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Assessing the distribution and protection status of two types of cool environment to facilitate their conservation under climate change

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Abstract
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Abstract

Strategies to mitigate climate change can protect different types of cool environments. Two are receiving much attention: protection of ephemeral refuges (i.e., places with low maximum temperatures) and of stable refugia (i.e., places that are cool, have a stable environment, and are isolated). Problematically, they are often treated as equivalents. Careful delineation of their qualities is needed to prevent misdirected conservation initiatives; yet, no one has determined whether protecting one protects the other. We mapped both types of cool environments across a large (~3.4M ha) mixed-use landscape with a geographic information system and conducted a patch analysis to compare their spatial distributions; examine relations between land use and their size and shape; and assess their current protection status. With a modest, but arbitrary, threshold for demarcating both types of cool environments (i.e., values below the 0.025 quantile) there were 146,523 ha of ephemeral refuge (62,208 ha) and stable refugia (62,319 ha). Ephemeral refuges were generally aggregated at high elevation, and more refuge area occurred in protected areas (55,184 ha) than in unprotected areas (7,024 ha). In contrast, stable refugia were scattered across the landscape, and more stable-refugium area occurred on unprotected (40,135 ha) than on protected land (22,184 ha). Although sensitivity analysis showed that varying the thresholds that define cool environments affects outcomes, it also exposed the challenge of choosing a threshold for adaptation strategies; there is no single value that is appropriate for all of biodiversity. The degree of overlap between ephemeral refuges and stable refugia revealed that targeting only the former for protection on currently unprotected land would capture ~17% of stable refugia. Targeting only stable refugia would capture ~54% of ephemeral refuges. Thus, targeting one type of cool environment did not fully protect the other.
Introduction

Earth’s atmosphere is warming rapidly (Duarte et al. 2012). While mitigation has been the chief policy response to climate warming and variability, adaptation (i.e. “adjustment in natural or human systems to a new or changing environment that exploits beneficial opportunities or moderates negative effects” [National Research Council 2010]) is becoming central to government policy (e.g. Anon. 2011). Options to implement adaptation for biodiversity conservation are urgently needed (Cross et al. 2013) and must aim to retain as much as possible of a region’s biodiversity while meeting the demands of a growing human population (Green et al. 2005; Fischer et al. 2006; Balmford et al. 2012). Various incentive programs to encourage private landowners to set aside land for conservation have been devised (e.g. Wilcove & Lee 2004; Kabii & Horwitz 2006; Burgin 2008), but there remains considerable uncertainty as to their efficacy.

Among 16 general strategies identified in a review of climate change adaptation strategies for biodiversity conservation (Mawdsley et al. 2009), one gaining most attention recently is the identification and protection of places that provide respite from warming global temperatures, that is, refuges and refugia (Keppel & Wardell-Johnson 2012). The identification of cool refugia in particular has increased in priority in conservation planning (Game et al. 2011; Noss 2001), although the difficulties in identifying them has also been acknowledged (Mackey et al. 2012). The terms refuge and refugium are often treated as equivalent, defined loosely, and generally confused (Davis et al. 2013; Keppel & Wardell-Johnson 2012; Mackey et al. 2012). Difficulties identifying different types of cool environments for adaptation are by no means minor. No one has compared their distributions, examined current levels of protection, or determined if protecting one also provides sufficient protection for the other. Complete discussion of their differences has been covered elsewhere.
(e.g. Keppel & Wardell-Johnson 2012), so here, we summarize the key attributes necessary for their identification.

There are two main approaches to identifying cool environments for biodiversity. The simplest is to identify patches that have the coolest maximum temperatures when regional temperatures are relatively high. This is a rather obvious tactic because under a future warmer climate (IPCC 2008), the coolest extremes of temperature gradients will be where heat-sensitive species can find respite. Studies of animal communities show animals retreat to cooler environments when the regional temperatures become too warm (Jiguet et al. 2011). Notably, the cool conditions at any one place could last only seconds, minutes, years, or decades. In other words, refuges can be thought of as operating over short ecological time scales or within the lifespan of an organism (Keppel et al. 2012). These transient cool conditions are thought to be important for highly mobile species where respite from high temperatures can easily be tracked (Davis et al. 2013). The genetic structure of species that depend on these cool environments is most likely complex because of influences of geographical proximity and connectivity of habitats (e.g., Meffe & Vrijenhoek 1988). We use the term *ephemeral refuge* to describe this type of cool environment.

The second approach is to identify the cooler maximum temperatures and to account for variability (or lack thereof) and the degree of isolation within a well-connected matrix. Such environments are considered to be decoupled from the regional climate and so can potentially offer longer-term protection within a climatically variable landscape (Dobrowski 2011). In contrast to ephemeral refuges, identifying these places in the landscape has attracted the most attention because they may offer the only hope for in situ persistence of species with poor dispersal abilities (Keppel & Wardell-Johnson 2012). High within- and low between-population gene flow are likely scenarios due to the extreme isolation among populations (e.g., Meffe & Vrijenhoek 1988). Although a lack of connectivity can be
problematic for metapopulation function (Fahrig & Merriam 1985), the isolation of places with low climate variability is thought to buffer species from antagonistic interactions with competitors, reduce extinction rates, and enable long-term persistence (Mosblech et al. 2011; Tzedakis et al. 2002). Palaeoecological studies have highlighted the importance of such isolation at macro-scales (i.e. continental scale) for retaining species during glaciation (Stewart et al. 2010). However, micro-scale patches (i.e. local scale) may also play a role in creating resilience under rapid climate change (Mosblech et al. 2011). The persistence of species over many millennia and multiple climate change events may have only been possible through the presence of these microrefugia because they serve as a source for recolonization when the regional climate becomes favourable again (Hampe & Jump 2011; Mosblech et al. 2011). We use the term stable refugia to describe this type of cool environment.

Considering the differences in these attributes it follows that the distribution of ephemeral refuges and stable refugia could be substantially different. Conversely, given their relatedness, a large degree of overlap is also possible. We assessed the distribution of both types using published fine-scale climate models (Ashcroft & Gollan 2012; Ashcroft et al. 2012) across a large (200 × 300km) mixed-use landscape in temperate Australia. The following questions were addressed: What are the spatial distributions of the two types of cool environments, how do they differ, and to what extent do they overlap? How might land use influence the characteristics of each type in terms of their distribution, size, shape, extent? and What proportion of each are currently not protected? Our objective was to reveal the disparity, errors, and potential losses of biodiversity that could arise if land managers target the ephemeral refuges that are important for mobile species rather than the stable refugia that offer long-term in situ protection for relatively sessile species.

**Methods**

**Study Area**
Our study was within the jurisdiction of three catchment management boundaries in New South Wales, Australia (Fig. 1). The area covered approximately 3.4 M ha and contained a range of production land for cattle, cropping, and mining (~74% of total land area). The remainder was made up of continuous expanses of protected land set aside for biodiversity conservation, including Wollemi (33°7'50.31"S 150°29'21.22"E) and Barrington Tops National Parks (32°2'56.82"S 151°32'13.06"E). The region encompasses sub-tropical, temperate, and sub-alpine thermal regimes; a wide range of vegetation communities was represented, including coastal forests and heathland, temperate and sub-tropical rainforests, perched swamps, and open grassy woodlands (Peake 2003). Human land uses are mostly concentrated in areas along the coast, with low topographic relief, and of fertile alluvial soils on the valley floors. Elevation ranges from sea level to around 1 600 m in Barrington Tops National Park (Fig. 1).

**Climate gradient for identifying ephemeral refuges**

We used the fine-grained (25 m) climate model published by Ashcroft and Gollan (2012). This model was created with 127 iButton data loggers deployed across the study area for 12 months (June 2009-May 2010). Fourteen potential climate-forcing factors, including topographic exposure, canopy cover, elevation, and susceptibility to cold air drainage, were used as predictors. Climate models often ignore canopy cover and cold air drainage (e.g. Bennie et al. 2008), but there is growing recognition that these factors must be considered to make accurate predictions of species distributions (Suggitt et al. 2011).

Extreme values of temperature are more relevant than quantities such as mean annual temperature for ecological systems (Pimm 2009). For example, climate extremes improve predictions of spatial patterns of tree species (Zimmermann et al. 2009). Thus, we used the 95th percentile of maximum temperatures (95MaxT) as the temperature gradient for identifying ephemeral refuges. This gradient identifies the hottest conditions at each location.
even if they do not occur simultaneously or on consecutive days. Our attention on extremes of temperature is different from the popular notion of climate, which is the “average of weather” (Lovejoy 2013). However, it is in line with the view of McGregor (2006), who defines climate as the array of conditions that are possible and how often those conditions occur.

**Climate gradient for identifying stable refugia**

We used the climate output of Ashcroft et al. (2012), which identified stable refugia across the study area. Their method produced a refugia index (RI) that was represented on a continuous gradient. This gradient utilised the same modelling approach as Ashcroft and Gollan (2012), although climatic data were collected over 2 years (June 2009-May 2011) so that temporal variability could be quantified. In summary the following steps were involved. First, a grid of climatic variability of the 95MaxT gradient was produced by averaging across three different time scales, intra-seasonal, intra-annual and inter-annual. The degree of isolation was then determined by calculating the difference between a location’s temperature and the average temperature within a 5 km radius moving window. All values were standardised to z-scores so that they were quantified on similar scales. The resulting RI ranged from -3.38 to +2.12. Increasing negative numbers translated to locations that were increasingly cooler, isolated, and less climatically variable. Values nearest zero represented conditions that were most climatically variable and least isolated. Increasing positive numbers were increasingly warm, isolated, and less climatically variable (see Ashcroft et al. 2012 for full details).

**Demarcation of ephemeral refuge and stable refugia**

For each climate gradient (Max95T and RI), we assembled data into nine quantiles (0.025, 0.050, 0.075,…, 0.225). To provide a contextual analysis, we considered that ephemeral refuges in the landscape were most likely to be places that experienced
temperatures below the lowest quantile on the 95MaxT gradient (i.e. \( \leq 0.025 \) or 29.8°C) and that stable refugia were places below the lowest quantile on the RI gradient (i.e. \( RI \leq -1.659 \)). We used GIS to produce maps of ephemeral refuges, stable refugia, and the overlap of the two as raster layers (ArcMap V10.1).

Maps were overlayed with a land use layer (NSW Landuse V2), provided by the NSW Office of Environment and Heritage, to relate patches of ephemeral refuges and stable refugium to land use and protection status. We used the terms *patch* or *patch type* because they imply areas with a relatively discreet spatial pattern but with no constraint on size (White & Pickett 1985). We determined how land use influenced the characteristics of the patch types in terms of their distribution, size, shape, and extent and quantified the current protection status by exporting layers in ASCII format. We used Fragstats 3.4 (McGarigal et al. 2002) to calculate the number of patches and mean patch size and the eight cell rule to determine patch neighbours. We used ArcMap (V10.1) to calculate number of hectares of different patch types.

The threshold quantile of 0.025 to delineate ephemeral refuge and stable refugia (as above) was somewhat arbitrary (as were the number and position of quantiles themselves), but it was needed for the categorical patch analysis. Thresholds should be based on what is relevant to biota when considering cool climate environments for climate adaptation. However, and as detailed later (see Discussion), the decision where to segregate data is not straightforward. Thus, we conducted a sensitivity analysis to explore how changes to thresholds affected results. Using the constructed raster layers for both gradients and at each of the nine quantiles (as above), we examined the distribution of data at each of the nine quantiles. In other words, we assessed how outcomes change as the restrictions on each patch type were eased (i.e. as quantiles were made larger). The effects on changes to thresholds
were assessed in terms of the number of hectares, the degree of overlap, and how the protection status of patches altered.

Results

*Spatial distribution of ephemeral refuges and stable refugia*

There were 62,208 ha of ephemeral refuge, 62,319 of stable refugia, and 21,996 ha that overlapped (~4.3% of the total study area). The majority of ephemeral refuge patches coincided with the high elevation areas in Barrington Tops National Park and along the northern edges of the study boundary (compare Figs. 1 and 2). The few ephemeral refuge patches that existed outside the central area of the study region were smaller. In contrast, the majority of stable refugia were located in the north-eastern portion of the study area. Stable refugia were not confined to high elevations; they were scattered across the entire region, including tracts along the coast within 200 m of mean sea level. The south and south western areas (corresponding to much of Wollemi National Park) also contained patches of stable refugia, although these were smaller and less dense than in the north-eastern portion. There was no obvious spatial patterning in relation to patches where ephemeral refuge and stable refugia overlapped, although most were positioned on the periphery or away from the extreme high elevation region in the central part of the study area (Fig. 2).

Overlay of satellite imagery with the grids of stable refugia showed patches on non-protected land tended to be covered by trees and shrubs (e.g. Fig. 3a). However, not all isolated tree cover was stable refugia (toward top of Fig. 3a). Stable refugia in protected areas tended to be not as conspicuous as those on non-protected land. They were often positioned within places with a relatively homogenous canopy cover (e.g. Fig. 3b).

*Ephemeral refuge, stable refugia, and their overlap*

We identified 62,208 ha (4,774 patches) of ephemeral refuge, which occupied ~1.8% of the total area. Nearly eight times more ephemeral refuge was found in protected land (55,184 ha)
compared with non-protected land (7,024 ha). The majority of ephemeral refuge on non-protected land was found within the tree and shrub cover category (6,038 ha). In protected area the average patch size was just over 6 times larger (20.49 ha) than those in non-protected area (3.38 ha; Table 1).

There were 62,319 ha (15,142 patches) of stable refugia, and, in contrast to ephemeral refuge, the majority was found on non-protected land (40,135 ha or ~1.2% of total land area). In common with ephemeral refuge, the majority of stable refugia on non-protected land was found in the tree and shrub cover category (32,616 ha). Grazing accounted for 6,466 ha of stable refugia, while other land use classes combined had 1,035 ha. Also in common with ephemeral refuge, the average patch size was larger on protected (4.34 ha) than non-protected land (3.86 ha; Table 1).

The overlap of ephemeral refuge and stable refugia occupied ~0.7% of the total land area or 21,996 ha, with the majority on protected land (13,727 ha). In non-protected land, nearly all overlap was of the tree and shrub category (~72.7%). Other land use categories combined accounted for 226 ha (Table 1).

**Changes with increasing threshold**

The area of ephemeral refuge and stable refugia in protected areas increased almost linearly as quantiles increased. Ephemeral refuge had consistently higher representation (Fig. 4a) when assessed independently. This trend was evident in the proportional protection as quantiles increased (Fig. 4b). At the 0.025 quantile, over 80% of ephemeral refuges were in protected areas, while only ~40% of stable refugia were protected. As quantiles increased, the level of protection status for ephemeral refuges declined to just over 50% at the 0.225 quantile. In contrast, the level of protection for stable refugia was fairly stable regardless of the quantile (Fig. 4b).
When considering the level of representation of both ephemeral refuge and stable refugia concurrently, the degree of overlap (i.e. locations that are both ephemeral refuge and stable refugia) increased almost linearly in protected areas as quantiles increased. However, the proportion of those locations in protected areas remained fairly constant across quantiles. In contrast, the amount of protection for locations that remained either ephemeral refuge or stable refugia did not increase as quantiles increased. Indeed, as quantiles increase, the proportion of ephemeral refuges in protected areas declined from nearly 90% at the 0.025 quantile to just over 50% at the 0.225 quantile. Representation of stable refugia sites was relatively impervious to changes in quantiles (Fig. 4b).

**Discussion**

Our analysis of ephemeral refuges, the coldest locations in the landscape, showed that they were aggregated in large areas and were well protected (~82% in protected areas). These are likely important for mobile species. Stable refugia (cold, stable, and isolated locations) in contrast had much lower protection (~58% in non-protected areas), which highlights a need to increase protection of these locations that are a high priority for conserving low mobility species. Many stable refugia were small and on private land, and our study highlights the need for off-reserve conservation measures. The differences in the distributions of ephemeral refuges and stable refugia highlight that a strategy based on finding and protecting the coolest places in the landscape will not necessarily protect the stable refugia that are hypothesised to be better for the persistence of populations of low mobility species over long time frames (Hopper 2009; Hampe & Jump 2011; Mosblech et al. 2011). Conversely, a focus on stable refugia may miss the places important for maintaining a metapopulation structure for more mobile species (Davis et al. 2013).

Using our approach, and provided that appropriate fine-grained climate models exist, managers will have opportunities for incorporating both types of cool environments into
climate change adaptation plans. For example, currently unprotected stable refugia could be added to existing protected area systems or targeted for conservation as part of incentive schemes on private land (e.g. biodiversity or mitigation banking) (Burgin 2008). Our results showed 40,135 ha of stable refugia that were not protected, which was almost double the amount protected (22,184 ha). However, to be considered in incentive schemes, sites with unique thermal properties (whether they be ephemeral refuge or stable refugia) will need to be valued as landscape assets and considered alongside more traditional indicators of habitat value derived from structural elements of vegetation or the presence of species of interest. Inclusion of stable refugia alongside conservation planning approaches that utilise novel abiotic conditions (e.g. Brost & Beier 2012) should be a high priority because of their importance for in situ persistence of poorly dispersed species (Game et al. 2011).

Ephemeral refuges are important for the maintenance of population dynamics of mobile species (Davis et al. 2013) and so cannot be overlooked for protection. However, our analysis indicated that much of this type of cool environment is already protected and concentrated in the high elevation areas. Reserves in Australia were historically selected in unprofitable, rugged and high elevation areas (Fitzsimons & Westcott 2001). Most of the ephemeral refuges in our analysis were aggregated at high elevations. The bias of reserves towards high-elevation areas is not confined to Australia; it also occurs, for example, in the United States (Scott et al. 2001). When considering cool environments on private land for adaptation strategies, conservation planners may only need to consider the small pockets of stable refugia.

Developing approaches to valuing and prioritising for protection is a further hurdle in bringing cool environments to climate change adaptation planning. Using systematic conservation planning tools such as reserve design software to ensure representativeness or to achieve certain targets could be one way. The overlap of the two cool environments could be
a priority; the overlap acts as both ephemeral refuge and stable refugia. Ephemeral refuges or stable refugia with predefined patch size, shapes, or patches with a high density of both types could be favoured depending on their importance for population dynamics and interactions (e.g. Harper et al. 1993; Orrock et al. 2003). Cool and climatically stable sites combined with sites important with respect to current patterns of biodiversity distribution might be areas for prioritization (Groves et al. 2012). However, the conservation value of those that do not contain rare species or high levels of biodiversity should not be forgotten because the processes they support may still offer future protection for species that are not currently rare or threatened (Mosblech et al. 2011).

Considerable opportunity and worth exists in identifying ephemeral refuges and stable refugia that are already protected as part of broader conservation initiatives (e.g. where they occur within existing protected areas). As illustrated, not all spaces in protected areas have the same capacity to avoid extreme temperature conditions (Figure 3b). Recognising this would lead to more targeted management plans. For example, more effort could be made to protect the largest patches of refuge or refugia from wildfire, while smaller ones could be considered expendable. Access roads, walking tracks, and recreational facilities could also be planned to avoid the most valued patches.

The finding that more refugia were contained within non-protected areas may be a direct result of fragmentation that has occurred through activities such as land clearing and water abstraction and diversion. These sites should be viewed as potential refugia because they may be degraded. The potential for isolation through land clearing is perhaps apparent in Figure 3a, where there is a sharp transition from dense vegetation to agricultural land. But seemingly similar patches of vegetation cover just to the north in Figure 3a were not identified as stable refugia. Moreover, some grazed areas with sparse canopy were stable refugia (not illustrated). We reiterate the important point that environmental factors other
than vegetation cover also influence the distribution of cool patches across the landscape. In the analysis to produce the climate grids we used (Ashcroft & Gollan 2012), canopy cover had less effect on maximum temperatures (effect size =7.8°C), elevation (effect size =13.3°C), and distance to coast (effect size =13.7°C). Canopy cover had only marginally more effect than topographic exposure (effect size =5.2°C) and latitude (effect size =5.5°C).

It is important to acknowledge that increasing temperatures are not the only threat to biodiversity under climate change and so areas offering protection from other threats should also be considered. Climate models predict that current trends may become more intensified such that wet areas become wetter and drought conditions become more pronounced (IPCC 2008). Mackey et al. (2012) introduced a metric for identifying potential micro-refuges based on a time series of remotely sensed vegetation greenness (i.e., locations that may function as drought and fire microrefugia for multiple species). Analysis of ecosystem vegetation greenness combined with our patch mosaic of cool climate environments could prove a powerful tool for prioritisation in adaptation strategies.

We have presented a pattern analysis of fine-grained climate models as a way forward in terms of practical adaptation strategies, but it is not without caveats that need careful consideration before implementing. For example, canopy cover is an unstable entity that could affect the thermal conditions at a site. Of course canopy cover can be modified by land clearing, disturbances such as fire, or even climate change itself. The degree of change, however, ultimately depends on the influence of tree canopy at any one site and the influence of the more enduring properties such as topographic position and complexity.

Another caveat is that our patches are represented by discrete areas of relatively homogeneous environmental conditions and the patch boundaries are abrupt discontinuities in temperature. In reality, boundaries are more likely to be a gradual transition in temperature. From an organism-centred perspective, the importance of the boundary’s sharpness will vary.
For some fauna there appears to be no disjunction coinciding with discreet edges (e.g. Dangerfield et al. 2003). Likewise, what constitutes a cool climate depends on an organism’s climatic tolerances and the distance between patches depends on the organism’s mobility and dispersal capabilities. The 5 km radius moving window that was used to delineate the degree of isolation will be far too large for species that live fairly sedentary lives or where propagules are dispersed over very short distances. Weighting climate variability differently, using different temperature gradients, and changing the radius of the moving window are all aspects that can vary results dramatically (see sensitivity analysis in supplementary material of Ashcroft et al. 2012). Identifying an ephemeral refuge or stable refugium for any one species might be easy when life history attributes are well known, but attempting a more holistic approach to consider all of biodiversity is not at all straightforward. This presents a considerable challenge that will need to be addressed by conservation biologists for some time to come. Our sensitivity analysis across thresholds is a useful way to explore these issues because it will aid in formulating the most conservative thresholds for biodiversity conservation.

Acknowledgments

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Literature cited


Table 1. Patch metrics for ephemeral refuges, stable refugia, and their overlap among land-use categories.

<table>
<thead>
<tr>
<th>Land-use category</th>
<th>Number of patches (ha)</th>
<th>Mean patch size (ha)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>ephemeral refuges</td>
<td>stable refugia</td>
</tr>
<tr>
<td>Protected area</td>
<td>861,062 (55,184)</td>
<td>5,112 (22,184)</td>
</tr>
<tr>
<td>Unprotected</td>
<td>2,508,428 (7,024)</td>
<td>10,389 (40,135)</td>
</tr>
<tr>
<td>Protected and</td>
<td>3,369,490 (62,208)</td>
<td>15,142 (62,319)</td>
</tr>
<tr>
<td>Unprotected Grazing</td>
<td>1,574,149 (940)</td>
<td>2,664 (6,466)</td>
</tr>
<tr>
<td>Trees &amp; shrubs</td>
<td>642,687 (6,038)</td>
<td>6,690 (32,616)</td>
</tr>
<tr>
<td>Infrastructure</td>
<td>16,839 (6)</td>
<td>45 (29)</td>
</tr>
<tr>
<td>corridors</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Urban</td>
<td>74,543 (&lt;1)</td>
<td>241 (556)</td>
</tr>
<tr>
<td>Drainage system</td>
<td>47,197 (61)</td>
<td>191 (81)</td>
</tr>
<tr>
<td>Special category</td>
<td>18,564 (27)</td>
<td>27 (59)</td>
</tr>
<tr>
<td>No data</td>
<td>1,486 (424)</td>
<td>359 (64)</td>
</tr>
<tr>
<td>Mining</td>
<td>63,627 (18)</td>
<td>18 (29)</td>
</tr>
<tr>
<td>Wetland</td>
<td>13,221 (150)</td>
<td>150 (232)</td>
</tr>
<tr>
<td>Horticulture</td>
<td>9,380 (&lt;1)</td>
<td>2 (&lt;1)</td>
</tr>
<tr>
<td>Cropping</td>
<td>42,463</td>
<td>1 (&lt;1)</td>
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<tr>
<td>Power generation</td>
<td>868 (&lt;1)</td>
<td>1 (&lt;1)</td>
</tr>
<tr>
<td>Animal production</td>
<td>3,406 (&lt;1)</td>
<td>1 (&lt;1)</td>
</tr>
</tbody>
</table>

*Lack of a value indicates an absence of that patch type.*
Figure legends

Fig. 1 Location of the three adjacent catchment areas (thin black line) in our study of the distribution of ephemeral refuge and stable refugium in relation to protected and unprotected area.

Fig. 2 Location of ephemeral refuge, stable refugia, and areas where the two overlap relation to protected and unprotected area (dashed circle, approximate location of the satellite image in Fig. 3a; solid circle, location of the satellite image in Fig. 3b. Inset shows greater detail. See Fig. 1 for location of catchments.
Fig. 3 Satellite image of a stable climate refugium (solid white lines) in (a) an unprotected and (b) a protected area. Locations in relation to the wider landscape are circled in Fig. 2 (Image source and date: Google Earth, 16 December 2008).
Fig. 4 (a) Number of hectares and (b) proportion of ephemeral refuge, stable refugium, and overlap of the two in protected area at each of nine quantiles