corymbia callophyla	FP18
			Scholtzia involucrata	FP19
			Corymbia ficifolia	FP20
			Acacia cyclops	FP21
			Melaleuca seriata	FP22
			Pithocarpa cordata	FP23
			Gompholobium tomentosum	FP24
			Taraxacum khatoonae	FP25
			Jacksonia floribunda	FP26

			Leucopogon propinquus	FP27
			Eucalyptus erythrocorys	FP28
			Schinus terebinthifolius	FP29
			Astaria scoparia	FP30
			Eucalyptus camaldulensis	FP31
			Pelargonium capitatum	FP32
			Eucalyptus leucoxylon	FP33
			Arctotheca calendula	FP34
			Conostylis candicans	FP35
			Callistemon viminalis	FP36
			Banksia prionotes	FP37
			Xanthorrhoea preissii	FP38
			Jacksonia gracillima	FP39
			Dasypogon bromeliifolius	FP40
			Chamelaucium uncinatum	FP41
Residential	Allodapini	Allo	Hibbertia scandens	FP1
garden year 1	Amegilla	Ameg	Corymbia callophyla	FP2
	Euryglossinae	Eury	Lophostemon confertus	FP3
	Homalictus	Hom	Jacaranda mimosifolia	FP4
	Hylaeinae	Hyl	Plumeria obtusa	FP5
	Lasioglossum	Las	Agapanthus (purple var)	FP6
	Lipotriches	Lipo	Solanum lycopersicum	FP7
	Leioproctus	Leio	Limonium perezii	FP8
	Megachile	Meg	Antirrhinum majus	FP9
	Honeybee	НВ	Melaleuca braceata	FP10
			Banksia attenuata	FP11
			Lechenaultia floribunda	FP12
			Eucalyptus rudis	FP13
			Regelia ciliata	FP14
			Ricinocarpos pinifolius	FP15

Carpobrutus edulis	FP16
Foeniculum vulgare	FP17
Nuytsia floribunda	FP18
Xanthorrhoea preissii	FP19
Anigozanthus manglesii	FP20
Salvia farinacea	FP21
Polygala myrtifolia	FP22
Callistemon viminalis	FP23
Agonis flexuosa	FP24
Syzygium paniculata	FP25
Melaleuca huegelii	FP26
Anigozanthus rufus	FP27
Alyogyne huegelii	FP28
Brassica oleracea	FP29
Agapanthus (white var)	FP30
Magnolia grandiflora	FP31
Trachelospermum jasminoides	FP32
Jacksonia furcellata	FP33
Gompholobium aristatum	FP34
Taraxacum khatoonae	FP35
Eucalyptus marginata	FP36
Lonicera japonica	FP37
Lobularia maritima	FP38
Scaevola albida	FP39
Jacksonia sternbergiana	FP40
Duranta repens	FP41
Rosa sp.	FP42
Wisteria floribunda	FP43
Oenothera laciniata	FP44
Callistemon salignus	FP45

Lantana camara	FP46
Ocimum basilicum	FP47
Tanacetum cinerariifolium	FP48
Lirope muscari	FP49
Sida fallax	FP50
Lagerstroemia indica	FP51
Rosmarinus officinalis	FP52
Buddleja davidii 'Monum' (purple)	FP53
Eucalyptus erythrocorys	FP54
Tipuana tipu	FP55
Pelargonium australe	FP56
Abelia grandiflora	FP57
Corymbia ficifolia	FP58
Pandorea jasminoides	FP59
Eucalyptus gomphocephala	FP60
Thryptomene saxicola	FP61
Tetragonia tetragonioides	FP62
Marianthus bicolor	FP63
Grevillea thelemanniana	FP64
Banksia media	FP65
Eruca sativa	FP66
Citrus latifolia	FP67
Melaleuca lanceolata	FP68
Verbesina encelioides	FP69
Wisteria sinensis	FP70
Grevillea "Moonlight"	FP71
Erigeron karvinskianus	FP72
Tagetes erecta	FP73
Lobelia erinus	FP74
Scholtzia involucrata	FP75

		Baeckea sp.	FP76
		Astartea 'eastern selection'	FP77
		Leucophyta brownii	FP78
		Melaleuca nesophila	FP79
		Senecio cineraria	FP80
		Grevillea "Yellow var."	FP81
		Triadica sebifera	FP82
		Cymbalaria muralis	FP83
		Argyranthemum frutescens	FP84
		Papaver rhoeas	FP85
		Pelargonium x domesticum	FP86
		Allium triquetrum	FP87
		Gazania linearis	FP88
		Nasturtium officinale	FP89
		Ceratopetalum gummiferum	FP90
		Centaurea cyanus	FP91
		Arctotheca calendula	FP92
		Lavandula angustifolia	FP93
		Banksia ashbyi	FP94
		Vitis vinifera	FP95
		Banksia blechnifolia	FP96
		Echeveria sp.	FP97
		Westringia fruticosa	FP98
		Lavandula dentata	FP99
		Malus pumila	FP100
		Grevillia leucopteris	FP101
Allodapini	Allo	Jacksonia gracillima	FP1
Amegilla	Ameg	Jacksonia furcellata	FP2
Euryglossinae	Eury	Astartea scoparia	FP3
Homalictus	Hom	Melaleuca preissiana	FP4

Urban bushland remnant year 2

Hylaeinae	Hyl
Lasioglossum	Las
Lipotriches	Lipo
Leioproctus	Leio
Megachile	Meg
Coelioxys	Coe
Thyreus	Thy
Trichocolletes	Tri
Honeybee	HB

Kunzea glabrescens	FP5
Melaleuca seriata	FP6
Acacia huegelii	FP7
Arctotheca calendula	FP8
Taraxacum khatoonae	FP9
Jacksonia sericea	FP10
Banksia attenuata	FP11
Eucalyptus marginata	FP12
Jacksonia sternbergiana	FP13
Thysanotus sparteus	FP14
Grevillea whitea	FP15
Rhagodia baccata	FP16
Galenia secunda	FP17
Jacksonia floribunda	FP18
Scholtzia involucrata	FP19
Gompholobium tomentosum	FP20
Hemiandra pungens	FP21
Corymbia callophyla	FP22
Melaleuca lanceolata	FP23
Calytrix fraseri	FP24
Corymbia ficifolia	FP25
Grevillea vestita	FP26
Tricoryne tenella	FP27
lsopogon trilobus	FP28
Pelargonium capitatum	FP29
Grevillea thelemanniana	FP30
Callistemon viminalis	FP31
Eucalyptus erythrocorys	FP32
Eucalyptus orbifolia	FP33
Raphanus raphanistrum	FP34

Solanum nigrum	FP35
Brassica napus	FP36
Schinus terebinthifolius	FP37
Melaleuca systena	FP38
Pithocarpa cordata	FP39
Arnocrinum preissii	FP40
Eucalyptus camaldulensis	FP41
Corynotheca micrantha	FP42
Regelia ciliata	FP43
Leucophyta brownii	FP44
Banksia prionotes	FP45
Rosmarinus officinalis	FP46
Dasypogon bromeliifolius	FP47
Dampiera diversifolia	FP48
Banksia ilicifolia	FP49
Petrophile linearis	FP50
Xanthorrea preissii	FP51
Wahlenbergia capensis	FP52
Patersonia occidentalis	FP53
Lotus subbiflorus	FP54
Daviesia divaricata	FP55
Dianella revoluta	FP56
Hibbertia hypericoides	FP57
Banksia sessilis	FP58
Carpobrutus edulis	FP59
Eucalyptus leucoxylon	FP60
Agonis flexuosa	FP61
Bauhinia variegata	FP62
Tamarix ramosissima	FP63
Hardenbergia comptoniana	FP64

			Scaevola repens	FP65
			Calothamnus quadrifidus	FP66
			Poaceae	FP67
			Scaevola albida	FP68
			Lavandula dentata	FP69
			Scaevola thesioides	FP70
			Hakea prostrata	FP71
			Hypocalymma robustum	FP72
			Anigozanthus manglesii	FP73
			Eutaxia obovata	FP74
			Leptospermum laevigata	FP75
			Daviesia physodes	FP76
			Euchilopsis linearis	FP77
			Thysanotus sparteus	FP78
			Hypocalymma angustifolium	FP79
			Senecio cineraria	FP80
			Scaevola nitida	FP81
			Conostylis candicans	FP82
			Euphorbia terracina	FP83
			Hibbertia cuneiformis	FP84
Residential	Allodapini	Allo	Regelia ciliata	F1
garden year 1	Amegilla	Ameg	Nuytsia floribunda	F2
	Euryglossinae	Eury	Melaleuca nesophila	F3
	Homalictus	Hom	Metrosideros thomasii	F4
	Hylaeinae	Hyl	Brachychiton discolor	F5
	Lasioglossum	Las	Callistemon viminalis	F6
	Lipotriches	Lipo	Aptenia cordifolia	F7
	Leioproctus	Leio	Calytrix aurea	F8
	Megachile	Meg	Melaleuca linariifolia	F9
	Thyreus	Thy	Abelia grandiflora	F10

Trichocolletes	Tri	Allium cepa	F11
Honeybee	HB	Hibbertia scandens	F12
		Microcitrus australasica	F13
		Duranta repens	F14
		Brassica oleracea	F15
		Melaleuca huegelii	F16
		Lophostemon confertus	F17
		Tanacetum cinerariifolium	F18
		Rosa sp.	F19
		Grevillea "pink"	F20
		Centranthus ruber	F21
		Buddleja davidii	F22
		Buddleja "white"	F23
		Lagerstroemia indica	F24
		Plumeria obtusa	F25
		Canna_lily	F26
		Punica granatum	F27
		Jacksonia furcellata	F28
		Eucalyptus torquata	F29
		Eucalyptus marginata	F30
		Banksia attenuata	F31
		Antigonon leptopus	F32
		Melaleuca nesophila	F33
		Pandorea jasminoides	F34
		Agapanthus (purple var)	F35
		Jacksonia sternbergiana	F36
		Jacksonia scoparia	F37
		Fragaria × ananassa	F38
		Brachysome angustifolia	F39
		Corymbia callophyla	F40

Cuphea hyssopifolia	F41
Limonium perezii	F42
Citrus × limon	F43
Jacobaea maritima	F44
Dahlia	F45
Banksia media	F46
Salvia farinacea	F47
Salvia officinalis (blue)	F48
Erigeron glaucus	F49
Eucalyptus erythrocorys	F50
Taraxacum khatoonae	F51
Corymbia callophyla white	F52
Sedum album	F53
Scholtzia involucrata	F54
Pelargonium australe	F55
Thryptomene saxicola	F56
Marianthus bicolor	F58
Syzygium paniculata	F59
Ocimum basilicum	F60
Leptospermum scoparium	F61
Chrysocephalum apiculatum	F62
Caesalpinia gilliesii	F63
Thymus serpyllum 'Albus'	F64
Thymus serpyllum (purple)	F65
Lantana camara	F66
Centranthus ruber	F67
Gazania linearis	F68
Rosmarinus officinalis	F69
Euphorbia cyathophora	F70
Liriope sp.	F71

Corymbia ficifolia	F72
Chamelaucium uncinatum	F73
Melaleuca lanceolata	F74
Erigeron glaucus	F75
Erigeron karvinskianus	F76
Scaevola aemula	F77
Pelargonium × hortorum	F78
Lobularia maritima	F79
Nemesia fruticans	F80
Capsicum annum	F81
Pisum sativum	F82
Eruca sativa	F83
Nasturtium officinale	F84
Nerium oleaner	F85
Coleonema pulchellum	F86
Euryops pectinatus	F87
Polygala myrtifolia	F88
Pelargonium x domesticum	F89
Banksia burdettii	F90
Agapanthus ("white)	F91
Vitex triflia	F92
Baekia sp.	F93
Tipuana tipu	F94
Petroselinum crispum	F95
Fragaria × ananassa	F96
Sambucus nigra	F97
Ozothamnus diosmifolius	F98
Calibrachoa	F99
Helianthus annuus	F100
Astartea 'eastern selection'	F101

Grevillea leucopteris	F102
Tagetes erecta	F103
Cuphea hyssopifolia	F104
Lavandula dentata	F105
Wisteria sinensis	F106
Hibiscus tiliaceus	F107
Tetragonia tetragonioides	F108
Citrus latifolia	F109
Gompholobium tomentosum	F110
Polemonium caeruleum	F111
Grevillea whitea	F112
Oenothera (prev. Gaura) lindheimeri	F113
Eucalyptus leucoxylon	F114
Eucalyptus leucoxylon var. rosea	F115
Melaleuca quinquenervia	F116
Westringia fruticosa	F117
Sida fallax	F118
Sida fallax Vinca major	F118 F119
Sida fallax Vinca major Banksia prionotes	F118 F119 F120
Sida fallax Vinca major Banksia prionotes Crassula capitella Campfire	F118 F119 F120 F121
Sida fallax Vinca major Banksia prionotes Crassula capitella Campfire Pelargonium peltatum	F118 F119 F120 F121 F122
Sida fallax Vinca major Banksia prionotes Crassula capitella Campfire Pelargonium peltatum Tithonia speciosa	F118 F119 F120 F121 F122 F123
Sida fallax Vinca major Banksia prionotes Crassula capitella Campfire Pelargonium peltatum Tithonia speciosa Grevillea excelsio	F118 F119 F120 F121 F122 F123 F124
Sida fallax Vinca major Banksia prionotes Crassula capitella Campfire Pelargonium peltatum Tithonia speciosa Grevillea excelsio Portulaca sp.	F118 F119 F120 F121 F122 F123 F124 F125
Sida fallax Vinca major Banksia prionotes Crassula capitella Campfire Pelargonium peltatum Tithonia speciosa Grevillea excelsio Portulaca sp. Lonicera japonica	F118 F119 F120 F121 F122 F123 F124 F125 F126
Sida fallax Vinca major Banksia prionotes Crassula capitella Campfire Pelargonium peltatum Tithonia speciosa Grevillea excelsio Portulaca sp. Lonicera japonica Banksia speciosa	F118 F119 F120 F121 F122 F123 F124 F125 F126 F127
Sida fallax Vinca major Banksia prionotes Crassula capitella Campfire Pelargonium peltatum Tithonia speciosa Grevillea excelsio Portulaca sp. Lonicera japonica Banksia speciosa Euphorbia milii	F118 F119 F120 F121 F122 F123 F124 F125 F126 F127 F128
Sida fallax Vinca major Banksia prionotes Crassula capitella Campfire Pelargonium peltatum Tithonia speciosa Grevillea excelsio Portulaca sp. Lonicera japonica Banksia speciosa Euphorbia milii	F118 F119 F120 F121 F122 F123 F124 F125 F126 F127 F128 F129
Sida fallax Vinca major Banksia prionotes Crassula capitella Campfire Pelargonium peltatum Tithonia speciosa Grevillea excelsio Portulaca sp. Lonicera japonica Banksia speciosa Euphorbia milii Arctotheca calendula Pelargonium capitatum	F118 F119 F120 F121 F122 F123 F124 F125 F126 F126 F127 F128 F129 F130

Callistemon salignus	F131
Lechenaultia floribunda	F132
Dasypogon bromeliifolius	F133
Rheum rhabarbarum	F134
Eucalyptus camaldulensis	F135
Malus pumila	F136
Lavandula white variety	F137
Lavandula penduculata	F138
Cymbalaria muralis	F139
Anigozanthus rufus	F140
Dianella revoluta	F141
Eremea paucifolia	F142
Gompholobium aristatum	F143
Leucospermum cordifolium	F144
Medicago polymorpha	F145
Melaleuca braceata	F146
Conostylis candicans	F147
Vicia faba	F148
Coriandrum sativum	F149
Grevillea crithmifolia	F150
Agonis flexuosa	F151
Pimelea ferruginea	F152
Grevillea thelemanniana	F153
Raphanus raphanistrum	F154
Ricinocarpos pinifolius	F155
Viburnum odoratissimum	F156
Anigozanthus manglesii	F157
Daviesia divaricata	F158
Xanthorrea preissii	F159
Hardenbergia comptoniana	F160

Calothamnus quadrifidus	F161
Eucalyptus camaldulensis	F162
Eucalyptus melliodora	F163
Olea europea	F164
Grevillea olivacea	F165
Eutaxia obovata	F166
Kalanchoe blossfeldiana	F167
Linaria vulgaris	F168
Oxalis pes-rapae	F169
Grevillea Peaches & Cream var	F170
Citrus tangerina	F171
Matthiola	F172
Macadamia	F173
Azelea	F174
Regelia inops	F175
Melaleuca rhaphiophylla	F176
Pyrus calleryana	F177

# **9.9. Appendix 9:** *Interactions between the introduced European honey bee and native bees in urban areas varies by year, habitat type, and native bee guild* **Supplementary Material**

Taxon	Family	Body-size	Foraging characteristics
Amegilla	Apidae	Large	Generalists
			Frequently visit plants that require sonication
			Long-tongued
Coelioxys	Megachilidae	Large	Kleptoparasite of Megachile
			Long-tongued
Euryglossinae	Colletidae	Small	Mainly specialists on Myrtaceae
			Short-tongued
Exoneura	Apidae	Small	Generalists
			Long-tongued
Homalictus	Halictidae	Small	Generalists
			Short-tongued
Hylaeus	Colletidae	Predominantly	Mainly specialists on Myrtaceae
		small	Short-tongued
Lasioglossum	Halictidae	Small – medium	Generalists
			Short-tongued
Leioproctus	Colletidae	Medium – large	Specialist to generalists
			Short-tongued
Lipotriches	Halictidae	Predominantly	Generalists
		medium	Short-tongued
Megachile	Megachilidae	Small - medium	Specialists to generalists, however many frequently
			forage on native Fabaceae
			Long-tongued
Meroglossa	Colletidae	Medium	Only collected from native flora
			Short-tongued
Thyreus	Apidae	Large	Kleptoparasite of Amegilla
			Long-tongued
Trichocolletes	Colletidae	Large	Mostly specialists on native Fabaceae
			Short-tongued

#### **Supporting Information 1:**

#### Table S1. Taxonomic categories of native bees

## Tables S2 – S12: Honeybee Competition Model Outputs: bold = significant (p<0.05); *italics* = *trending towards significance* (0.05>p<1.0)

**Table S2.** Model outputs for interactions between explanatory variables (honeybee abundance \*habitat and honeybee abundance \* floral variables). Test statistics are derived from an ANOVAbetween two models (with and without the interaction effect).

Year	Model	<i>X</i> <sup>2</sup>	P-value
one	In(native bee N) ~	3.95	0.047
	In (honeybee N) *		
	Habitat		
	native bee N ~ In	2.58	0.108
	(honeybee N) * In		
	(flower N)		
	ln(native bee N) ~	1.09	0.296
	In (honeybee N) *		
	flower R		
	ln(native bee N) ~ ln	0.07	0.790
	(honeybee N) *		
	proportion native		
	flowers		
	ln(native bee N) ~ ln	1.05	0.305
	(honeybee N) *		
	proportion native		
	flower species		
two	ln(native bee N) ~ ln	0.27	0.607
	(honeybee N+1) *		
	Habitat		
	native bee N ~ In	3.71	0.054
	(honeybee N+1) * In		
	(flower N)		
	ln(native bee N) ~	3.06	0.080
	In (honeybee N+1) *		
	flower R		

	In(native bee N) ~ In	2.35	0.126
	(honeybee N+1) *		
	proportion native		
	flowers		
	ln(native bee N) ~ In	1.95	0.163
	(honeybee N+1) *		
	proportion native		
	flower species		
one	native bee R ~ In	6.35	0.012
	(honeybee N) *		
	habitat		
	native bee R ~ In	3.15	0.076
	(honeybee N) * In		
	(flower N)		
	native bee R ~ In	1.28	0.26
	(honeybee N) *		
	flower R		
	native bee R ~ In	0.002	0.966
	(honeybee N) *		
	proportion native		
	flowers		
	native bee R ~ In	0.19	0.659
	(honeybee N) *		
	proportion native		
	flower species		
two	native bee R ~ In	0.005	0.945
	(honeybee N+1) *		
	habitat		
	native bee R ~ In	5.7	0.017
	(honeybee N+1) *		
	ln (flower N)		
	native bee R ~ In	1.13	0.288
	(honevbee N+1) *		
	(		

native bee R ~ In	0.02	0.878
(honeybee N+1) *		
proportion native		
flowers		
native bee R ~ In	010	0.755
(honeybee N+1) *		
proportion native		
flower species		

**Table S3.** Relationship between honeybee abundance and native bee abundance and species richness.  $X^2$  and *P*-value are derived from an ANOVA between models with and without honeybee abundance. Estimate, standard error (S.E.) and R<sup>2</sup> values (conditional and marginal) are from the summary output of the model with honeybee abundance as the main effect.

Year	Model	Estimate	S.E.	R <sup>2</sup> c	<i>R</i> <sup>2</sup> m	X <sup>2</sup>	P-value
one	In (native bee	0.07	0.08	0.213	0.014	0.7	0.403
	N) ~ ln						
	(honeybee N)						
	Bushland: In	-0.06	0.09	0.015	0.015	0.4	0.528
	(native bee N)						
	~ In (honeybee						
	N)						
	Residential	0.24	0.12	0.167	0.119	3.7	0.055
	garden: In						
	(native bee N)						
	~ In (honeybee						
	N)						
two	In (native bee	-0.12	0.07	0.206	0.034	2.7	0.101
	N) ~ ln						
	(honeybee						
	N+1)						
one	native bee R ~	0.14	0.03	0.611	0.185	17.2	<0.001
	In (honeybee						
	N)						
	Bushland:	0.08	0.04	0.330	0.142	4.0	0.046
	native bee R ~						
	In (honeybee						
	N)						
	Residential	0.25	0.06	0.480	0.480	19.1	<0.001
	garden: native						
	bee R ~ In						
	(honeybee N)						
two	native bee R ~	-0.06	0.03	0.584	0.046	6.4	0.011
	In (honeybee						
	N+1)						

**Table S4.** Model output between native bee abundance and species richness in the second year of surveys with honeybee abundance in the first year (i.e. carry-over effects).  $X^2$  and P-value are derived from an ANOVA between models with and without honeybee abundance; estimate, standard error (S.E.) and R<sup>2</sup> values (conditional and marginal) are from the summary output of the model with honeybee abundance as the main effect.

Model	Estimate	S.E.	<b>R</b> <sup>2</sup> c	<i>R</i> <sup>2</sup> m	<b>X</b> <sup>2</sup>	P-value
In (native bee	0.11	0.09	0.207	0.025	1.2	0.249
N yr2) ~ ln						
(honeybee N						
yr1)						
In (native bee	-0.01	0.04	0.468	0.0001	0.1	0.876
R yr2) ~ In						
(honeybee N						
yr1)						

**Table S5.** Relationship between honeybee abundance and native bee abundance and species richness of different body size categories.  $X^2$  and P-value are derived from an ANOVA between models with and without honeybee abundance; estimate, standard error (S.E.) and R<sup>2</sup> values (conditional and marginal) are from the summary output of the model with honeybee abundance as the main effect.

Year	Model	Estimate	S.E.	<i>R</i> <sup>2</sup> c	<i>R</i> <sup>2</sup> m	<b>X</b> <sup>2</sup>	P-value
one	In (small N	0.22	0.11	0.379	0.064	3.8	0.051
	+1) ~ ln						
	(honeybee N)						
	ln (medium N	0.11	0.07	0.391	0.042	2.6	0.104
	+1) ~ ln						
	(honeybee N)						
	In (large N +1)	0.05	0.10	0.44	0.005	0.3	0.576
	~ In						
	(honeybee N)						
two	In (small N+1)	-0.02	0.08	0.253	0.001	0.1	0.807
	~ In						
	(honeybee						
	N+1)						
	ln (medium N	-0.07	0.07	0.307	0.012	1.0	0.317
	+1) ~ ln						
	(honeybee						
	N+1)						
	ln (large N +1)	-0.14	0.08	0.441	0.034	3.3	0.069
	~ In						
	(honeybee						
	N+1)						
one	In (small R +1)	0.21	0.07	0.454	0.137	8.5	0.004
	~ In						
	(honeybee N)						
	medium R ~ In	0.05	0.05	0.384	0.017	1.1	0.287
	(honeybee N)						

	large R ~ In	0.10	0.05	0.276	0.066	3.6	0.053
	(honeybee N)						
two	In (small R +1)	-0.003	0.06	0.300	<0.001	<0.001	0.990
	~ In						
	(honeybee						
	N+1)						
	medium R ~	-0.15	0.04	0.414	0.145	16.2	<0.001
	In (honeybee						
	N+1)						
	large R ~ In	-0.06	0.04	0.556	0.013	1.73	0.189
	(honeybee						
	N+1)						

**Table S6.** Model outputs for the effect of time period on number of native bees and honeybeesobserved. Test statistics are derived from an ANOVA between two models (with and without themain effect or interaction effect).

Year	Model	<b>Х</b> <sup>2</sup>	P-value
one	Nativebees(In+1)~time.period	3.63	0.163
	Honeybees(In+1) ~time.period	0.34	0.845
	Nativebees(In+1)~	7.58	0.023
	Honeybees(In+1) *time.period		
two	Nativebees(In+1)~time.period	1.70	0.428
	Honeybees(In+1) ~time.period	0.43	0.806
	Nativebees(In+1)~ Honeybees(In+1)	5.92	0.052
	*time.period		
**Table S7.** Relationship between honeybee abundance and native bee abundance in the morning, midday, and afternoon time periods.  $X^2$  and *P*-value are derived from an ANOVA between models with and without honeybee abundance; estimate, standard error (S.E.) and R<sup>2</sup> values (conditional and marginal) are from the summary output of the model with honeybee abundance as the main effect.

Year	Model	Estimate	S.E.	<i>R</i> <sup>2</sup> c	<i>R</i> <sup>2</sup> m	X <sup>2</sup>	P-value				
one	Morning:	-0.19	0.07	0.159	0.106	6.4	0.012				
	Nativebees(In+1)~										
	Honeybees(ln+1)										
	Midday:	-0.04	0.08	0.070	0.005	0.3	0.588				
	Nativebees(In+1)~										
	Honeybees(In+1)										
	Afternoon:	0.11	0.09	0.282	0.023	1.3	0.254				
	Nativebees(In+1)~										
	Honeybees(In+1)										
two	Morning:	-0.23	0.06	0.320	0.160	13.8	0.0002				
	Nativebees(In+1)~										
	Honeybees(In+1)										
	Midday:	-0.18	0.08	0.140	0.061	5.0	0.0254				
	Nativebees(In+1)~										
	Honeybees(In+1)										
	Afternoon:	-0.02	0.08	0.149	0.001	0.1	0.784				
	Nativebees(In+1)~										
	Honeybees(In+1)										

**Table S8.** Model output for relationships between abundance of native bee taxa and resource overlap with honeybees (measured as Potential for Apparent Competition with honeybees). Test statistics are derived from an ANOVA between two models (with and without the main effect of resource overlap).

Year	Model	Estimate	S.E.	<b>R</b> <sup>2</sup> c	<i>R</i> <sup>2</sup> m	<b>X</b> <sup>2</sup>	P-value
one	In(abundance+1)~PAC	-0.05	0.27	0.019	0.019	3.6	0.058
	Bushland:	-1.02	0.43	0.053	0.053	5.5	0.019
	In(abundance+1)~PAC						
	Residential garden:	0.07	0.35	0.0005	0.0005	0.04	0.844
	In(abundance+1)~PAC						
two	In(abundance+1)~PAC	-0.84	0.22	0.042	0.042	14.8	0.0001

**Table S9.** Model output for interaction effects with habitat type for relationships betweenabundance of native bee taxa and resource overlap with honeybees (measured as Potential forApparent Competition with honeybees). Test statistics are derived from an ANOVA between twomodels (with and without the interaction effect).

Year	Model	X <sup>2</sup>	P-value
one	In(native bee	3.79	0.052
	N+1)~Apparent.Cor	пр	
	* Habitat		
two	In(native bee	0.20	0.655
	N+1)~Apparent.Cor	np	
	* Habitat		

**Table S10.** Model output for PAC by habitat and taxon. Test statistics are derived from an ANOVAbetween two models (with and without habitat type or taxon).

Year	Model	Х <sup>2</sup>	P-value
one	Apparent.Comp ~	6.84	0.009
	Habitat		
two	Apparent.Comp ~	3.63	0.057
	Habitat		
one	Apparent.Comp ~	45.2	<0.0001
	Taxon		
two	Apparent.Comp ~	55.62	<0.0001
	Taxon		

	Amegilla	Coelioxys	Euryglossinae	Exoneura	Homalictus	Hylaeus	Lasioglossum	Leioproctus	Liopotriches	Megachile	Meroglossa	Thyreus	Trichocolletes
Amegilla													
Coelioxys	1.00												
Euryglossinae	0.722	1.00											
Exoneura	0.793	1.00	1.00										
Homalictus	0.374	0.981	0.997	1.00									
Hylaeus	0.0001	1.00	0.087	0.836	0.861								
Lasioglossum	0.903	1.00	1.00	1.00	1.00	0.158							
Leioproctus	1.00	1.00	0.993	0.985	0.850	0.008	0.999						
Liopotriches	0.999	1.00	0.999	0.997	0.931	0.012	1.00	1.00					
Megachile	1.00	1.00	0.189	0.471	0.087	<0.001	0.535	0.995	0.939				
Meroglossa	0.999	1.00	1.00	0.999	0.997	0.361	1.00	1.00	1.00	0.996			
Thyreus	0.999	1.00	1.00	1.00	1.00	0.998	1.00	1.00	1.00	0.994	1.00		
Trichocolletes	1.00	1.00	1.00	1.00	1.00	0.990	1.00	1.00	1.00	1.00	1.00	1.00	

	Amegilla	Coelioxys	Euryglossinae	Exoneura	Homalictus	Hylaeus	Lasioglossum	Leioproctus	Liopotriches	Megachile	Meroglossa	Thyreus	Trichocolletes
Amegilla													
Coelioxys	1.00												
Euryglossinae	0.651	1.00											
Exoneura	0.095	0.893	0.909										
Homalictus	0.012	0.756	0.997	1.00									
Hylaeus	0.001	0.825	0.836	1.00	1.00								
Lasioglossum	0.006	0.905	0.934	1.00	1.00	1.00							
Leioproctus	0.026	1.00	1.00	1.00	1.00	1.00	1.00						
Liopotriches	0.987	0.435	1.00	0.553	0.357	0.119	0.237	0.382					
Megachile	1.00	1.00	0.86	0.059	0.003	<0.001	0.010	0.007	0.951				
Meroglossa	0.999	1.00	0.234	1.00	1.00	1.00	1.00	1.00	1.00	0.999			
Thyreus	1.00	0.981	0.923	0.952	0.978	0.972	0.968	0.974	1.00	1.00	1.00		
Trichocolletes	0.520	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.867	0.454	1.00	0.968	

#### Table S12. Pairwise differences between taxa in PAC in year two

#### 9.10. Appendix 10: Copyright Statements

# Chapter 2: A global review of determinants of native bee assemblages in urbanised landscapes

To whom it may concern, I, Kit Stasia Prendergast, conceived the ideas and conducted the literature search and review, analysed the data, wrote the manuscript, and created all figures and tables; all authors contributed to the revisions of the manuscript for the following publication:

**Prendergast, K. S.,** Dixon, K. W., & Bateman, P. W. (2020). A global review of determinants of native bee assemblages in urbanised landscapes. *Journal of Insect Conservation & Diversity, under review*.

Signed:

Date: 3 June 2020

I, as Co-Author, endorse that this level of contribution by the candidate indicated above is appropriate

Prof Kingsley W. Dixon

Signature:

Date: 28 July 2020

Assoc. Prof Bill W. Bateman

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### Chapter 3: The relative performance of sampling methods for native bees: an empirical test and review of the literature

To whom it may concern, I, Kit Stasia Prendergast, conducted the literature review, collected the data; identified the specimens; wrote the manuscript; created the figures and tables; and analysed the data with guidance from MHM. All authors contributed to conceiving the study, and revisions of the manuscript for the following publication:

Prendergast, K. S., Menz, M. H. M., Dixon, K. W., & Bateman, P. W. (2020). The relative performance of sampling methods for native bees: an empirical test and review of the literature. *Ecosphere*, 11(5), e03076. doi:10.1002/ecs2.3076

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Date: 3 June 2020

I, as Co-Author, endorse that this level of contribution by the candidate indicated above is appropriate

Dr Myles H. Menz

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Date: 28 July 2020

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Date: 28 July 2020

Assoc. Prof Bill W. Bateman

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### Chapter 4: Residential gardens are a poor alternative to urban native vegetation remnants in supporting native bee communities

To whom it may concern, I, Kit Stasia Prendergast, collected the data; identified the specimens; wrote the manuscript; created the figures with MHM and ST; and analysed the data with MHM and ST. Myself, MHM, KD and BB contributed to conceiving the study, and all authors contributed to revisions of the manuscript.

**Prendergast, K. S.,** Tomlinson, S., Dixon, K.W., Bateman, P. W. & Menz, M. H. M., (2020). Residential gardens are a poor alternative to urban native vegetation remnants in supporting native bee communities. *Biological Conservation, under review*.

Signed:

Date: 3 June 2020

I, as Co-Author, endorse that this level of contribution by the candidate indicated above is appropriate

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Date: 28 July 2020

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## Chapter 5: Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens

To whom it may concern, I, Kit Stasia Prendergast, conceived of the study; collected the data; identified the specimens; wrote the manuscript; created the figures and tables; and analysed the data with guidance from JO. All authors contributed to revisions of the manuscript for the following publication:

Prendergast, K. S. & Ollerton, J. (2020) Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens, *Urban Ecosystems* (Online Early). <u>https://doi.org/10.1007/s11252-020-01089-w</u>

Signed:

Date: 3 June 2020

I, as Co-Author, endorse that this level of contribution by the candidate indicated above is appropriate

Prof Jeff Ollerton

Signature:

Date: 4 June 2020

## Chapter 6: Impacts of the introduced European honeybee on Australian bee-flower network properties in urban bushland remnants and residential gardens

To whom it may concern, I, Kit Stasia Prendergast, conceived of the study; collected the data; identified the specimens; wrote the manuscript; created the figures and tables; and analysed the data with guidance from JO. All authors contributed to revisions of the manuscript for the following publication:

Prendergast, K. S. & Ollerton, J. (2020) Impacts of the introduced European honeybee on Australian bee-flower network properties in urban bushland remnants and residential gardens. *Austral Ecology* (Online Early). DOI: 10.1111/aec.13040

Signed:

Date: 3 June 2020

I, as Co-Author, endorse that this level of contribution by the candidate indicated above is appropriate

Prof Jeff Ollerton

Signature:

Date: 4 June 2020

#### Chapter 7: Interactions between the introduced European honey bee and native bees in urban areas varies by year, habitat type and native bee guild

To whom it may concern, I, Kit Stasia Prendergast, conceived of the study; collected and analysed the data; identified the specimens; wrote the manuscript; and created the figures and tables. All authors (myself, KD and PW) conceived the ideas and contributed to revisions of the manuscript.

Prendergast, K. S., Dixon, K.W. & Batemn, P.W. (2020) Interactions between the introduced European honey bee and native bees in urban areas varies by year, habitat type and native bee guild. *Biological Journal of the Linnaean Society*. (Online Early). DOI: 10.1093/biolinnean/blab024

Signed:

Date: 3 June 2020

I, as Co-Author, endorse that this level of contribution by the candidate indicated above is appropriate

Prof Kingsley W. Dixon

Signature:

Date: 28 July 2020

Assoc. Prof Bill W. Bateman

Signature:



Megachile monstrosa © Kit Prendergast