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A low-altitude mountain range as an important refugium for two narrow endemics in the Southwest Australian Floristic Region biodiversity hotspot

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- **Background and Aims** Low-altitude mountains constitute important centres of diversity in landscapes with little topographic variation, such as the Southwest Australian Floristic Region (SWAFR). They also provide unique climatic and edaphic conditions that may allow them to function as refugia. We investigate whether the Porongurups (altitude 655 m) in the SWAFR will provide a refugium for the endemic *Ornduffia calthifolia* and *O. marchantii* under forecast climate change.
- **Methods** We used species distribution modelling based on WorldClim climatic data, 30-m elevation data and a 2-m-resolution LiDAR-derived digital elevation model (DEM) to predict current and future distributions of the *Ornduffia* species at local and regional scales based on 605 field-based abundance estimates. Future distributions were forecast using RCP2.6 and RCP4.5 projections. To determine whether local edaphic and biotic factors impact these forecasts, we tested whether soil depth and vegetation height were significant predictors of abundance using generalized additive models (GAMs).
- **Key Results** Species distribution modelling revealed the importance of elevation and topographic variables at the local scale for determining distributions of both species, which also preferred shadier locations and higher slopes. However, *O. calthifolia* occurred at higher (cooler) elevations with rugged, concave topography, while *O. marchantii* occurred in disturbed sites at lower locations with less rugged, convex topography. Under future climates both species are likely to severely contract under the milder RCP2.6 projection (approx. 2 °C of global warming), but are unlikely to persist if warming is more severe (RCP4.5). GAMs showed that soil depth and vegetation height are important predictors of *O. calthifolia* and *O. marchantii* distributions, respectively.
- **Conclusions** The Porongurups constitute an important refugium for *O. calthifolia* and *O. marchantii*, but limits to this capacity may be reached if global warming exceeds 2 °C. This capacity is moderated at local scales by biotic and edaphic factors.

Key words: Anthropogenic climate change, extinction, interspecific interactions, localized endemic, low-altitude mountain, refugia, microclimate, Southwest Australian Floristic Region (SWAFR), *Ornduffia calthifolia*, *Ornduffia marchantii*, species distribution 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 (Rebelo *et al*., 2006; Barrett and Yates, 2015). Hence, they probably constitute important microrefugia that may provide important safe havens for biodiversity under anthropogenic climate change (Ashcroft, 2010; Keppel and Wardell-Johnson, 2012).

The Southwest Australian Floristic Region (SWAFR) and Cape Floristic Region are globally significant centres of plant diversity where low-altitude mountains provide important topography, and hence potential microrefugia. Climate change is predicted to have a substantial impact on biodiversity in both regions (Midgley *et al*., 2002; Fitzpatrick *et al*., 2008; Klausmeyer and Shaw, 2009), and species in mountainous areas at higher elevations may be disproportionally vulnerable (McCullough *et al*., 2016). Indeed, both regions contain high concentrations of species vulnerable to climate change (Yates *et al*., 2010; Foden *et al*., 2013).

In the SWAFR, the Stirling Range (1090 m a.s.l.) and Porongurup Range (Porongurups 655 m a.s.l.) on the region's south coast provide distinctly montane environments, with numerous endemic species restricted to higher and cooler elevations (Barrett, 1996; Barrett and Yates, 2015). Here we use species distribution modelling to forecast the likely impacts of climate change on two narrowly endemic, iconic species of the genus *Ornduffia* Tippery & Les in the Porongurups. We also test whether *in situ* edaphic (soil depth) and biotic (vegetation height) factors, which are difficult to include in species distribution modelling, significantly affect the distribution of the two species and hence the capacity of potential microrefugia. We thus determine whether the Porongurups, or other proximal locations, have the potential to act as refugia for *Ornduffia* species under anthropogenic climate change.

MATERIALS AND METHODS

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 probably acted as refugia during past periods of climate change (Schut *et al*., 2014; Tapper *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 1100 Mya (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 distributions are centred on the Porongurups, including *Ornduffia marchantii*, a close relative of *O. calthifolia*.

Study species

Ornduffia is a genus of eight southern Australian taxa (five confined to south-western Australia) that has been recently recognized as distinct from *Villarsia* in the morphologically diverse and cosmopolitan family Menyanthaceae, which includes 60–70 aquatic and wetland species (Tippery and Les, 2009). *Ornduffia calthifolia* (Fig. 1A–C) is an erect, robust perennial, locally endemic to moist sheltered sites on the upper slopes of granite outcrops of the Porongurups (Brown *et al*., 1998). The fleshy-leaved species is widely recognizable, and iconic to the Porongurups (Barrett, 1996; Brown *et al*., 1998). The stem bearing the inflorescence (culm) rises to a metre or more. Adventitious roots arise from a fleshy underground organ, providing a reserve of water and nutrients, and enabling rapid growth under favourable conditions (Pate & Dixon, 1982). However, the species is apparently drought-susceptible, as evidenced by observations of dead plants after the extreme heat of January 1991 (Robinson and Coates, 1995). *Ornduffia calthifolia* is killed by fire and relies on seedling regeneration for persistence. Fire may enhance germination, but inter-fire seedling establishment also occurs (Gilfillan and Barrett, 2004).

Ornduffia calthifolia was declared as Rare Flora under the Western Australian *Wildlife Conservation Act 1950* in November 1980, ranked as Endangered (EN) in 1997, and listed under the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act – Gilfillan and Barrett, 2004). This species also meets World Conservation Union (IUCN, 2012) Red List Category EN (but is not currently listed), under Criteria C2a, due to a continuing decline in the number of mature individuals, with no population estimated to include more than 250 mature individuals. Nine populations and 582 mature plants were known when the species Interim Recovery Plan (Gilfillan and Barrett, 2004) was published.

Abbott (1982) originally listed *O. calthifolia* from karri forest at the 300-m contour in the Mira Flores estate on the southern slopes of the Porongurups, prior to recognition of a second species in the area. Ornduff (1990) described the closely related *O. marchantii* (Fig. 1D, E) from a small population at

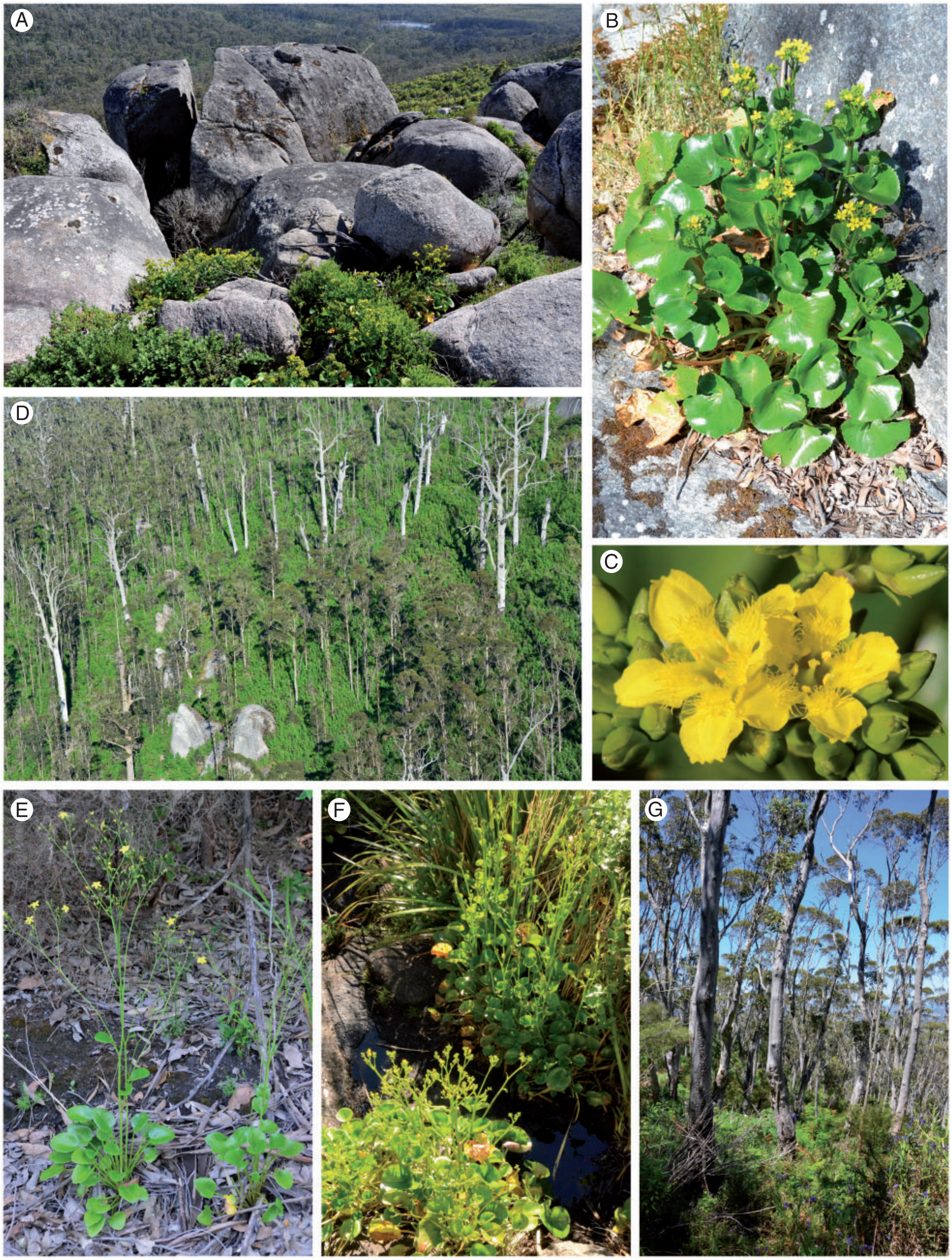


FIG. 1. *Ornduffia* species and habitat in the Porongurup Range, south-western Australia. (A) Habitat of *Ornduffia calthifolia* (yellow-flowered plants in granite rock crevices) at 640 m elevation. (B) Single plant of *O. calthifolia*. (C) Flowers of *O. calthifolia*. (D) Karri (*Eucalyptus diversicolor*)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

an elevation of 450 m in a boggy site amongst karri forest. *Ornduffia marchantii* is similar, but much smaller, and occurs in seasonally wet loams on lower to mid slopes at altitudes below populations of *O. calthifolia* (Gilfillan and Barrett, 2004). Ornduff (1990) also noted the capacity for hybridization and putative hybrids between the two species have been reported in the overlap zone (Robinson and Coates, 1995). *Ornduffia marchantii* is currently known from eight specimens in the WA Herbarium, with six originating from the Porongurups. The remaining two specimens are from populations in now degraded vegetation within 10 km to the north and west of the Porongurups. Extensive searches by G.W.J. did not find the species and these populations are likely to be no longer extant.

Field-based variables

In February 2012 and November 2013, we recorded the abundance of *O. calthifolia* and *O. marchantii*, and their putative hybrid, throughout the Porongurups and surrounds. We used strategic random sampling to obtain the abundance of *Ornduffia* species, vegetation height (m), soil depth (cm) and GPS coordinates for 606 locations (207 with *O. calthifolia* present, 55 with *O. marchantii*, 14 with the putative hybrid, and 362 absences with neither species present; note that more than one taxon occurred in some locations). Abundance of each *Ornduffia* taxon was recorded using a modified Braun–Blanquet scale ($5 = \geq 75$ %, $4 = 50–74$ %, $3 = 25–50$ %, $2 = 10–25$ %, $1 = <10$ %), estimating cover in circular 27-m^2 plots. Plots 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 were obtained by airplane using a Leica ALS 50-II scanner, flying in April 2011. Flight height was approx. 1700–2200 m, resulting in 0·63 points m^{-2}, which was interpolated into a 2-m grid using triangulation. Horizontal and vertical accuracy was <0·35 and <0·15 m, respectively. Further details can be found in Schut *et al.* (2014). The data were used for fine-scale, localized species distribution modelling of the Porongurups. Elevation data at 30-m resolution (1-arc second) from the Shuttle Radar Topography Mission (SRTM) were 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, Garbutt, QLD) series data logger, and sensors for air temperature and relative humidity (CS215 CSL; manufacturer: Campbell Scientific Australia), precipitation (CS702 tipping bucket rain gauge; manufacturer: Hydrological Services Pty. Ltd, Warwick Farm, NSW), solar radiation (SP210 pyranometer; manufacturer: Apogee Instruments Inc., Logan, UT, USA) and soil moisture (CS625 water content reflectometer; manufacturer: Campbell Scientific Australia).

Each climate station was equipped with an iButton data logger (DS1923 Hygrochron; manufacturer: Maxim Integrated, San Jose, CA, USA), which was attached to the climate station in a plastic cup insulated with duct tape. This was to facilitate comparison with other iButtons placed in various locations with different aspects and radiation intensities. The two climate stations were placed at different altitudes (385 m – foothill climate station, 590 m – hilltop climate station), but were both located on the northern side of the Porongurups. We compared the temperatures recorded by the iButton on the north-facing hilltop climate station with that of a south-facing iButton of similar altitude (580 m; 34°40′21·10″S, 117°50′28·19″E).

Bioclimatic variables (annual mean temperature and precipitation) were acquired from WorldClim, which are generated at a resolution of 1 km^2 via interpolation of average monthly weather station data (Hijmans *et al.*, 2005). Future condition bioclimatic variables were used to assess species distribution under a projected climate based on two representative concentration pathway scenarios – 2·6 (RCP2.6) and 4·5 (RCP4.5). RCP2.6 projections are based on the lowest emission scenario, assuming a global mean temperature increase limited to 2 °C and requiring substantial reductions in greenhouse gas emissions (van Vuuren *et al.*, 2011). RCP4.5 assumes medium to low emissions producing a global mean temperature increase of around 3 °C (Thomson *et al.*, 2011). For the regional-scale model, cell size was downscaled to 30 m using cubic convolution resampling to be commensurate with the SRTM elevation data and regional-scale topographic derivatives.

Topographic derivatives

A suite of raster surfaces were derived from both elevation data sources (LiDAR and SRTM) including slope (first derivative of elevation), aspect (degrees from north) and curvature (second derivative of elevation). A curvature of 0 suggests the terrain is flat, negative curvature is upwardly concave (convex) and positive curvature is upwardly convex (concave). Relative Topographic Position, a measure of terrain ruggedness, was calculated using methods described in Cooley (2015). Total solar radiation for 2011 was calculated in ArcGIS (ESRI, 2015) using the techniques outlined by Fu and Rich (2000). This approximates incoming solar radiation over the year (WH m^{-2}) by summing monthly intervals. The Topographic Wetness Index (TWI), a surrogate for soil moisture, was calculated using eqn (1) (Gessler *et al.*, 1995):

$$TWI = ln\left(\frac{a}{tan\ \beta}\right) \tag{1}$$

where α is calculated as (flow accumulation + 1) × (pixel area in m^2) and β is the slope in radians. Flow accumulation measures the number of cells that drain into an individual cell (Olivera *et al.*, 2002).

Table 1. *Mean (standard deviation; range) of variables considered for inclusion in the starting model for all three taxa*

	Soil depth	Vegetation height	Elevation	Topographic wetness index	Aspect	Curvature	Roughness	Solar radiation
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)	189·6 (81·6; 8·3–358·9)	14·4 (101·8; −1039·9–520·6)	0·5 (0·09; 0·3–0·8)	1113215 (257414; 110825–1556341)
Ornduffia marchantii ($n = 55$)	36·8 (16·6; 10·0–50·0)	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 (179749 784041–1485304)
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; 78041–15102717)

Species distribution modelling

Modelling was conducted at local and regional scales using 2- and 30-m resolution surfaces, respectively, using MaxEnt version 3.3.3k, which uses the concept of maximum entropy to predict potential distributions (Phillips *et al*., 2006). A logistic output format was used for all models, whereby suitability ranges from 0 to 1 for each grid cell. The local-scale model used elevation and topographic derivatives but not bioclimatic variables, as none are available at such fine-scale resolution. We used this model to explore habitat preferences of the two species by dividing predicted suitability into four equal-interval classes and extracting the mean value of all variables at 1000 random locations within each class. Differences between classes were tested using Tukey's honestly significantly different test (Kramer, 1956).

At the regional scale, elevation was strongly and significantly correlated with mean annual temperature ($r = -0{\cdot}8$, $P < 0{\cdot}01$) and discarded (only from regional-scale modelling) to avoid masking the influence of temperature. In addition, we added mean annual precipitation to enable projections of both a warmer and drier climate under two climate change scenarios to 2070. Predictions of potential distributions (suitability) based on current conditions and climate change forecasts were calculated. As the convex hull of the sampling design covered the majority of the LiDAR image, no bias file (Fourcade *et al*., 2014) was deemed necessary for the local-scale model. However, to avoid potential overfitting, the convex hull of presence points was used to mitigate sampling bias (Young *et al*., 2011; Brown, 2014) for regional-scale modelling.

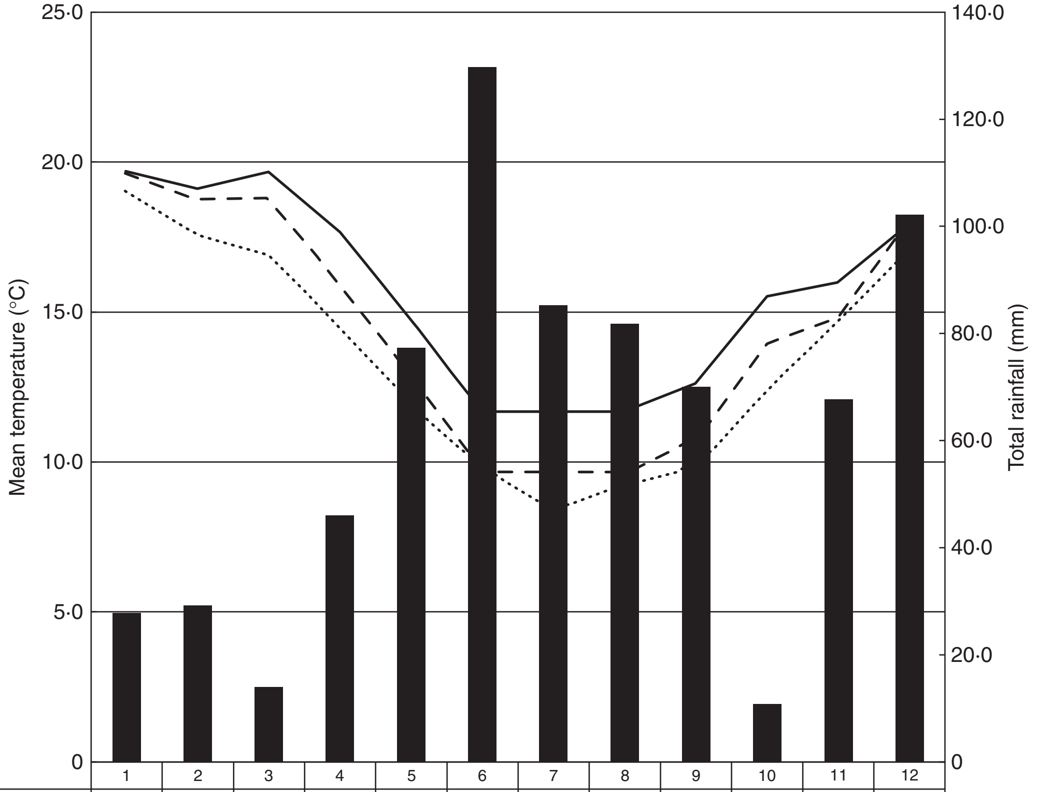
Species presence records were randomly subset, with 90 % used for model training ('training subset') and 10 % used as an independent source for model validation ('testing subset'). Validation was conducted using both the training and the testing datasets by computing the area under the curve (AUC) of receiver operating characteristic (ROC) graphs (Fielding and Bell, 1997). Interpretation of discrimination potential used the ranges presented by Hosmer and Lemeshow (2000).

Ecological modelling

The abundances (*Ab*) of *O. calthifolia* (OC) and *O. marchantii* (OM) were the response variables. We did not model the distribution of the putative hybrid between the two species (OX) because of the low sample size ($n = 14$). A combination of field-based and remotely-sensed variables was used to determine the key ecological factors driving species distribution and abundance. We initially considered the following predictor variables for the starting model: soil depth (S); vegetation height (V); insolation (I) in winter (calculated as the average insolation during the month of June, I_w), summer (average insolation during the month of December, I_s) and throughout the year (average insolation throughout the year, I_a); aspect (A); curvature (C); elevation (E); roughness (R); and topographic wetness index (T). The averages, variation and ranges of these variables are summarized for the three taxa in Table 1. All analyses were implemented in R software 2.15.1 (R Development Core Team).

To avoid concurvity, we tested for correlation among explanatory variables using Pearson's correlation coefficient, removing variables with a coefficient $>0{\cdot}5$. If correlation was detected, we retained variables that were ecologically more relevant and more proximal (rather than distant) predictors (Dormann *et al*., 2013). Because winter (I_w) and summer insolation (I_s) were positively correlated to each other ($r = 0{\cdot}518$) and to annual insolation (I_a; $r = 0{\cdot}905$ and $0{\cdot}828$, respectively), we excluded summer and winter insolation from starting models. In addition, strong correlations were observed between vegetation height (V), elevation (E), roughness (R) and topographic wetness index (T) (Supplementary Data Table S2). To address this, we removed R, which (in our opinion) was ecologically the least meaningful variable. Because *O. calthifolia* appeared to be restricted by elevation (no presences below 447 m, Table 1) and *O. marchantii* by vegetation height (no presences below 3 m, Table 1), we decided to include these variables instead of the correlated terms in the respective models. Because of the correlation between vegetation height and soil depth ($r = 0{\cdot}511$), we excluded the latter from the model for *O. marchantii*.

We therefore built two generalized additive models (GAMs) including all retained variables. The 'mgcv' package (Wood, 2016) was used to implement the models with the following function calls: gam(as.factor(Ab_{OC}) $\sim$ s(S) + s(I_a) + s(A) + s(C) + s(E)), gam(as.factor (Ab_{OM}) $\sim$ s(I_a) + s(A) + s(C) + s(V)). We assumed a binomial error distribution and used a logistic-link function. Independent variables in the model were selected using backwards stepwise regression. Non-significant terms ($P < 0{\cdot}05$) based on the likelihood ratio were consequently removed. The significance and fraction of variance explained were determined for each selected independent variable. In addition, we used the Akaike information criterion (AIC; Akaike, 1974) to test model performance. We used a



	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 temp. 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 temp. 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 temp. 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

Month

FIG. 2. Climate diagram for the Porongurup Range from 1 November 2011 (1) to 31 October 2012 (12), showing the total rainfall for the foothill climate station (black bars) and mean monthly temperatures for iButtons at the foothill climate station (385 m elevation), at the hilltop climate station (590 m, north-facing), and at a south-facing location (580 m).

second-order AIC: AICc = AIC + 2(*K*(*K* + 1)/(*n* − *K* − 1)), where *K* is the number of parameters in the model and *n* is the number of sample points (Burnham and Anderson, 1998).

RESULTS

Climate

As expected for Mediterranean climates, high rainfall was recorded in winter and spring (June to September). In addition, high rainfall was recorded in November and December as a result of storm systems causing high precipitation on 3 November (27·4 mm) and from 6 to 8 December (53·8 mm) (Fig. 2). Temperatures were lower at higher elevations (the hilltop climate station at 590 m and the south-facing iButton at 580 m), where monthly average temperatures were about 2–3 °C lower than at the foothill climate station (385 m elevation). The south-facing iButton recorded consistently lower temperatures (0·95 °C on average) than the iButton facing north.

The hilltop climate station had lower average temperatures, lower precipitation, higher humidity, higher soil moisture and lower insolation than the foothill climate station (Supplementary Data Table S1). Differences were most pronounced for soil moisture (the annual average was 110·7 % higher in the hilltop climate station) and precipitation (24·5 % more total rainfall at the foothill climate station). Differences in climate variables between the two climate stations were most pronounced during winter (June to August) and least pronounced during summer (December to February).

Species distribution modelling

Elevation had the greatest explanatory power for local models (LiDAR-based) of the two species (Table 2A), although its effect was less pronounced for *O. marchantii* with roughness, aspect, solar radiation and TWI contributing strongly to the model (Table 2A). At the regional scale, temperature (correlated with elevation) and precipitation contributed >97 % for both species (Table 2B). Considering the qualitative interpretation of AUC values proposed by Hosmer and Lemeshow (2000), discrimination potential ranged from excellent (*O. marchantti*) to outstanding (*O. calthifolia*; Table 2).

Under current conditions, both species preferred cooler environments. The most suitable habitats occurred at higher average elevations, being approx. 630 m for *O. calthifolia* and approx.

TABLE 2. *Percentage 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*

Species distribution model	Percentage contribution										Accuracy	
	Annual temp. (°C × 10)	Annual precipitation (mm)	Elevation (m a.s.l.)	Roughness	Aspect (°)	Solar radiation (WH m^{-2})	TWI	Slope (°)	Curvature	Σ	AUC$_{\mathrm{Train}}$* ± s.e.	AUC$_{\mathrm{Test}}$† ± s.e.
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

*Computed using the training subset.
†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* $\alpha = 0{\cdot}05$ *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}	1 075 442^{a}	2·8^{a}	38·0^{a}	6·5^{a}
	0·50–0·75	1000	610·9^{b}	0·51^{b}	196·3^{b}	1 133 720^{b}	3·4^{b}	31·3^{b}	2·5^{a}
	0·25–0·50	1000	574·2^{c}	0·50^{c}	192·2^{b}	1 164 544^{c}	3·8^{c}	28·2^{c}	1·8^{a}
	0·00–0·25	1000	342·2	0·50^{c}	169·2^{c}	1 335 118^{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}	1 239 289^{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}	1 302 324^{b}	5·3^{b}	13·2^{b}	–1·5^{a}
	0·25–0·50	1000	361·9^{c}	0·49^{b}	139·0^{b}	1 300 151^{b}	5·2^{b}	12·3^{b}	–0·4^{a}
	0·00–0·25	1000	335·3^{d}	0·50^{c}	178·2^{c}	1 344 218^{c}	5·2^{b}	12·5^{b}	0·3^{a}

550 m for *O. marchantii* (Table 3). In addition, both species preferred southerly (shadier) aspects that receive less solar radiation over the year, although aspect preferences were more south-west for *O. calthifolia* and south-east for *O. marchantii*. Both species preferred steeper slopes, although this relationship was far more prominent for *O. calthifolia*. The two species differed in terms of curvature preference and ruggedness with *O. calthifolia* preferring concave, rugged terrain and *O. marchantii* convex, less rugged locations although curvature was not a significant variable between suitability classes within species.

Suitable locations for *O. marchantii* modelled at the local scale with elevation and associated topographic derivatives were far more widespread than for *O. calthifolia* – the latter restricted to higher altitude areas (Fig. 3). Regional modelling also identified the Porongurups as suitable habitat with few other suitable sites (e.g. Mount Barrow and Mount Manypeaks) in the region likely to host either species (Fig. 4A). However, even under the mildest temperature prediction for 2070 (RCP2.6), the range of both species contracted significantly. Remaining sites were only moderately suitable and restricted to the Porongurups (Fig. 4B, E), suggesting no opportunities for translocation. Under more severe warming and drying (RCP4.5), modelling suggests no suitable habitat for either species by 2070 (Fig. 4C, F).

Ecological modelling

The best model for *Ornduffia calthifolia* included elevation, insolation, soil depth and curvature and explained almost 48 % of the observed deviance (Table 4). Although curvature was marginally not significant ($P = 0{\cdot}055$) in the overall model, removing it significantly reduced the performance of the model ($\chi^2 = 16{\cdot}64$, $P = 8{\cdot}4 \times 10^{-4}$, likelihood ratio test). Of these variables, elevation explained the greatest amount of variance (33 %; Table 5). For *O. marchantii*, the best model included vegetation height and aspect, and explained 46 % of the total deviance. Vegetation height alone explained almost 38 % of the observed deviance.

The putative hybrid between the two species was generally found in conditions that are intermediate between the two species (soil depth, vegetation height, TWI, solar insolation; Table 1). However, the average and range of elevation for the putative hybrid were similar to those of *O. calthifolia*, suggesting that the hybrid can only form in close proximity to this species.

DISCUSSION

Climate

Climatic conditions differed considerably with elevation and aspect over small distances. Such differences in soil and air temperature are well established (Rorison *et al*., 1986; Fridley, 2009). High variability in climatic conditions on fine scales is usually related to topographic complexity and indicates that microrefugia may be present (Dobrowski, 2011; Ashcroft *et al*., 2012; Keppel *et al*., 2015).

Species distribution modelling

Species distribution modelling of two species endemic to the Porongurups (*O. calthifolia* and *O. marchantii*) identified suitable habitat that closely matched descriptions in the literature

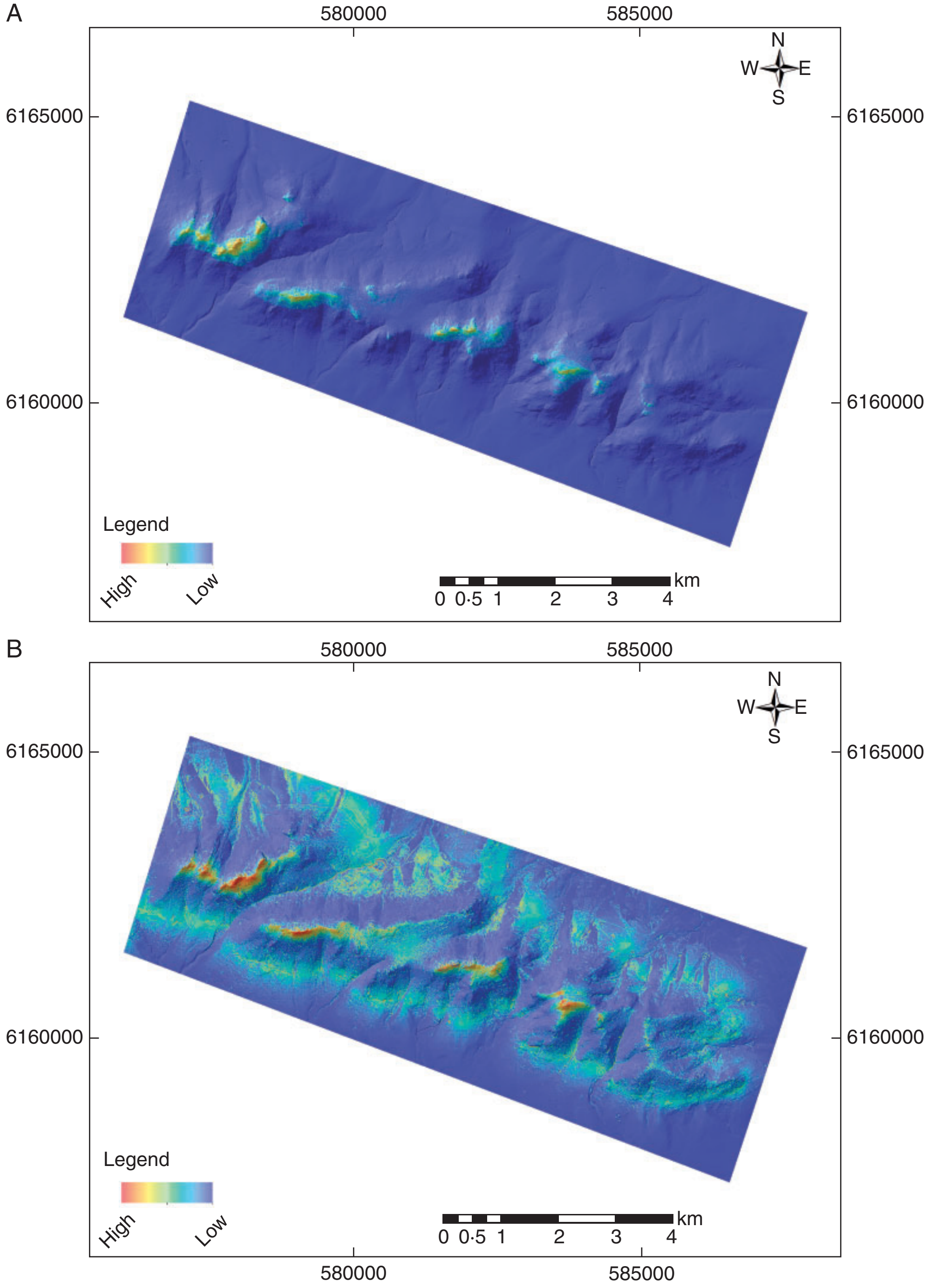


FIG. 3. Local-scale species distribution models of *Ornduffia* species in the Porongurup Range based on topopgraphic derivatives of LiDAR data: (A) *O. calthifolia*, (B) *O. marchantii*.

(e.g. Robinson and Coates, 1995; Gilfillan and Barrett, 2004) as well as our validation data. Elevation, used in the local modelling as a surrogate for temperature, contributed strongly (58–85 %) to both models. At this scale, other variables, particularly aspect, roughness and solar radiation, were also of importance. At 30-m resolution (regional modelling), temperature was the key variable (74–86 %) which was also strongly (negatively) correlated to elevation. The combination of temperature and precipitation was clearly the most important driver of the regional-scale model (96–99 %).

Spatial clustering of sampling points, difficult to avoid for rare endemic species with very specific habitat preferences, probably contributes to the high model accuracy, despite random selection and the use of an independent subset. Nonetheless, projected distributions under climate change indicate that the distribution of both species will reduce markedly.

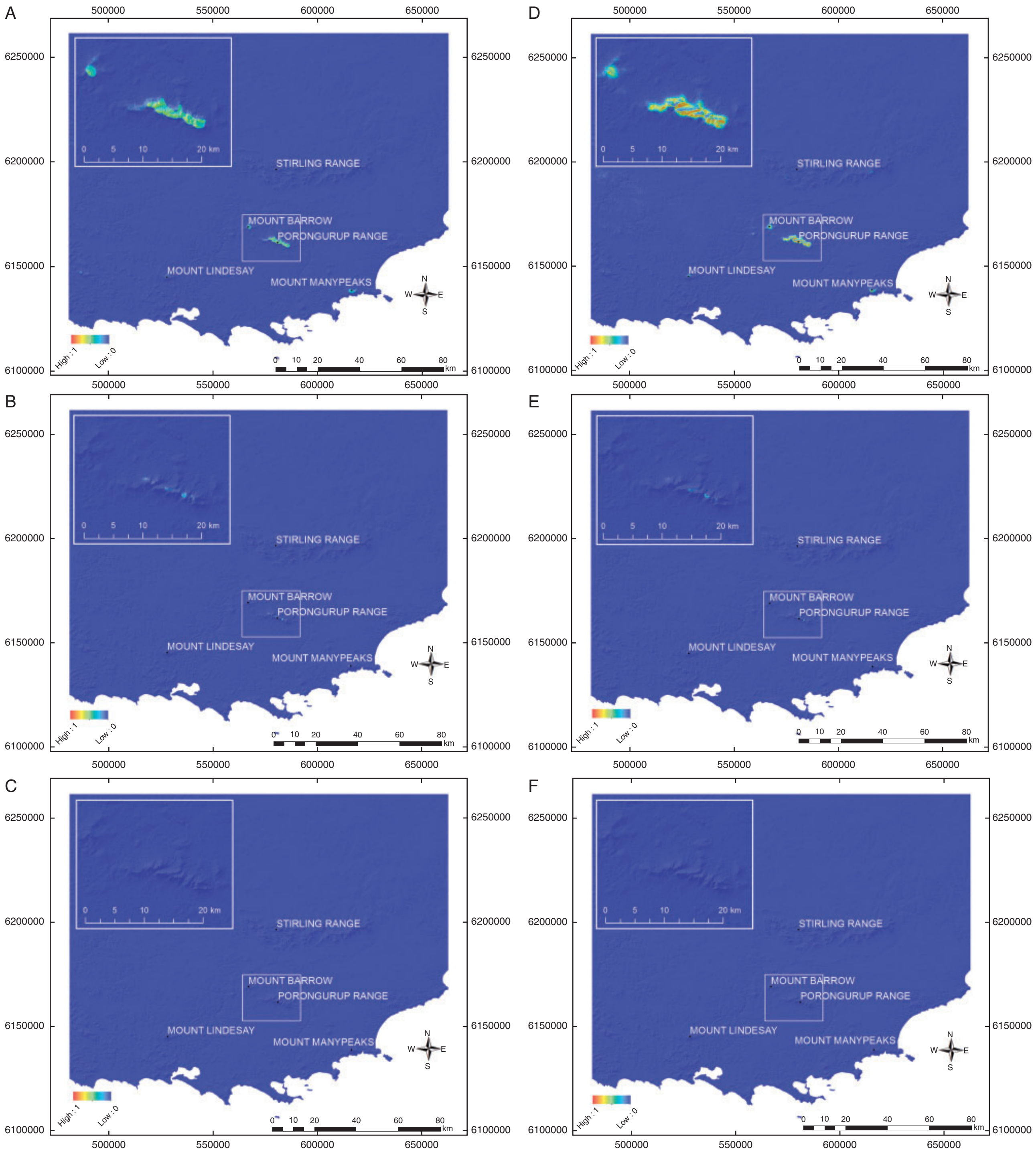


Fig. 4. Regional-scale species distribution models of *Ornduffia* species in southern Western Australia using topographic derivatives of 30-m STRM data and bioclimatic variables (resampled to 30 m): (A) *O. calthifolia* – current climatic conditions; (B) *O. calthifolia* – climatic conditions 2070 based on RCP2.6; (C) *O. calthifolia* – climatic conditions 2070 based on RCP4.5; (D) *O. marchantii* – current climatic conditions; (E) *O. marchantii* – climatic conditions 2070 based on RCP2.6; (F) *O. marchantii* – climatic conditions 2070 based on RCP4.5.

Although considerable range reductions are predicted for both species, persistence is likely under the milder RCP2.6 scenario. However, both species are at high risk under the more severe RCP4.5 projection, with probable extinction and no regional opportunities for translocation.

The Porongurups constitute an important refugium for both species under anthropogenic climate change, despite being a low-altitude mountain range. Few areas outside of this mountain range contain potentially suitable climate. However, our modelling highlights important limits to refugial capacity,

TABLE 4. *Performance indicators of the best generalized additive models (highest deviance explained, no correlated variables) describing the abundance of* Ornduffia calthifolia *and* O. marchantii

	d.f.	*P*-value	Deviance explained (%)	Adjusted r^2
Ornduffia calthifolia				
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	$7{\cdot}8 \times 10^{-7}$		
Insolation (I_a)	1·00	$5{\cdot}7 \times 10^{-10}$		
Curvature (*C*)	4·49	0·06		
Soil depth (*S*)	3·21	$3{\cdot}5 \times 10^{-7}$		
Ornduffia marchantii				
Best model: $Ab_{OM} \sim s(A) + s(V)$				
Model overall			46·0	0·383
Vegetation height (*H*)	3·75	$9{\cdot}7 \times 10^{-4}$		
Aspect (*A*)	8·66	$2{\cdot}1 \times 10^{-9}$		

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

	d.f.	*P*-value	Deviance explained (%)
Ornduffia calthifolia			
Elevation (*E*)	5·30	$1{\cdot}0 \times 10^{-5}$	33·1
Insolation (I_a)	5·01	$<2{\cdot}0 \times 10^{-16}$	18·7
Curvature (*C*)	6·97	$6{\cdot}1 \times 10^{-12}$	13·2
Soil depth (*S*)	3·52	$1{\cdot}0 \times 10^{-7}$	7·6
Ornduffia marchantii			
Vegetation height (*H*)	8·58	$4{\cdot}8 \times 10^{-9}$	37·8
Aspect (*A*)	3·09	0·016	4·84

indicating that the range could cease to act as a refugium for both species if global warming exceeds 2 °C of pre-industrial levels. Our study therefore highlights both the potential (through provision of unique microhabitats) and the limitations (due to restricted elevational range) of low-altitude mountains to act as refugia under anthropogenic climate change. Furthermore, because of their lower elevation and the associated smaller geographical extent compared with major mountain ranges, the protected areas in which they lie tend to be smaller and surrounded by highly modified and populated landscapes (Rebelo *et al*., 2006; Barrett and Yates, 2015). 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 species distribution modelling ignore biological and edaphic factors. Based on ecological modelling, soil depth affects the distribution of *O. calthifolia* and vegetation height of *O. marchantii*. Deeper soils increase the habitat suitability for *O. calthifolia*, and vegetation height (probably 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.

Hybridization 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 hybridization 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 undertaken has crucial impacts on the outcome. Unfortunately, gridded climatic data are currently only available at a resolution of 1 km (or greater), which is considerably poorer than the 2-m LiDAR used for local modelling and 30-m SRTM used for regional modelling. Although interpolation algorithms were used to change cell size, it does not replicate the resolution of the other datasets driving the model and masks local heterogeneities (e.g. microclimate) that may facilitate persistence of the species. This is particularly relevant in topographically complex areas, resulting in exaggerated predictions of extinction risk (Randin *et al*., 2009; Austin and Van Niel, 2011*b*; Franklin *et al*., 2013).

Species distribution models do not consider interspecific interactions. This is especially pertinent for *O. marchantii*, the distribution of which seems to be closely linked to the presence of karri (*Eucalyptus diversicolor*), which is the dominant species in the only community with vegetation heights of 20 m or more. The absence of *O. marchantii* in areas of currently suitable climate appears to be a result of the requirement for shade provided by high vegetation of the karri forest. In addition, most individuals of *O. marchantii* were found at the margins of tracks (i.e. edges of disturbance) in these karri forest sites, suggesting some level of disturbance is important to the growth of this species in the otherwise dense understorey of the karri forest. Whilst it is possible to include vegetation height as a variable in local models, its permanency, relative to topographic variables, is questionable. For example, fire could remove large proportions, and the range of the karri forest at this location is predicted to contract strongly under forecast climate change (Wardell-Johnson *et al*., 2015). Vegetation height therefore is unreliable for forecasting *O. marchantii* distributions.

Species distribution models require continuous and complete coverage (surfaces) of all variables, which is not always feasible. For example, soil depth is an important factor affecting the assembly and structure of granite outcrop plant communities (Poot *et al*., 2012; Schut *et al*., 2014; do Carmo and Jacobi, 2016). 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 hybridization 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.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Table S1: temperature, rainfall, relative humidity, soil moisture and insolation recorded for two climate stations from 1 November 2011 to 31 October 2012. Table S2: Pearson's correlation coefficient (based on all 626 data points) for all variables considered for inclusion in the starting model.

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