

Identifying refugia from climate change

Michael B. Ashcroft*

Australian Museum, 6 College Street, Sydney,
NSW 2010, Australia

ABSTRACT

This article highlights how the loose definition of the term ‘refugia’ has led to discrepancies in methods used to assess the vulnerability of species to the current trend of rising global temperatures. The term ‘refugia’ is commonly used without distinguishing between macrorefugia and microrefugia, *ex situ* refugia and *in situ* refugia, glacial and interglacial refugia or refugia based on habitat stability and refugia based on climatic stability. It is not always clear which definition is being used, and this makes it difficult to assess the appropriateness of the methods employed. For example, it is crucial to develop accurate fine-scale climate grids when identifying microrefugia, but coarse-scale macroclimate might be adequate for determining macrorefugia. Similarly, identifying *in situ* refugia might be more appropriate for species with poor dispersal ability but this may overestimate the extinction risk for good dispersers. More care needs to be taken to properly define the context when referring to refugia from climate change so that the validity of methods and the conservation significance of refugia can be assessed.

Keywords

Bioclimatic envelope models, climatic stability, conservation biogeography, cryptic refugia, ecological niche models, extinction risk, interglacial refugia, macrorefugia, microclimate, microrefugia.

*Correspondence: Michael B. Ashcroft,
Australian Museum, 6 College Street, Sydney,
NSW 2010, Australia.
E-mail: mick.ashcroft@austmus.gov.au

INTRODUCTION

The importance of refugia is increasingly being recognized (Noss, 2001; Petit *et al.*, 2003; Bennett & Provan, 2008). While the term was originally introduced to refer to locations where species survived the last glacial period (Bennett & Provan, 2008), it is now increasingly used to refer to areas that should be conserved to limit the impacts of rising global temperatures in the 21st century (Barnosky, 2008; Trivedi *et al.*, 2008; Williams *et al.*, 2008; Rull, 2009). However, the broadening usage of the term has introduced apparent contradictions in methodology and potentially decreased its usefulness (Bennett & Provan, 2008). This article provides an overview of different interpretations of climate change refugia and highlights some of the methodological discrepancies and potential problems that can result (Table 1). Authors need to explicitly address these inconsistencies or the ecological significance of refugia will be ambiguous, thus confounding their conservation value.

REFUGIA FROM CLIMATE CHANGE

Taxa that prefer warmer climates generally contract their distributions to refugia during glacial periods, while taxa that

prefer cooler climates are generally restricted to refugia during interglacial periods (Stewart *et al.*, 2010). Both glacial and interglacial refugia should be conserved to ensure long-term persistence of species (Skov & Svenning, 2004); however, it is the species that prefer cooler conditions that are of most immediate concern as they are currently restricted to interglacial refugia and face increased threat with further rises in global temperatures. Present-day average global temperatures are *c.* 2 °C cooler than the previous interglacial (Jouzel *et al.*, 1987), but there are spatial and seasonal differences in this relationship and some locations are already warmer than the last interglacial during some seasons (Kubatzki *et al.*, 2000; Montoya *et al.*, 2000; Kaspar *et al.*, 2005). In addition, temperatures are expected to rise by a further 1.1–6.4 °C during the 21st century (IPCC, 2007), and this will place additional stress on species that prefer cooler temperatures and are currently restricted to interglacial refugia.

Refugia from 21st century climate change will differ from current interglacial refugia in that temperatures will be warmer and species will have to cope with landscapes that have been fragmented by humans (Vos *et al.*, 2008). If refugia are restricted to locations that remain suitable for a species (*in situ* refugia; Attorre *et al.*, 2007; VanDerWal *et al.*, 2009), then

Table 1 A list of potential issues that could arise when identifying refugia from climate change.

Potential methodological issues
Limiting studies to <i>in situ</i> refugia might exaggerate extinction risk for good dispersers, while including <i>ex situ</i> refugia might underestimate extinction risk for poor dispersers or where there are barriers to dispersal
The minimum viable size of refugia depends on body size and area required to support the population, and therefore the relevant scale of macrorefugia and microrefugia will be taxon specific
Macrorefugia can be identified using commonly used climate grids based on elevation-sensitive interpolations (e.g. BioClim and WorldClim), but microrefugia require fine-scale climate surfaces that consider a broader range of climate-forcing factors
Refugia based only on climate stability are limited to <i>in situ</i> refugia, and may be misleading if species in more climatically stable areas are more sensitive to change
Refugia based on habitat stability may be biased towards cooler locations if climate stability is ignored (uniform warming), and these will be biased towards high elevations if climate surfaces neglect other climate-forcing factors
Refugia based on climate stability or community composition may include non-refugial species unless they demonstrate a contraction in distribution for individual species
Species distribution models (SDMs) need to predict where, and for how long, species can persist in areas where habitat has become unfavourable if they are to comprehensively predict species persistence

refugia from 21st century climate change will occupy a subset of the locations where interglacial refugia currently occur (areas that are cooler than the surrounding region are expected to shrink as the climate warms; Ohlemüller *et al.*, 2008). However, some species can survive periods of unfavourable climate in locations that they did not occupy previously (*ex situ* refugia; Loarie *et al.*, 2008; Holderegger & Thiel-Egenter, 2009). Identifying *in situ* refugia from climate change might be more appropriate for species with poor dispersal or where human land-use changes have created barriers, but this might exaggerate the extinction risk for good dispersers. Potential *ex situ* refugia that were previously unreachable may become available if humans assist colonizations or create new corridors (Hunter, 2007; Vos *et al.*, 2008). The choice between *in situ* and *ex situ* climate change refugia is therefore an important aspect that should be justified in terms of species dispersal capabilities. This choice is analogous to the assumption in species distribution models that species either have no dispersal (*in situ* refugia only) or universal dispersal (both *in situ* and *ex situ* refugia; Thomas *et al.*, 2004; Pearson, 2006).

The differences between *in situ* and *ex situ* refugia illustrate the confusion that arises when the term 'refugia' is used without clarifying definitions and context. For example, the terms 'refugia' and 'refuge' are used at a variety of spatial and temporal scales, including intra-day shelters from predators (Monasterio *et al.*, 2009), small patches of forest left undisturbed during forest harvesting (Perhans *et al.*, 2009) and

inter-annual protection from drought conditions (Manning *et al.*, 2007). These definitions of refugia could also be extended to include climate change impacts, for example by management actions that create thermally buffered environments such as nest boxes (Williams *et al.*, 2008). While attempts have been made to distinguish between refugia and refuges (e.g. Rull, 2009), corresponding rules are not always followed. This highlights the need to replace the term 'refugia' with a more descriptive term and to clarify the context in which refugia is used (Bennett & Provan, 2008).

Throughout this article the term 'refugia' is used for areas that are at least large enough to support a small population of some species (e.g. *c.* 100–10,000 m² or more), while individual shelters such as rocks and nest boxes are regarded as 'refuges' and are not considered further. However, this arbitrary classification is biased towards plants and vertebrates, and smaller species, such as invertebrates, may be able to maintain viable populations in climate change refugia at finer scales. Once again, the taxon specific variations in the scale of refugia highlight the need to clarify the definition and interpretation of refugia.

MICROREFUGIA AND MACROREFUGIA

Although refugia can be examined at a continuum of scales, they have been broadly classified as either macrorefugia (classical refugia) or microrefugia (cryptic refugia; Bennett & Provan, 2008; Holderegger & Thiel-Egenter, 2009; Rull, 2009). For example, during the last glacial period large areas with favourable regional climate in southern Europe acted as macrorefugia for temperate taxa, while small areas with unusual microclimate in northern Europe acted as microrefugia. The climate grids needed to identify microrefugia differ from those needed to identify macrorefugia, yet the term 'refugia' is sometimes used without distinguishing between the two. This is an unfortunate oversight, as it makes it difficult to assess the appropriateness of the climate grids used.

The responses of species to climate change are often identified using coarse-scale species distribution models (SDMs; Pearson & Dawson, 2003; Thomas *et al.*, 2004), yet these may overestimate extinction risk because the climate grids used by these models are too coarse to predict the location of microrefugia (Thuiller *et al.*, 2005; Araújo & Rahbek, 2006; Pearson, 2006). For example, commonly used climate grids, such as BioClim (Houlder *et al.*, 2003) and WorldClim (Hijmans *et al.*, 2005), are developed using elevation-sensitive interpolations from weather stations. While these methods are suitable at coarse resolutions, the climate surfaces cannot simply be downscaled to finer resolutions as they neglect climate-forcing factors that operate over small distances (< 10 km; Daly, 2006). Local climates are also affected by cold air drainage, streams, oceans, lakes and topographic exposure to winds and radiation (Lookingbill & Urban, 2003; Daly, 2006; Ashcroft *et al.*, 2008; Fridley, 2009; Bennie *et al.*, 2010), all of which are neglected when temperatures are interpolated or downscaled based only on elevation

or other simplistic methods (e.g. Saxon *et al.*, 2005; Trivedi *et al.*, 2008; Vos *et al.*, 2008; VanDerWal *et al.*, 2009).

Studies that use simplified climate grids based only on elevation need to be clear that they can only capture macrorefugia, regardless of spatial resolution, because they do not consider the climate-forcing factors that create unusual local variations from the regional climate. Studies that attempt to identify microrefugia need to provide specific details on how the fine-scale climate surfaces were derived, as the climate surfaces are crucial for assessing the appropriateness of the methods. Fine-scale climate grids need to be developed using large networks of temperature sensors across a broad range of environments. It is not possible to simply interpolate observations from a sparse network of weather stations that are biased towards environments such as flat, low-elevation or unvegetated areas (Lookingbill & Urban, 2003; Ashcroft *et al.*, 2008; Fridley, 2009; Bennie *et al.*, 2010).

Another alternative is to use coarse-scale climate surfaces and the within-cell elevational range to predict whether there are microrefugia somewhere within grid cells (Luoto & Heikkinen, 2008; Vetaas & Ferrer-Castán, 2008; Randin *et al.*, 2009). Ironically, this coarse-scale method may be more successful at identifying the approximate location of microrefugia than fine-scale models that use climate surfaces only based on elevation (Trivedi *et al.*, 2008; VanDerWal *et al.*, 2009). This is because topography creates complex mosaics of exposure to wind and radiation, and sheltered locations may be buffered from regional climate change (Hampe & Petit, 2005; Williams *et al.*, 2008; Ashcroft *et al.*, 2009). Deep gorges, such as those that provide microrefugia for the Wollemi pine (*Wollemia nobilis*) in Australia (Offord *et al.*, 1999), are predicted to be warmer than the surrounding area if climate surfaces are based only on elevation, but are actually cooler when topographic shelter is considered (Ashcroft *et al.*, 2008).

Both microrefugia and macrorefugia are of conservation interest. Larger refugia are expected to provide a more secure buffer against extinction, and will be needed for large-bodied animals or species with large home ranges (Stewart *et al.*, 2010). However, as temperatures increase, microrefugia can persist even once the regional climate is unsuitable and no macrorefugia remain. This means that microrefugia have the potential to withstand a greater amount of warming than macrorefugia. Microrefugia may also be the only conservation option for rare or threatened species that exist in small fragmented populations (Maschinski *et al.*, 2006).

ARE REFUGIA STABLE IN CLIMATE OR HABITAT?

There is confusion as to whether refugia should be defined with respect to stability in climate or habitat. Some have suggested that microrefugia are locations where the climate is more stable (or has less warming) than the surrounding areas (Saxon *et al.*, 2005; Ashcroft *et al.*, 2009; Fridley, 2009; Rull, 2009). However, SDMs are typically used to predict stability in habitat rather than stability in climate (Attorre *et al.*, 2007;

VanDerWal *et al.*, 2009). Although locations that are stable in climate are likely to be stable in habitat for many species, the methodological issues that arise from the two different definitions deserve closer attention and are discussed in detail in the remainder of this section.

Locations that are stable in climate are defined without reference to any particular species, yet they are topographically and geographically biased in their locations and will only capture a subset of species in a region (Ashcroft *et al.*, 2009; Fridley, 2009). In some landscapes, localities with low summer maximum temperatures have received less warming than warmer localities, and therefore microrefugia are expected to help protect the species that are most at risk in a warming climate (Ashcroft *et al.*, 2009). In these cases, as warmer localities experience larger increases in temperature than cooler localities, it also raises the possibility that climate change will increase the length of landscape-scale temperature gradients (Fridley, 2009). This could create higher environmental diversity (Faith & Walker, 1996; Faith, 2003), and therefore lead to higher landscape-scale biological diversity if new species that prefer warmer conditions are able to disperse to the area.

This trend of cooler locations warming less than warmer locations is not universally applicable, however. At the global scale the colder polar regions are warming more than the global average and overall global diversity is predicted to decrease (Hughes, 2000; Thomas *et al.*, 2004). At the landscape scale, winter minimum temperatures decrease further from the coast and more warming is expected to occur in these cooler locations (Ashcroft *et al.*, 2008, 2009). Winter minima are generally increasing more than summer maximum temperatures (Hughes, 2000; Ashcroft *et al.*, 2009), and therefore refugia from rising winter minimum temperatures may have greater conservation significance.

In the context of the current warming trend, less warming is generally expected to occur in locations that are nearer to streams or coastlines, or where there is cold air drainage, higher soil moisture, higher canopy cover, higher elevation or less exposure to hot winds and radiation (Kennedy, 1997; Noss, 2001; Bennett & Provan, 2008; Ashcroft *et al.*, 2009; Fridley, 2009). However, the relative effect of these factors will vary between seasons and locations. For example, the trend of decreased warming with elevation is stronger in tropical zones, with the trend outside the tropics obscured by snow-ice feedback and greater warming near the 0 °C isotherm (Pepin & Lundquist, 2008).

One problem with defining refugia with respect to climatic stability is that species that are adapted to climatically stable locations may be more susceptible to changes than are other species (Williams *et al.*, 2008). Even if a cool gorge experiences half the warming of more exposed ridges, the biological impacts may be equivalent. Another problem is that climatic stability could be defined with respect to a number of factors, including winter minimum temperatures, summer maximum temperatures or humidity (Barnosky, 2008). The location of refugia from climate change would vary according to which

parameters were chosen, and this would also affect which species were protected. Although climatic stability may play a large role in determining the location of *in situ* refugia, SDMs are still needed to determine which species may be able to persist in *ex situ* refugia, and to determine the species-specific risks of extinction based on changes in multiple environmental factors.

Habitat stability is species specific, and therefore the location of refugia will differ among species. While habitat stability is undoubtedly influenced by climatic stability, SDMs sometimes assume there is uniform warming or downscale global climate models in a manner that would result in nearly uniform warming at fine scales (see references in Beaumont *et al.*, 2007; Trivedi *et al.*, 2008; and VanDerWal *et al.*, 2009). Under these circumstances, cooler locations will almost inevitably be less susceptible to warming than warmer locations as they can withstand a larger increase in regional climate before the habitat becomes unsuitable (Fig. 1a). However, it is possible that a warmer site could have higher habitat stability if it had higher climatic stability (Fig. 1b). The differences are more apparent when considering refugia from a cooling climate. Under these circumstances, the cooler site,

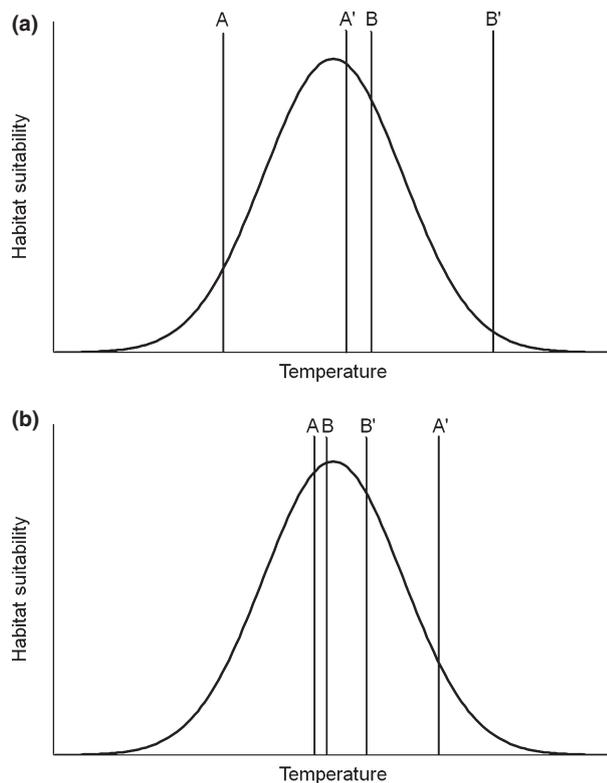


Figure 1 The bell curves illustrate the relationship between habitat suitability and temperature for a hypothetical species. Two locations, A and B, are subjected to global warming which raises their temperature to A' and B' respectively. Site A is less susceptible to global warming under the assumption of uniform warming (a) because it is a cooler location. However, if site B was more climatically stable (b), then it could be less susceptible to warming than site A even if it was originally warmer.

which is at least risk under a warming climate, is at most risk under a cooling climate if climatic stability is ignored (Fig. 1a). However, the same site can have higher habitat stability under both warming and cooling climates when climatic stability is considered (Fig. 1b).

The implications are even more dramatic when considering that commonly used climate surfaces such as BioClim (Houlder *et al.*, 2003) and WorldClim (Hijmans *et al.*, 2005) are based on elevation-sensitive interpolations. The assumption of uniform warming will potentially over-emphasize the importance of the coldest locations in the landscape (Fig. 1), and the assumption that temperatures are correlated with elevation will result in these being at higher elevations. There is thus the danger that SDMs will identify refugia from climate change at higher elevations simply based on the assumptions that were made during the modelling process rather than based on the ecology or distribution of the species. Microrefugia are known to occur in sheltered locations at lower elevations, and the methods employed to locate them should be capable of capturing the unique climates in these topographic positions. Therefore, it is important to consider variations in climatic stability, even when using a definition of refugia based on habitat stability.

Studies therefore need to include both climatic stability and habitat stability in studies of refugia. While this may not be a problem at coarse scales, where SDMs are widely employed and spatial variations in climate change are well studied, further work is needed to adequately address both these factors when locating microrefugia.

REDUCTION IN DISTRIBUTION

A key attribute of refugia is a reduction in species distributions. This usually involves a reduction in overall range size, but it is also possible that a species' overall range may be more or less maintained while it contracts its distribution to a number of microrefugia within that range (Bennett & Provan, 2008). While the term 'refugia' is generally used with respect to contractions and expansions that have occurred over glacial and interglacial periods in the Quaternary (e.g. Stewart *et al.*, 2010), there are also contractions and expansions that have been occurring over longer time periods. For example, Bennett & Provan (2008) highlight examples of species that have been expanding their range sizes in a stepwise manner during the glacial and interglacial periods of the Quaternary. Conversely, the gradual shift of Australia and South America towards the equator has caused some species to contract their ranges in a stepwise manner (Kershaw, 1986; Ledru *et al.*, 2007). Climate change could further reduce the distribution of these species, demonstrating that climate change refugia need not be limited to species that expand and contract their ranges in the glacial and interglacial periods. Similarly, even species that prefer warmer conditions and have initially expanded during the current interglacial period may eventually reach a limit and begin to contract.

Species distribution models typically predict that many species will contract their distributions under climate change (e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Svenning & Skov, 2006; Coetzee *et al.*, 2009). Therefore, restricting the term 'refugia' to species that have contracted in range size is unlikely to hinder studies predicting refugia from 21st century climate change. Indeed, any study that uses coarse-scale SDMs to predict future distributions is effectively identifying macrorefugia from climate change if a range contraction occurs. Nevertheless, if a contraction in distribution is a requirement for the use of the term 'refugia', then this needs to be demonstrated. A species that has continued to exist in a small area is unlikely to be regarded as a refugial population if there is no expansion and contraction (Bennett & Provan, 2008).

Range contractions are also problematic for methods that identify refugia based on climatic stability (see the previous section), the compositional irreplaceability of locations (Coetzee *et al.*, 2009) or other methods based on the expected response of multiple species. Unless these methods estimate the range change for individual species, they may be based to some degree on rare or restricted species where no contraction in distribution occurs. Indeed, as species respond individually to climate change, it makes sense to limit the definition of refugia to individual species (as per Stewart *et al.*, 2010). This does not prevent other terms, such as 'ecosystem hotspots' (Vos *et al.*, 2008), being used to refer to locations where refugia for multiple species coincide, and this might be beneficial from a conservation perspective.

SPECIES PERSISTENCE

The conservation value of refugia reflects their ability to allow species to persist during periods of unfavourable climate. As the distribution of the species contracts to a smaller area, the probability of extinction is increased, and this risk increases the longer the unfavourable conditions last (Stewart *et al.*, 2010). However, species persistence is also affected by the quality of the habitat in refugia. Species may even be able to persist for a limited time after their habitat becomes unsuitable. Examples include seeds stored in the soil bank, or species that can survive as adults for long periods even when conditions are not suitable for reproduction. These species are effectively committed to extinction (Thomas *et al.*, 2004), and it may be more appropriate to refer to these as relict populations than refugial populations (Hampe & Petit, 2005). However, even these relicts could have conservation value if the trend in climate change reversed in future, and they can recover when conditions become favourable again.

If the term 'refugia' is used to refer purely to species that have contracted in range, then this definition would also include long-lived species surviving in unsuitable habitat. This is problematic for SDMs, as it requires them to identify previously suitable habitat, estimate how long the adults or seeds could survive under unfavourable conditions, and determine whether they could recover in future. Even if these relicts are excluded from the definition of refugia, it is still

necessary to know how long the climate will be warmer than 'normal' interglacial conditions so that the probability of persistence in refugia can be estimated.

CONCLUDING REMARKS

Refugia need to be identified and protected across multiple spatial and temporal scales (Noss, 2001). While the trend of rising global temperatures poses immediate threats, long-term survival of species depends on protecting both glacial and interglacial refugia (Skov & Svenning, 2004) as well as refugia from climate change, and these may not coincide. The variety of species responses to climate change (Bennett & Provan, 2008) and the methodological discrepancies highlighted in this article illustrate the need to improve the terminology and clarify the context to which the term 'refugia' is applied. This article has highlighted a number of potential methodological issues that could arise when identifying refugia from climate change (Table 1), and clarifying the context of refugia in each study would help avoid these pitfalls. It would be beneficial to replace the general term 'refugia' with more distinct terms such as 'interglacial microrefugia' (Rull, 2009) or 'microclimatic refugia' (Trivedi *et al.*, 2008); however, even these leave some ambiguities with regard to *in situ* versus *ex situ* refugia and climatic stability versus habitat stability. If studies are based on a clearer definition of refugia (e.g. Stewart *et al.*, 2010), it will help others to assess the appropriateness of the methods employed and place their results in the appropriate ecological context.

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BIOSKETCH

Michael B. Ashcroft is a spatial analyst at the Australian Museum. His research interests include the spatial and temporal distribution of plants, invertebrates and associated environmental factors.

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