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A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix

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A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix

Running title: Quantifying and locating microrefugia

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Abstract

Ecologists are increasingly recognising the conservation significance of microrefugia, but it is inherent difficult to locate these small patches with unusual climates, and hence they are also referred to as cryptic refugia. Here we introduce a new methodology to quantify and locate potential microrefugia using fine-scale topoclimatic grids that capture extreme conditions, stable climates, and distinct differences from the surrounding matrix. We collected hourly temperature data from 150 sites in a large (200km by 300km) and diverse region of New South Wales, Australia, for a total of 671 days over two years. Sites spanned a range of habitats including coastal dune shrublands, eucalypt forests, exposed woodland ridges, sheltered rainforest gullies, upland swamps, and lowland pastures. Climate grids were interpolated using a regional regression approach based on elevation, distance to coast, canopy cover, latitude, cold-air drainage and topographic exposure to winds and radiation. We identified extreme temperatures on two separate climatic gradients: the 5th percentile of minimum temperatures and the 95th percentile of maximum temperatures. For each gradient, climatic stability was assessed on three different time scales (intra-seasonal, intra-annual and inter-annual). Differences from the matrix were assessed using a moving window with a 5km radius. We averaged the Z-scores for these extreme, stable and isolated climates to identify potential locations of microrefugia. We found that our method successfully predicted the location of communities that were considered to occupy refugia, such as rainforests that have progressively contracted in distribution over the last 2.5 million years, and alpine grasslands that have contracted over the last 15 thousand years. However, the method was inherently sensitive to the gradient selected and other aspects of the modelling process. These uncertainties could be dealt with in a conservation planning context by repeating the methodology with various parameterisations and identifying areas that were consistently identified as microrefugia.

Introduction

The conservation of biodiversity has traditionally been based on static maps of species' distributions (Margules & Pressey, 2000), but there is increasing awareness that conservation planning needs to evolve to cope with the dynamic nature of biodiversity (Pressey *et al.*, 2007). One way this can be achieved is by protecting locations that are important for ongoing ecological and evolutionary processes, an important example of which is refugia (Klein *et al.*, 2009). Refugia are locations that have stable and unusual climates with intrinsic conservation value because they: (1) buffer species from climate variability and therefore enhance the ability of species to persist when the climate is unsuitable elsewhere; (2) foster genetic isolation that can enhance evolutionary processes; and, (3) enhance the diversity of environmental conditions and thus increase the potential for higher biodiversity (Noss, 2001; Tzedakis *et al.*, 2002; Forest *et al.*, 2007; Johnson & Stinchcombe, 2007; Kozak *et al.*, 2008; Stewart *et al.*, 2010). Some refugia are also known to harbour rare or endemic genotypes or species (e.g. the Wollemi pine; *Wollemia nobilis*; Offord, 2011), but even those that do not contain these have conservation value because the processes they support may still offer future protection for species that are not currently rare or threatened (Mosblech *et al.*, 2011).

Refugia have been broadly classified as either macrorefugia or microrefugia, where macrorefugia are regions with favourable climate and microrefugia are small areas of favourable climate within a region of generally unfavourable climate (Bennett & Provan, 2008; Rull, 2009). The locations of macrorefugia can be estimated using coarse-grained species distribution models based on macroclimatic surfaces and readily available data and software make this a relatively simple way to estimate broad-scale latitudinal and altitudinal shifts in species' distributions (e.g. Svenning *et al.*, 2008). On the other hand, locating microrefugia is more challenging and has not been sufficiently addressed because it requires accurate fine-scale climatic grids based on a wider variety of climate forcing factors

(Ashcroft, 2010). Indeed, microrefugia are often referred to as cryptic refugia due to the inherent difficulty in determining their exact location (Bennett & Provan, 2008; Rull, 2009).

A number of methods have been utilised to investigate the location of microrefugia, though all have their weaknesses. Fossil and pollen records can provide historical information on species' distributions and be used as evidence of long-term persistence *in-situ*. However, these sources of information are often incomplete and not available in all locations and therefore need to be supplemented with data from other sources (Keppel *et al.*, 2011). Analysing current distributions of genotypes can provide evidence of the existence of past microrefugia, but this does not provide direct evidence of exactly where those genotypes survived or evolved if there have been subsequent range expansions or shifts (e.g. Petit *et al.*, 2003; Wang *et al.*, 2009). Coarse-scale species distribution models can also be used to infer the approximate location of microrefugia as they are likely to exist in topographically complex areas and this can be introduced into models using a within-cell elevational range predictor (Luoto & Heikkinen, 2008). However, this method does not provide information on exactly where the microrefugia exist within those coarse-grained grid cells.

Given the difficulties in locating microrefugia, it is not surprising that authors have discussed their locations qualitatively or generalised that they occur in distinct habitats such as topographic depressions, boulder fields, granite outcrops, or sheltered gorges (e.g. Shoo *et al.*, 2010a; Hopper, 2009; Ashcroft, 2010; Dobrowski, 2011; Keppel *et al.*, 2011; Mosblech *et al.*, 2011). Indeed, most authors have not actually quantified what constitutes a microrefugium or produced maps of expected locations (Hampe & Jump, 2011). Some authors have identified fine-scale variations in warming that indicate higher climatic stability (e.g. Ashcroft *et al.*, 2009), while others have considered a broad range of climate forcing factors whilst still assuming uniform warming (e.g. Dobrowski, 2011). There is a pressing need to combine both these approaches in order to quantify both the uniqueness and

variability of climate in microrefugia using a broad range of fine-scale climate-forcing factors.

Here we introduce a novel methodology to identify the potential locations of microrefugia by quantifying areas that: (1) have the lowest or highest temperatures when assessed using fine-scale topoclimatic grids; (2) have relatively stable climates; and, (3) are distinctly different from the climate in the surrounding area (hereafter referred to as the matrix). The justifications for each of these interrelated criteria as well as the methodological issues that need to be addressed to quantify them are discussed in the following sections.

Extreme temperatures

Cold-adapted species tend to contract to refugia during interglacial periods, while warm-adapted species tend to contract during glacial periods (Stewart *et al.*, 2010). Those locations at the coldest and warmest extremes of the temperature gradients respectively will remain most climatically favourable during harsher times, and therefore it is important to identify locations with conditions at the extreme ends of temperature gradients. Cold-adapted species are currently facing the greatest threat from rising temperatures, but we focus on both extremes in this study because it is important to conserve both warm and cold refugia to protect species over the long-term (Svenning & Skov, 2006). Changes in geomorphology and vegetation over long time scales and large climatic fluctuations will undoubtedly reduce the applicability of models based on current conditions, but the intent is to estimate where species can survive or evolve over many millennia (see also Discussion).

Quantifying locations with extreme climates will depend on the climatic gradient considered. For example, if the environmental gradient of interest was average winter minimum temperatures then the coldest conditions might be found in topographic depressions where cold-air could accumulate (Dobrowski, 2011). Alternatively, if the environmental

gradient of interest was average summer maximum temperatures then the coldest conditions might be found in topographically sheltered locations where there was protection from radiation and hot drying winds (Ashcroft *et al.*, 2009). Therefore, identifying the location of extreme climates is obviously dependent on which climatic gradients are considered, and this in turn affects which species could potentially persist in the associated microrefugia (Barnosky, 2008; Dobrowski, 2011).

Stable climates

Climatic stability is a second important attribute of refugia because higher variability is expected to lead to higher extinction rates and therefore reduce the long-term persistence of species (Tzedakis *et al.*, 2002; Mosblech *et al.*, 2011). While climate stability has been studied at both coarse (Saxon *et al.*, 2005; Iwamura *et al.*, 2010) and fine scales (Lundquist & Cayan, 2007; Ashcroft *et al.*, 2009), it is at the fine-scale where stability will be especially crucial. This is because populations that are restricted to small areas are more prone to extinction, and the persistence of species for many millennia may only be possible in microrefugia where climatic stability lowers the risk of local extinctions (Hopper, 2009; Hampe & Jump, 2011; Mosblech *et al.*, 2011).

Climate stability can be measured over many different time frames, each of which may have an impact on extinction rates for different species. Depending on the life cycle and traits of a species it may be particularly sensitive to day-to-day variability within a certain season, the seasonal variation within a year, or the year-to-year variation in climate. The effect of different climate-forcing factors varies between seasons and weather patterns (e.g. Lundquist & Cayan, 2007; Ashcroft *et al.*, 2009; Ashcroft & Gollan, 2012) and hence a site may vary in climatic stability over these time frames. Therefore, any methodology that is introduced to quantify climatic stability needs to consider a range of different time scales.

Isolation from the matrix

The third important trait of microrefugia is the difference in climate from the surrounding matrix, as this is indicative of the climatic isolation of the location (Hampe & Jump 2011; Mosblech *et al.*, 2011). The importance of this isolation is best illustrated by an example. Consider a species that occupies a microrefugium within its realised niche and can maintain or increase population size even in the presence of competitors (Pulliam, 2000; Fig. 1A). Climate stability will increase the probability that the climate of the microrefugium stays within the species' realised niche, but continued warming (or cooling) may cause the climate to shift outside the realised niche, but remain within the fundamental niche (Fig. 1B). In this situation the species would no longer be able to maintain a population if antagonistic species were present, hence the contrast from the matrix becomes crucial. If the microrefugium is very different environmentally from the matrix then the matrix could act as a barrier that prevents competitors, pathogens and parasites dispersing to the site and the species may be able to persist even though it is now occupying conditions outside its realised niche (Pulliam, 2000; Hopper, 2009; Hampe & Jump, 2011). Further warming may mean that the species experiences conditions outside its fundamental niche, and while individuals of the species can survive within their persistence niche, they are no longer able to produce sufficient offspring to maintain the species' population in the long-term (Pulliam, 2000; Fig. 1C). Under these circumstances, life history traits become important as, for example, clonal growth, longevity or a persistent soil seed bank may allow existing individuals to persist long enough for conditions to return to within the fundamental niche (Ashcroft, 2010; Hampe & Jump, 2011; Mosblech *et al.*, 2011). The population would inevitably go extinct if conditions exceeded the limits of the persistence niche (Fig. 1D), but isolation from the matrix would nevertheless

help the population survive a broader range of conditions outside its realised niche (Fig. 1B, C).

The topographic heterogeneity that allows some areas to be climatically isolated from the matrix (Mosblech *et al.*, 2011) also creates sharp climatic gradients. These transitions in climate may also allow species to persist *ex-situ* by migrating over small geographic distances (Hampe & Jump, 2011). Although we acknowledge that climatic heterogeneity and differences from the matrix may differ in some respects, we assume these are largely inter-related and focus only on difference from the matrix in this article.

New methodological framework

The methodological framework we introduced in this study consisted of three steps. First, we quantified the three aspects of refugia (extreme, stable, and isolated climates) using fine-resolution climate grids based on a range of climate-forcing factors. Second, we standardised each aspect so that all three were quantified on similar scales. Third, we averaged the standardised results to identify locations that were extreme, stable and/or isolated. Importantly, our methodology does not rely on all sites having to satisfy all three criteria as, for example, extremely stable sites may not need much environmental heterogeneity for persistence (see Fig. 1 in Hampe & Jump, 2011). It should be noted that refugia are not an all or nothing concept, and our methodology captured a continuum of sites varying in temperature, stability and isolation.

Materials and methods

Study area

This study was conducted in and around the Hunter Valley in New South Wales, Australia (31.4–33.4°S, 149.4–152.6°E; Fig. 2). Although all our analyses were conducted over this entire area, microrefugia were small and hard to discern in maps of the entire study area, and so we focused only on results in two world heritage areas either side of the valley that have particular conservation significance. The first was the Greater Blue Mountains World Heritage Area (GBMWHa), which includes parts of eight different conservation reserves. We focused on the northern-most section of the GBMWHa, including most of Wollemi National Park and Yengo National Park. The second area of focus comprised Mount Royal National Park, Barrington Tops National Park and Barrington Tops State Conservation Area; the former two contain parts of the Gondwana Rainforests of Australian World Heritage Area. We hereafter refer to these two areas as the Wollemi and Barrington regions.

The Wollemi region is topographically complex and includes basalt capped mountains, deep gorges, and sandstone cliffs. Elevation ranges from less than 100m in the deep gorges to over 1200m at the highest peaks (Fig. 2). It is dominated by eucalypt forests and woodlands, but also contains areas of heath, upland swamps and warm temperate rainforests (NPWS, 2001). The Wollemi region contains a number of highly restricted local endemics, including *Apatophyllum constablei*, *Acacia asparagoides*, *Eucalyptus bensonii*, *Wollemia nobilis* and *Rupicola decumbens* (NPWS, 2001). The recent discovery of the ancient Wollemi pine (*Wollemia nobilis*) in particular highlights the remote and unexplored nature of the region, and there are potentially other localised endemics in isolated microrefugia within the park.

In contrast, the Barrington region is dominated by a plateau at an elevation of 1400–1600m, and steep slopes down to 200–300m (Fig. 2). Eucalypt forests dominate on exposed

ridges on the plateau with rainforests in more sheltered locations (NPWS, 2010). The shallow, broad valleys on the plateau trap cold-air, which excludes trees, and the vegetation forms upland swamps and grasslands (Dodson, 1987). These communities in particular have endemic species of high conservation value (NPWS, 2010) and the vegetation in the upland swamps is listed as an Endangered Ecological Community (NSW Scientific Committee, 2004).

Historical context

Rainforests were widespread in south-east Australia in the early Miocene (~23–15Mya) and Pliocene (~5.3–2.5Mya), although they contracted during the late Miocene during a period of increased fire activity and sclerophyllous vegetation expansion (White, 1994). The Pleistocene glacial and interglacial cycles (~2.5Mya–present) were accompanied by further and more sustained drying. While this saw rainforests progressively contract to the small refugia they occupy today, their current distribution is broader than that during the drier times of the last glacial period (~18kya; White, 1994; Bowman, 2000). The current fragmented distribution of rainforests has been variously attributed to nutrients, climate and fire (Bowman, 2000), although these factors are interrelated and may not act independently.

During the last glacial maximum (~18–15kya), south-east Australia was cold and dry, with alpine grasslands widespread and extending to low elevations (White, 1994; Williams *et al.*, 2006). The forests that survived these times in refugia have since expanded their distributions, while the alpine grasslands and the species they support have contracted to small refugia at higher elevations (Dodson, 1987; Dodson *et al.*, 1994; NSW Scientific Committee, 2001). These refugia may include the topographic depressions on the Barrington Plateau where grasslands and upland swamps are found, although the swamps will be moister than many locations during the drier glacial period. Therefore, there are at least two relict

communities that are of particular interest in this study area: the rainforests that have been progressively contracting to refugia over the last 2.5 million years, and the alpine grasslands that have contracted to refugia over the last 15 thousand years.

Fine-resolution topoclimatic grids

Standardised weather stations are inappropriate for the study of microrefugia because they are sparsely distributed and are biased against forests and topographically complex areas (Ashcroft, 2010). Therefore, we deployed 150 DS1923 iButton dataloggers (Maxim; Fig. 2) to capture the climate in a range of habitats, recording hourly temperature and humidity for a total of 671 days over two years (1st June to 24th August 2009, 2nd September to 25th November 2009, 3rd December 2009 to 25th February 2010, 5th March to 28th May 2010, 5th June to 21st November 2010, and 11th December 2010 to 15th May 2011). Sensors were placed ~5cm above the ground inside an inverted PVC jar, with holes drilled in the sides to allow airflow while still providing protection from direct radiation and rainfall. A diversity of environments were sampled, including coastal dune shrublands, eucalypt forests, exposed woodland ridges, sheltered rainforest gullies, upland swamps, and lowland pastures. While many of the sensors were located outside the two regions of focus in this study, these locations were selected to minimise the correlations between different climate-forcing factors, reduce spatial autocorrelation, and increase the range of each factor so that more robust climate grids could be produced (Ashcroft & Gollan, 2012).

A wide range of environmental gradients could have been analysed to identify locations with extreme climates. In this paper we chose to demonstrate our methodology using two temperature gradients that capture the hottest and coldest conditions at each location, as these are likely to be physiologically limiting for many species. Temperature gradients such as mean annual temperature or average summer maximum temperature can

obscure which locations experience the hottest and coldest temperatures as they are based on predefined periods that include many different weather patterns (Ashcroft & Gollan, 2012). Extreme temperatures at any site occur under specific weather conditions at that site, and so we used gradients based on the 5th percentile of minimum temperatures and the 95th percentile of maximum temperatures so we could focus on the extreme conditions at each site even if they did not occur simultaneously or on consecutive days.

To produce topoclimatic grids representing the two gradients we first analysed the data at each site to determine the daily maximum and minimum temperatures, and then calculated the 5th percentile of minimum temperatures and the 95th percentile of maximum temperatures to examine the extremes at each site. These variables were interpolated to form climate grids using a regional regression approach (Lookingbill & Urban 2003; Daly, 2006) based on elevation, distance to coast, canopy cover, latitude, cold-air drainage and topographic exposure to the northwest, northeast, and south. We first used Generalised Additive Models (GAMs in SPlus v8.0.4, Insightful Corp.; Gaussian family) to examine the shape of responses and transformed predictors to ensure that relationships were reasonably linear for use in the regional regression. We then performed a stepwise regression (forward-backward using default values in SPlus) using the climate-forcing factors and used the resulting models to interpolate climate grids in ArcMap (ESRI). Models were assessed by the strengths of the correlations and the root-mean-square (RMS) errors. Further details of the sampling and interpolation method implemented can be found in Ashcroft & Gollan (2012).

Similarly, we interpolated six different grids of climate variability, capturing three different time scales of variability relevant for the two temperature gradients detailed above. The variability grids were: (i) intra-seasonal variation in maximum temperatures, calculated as the 95th percentile of summer (December–February) maximums minus the 5th percentile of summer maximums; (ii) intra-annual variation in maximum temperatures, calculated as the

95th percentile of summer maximum temperatures minus the 95th percentile of winter (June–August) maximum temperatures; (iii) inter-annual variation in maximum temperatures, calculated as the difference in the 95th percentile of maximum temperatures between the two years; (iv) intra-seasonal variation in minimum temperatures, calculated as the 95th percentile of winter minimum temperatures minus the 5th percentile of winter minimum temperatures; (v) intra-annual variation in minimum temperatures, calculated as the 5th percentile of summer minimum temperatures minus the 5th percentile of winter minimum temperatures; and, (vi) inter-annual variation in minimum temperatures, calculated as the difference in the 5th percentile of minimum temperatures between the two years. These six estimates of climatic variability were calculated at 113 of the 150 sites (some iButtons failed and some sites were disturbed) and interpolated to produce climate variability grids using the same methodology as detailed above.

Identifying potential locations of microrefugia

As proposed above, the locations of potential microrefugia were identified by combining: 1) the coldest/hottest locations; 2) the locations that were most climatically stable; and, 3) the locations that were most different from the matrix. These three aspects of refugia were combined by averaging their Z-scores ($[x - \text{mean}] / \text{s.d.}$). This standardisation ensured that all three aspects were on comparable scales before they were averaged. Negative Z-scores reflected sites that were extremely cold, colder than the matrix, or very stable. Positive Z-scores reflected sites that were extremely warm, warmer than the matrix, or highly variable. Therefore, we had to vary the sign of the variability Z-score depending on whether the site was warmer or cooler than the matrix to ensure warm refugia were also stable. The formula for our refugia index (RI) was given by:

$$\text{RI} = (Z_{\text{temp}} + \text{sign}(Z_{\text{matrix}}) \cdot Z_{\text{var}} + Z_{\text{matrix}}) / 3 \quad (1)$$

where RI is the refugia index, Z_{temp} is the Z-score based on temperature, Z_{var} is the Z-score based on variability, Z_{matrix} is the Z-score for difference from the matrix, and $\text{sign}(Z_{\text{matrix}})$ indicates whether the site is cooler (-1) or warmer (+1) than the matrix.

Z-scores for the coldest and hottest locations were calculated for both the 5th percentile of minimum temperature and 95th percentile of maximum temperature gradients. We calculated Z-scores for the six variability grids separately. Z-scores for the three variability grids associated with the 95th percentile of maximum temperatures were averaged to estimate overall climate stability, and the same was done for the three variability grids associated with the 5th percentile of minimum temperatures. Z-scores for difference from the matrix were determined for both gradients by calculating the difference between the site temperature and the average temperature within a 5km radius moving window. This 5km radius was chosen arbitrarily and could be varied to capture a continuum from microrefugia to macrorefugia and to cater for variations in dispersal ability among species. This is addressed further in the discussion.

Results

Extreme temperatures

The 5th percentiles of minimum temperatures were predominately determined by cold-air drainage, and to a lesser extent elevation, distance to coast, and canopy cover (Ashcroft & Gollan, 2012). Coldest sites on this gradient occurred in topographic depressions, at high elevations, inland, and where there was low canopy cover. The 95th percentiles of maximum temperatures were predominated determined by canopy cover, elevation, distance to coast, and to a lesser extent topographic exposure and latitude (Ashcroft & Gollan, 2012). In contrast to the 5th percentiles of minimum temperatures, coldest sites on this gradient had high canopy cover, high elevation, were near the coast, and were sheltered from the northwest. The 5th percentile of minimum temperatures ($r^2 = 0.74$; range of -8.6 – 9.3°C ; RMS error = 1.7°C) could be predicted more accurately than the 95th percentile of maximum temperatures ($r^2 = 0.58$; range of 26.6 – 53.2°C ; RMS error = 3.4°C), in part because the remotely sensed canopy cover layer was not as accurate as the canopy cover observed at the sites (Ashcroft & Gollan, 2012).

Differences from the matrix

The difference from the matrix grids highlighted small locations with unusual climate. For example, the Barrington plateau was consistently at the cooler end of the 95th percentile of maximum temperature gradient (Fig. 3a) and so there were few locations that were colder than the matrix (Fig. 3b). However, the steep climatic gradients caused by cold-air drainage in the topographic depressions created areas of unusual minimum temperatures (Fig. 4a), and led to large differences (Fig. 4b).

Climatic variability

Intra-seasonal variation in maximum temperatures varied from 7.5°C to 31.0°C, but could not be modelled as well as the temperature gradients described above ($r^2 = 0.40$; RMS error = 3.3°C). Stability was predominately determined by distance to coast, with coastal areas more stable than inland. Stability was also higher at sites with higher canopy cover, in northern areas, at higher elevations, and at sites sheltered from the northwest or exposed to the south.

Intra-annual variation in maximum temperatures varied from 5.1°C to 31.2°C, and the model performed similarly to intra-seasonal variability ($r^2 = 0.39$; RMS error = 1.8°C). While coastal forests with high canopy cover were stable in terms of both intra-seasonal and intra-annual variability, the dominant factor affecting intra-annual variability was exposure to the south. Four of the 12 most stable sites (variation < 13.5°C) were drier sites in more inland locations where protection from cold, moist southerly winds in winter allowed winter maximum temperatures to remain high. Exposure to radiation may also have contributed to this effect, although these four sites had some protection due to canopy cover, and other sites that were exposed to the northwest but not sheltered from the south did not have low variability. Stability was higher at sites that were sheltered from the south, nearer the coast, further north, or at higher elevation.

The model for inter-annual variability of maximum temperatures was weaker ($r^2 = 0.18$; RMS error = 1.8°C), with an observed range of 0°C to 8.3°C. In contrast to the previous two models, the most climatically stable areas were at lower elevation, although northern areas were still predicted to be more stable.

Intra-seasonal variability in minimum temperatures ranged from 5.6°C to 15.6°C, with a model performance better than those for maximum temperatures ($r^2 = 0.72$; RMS error = 1.1°C). While topographic depressions where cold air could pool had temperatures that were much lower than the surrounding matrix, this was also the dominant factor leading to higher

intra-seasonal variability in minimum temperatures (e.g. topographic depressions in Fig. 4). Sites with high canopy cover or that were closer to the coast had high stability.

Intra-annual variability in minimum temperatures ranged from 8.6°C to 15.4°C and was also better modelled than maximum temperatures ($r^2 = 0.61$; RMS error = 0.9°C). Similarly to the intra-seasonal variability, stability was higher at coastal locations, at sites with higher canopy cover, and at perched sites where cold air could drain away. However, elevation was also included in this model, with higher stability at higher elevations.

Inter-annual variability in minimum temperatures ranged from 0°C to 2.6°C, with the model explaining very little variation ($r^2 = 0.10$; RMS error = 0.5°C). Variability was lower at lower elevations and at perched sites where cold air could drain away.

Refugia in the Barrington region

The Barrington region was consistently at the coldest extreme of the 95th percentile of maximum temperature gradient (Fig. 3a), however, the plateau itself was relatively uniform and hence there were few areas that were different from the matrix (Fig. 3b). The Barrington region was predicted to be quite stable in terms of intra-seasonal variability due to the high elevation and canopy cover (Fig. 3c), but the higher elevation also meant it was predicted to be less stable in terms of inter-annual variability (Fig. 3e). Cold refugia were generally found around the periphery of the reserve, where greater topographic complexity and land clearing created larger contrasts from the surrounding matrix, and topographic shelter led to higher intra-annual stability (Fig. 3f). Very few warm refugia were in the region; those that were, were restricted to lowland gullies.

The Barrington plateau contains a number of grasslands and upland swamps in topographic depressions where cold air pools, and these were predicted to be more than 7°C colder than the surrounding matrix (Fig. 4b). However, while cold-air drainage created

environments that were unusually cold, it also caused these locations to be more variable than the surrounding areas (Fig. 4c, e). Nevertheless, these grasslands and upland swamps on the plateau were still identified as cool refugia, as the large contrast from the matrix more than compensated for the higher variability (Fig. 4f). The forested slopes around the plateau were predicted to be warmer (Fig. 4a) and more stable (Fig. 4c-e), as these locations have less cold air drainage and higher canopy cover. Although this was sufficient to classify them as warm refugia, the contrast from the matrix was low (Fig. 4b) and the warm refugia were not as isolated as the cool refugia (Fig. 4f).

Refugia in the Wollemi region

The Wollemi region is more topographically complex than the Barrington region, resulting in a more complex pattern of 95th percentile of maximum temperatures (Fig. 5a). Both the hottest and coldest locations were restricted to smaller patches than in the Barrington region, and these patches had larger contrasts from the matrix (Fig. 5b). Warm and cool refugia on the 95th percentile of maximum temperature gradient were restricted to these small patches (Fig. 5f), many of which also exhibited a large degree of climatic stability (Fig. 5c-e).

For 5th percentile of minimum temperatures, the matrix in the Wollemi region consisted of woodland ridges, where canopy cover and an absence of cold air drainage lead to warm (Fig. 6a) and stable temperatures (Fig. 6c-e). Topographic depressions and gullies were cooler than the matrix (Fig. 6b), but the contrast was not as great as the Barrington region, and the higher variability caused by cold-air drainage meant that cool refugia were predicted to be rare and generally located in cleared areas just outside the reserve boundary (Fig. 6f). Warm refugia were predicted to be more widespread, and were found on the steeper slopes that are unaffected by cold-air drainage, and hence warmer and more stable.

Discussion

The primary objective of this study was to demonstrate a method for locating potential microrefugia by quantifying extreme climates, climatic stability, and differences from the matrix. As few studies have attempted to quantify or map microrefugia (Hampe & Jump, 2011), this is a valuable first step. However, our results also raised many issues with the concept of microrefugia that warrant further attention.

First, we found that areas with extreme climates do not necessarily correspond with areas of high climatic stability. For example, while cold-air drainage has been identified as a factor affecting refugia because it leads to temperatures that are much colder than the matrix (Dobrowski, 2011), we found that it also causes these locations to be more climatically variable (Fig. 4a, c). Whether or not topographic depressions where cold air pools can function as refugia depends on the relative importance of climatic stability and differences from the matrix. Our methodology made arbitrary decisions regarding the relative importance of the three aspects of refugia when we combined them using their Z-scores, but they each have very different distributions (e.g. Fig. 3a–e), and results are vastly different if they are combined differently. For example, if we weighted variability twice as highly as the other two aspects, then there were much fewer cool refugia in the Barrington region (Fig. S1 in Supporting Information). Similarly, if we linearly scaled each aspect to a range of -1 to 1 instead of using Z-scores then this had a large effect on the cool refugia that were identified at lower elevations (Fig. S2 in Supporting Information). Given that the true location of microrefugia is cryptic, obtaining data to validate which method performs best is problematic.

Second, it is worth noting the difference in the location of refugia when assessed using two different climatic gradients (5th percentile of minimum temperatures and 95th percentile of maximum temperatures). Some locations that were identified as being cool refugia in terms of the 95th percentile of maximum temperature were classified as warm

refugia according to the 5th percentile of minimum temperatures (e.g. Fig. 3, 4). As different species will respond to different climatic gradients there is no right or wrong answer to which gradients should be examined, yet results are obviously highly sensitive to which gradients are selected.

Third, climatic stability has already been utilised to recommend areas for conservation (e.g. Saxon *et al.*, 2005; Iwamura *et al.*, 2010), yet our results demonstrate that the location of stable climates varies according to the time frame over which stability is considered (e.g. Fig. 3c–e). Different climate-forcing factors were identified as affecting our six estimates of variability, with elevation in particular having both positive and negative effects in different models.

Finally, the results were dependent on the radius that was used to identify differences from the matrix. While we used a radius of 5km in all our analyses, it can be shown that results vary dramatically if the radius is varied from 1km to 25km (Fig. S3 in Supporting Information), reflecting a continuum of microrefugia to macrorefugia. Once again, there is no correct answer for which scale should be used, as different species vary in dispersal ability and home range and hence a range of scales would be appropriate.

All the above sensitivities highlight how the identified locations of microrefugia are inherently dependent on the details of the methodology utilised. We considered two climatic gradients and both warm and cool refugia, yet there are many more possibilities that could be considered. Our results demonstrate the applicability of the methodology, but if it were applied in a conservation planning context then more gradients and more radii should be considered, as well as different combinations of the three aspects of refugia. The intent would be to identify locations that are consistently identified as refugia across a number of spatial scales and environmental gradients and are robust to the uncertainties surrounding the relative contributions of different aspects.

Limitations, errors, and potential future applications

All climatic grids we produced were interpolated using a remotely-sensed canopy cover layer that is known to contain inaccuracies at higher canopy covers (DECC, 2008). We previously reported that these errors affected our ability to identify sites with low maximum temperatures (Ashcroft & Gollan, 2012), and this also means that we probably failed to identify some refugia where the 95th percentiles of maximum temperatures were low in this study. Improving the accuracy of the canopy cover layer remains a high priority.

One limitation of our approach is that the microrefugia we identified can form somewhat continuous patches (e.g. cool refugia in Fig. 3 or warm refugia in Fig. 4). Although we considered the difference from the matrix using a 5km-radius moving window, this does not prevent continuity when linear elements are present or extreme climates or stability override the fact that there is little difference from the matrix. Where isolation is a crucial aspect of refugia (e.g. for allopatric evolutionary processes), the maps we produced could be enhanced by conducting landscape analysis (e.g. calculating metrics based on fragmentation and isolation; Fahrig, 2003).

The models for inter-annual variability were poorer (lower r^2) than those for intra-seasonal and intra-annual variability. This is probably because the differences between the two years were much smaller than the differences within or between seasons, and hence there was more noise in the data and the accuracy of the iButtons ($\pm 0.5^\circ\text{C}$) had more effect. It is also worth noting that inter-annual variability was based on only two years of data, and trends may be more apparent with a longer time series. Nevertheless, it is also worth highlighting that inter-annual variability displayed some different trends, and there would be dangers in assuming that inter-seasonal or intra-annual variability represented inter-annual variability.

Another limitation of our approach is that it only considers isolation from the matrix

in terms of the difference in temperature. In actual landscapes, isolation may be enhanced by a number of other environmental factors including geology, disturbance frequency (e.g. bushfire), land-use, or soil nutrients. Indeed, microrefugia in deep gorges within Wollemi National Park could be enhanced where the gorges are much richer in nutrients than the surrounding sandstone ridges and have lower fire frequency. Similarly, species that occupy outcrops with distinct geologies, such as limestone, may act as litho-refugia (Shoo *et al.*, 2010a) if the substrate acts as a barrier that prevents antagonistic species from the matrix migrating onto that geology.

Moisture is another factor that could have been included in our analysis. Indeed, our sensors also recorded humidity and we have produced grids of extreme humidities as well as temperature (Ashcroft & Gollan, 2012). Humidity may be especially important for rainforests, which contracted as Australia became drier (White, 1994). However, our data indicate that locations with the lowest maximum temperatures are similar to the areas with the highest minimum humidities (Ashcroft & Gollan, 2012). Therefore, results for high humidity refugia may be similar to the cool refugia identified in this study. Refugia based on areas with high soil moisture are not necessarily the same as those for high near-surface humidity, and further investigation is needed into refugia based on soil moisture.

Implications for conservation planning

There are a few microrefugia that deserve attention in our study area. The upland swamps and grasslands in the topographic depressions at Barrington Tops are more than 7°C colder than the surrounding matrix according to both our observations and our models (Fig. 4b), and this results in distinctly isolated climates that were identified as cool refugia (Fig. 4f). Indeed, the depressions where these communities occur are a classic example of a vegetation inversion due to cold-air drainage (Dobrowski, 2011). These communities contain relict species from

the last interglacial, including rare, endemic and threatened species (NSW Scientific Committee, 2001; NPWS, 2010). One of the threats these locations face in a warming climate is an encroachment of woody vegetation, such as Scotch broom (*Cytisus scoparius*), which might transform these environments and increase minimum temperatures even further (NSW Scientific Committee, 2008; Hampe & Jump, 2011).

The microrefugia we identified within the Wollemi region were smaller and more isolated than those in the Barrington region, and reflect the greater complexity in canopy cover and topographic shelter. Although the rare Wollemi Pine (*Wollemia nobilis*) is only known from four deep gorges within this region (Benson & Allen, 2007; Offord, 2011), the locations are not publicly available and we cannot confirm whether or not they are captured in our maps. There are many rainforest patches within the region that were not identified as refugia, and we highlight once again that the limitations of our remotely-sensed canopy cover layer may have reduced the accuracy of our method in these locations. However, given that rainforests have expanded since the last glacial maximum, it is also possible that only a subset of the moist sheltered gorges that are currently occupied by rainforest offer long-term protection.

The data on which we have estimated the location of potential microrefugia reflects current conditions, and is most appropriate for addressing issues relating to contemporary climate change and conservation issues. Over longer time frames and larger climatic fluctuations the effects of different climate-forcing factors may vary dramatically. For example: as sea levels change the distance from coast effect will vary accordingly; as vegetation changes, the canopy cover effect will also vary; changes in moisture will affect the effect of elevation as dry air has a higher lapse rate than moist air; erosion and deposition will alter the topography and affect cold-air drainage and topographic exposure; and, sustained periods of snow cover or aridity will reduce the availability of certain areas during colder or

drier times. Indeed, the topographic depressions at Barrington Tops probably reflect *ex-situ* microrefugia, with species migrating from lower elevations as the landscape changed since the last glacial maximum (Dodson, 1987). The refugia indices we calculated in this study will not be stable over longer time periods, but the topographic features we have identified will still be affected by a similar set of climate-forcing factors, and will hold their conservation significance to some degree. For example, the sheltered gorges that currently support rainforest are expected to remain cooler and moister than the surrounding landscape, and are likely to continue to support unusual climates and communities even if disturbance or climate change reduce the buffering effect of the existing canopy cover.

The methodology we introduced in this study was designed to identify areas that have extreme, stable, and unusual climates as determined using fine-scale topoclimatic grids. An important next step will be to validate the conservation value of these locations using biotic data. One way this could be done is by using the current or past distributions of species or genotypes (Keppel *et al.*, 2011), but it is worth making the distinction between refugia (locations with reduced exposure to climate change) and relict populations (biota with traits that allow them to utilise refugia to reduce sensitivity to climate change; Williams *et al.*, 2008; Hampe & Jump, 2011). Not all refugia contain relict species, and a pattern-based approach using species' distributions would not provide direct evidence of the processes that make microrefugia valuable (Mosblech *et al.*, 2011). This is especially true for warm refugia, as species that survived the last glacial period in these locations may since have expanded their distributions. A more relevant validation would examine the stability of biotic communities in microrefugia to confirm whether the isolation and climatic stability reduce local extinction rates and increase community stability. This may be difficult with trees or other long-lived species, but may be feasible using short-lived species such as invertebrates.

Once the locations of microrefugia are confirmed there are numerous conservation options available. Firstly, unprotected microrefugia could be targeted for inclusion in the reserve system. Secondly, environments could be engineered to enhance isolation or climatic stability by, for example, manipulating canopy cover or engineering works to manipulate cold-air drainage or topographic exposure (Williams *et al.*, 2008). Restoring degraded forests has the potential to increase the amount of refugial habitat available (Shoo *et al.*, 2010b), however, given the importance of isolation for microrefugia (Mosblech *et al.*, 2011), this may be a strategy that needs to be employed with care and may only be appropriate for macrorefugia. Indeed, connecting microrefugia may do more harm than good if it assists the colonisation opportunities for antagonistic species (Hopper, 2009; Mosblech *et al.*, 2011; Fig. 1).

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Supporting Information:

SupplementaryMaterial.doc – Figures S1 to S3 and captions showing sensitivity of refugia to variations in methods.

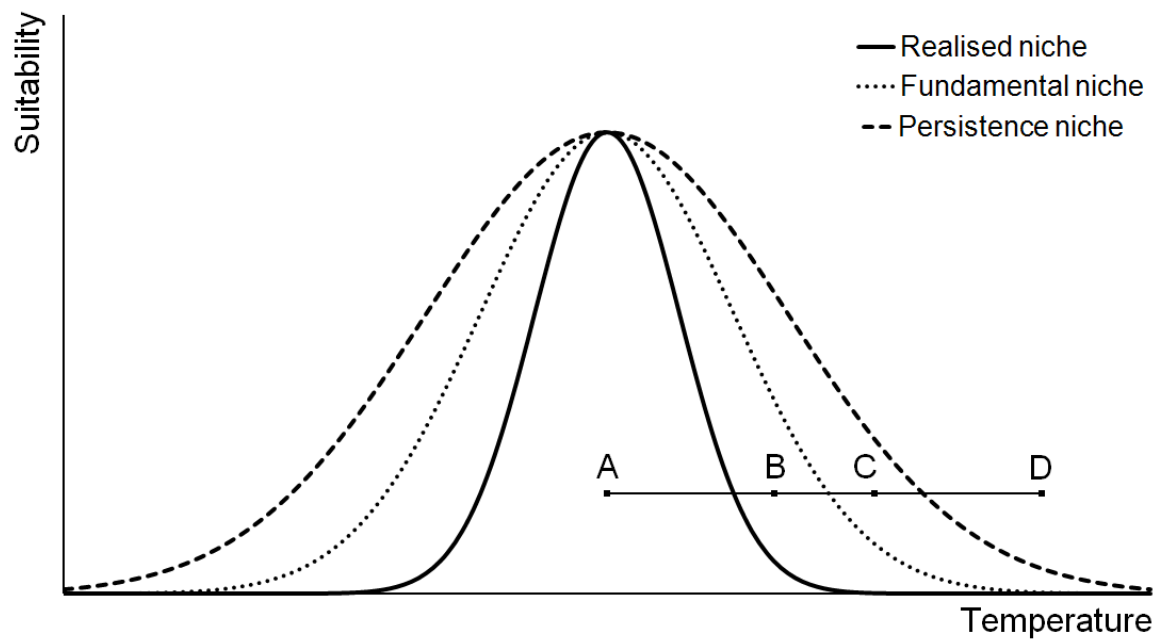


Fig. 1 The climate within a microrefugium could be: within a species' realised niche and hence able to survive even in the presence of antagonistic species (A); outside the realised niche but within the fundamental niche and hence only able to survive in isolated fragments that antagonistic species cannot reach (B); outside the fundamental niche but within the persistence niche where individuals of the species may be able to survive for some time if they have traits that favour persistence even though the growth rate of the population is negative (C); or outside the persistence niche where the species cannot survive (D).

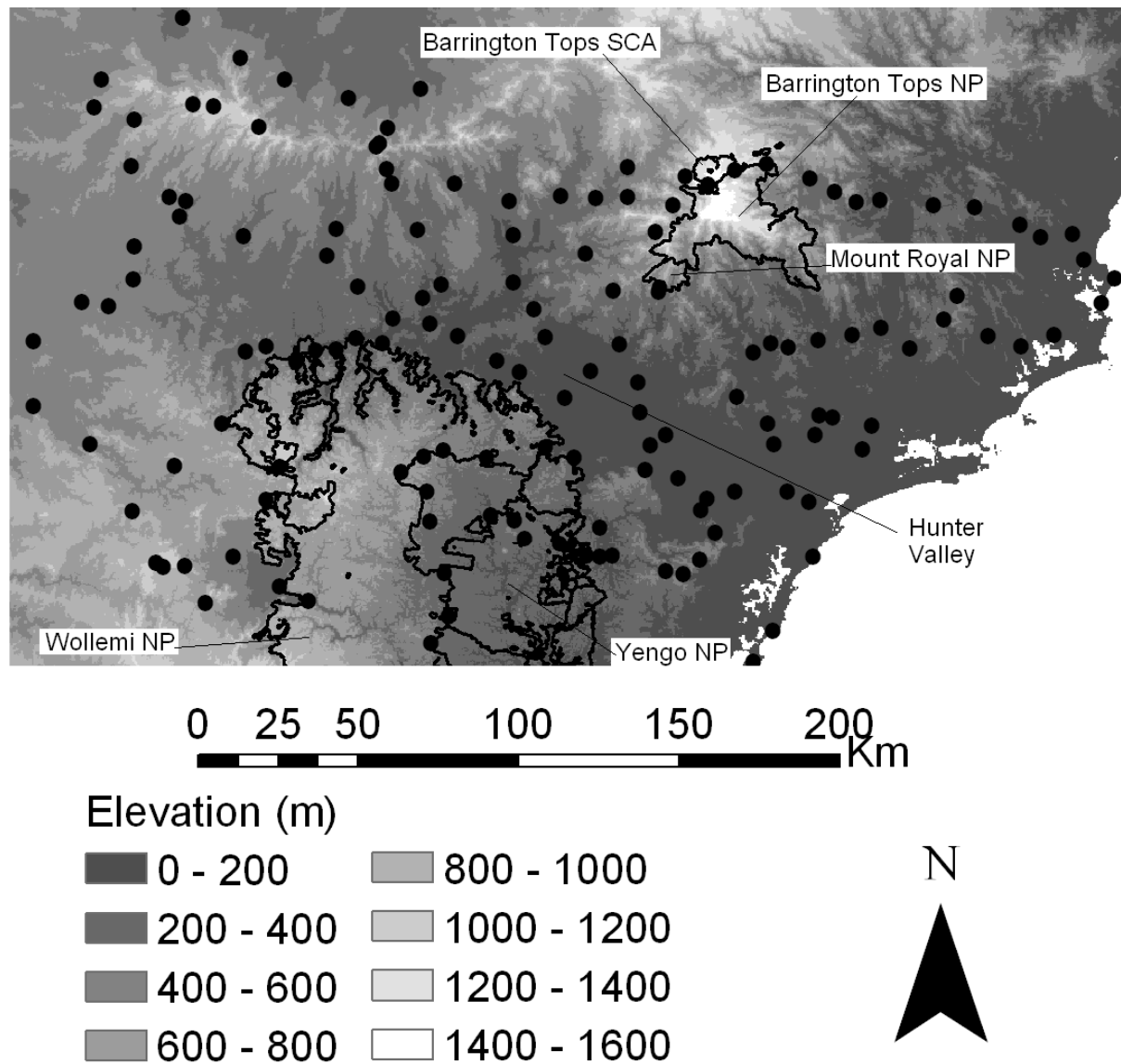


Fig. 2 The topography around the Hunter Valley, NSW, Australia (31.4–33.4°S, 149.4–152.6°E). Black dots indicate the locations of 150 locations where iButton hygrochron loggers were used to record hourly temperature and humidity between June 2009 and May 2011. The black lines indicate the boundaries of the conservation areas.

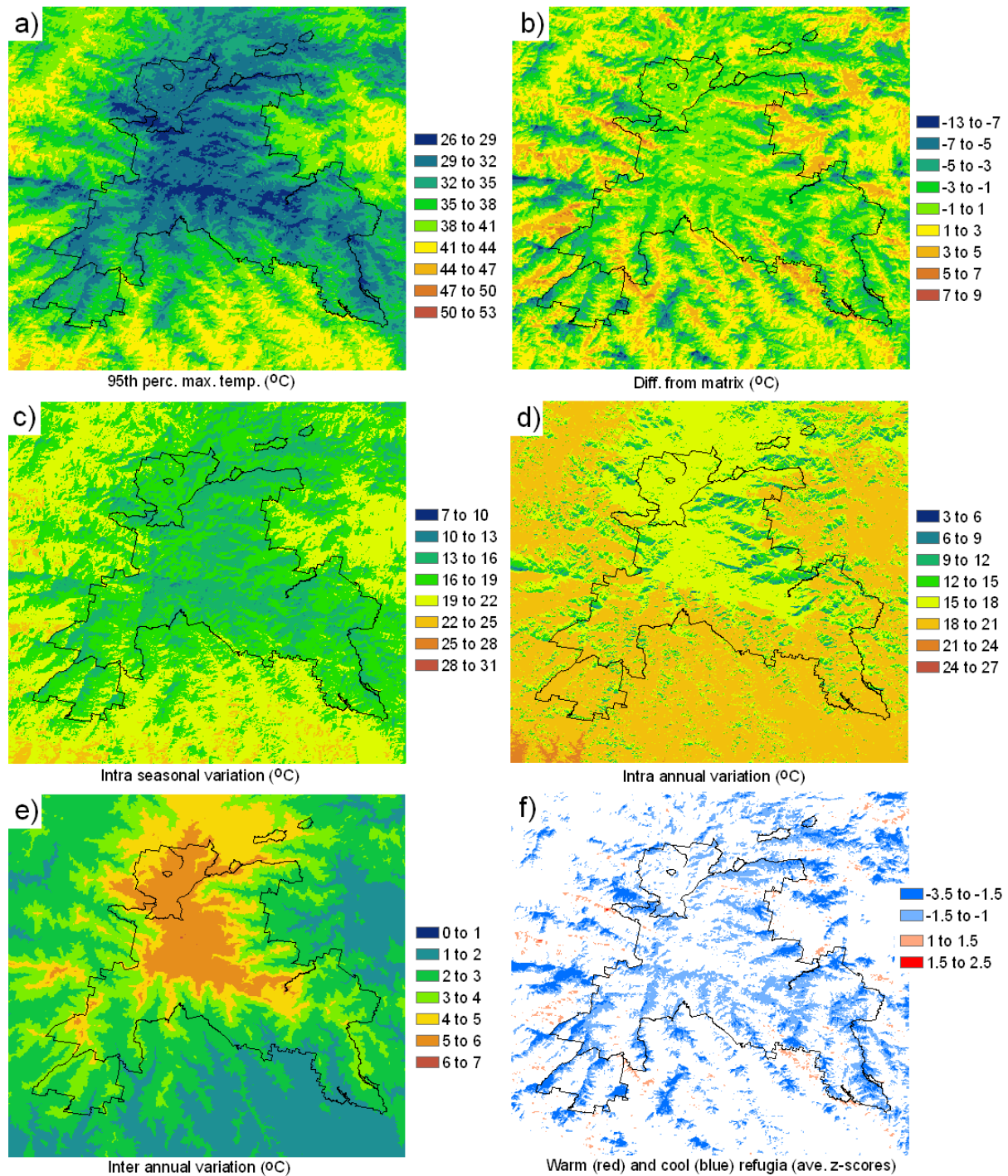


Fig. 3 The warm and cool refugia on the 95th percentile of maximum temperature gradient in the Barrington Region. Refugia are identified by averaging the Z-scores for extreme climates (a), differences from the matrix (b), and three estimates of climate variability over different time scales (c-e). The black lines indicate the boundaries of the conservation areas (see Fig. 2).

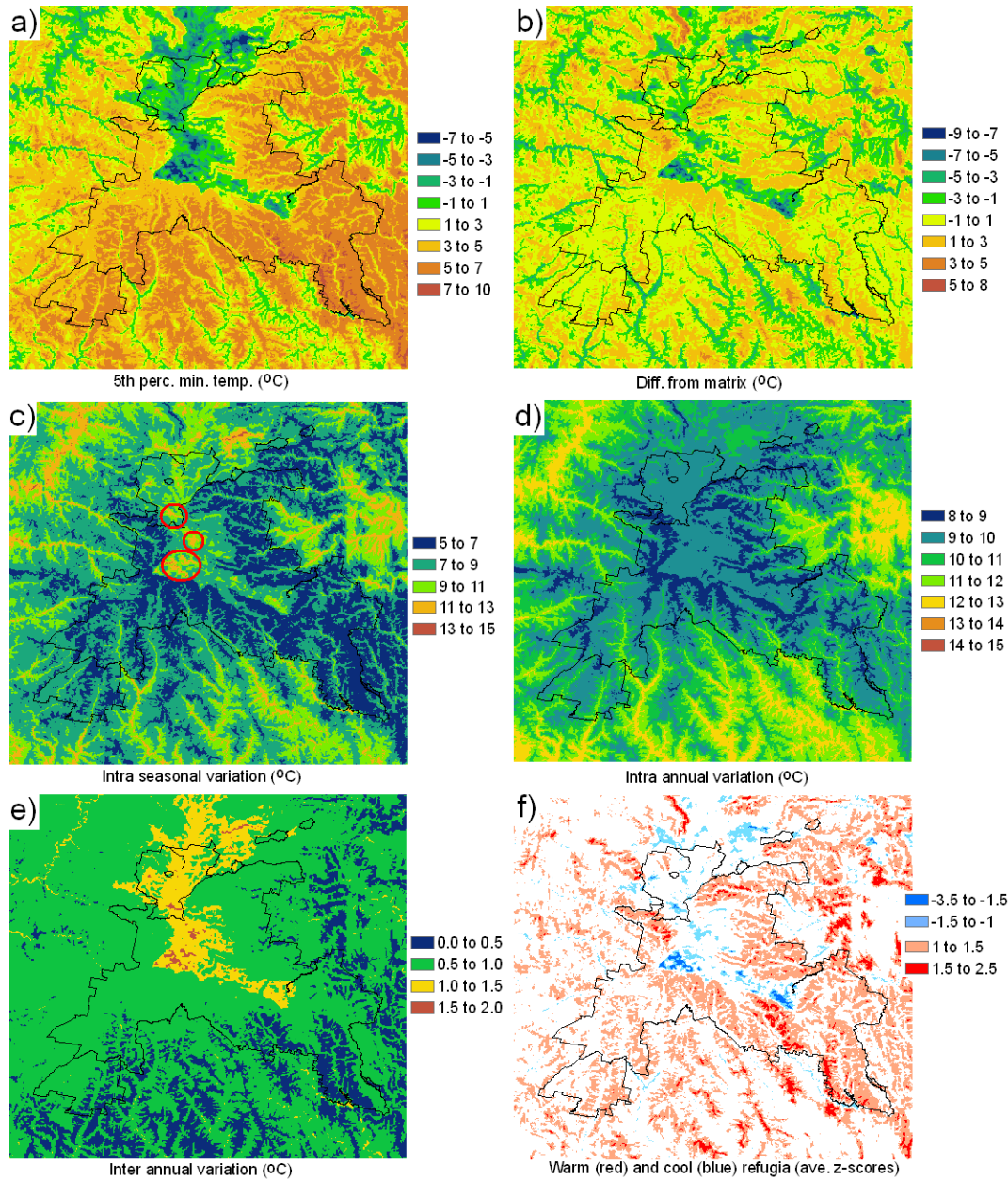


Fig. 4 The warm and cool refugia on the 5th percentile of minimum temperature gradient in the Barrington Region. Refugia are identified by averaging the Z-scores for extreme climates (a), differences from the matrix (b), and three estimates of climate variability over different time scales (c-e). The black lines indicate the boundaries of the conservation areas (see Fig. 2). Red ellipses indicate approximate locations of some of the topographic depressions, with the distinct climate of the depressions apparent in all panels apart from (d).

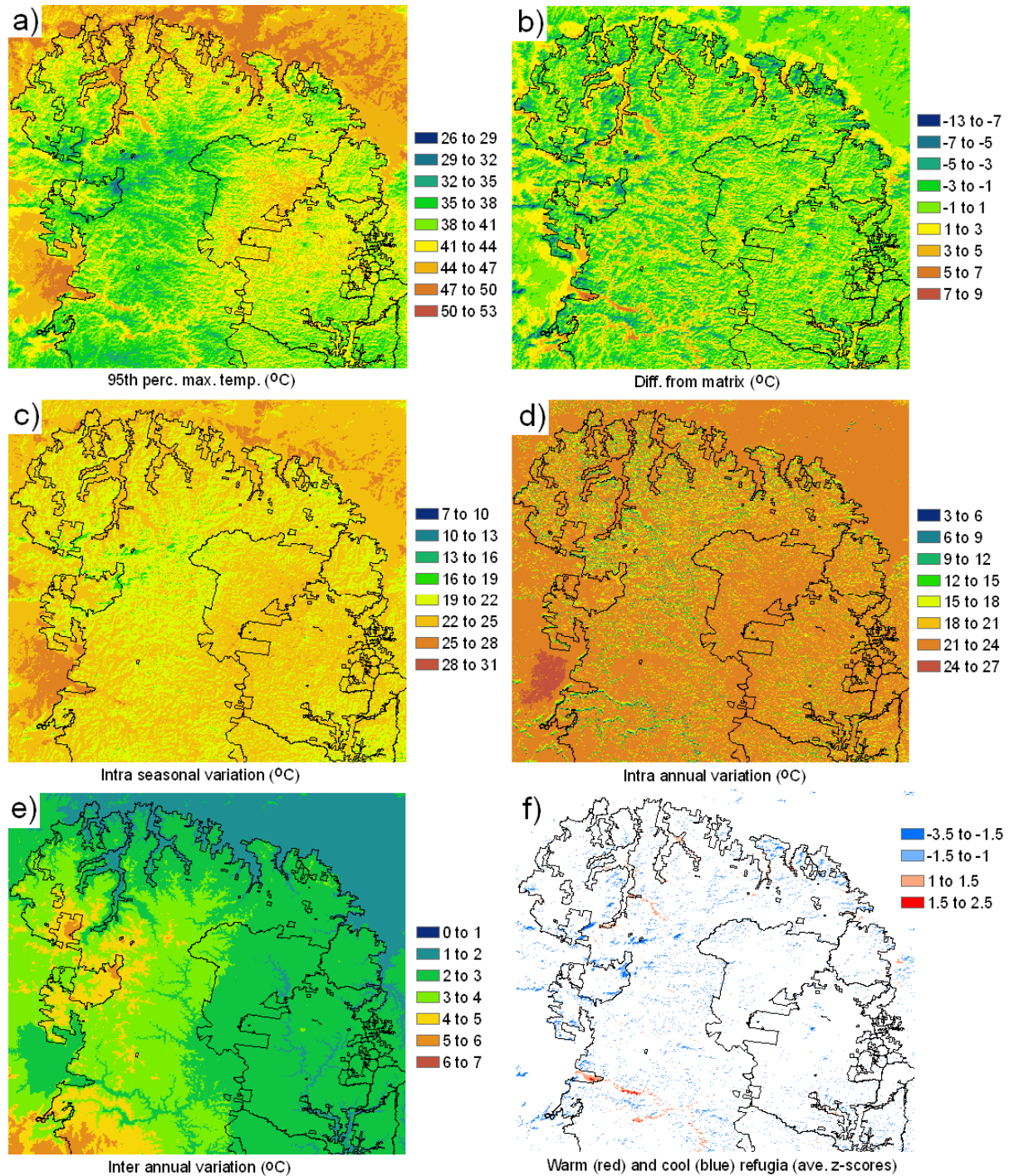


Fig. 5 The warm and cool refugia on the 95th percentile of maximum temperature gradient in the Wollemi Region. Refugia are identified by averaging the Z-scores for extreme climates (a), differences from the matrix (b), and three estimates of climate variability over different time scales (c-e). The black lines indicate the boundaries of the conservation areas (see Fig. 2).

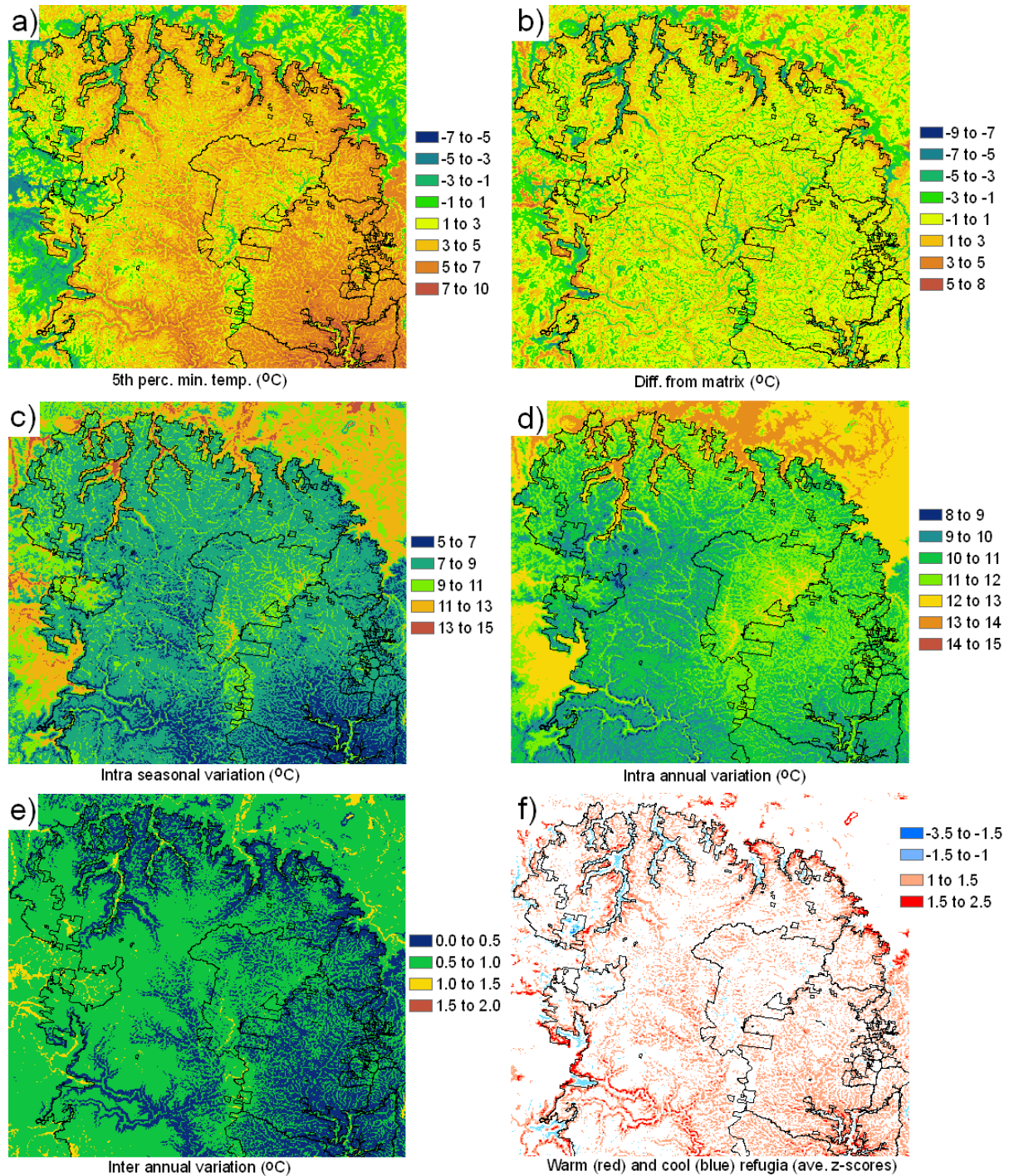


Fig. 6 The warm and cool refugia on the 5th percentile of minimum temperature gradient in the Wollemi Region. Refugia are identified by averaging the Z-scores for extreme climates (a), differences from the matrix (b), and three estimates of climate variability over different time scales (c-e). The black lines indicate the boundaries of the conservation areas (see Fig. 2).

