The canopy, bark, soil and litter invertebrate fauna of the Darling Plateau and adjacent woodland near Perth, Western Australia, with reference to the diversity of forest and woodland invertebrates

J. D. MAJER[1], H. F. RECHER[2], B. E. HETERICK[1] and A. C. POSTLE[1,3]

This paper tables and reports on pooled taxonomic data from three separate research projects involving aspects of eucalypt invertebrate ecology: canopy invertebrates in jarrah and marri forest; bark invertebrates on four eucalypt species in forest and woodland; and soil and litter fauna in jarrah and marri forest. The data support the concept of a high invertebrate biodiversity on and under southwestern eucalypts, with 1 234 adult morphospecies of invertebrates being collected from the bark alone. Despite different trapping methods used in each of the three studies, we were able to find a high degree of overlap at the family level between bark and canopy fauna (126 families were found on both bark and in the canopy representing 79.2% of 159 canopy families). Eighty identified genera were also found on both bark and canopy, which represents 46.2% of the 173 identified canopy genera. The soil and litter fauna data are not complete (a taxonomic inventory of Acarina and Formicidae is not available) but appears to be more distinctive, sharing only 24 families (= 60% of the 40 identified soil-litter families) with bark, and 17 families (= 42.5% of the soil-litter families) with the canopy. At the generic level, only seven identified genera (= 8.6% of 22 soil-litter genera) were shared between soil-litter and bark, and five genera (= 6.2% of soil-litter genera) were shared between soil-litter and the canopy.

An examination of the trophic guilds reveals that fungivores-decomposers were very diverse in soil and litter (accounting for approximately 50% of the biodiversity in these substrates). This guild was much less diverse on the canopy (21.6% of the canopy diversity) and the bark (16.9% of bark diversity). Sap-sucking organisms were more diverse in soil (13.9%) and litter (12.8%) than on the canopy (5.3%) or on bark (5.9%). The canopy result is surprising, and suggests that not many invertebrate species are able to feed on the sap of southwestern eucalypts, the sap of which may contain a high proportion of toxic compounds. Predators were more diverse on the canopy and on bark (≈19–23% of total taxa) than in soil and litter (≈ 9–9.5%), as were parasitoids (18.7% and 22.5% compared with 10.5% and 14.8%). Epiphyte grazers and phytophages were not very diverse (≤11%) on any of the substrates, and representatives of other guilds or organisms whose diet was unknown accounted for less than 2.5% of the total diversity. Tourist species were not recognised among the soil and litter fauna, though they were found in the canopy and on bark, and ants were not quantified for soil and litter.

INTRODUCTION

PROBABLY one of the main effects of the cooling and drying of the Australian continent that took place in the early Oligocene (about 38 mybp) was the diversification of the Myrtaceae (Cranston and Naumann 1990). Within this family in Australia, the most conspicuous representative is the genus *Eucalyptus*, with an estimated 700 or so species (Brooker and Kleinig 1990). Representatives of this genus are usually moderate to large trees, and are ubiquitous in the Australian environment, except for rainforests and some desert areas (Recher *et al.* 1996). One might expect that such a significant life-form would be an important substrate for a large proportion of Australia's vertebrates and invertebrates but, while detailed analyses of the vertebrates on eucalypts have been published (e.g., Woinarski *et al.* 1997), the diversity and ecology of the invertebrate biota is yet largely unexamined in publications (e.g., Woinarski and Cullen 1984; Fensham 1994; Majer *et al.* 1994).

This paper brings together summaries of invertebrate taxonomic data for four eucalypt species: jarrah (*Eucalyptus marginata*), marri (*Corymbia calophylla*), powderbark wandoo (*E. accedens*), and wandoo (*E. wandoo*) found in the Perth hinterland, but most particularly the information obtained from jarrah and marri. The aim of this paper is to provide an integrated overview of the biodiversity and trophic guild structure of invertebrate taxa found at various levels on a number of representatives of each of the four species of eucalypt, and in the litter and soil around roots. A full checklist of the invertebrate species that were found is provided in Heterick *et al.* (2001).

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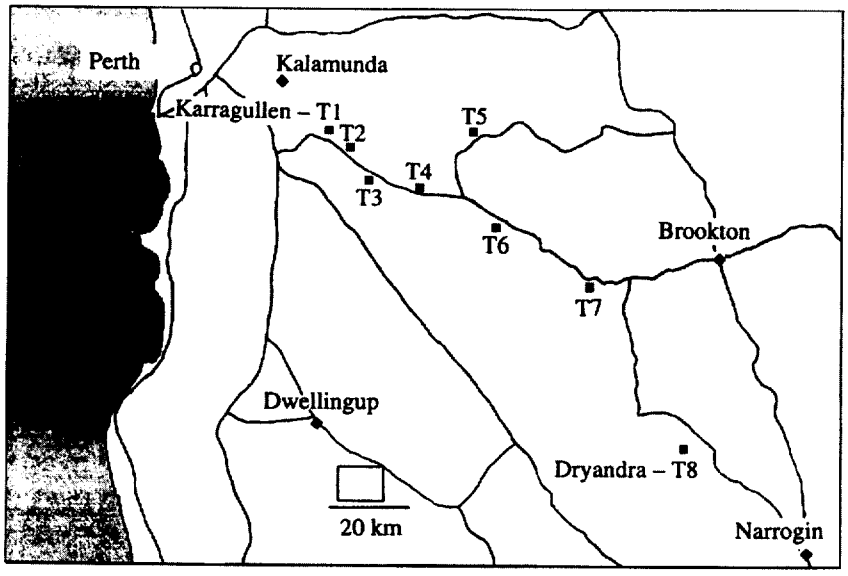
METHODS

Canopy fauna

The sampling area map is shown in Figure 1a. and is depicted in Figure 2a. Sampling was carried out once in each of the four seasons from April 1987 through to January 1988 at Karragullen, Western Australia, on marri and jarrah. During each season, samples were taken from the canopy (>7 m) of each tree species using chemical knockdown procedures. Because the study was primarily concerned with foliage-associated invertebrates, sampling of flowering trees was avoided.

Details of the procedures used and the habitats sampled are presented in Majer and Recher (1988) and Majer *et al.* (1990, 1992, 2000). In brief, in each season 10 trees of each species were selected for sampling. No tree was sampled more than once. Within each tree, 10 funnel-shaped nets of area 0.5 m^2 were suspended using a cherry-picker. Nets were positioned so as not to overlap and to sample different parts of the tree canopy. The following day, the trees were sprayed using a Stihl® motorised knapsack mistblower to deliver a fast-acting pyrethrin insecticide (0.2% Karate® synergized with piperonyl butoxide) (Fig. 3a). Spraying was carried out only under calm conditions during

a.



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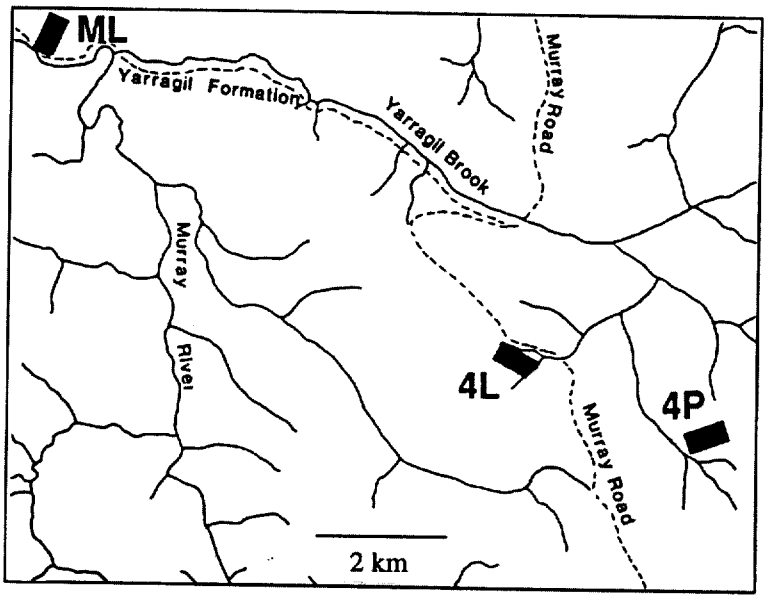
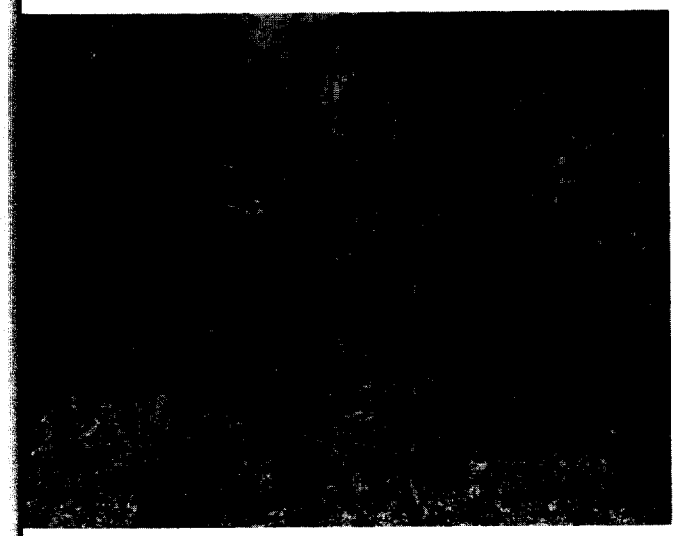
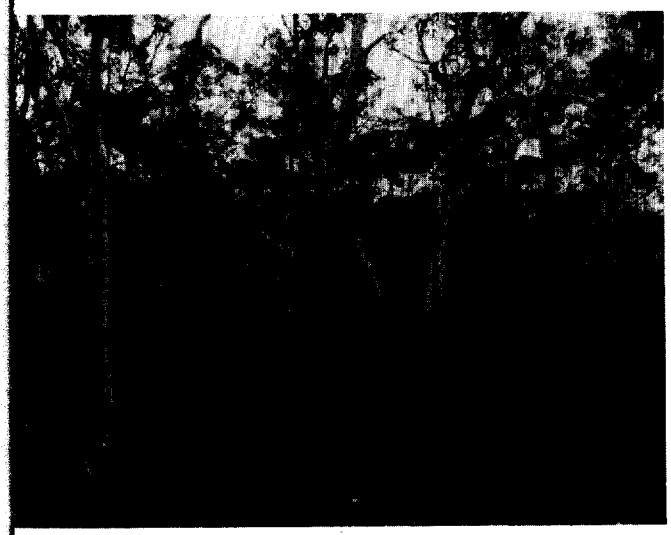


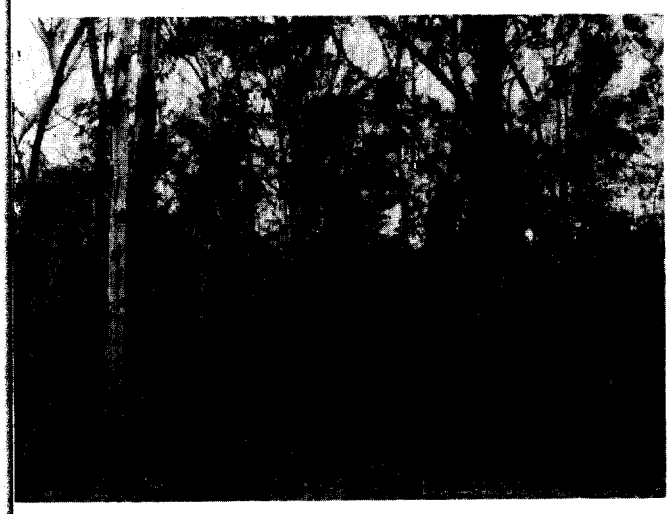
Fig. 1. Study area for (a) the canopy and bark, and (b) the soil and litter projects. Note that at the Karragullen site (T1) jarrah and marri trees were sampled; at Sites T2–T7 marri only was sampled and at site T8 jarrah, marri, powderbark wandoo and wandoo trees were sampled. The open rectangle in (a) shows the location of the soil and litter project and the black rectangle in (b) shows the positions of the soil and litter sample sites. ML = loam sites, 4L and 4P = lateritic sites.



(a) Jarrah-marri forest — Karragullen



(b) Powderbark wandoo woodland — Dryandra



(c) Wandoo woodland — Dryandra

Fig. 2. General views of the three main habitats where invertebrates were sampled.

the early morning. The invertebrates collected by the nets were stored in 70% ethanol until sorting commenced.

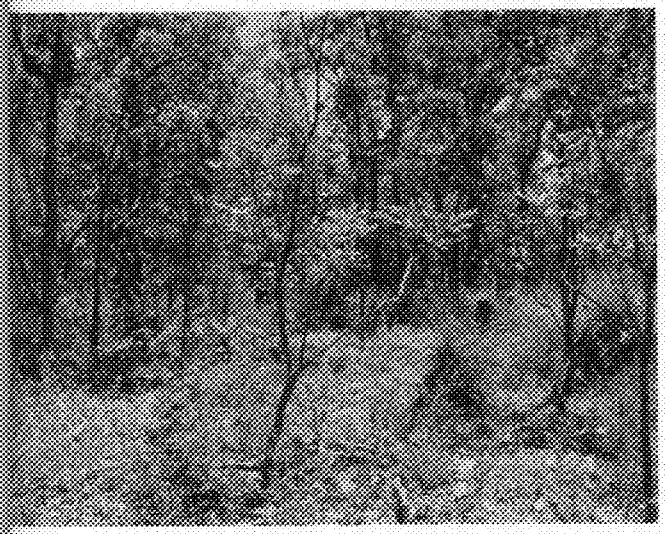
The samples from each of the 10 nets were combined to form the tree samples used in this analysis. Except for endopterygote larvae, which were not identified further, the invertebrates from each sample period and from each of the two tree species were sorted to morphospecies level, as described by Oliver and Beattie (1996) and Longino and Colwell (1997). With the exception of the mites, all animals were assigned to families and morphospecies. Because such a high proportion of the Australian invertebrate fauna is still undescribed (Taylor 1976), a coding system was adopted to refer to individual morphospecies. The task of converting morphospecies to named species, particularly with the smaller-bodied taxa (Lawton *et al.* 1998), was too great for the scope of this study. However, selected groups were sent to specialists in order to obtain more definitive names. Because of the taxonomic complexity of dealing with large numbers of juvenile spiders and also with the extremely high richness of Hymenoptera, these two groups were sorted only for the first two seasons. Only adult invertebrates were considered in this paper.

The invertebrates were also categorized by feeding guild following the procedure of Moran and Southwood (1982). Some guilds contained insufficient species to allow statistical analysis, and were therefore amalgamated into larger guilds.

Bark fauna

In 1998, eight study sites, each approximately 3 ha in area, were selected along a transect south-east from Perth (Fig. 1a). The Karragullen site (T1) is located closest to Perth on the Darling Scarp, while Dryandra Woodland (T8) is located at the other end of the moisture gradient, close to Narrogin. Sites T2–T4 are distributed at approximately 10 km intervals along the Brookton Highway between Karragullen and Brookton. The distance between the remaining sites is somewhat greater (≈15–20 km). The five sites closest to Perth are in jarrah/marri open-forest. Site T5, the last of the jarrah/marri sites, is an outlier located within wandoo and powderbark wandoo woodland. Powderbark wandoo (Fig. 2b) and wandoo (Fig. 2c) woodlands characterize the sites from T6 through to Dryandra (T8).

Site selection was based on the availability of trees large enough to accommodate invertebrate traps, accessibility, and fire history. All sites, except T1 and T8, were located near main roads. No study site had been burnt in the two years preceding the project, and no fires occurred during the study.



(a) Jarrah-marri forest — Karragullen

(b) Powderbark wandoo woodland — Dryandra

(c) Wandoo woodland — Dryandra

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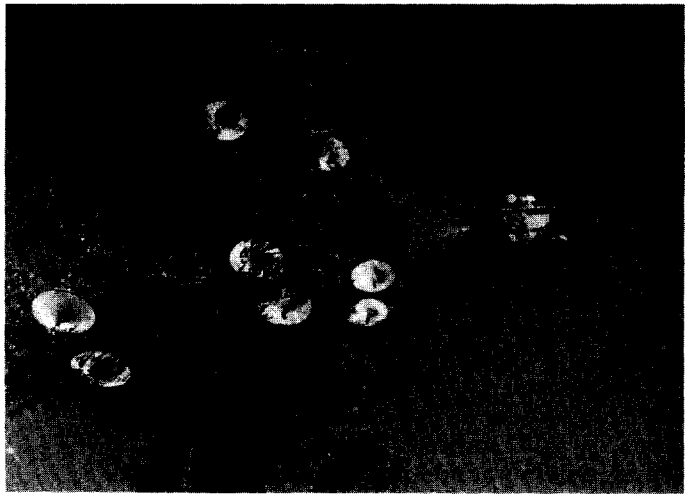
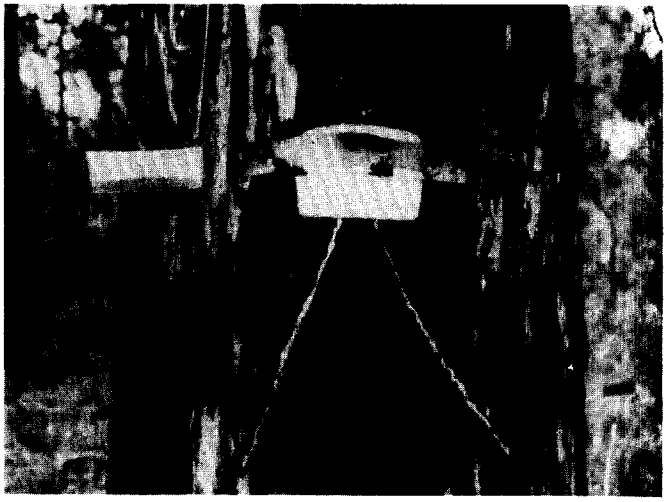
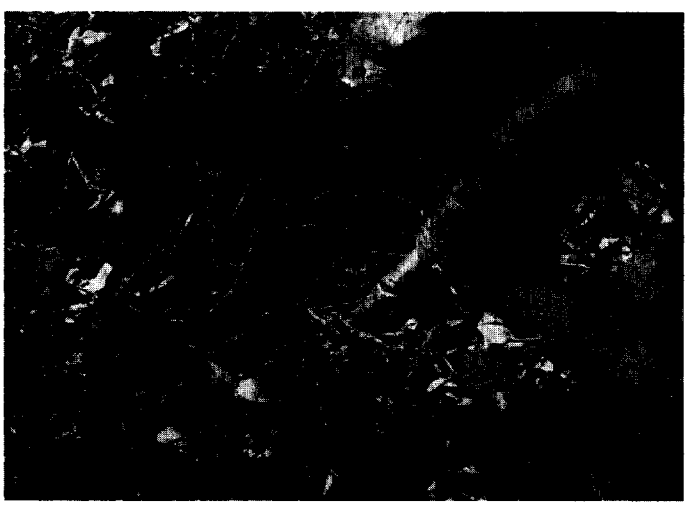


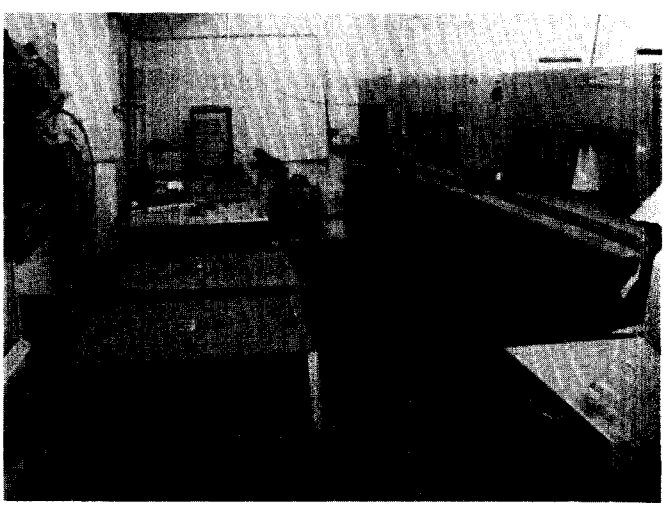
(a) Canopy knockdown procedure



(b) Intercept (left) and bark (right) traps on trunk



(c) Collecting leaf litter from quadrat. Soil is collected by coring in centre of quadrat.



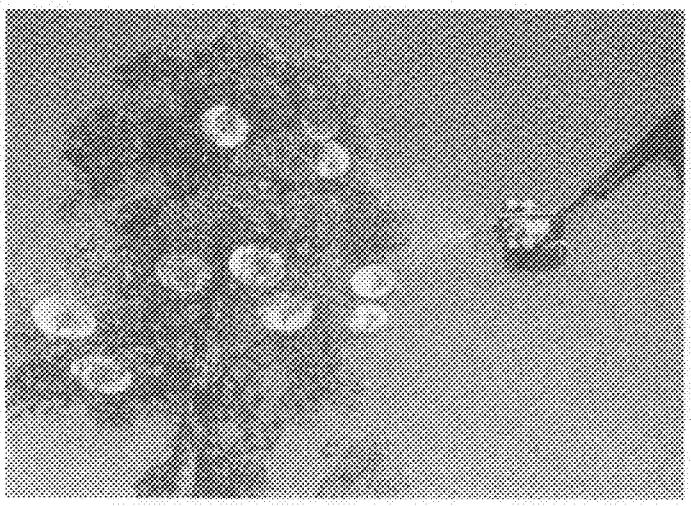
(d) Berlese Funnels (left) and heat extractors (right) for extracting invertebrates from litter and soil, respectively.

Fig. 3. Collecting procedures for sampling canopy, trunk, soil and litter fauna.

Ten mature trees were selected at each site in mid-1998. Marri trees were the focus of the moisture gradient investigation because this was the only tree species that occurred along the entire length of the transect. T1 and T8 were the only sites where other tree species were also sampled, with Jarrah being sampled at both sites. At T8, both wandoo plus powderbark wandoo were also sampled.

Invertebrates were sampled using two methods: a modified arboreal bark trap (Moeed and Meads 1983) and a perspex intercept trap (Fig. 3b). These traps were attached to the northern side of trunks at breast height (1.5m) on large eucalypt trees. Where the bark was unsuitable for attaching traps, due to damage or surface irregularities, the traps were placed on the first suitable surface of the trunk moving in an easterly direction around the tree.

Bark traps were nailed to the bark and were designed to sample invertebrates that were moving, or living, on the trunk. An open triangular configuration of 90 cm-long drift fences, separated by a distance of 60 cm at the lower end, was used to channel invertebrates moving vertically up the bark into the trap's entrance. The drift fences were nailed into grooves cut into the rough bark or nailed into place on smooth barked trees. Silicone sealant was used to fill in gaps along the 40 mm high drift fences. Invertebrates caught in the trunk traps were preserved in a 50% ethylene or propylene glycol solution until traps were emptied.



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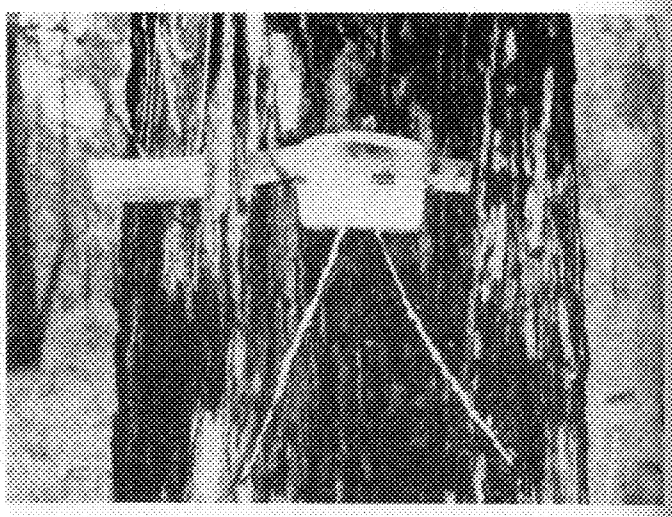

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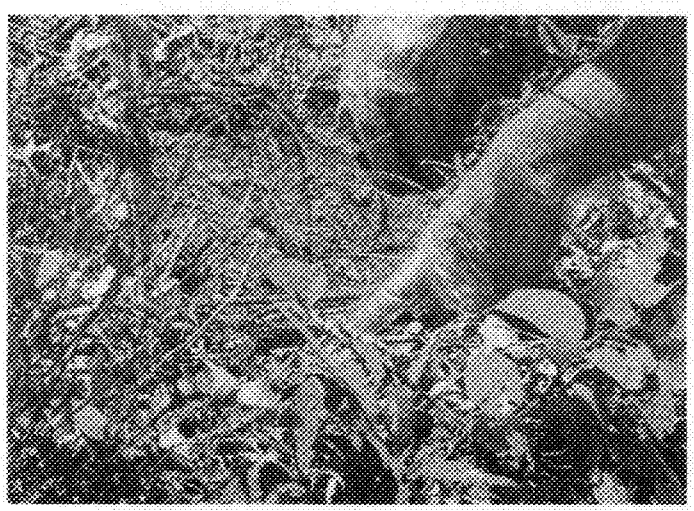

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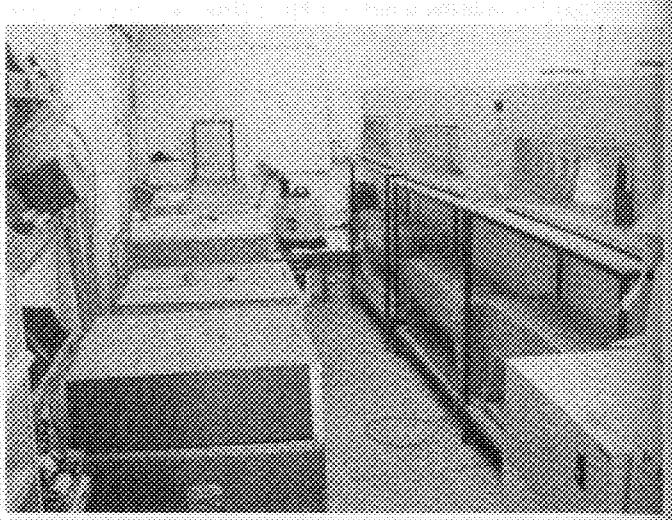

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Intercept traps were designed to catch invertebrates attempting to land on the bark surface. Plates were placed to the left and slightly above the bark traps. A flat piece of perspex 130 mm × 300 mm was nailed to the trunk with a collecting tray clipped onto the bottom 30 mm using alligator clips and supported underneath by nails. The collecting vessel, which contained ethylene or propylene glycol, had small perforations half-way up the sides to allow overflow when rain occurred during sampling.

Invertebrate sampling was undertaken between October 1998 and October 1999. Sampling took place at 8-week intervals, with traps remaining active for two weeks before being cleared. Samples were transferred to 70% ethanol for subsequent sorting. The samples for Spring (October-November) 1998 and Winter (August) 1999 were sorted to morphospecies level, with various taxonomic groups forwarded to available taxonomic specialists. Ants and some wasps were identified using local expertise.

As with the canopy fauna, invertebrates were also categorized by feeding guild. Moran and Southwood (1982) was the main authority used for assigning guilds, but CSIRO "Insects of Australia" (1990) was utilized for some other insect groups. Invertebrates were assigned to more than one guild where this was warranted (e.g., larvae and adults have different diets, or the invertebrate taxon is polyphagous).

Soil and litter fauna

The study area was distinct from that used for the previous two exercises, and was situated 10 km SE of Dwellingup (Fig. 1a). Within the general study area (Fig. 1b) two of the sites selected were near Yarragil Brook, in micro-catchments 4P and 4L. The soil here was laterite, and the trees were jarrah and marri. A third site (ML) was situated on the Murray River bank on Murray River loam soil and was partly under flooded gum (*Eucalyptus rudis*). Each site comprized three 40 m × 20 m plots arranged at 15–40 m intervals in a transect perpendicular to the bank of the stream.

Between June 1980 and September 1981, soil and litter fauna were sampled every month from each of 20 stratified, randomly selected points within each plot (Fig. 3c). At each point the litter was removed from a 19 cm × 19 cm quadrat and sealed in plastic bags. Soil cores (54 mm diameter, 97 mm depth) were then taken from beneath the litter, and the soil extruded into 54 mm internal diameter plastic sleeves with a 3 mm mesh base. Both sets of samples were returned to the laboratory and the soil fauna extracted using a multiple canister heat extractor (Fig. 3d, on right) (Southwood 1966) in which the temperature was raised from ambient to 40°C over a week.

Only nine Berlese funnels (Fig. 3d, on left) were available, so the 20 replicate samples from each of the three plots at a site were bulked, mixed and placed in the funnels. Each funnel had a mesh of 43 cm × 43 cm that had a 1.2 mm × 1.6 mm hole size. This stopped small litter fragments falling into the alcohol preservative, but also prevented the passage of large litter animals. Consequently, the small mesh was surrounded by an 8.5 cm boundary of 6 mm × 6 mm mesh hole size to allow the passage of larger animals. The temperature above the litter was raised using the same regime as for the soil.

Invertebrates from the soil and litter samples were sorted and counted to class and/or order, and the data have already been presented in an unpublished thesis by Postle (1989) and in Postle *et al.* (1991). Selected taxa were sorted to morphospecies and sent to specialists for identification. Taxa were selected on the basis of their being common in the samples, the availability of taxonomists and, to a large extent, their relevance to litter decomposition. The Protura, Diplura, Orthoptera and certain Coleoptera play a role in decomposition, but were not identified to species level, nor were insect larvae (which are difficult to sort to species level). In many cases the species or genera are undescribed or unknown. Trophic guilds have been assigned to the soil and litter fauna, employing the same principles used for the bark and canopy faunas.

Climatic patterns

All sites experience a Mediterranean climate with warm summers and cool winters. Rainfall occurs predominantly in the winter months, with annual averages of 1 078, 1 266, 459, and 504 mm respectively for Kalamunda, Dwellingup, Brookton and Narrogin, the closest meteorological recording stations (Fig. 1). Thus, the Dwellingup sampling location is slightly wetter than the Karragullen area. Also, although recording stations were not present at the eight sites along the bark sampling transect, it can be assumed that rainfall drops from T1 through to T7, and that T8 is slightly wetter than T7, on account of its more southerly location.

RESULTS AND DISCUSSION

In the foregoing, we do not discuss the invertebrate species collected on bark from trees outside of Karragullen or from soil and litter in the Murray Valley loam soil area in any detail, but rather we concentrate on those collected at Karragullen and the equivalent community at Dwellingup.

General trends

The results are summarized in Table 1 for canopy, bark and soil/litter respectively. The number of families for soil and litter is an underestimate because data on Acarina at family level were not available. However, the data on taxa collected from jarrah and marri at Karragullen are sufficient to enable a general statement to be made concerning invertebrate species richness on eucalypts in this region. We have also assumed that the data on soil and litter fauna from Dwellingup are what might be expected from the same substrates at Karragullen, since the two study areas are relatively close and on approximately the same longitude. The two areas are also on the same lateritic soil type and share similar plant communities, having a mid-storey of *Allocasuarina fraseriana*, *Banksia grandis* and *Persoonia longifolia*. Although we primarily consider invertebrates at the Karragullen/Dwellingup area, Table 1 also provides a summary of numbers of species and families from all sampling locations in order to provide a record of invertebrate diversity in these situations.

For the canopy study, 422 species in 133 invertebrate families were collected from jarrah, and 417 species from 146 invertebrate families were collected from marri. Overall, 561 species in 161 invertebrate families were collected from the canopy of both tree species at Karragullen. The Karragullen data for the bark study reveal that 313 species in 136 invertebrate families were collected from jarrah, and 276 species from 121 invertebrate families were collected from marri. The overall count was 416 species in 162 invertebrate families for both tree species combined. Finally, the incomplete data for the soil and litter study reveal that 242 species in 37 invertebrate families were taken from lateritic soil, and 222 species from 38 invertebrate families were taken from litter above this soil type. Three hundred and five species from over 38 families were sampled from soil and litter combined.

Overlap between strata

The pooled data for this four-tiered survey of invertebrate fauna to be found on and under eucalypt species near Perth is far from comprehensive. In particular, information on important taxa is lacking for the soil and litter study. (For example, ants and Acarina were collected in considerable numbers from all soil and litter sites, but taxonomic detail is not available.) The sampling methods also differ in each case. Moreover, the taxonomic expertise available varied with each of the studies, so that detailed treatment was often given to different taxonomic groups. However, there is clearly a degree of overlap, particularly at a higher

Table 1. Summary of total species and families sampled from (a) the canopy of jarrah (J) and marri (M) trees at Karragullen, (b) the bark of jarrah, marri, powderbark wandoo (P) and wandoo (W) trees along a west-east transect between Karragullen and Dryandra, and (c) from soil and litter associated with loam and lateritic soils at Dwellingup. Sites are shown in Figure 1.

(a)

	J	M
Total species	422	417
Total families	133	146
Total species overall	561	
Total families overall	161	

(b)

	Karragullen		W-E Transect						Dryandra			
	J1	M1	M2	M3	M4	M5	M6	M7	M8	J8	P8	W8
Total species	313	276	290	285	271	288	383	335	396	320	422	497
Total families	136	121	124	119	121	119	133	128	138	127	140	159
Total species at Karragullen	416											
Total families at Karragullen	162											
Total species overall	1 234											
Total families overall	269											

(c)

	Soil Type		Stratum	
	Loam	Laterite	Soil	Litter
Total species	189	242	180	222
Total families	32	37	25	38
Total species overall	305			
Total families overall	>38			

taxonomic level, for the bark and canopy fauna. These two substrates shared 126 identified families in common, or 79.2% of the 159 families identified for the canopy, and 80 genera (46.2% of the 173 identified canopy genera). Had more specialist identifications been made, we consider it very likely that these figures would be higher. Too few taxa were identified to species to compare these two substrates at the level of the fundamental evolutionary unit. Nonetheless, we can reasonably assume that many relatively mobile invertebrates are likely to move up the tree trunk into the canopy and back again, depending on their need for forage. This is certainly true for ants. A large number of ants (>100 species) were collected from the bark, and many of these species are known to travel up the trunk into the canopy in search of nectar, honeydew and prey (CSIRO 1990).

Are the taxa from the different strata different or is there overlap? With regard to the available data, the fauna of the soil and litter is distinct compared with the bark and canopy fauna. At a family level 24 taxa (60.0% of the 40 identified soil-litter families) were shared between soil-litter and bark, but soil-litter and canopy shared only 17 taxa (42.5% of identified soil-litter families). At the level of genus (where known) very few taxa were shared by soil-litter and canopy (5 = 6.2% of 81 soil-litter genera) or soil-litter and bark (7 = 8.6%). Many of the identified soil-litter organisms are minute and specialized, and not highly mobile. An example of this is the Class Pauropoda. No less than 40 species of these minute arthropods were identified from the soil-litter, one of the richest pauropod faunas identified in the world [U. Scheller, pers. comm.]. However, only one pauropod was collected from bark, and none from the canopy. The soil-litter collembolan fauna was also rich, with 47 species from 10 families and at least 38 genera represented here. This is not surprising, as most Collembola are decomposers and fungivores. Bark-dwelling Collembola were less numerous (30 species from 7 families, few identified to genus) and canopy-dwelling Collembola were relatively sparse (9 species from 5 families, and approximately 7 genera). However, Acarina collected from the bark were an exception to this pattern, with many of the Endeostigmata and Prostigmata typical of soil-litter fauna rather than arboricolous fauna [H. Proctor, pers. comm.]. The bulk of these are known to be predatory or fungivorous, but a reasonable proportion is also parasitic on insects in the larval stage. Some mites, such as the Uropodidae (Mesostigmata), are phoretic on insects, while other taxa may move up and down the bark surface independently.

In order to obtain a crude measure of the degree of similarity between fauna from the various strata, Sørensen's quotient of similarity was calculated for each combination of strata, using the overlap, and numbers of families in each stratum. Figure 4 is a diagrammatic representation of the similarity between strata, with the length of lines connecting strata being proportional to the inverse of the similarity quotient value. It clearly indicates that the fauna of soil and litter is most closely related in terms of families, followed, to a lesser extent, by the fauna of the canopy and trunk. The soil/litter

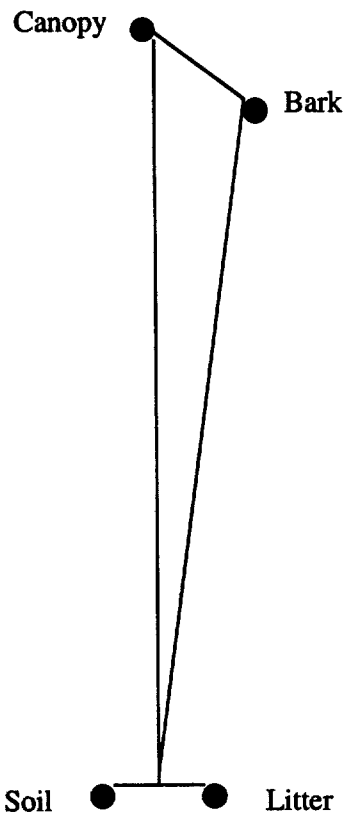

Fig. 4. Constellation diagram showing the degree of overlap between families of invertebrates in the four strata within the forest. Length of lines are proportional to the inverse of Sørensen's quotient of similarity between strata. For reasons of clarity, lines from soil and litter are the average for the respective values for soil and litter versus the other two strata.

fauna combined is most closely related to that of the trunk, and the least similar relationship is that between the soil/litter and the canopy.

The lack of species-level identifications makes precise comparison between the various strata impossible, and any estimation of biodiversity for a typical south-west *Eucalyptus* tree must take into account the mobility of the invertebrate community. To some degree the fauna of the canopy and the trunk is interchangeable, as, to a lesser extent, is that of the trunk and the surrounding soil and litter. Nonetheless, the overall biodiversity is high, with the bark fauna alone consisting of 1 234 adult morphospecies

of invertebrates (in 280 identified families and 426 identified genera). The canopy fauna was also rich, with 562 adult morphospecies of invertebrates identified (although the sampling method used is biased towards the larger specimens and those more easily dislodged from the canopy).

Trophic guilds

The different roles played in the ecosystem by the taxa from canopy, bark, litter and soil was assessed using trophic (feeding) guilds (Fig. 5a–d). The most salient feature is the high diversity of fungivores and decomposers (≈50% of the total taxa) present in soil and litter. Even were Acarina and ants to be factored in, the proportion would probably not change substantially since many mites are fungivorous. Fungivores-decomposers were far less diverse in the canopy (21.6%) and bark (16.9%). Sap-suckers were also more prominent in the soil and litter (13.9% and 12.8%, respectively)

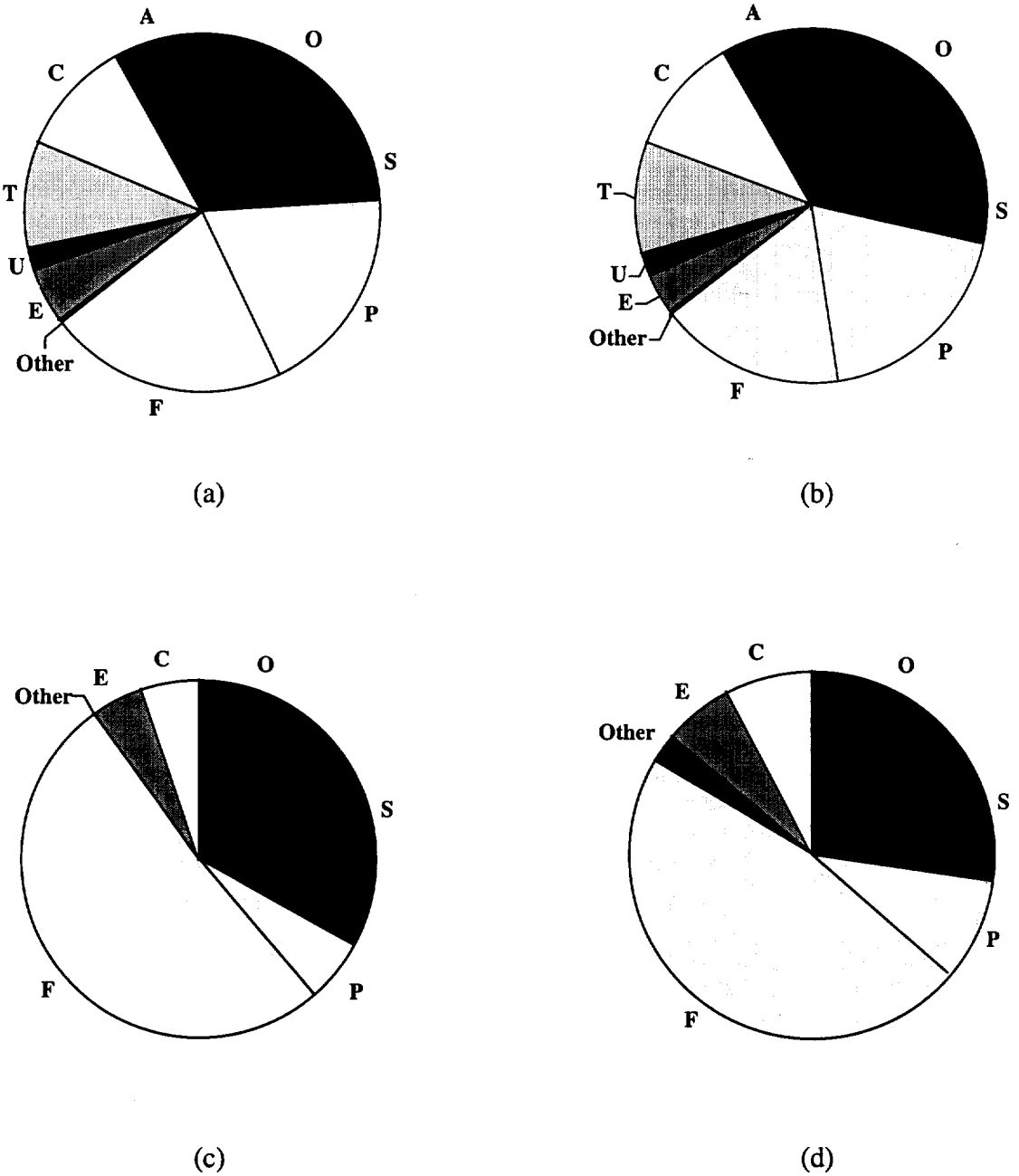

Fig. 5a–d. Profile of invertebrate trophic guilds in the four substrates mentioned in this paper. a. Canopy. b. Bark. c. Laterite. d. Litter. (Note that details of Acarina and ants (Hymenoptera) were not available for c and d). Abbreviations: A. — Ants. C. — Phytophages. E. — Epiphyte grazers. F. — Fungivores, scavengers and dead wood feeders. O. — Parasitoids. P. — Predators. S. — Sap-suckers. T. — Tourists. Other — Other trophic categories. U — Unknown (categories follow Moran and Southwood 1982).

compared with the canopy (5.3%) and bark (5.9%). On the other hand, the diversity of soil and litter predators was low (≈9–9.5% of the total taxa) compared with that of predators on bark and canopy (≈19–23%). This was also true of parasitoids (10.5% and 14.8% compared with 18.7% and 22.5%). Representatives of epiphyte grazers and phytophages formed a low proportion of the taxa (≤11%) at all levels. Tourists were not identified among the soil and litter fauna, although these were prominent among the canopy and bark faunas, and ants were not quantified for soil and litter. Representatives of other trophic guilds or organisms whose dietary habits are unknown were absent or represented only by few taxa (always ≤2.5%).

Fungivores–decomposers have an important role in the breakdown of vegetative and animal matter (Postle *et al.* 1986). These are often tiny organisms, well adapted to moving in the interstices between soil particles and closely packed debris. They are present in lesser numbers on the tree surface. What is perhaps surprising is that a greater diversity of fungivores-decomposers appears to reside in the canopy rather than on the bark (especially since there are more collembolan species on the bark than in the canopy). The relatively low richness of sap-sucking invertebrates in the canopy compared with other substrates is also surprising. However, some caution must be followed in interpreting this result, since the dietary habits of Australian pauropods (here assumed to be fungivores and sap-suckers) are not perfectly known (Harvey and Yen 1997). Also of interest is the low biodiversity of phytophages at all levels, this despite the fact that Coleoptera and Lepidopteran larvae are often conspicuous and may occur in damaging numbers on eucalypts. The low proportion of sap-sucking species in the canopy may, in part, result from undersampling of animals that are attached to the foliage through their mouthparts. This is evidenced by the fact that, using branch-clipping procedures, Abbott *et al.* (1992) found proportionately higher abundances of phytophages on jarrah than we did. However, the high level of secondary compounds, such as tannins, found in leaves and cambium in southern Australian eucalypts, are believed by some to have selected for a relatively small suite of phytophages that are evolutionarily suited to feeding on such forage (see discussion by Landsberg and Cork 1997).

We therefore concur with Abbott (1995) that a typical southwestern eucalypt supports a wide diversity of organisms, occupying a variety of trophic guilds. The number of species of macroscopic invertebrates to be found on and around a typical eucalypt species is certainly several thousand, possibly many more.

Diversity of invertebrates in eucalypt formations

Erwin's (1982) seminal paper on rainforest canopy invertebrates produced a global estimate of 30 million arthropods, a figure that is regarded by some to be an overestimate and by others to be too low (Stork 1988; May 1990; Gaston 1991). Erwin assumed that most diversity was contained within the tropics. Our own findings leave us to conclude that eucalypt communities are also extraordinarily rich in invertebrate species. If the current estimates of 140 000 Australian *insect* species are taken (Nielsen and West 1994), the insect component of the samples described here represent about 1% of the total Australian insect fauna. As this study only sampled four of the 700 or so Australian eucalypt species and the litter beneath them, and only sampled at a range of extremely localized sites, it is unlikely that we sampled as great a percentage as this of the Australian insect fauna. Apart from the bark transect, our study sites are localized and do not account for variation in species composition across the landscape. The results from the bark transect (J. D. Majer and H. F. Recher, unpubl. data), and the surveys of canopy arthropods over wide ranging sites by Burgman and Williams (1995) and Abbott *et al.* (2001) indicate that there is a high degree of species turnover across the landscape. This fact, and the high richness of arthropods from the different strata at the Karragullen/Dwellingup sites, therefore leads us to conclude that the current estimates of Australian insect and other terrestrial invertebrate richness are underestimates.

The work of Walter and Proctor (1998) and Walter *et al.* (1998) on the richness of mite faunas in Australian rainforest canopies also supports the contention that continental insect and arthropod species richness is much greater than acknowledged. While there may be little gain in replicating Erwin's estimates using Australian experience, it is hard to escape the conclusion that insect and other invertebrate species richness in eucalypt formations must be enormous, and that continental richness must be vastly greater than the current estimate of 225 000 terrestrial *arthropod* species (Nielsen and West 1994). This suggestion highlights two important facts. First, global species richness may well be much higher than even Erwin (1982) estimated. Second, the loss of biodiversity as forests and native vegetation are modified, fragmented, cleared, and degraded may also be considerably higher than current estimates suggest.

The figures for invertebrate species richness for tree species presented here are intermediate between the high values for the canopy of

tropical forests (e.g., see Erwin 1982, 1983a,b; Stork 1987; Basset and Arthington 1992) and the lower values for temperate deciduous (e.g., see Southwood *et al.* 1982a,b) and coniferous (e.g., see Ozanne *et al.* 1997; Winchester 1997) forests. Most of the contributions to the debate on global invertebrate species richness are based on data obtained from the tropics, with only moderate consideration being given to data from temperate forests. The data presented in this paper support the statement that Australia is one of the 12 megadiverse countries that, together, account for 75% of the total biodiversity of the planet (McNeely *et al.* 1992). They also concur with Platnick's (1991) statement that far more attention should be given to the temperate regions when estimating global biodiversity. It is likely that current estimates of invertebrate species richness would then be elevated to even higher levels.

Further research

The data reported here relate to the northern jarrah forest. It would be worthwhile repeating these observations along east-west transects in the central and southern jarrah forests and also in the karri (*Eucalyptus diversicolor*) forest. The resulting data-set would inform us on the regional variation in forest diversity and provide information on the adequacy of current reserve systems to conserve this biodiversity.

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