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Low-altitude mountain range is an important refugium for two narrow endemics in the Southwest Australian Floristic Region biodiversity hotspot

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22 Running title: Low-altitude mountain refugium for endemic species

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1   • **Background and Aims** Low-altitude mountains constitute important centres of

2 diversity in landscapes with little topographic variation, such as the Southwest Australian

3 Floristic Region (SWAFR). They also provide unique climatic and edaphic conditions that

4 may allow them to function as refugia. We investigate whether the Porongurups (altitude

5 655 m) in the SWAFR will provide a refugium for the endemic *Ornduffia calthifolia* and

6 *O. marchantii* under forecast climate change.

7   • **Methods** We used species distribution modelling based on WorldClim climatic data, 30

8 m elevation data and a 2 m resolution LiDAR-derived digital elevation model (DEM) to

9 predict current and future distributions of the *Ornduffia* species at local and regional scales

10 based on 605 field-based abundance estimates. Future distributions were forecast using

11 RCP2.6 and RCP4.5 projections. To determine whether local edaphic and biotic factors

12 impact these forecasts, we tested whether soil depth and vegetation height were significant

13 predictors of abundance using generalized additive models (GAMs).

14   • **Key Results** Species distribution modelling revealed the importance of elevation and

15 topographic variables at the local scale for determining distributions of both species,

16 which also preferred shadier locations and higher slopes. However, *O. calthifolia* occurred

17 at higher (cooler) elevations with rugged, concave topography, while *O. marchantii*

18 occurred in disturbed sites at lower locations with less rugged, convex topography. Under

19 future climates both species are likely to severely contract under the milder RCP2.6

20 projection (approximately 2°C of global warming), but are unlikely to persist if warming

21 is more severe (RCP4.5). GAMs showed that soil depth and vegetation height are

22 important predictors of *O. calthifolia* and *O. marchantii* distributions, respectively.

23   • **Conclusions** The Porongurups constitute an important refugium for *O. calthifolia* and

24 *O. marchantii*, but limits to this capacity may be reached if global warming exceeds 2°C.

25 This capacity is moderated at local scales by biotic and edaphic factors.

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2 **Key words:** anthropogenic climate change; extinction; interspecific interactions; localised

3 endemic; low-altitude mountain; refugia; microclimate; Southwest Australian Floristic

4 Region (SWAFR); *Ornduffia calthifolia*; *Ornduffia marchantii*; species distribution

5 modelling

INTRODUCTION

The world's mountains are centres of diversity and endemism (Kessler and Kluge, 2008; Ohlemüller *et al.*, 2008). Mountain species may also be particularly vulnerable to anthropogenic global warming and attendant climate change (Thuiller *et al.*, 2005; La Sorte and Jetz, 2010). Upward migration of species along elevational temperature gradients is resulting in range reductions for many species, as the total area available at a given altitude generally decreases with elevation on mountains (Wilson *et al.*, 2005; Parmesan, 2006). Where no suitable habitats are available at higher altitudes, climate change may lead to extinctions (Pauli *et al.*, 2003; La Sorte and Jetz, 2010). Species with narrow ranges that are restricted to mountaintops may therefore be amongst the most threatened by habitat loss leading to extinction (Pounds and Crump, 1994; Dirnböck *et al.*, 2011).

Although mountain species may be particularly vulnerable to anthropogenic climate change, steep environmental gradients and topographic complexity may provide important microrefugia for species (Byrne *et al.*, 2008; Médail and Diadema, 2009; Tapper *et al.*, 2014). Such refugia are often not detectable at the scale of most modelling studies, resulting in exaggerated predictions of extinction risk (Randin *et al.*, 2009; Austin and Van Niel, 2011*a*; Franklin *et al.*, 2013). However, microrefugia have facilitated the persistence of species during past climate change (Byrne *et al.*, 2008; Provan and Bennett, 2008) and are likely to play an important role in facilitating *in situ* persistence under ongoing and future climate change. Identifying and protecting refugia with the highest capacity to facilitate persistence is therefore critically important for effective conservation (Keppel *et al.*, 2012, 2015).

Low-altitude mountains often have significant conservation value but face particularly high conservation threats (Watson and Barrett, 2004; Guerin and Lowe, 2013; Barrett and Yates, 2015). Irrespective of their size, they are often the highest points in the landscape and provide unique climate and edaphic environments with attendant endemic species (Barrett

1   and Yates, 2015; Rebelo *et al*., 2006). Hence, they likely constitute important microrefugia

2   that may provide important safe havens for biodiversity under anthropogenic climate change

3   (Ashcroft, 2010; Keppel and Wardell-Johnson, 2012).

4   The Southwest Australian Floristic Region (SWAFR) and Cape Floristic Region are

5   globally significant centres of plant diversity where low-altitude mountains provide important

6   topography, and hence potential microrefugia. Climate change is predicted to have a

7   substantial impact on biodiversity in both regions (Midgley *et al*., 2002; Fitzpatrick *et al*.,

8   2008; Klausmeyer and Shaw, 2009), and species in mountainous areas at higher elevations

9   may be disproportionally vulnerable (McCullough *et al*., 2015). Indeed, both regions contain

10 high concentrations of species vulnerable to climate change (Yates *et al*., 2010; Foden *et al*.,

11 2013).

12   In the SWAFR, the Stirling Range (1090 m asl) and Porongurup Range (Porongurups 655

13 m asl) on the region's south coast provide distinctly montane environments, with numerous

14 endemic species restricted to higher and cooler elevations (Barrett, 1996; Barrett and Yates

15 2015). Here we use species distribution modelling to forecast the likely impacts of climate

16 change on two narrowly endemic, iconic species of the genus *Ornduffia* Tippery & Les in the

17 Porongurups. We also test whether *in situ* edaphic (soil depth) and biotic (vegetation height)

18 factors, which are difficult to include in species distribution modelling, significantly affect

19 the distribution of the two species and hence the capacity of potential microrefugia. We thus

20 determine whether the Porongurups, or other proximal locations, have the potential to act as

21 refugia for *Ornduffia* species under anthropogenic climate change.

22

23

24   MATERIALS AND METHODS

25 *Study Site*

The SWAFR constitutes a global biodiversity hotspot, with high plant species richness and endemism, and highly modified landscapes (Myers *et al.*, 2000; Hopper and Gioia, 2004). This high diversity exists in landscapes displaying little topographic variation, with only a few areas of moderate elevation and limited scope for altitudinal migration (Hopper and Gioia, 2004; Rix *et al.*, 2014). Granite outcrops provide important topography in this landscape, and likely acted as refugia during past periods of climate change (Tapper *et al.*, 2014; Schut *et al.*, 2014).

The Porongurups constitute Australia's most massive granite outcrop, covering an area of about 12×3 km with several peaks exceeding 600 m in altitude (maximum: 655 m a.s.l.). It consists of a series of granite domes dating to about 1,100 million years ago (Abbott, 1982). The climate is Mediterranean, with cool, wet winters and hot dry summers, and attracts considerable orographic moisture due to its size and height. The summits are mostly bare or covered with lichens, herbaceous plants and scattered shrubs. Lower down, a belt of *Eucalyptus cornuta* and *E. megacarpa* leads into extensive karri (*E. diversicolor*) forest on the lower slopes. This karri forest is a significant outlier for mesic species from the cooler-higher rainfall zone of the SWAFR, considerably extending the species' ranges at their arid margins, presumably in response to favourable local climates and soil moisture created by the range's topography (Churchill, 1968; Abbott, 1982; Schut *et al.*, 2014). The Porongurups are a highly important, traditional ceremonial place for the Nyoongar people.

Although floristically not among the richest of the south-western Australian granite outcrops, the Porongurups include about 750 native species. These include five species of local endemics (Barrett, 1996); *Brachysema subcordatum* (Fabaceae), *Hibbertia bracteosa* (Dilleniaceae), *Billardiera granulata* (Pittosporaceae), *Apium prostratum* ssp. *phillipii* (Apiaceae) and *Ornduffia calthifolia* (Menyanthaceae). There are also several species whose

1   distributions are centred on the Porongurups, including *Ornduffia marchantii*, a close relative

2   of *O. calthifolia*.

3

4   *Study Species*

5   *Ornduffia* is a genus of eight southern Australian taxa (five confined to south-western

6   Australia), that has been recently recognised as distinct from *Villarsia* in the morphologically

7   diverse and cosmopolitan family Menyanthaceae, which includes 60-70 aquatic and wetland

8   species (Tippery and Les, 2009). *Ornduffia calthifolia* (Fig. 1A-C) is an erect, robust

9   perennial, locally endemic to moist sheltered sites on the upper slopes of granite outcrops of

10   the Porongurups (Brown *et al*., 1998). The fleshy-leaved species is widely recognizable, and

11   iconic to the Porongurups (Barrett, 1996; Brown *et al*., 1998). The stem bearing the

12   inflorescence (culm) rises to a metre or more. Adventitious roots arise form a fleshy

13   underground organ, providing a reserve of water and nutrients, and enabling rapid growth

14   under favourable conditions (Pate & Dixon, 1982). However, the species is apparently

15   drought susceptible, evidenced by observations of dead plants after the extreme heat of

16   January 1991 (Robinson and Coates, 1995). *Ornduffia calthifolia* is killed by fire and relies

17   on seedling regeneration for persistence. Fire may enhance germination, but inter-fire

18   seedling establishment also occurs (Gilfillan and Barrett, 2004).

19   *Ornduffia calthifolia* was declared as Rare Flora under the Western Australian *Wildlife*

20   *Conservation Act 1950* in November 1980, ranked as Endangered (EN) in 1997, and listed

21   under the Commonwealth *Environment Protection and Biodiversity Conservation* Act 1999

22   (EPBC Act - Gilfillan and Barrett, 2004). This species also meets World Conservation Union

23   (IUCN, 2012) Red List Category EN (but is not currently listed), under Criteria C2a, due to a

24   continuing decline in the number of mature individuals, with no population estimated to

1   include more than 250 mature individuals. Nine populations and 582 mature plants were

2   known when the species Interim Recovery Plan (Gilfillan and Barrett, 2004) was published.

3   Abbott (1982) originally listed *O. calthifolia* from karri forest at the 300 m contour in the

4   Mira Flores estate on the southern slopes of the Porongurups, prior to recognition of a second

5   species in the area. Ornduff (1990) described the closely related *O. marchantii* (Fig. 1D,E)

6   from a small population at 450 m elevation in a boggy site amongst karri forest. *Ornduffia*

7   *marchantii* is similar, but much smaller, and occurs in seasonally wet loams on lower to mid

8   slopes at altitudes below populations of *O. calthifolia* (Gilfillan and Barrett, 2004). Ornduff

9   (1990) also noted the capacity for hybridisation and putative hybrids between the two species

10 have been reported in the overlap zone (Robinson and Coates, 1995). *Ornduffia marchantii* is

11 currently known from eight specimens in the WA Herbarium, with six originating from the

12 Porongurups. The remaining two specimens are from populations in now degraded vegetation

13 within 10 km to the north and west of the Porongurups. Extensive searches by GWJ did not

14 find the species and these populations are likely to be no longer extant.

15

16 *Field-based variables:*

17 In February 2012 and November 2013, we recorded the abundance of *O. calthifolia* and *O.*

18 *marchantii*, and their putative hybrid, throughout the Porongurups and surrounds. We used

19 strategic random sampling to obtain the abundance of *Ornduffia* species, vegetation height

20 (m), soil depth (cm) and GPS coordinates for 606 locations (207 with *O. calthifolia* present,

21 55 with *O. marchantii*, 14 with the putative hybrid, and 362 absences with neither species

22 present; note that more than one taxon occurred in some locations). Abundance of each

23 *Ornduffia* taxon was recorded using a modified Braun-Blanquet scale (5 = ≥75%, 4 = 50-

24 74%, 3 = 25-50%, 2 = 10-25%, 1 = <10%), estimating cover in circular 27 m^2 plots. Plots

25 were at least 20 m apart. Vegetation height was estimated using a ruler and a 2 m pole. Soil

depth was determined as the average of five soil depth measures from around the main stem

of an individual plant by inserting a scaled (cm) soil probe (with a maximum range of 50 cm),

following the approach of Houle and Phillips (1989). GPS co-ordinates were collected using

a Garmin Etrex 10 GPS.

Elevation Data Sources

LiDAR data was obtained by airplane using a Leica ALS 50-II scanner, flying in April 2011.

Flight height was approximately 1700-2200 m resulting in 0.63 points per m^2, which was

interpolated into a 2 m grid using triangulation. Horizontal and vertical accuracy was <0.35

m and <0.15 m, respectively. Further details can be found in Schut *et al.* (2014). This data

was used for fine scale, localised species distribution modelling of the Porongurups.

Elevation data at 30 m resolution (1-arc second) from the Shuttle Radar Topography Mission

(SRTM) was used for regional scale modelling, which extended to other proximal ranges

(e.g. Stirling Range) in the south-west.

Climatic Data

Climatic variables were recorded for one year (1 November 2011 to 31 October 2012) using

two climate stations with a CR200X (CS215 CSL; manufacturer: Campbell Scientific

Australia Pty Ltd.) series data logger, and sensors for air temperature and relative humidity

(CS215 CSL; manufacturer: Campbell Scientific Australia Pty Ltd.), precipitation (CS702

tipping bucket rain gauge; manufacturer: Hydrological Services Pty. Ltd.), solar radiation

(SP210 pyranometer; manufacturer: Apogee Instruments Inc.), soil moisture (CS625 water

content reflectometer; manufacturer: Campbell Scientific Australia Pty Ltd.).

Each climate station was equipped with an iButton data logger (DS1923 Hygrochron;

manufacturer: Maxim Integrated), which was attached to the climate station in a plastic cup

1 insulated with duct tape. This was to facilitate comparison with other iButtons placed in

2 various locations with different aspects and radiation intensities. The two climate stations

3 were placed at different altitudes (385 m – foothill climate station, 590 m – hilltop climate

4 station), but were both located on the northern side of the Porongurups. We compared the

5 temperatures recorded by the iButton on the north-facing hilltop climate station with that of a

6 south-facing iButton of similar altitude (580 m; 34°40'21.10"S; 117°50'28.19"E).

7   Bioclimatic variables (annual mean temperature and precipitation) were acquired from

8 WorldClim, which are generated at a resolution of 1 km^2 via interpolation of average monthly

9 weather station data (Hijmans *et al.*, 2005). Future condition bioclimatic variables were used

10 to assess species distribution under a projected climate based on two representative

11 concentration pathway scenarios - 2.6 (RCP2.6) and 4.5 (RCP4.5). RCP2.6 projections are

12 based on the lowest emission scenario, assuming a global mean temperature increase limited

13 to 2°C and requiring substantial reductions in greenhouse gas emissions (van Vuuren *et al.*,

14 2011). RCP4.5 assumes medium-low emissions producing a global mean temperature

15 increase of around 3°C (Thomson, 2011). For the regional-scale model, cell size was

16 downscaled to 30 m using cubic convolution resampling to be commensurate with the SRTM

17 elevation data and regional scale topographic derivatives.

18

19 *Topographic Derivatives*

20 A suite of raster surfaces were derived from both elevation data sources (LiDAR and SRTM)

21 including slope (first derivative of elevation), aspect (degrees from north), and curvature

22 (second derivative of elevation). A curvature of 0 suggests the terrain is flat, negative

23 curvature is upwardly concave (convex) and positive curvature is upwardly convex

24 (concave). Relative Topographic Position, a measure of terrain ruggedness, was calculated

25 using methods described in Cooley (2015). Total solar radiation for 2011 was calculated in

1   ArcGIS (ESRI, 2015) using the techniques outlined by Fu and Rich (2000). This

2   approximates incoming solar radiation over the year (WH/m^2) by summing monthly intervals.

3   The Topographic Wetness Index (TWI), a surrogate for soil moisture, was calculated using

4   Eq. 1 (Gessler *et al.*, 1995):

5   $$TWI = ln\left(\frac{a}{tan\,\beta}\right) \qquad\qquad\qquad (Eq.1)$$

6   where α is calculated as (flow accumulation + 1)×(pixel area in m^2). β is the slope in radians.

7   Flow accumulation measures the number of cells that drain into an individual cell (Olivera *et*

8   *al.*, 2002).

9

10   *Species Distribution Modelling*

11   Modelling was conducted at local and regional scales using 2 m and 30 m resolution surfaces,

12   respectively using MaxEnt version 3.3.3k, which uses the concept of maximum entropy to

13   predict potential distributions (Phillips *et al.*, 2006). A logistic output format was used for all

14   models, whereby suitability ranges from 0 to 1 for each grid cell. The local scale model used

15   elevation and topographic derivatives but not bioclimatic variables, as none are available at

16   such fine scale resolution. We used this model to explore habitat preferences of the two

17   species by dividing predicted suitability into four equal-interval classes and extracting the

18   mean value of all variables at 1000 random locations within each class. Differences between

19   classes were tested using Tukey's Honestly Significantly Different test (Kramer, 1956).

20   At the regional scale, elevation was strongly and significantly correlated with mean annual

21   temperature (r = -0.8, p < 0.01) and discarded from regional scale modelling to avoid

22   masking the influence of temperature. In addition, we added mean annual precipitation to

23   enable projections of both a warmer and drier climate under two climate change scenarios to

24   2070. Predictions of potential distributions (suitability) based on current conditions and

1 climate change forecasts were calculated. As the convex hull of the sampling design covered

2 the majority of the LiDAR image, no bias file (Fourcade *et al.*, 2014) was deemed necessary

3 for the local-scale model. However, to avoid potential overfitting, the convex hull of presence

4 points was used to mitigate sampling bias (Young *et al.*, 2011; Brown, 2014) for regional

5 scale modelling.

6   Species presence records were randomly subset, with 90% used for model training

7 ("training subset") and 10% used as an independent source for model validation ("testing

8 subset"). Validation was conducted using both the training and testing datasets by computing

9 the area under the curve (AUC) of receiver operating characteristic (ROC) graphs (Fielding

10 and Bell, 1997). Interpretation of discrimination potential used the ranges presented by

11 Hosmer and Lemeshow (2000).

12

13 *Ecological Modelling*

14 The abundances (*Ab*) of *O. calthifolia* (OC) and *O. marchantii* (OM) were the response

15 variables. We did not model the distribution of the putative hybrid between the two species

16 (OX) because of the low sample size ($n = 14$). A combination of field-based and remotely-

17 sensed variables was used to determine the key ecological factors driving species distribution

18 and abundance. We initially considered the following predictor variables for the starting

19 model: soil depth (*S*); vegetation height (*V*); insolation (*I*) in winter (calculated as the average

20 insolation during the month of June, I_w), summer (average insolation during the month of

21 December, I_s), and throughout the year (average insolation throughout the year, I_a); aspect

22 (*A*); curvature (*C*); elevation (*E*); roughness (*R*); and topographic wetness index (*T*). The

23 averages, variation and ranges of these variables are summarised for the three taxa in Table 1.

24 All analyses were implemented in R software 2.15.1 (R Development Core Team).

1   To avoid concurvity, we tested for correlation among explanatory variables using

2 Pearson's correlation coefficient, removing variables with a coefficient >0.5. If correlation

3 was detected, we retained variables that were ecologically more relevant and more proximal

4 (rather than distant) predictors (Dormann *et al.*, 2013). Because winter (I_w) and summer

5 insolation (I_s) were positively correlated to each other ($r = 0.518$) and to annual insolation (I_a;

6 $r = 0.905$ and 0.828, respectively), we excluded summer and winter insolation from starting

7 models. In addition, strong correlations were observed between vegetation height (V),

8 elevation (E), roughness (R), and topographic wetness index (T) (Table S2). To address this,

9 we removed R, which (in our opinion) was ecologically the least meaningful variable.

10 Because *O. calthifolia* appeared to be restricted by elevation (no presences below 447 m,

11 Table 1) and *O. marchantii* by vegetation height (no presences below 3 m, Table 1), we

12 decided to include these variables instead of the correlated terms in the respective models.

13 Because of the correlation between vegetation height and soil depth ($r = 0.511$), we excluded

14 the latter from the model for *O. marchantii*.

15   We therefore built two generalised additive models (GAMs) including all retained

16 variables. The 'mgcv' package (Wood, 2016) was used to implement the models with the

17 following function calls: gam(as.factor(Ab_{OC}) ~ s(S) + s(I_a) + s(A) + s(C) + s(E)),

18 gam(as.factor (Ab_{OM}) ~ s(I_a) + s(A) + s(C) + s(V)). We assumed a binomial error distribution

19 and used a logistic-link function. Independent variables in the model were selected using

20 backwards stepwise regression. Non-significant terms ($p <0.05$) based on the likelihood ratio

21 were consequently removed. The significance and fraction of variance explained were

22 determined for each selected independent variable. In addition, we used the Akaike

23 Information Criterion (AIC; Akaike, 1974) to test model performance. We used a second-

24 order AIC: AICc = AIC $+2(K(K + 1)/(n - K - 1))$, where K is the number of parameters in

25 the model and n is the number of sample points (Burnham and Anderson, 1998).

1

2

3   RESULTS

4   *Climate*

5   As expected for Mediterranean climates, high rainfall was recorded in winter and spring

6   (June to September). In addition, high rainfall was recorded in November and December as a

7   result of storm systems causing high precipitation on 3 November (27.4 mm) and from 6-8

8   December (53.8 mm) (Fig. 2). Temperatures were lower at higher elevations (the hilltop

9   climate station at 590 m and the south-facing iButton at 580 m), where monthly average

10   temperatures were about 2-3°C lower than at the foothill climate station (385 m elevation).

11   The south-facing iButton recorded consistently lower temperatures (0.95° on average) than

12   the iButton facing north.

13   The hilltop climate station had lower average temperatures, lower precipitation, higher

14   humidity, higher soil moisture, and lower insolation than the foothill climate station (Table

15   S1). Differences were most pronounced for soil moisture (the annual average was 110.7%

16   percent higher in the hilltop climate station) and precipitation (24.5% more total rainfall at

17   the foothill climate station). Differences in climate variables between the two climate stations

18   were most pronounced during winter (June to August) and least pronounced during summer

19   (December to February).

20

21   *Species Distribution Modelling*

22   Elevation had the greatest explanatory power for local models (LiDAR-based) of the two

23   species (Table 2A), although its effect was less pronounced for *O. marchantii* with

24   roughness, aspect, solar radiation and TWI contributing strongly to the model (Table 2A). At

25   the regional scale, temperature (correlated with elevation) and precipitation contributed >

1   97% for both species (Table 2B). Considering the qualitative interpretation of AUC values

2   proposed by Hosmer and Lemeshow (2000), discrimination potential ranged from excellent

3   (*O. marchantti*) to outstanding (*O. calthifolia;* Table 2).

4   Under current conditions, both species preferred cooler environments. The most suitable

5   habitats occurred at higher average elevations, being c. 630 m for *O. calthifolia* and c. 550 m

6   for *O. marchantii* (Table 3). In addition, both species preferred southerly (shadier) aspects

7   that receive less solar radiation over the year, although aspect preferences were more south-

8   west for *O. calthifolia* and south-east for *O. marchantii*. Both species preferred steeper

9   slopes, although this relationship was far more prominent for *O. calthifolia*. The two species

10   differed in terms of curvature preference and ruggedness with *O. calthifolia* preferring

11   concave, rugged terrain and *O. marchantii* convex, less rugged locations although curvature

12   was not a significant variable between suitability classes within species.

13   Suitable locations for *O. marchantii* modelled at the local scale with elevation and

14   associated topographic derivatives were far more widespread than for *O. calthifolia* – the

15   latter restricted to higher altitude areas (Fig. 3A,B). Regional modelling also identified the

16   Porongurups as suitable habitat with few other suitable sites (e.g. Mount Barrow and Mount

17   Manypeaks) in the region likely to host either species (Fig. 4A). However, even under the

18   mildest temperature prediction for 2070 (RCP2.6), the range of both species contracted

19   significantly. Remaining sites were only moderately suitable and restricted to the

20   Porongurups (Fig. 4B,E), suggesting no opportunities for translocation. Under more severe

21   warming and drying (RCP4.5), modelling suggests no suitable habitat for either species by

22   2070 (Fig. 3C,F).

23

24   *Ecological Modelling*

1   The best model for *Ornduffia calthifolia* included elevation, insolation, soil depth and

2   curvature and explained almost 48% of the observed deviance (Table 4). Although curvature

3   was marginally not significant ($p = 0.055$) in the overall model, removing it significantly

4   reduced the performance of the model ($X^2 = 16.64$, $p = 8.4 \times 10^{-4}$, likelihood ratio test). Of

5   these variables, elevation explained the greatest amount of variance (33%; Table 5). For *O.*

6   *marchantii*, the best model included vegetation height and aspect, and explained 46% of the

7   total deviance. Vegetation height alone explained almost 38% of the observed deviance.

8   The putative hybrid between the two species was generally found in conditions that are

9   intermediate between the two species (soil depth, vegetation height, topographical wetness

10   index, solar insolation; Table 1). However, the average and range of elevation for the putative

11   hybrid were similar to those of *O. calthifolia*, suggesting that the hybrid can only form in

12   close proximity to this species.

13

14

15   DISCUSSION

16   *Climate*

17   Climatic conditions differed considerably with elevation and aspect over small distances.

18   Such differences in soil and air temperature are well-established (Rorison *et al*., 1986;

19   Fridley, 2009). High variability in climatic conditions on fine scales is usually related to

20   topographic complexity and indicates that microrefugia may be present (Dobrowski, 2011;

21   Ashcroft *et al*., 2012; Keppel *et al*. 2015).

22

23   *Species distribution modelling*

24   Species distribution modelling of two species endemic to the Porongurups (*O. calthifolia* and

25   *O. marchantii*) identified suitable habitat that closely matched descriptions in the literature

1 (e.g. Robinson and Coates, 1995; Gilfillan and Barrett, 2004) as well as our validation data.

2 Elevation, used in the local modelling as a surrogate for temperature, contributed strongly

3 (58-85%) to both models. However, at this scale, we were also able to capture the influence

4 of other variables, particularly aspect, roughness and solar radiation, which was not possible

5 at the 30 m resolution. At 30 m resolution, temperature was the key variable (74-86%) which

6 was also strongly (negatively) correlated to elevation. The combination of temperature and

7 precipitation were clearly the most important drivers of the regional-scale model (96-99%).

8 Spatial clustering of sampling points, difficult to avoid for rare endemic species with very

9 specific habitat preferences, likely contributes to the high model accuracy, despite random

10 selection and the use of an independent subset. Nonetheless, projected distributions under

11 climate change indicate that the distribution of both species will reduce markedly. Although

12 considerable range reductions are predicted for both species, persistence is likely under the

13 milder RCP2.6 scenario. However, both species are at high risk under the more severe

14 RCP4.5 projection, with likely extinction and no regional opportunities for translocation.

15 The Porongurups constitute an important refugium for both species under anthropogenic

16 climate change, despite being a low-altitude mountain range. Few areas outside of this

17 mountain range contain potentially suitable climate. However, our modelling highlights

18 important limits to refugial capacity, indicating that the range could cease to act as a refugium

19 for both species if global warming exceeds 2°C of pre-industrial levels. Our study therefore

20 highlights both the potential (through provision of unique microhabitats) and limitations (due

21 to restricted elevational range) of low-altitude mountains to act as refugia under

22 anthropogenic climate change. Furthermore, because of their lower elevation and the

23 associated smaller geographical extent compared with major mountain ranges, the protected

24 areas in which they lie tend to be smaller and surrounded by highly modified and populated

25 landscapes (Barrett and Yates, 2015; Rebelo *et al.*, 2006). Low-altitude mountain

communities and their endemic species are therefore particularly susceptible to a whole suite

of threatening processes in addition to climate change (Watson and Barrett 2004; Barrett and

Yates 2015).

Ecological modelling

It is important to note that predictions from SDM ignore biological and edaphic factors.

Based on ecological modelling, soil depth affects the distribution of *O. calthifolia* and

vegetation height that of *O. marchantii*. Deeper soils increase the habitat suitability for *O.*

calthifolia, and vegetation height (likely through shade provided by the karri forest) enhances

habitat suitability for *O. marchantii*. Our findings therefore highlight the importance of

considering the effects of forest on local climate (Scheffers *et al.*, 2014; De Frenne and

Verheyen 2016). Biological and edaphic factors therefore may significantly modify the

capacity of the Porongurups to act as refugia for both species.

Hybridisation has been observed between *O. calthifolia* and *O. marchantii* and presents a

potential threat to both species but particularly to the rare *O.calthifolia*. With climate change

causing upward migration of species, hybridization has recently been identified as a potential

threat for narrow-range congeners (Gómez *et al.*, 2015). Introgression of genetic material

from a common to a rare species can pose considerable conservation threats through genetic

assimilation of the rare species (Keppel *et al.*, 2011; Beatty *et al.*, 2015). Given that the

hybrids were most commonly found associated with *O. calthifolia*, asymmetric hybridisation

with *O. calthifolia* as the maternal parent could thus be a significant threat to this rare species.

Limitations of species distribution models

Our study highlights some of the limitations of species distribution models (Pearson and

Dawson, 2003; Sinclair *et al.*, 2010). The scale at which species distribution modelling is

1 undertaken has crucial impacts on the outcome. Unfortunately, gridded climatic data are

2 currently only available at a resolution of 1 km (or greater), which is considerably poorer than

3 the 2 m LiDAR used for local modelling and 30 m SRTM used for regional modelling.

4 Although interpolation algorithms were used to change cell size, it does not replicate the

5 resolution of the other datasets driving the model and masks local heterogeneities (e.g.

6 microclimate) that may facilitate persistence of the species. This is particularly relevant in

7 topographically complex areas, resulting in exaggerated predictions of extinction risk

8 (Randin *et al.*, 2009; Austin and Van Niel, 2011*b*; Franklin *et al.*, 2013).

9 Species distribution models do not consider interspecific interactions. This is especially

10 pertinent for *O. marchantii*, the distribution of which seems to be closely linked to the

11 presence of karri (*Eucalyptus diversicolor*), which is the dominant species in the only

12 community with vegetation heights of 20 m or more. The absence of *O. marchantii* in areas

13 of currently suitable climate appears to be a result of the requirement for shade provided by

14 high vegetation of the karri forest. In addition, most individuals of *O. marchantii* were found

15 at the margins of tracks (i.e. edges of disturbance) in these karri forest sites, suggesting some

16 level of disturbance is important to the growth of this species in the otherwise dense

17 understorey of the karri forest. Whilst it is possible to include vegetation height as a variable

18 in local models, its permanency, relative to topographic variables, is questionable. For

19 example, fire could remove large proportions and the range of the karri forest at this location

20 is predicted to contract strongly under forecast climate change (Wardell-Johnson et al., 2015).

21 Vegetation height therefore is unreliable for forecasting *O. marchantii* distributions.

22 Species distribution models require continuous and complete coverage (surfaces) of all

23 variables, which is not always feasible. For example, soil depth is an important factor

24 affecting the assembly and structure of granite outcrop plant communities (Poot *et al.*, 2012;

25 Schut *et al.*, 2014; do Carmo and Jacobi, 2015). Soil depth is seemingly important for

determining the distribution of *O. calthifolia* but cannot currently be captured using remote

sensing – nor are relevant maps or GIS layers available. Consequently, models can be mis-

specified if an important parameter cannot be incorporated into the model because it does not

exist, or cannot easily be derived as a surface.

Conclusions

We have demonstrated that the Porongurups have the capacity to continue acting as a

refugium for the target species, *O. calthifolia* and *O. marchantii*, and that edaphic (soil depth)

and biotic (vegetation height) factors may have strong impacts on this capacity. This

highlights the importance of considering such factors when interpreting the results of species

distribution modelling. Climate change exceeding 2°C of pre-industrial levels would have

significant consequences for these two species of *Ornduffia*. While climate change possibly

poses the most severe threat to the persistence of the two species, there are numerous other

threats such as potential hybridisation among the two species. Conservation planning

therefore needs to consider a complex array of factors under anthropogenic climate change to

facilitate persistence of low mountain endemics.

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5

TABLE 1. *Mean, standard deviation and range of variables considered for inclusion in the starting model for all three taxa.*

	Soil depth (cm)	Vegetation height (m)	Elevation (m a.s.l)	Topographic wetness index	Aspect (°)	Curvature	Roughness	Solar Radiation (WH m^{-2})
Ornduffia calthifolia (n=207)	21.2 (10.8; 3.0-50.0)	2.5 (5.1; 0.1-25.0)	596.2 (48.8; 447.2-669.6)	3.7 (1.9; 0-11.2)	186.9 (81.6; 8.3-358.9)	-14.4 (101.8; -1039.9-520.6)	0.5 (0.09; 0.3-0.8)	1113215 (257414.3; 110824.5-1556341)
*Ornduffia marchanti*i (n=55)	36.8 (16.6; 10-50)	20.9 (12.3; 3.0-40.0)	422.2 (143.2; 238.8-648.6)	5.3 (2.5; 1.7-12.7)	153.8 (104.3; 3.4-352.2)	-2.9 (17.8; -55.3-82.3)	0.5 (0.08; 0.3-0.6)	1271651 (179748.6; 784041.1-1485304)
Putative hybrid (n=14)	29.4 (17.1; 12.0-50.0)	14.4 (16.88; 3.0-40.0)	579.7 (61.6; 447.2-648.6)	4.9 (2.6; 2.2-10.5)	165.8 (70.4; 101.2-343.8)	-5.5 (31.6; -55.3-82.3)	0.5 (0.09; 0.4-0.7)	1179334 (201629.3; 784041.1-1510217)

TABLE 2: *Percent contribution of each variable to the species distribution model. (A) Local model (2 m resolution). (B) Regional model (30 m resolution). See text for variable definitions and variable selection.*

	SDM	Percent Contribution										Accuracy	
		Annual Temp (°C x 10)	Annual Precipitation (mm)	Elevation (m asl)	Roughness	Aspect (°)	Solar Radiation (WH/m^2)	TWI	Slope (°)	Curvature	Σ	AUC$_{Train}$[1] ± SE	AUC$_{Test}$[2] ± SE
A	*O. calthifolia*	-	-	85.2	0.7	0.6	3.1	3.8	2.1	4.4	100	0.991 ± 0.003	1.000 ± 0.000
	O. marchantii	-	-	58.0	12.8	12.7	6.0	5.4	4.3	0.8	100	0.905 ± 0.027	0.914 ± 0.092
B	*O. calthifolia*	86.3	13.2	-	0.1	0.2	0.1	0.1	0.0	0.0	100	0.946 ± 0.013	0.944 ± 0.042
	O. marchantii	74.5	22.5	-	0.0	0.3	1.7	0.0	0.9	0.0	100	0.812 ± 0.049	0.857 ± 0.132

[1] Computed using the training subset.

[2] Computed using the testing subset.

TABLE 3: *Average statistics of variables for each model for different habitat suitability class breaks. (A)* O. calthifolia. *(B)* O. marchantii.

Variables annotated with the same letter are not significantly different at α = 0.05 for those class intervals.

	Class	N	Elevation (m)	Roughness	Aspect (°)	Solar Radiation (WH/m^2)	TWI	Slope (°)	Curvature
A	0.75-1.00	1000	631.7[a]	0.53[a]	215.5[a]	1075442[a]	2.8[a]	38.0[a]	6.5[a]
	0.50-0.75	1000	610.9[b]	0.51[b]	196.3[b]	1133720[b]	3.4[b]	31.3[b]	2.5[a]
	0.25-0.50	1000	574.2[c]	0.50[c]	192.2[b]	1164544[c]	3.8[c]	28.2[c]	1.8[a]
	0.00-0.25	1000	342.2	0.50[c]	169.2[c]	1335118[d]	5.3[d]	12.0[d]	0.4[a]
B	0.75-1.00	1000	548.5[a]	0.45[a]	156.5[a]	1239289[a]	4.7[a]	17.4[a]	-2.1[a]
	0.50-0.75	1000	427.2[b]	0.46[a]	146.0[a,b]	1302324[b]	5.3[b]	13.2[b]	-1.5[a]
	0.25-0.50	1000	361.9[c]	0.49[b]	139.0[b]	1300151[b]	5.2[b]	12.3[b]	-0.4[a]
	0.00-0.25	1000	335.3[d]	0.50[c]	178.2[c]	1344218[c]	5.2[b]	12.5[b]	0.3[a]

7　TABLE 4: *Performance indicators of the best generalized additive models (highest deviance*

8　*explained, no correlated variables) describing the abundance of* Ornduffia calthifolia *and* O.

9　marchantii.

	d.f.	p-value	Deviance explained	Adjusted r^2
Ornduffia calthifolia				
Best model: Best model: $Ab_{OC} \sim s(S) + s(I_a) + s(A) + s(C) + s(E)$				
Model overall			47.8%	0.492
Elevation (E)	5.71	7.8×10^{-7}		
Insolation (I_a)	1.00	5.7×10^{-10}		
Curvature (C)	4.49	0.06		
Soil Depth (S)	3.21	3.5×10^{-7}		
Ornduffia marchantii				
Best model: $Ab_{OM} \sim s(A) + s(V)$				
Model overall			46.0%	0.383
Vegetation height (H)	3.75	9.7×10^{-4}		
Aspect (A)	8.66	2.1×10^{-9}		

10

TABLE 5: *Deviance explained,* p-*values and degrees of freedom (d.f.) for significant variable explaining the abundance of* Ornduffia calthifolia *and* O. marchantii.

	d.f.	*p*-value	Deviance explained
Ornduffia calthifolia			
Elevation (E)	5.30	1.0×10^{-5}	33.1%
Insolation (I_a)	5.01	$<2.0 \times 10^{-16}$	18.7%
Curvature (C)	6.97	6.1×10^{-12}	13.2%
Soil Depth (S)	3.52	1.0×10^{-7}	7.6%
Ornduffia marchantii			
Vegetation height (H)	8.58	4.8×10^{-9}	37.8%
Aspect (A)	3.09	0.016	4.84%

15 FIG. 1. *Ornduffia* species and habitat in the Porongurup Range, south-western Australia. (A)

16 Habitat of *Ornduffia calthifolia* (yellow-flowered plants in granite rock crevices) at 640 m

17 elevation; (B) Single plant of *O. calthifolia*; (C) Flowers of *O. calthifolia*; (D) Karri

18 (*Eucalyptus diversicolor*) forest habitat of *O. marchantii* at 330 m elevation. The karri trees

19 are approximately 50 m high and the site had been burnt by high intensity fire 5 years

20 previously (2008); (E) *O. marchantii* along disturbed firebreak in karri forest at 330 m

21 elevation; (F) Intermediate form along walk track in bullich (*E. megacarpa*) forest at 450 m

22 elevation; (G) Bullich forest habitat of intermediate form of *Ornduffia* at 450 elevation. The

23 bullich trees are approximately 10 m high. Photo credits A: Klaus Braun, B-G Grant Wardell-

24 Johnson.

25

26 FIG. 2. Climate diagram for the Porongurup Range from 1 November 2011 (11) to 31 October

27 2012 (10), showing the total rainfall for the foothill climate station (black bars) and the mean

28 monthly temperatures for iButtons at the foothill climate station (385 m elevation), at the

29 hilltop climate station (590m, north-facing), at a south-facing location (580m).

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31 FIG. 3. Local-scale species distribution models of *Ornduffia* species in the Porongurup Range

32 based on topopgraphic derivatives of LiDAR data. A) *O.calthifolia*; and (B) *O. marchantii*.

33

34 FIG. 4. Regional-scale species distribution models of *Ornduffia* species in southern Western

35 Australia using topographic derivatives of 30 m STRM data and bioclimatic variables

36 (resampled to 30 m). (A) *O.calthifolia* – current climatic conditions; (B) *O.calthifolia* –

37 climatic conditions 2070 based on RCP2.6; (C) *O.calthifolia* – climatic conditions 2070

38 based on RCP4.5; (D) *O. marchantii* – current climatic conditions; (E) *O. marchantii* –

39   climatic conditions 2070 based on RCP2.6; (F) *O. marchantii* – climatic conditions 2070

40   based on RCP4.5.

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Table S1: *Temperature, rainfall, relative humidity, soil moisture and insolation recorded for two climate stations from 1 November 2011*

to 31 October 2012. The two climate stations were placed at different altitudes (590 m – hilltop ; 385 m – foothill), but were both located

on the northern side of the PorongurupRange. See text for equipment details.

	Hilltop Climate Station (590m) 34°40'19.70" S; 117°50'27.51" E					Foothill Climate Station (385m) 34°39'47.17" S; 117°51'37.76" E				
Month	Temp. (°C)	Rainfall (mm)	Relative Humidity (%)	Soil Moisture (Vw)	Insolation (kW/m^2)	Temp. (°C)	Rainfall (mm)	Relative Humidity (%)	Soil Moisture (Vw)	Insolation (kW/m^2)
Nov 11	14.8	65.2	77.8	0.166	0.275	16.0	67.6	75.6	0.090	0.269
Dec 11	18.0	113.2	77.8	0.222	0.258	18.0	102.2	79.8	0.097	0.283
Jan 12	19.6	17.2	74.1	0.061	0.259	19.7	27.8	75.9	0.060	0.264
Feb 12	18.7	27.0	75.3	0.047	0.241	19.1	29.2	75.8	0.052	0.241
Mar 12	18.8	17.4	67.9	0.034	0.226	19.7	13.8	66.8	0.041	0.228
Apr 12	15.9	35.6	75.2	0.046	0.143	17.7	46.0	71.9	0.049	0.158
May 12	12.9	40.8	82.7	0.082	0.104	14.7	77.2	78.6	0.079	0.115
Jun 12	9.6	78.8	89.8	0.331	0.083	11.7	129.6	85.8	0.157	0.092

Jul 12	9.7	60.0	84.4	0.332	0.099	11.7	85.2	80.0	0.107	0.111
Aug 12	9.7	52.0	85.4	0.318	0.128	11.7	81.8	81.6	0.092	0.137
Sep 12	10.7	72.0	84.8	0.325	0.175	12.6	70.0	81.4	0.105	0.188
Oct 12	13.9	16.4	74.9	0.160	0.228	15.5	10.8	71.6	0.080	0.263
Total/Average	**14.4**	**595.6**	**79.2**	**0.177**	**0.185**	**15.7**	**741.2**	**77.1**	**0.084**	**0.196**

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TABLE S2: *Pearson's correlation coefficient (based on all 626 data points) for all variables considered for inclusion in the starting*

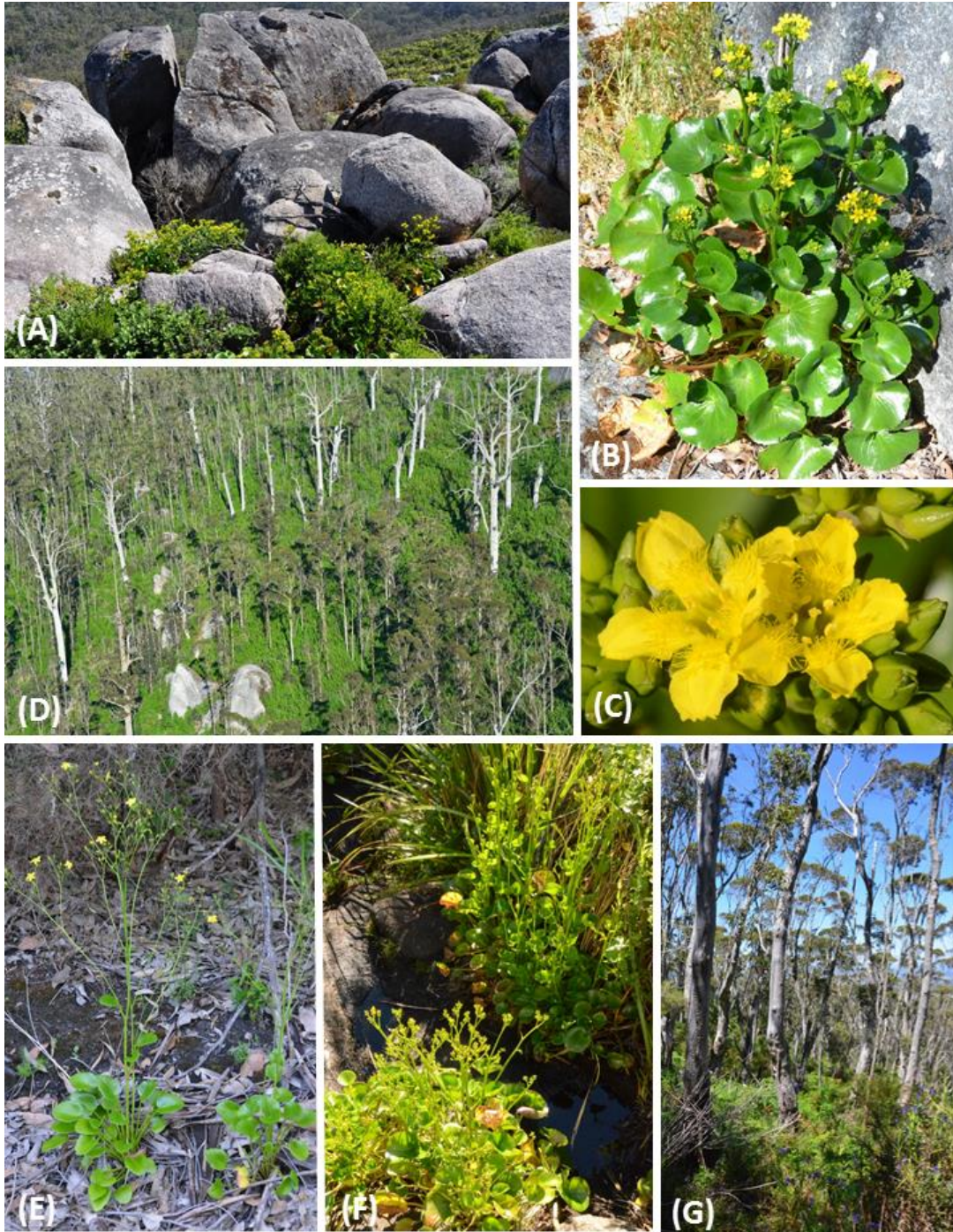model. *Bold print indicates coefficients significant at* $p \leq 0.05$.

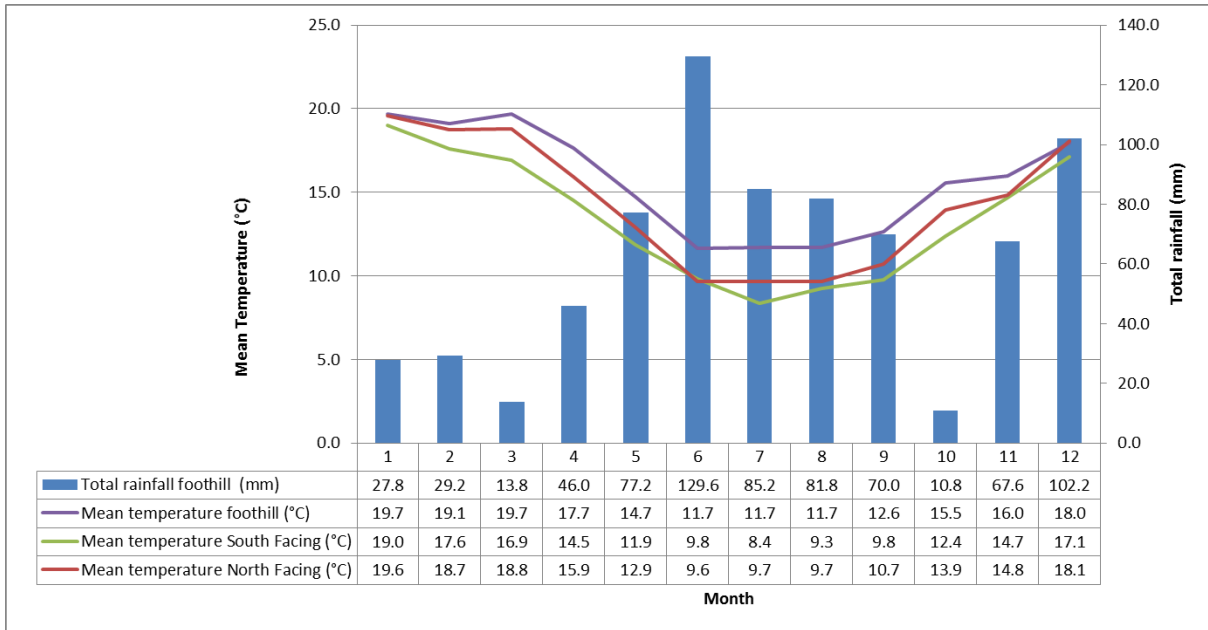|	Solar radiation	Roughness	Curvature	Aspect	Elevation	Vegetation height	Soil Depth	Topographic Wetness Index
Solar radiation		**- 0.637**	0.187	0.072	-0.325	0.252	0.181	0.450
Roughness			0.098	0.148	**0.639**	-0.561	-0.368	**-0.753**
Curvature				0.093	0.116	0.012	0.001	0.062
Aspect					0.143	-0.126	-0.133	-0.111
Elevation						**-0.797**	-0.455	**-0.694**
Vegetation height							0.511	**0.629**
Soil Depth								0.363

Fig. 1. *Ornduffia* species and habitat in the Porongurup Range, south-western Australia. (A) Habitat of *Ornduffia calthifolia* (yellow-flowered plants in granite rock crevices) at 640 m elevation; (B) Single plant of *O. calthifolia*; (C) Flowers of *O. calthifolia*; (D) Karri (*Eucalyptus diversicolor*) forest habitat of *O. marchantii* at 330 m elevation. The karri trees are approximately 50 m high and the site had been burnt by high intensity fire 5 years previously (2008); (E) *O. marchantii* along disturbed firebreak in karri forest at 330 m elevation; (F) Intermediate form along walk track in bullich (*E. megacarpa*) forest at 450 m elevation; (G) Bullich forest habitat of intermediate form of *Ornduffia* at 450 elevation. The bullich trees are approximately 10 m high. Photo credits A: Klaus Braun, B-G Grant Wardell-Johnson.

Month	1	2	3	4	5	6	7	8	9	10	11	12
Total rainfall foothill (mm)	27.8	29.2	13.8	46.0	77.2	129.6	85.2	81.8	70.0	10.8	67.6	102.2
Mean temperature foothill (°C)	19.7	19.1	19.7	17.7	14.7	11.7	11.7	11.7	12.6	15.5	16.0	18.0
Mean temperature South Facing (°C)	19.0	17.6	16.9	14.5	11.9	9.8	8.4	9.3	9.8	12.4	14.7	17.1
Mean temperature North Facing (°C)	19.6	18.7	18.8	15.9	12.9	9.6	9.7	9.7	10.7	13.9	14.8	18.1

Fig. 2. Climate diagram for the Porongurup Range from 1 November 2011 (11) to 31 October 2012 (10), showing the total rainfall for the foothill climate station (black bars) and the mean monthly temperatures for iButtons at the foothill climate station (385 m elevation), at the hilltop climate station (590m, north-facing), at a south-facing location (580m).
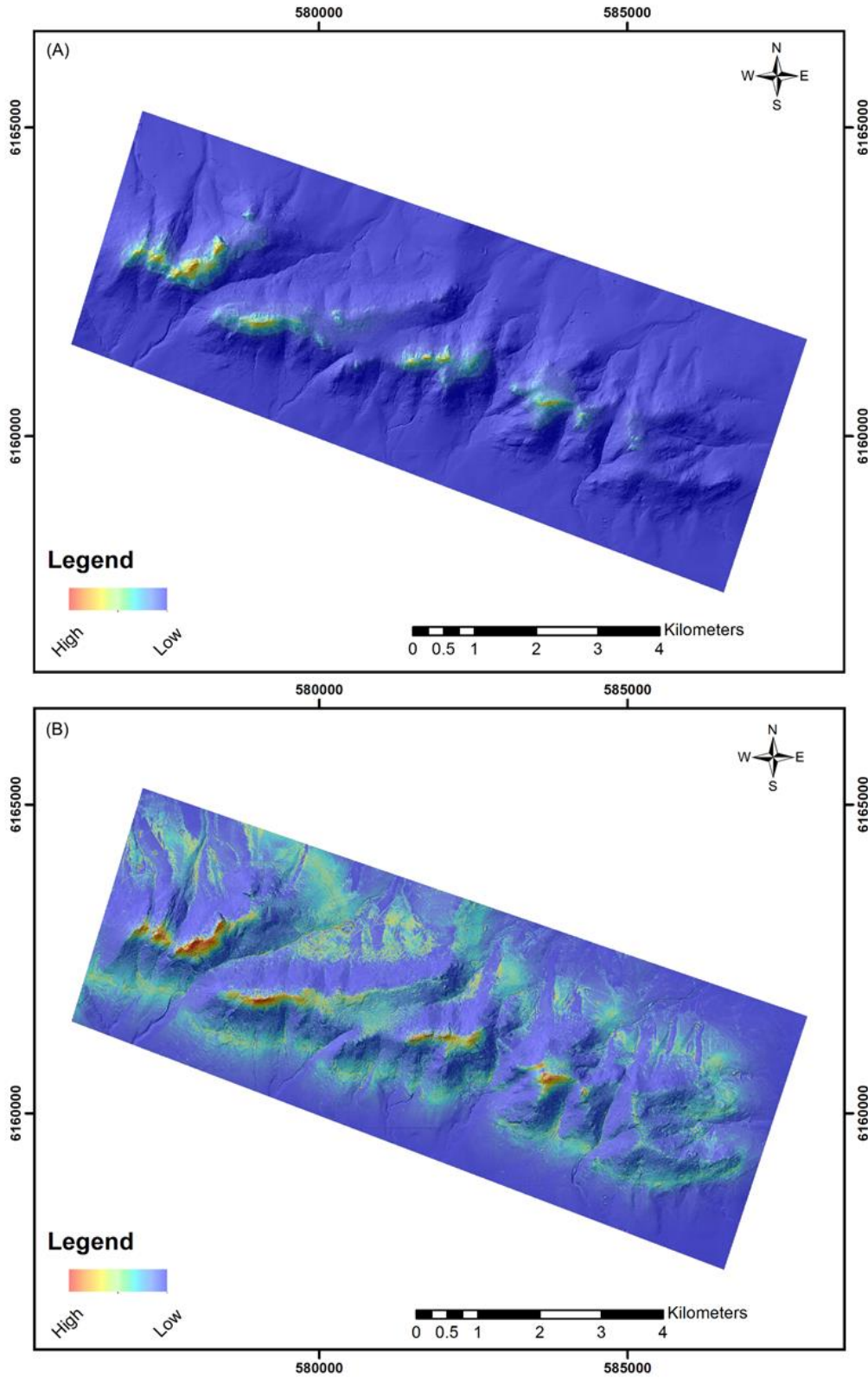
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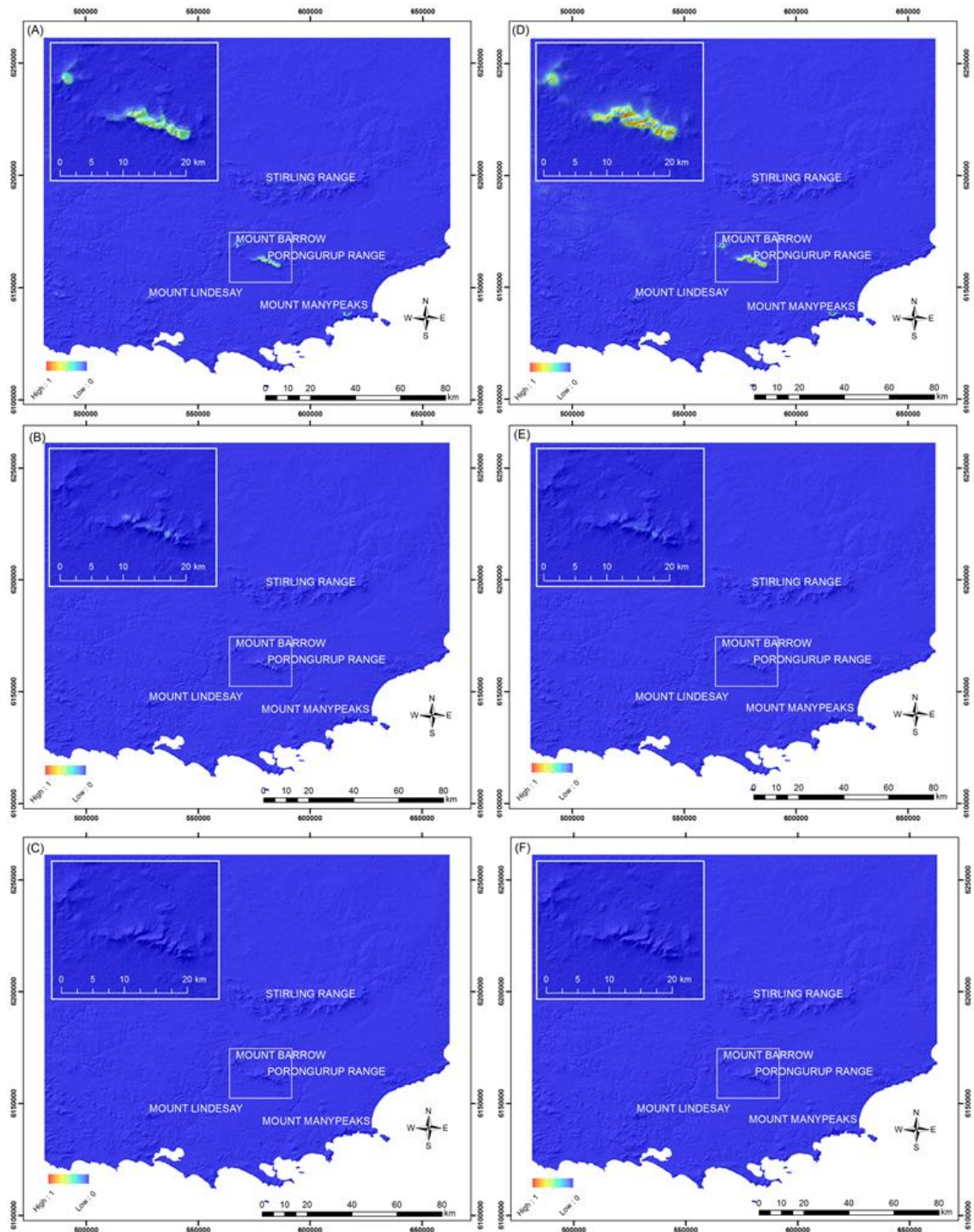
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