



A short distance to the last glacial coast best explains a Tasmanian centre of endemism

Joe Atkinson^{1*}  and James B. Kirkpatrick¹ 

¹ Discipline of Geography and Spatial Sciences, School of Technology Environment and Design, University of Tasmania, Churchill Avenue, Sandy Bay, Tasmania, Australia. *Corresponding author: Joe Atkinson: j.atkinson@unsw.edu.au

Abstract

At the small scales of world, continent and region, centres of local endemism have been hypothesised to be related to refugia and/or distinctive environmental conditions. We consider patterning of local endemics at a large scale to help test the validity of these two hypotheses for centres of local endemism recognised at smaller scales. Our study area was a centre of local endemism on the Tasman and Forestier peninsulas, Tasmania, Australia. We tested the distinctiveness of both the current climatic and edaphic conditions and the potential for refugia during Quaternary climatic fluctuations, using databases, published maps, and direct observation of climate. Inverse rarity analyses at 1 km² showed a pattern of concentration of local endemics near the east and southeast coasts of the peninsulas. However, the ranges of species at a larger scale were largely non-overlapping. Climate did not differ from other coastal areas in southeastern Tasmania that lacked local endemics. Climatically similar areas to the centre of local endemism on and outside the peninsulas also had treeless vegetation on skeletal soils on dolerite and mudstone that were habitat for many of the species in the peninsulas centre of local endemism. The areas with high concentrations of local endemics on the peninsulas were located close to the coastline of the Last Glacial Maximum, unlike other areas with the same climatic and edaphic environments inside and outside the peninsulas. The conclusion that the centre of local endemism relates to a closely adjacent glacial refugium, rather than being a response to a distinctive environment, was reinforced by the non-overlapping distributions of the most locally endemic species at a large scale, and the variability in the habitat of the most locally endemic species. This study illustrates the value of investigating the causes of centres of local endemism at a range of scales and confirms the tight link between centres of endemism and refugia.

Highlights

- We investigate patterning of local endemic plant species on two southeastern Tasmanian peninsulas at different scales to help unravel the cause of their concentration.
- In doing so, we identify ten species previously not recognized as local endemics, largely due to their recent descriptions.
- The coincidence of distributions of local endemics decreases with increasing scale with strong very local segregation.
- We show that local endemics on the peninsula are concentrated in areas close to coastlines at the last glacial maximum, suggesting, along with their local distribution patterns, a long-term stable climate refugium.

Keywords: Local endemism, glacial coastline, glacial refugia, plant endemism, endemism hotspot

Introduction

It is axiomatic to say that the presence of an organism in an area indicates that the habitat is or has been suitable for its establishment. However, the

absence of an organism from an area does not indicate a lack of habitat suitability (Tivy 1993), making it no simple task to unpack the historical and ecological explanations for the distributions of geographically

restricted species. The word “endemic” is used to describe species restricted to a defined geographic area (Tivy 1993). Organisms can be endemic at a wide range of spatial scales. Those restricted to a very local distribution are often referred to as ‘local’ (or sometimes ‘range-restricted’) endemics (Kirkpatrick and Brown 1984, Harvey 2002, Bossuyt et al. 2004, Garrick et al. 2004, Murienne et al. 2005, Muñoz et al. 2008, Krosch et al. 2009, Köhler 2010, Schaefer et al. 2011). Understanding the patterns of occurrence of local endemic plants and the causes of any aggregations of such species in centres of local endemism is important in planning and management for nature conservation. Local endemics can also provide an opportunity to investigate the drivers of biodiversity generation and maintenance. Consequently, there is a large literature on local endemism (see Harrison and Noss 2017 for a comprehensive overview).

Endemics are commonly divided into palaeoendemics and neoendemics. Palaeoendemics were more widespread in the past, whereas neoendemics are species that have recently evolved (Stebbins and Major 1965, Molina-Venegas et al. 2017, Thornhill et al. 2017). Both neo- and palaeoendemics can be local endemics. The definition of a local endemic relies entirely on a clear spatial definition on a case by case basis, as there is no standard maximum range for ‘local’.

Stable climates and insularity are associated with refugia as well as being important drivers of endemism (Harrison and Noss 2017, Keppel et al. 2018). Hotspots of local endemic plant species have been shown to be concentrated in coastal areas and islands where temperatures are moderated by the sea (Crisp et al. 2001, Linder 2001, Mittermeier et al. 2005, Kier et al. 2009). The importance of the capacity of refugia (Keppel et al. 2015) to facilitate species persistence in an area to buffer climate shifts during the Pleistocene (2.58 – 0.012 MYA) climatic oscillations is regarded as critical in understanding patterns of local endemism (Jansson 2003, Sandel et al. 2011, Castellanos-Morales et al. 2016, Harrison and Noss 2017), although support for the climatic stability hypothesis is not universal (e.g., Zuloaga et al. 2019). Distinctive edaphic conditions have also been associated with concentrations of local endemic plants (e.g., Kirkpatrick and Brown 1984, Gibson et al. 1992, Morat 1993, Bredenkamp et al. 2001, Stevanović et al. 2003, Molina-Venegas et al. 2013; Anacker & Strauss 2014, Molina-Venegas et al. 2015). Therefore, research aimed at testing these hypotheses is particularly relevant in conservation biogeography (Richardson and Whittaker 2010).

Major concentrations of local endemic plants in Australia are associated with the coast (Crisp et al. 2001). Tasmania is one of three major centres of corrected weighted endemism (endemic species/total species richness, CWE) in Australia at the 1° x 1° scale (Crisp et al. 2001). The only other major centres of CWE in Australia are the wet tropics in northern Australia and southwest Western Australia, the latter of which is widely considered as a globally significant centre of

endemism (Boden and Given 1995, Crisp et al. 2001, Hopper and Gioia 2004, Harrison and Noss 2017).

Crisp et al. (2001) suggested that finer-grained analyses of distributions of species within their continent-scale centres of local endemism could help explain their genesis. A well-recognised centre of local endemism within the Tasmanian centre of Crisp et al. (2001) is centred on the Tasman Peninsula, extending to the directly adjacent Forestier Peninsula. It is characterised by the coincident distributions at a cell size of 100 km² of *Epacris marginata*, *Euphrasia phragmostoma*, and *Euphrasia semipicta* (Kirkpatrick and Brown 1984, Brown and Duncan 1986, Hill and Orchard 1999, Kirkpatrick 1999). This centre has been explained by a distinctive edaphic and climatic environment (Kirkpatrick and Brown 1984, Brown and Duncan 1986). Yet, the composition of pollen in the sediments near Remarkable Cave indicates vegetation in the centre of local endemism similar to the present since the early Last Glacial (Colhoun 1977), consistent with the refugial hypothesis for endemism hotspots.

We describe patterns of local endemism on the Tasman Peninsula and Forestier Peninsula at several scales to test the alternative hypotheses that the centre of local endemism is related to: 1) the proximity of a coastal refugium during colder times; 2) distinctive environmental conditions.

Methods

Study area

The Tasman and Forestier Peninsulas (‘the peninsulas’) are found in the southeast of Tasmania, Australia (Figure 1). They are largely composed of Jurassic dolerite, with Triassic sediments in the northeast and southwest. There are bands of Permian mudstone on the eastern coast and a small pocket of Devonian granite at Cape Surville. The area has the highest vertical sea cliffs in the southern hemisphere. At Cape Pillar, the columnar jointed dolerite pillars tower 300 m over the Tasman Sea. Heathlands occur on rudosols on dolerite and podosols on sands on the most exposed parts of the cliff tops. Elsewhere, the remaining natural vegetation is largely eucalypt-dominated forest (Brown and Duncan, 1986).

Data collection

Distribution data for all Tasmanian endemic vascular plant taxa were downloaded from the Natural Values Atlas¹ (NVA). The NVA compiles verified user-submitted observations, research-grade iNaturalist records, and all Tasmanian herbarium species. Data are collected as point data with accuracy reported for each observation. The mean reported spatial accuracy of data included in the analysis is 262 m and the median 10 m. Unvouchered observations were included in the analyses reported in the present paper.

Climate data for 42 Tasmanian long-term weather stations were downloaded from the Bureau of Meteorology

1 <https://www.naturalvaluesatlas.tas.gov.au/>, last accessed on 18th February 2019

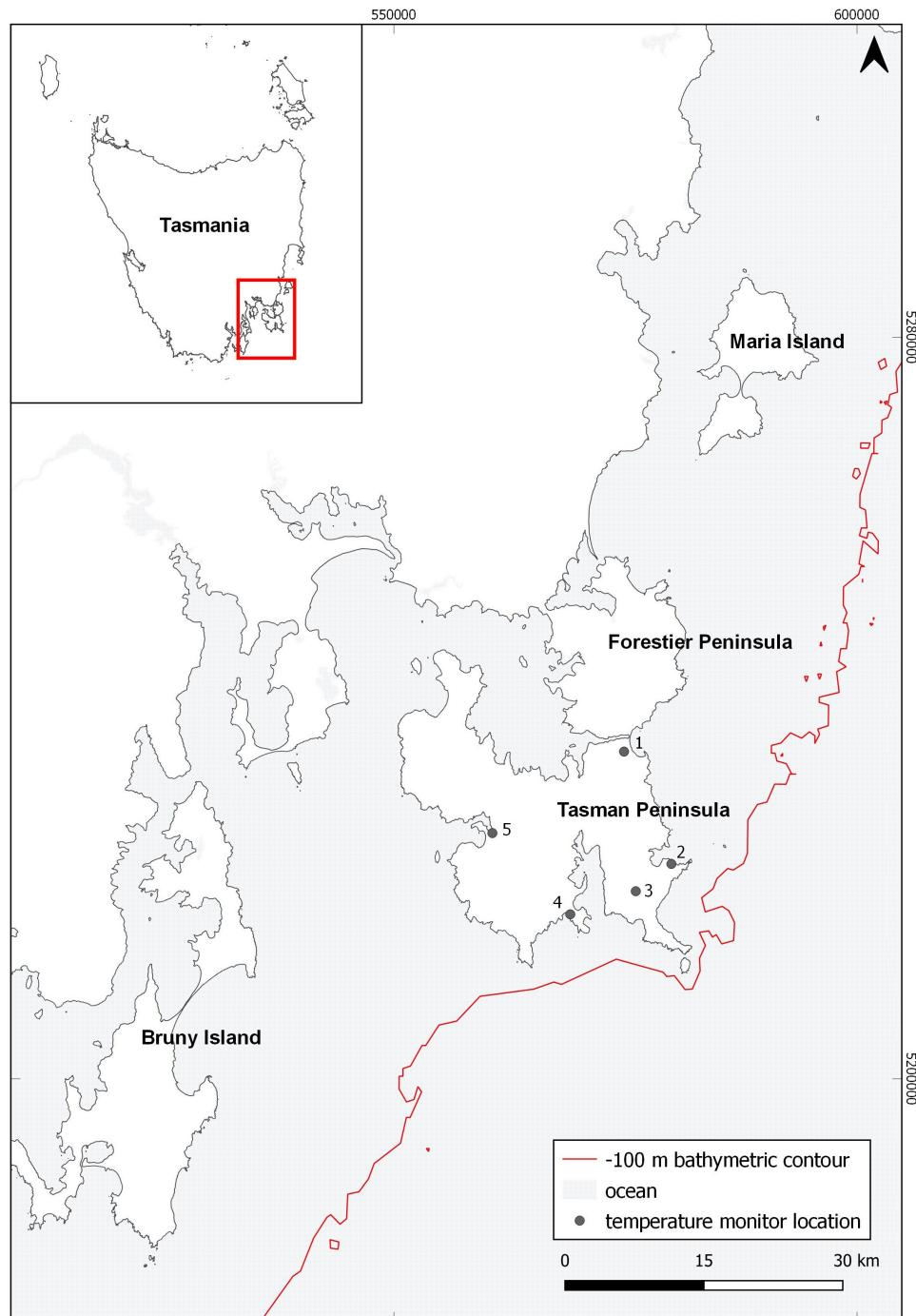


Figure 1. The Tasman and Forestier Peninsulas, Tasmania (inset), Australia, with the -100 m bathymetric contour highlighted. Locations of LogTag temperature monitors used in analyses are shown in grey. Numbered locations are as follows: 1 – Cashes Lookout, 2 – Cape Hauy, 3 – Snake Hill, 4 – Remarkable Cave, 5 – White Beach. Coastline and bathymetric data © Geoscience Australia.

(BOM) website on the 17th of July 2018. Stations with less than ten years of measurements were excluded, except for Dunalley, to the immediate north of the study area. Rainfall data for Dunalley are obtained from Bangor and temperature data from Stroud Point. Stroud Point is a five-year average. Climate data for Port Arthur (Palmer's Lookout) on the Tasman Peninsula were collected from 1980 to 2005 for temperature and 1980 to 2009 for rainfall. The metric of temperature

amplitude was the difference between the average temperatures of the warmest and coldest months.

Temperatures at White Beach, Snake Hill, the Cape Hauy walking track, Cash's Lookout, and between Remarkable Cave and Mt Brown (Figure 1) were recorded hourly between October 2018 and April 2019 using calibrated LogTag temperature monitors. Sites were selected to capture a range of local endemic taxon richness. Cape Hauy, Cashes Lookout, and Remarkable

Cave sites are all close to concentrations of peninsula endemics. White Beach and Snake Hill are coastal sites depauperate in peninsula endemics. The monitors were secured on stakes, inside plastic buckets with holes drilled in the sides to reduce the effect of solar radiation, wind, and rain on temperature readings.

Bathymetric spatial data was obtained from the Australian Bathymetry and Topo (2009) dataset, copyright Geoscience Australia (GA). These data are accurate to a 250 m resolution (GA 2009). The -100 m bathymetric contour was chosen for comparison to endemism as it is a close proxy to past coastlines during glacial periods in Tasmania when sea levels were approximately 130–120 m lower than at present (Lambeck and Chappell 2001, Lambeck et al. 2002, DPAC 2012).

The distribution of vegetation types on the peninsulas was obtained from TASVEG 3.0 mapping (DPIPWE 2013). The geology map used for analyses was at a scale of 1:250,000, compiled by Mineral Resources Tasmania to an accuracy of +/- 250 m (Mineral Resources Tasmania 2010).

Data analysis

All data analysis was conducted using Minitab 19, R Version 3.4.4 and RStudio Version 1.1.447. All GIS analysis was conducted using QGIS version 3.4.7 – Madeira. Categorized symbology used in distribution maps uses Jenks natural breaks optimization (Jenks 1967).

To investigate spatial patterns in endemism, species are often weighted by the inverse of their range (1 / number of grid cells occupied by an organism; Crisp et al. 2001, Kessler 2002, Christman et al. 2005, Baldwin et al. 2017, Zuloaga et al. 2019). When summed for all species in a cell of a defined area, the resulting metric is called weighted endemism (Crisp et al. 2001). However, weighted endemism is strongly predicted by species richness (Crisp et al. 2001, Zuloaga et al. 2019). Thus, weighted endemism is often corrected for species richness within any given area to give corrected weighted endemism (Crisp et al. 2001). Guerin et al. (2015) suggest that this correction of endemism scores has the potential in some instances to mask hotspots where species richness is high (e.g., Slatyer et al. 2007). In the present study, species were scored by the inverse of their distribution in 1 x 1 km grid squares. The values for all taxa were added for each grid squares. Weighted endemism and corrected-weighted endemism were calculated for each cell.

The Tasmanian endemic taxa that had half or more of the 10 x 10 km grid squares in which they were recorded on the peninsulas were called peninsula endemics. Records of these species on the peninsulas were intersected with TASVEG 3.0 vegetation type data and the MRT 1:250000 state-wide geology layer (Mineral Resources Tasmania 2010). The classes were simplified to allow the use of statistics to determine whether the peninsula endemics were consistently associated with particular environments. A small area of granite was subsumed in Jurassic dolerite and all sedimentary rocks were grouped. The vegetation types were reduced to treeless, dry forest (following

Brown and Duncan 1996) and wet forest, which included both wet eucalypt forest and a small area of temperate rainforest. The significance of the association between the occurrence of peninsula endemics and each vegetation type and geological type in 1 x 1 km grid squares was tested using chi-squared. Expected values for the chi-squared analysis were calculated from the areas for each of the types on the peninsulas.

To test the hypothesis that the equable temperatures associated with maritime locations were associated with the occurrence of peninsula endemics on the peninsulas, we calculated the mean range between the 25 and 75 percentiles of temperature from our five stations, then related these data to the mean number of peninsula endemics in the nine 1 x 1 km cells closest to each of the stations. We used Pearson's product-moment correlation coefficient and fitted a regression line to the scatter of points.

To test the hypothesis that the occurrence of peninsula endemics on the peninsulas was related to the location of a long-term stable coastal refugium, distance to the -100 m bathymetric contour was measured for all 1 x 1 km grid squares. Welch's ANOVA was used to determine whether the number of peninsula endemics (classes = 0, 1, 2, 3, >3) in 1 x 1 km grid cells on the peninsulas with any Tasmanian endemic species records was related to this distance.

To further test the hypothesis that the centre of endemism on the peninsulas was related to the location of a long term stable coastal refugium rather than a distinctive environment, we located all 10 x 10 km grid areas in Tasmania that had the same environmental conditions as the 10 x 10 km grid squares with local endemics on the peninsulas. Such grid squares intersected with the coast, had dolerite, mudstone, or Quaternary sand substrates and had at least part of the square in the mean annual rainfall range of 750-1050 mm. We used the two-sample t-test to determine whether these grid squares that were on the peninsulas were closer to the - 100 m bathymetric contour than those outside the peninsulas. Average annual rainfall data for this analysis used an Australia-wide 30-year average from 1961-1990 from the Bureau of Meteorology with a spatial resolution of 0.05 degrees (approximately 5 x 5 km).

Results

Eight out of 532 Tasmanian endemic vascular plant taxa were confined to the peninsulas: *Allocasuarina crassa*, *Bedfordia linearis* ssp. *oblongifolia* var. *curvifolia*, *Boronia pilosa* ssp. *tasmanensis*, *Craspedia cynurica*, *Euphrasia amphisysepala*, *Euphrasia phragmostoma*, *Euphrasia semipicta* and *Euphrasia* sp. Bivouac Bay. *Boronia pilosa* ssp. *tasmanensis* has two records outside of the peninsulas, both of which are over 70 years old with an accuracy of 20 km. The most recent taxonomic work on the subspecies states that it is restricted to the peninsulas (Duretto 2003).

Five taxa occurred outside the peninsulas but had half or more of their range on them: *Cyathodes platystoma* (69%), *Prasophyllum castaneum* (67%),

Correa alba var. *rotundifolia* (55%), *Epacris marginata* (53%) and *Limonium australe* var. *baudinii* (50%).

Corrected weighted endemism and the number of peninsula endemic taxa show similar patterns, with the eastern and southern part of the Tasman Peninsula having high values (Figure 2). The rest of southeastern Tasmania had only sporadic occurrences of peninsula endemics (Figure 2). At a larger scale, the peninsula endemics did not display strongly overlapping ranges (Figure 3). Members of the genus *Euphrasia* have very fine-scale geographical separation from one another (Figure 3c). The peninsula endemics with several locations on the far west and far north of the peninsulas were confined to vegetation strongly influenced by coastal processes. These taxa were the saltmarsh taxon *Limonium australe* var. *baudinii* and the sand dune/rocky coast taxon *Correa alba* var. *rotundifolia* (Figure 3b).

Climatically analogous weather stations to Tasman Island, which is close to the greatest concentration of peninsula endemics, are located on exposed coastal sites at Cape Bruny, Cape Grim, and Bicheno (Supplementary figure S1). Temperature amplitude at Port Arthur was most similar to Friendly Beaches, Flinders Island, Orford, St Helens, Wynyard and Dunalley, all of which are close to the coast and, with the exception of Wynyard, are in eastern Tasmania. Port Arthur, but

not Tasman Island, had more rainfall than most of the above-mentioned stations (Supplementary figure S2). There was an increase in the temperature range at our short-term climate stations as the number of peninsula endemic species increased ($r = 0.987$, $df = 4$, $P = 0.002$, Supplementary figure S3).

Seven of the peninsula endemic taxa were most frequently observed in treeless vegetation, five in dry forest, and one in wet forest (Table 1). Ten peninsula endemic taxa were most common on dolerite, two on Quaternary deposits, and one on sedimentary rocks (Table 1). Few of these species were confined to a particular vegetation or geology (Table 1).

The southeastern extremities of the peninsulas are in close proximity to the Last Glacial coastline (Figure 1). Within the peninsulas, the highest concentrations of peninsula endemic plant species are closest to the Last Glacial shorelines (Figure 4). There was a strong relationship between distance classes and the number of peninsula endemics (Welch's ANOVA, $F_{4,591} = 54.8$, $P < 0.001$). The grid squares outside the peninsula that shared coastal proximity, geology, and mean annual precipitation with the grid squares on the peninsulas were more remote from the Last Glacial coastline than the peninsulas grid squares (means (sd) 26 (9.9) vs 11 (9.0) km; Two sample $t = 4.06$, $df = 1, 27$, $P < 0.001$).

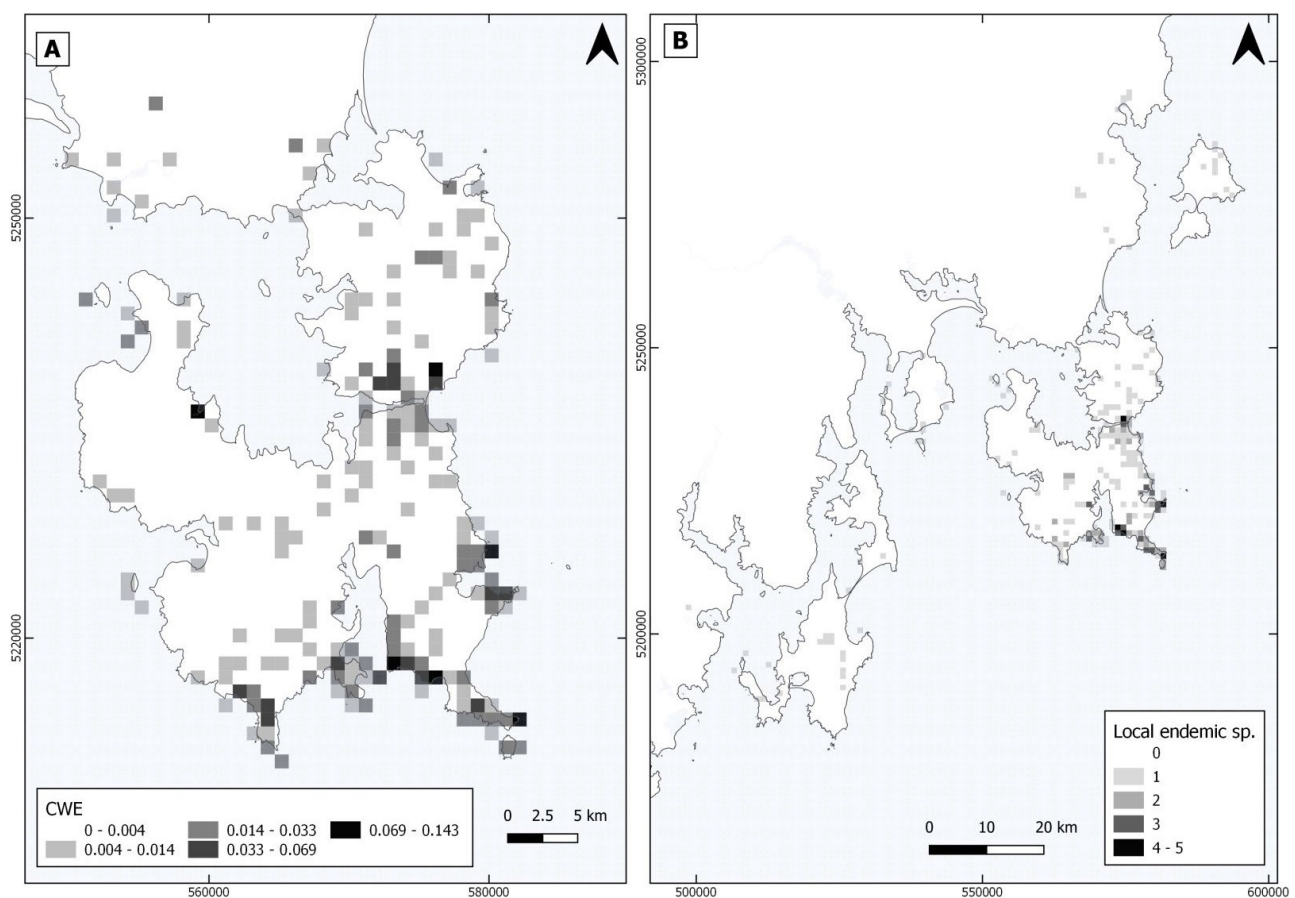


Figure 2. Corrected weighted endemism (CWE) (A) and numbers of peninsula endemic plant taxa (B). Grid squares are 1 km², UTM coordinates are in GDA 94, 55 G.

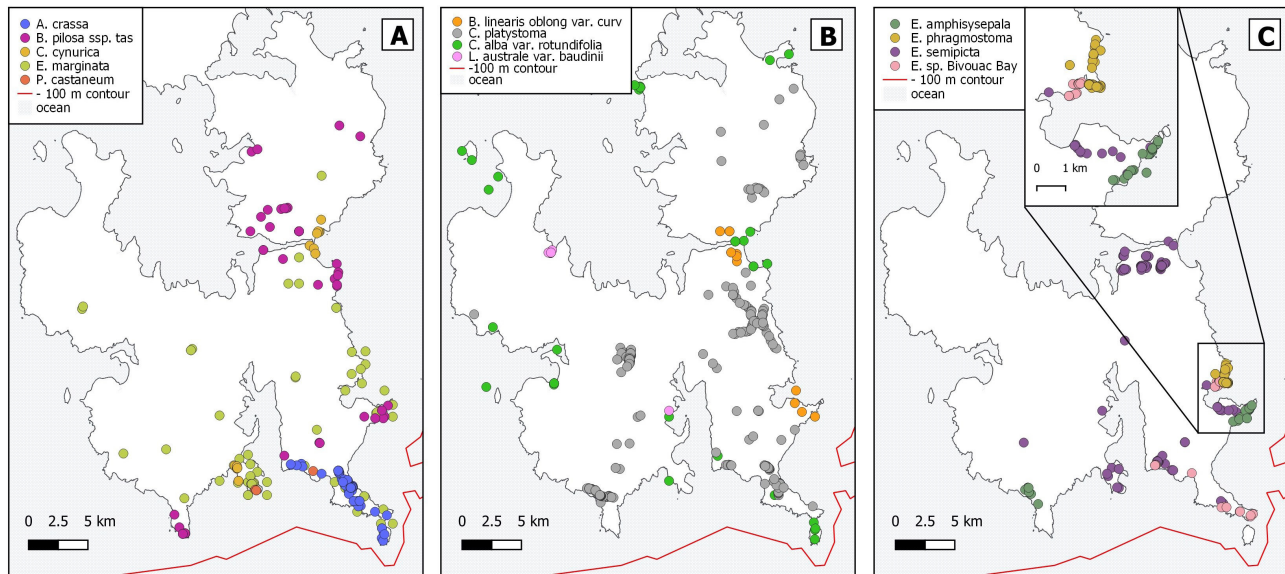


Figure 3. Distribution of peninsula endemic plant taxa. Peninsula endemics have half or more of their overall known distribution on the Tasman and Forestier peninsulas. The red line shown the -100 m bathymetric contour as a proxy for the coastline location during the Last Glacial Maximum. Species abbreviations are as follows for maps A and B: *Allocasuarina crassa*, *Boronia pilosa* subsp. *tasmanensis*, *Craspedia cynurica*, *Epacris marginata*, *Prasophyllum castaneum*, *Bedfordia linearis* subsp. *oblongifolia* var. *curvifolia*, *Cyathodes platystoma*, *Correa alba* var. *rotundifolia*, *Limonium australe* var. *baudinii*. All species in C are in the genus *Euphrasia*.

Table 1. Associations of peninsula endemic plant taxa with broad vegetation types (Tless = treeless vegetation types, Dryf = dry forest, Wetf = wet forest) and broad geologic type (Dol = Jurassic dolerite, Sed = sedimentary rocks, Qua = Quaternary deposits), shown as a percentage of 1 x 1 km grid squares in which each taxon is recorded. Probabilities from chi-squared are shown. Expected values for chi-squared were calculated from the percentages for vegetation types and geologic types for the peninsulas as a whole (shown in the final row). (1) = classes were reduced to two for analysis. NA = analysis not applicable. Percentages more than 1.5 times the expected are underlined.

Taxon	<i>n</i>	Tless	Dryf	Wetf	<i>p</i>	Dol	Sed	Qua	<i>p</i>
<i>Allocasuarina crassa</i>	158	13	84	4	<0.001	99	0	1	<0.001
<i>Bedfordia linearis</i> subsp. <i>oblongifolia</i> var. <i>curvifolia</i>	9	11	78	11	<0.05 (1)	100	0	0	<0.01 (1)
<i>Boronia pilosa</i> subsp. <i>tasmanensis</i>	49	30	63	6	<0.01	76	16	8	<0.05
<i>Correa alba</i> var. <i>rotundifolia</i>	30	40	53	7	<0.01	37	9	53	<0.001
<i>Craspedia cynurica</i>	20	90	10	0	<0.001	0	14	86	<0.001
<i>Cyathodes platystoma</i>	377	14	22	64	<0.001	85	7	8	<0.001
<i>Epacris marginata</i>	56	61	23	16	<0.001	74	10	15	<0.001
<i>Euphrasia amphisysepala</i>	34	76	21	3	<0.001	97	3	0	<0.001
<i>Euphrasia phragmostoma</i>	53	32	64	4	<0.001	100	0	0	<0.001
<i>Euphrasia semipicta</i>	171	55	39	6	<0.001	87	1	12	<0.001
<i>Euphrasia</i> sp. Bivouac Bay	33	70	30	0	<0.01	100	0	0	<0.001
<i>Limonium australe</i> var. <i>baudinii</i>	9	100	0	0	<0.001 (1)	2	79	19	<0.001 (1)
<i>Prasophyllum castaneum</i>	5	100	0	0	NA	100	0	0	NA
Expected values		31	43	26		28	58	14	

Discussion

The number of taxa in our centre of local endemism has increased from the three recognised in the 20th century to thirteen, as a result of recent taxonomic revisions (e.g., Weiller 1996, Schahinger 2002, Duretto 2003, Orchard 2004, Jeanes 2011, Rozefelds 2011, Baker et al.

2015, de Salas and Schmidt-Lebuhr 2018). A new species of *Ozothamnus* (de Salas and Schmidt-Lebuhr, 2018) may also prove to be a peninsula endemic.

We reject the hypothesis that the peninsulas centre of endemism is the product of a distinct set of contemporary environmental conditions. There are places, such as South Bruny Island, that have

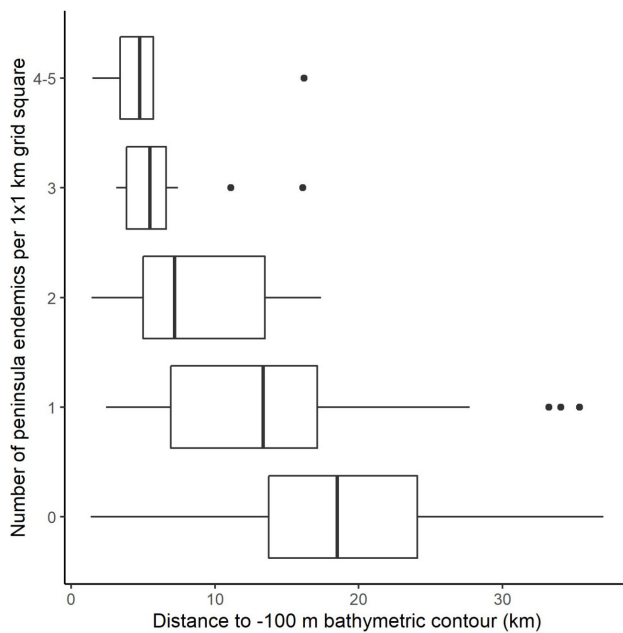


Figure 4. The number of peninsula endemic taxa in each 1x1 km grid square by distance to -100 m bathymetric contour. Peninsula endemics have over half of their known distribution on the Tasman and Forestier Peninsulas. Grid squares with 0 local endemics were only included where they contained other Tasmanian endemic taxa. The box contains 50% of the observations about the median (bold line). Outliers are shown by points. There is a significant relationship between distance and these classes of the number of endemics (Welch's ANOVA, $F_{4,591} = 54.8$, $P < 0.001$).

the same climate as Cape Pillar and Cape Hauy on the Tasman Peninsula. The same places also have substantial areas of the same shallow soils on dolerite that support many of the local endemics on the peninsulas. Nevertheless, the peninsula endemic taxa have individualistic distributions in relation to geology and vegetation type. The soil types and vegetation types on which they are found on the peninsulas all occur outside the peninsulas in similar climates. If the centre of endemism was related to a distinctive set of environmental conditions, we would expect that all local endemic species would occur in the same environments at a local scale. Such a coincidence is not the case.

The pattern of concentration of local endemics near the coast we observed for the peninsulas is widespread (e.g., Burgess et al. 1998, Taberlet et al. 1998, Sorrie and Weakley 2001, Silvertown 2004, Kier et al. 2009). The most feasible explanation for this patterning of our centre for local endemism is that the local endemic species have been able to survive fluctuations in sea level and climate because of the proximity of the Last Glacial coast. The moderating effects on both temperature variability and long-term climate of this coastal situation (Kier et al. 2009) may have played a role in providing refugial conditions (Harrison and Noss 2017, Keppel et al. 2018). However, temperature

moderation by itself seems not to be an explanation in this case, as such effects are widespread in coastal areas across southern and eastern Tasmania.

The proximity to the Last Glacial coast of the concentrations of peninsula endemic species, and the lack of such proximity in places with identical climatic and geologic environments outside the peninsulas, are strongly consistent with the stable climatic refugium hypothesis. The ability of the environment to buffer against the speed of changes in the climate (i.e., reduce climate change velocity; Keppel et al. 2015) has been shown to relate to high levels of local endemism (Jansson 2003, Sandel et al. 2011, Abellán and Svenning 2014, Fordham et al. 2019). Climate buffering is an important concept to explain biodiversity patterns in both the OCBIL (old, climatically buffered, infertile landscapes; Hopper 2009) and OSL (old, stable landscapes; Mucina and Wardell-Johnson 2011) theories. Within such climatically buffered areas, particular microhabitats, such as the cliffs in our study area, are likely to provide microrefugia to species that are threatened by changing environments (Harrison and Noss 2017; Keppel et al. 2018). In the case of our putative peninsula refugium, the steep topographic gradient to the Last Glacial coast may have enabled the peninsula endemics to escape inclement conditions in their present ranges and to return with climatic amelioration.

Two of the OCBIL regions as identified by Hopper (2009) are situated in areas that are likely to have had maritime climates for millions of years; however, it is unlikely that maritime conditions extended as far back as the Cretaceous (Hopper 2009, Mucina and Wardell-Johnson 2011). The maritime influence on southeastern parts of the peninsulas may have produced buffering of extreme temperatures over millions of years.

The refugial hypothesis is further supported by the finer level analysis. In particular, the *Euphrasia* species demonstrated little to no overlap in their distributions. Such a lack is likely to occur where the persistence of a set of environments occurs because of unusually short migration routes. *Euphrasia* is characterised by polyploidy, frequent self-fertilisation, species divergence, and widespread hybridisation (Karlsson 1974, Karlsson 1986, French et al. 2005, Wang et al. 2014). The genus is thought to have spread from Eurasia approximately 11-8 Mya and has been shown to have achieved bipolarity by 7-5 Mya (Gussarova et al. 2008). A global phylogenetic analysis of *Euphrasia* species determined local endemic *E. phragmostoma* to be more closely related to *E. hookeri* than to another lowland Tasmanian species *E. collina* (Gussarova et al. 2008). The same study estimated the age of divergence of *E. phragmostoma* from *E. hookeri* at approximately 2.5 Mya, and from the endangered *E. scabra* at approximately 4 Mya. It may be that the set of putatively neo-endemic *Euphrasia* species on the peninsulas are almost as ancient as these species, as intermediacy and hybridisation can persist from deep time, as in the case of the widespread hybrid between

the Tasmanian Cretaceous palaeoendemics, *Athrotaxis cupressoides* and *A. selaginoides* (Jordan et al. 2016).

In conclusion, we have added to the literature on the effects of the history of geographic patterns of climate on distributions of endemic organisms (Fjeldså and Lovett 1997, Hopper 2009, Mucina and Wardell-Johnson 2011, Sandel et al. 2011, Harrison and Noss 2017, Molina-Venegas et al. 2017; Fordham et al. 2019). In doing so, we have provided the first example of a contemporary local endemic concentration relating to the proximity of glacial era coastlines. Non-overlapping distributions of the most locally endemic species at a large scale and the variability in the habitat of the most locally endemic species reinforce the conclusion that the centre of local endemism relates to a closely adjacent glacial refugium, rather than being a response to a distinctive environment. The present study illustrates the value of investigating the causes of centres of local endemism at a range of scales and confirms the tight link between centres of endemism and refugia (Richardson and Whittaker 2010).

Acknowledgements

The authors would like to acknowledge the two reviewers and the journal editor who provided constructive feedback that greatly enhanced the overall structure and content of this research article.

Data Availability Statement

All data used for analyses can be found at <https://osf.io/rsdmq/>

Supplementary Materials

The following materials are available as part of the online article from <https://escholarship.org/uc/fb> **Figures S1-S3**. Additional climate figures

References

- Abellán, P. & Svenning, J.C. (2014) Refugia within refugia – patterns in endemism and genetic divergence are linked to Late Quaternary climate stability in the Iberian Peninsula. *Biological Journal of the Linnean Society*, 113, 13–28.
- Anacker, B.L. & Strauss, S.Y. (2014). The geography and ecology of plant speciation: range overlap and niche divergence in sister species. *Proceedings of the Royal Society B*, 281, 20132980.
- Baker, A., Mutton, T., Mason, E. & Gray, E. (2015) A taxonomic assessment of the Australian dusky Antechinus complex: a new species, the Tasman Peninsula dusky Antechinus (*Antechinus vandycki* sp. nov.) and an elevation to species of the mainland dusky Antechinus (*Antechinus swainsonii mimetes* (Thomas)). *Memoirs of the Queensland Museum*, 59, 75–126.
- Baldwin, B.G., Thornhill, A.H., Freyman, W.A., Ackerly, D.D., Kling, M.M., Morueta-Holme, N. & Mishler, B.D. (2017) Species richness and endemism in the native flora of California. *American Journal of Botany*, 104, 487–501.
- Boden, R. & Given, V.H. (1995) Centres of plant diversity: a guide and strategy for their conservation. World Wide Fund for Nature (WWF) and ICUN - World Conservation Union, Cambridge, U.K.
- Bossuyt, F., Meegaskumbura, M., Beenaerts, N., Gower, D.J., Pethiyagoda, R., Roelants, K., Mannaert, A., Wilkinson, M., Bahir, M.M., Manamendra-Arachchi, K., Ng, P.K.L., Schneider, C.J., Oommen, O.V. & Milinkovitch, M.C. (2004) Local endemism within the Western Ghats-Sri Lanka biodiversity hotspot. *Science*, 306, 479–481.
- Bredenkamp, G.J., Van Wyk, A.E. & Siebert, S.J. (2001) Endemism in the flora of ultramafic areas of Sekhukhuneland, South Africa. *South African Journal of Science*, 97, 529–532.
- Brown, M.J. & Duncan, F. (1986) The vegetation of the Tasman Peninsula, in: is history enough? Past, present and future use of the resources of Tasman Peninsula. Royal Society of Tasmania, Hobart, Australia.
- Burgess, N.D., Clarke, G.P. & Rodgers, W.A. (1998) Coastal forests of eastern Africa: status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society*, 64, 337–367.
- Castellanos-Morales, G., Gámez, N., Castillo-Gámez, R.A. & Eguiarte, L.E. (2016) Peripatric speciation of an endemic species driven by Pleistocene climate change: the case of the Mexican prairie dog (*Cynomys mexicanus*). *Molecular Phylogenetics and Evolution*, 94, 171–181.
- Christman, M.C., Culver, D.C., Madden, M.K. & White, D. (2005) Patterns of endemism of the eastern North American cave fauna. *Journal of Biogeography*, 32, 1441–1452.
- Crisp, M.D., Laffan, S., Linder, H.P. & Monro, A. (2001) Endemism in the Australian flora. *Journal of Biogeography*, 16, 183–198.
- de Salas, M. & Schmidt-Lebuhn, A.N. (2018) Integrative approach resolves the taxonomy of the *Ozothamnus ledifolius* (Asteraceae):

- Gnaphalidae) species complex in Tasmania, Australia. *Phytotaxa*, 358, 117–138.
- DPAC (2012) Derivation of the Tasmanian sea level rise planning allowances. Department of Premier and Cabinet, Tasmania, Australia.
- DPIPWE (2013) TASVEG 3.0. Tasmanian vegetation monitoring and mapping program. Resource Management and Conservation Division, Tasmania, Australia.
- Duretto, M.F. (2003) Notes on *Boronia* (Rutaceae) in eastern and northern Australia. *Muelleria*, 17, 19–135.
- Fjelds , J. & Lovett, J.C. (1997) Biodiversity and environmental stability. *Biological Conservation*, 6, 315–323.
- Fordham, D.A., Brown, S.C., Wigley, T.M.L. & Rahbek, C. (2019) Cradles of diversity are unlikely relics of regional climate stability. *Current Biology*, 29, R356–R357.
- French, G.C., Ennos, R.A., Silverside, A.J. & Hollingsworth, P.M. (2005) The relationship between flower size, inbreeding coefficient and inferred selfing rate in British *Euphrasia* species. *Heredity*, 94, 44–51.
- Garrick, R.C., Sands, C.J., Rowell, D.M., Tait, N.N., Greenslade, P. & Sunnucks, P. (2004) Phylogeography recapitulates topography: very fine-scale local endemism of a saproxylic ‘giant’ springtail at Tallaganda in the Great Dividing Range of south-east Australia. *Molecular Ecology*, 13, 3329–3344.
- Gibson, N., Brown, M.J., Williams, K. & Brown, A.V. (1992) Flora and vegetation of ultramafic areas in Tasmania. *Australian Journal of Ecology*, 17, 297–303.
- Guerin, G.R. & Lowe, A.J. (2015) ‘Sum of inverse range-sizes’ (SIR), a biodiversity metric with many names and interpretations. *Biodiversity and Conservation*, 24, 2877–2882.
- Guerin, G.R., Ruokolainen, L. & Lowe, A.J. (2015) A georeferenced implementation of weighted endemism. *Methods in Ecology and Evolution*, 6, 845–852.
- Gussarova, G., Popp, M., Vitek, E. & Brochmann, C. (2008) Molecular phylogeny and biogeography of the bipolar *Euphrasia* (Orobanchaceae): recent radiations in an old genus. *Molecular Phylogenetics and Evolution*, 48, 444–460.
- Harrison, S. & Noss, R. (2017) Endemism hotspots are linked to stable climatic refugia. *Annals of Botany*, 119, 207–214.
- Harvey, M.S. (2002) Short-range endemism amongst the Australian fauna: some examples from non-marine environments. *Invertebrate Systematics*, 16, 555–570.
- Hill, R.S. & Orchard, A.E. (1999) Composition and endemism of vascular plants. Chapter 5 in: Reid, J.B., Hill, R.S., Brown, M.J. & Hovenden, M.J. (Eds.), pp 89–123. *Vegetation of Tasmania*. Australian Biological Resources Study, Canberra, Australia.
- Hobohm, C. (Ed.) (2013) *Endemism in vascular plants*, Springer, Dordrecht, Netherlands.
- Hopper, S. D. & Gioia, P. (2004) The Southwest Australian Floristic region: evolution and conservation of a global hot spot of biodiversity. *Annual Review of Ecology Evolution and Systematics*, 35, 623–50.
- Hopper, S.D. (2009) OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil*, 322, 49–86.
- Jansson, R. (2003) Global patterns in endemism explained by past climatic change. *Proceedings of the Royal Society B*, 270, 583–590.
- Jeanes, J.A., (2011) Resolution of the *Thelymitra aristata* (Orchidaceae) complex of south-eastern Australia. *Muelleria*, 29, 110–129.
- Jenks, G.F. (1967) The data model concept in statistical mapping. *International Yearbook of Cartography*, 7, 186–190.
- Johnson, L.A.S. (1989) *Flora of Australia 3:194*. Australian Government Publishing Service, Canberra, Australia.
- Jordan, G.J., Harrison, P.A., Worth, J.R.P., Williamson, G.J. & Kirkpatrick, J.B. (2016) Palaeoendemic plants provide evidence for persistence of open, well-watered vegetation since the Cretaceous. *Global Ecology and Biogeography*, 25, 127–140.
- Karlsson, T. (1986) The evolutionary situation of *Euphrasia* in Sweden. *Acta Universitet Upsala Symbolae Botanicae Upsaliensis*, 27, 2–61.
- Karlsson, T. (1974) Recurrent ecotypic variation in Rhinanthae and Gentianaceae in relation to hemiparasitism and mycotrophy. *Botaniska Notiser*, 127, 527–539.
- Keppel, G., Mokany, K., Wardell-Johnson, G.W., Phillips, B.L., Welbergen, J.A. & Reside, A. (2015). The capacity of refugia for conservation planning

- under climate change. *Frontiers in Ecology and the Environment*, 13, 106–112.
- Keppel, G., Ottaviani, G., Harrison, S., Wardell-Johnson, G.W., Marcantonio, M. & Mucina, L. (2018) Towards an eco-evolutionary understanding of endemism hotspots and refugia. *Annals of Botany*, 122, 927–934.
- Kessler, M. (2002) The elevational gradient of Andean plant endemism: varying influences of taxon-specific traits and topography at different taxonomic levels. *Journal of Biogeography*, 29, 1159–1165.
- Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J. & Barthlott, W. (2009) A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences USA*, 106, 9322–9327.
- Kirkpatrick, J.B. (1999) *A Continent Transformed*. Oxford University Press, Melbourne, Australia.
- Kirkpatrick, J.B. & Brown, M.J. (1984) The paleogeographic significance of local endemism in Tasmanian higher plants. *Search*, 15, 112–113.
- Köhler, F. (2010) Uncovering local endemism in the Kimberley, Western Australia: description of new species of the genus *Amplirhagada* Iredale, 1933 (Pulmonata: Camaenidae). *Records of the Australian Museum*, 62, 217–284.
- Krosch, M.N., Baker, A.M., Mckie, B.G., Mather, P.B. & Cranston, P.S. (2009) Deeply divergent mitochondrial lineages reveal patterns of local endemism in chironomids of the Australian Wet Tropics. *Austral Ecology*, 34, 317–328.
- Lambeck, K. & Chappell, J. (2001) Sea level change through the Last Glacial Cycle. *Science*, 292, 679–686.
- Lambeck, K., Yokoyama, Y. & Purcell, T. (2002) Into and out of the Last Glacial Maximum: sea-level change during Oxygen Isotope Stages 3 and 2. *Quaternary Science Reviews*, 21, 343–360.
- Linder, H.P. (2001) Plant diversity and endemism in sub-Saharan tropical Africa. *Journal of Biogeography*, 28, 169–182.
- Mineral Resources Tasmania (2010) 1:250 000 Digital Geology, Mineral Resources Tasmania, Tasmania, Australia.
- Mittermeier, R.A., Gil, P.R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J. & da Fonseca, G.A.B. (2005) Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions. Cemex, Mexico City, Mexico.
- Molina-Venegas, R., Aparicio, A., Pina, F. J., Valdés, B. & Arroyo, J. (2013) Disentangling environmental correlates of vascular plant biodiversity in a Mediterranean hotspot. *Ecology and Evolution*, 3, 3879–3894.
- Molina-Venegas, R., Aparicio, A., Slingsby, J. A., Lavergne, S. & Arroyo, J. (2015) Investigating the evolutionary assembly of a Mediterranean biodiversity hotspot: deep phylogenetic signal in the distribution of eudicots across elevational belts. *Journal of Biogeography*, 42, 507–518.
- Molina-Venegas, R., Aparicio, A., Lavergne, S. & Arroyo, J. (2017) Climatic and topographical correlates of plant palaeo- and neoendemism in a Mediterranean biodiversity hotspot. *Annals of Botany*, 119, 229–238.
- Morat, P. (1993) Our knowledge of the flora of New Caledonia: endemism and diversity in relation to vegetation types and substrates. *Biodiversity Letters*, 1, 72–81.
- Mucina, L. & Wardell-Johnson, G.W. (2011) Landscape age and soil fertility, climatic stability, and fire regime predictability: beyond the OCBIL framework. *Plant and Soil*, 341, 1–23.
- Muñoz, J., Gómez, A., Green, A.J., Figuerola, J., Amat, F. & Rico, C. (2008) Phylogeography and local endemism of the native Mediterranean brine shrimp *Artemia salina* (Branchiopoda: Anostraca). *Molecular Ecology*, 17, 3160–3177.
- Murienne, J., Grandcolas, P., Piulachs, M.D., Bellés, X., D'Haese, C., Legendre, F., Pellens, R. & Guilbert, E. (2005) Evolution on a shaky piece of Gondwana: is local endemism recent in New Caledonia? *Cladistics*, 21, 2–7.
- Orchard, A.E. (2004) A revision of *Bedfordia* DC. (Asteraceae). *Muelleria*, 19, 81–94.
- Richardson, D.M. & Whittaker, R.J. (2010) Conservation biogeography – foundations, concepts and challenges. *Diversity and Distributions*, 16, 313–320.
- Rozefelds, A. (2011) New species of *Craspedia* from Tasmania and an evaluation of the status of *Craspedia macrocephala* Hook. *Kanunnah*, 4, 93–116.
- Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. & Svenning, J.-C. (2011) The influence of late Quaternary climate-change velocity on species endemism. *Science*, 334, 660–664.

- Schaefer, S.A., Chakrabarty, P., Geneva, A.J. & Sabaj Pérez, M.H. (2011) Nucleotide sequence data confirm diagnosis and local endemism of variable morphospecies of Andean astrolepid catfishes (Siluriformes: Astroblepidae). *Zoological Journal of the Linnaean Society*, 162, 90–102.
- Schahinger, R. (2002) *Allocasuarina crassa* L. Johnson (Casuarinaceae): a revised description, with notes on distribution and habitat. *Papers and Proceedings of the Royal Society of Tasmania*, 136, 101–106.
- Silvertown, J. (2004) The ghost of competition past in the phylogeny of island endemic plants. *Journal of Ecology*, 92, 168–173.
- Slatyer, C., Rosauer, D. & Lemckert, F. (2007) An assessment of endemism and species richness patterns in the Australian Anura. *Journal of Biogeography*, 34, 583–596.
- Sorrie, B.A. & Weakley, A.S. (2001) Coastal Plain vascular plant endemics: phytogeographic patterns. *Castanea*, 66, 50–82.
- Stebbins, G.L. & Major, J. (1965) Endemism and speciation in the California flora. *Ecological Monographs*, 35, 1–35.
- Stevanović, V., Tan, K. & Iatrou, G. (2003) Distribution of the endemic Balkan flora on serpentine I. – obligate serpentine endemics. *Plant Systematics and Evolution*, 242, 149–170.
- Taberlet, P., Fumagalli, L., Wust-Saucy, A.-G. & Cosson, J.-F. (1998) Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology*, 7, 453–464.
- Thornhill, A.H., Baldwin, B.G., Freyman, W.A., Nosratinia, S., Kling, M.M., Moruete-Holme, N., Madsen, T.P., Ackerly, D.D. & Mishler, B.D. (2017) Spatial phylogenetics of the native California flora. *BMC Biology*, 15, 96
- Threatened Species Section (2019a) *Epacris virgata* (pretty heath): Species management profile for Tasmania's Threatened Species Link. Department of Primary Industries, Parks, Water and Environment, Tasmania, Australia. Viewed 16th October 2019, <<https://www.threatenedspecieslink.tas.gov.au/Pages/Epacris-virgata.aspx>>.
- Threatened Species Section (2019b) *Tetratheca gunnii* (shy pinkbells): Species management profile for Tasmania's Threatened Species Link. Department of Primary Industries, Parks, Water and Environment, Tasmania, Australia. Viewed 16th October 2019, <<https://www.threatenedspecieslink.tas.gov.au/Pages/Tetratheca-gunnii.aspx>>.
- Tivy, J. (1993) *Biogeography - A study of plants in the ecosphere*, 3rd ed. Longman Scientific & Technical and John Wiley & Sons, Inc., New York.
- Wang, Y., Wang, J., Lai, L., Jiang, L., Zhuang, P., Zhang, L., Zheng, Y., Baskin, J.M. & Baskin, C.C. (2014) Geographic variation in seed traits within and among forty-two species of *Rhododendron* (Ericaceae) on the Tibetan plateau: relationships with altitude, habitat, plant height, and phylogeny. *Ecology and Evolution*, 4, 1913–1923.
- Weiller, C. (1996) Reassessment of *Cyathodes* (Epacridaceae). *Australian Systematic Botany*, 9, 491.
- Zuloaga, J., Currie, D.J. & Kerr, J.T. (2019) The origins and maintenance of global species endemism. *Global Ecology and Biogeography*, 28, 170–183.
- Submitted: 26 March 2020
 First decision: 30 April 2020
 Accepted: 15 June 2020
- Edited by Janet Franklin and Robert J. Whittaker