



# Refugia: identifying and understanding safe havens for biodiversity under climate change

Gunnar Keppel<sup>1\*</sup>, Kimberly P. Van Niel<sup>2</sup>, Grant W. Wardell-Johnson<sup>1</sup>, Colin J. Yates<sup>3</sup>, Margaret Byrne<sup>3</sup>, Ladislav Mucina<sup>1</sup>, Antonius G. T. Schut<sup>1</sup>, Stephen D. Hopper<sup>4</sup> and Steven E. Franklin<sup>5</sup>

<sup>1</sup>Curtin Institute for Biodiversity and Climate, Department of Environment and Agriculture, PO Box U1987, Perth, 6845 WA, Australia,

<sup>2</sup>School of Earth and Environment, The University of Western Australia, Crawley, WA 6009, Australia, <sup>3</sup>Science Division, Department of Environment and Conservation, Locked Bag 104, Bentley Delivery Centre, WA, Australia,

<sup>4</sup>Royal Botanic Gardens Kew, Richmond, Surrey TW9 3AB, UK and School of Plant Biology, The University of Western Australia, Crawley WA 6009, Australia, <sup>5</sup>Trent University, 1600 West Bank Drive, Peterborough, Ontario, Canada K9J 7B8

## ABSTRACT

**Aim** Identifying and protecting refugia is a priority for conservation under projected anthropogenic climate change, because of their demonstrated ability to facilitate the survival of biota under adverse conditions. Refugia are habitats that components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions. However, the study and discussion of refugia has often been *ad hoc* and descriptive in nature. We therefore: (1) provide a habitat-based concept of refugia, and (2) evaluate methods for the identification of refugia.

**Location** Global.

**Methods** We present a simple conceptual framework for refugia and examine the factors that describe them. We then demonstrate how different disciplines are contributing to our understanding of refugia, and the tools that they provide for identifying and quantifying refugia.

**Results** Current understanding of refugia is largely based on Quaternary phylogeographic studies on organisms in North America and Europe during significant temperature fluctuations. This has resulted in gaps in our understanding of refugia, particularly when attempting to apply current theory to forecast anthropogenic climate change. Refugia are environmental habitats with space and time dimensions that operate on evolutionary time-scales and have facilitated the survival of biota under changing environmental conditions for millennia. Therefore, they offer the best chances for survival under climate change for many taxa, making their identification important for conservation under anthropogenic climate change. Several methods from various disciplines provide viable options for achieving this goal.

**Main conclusions** The framework developed for refugia allows the identification and description of refugia in any environment. Various methods provide important contributions but each is limited in scope; urging a more integrated approach to identify, define and conserve refugia. Such an approach will facilitate better understanding of refugia and their capacity to act as safe havens under projected anthropogenic climate change.

## Keywords

Climate change, conservation, disturbance, habitat, microclimate, palaeobiology, phylogeography, refuges, refugia, species distribution models.

\*Correspondence: Gunnar Keppel, Curtin Institute for Biodiversity and Climate, Department of Environment and Agriculture, PO Box U1987, Perth, 6845 WA, Australia. E-mail: g.keppel@curtin.edu.au

## INTRODUCTION

Refuges and refugia are receiving increasing attention in the biological literature (see Fig. S1 in Supporting Information). Refugia have facilitated the persistence of components of biodiversity over millennia and under changing climates (Tzedakis *et al.*, 2002). Thus the identification and protection of refugia has increased in priority for conservation planning under projected anthropogenic climate change (Noss, 2001; Taberlet & Cheddadi, 2002; Loarie *et al.*, 2008), which includes increasing global temperatures of 2 to 4.5°C by 2100 and more intense, frequent heat waves of longer duration (IPCC, 2007). Despite this increase in interest, refugia are currently loosely defined and their study is often based on *ad hoc* descriptive data sources. Therefore, clarification of the terminology surrounding refugia and related concepts, as well as evaluation of the status of knowledge about refugia (Ashcroft, 2010) is warranted, allowing the development of protocols for their identification and conservation.

Here, we review the concepts of refugia and methodologies for their identification. Based on an extensive literature search, we identify a bias towards Northern Hemisphere and Quaternary glaciations in the current understanding of refugia. We propose a process-based definition for refugia, centred on species-specific requirements in a multidimensional domain of environmental variables, space and time, as well as spatial requirements that encompasses past glacial fluctuations and current and future anthropogenic climate change. Thus the definition should be both globally and temporally applicable. The utility of available methods from various disciplines is then considered for describing and identifying refugia to facilitate understanding of ecological and evolutionary processes and safeguarding threatened biota under anthropogenic climate change. We suggest that an integrated approach based on multiple sources of evidence will be most efficient in providing an ecological and evolutionary understanding of refugia. Such an approach is also likely to provide the best opportunity to guide conservation approaches in the future.

## REFUGES AND REFUGIA IN BIOLOGY

The terms 'refugium' and 'refuge' have been widely, and sometimes interchangeably (e.g. Magoulick & Kobza, 2003; Svenning & Skov, 2007), used in biological sciences. To assess the scope of refuge and refugium in the biological sciences, we surveyed the literature between 1991 and 2009 and identified more than 6000 references (see Appendix S1 for methodology) with a continuous increase over time. Generally, the term refuge was used to denote temporal and/or spatial protection from disturbances (e.g. Magoulick & Kobza, 2003), predation (e.g. Brown, 2003), herbivory (e.g. Beschta, 2005) or competition (e.g. Sebens, 1982), and hence refers to microhabitats providing spatial and/or temporal protection from disturbances or advantages in biotic interactions. The term has also been used to denote areas legally, customarily or circumstantially protected from

anthropogenic disturbance (e.g. Quinn *et al.*, 1993), which should be referred to as reserves.

The term refugium was first used in biological sciences to describe places of limited spatial extent to which components of the biota retreated to, in which they survived periods of glaciation during the Last Glacial Maximum (LGM), and which they subsequently expanded from into the surrounding landscape (Dahl, 1946; Bennett & Provan, 2008). Although difficult to quantify, the concept of refuges is based on shorter ecological time-scales of minutes to decades, while refugia operate over longer evolutionary time-scales of millennia. To avoid confusion we suggest using the term refugia when considering species range dynamics and climate change.

The greatest increase in the number of publications has been on refugia in a Quaternary climate change context, mainly facilitated by increases in phylogeographic studies (Beheregaray, 2008), accounting for about 76% of all such publications in 2009. They are also biased towards the Northern Hemisphere (Fig. 1), and Europe has almost twice as many studies as North America (cf. Beheregaray, 2008). Many studies have demonstrated the critical role that refugia played in the survival and evolution of biota during and after the Pleistocene glaciations (Soltis *et al.*, 1997; Taberlet *et al.*, 1998; Binney *et al.*, 2009). More recently, an increasing number of studies have considered refugia and species range dynamics in landscapes that were not affected by moving ice sheets. In these regions, glacial periods were often associated with increasing aridity (Nichol, 1999; Fuijoka *et al.*, 2009), and there is evidence for mesic refugia in such landscapes in North America (e.g. Fehllberg & Ranker, 2009), South America (e.g. Carnaval *et al.*, 2009), Africa (e.g. Arctander *et al.*, 1999), Asia (e.g. Gathorne-Hardy *et al.*, 2002) Australia (e.g. Byrne, 2008) and the Pacific (Pillon *et al.*, 2009). While many refugia in non-glaciated landscapes are associated with complex landscape topography, such as mountain ranges and deep valleys (Stebbins & Major, 1966; Taberlet & Cheddadi, 2002; Médail & Diadema, 2009), refugia also occur in topographically subdued landscapes, but the characteristics and spatial extent of these places remain cryptic (Hopper, 1979; Byrne, 2008).

Common to studies of species Quaternary range dynamics in both glaciated and unglaciated regions is the idea that when regional climate became unsuitable for species, their ranges contracted to places of limited spatial extent that provided suitable environments. They persisted in these sites and subsequently expanded from them when climatic conditions improved. Often a refugium will be a place providing environmental diversity and stability, facilitating persistence as regional biotic and abiotic environments change (i.e. an *in situ* refugium). However, refugia may also be of transient nature outside a species' range (i.e. *ex situ* refugia), for example southern European glacial refugia (Petit *et al.*, 2003; Bennett & Provan, 2008; Birks & Willis, 2008). The key point is that these habitats retain conditions that once were common in the landscape. Hence refugia are habitats that components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions.

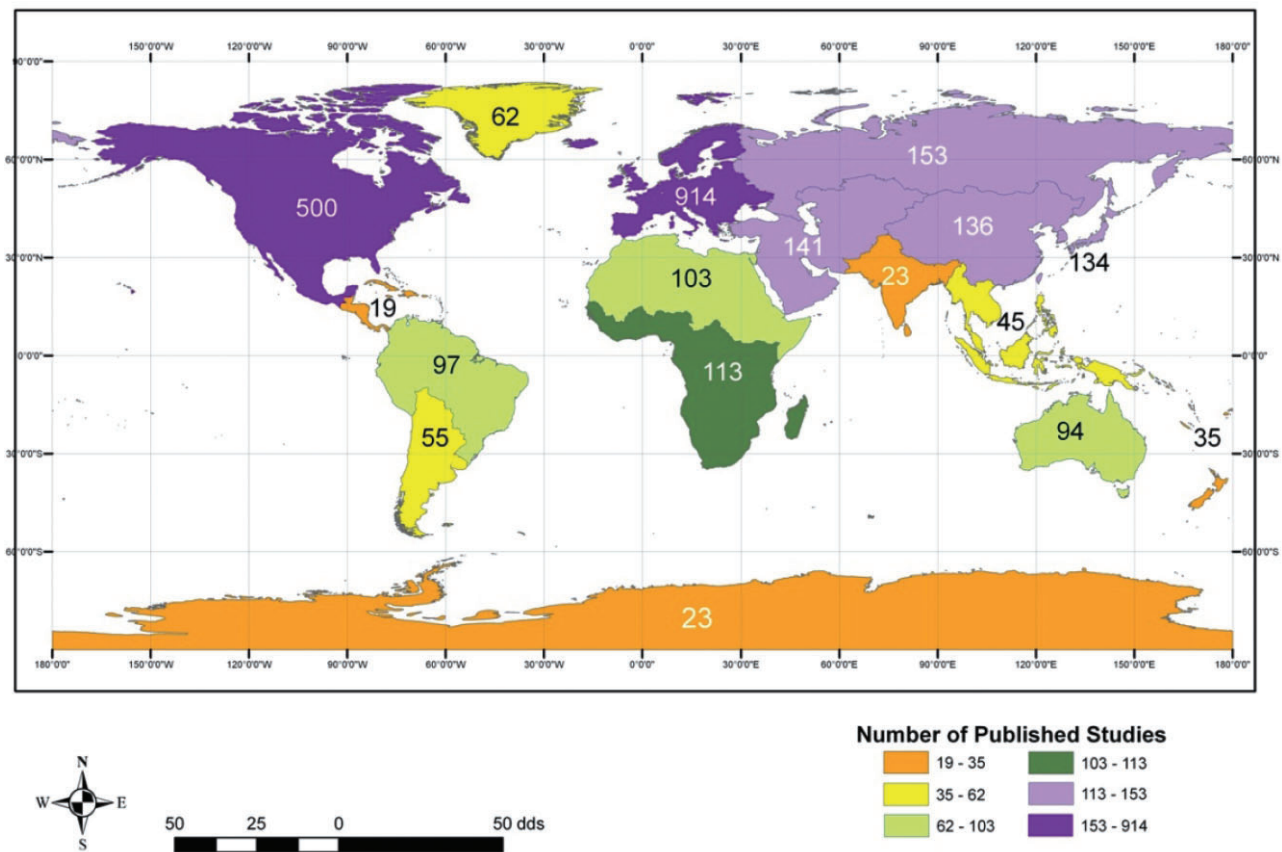


Figure 1 Regional distribution of refugia studies. Numbers indicate number of studies per region.

The emerging broader view of refugia describes a multidimensional domain of environmental variables, space and time, and incorporates various climate and spatial extremes [e.g. glacial versus interglacial (Bennett & Provan, 2008), mesic versus arid (Byrne, 2008) and macro versus micro (Rull, 2009) refugia], and recognizes they are end points along spatial and temporal continua. The concept may be applied to genes, taxa or multiple taxa with similar functional traits, which may respond in a roughly similar manner as climates change (Tzedakis *et al.*, 2002; Bhagwat & Willis, 2008; although see Austin *et al.*, 2009, for an alternative outcome). Although the study of refugia has been largely restricted to the Quaternary, we argue that the concept is applicable to biodiversity under potential future climates arising from the enhanced greenhouse effect.

### Habitat, space and time

The habitat is an essential property of a refugium, definable by environmental parameters. These continuous environmental variables along which different taxa may respond individually will have thresholds (such as 0°C) that affect a large number of taxa in a similar manner, defining the spatial dimensions of a refugium. In terrestrial environments, these parameters are direct and often inter-related gradients, such as temperature and water availability.

Temperature refugia are well-studied, especially glacial refugia that are associated with ice ages and caused by advancing and retreating ice sheets and the minimum temperature tolerance levels of organisms. These have been described in the Northern (Taberlet *et al.*, 1998; Soltis *et al.*, 2006; Opgenoorth *et al.*, 2010) and Southern (Buckley *et al.*, 2010; Cosacov *et al.*, 2010) Hemispheres. Refugia during interglacials based on maximum temperature tolerance levels and frost dependence of organisms have also been described (Ledig *et al.*, 2000; Ikeda *et al.*, 2006).

Organisms differ widely in their water requirements, and water balance is one of the major environmental factors determining the distribution of terrestrial vegetation (Stephenson, 1990; Neilson, 1995). Long-term changes in precipitation, such as increasing aridity in many areas during glacial periods (Nichol, 1999; Bowler & Wyrwoll, 2001), therefore greatly affect organisms and may result in the formation of mesic refugia. Prolonged and extreme aridity has also been shown to have resulted in the mobilization and expansion of sand dune systems, which had an effect similar to expanding ice sheets, in Africa (Nichol, 1999) and Australia (Byrne *et al.*, 2008; Fuijoka *et al.*, 2009). Arid refugia from mesic conditions have also been proposed (e.g. Hopper, 1979).

Despite this central role of habitat, several types of refugia have been described based on their location and spatial extent

(Bennett & Provan, 2008; Rull, 2009). However, delineating the extent of a refugium is often difficult, unless it is strongly associated with distinct topographic features, such as mountains and deep gorges (Médail & Diadema, 2009). In addition, the extent of a refugium varies with changes in environmental conditions and may be taxon specific. We argue that ecological habitat characteristics, which drive the processes leading to the formation of refugia, be primarily used to classify refugia across time as habitats arise, disintegrate, contract or expand. Considering that different species will show independent responses in spatial extent over time, refugia must be considered as complex and dynamic entities in both time and space.

## REFUGIA AND ANTHROPOGENIC CLIMATE CHANGE

Evidence for anthropogenic climate change and its impact on biodiversity continues to accumulate (Rosenzweig *et al.*, 2008; Stott *et al.*, 2010). Based on a substantial increase in fossil fuel use since 2000, an emissions trajectory that fits into the 'business as usual' or worst case A1FI scenario drawn up by the IPCC (2007), the probability of exceeding 2°C warming by 2100 relative to pre-industrial times continues to grow (Meinshausen *et al.*, 2009). A recent analysis indicates that a cautious implementation of the non-binding commitments under the Copenhagen Accord puts earth on a course to warm 3.5°C by 2100 (IEA, 2010). Recognizing these likelihoods and the difficulties in achieving mitigation, attention is increasingly turning towards living with climate change and minimizing the impacts on natural and human systems.

Because species contracted to and persisted in refugia when regional climates were unsuitable in the past, refugia are likely to facilitate survival (within limits) during anticipated anthropogenic climate change (Taberlet & Cheddadi, 2002; Hampe & Petit, 2005). A potential problem is that the refugia concept has arisen from studies of species range dynamics in response to cyclical warming and cooling in the Quaternary, with most studies focused on the LGM, a cooler and drier period. However, earth's climate is currently undergoing a monotonic warming, and it is expected that if carbon emissions are stabilized and reduced to zero then warming will stop, but whether pre-industrial climate conditions will return remains uncertain. We argue that the refugia concept still remains useful in at least identifying areas where negatively impacted biota can persist as anthropogenic climate change progresses with the potential to expand if suitable regional climate conditions return. We are not suggesting that all LGM refugia will act as refugia as anthropogenic climate change progresses, but that in some circumstances the characteristics of these places may allow them to act as safe havens under both warming and cooling, and they are at least worthy of investigation to understand how refugia may operate.

Projected climate change will stretch the ability of known refugia to continue acting as safe havens for species, and will depend on: (1) a species' requirements, (2) the extent to which the climate in refugia is decoupled from prevailing climatic conditions, and (3) whether microhabitat diversity and decoupling

can be maintained under continued warming (Dobrowski, 2011). The risk under potential future climate is that the greater the amplitude and rate of change, the more likely it is that *in situ* refugia will not be able to survive in safe havens and the less likely that species will be able to move fast enough to reach suitable habitat (*ex situ* refugia). Despite these issues, refugia are likely to offer the best chance for a species negatively impacted by climate change to survive under future climates.

As a result, identification of past and future refugia is now considered important in the management of anthropogenic climate change impacts (Noss, 2001; Loarie *et al.*, 2008) and developing methodologies for their identification and description is a high research priority (Steffen *et al.*, 2009). The climatic stability of refugia is often facilitated by high spatial heterogeneity and diversity, resulting in microclimate variation (Taberlet & Cheddadi, 2002; Virah-Sawmy *et al.*, 2009; Ackerly *et al.*, 2010). Understanding the impact of spatial heterogeneity on the ecology and evolution of biota in refugia is important for identifying likely locations of refugia under future climate change.

## IDENTIFYING AND DESCRIBING REFUGIA

There are two major approaches to identifying and describing refugia. One is to rely on biogeographic patterns (as proxies for processes) suggesting that refugia existed in an area at some stage in the past. This approach involves collecting data on the palaeobiology, ecology and/or genetics of target biota (Fig. 2), providing data for quantifying the spatial and temporal dimensions of refugia. The other, often neglected, approach for identifying refugia is to investigate the processes likely to produce refugial habitats. This approach (which may be more fruitful for identifying refugia in the face of anthropogenic climate change), involves identifying and quantifying the environmental and physical geographic processes (i.e. the habitat parameters) that define the environmental conditions conducive to the formation and maintenance of refugia. Below, we outline disciplines contributing to the identification of refugia (see Fig. 2), recognizing that boundaries are increasingly integrated and that each can contribute to both pattern and process.

### Palaeobiology

Pollen records (microfossils) preserved in lakes and swamps are powerful tools for identifying refugia (e.g. Colinvaux *et al.*, 2000; Carrión *et al.*, 2003), potentially providing continuous records of species composition. The continuous presence of plant taxa under changing climatic conditions demonstrates *in situ* refugia, as shown for temperate tree genera through several Pleistocene glaciations in Greece (Tzedakis *et al.*, 2002). Comprehensive databases of regional or continental pollen records can provide a more complete picture (Huntley & Birks, 1983; Binney *et al.*, 2009) and can potentially be used to reconstruct migration routes and to identify *ex situ* refugia. Macrofossils provide similar windows into the past, and the characteristics of fossilized leaves can be used to reconstruct prevalent local climates (Greenwood, 2005; Traiser *et al.*, 2005) and infer ploidy levels

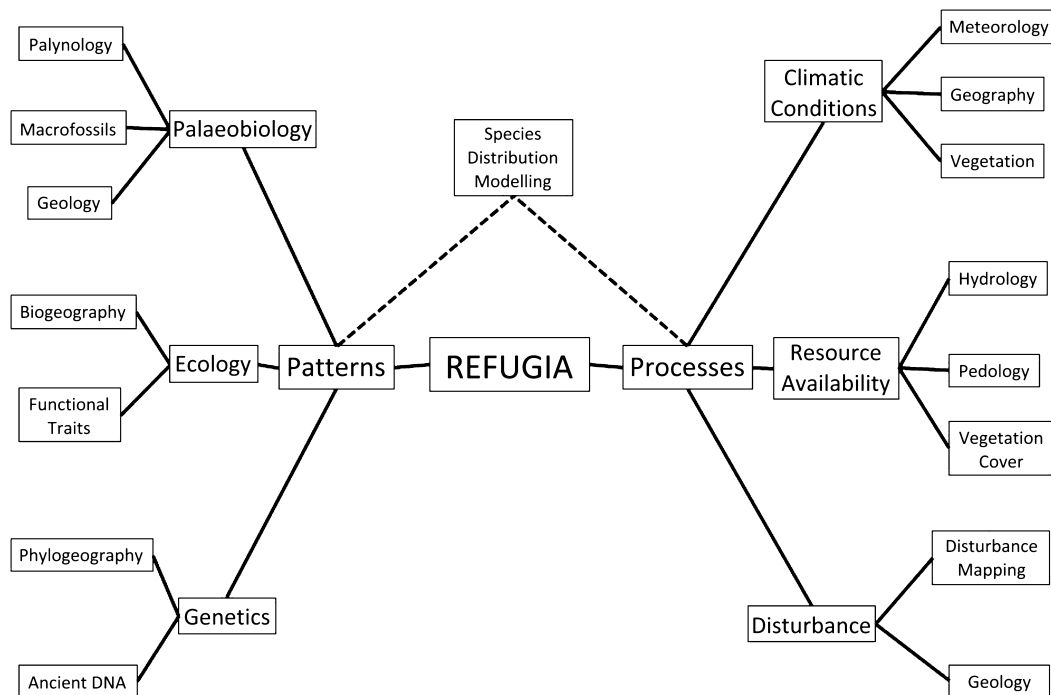


Figure 2 Schematic outline of pattern- and process-based approaches to the identification of refugia.

(Hunter *et al.*, 2001), which may be related to past refugia. In addition, the physical and chemical composition of lake and oceanic sediments can be used to infer past climatic and environmental conditions and thus possible refugia (Steig *et al.*, 1998; Kastner & Goñi, 2003).

While palaeontological sources provide the most unequivocal records of the past (Burke *et al.*, 1990), they often suffer from incompleteness, patchiness and spatial inaccuracy (Birks & Birks, 2000; Taberlet & Cheddadi, 2002). Therefore, an integrated approach utilizing all available palaeontological and other data is preferable when identifying refugia. Moreover, in arid and subdued landscapes, water bodies often do not persist long enough to provide reliable palaeontological records, although such records may occasionally be preserved by other means (Thompson & Anderson, 2000).

### Ecology

The historical and current distributions of species provided some of the earliest evidence for refugia (e.g. Hooker, 1862; Dahl, 1946). Species retract to refugia, and subsequent expansion is a slow process for many species (Svenning & Skov, 2007; Willner *et al.*, 2009). Thus refugia have been reported to have higher species diversity than the surrounding landscape (Lawes *et al.*, 2007; Médail & Diadema, 2009) and to have a relatively high number of endemic species and relict lineages (Fjeldså & Lovett, 1997). This implies that past climatic and landscape stability, often within small refugial areas (Birks & Willis, 2008), probably played a major role in shaping current diversity patterns, complementing other global drivers (Gaston, 2000; Whittaker *et al.*, 2001).

Ecological traits provide information about community assembly processes (McGill *et al.*, 2006) and may indicate locations of climatic stability over prolonged periods (i.e. *in situ* refugia). Thus some of the resident taxa in *in situ* refugia would be expected to display ecological traits such as reduced dispersability, long-term persistence (such as long life spans and asexual reproduction) and other traits less suitable for persistence outside the refugium. These traits should occur with higher frequency in refugia than elsewhere and could be used as signals to identify current refugia (reviewed in Hopper, 2009).

### Genetics

Genetic analysis, particularly phylogeography, uses the spatial distribution of genealogical lineages to deduce the influence of historical processes on the evolution of populations and species (Avice, 2000). These tools can identify the presence of refugia and likely post-refugial migration routes due to the genetic signatures of historical processes in extant species (Hewitt, 2000, 2004). Phylogeography may detect refugia that are not readily identified using classic biogeographical methods. Contraction and expansion to and from refugia leave genetic signatures of high diversity in refugial areas and low diversity in areas of expansion (Lewis & Crawford, 1995; Hewitt, 2000, 2004), although this is not always the case (Petit *et al.*, 2003). Thus low diversity with sharp allele frequency changes may indicate expansion from different refugia, or be the result of genetic drift in expanding populations promoting gene segregation (Excoffier & Ray, 2008). In addition, persistence in refugia leads to signatures of highly divergent lineages, which is indicative of

long-term isolation and persistence through multiple glacial cycles (Gómez & Lunt, 2007; Byrne, 2008; Byrne & Hopper, 2008).

Comparative phylogeography, involving the study of multiple species from a region, is a powerful means of inferring the presence of refugia and post-refugial colonization routes common to many species (Taberlet *et al.*, 1998; Soltis *et al.*, 2006; Médail & Diadema, 2009). If available, analysis of ancient DNA allows the identification of genetic patterns in the former distributions of species, providing genetic information to infer processes influencing species distributions during previous climatic conditions (Hofreiter *et al.*, 2004; Dalén *et al.*, 2007). Phylogeographic analysis is applicable in all landscapes, but may be particularly beneficial in subdued or non-glaciated landscapes. In these environments refugial areas are not readily identified by large-scale geographic features and other lines of evidence, such as palaeontology, are more restricted. Finally, the distribution of chromosomal races may also contribute evidence to identifying refugia and colonization routes (e.g. Hunter *et al.*, 2001).

### Climatic conditions

Although major climate zones are mostly determined by air circulation patterns, regional topography has a great impact on these global climatic patterns (Osborne, 2000), and fine-scale topography can produce large variations in microclimate (Weiss *et al.*, 1988; Ackerly *et al.*, 2010). Key factors in producing refugia from prevalent climate conditions include: decoupling of site climate from regional climate, a high diversity of site climatic conditions, and the more fine-scale influence of compounding topographic and climatic effects such as free-air advection, surface radiation and sheltered topographic depressions. Tight coupling to free-air advection can be caused by windy conditions which may also reduce boundary layer effects and enhance transpiration, while surface radiation can drive local heating, increasing boundary effects, decoupling them from regional climates. Similarly decoupling can occur via topographic depressions which can facilitate cold air drainage and pooling (Pepin & Lundquist, 2008). This decoupling of regional climates from microclimates, resulting in wide ranges of temperature across short distance (tens to hundreds of metres), has been documented (e.g. Ackerly *et al.*, 2010; Austin & Van Niel, 2011a,b). For example, Rorison *et al.* (1986) found a variation of 12°C from north- to south-facing slopes in subdued topography in the UK, and Ackerly *et al.* (2010) report an 8°C range in site temperatures due to radiation effects across different aspects and slopes. Areas with strong and consistent topoclimate decoupling from regional climate are likely to act as refugia for longer than sites coupled with regional climate (Dobrowski, 2011).

Climatic maps are based on the extrapolation of climatic (from available climate stations) and geographic data using standard lapse rates (Hijmans *et al.*, 2005). These modelled outcomes have been used to identify refugia (e.g. Hugall *et al.*, 2002) but are often flawed because they fail to consider microclimatic variation (Daly *et al.*, 2010). Climatic data-loggers are small

sensors that can provide spatio-temporal assessment of variability in microclimate (e.g. temperature, solar radiation). These data can be used in combination with remote sensing techniques, such as LiDAR, to provide fine-scale digital elevation models (DEMs) that can then be modelled to identify levels of radiation, water flow patterns, plant shading and other fine-scale factors that may provide critical microhabitats. Such fine-scale landscape features create local microclimates that can facilitate the persistence of biota in regions outside their physiological limits by modification of regional weather (Boyko, 1947; Dobrowski, 2011; Austin & Van Niel, 2011a,b). Variation in microclimate can then be compared with that predicted under various climate change scenarios, which can be downscaled to provide fine-scale microclimate using landscape features (Fridley, 2009; Ackerly *et al.*, 2010). Sites would be expected to serve as climate refugia if current microclimatic variation within the hypothesized refugium lies within the bounds of predicted climate change.

Such approaches, utilizing microtopographic and microclimatic data, are very promising for identifying and describing refugia in subdued landscapes with little large-scale topographic variation. This is because fine-scale modification of prevailing environmental conditions (e.g. wind and radiation) by topographic features and variation in edaphic conditions can affect how plants take up and process inputs.

### Resource availability

The distribution of resources across the landscape can be described and mapped to identify habitats that are high in resources and hence may enable species to persist as regional climates change. Resources (e.g. soil water balance and nutrients) and climatic conditions can be measured directly, or estimated using proxies such as net primary productivity (NPP) or cover/height of vegetation. Understanding limiting resources for species in particular regions can assist the identification of the most critical variables to measure. For example, water is a critically limiting resource affecting the composition and structure of vegetation in seasonally arid Mediterranean climate biomes, which will become drier under projected anthropogenic climate change (Bates *et al.*, 2008; Klausmeyer & Shaw, 2009). Pedological and hydrological data may enable understanding of how water balance is affected by topography and soils. Knowledge of variation across the landscape may thus identify areas likely to continue to act as refugia (Yates *et al.*, 2010). Measures of such variation include geodiversity, closely linked to biodiversity in Finland (Hjort & Luoto, 2010), soil diversity (Hopper, 2009) and associated differences in physiological performance based on soil nutrients (e.g. Anderson *et al.*, 2000).

The use of remotely sensed imagery can identify heterogeneity of resources and topography and information on the range of habitats and resource availability, which may enhance the survival of species during climatic perturbations or disturbance (Virah-Sawmy *et al.*, 2009). Therefore, remote sensing can potentially be used for predicting the location of areas of high biodiversity (Rocchini *et al.*, 2010) and refugia (Dubbin *et al.*,

2006). It can also be integrated with other forms of georeferenced data, such as DEMs and canopy height/ structure derived from LiDAR data (Koukoulas & Blackburn, 2005; Miura & Jones, 2010), to study patterns and processes at multiple spatial (Wulder & Franklin, 2007) and temporal (e.g. Hill & Donald, 2003) scales. Such combined data can provide an understanding of the fine-scale spatial distribution of limiting resources, hence facilitating the prediction of refugial sites.

## Disturbance

Disturbance is intrinsically linked to refugia because events such as glaciations, global warming, expanding systems of sand dunes and frequent, high-intensity fires have been shown to lead to the formation of refugia (Mackey *et al.*, 2002). Two major categories of disturbances can be differentiated. *Tabula rasa* disturbances (after Nordal, 1987), such as glaciers, volcanic lava flows and sand dune systems, denude all or parts of the affected landscape of all plants and animals and would generally lead to primary succession (Nordal, 1987; Nichol, 1999). Mosaic disturbances, such as fire (Verdú & Pausas, 2007; Bowman *et al.*, 2009), herbivory (Cantor & Whitham, 1989; Beschta, 2005) and cyclones (Curran *et al.*, 2008; Keppel *et al.*, 2010), will lead to secondary succession and may exclude taxa from parts of the landscape that are regularly affected by these disturbances. Habitats protected from these disturbances may initially be considered refuges but develop into refugia for disturbance-sensitive taxa, if the habitat remains buffered against the disturbance over evolutionary time-scales. Similarly, refugia of high disturbance in low-disturbance landscapes can be envisaged.

*Tabula rasa* disturbances often leave a distinct signature in the landscape that can be identified using geological or remote sensing technologies. The former presence of glaciers can be detected from erosion marks created by glacial ice (Meneghel *et al.*, 1999). Similarly, moving sand dunes may leave distinct marks in the landscape (Nichol, 1999) and signatures in lake sediments (Bowler & Wyrwoll, 2001). Areas shown not to have been affected by *tabula rasa* disturbances would constitute potential refugia.

Mosaic disturbances, such as fire, are difficult to document, as they often occur randomly in space and time. They are often strongly related to environmental heterogeneity (Turner *et al.*, 1994), and boundaries to recurrent disturbances can lead to disturbance refugia (e.g. Steffen *et al.*, 2009), even in subdued landscapes (Wardell-Johnson & Roberts, 1993). Therefore, the identification of refugia from such disturbances requires mapping of multiple disturbance events in the same landscape. Because the spectral signature from disturbance events may remain for decades, various remote sensing tools can be used for mapping. However, the limited period of detailed spatial records within any landscape does limit capacity to ascertain refugia from such disturbances. Multiple lines of evidence are therefore required to document refugia from mosaic disturbances. For example, there is evidence for refugia from recurring fires, derived from palaeobiology (Jasinski & Angelstam, 2002;

Niklasson *et al.*, 2002) and the local abundance of species with functional traits considered fire-sensitive (Bond *et al.*, 2004).

## Species distribution modelling

Correlative species distribution models (SDMs; Guisan & Thuiller, 2005; Elith & Leathwick, 2009) are widely used in biogeography and phylogeography to predict species distributions and have been applied to identify refugia (Hugall *et al.*, 2002; Fløjgaard *et al.*, 2009). SDMs relate the known occurrences of taxa to climate variables (taken as surrogates for physiologically relevant variables), and other factors such as soil and land cover, to define suitable abiotic conditions for populations. In turn the modelled environmental domains of species are projected onto spatially interpolated climate and other environmental surfaces to define a geographic range for a species (Yates *et al.*, 2010). Assuming that species' physiological limits and biotic interactions are constant over time (i.e. niche stability), the modelled environmental domains of species can be projected onto inferred climate surfaces to predict past or future distributions (Nogués-Bravo, 2009). Where modelled present distributions intersect with projected distributions, putative refugia may be inferred (Hugall *et al.*, 2002; Fløjgaard *et al.*, 2009).

Molecular phylogeographic data can also be included in the modelling approach, termed phyloclimatic modelling (Yesson & Culham, 2006; Waltari *et al.*, 2007; Carnaval *et al.*, 2009). The use of both species distribution and phylogeographic models provides more spatially and temporally explicit outcomes than either approach alone (Waltari *et al.*, 2007). For example, Yesson & Culham (2006) found that for the carnivorous plant genus *Drosera*, many clades diversified during the development of the Mediterranean climate in south-western Australia, resulting in both generalists and Mediterranean climate specialists. Waltari *et al.* (2007) found good agreement between ecological niche models and phylogeographic and molecular genetic models for predicting relictual species distributions, and recommended that the two approaches be used together to provide more spatially and temporally explicit outcomes. Examining both the genetic distribution and the change in climates at similar time frames enables the assessment of the links between times of climatic change and species diversification. Thus, there is potential for these methods to be combined to assess whether niche conservatism is a critical driver of the past and present distribution of relictual species, although this has yet to be tested.

Multidisciplinary information can be combined using modelling approaches to facilitate testing links between past climate change, phylogeography and modern distributions and responses with high spatial resolution. The flexibility of modelling approaches and their ability to incorporate almost unlimited datasets (Guisan & Thuiller, 2005) demonstrates the increasing value of multidisciplinary in the identification of refugia. However, to achieve reliable predictions it is necessary that models are sufficiently fine-scaled to capture 'microclimatic buffering' and the adaptive capacity of the biota (Willis & Bhagwat, 2009). This is important as retrospective and future projection modelling studies are limited by information on

precise climatic and landscape conditions and by design weaknesses (Elith & Leathwick, 2009; Austin & Van Niel, 2011a,b).

## CONCLUSIONS

The globally applicable principles and approaches described here facilitate the identification and quantitative description of refugia. The latter can be achieved by defining environmental and edaphic habitat parameters and by specifying the relevant temporal and spatial dimensions. This approach provides a globally applicable framework with parameters that need to be identified separately for specific refugia. This framework also encapsulates the dynamic nature of refugia, as their extent and sometimes location will change with the prevailing climatic conditions through time.

Each of several disciplines may contribute to the identification and understanding of refugia. However, while particular disciplines have the potential to contribute to the identification of refugia, they also each have limitations and shortcomings. For example, while phylogeographic methods have provided excellent insights into the histories of many species, their spatial and temporal resolution is usually limited. An integrated approach, using multiple lines of evidence, is therefore warranted (Taberlet & Cheddadi, 2002). Combinations across disciplines (e.g. using SDMs, topoclimatic modelling and genetics together), will improve our ability to identify future refugia under anthropogenic climate change. It is therefore appropriate that a cross-disciplinary approach be used to bring together different perspectives and approaches to produce new, testable hypotheses to further advance this emerging field of research.

Multiple lines of evidence are essential to examine the capacity of species to survive in refugia under projected anthropogenic climate change, and to explicitly relate these outcomes to conservation planning. Such an approach would contribute towards developing Climate Change Integrated Conservation Strategies (CCS; Hannah *et al.*, 2002), and to link regional modelling with a fine-scale understanding of the past and present distributions of species for spatial biodiversity conservation planning.

Refugia play an important role in understanding the evolutionary history of the world's biota and could contribute to protecting it against climate change. Therefore, research and conservation interest in refugia will continue to increase as more biodiversity is threatened and the impacts of anthropogenic climate change are increasingly fulfilled. Because limited resources are available for conservation, research investment will continue to be prioritized. Thus conservation priorities will increasingly be linked to areas of potential refugia that have an inherent resilience to climate change, providing safe havens where biota can be safeguarded for longest.

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## REFERENCES

- Ackerly, D.D., Loarie, S.R., Cornwell, W.K., Weiss, S.B., Hamilton, H., Branciforte, R. & Kraft, N.J.B. (2010) The geography of climate change: implications for conservation biogeography. *Diversity and Distributions*, **16**, 476–487.
- Anderson, J.E., Kriedemann, P.E., Austin, M.P. & Farquhar, G. (2000) Eucalypts forming a canopy functional type in dry sclerophyll forests respond differently to environment. *Australian Journal of Botany*, **48**, 759–775.
- Arctander, P., Johansen, C. & Coutellec-Vreto, M.-A. (1999) Phylogeography of three closely related African bovids (tribe Alcelaphini). *Molecular Biology and Evolution*, **16**, 1724–1739.
- Ashcroft, M.B. (2010) Identifying refugia from climate change. *Journal of Biogeography*, **37**, 1407–1413.
- Austin, M.P. & Van Niel, K.P. (2011a) Impact of landscape predictors on climate change modelling of species distributions: a case study with *Eucalyptus fastigata* in southern New South Wales, Australia. *Journal of Biogeography*, **38**, 9–19.
- Austin, M.P. & Van Niel, K.P. (2011b) Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeography*, **38**, 1–8.
- Austin, M.P., Smith, T.M., Van Niel, K.P. & Wellington, A.B. (2009) Physiological responses and statistical models of the environmental niche: a comparative study of two co-occurring *Eucalyptus* species. *Journal of Ecology*, **97**, 496–507.
- Avise, J.C. (2000) *Phylogeography. The history and formation of species*. Harvard University Press, Cambridge, MA.
- Bates, B.C., Hope, P., Ryan, B., Smith, I. & Charles, S. (2008) Key findings from the Indian Ocean Climate Initiative and their impact on policy development in Australia. *Climatic Change*, **89**, 339–354.
- Beheregaray, L.B. (2008) Twenty years of phylogeography: the state of the field and the challenges for the Southern Hemisphere. *Molecular Ecology*, **17**, 3754–3774.
- Bennett, K.D. & Provan, J. (2008) What do we mean by 'refugia'? *Quaternary Science Reviews*, **27**, 2449–2455.
- Beschta, R.L. (2005) Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's northern range. *Ecology*, **86**, 391–403.
- Bhagwat, S.A. & Willis, K.J. (2008) Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? *Journal of Biogeography*, **35**, 464–482.
- Binney, H.A., Willis, K.J., Edwards, M.E., Bhagwat, S.A., Anderson, P.M., Andreev, A.A., Blaauw, M., Dambon, F., Haesaerts, P., Kienast, F., Kremenetski, K.V., Krivonogov, S.K., Lozhkin, A.V., MacDonald, G.M., Novenko, E.Y., Oksanen, P., Sapelko, T.V., Valiranta, M. & Vazhenina, L. (2009) The distribution of late-Quaternary woody taxa in northern Eurasia: evidence from a new macrofossil database. *Quaternary Science Reviews*, **28**, 2445–2464.
- Birks, H.H. & Birks, H.J.B. (2000) Future uses of pollen analysis must include plant macrofossils. *Journal of Biogeography*, **27**, 31–35.



- Birks, H.J.B. & Willis, K.J. (2008) Alpines, trees, and refugia in Europe. *Plant Ecology and Diversity*, **1**, 147–160.
- Bond, W.J., Dickinson, K.J.M. & Mark, A.F. (2004) What limits the spread of fire-dependent vegetation? Evidence from geographic variation of serotiny in a New Zealand shrub. *Global Ecology and Biogeography*, **13**, 115–127.
- Bowler, J.M. & Wyrwoll, K.H. (2001) Variations of the north-west Australian summer monsoon over the last 300,000 years: the paleohydrological record of the Gregory (Mulan) Lakes system. *Quaternary International*, **83–85**, 63–80.
- Bowman, D.M.J.S., Balch, J.K., Artaxo, P. *et al.* (2009) Fire in the Earth system. *Science*, **324**, 481–484.
- Boyko, H. (1947) On the role of plants as quantitative climate indicators and the geo-ecological law of distribution. *Journal of Ecology*, **35**, 138–157.
- Brown, B.L. (2003) Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecology Letters*, **6**, 316–325.
- Buckley, T.R., Marske, K. & Attanayake, D. (2010) Phylogeography and ecological niche modelling of the New Zealand stick insect *Clitarchus hookeri* (White) support survival in multiple coastal refugia. *Journal of Biogeography*, **37**, 682–695.
- Burke, K., Francis, P. & Wells, G. (1990) Importance of the geological record in understanding global change. *Global and Planetary Change*, **89**, 193–204.
- Byrne, M. (2008) Evidence for multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography. *Quaternary Science Reviews*, **27**, 2576–2585.
- Byrne, M. & Hopper, S.D. (2008) Granite outcrops as ancient islands in old landscapes: evidence from the phylogeography and population genetics of *Eucalyptus caesia* (Myrtaceae) in Western Australia. *Biological Journal of the Linnean Society*, **93**, 177–188.
- Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A.J., Cooper, S., Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porch, N. & Wyrwoll, K.-H. (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology*, **17**, 4398–4417.
- Cantor, L.F. & Whitham, T.G. (1989) Importance of below-ground herbivory: pocket gophers may limit aspen to rock outcrop refugia. *Ecology*, **70**, 962–970.
- Carnaval, A.C., Hickerson, M.J., Haddad, C.F.B., Rodrigues, M.T. & Moritz, C. (2009) Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science*, **323**, 785–789.
- Carrión, J.S., Yll, E.I., Walker, M.J., Legaz, A.J., Chaín, C. & López, A. (2003) Glacial refugia of temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: new evidence from cave pollen at two Neanderthal man sites. *Global Ecology and Biogeography*, **12**, 119–129.
- Colinvaux, P.A., De Oliveira, P.E. & Bush, M.B. (2000) Amazonian and Neotropical plant communities on glacial timescales: the failure of the aridity and refuge hypotheses. *Quaternary Science Reviews*, **19**, 141–169.
- Cosacov, A., Sérsic, A.N., Sosa, V., Johnson, L.A. & Cocucci, A.A. (2010) Multiple periglacial refugia in the Patagonian steppe and post-glacial colonization of the Andes: the phylogeography of *Calceolaria polyrhiza*. *Journal of Biogeography*, **37**, 1463–1477.
- Curran, T.J., Brown, R.L., Edwards, E., Hopkins, K., Kelley, C., McCarthy, E., Pounds, E., Solan, R. & Wolf, J. (2008) Plant functional traits explain interspecific differences in immediate cyclone damage to trees of an endangered rainforest community in North Queensland. *Austral Ecology*, **33**, 451–461.
- Dahl, E. (1946) On different types of unglaciated areas during the ice ages and their significance to phytogeography. *New Phytologist*, **45**, 225–242.
- Dalén, L., Nyström, V., Valdiosera, C., Germonpré, M., Sablin, M., Turner, E., Angerbjörn, A., Arsuaga, J.L. & Götherström, A. (2007) Ancient DNA reveals lack of postglacial habitat tracking in the arctic fox. *Proceedings of the National Academy of Sciences USA*, **104**, 6726–6729.
- Daly, C., Conklin, D.R. & Unsworth, M.H. (2010) Local atmospheric decoupling in complex topography alters climate change impacts. *International Journal of Climatology*, **30**, 1857–1864.
- Dobrowski, S.Z. (2011) A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*, **17**, 1022–1035.
- Dubbin, W.E., Penn, M.G. & Hodson, M.E. (2006) Edaphic influences on plant community adaptation in the Chiquibul forest of Belize. *Geoderma*, **131**, 76–88.
- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution and Systematics*, **40**, 677–697.
- Excoffier, L. & Ray, N. (2008) Surfing during population expansions promotes genetic revolutions and structuration. *Trends in Ecology and Evolution*, **23**, 347–351.
- Fehlberg, S.D. & Ranker, T.A. (2009) Evolutionary history and phylogeography of *Encelia farinosa* (Asteraceae) from the Sonoran, Mojave, and Peninsular Deserts. *Molecular Phylogenetics and Evolution*, **50**, 326–335.
- Fjeldså, J. & Lovett, J.C. (1997) Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodiversity and Conservation*, **6**, 325–346.
- Fløjgaard, C., Normand, S., Skov, F. & Svenning, J.-C. (2009) Ice age distributions of European small mammals: insights from species distribution modelling. *Journal of Biogeography*, **36**, 1152–1163.
- Fridley, J.D. (2009) Downscaling climate over complex terrain: high finescale (<1000 m) spatial variation of near-ground temperatures in a montane forested landscape (Great Smoky Mountains). *Journal of Applied Meteorology and Climatology*, **48**, 1033–1049.
- Fuijoka, T., Chappell, J., Fitfield, L.K. & Rhodes, E.J. (2009) Australian desert dune fields initiated with Pliocene–Pleistocene global climatic shift. *Geology*, **37**, 51–54.

- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Gathorne-Hardy, F.J., Syaukani, Davies, R.G., Eggleton, P. & Jones, D.T. (2002) Quaternary rainforest refugia in south-east Asia: using termites (Isoptera) as indicators. *Biological Journal of the Linnean Society*, **75**, 453–466.
- Gómez, A. & Lunt, D.H. (2007) Refugia within refugia: patterns of phylogeographic concordance in the Iberian Peninsula. *Phylogeography of southern European refugia* (ed. by S. Weiss and N. Ferrand), pp. 155–188. Springer-Verlag, Amsterdam.
- Greenwood, D.R. (2005) Leaf form and the reconstruction of past climates. *New Phytologist*, **166**, 355–357.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Hampe, A. & Petit, R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.
- Hannah, L., Midgley, G.F. & Millar, D. (2002) Climate-change-integrated conservation strategies. *Global Ecology and Biogeography*, **11**, 485–495.
- Hewitt, G.M. (2000) The genetic legacy of the Quaternary ice ages. *Nature*, **405**, 907–913.
- Hewitt, G.M. (2004) Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 183–195.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hill, M.J. & Donald, G.E. (2003) Estimating spatio-temporal patterns of agricultural productivity in fragmented landscapes using AVHRR NDVI time series. *Remote Sensing of Environment*, **84**, 367–384.
- Hjort, M. & Luoto, M. (2010) Geodiversity of high-latitude landscapes in northern Finland. *Geomorphology*, **115**, 109–116.
- Hofreiter, M., Serre, D., Rohland, N., Rabeder, G., Nagel, D., Conard, N., Münzel, S. & Pääbo, S. (2004) Lack of phylogeography in European mammals before the last glaciation. *Proceedings of the National Academy of Sciences USA*, **101**, 12963–12968.
- Hooker, J.D. (1862) Outlines on the distribution of arctic plants. *Transactions of the Linnean Society of London*, **23**, 251–348.
- Hopper, S.D. (1979) Biogeographical aspects of speciation in the southwest Australian flora. *Annual Review of Ecology and Systematics*, **10**, 399–422.
- Hopper, S.D. (2009) OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil*, **322**, 49–86.
- Hugall, A., Moritz, C., Moussalli, A. & Staniscic, J. (2002) Reconciling paleodistribution models and comparative phylogeography in the wet tropics rainforest land snail *Gnarosiphia bellendenkerensis* (Brazier 1875). *Proceedings of the National Academy of Sciences USA*, **99**, 6112–6117.
- Hunter, K.L., Betancourt, J.L., Riddle, B.R., Van Devender, T.R., Cole, K.L. & Spaulding, W.G. (2001) Ploidy race distributions since the Last Glacial Maximum in the North American desert shrub, *Larrea tridentata*. *Global Ecology and Biogeography*, **10**, 521–533.
- Huntley, B. & Birks, H.J.B. (1983) *An atlas of past and present pollen maps of Europe: 0–13,000 years ago*. Cambridge University Press, Cambridge.
- IEA (2010) *World energy outlook*. International Energy Agency, Paris.
- Ikeda, H., Senni, K., Fujii, N. & Setoguchi, H. (2006) Refugia of *Potentilla matsumurae* (Rosaceae) located at high mountains in the Japanese archipelago. *Molecular Ecology*, **15**, 3731–3740.
- IPCC (2007) Summary for policy makers. *Climate change 2007: the physical science basis. Contribution of Working Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), pp. 1–18. Cambridge University Press, Cambridge.
- Jasinski, K. & Angelstam, P. (2002) Long-term differences in the dynamics within a natural forest landscape – consequences for management. *Forest Ecology and Management*, **161**, 1–11.
- Kastner, T.P. & Goñi, M.A. (2003) Constancy in the vegetation of the Amazon Basin during the late Pleistocene: evidence from the organic matter composition of Amazon deep sea fan sediments. *Geology*, **31**, 291–294.
- Keppel, G., Buckley, Y.M. & Possingham, H.P. (2010) Drivers of lowland rain forest community assembly, species diversity and forest structure on islands in the tropical South Pacific. *Journal of Ecology*, **98**, 87–95.
- Klausmeyer, K.R. & Shaw, M.R. (2009) Climate change, habitat loss, protected areas and the climate adaptation potential of species in Mediterranean ecosystems worldwide. *PLoS ONE*, **4**, e6392.
- Koukoulas, S. & Blackburn, G.A. (2005) Mapping individual tree location, height and species in broadleaved deciduous forest using airborne LIDAR and multi-spectral remotely sensed data. *International Journal of Remote Sensing*, **26**, 431–455.
- Lawes, M.J., Eeley, H.A.C., Findlay, N.J. & Forbes, D. (2007) Resilient forest faunal communities in South Africa: a legacy of palaeoclimatic change and extinction filtering? *Journal of Biogeography*, **34**, 1246–1264.
- Ledig, F.T., Bermejo-Velázquez, B., Hodgskiss, P.D., Johnson, D.R., Flores-López, C. & Jacob-Cervantes, V. (2000) The mating system and genic diversity in Martínez spruce, an extremely rare endemic of Mexico's Sierra Madre Oriental: an example of facultative selfing and survival in interglacial refugia. *Canadian Journal of Forest Research*, **30**, 1156–1164.
- Lewis, P.O. & Crawford, D.J. (1995) Pleistocene refugium endemics exhibit greater allozymic diversity than widespread congeners in the genus *Polygonella* (Polygonaceae). *American Journal of Botany*, **82**, 141–149.

- Loarie, S.R., Carter, B.E., Hayhoe, K., McMahon, S., Moe, R., Knight, C.A. & Ackerly, D.D. (2008) Climate change and the future of California's endemic flora. *PLoS ONE*, **3**, e2502.
- McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.
- Mackey, B., Lindenmayer, D., Gill, M., McCarthy, M. & Lindsay, J. (2002) *Wildlife, fire and future climate: a forest ecosystem analysis*. CSIRO, Collingwood, ON.
- Magoulick, D.D. & Kobza, R.M. (2003) The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology*, **48**, 1186–1198.
- Médail, F. & Diadema, K. (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography*, **36**, 1333–1345.
- Meinshausen, M., Meinshausen, H., Hare, W., Raper, S.B., Frieler, K., Knutti, R., Frame, D.J. & Allen, M.R. (2009) Greenhouse gas emission targets for limiting global warming to 2°C. *Nature*, **458**, 1158–1163.
- Meneghel, M., Bondesan, A., Salvatore, M.C. & Orombelli, G. (1999) A model of the glacial retreat of Upper Rennick Glacier, Victoria Land, Antarctica. *Annals of Glaciology*, **29**, 225–230.
- Miura, N. & Jones, S.D. (2010) Characterizing forest ecological structure using pulse types and heights of airborne laser scanning. *Remote Sensing of Environment*, **114**, 1069–1076.
- Neilson, R.P. (1995) A model for predicting continental-scale vegetation distribution and water balance. *Ecological Applications*, **5**, 362–385.
- Nichol, J.E. (1999) Geomorphological evidence and Pleistocene refugia in Africa. *The Geographical Journal*, **165**, 79–89.
- Niklasson, M., Lindbladh, M. & Björkman, L. (2002) A long-term record of *Quercus* decline, logging and fires in a southern Swedish *Fagus–Picea* forest. *Journal of Vegetation Science*, **13**, 765–774.
- Nogués-Bravo, D. (2009) Predicting the past distribution of species climatic niches. *Global Ecology and Biogeography*, **18**, 521–531.
- Nordal, I. (1987) *Tabula rasa* after all? Botanical evidence for ice-free refugia in Scandinavia reviewed. *Journal of Biogeography*, **14**, 377–388.
- Noss, R.F. (2001) Beyond Kyoto: forest management in a time of rapid climate change. *Conservation Biology*, **15**, 578–590.
- Opgenoorth, L., Vendramin, G.G., Mao, K.S., Miehe, G., Miehe, S., Liepelt, S., Liu, J.-Q. & Ziegenhagen, B. (2010) Tree endurance on the Tibetan Plateau marks the world's highest known tree line of the Last Glacial Maximum. *New Phytologist*, **185**, 332–342.
- Osborne, P.L. (2000) *Tropical ecosystems and ecological concepts*. Cambridge University Press, Cambridge.
- Pepin, N.C. & Lundquist, J.D. (2008) Temperature trends at high elevations: patterns across the globe. *Geophysical Research Letters*, **35**, L14701, doi:10.1029/2008GL034026.
- Petit, R.J., Aguinagalde, I., de Beaulieu, J.-L., Bittkau, C., Brewer, S., Cheddadi, R., Ennos, R., Fineschi, S., Grivet, D., Lascoux, M., Mohanty, A., Müller-Starck, G., Demesure-Musch, B., Palmé, A., Martín, J.P., Rendell, S. & Vendramin, G.G. (2003) Glacial refugia: hotspots but not melting pots of genetic diversity. *Science*, **300**, 1563–1565.
- Pillon, Y., Munzinger, J., Amir, H., Hopkins, H.C.F. & Chase, M.W. (2009) Reticulate evolution on a mosaic of soils: diversification of the New Caledonian endemic genus *Codia* (Cunoniaceae). *Molecular Ecology*, **18**, 2263–2275.
- Quinn, J.F., Wing, S.R. & Botsford, L.W. (1993) Harvest refugia in marine fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *American Zoologist*, **33**, 537–550.
- Rocchini, D., Balkenhol, N., Carter, G.A., Foody, G.M., Gillespie, T.W., He, K., Kark, S., Levin, N., Lucas, K., Luoto, M., Nagendra, H., Oldeland, J., Ricotta, C., Southworth, J. & Neteler, M. (2010) Remotely sensed spectral heterogeneity as a proxy of species diversity: recent advances and open challenges. *Ecological Informatics*, **5**, 318–329.
- Rorison, I.H., Sutton, F. & Hunt, R. (1986) Local climate, topography and plant growth in Lathkill Dale NNR. I. A twelve-year summary of solar radiation and temperature. *Plant, Cell and Environment*, **9**, 49–56.
- Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T.L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S. & Imeson, A. (2008) Attributing physical and biological impacts of anthropogenic climate change. *Nature*, **453**, 353–357.
- Rull, V. (2009) Microrefugia. *Journal of Biogeography*, **36**, 481–484.
- Sebens, K.P. (1982) Competition for space: growth rate, reproductive output, and escape in size. *The American Naturalist*, **120**, 189–197.
- Soltis, D.E., Gitzendanner, M.A., Strenge, D.D. & Soltis, P.S. (1997) Chloroplast DNA intraspecific phylogeography of plants from the Pacific Northwest of North America. *Plant Systematics and Evolution*, **206**, 353–373.
- Soltis, D.E., Morris, A.B., McLachlan, J.S., Manos, P.S. & Soltis, P.S. (2006) Comparative phylogeography of unglaciated eastern North America. *Molecular Ecology*, **15**, 4261–4293.
- Stebbins, G.L. & Major, J. (1966) Endemism and speciation in the California flora. *Ecological Monographs*, **35**, 1–35.
- Steffen, W., Burbidge, A.A., Hughes, L., Kitching, R., Lindenmayer, D., Musgrave, W., Smith, M.S. & Werner, P.A. (2009) *Australia's biodiversity and climate change*. CSIRO Publishing, Collingwood, ON.
- Steig, E.J., Wolfe, A.P. & Miller, G.H. (1998) Wisconsinan refugia and the glacial history of eastern Baffin Island, Arctic Canada: coupled evidence from cosmogenic isotopes and lake sediments. *Geology*, **26**, 835–838.
- Stephenson, N.L. (1990) Climatic control of vegetation distribution: the role of the water balance. *The American Naturalist*, **135**, 649–670.
- Stott, P.A., Gillett, N.P., Hegerl, G.C., Karoly, D.J., Stone, D.A., Zhang, X. & Zwiers, F. (2010) Detection and attribution of

- climate change: a regional perspective. *Wiley Interdisciplinary Reviews: Climate Change*, **1**, 192–211.
- Svenning, J.-C. & Skov, F. (2007) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters*, **10**, 453–460.
- Taberlet, P. & Cheddadi, R. (2002) Quaternary refugia and persistence of biodiversity. *Science*, **297**, 2009–2010.
- Taberlet, P., Fumagalli, L., Wust-Saucy, A.G. & Cosson, J.F. (1998) Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology*, **7**, 453–464.
- Thompson, R.S. & Anderson, K.H. (2000) Biomes of western North America at 18,000, 6000 and 0 <sup>14</sup>C yr BP reconstructed from pollen and packrat midden data. *Journal of Biogeography*, **27**, 555–584.
- Traiser, C., Klotz, S., Uhl, D. & Mosbrugger, V. (2005) Environmental signals from leaves – a physiognomic analysis of European vegetation. *New Phytologist*, **166**, 465–484.
- Turner, M.G., Hargrove, W.W., Gardner, R.H. & Romme, W.H. (1994) Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science*, **5**, 731–742.
- Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M. & Preece, R.C. (2002) Buffered tree population changes in a Quaternary refugium: evolutionary implications. *Science*, **297**, 2044–2047.
- Verdú, M. & Pausas, J.G. (2007) Fire drives phylogenetic clustering in Mediterranean Basin woody plant communities. *Journal of Ecology*, **95**, 1316–1323.
- Virah-Sawmy, M., Gillson, L. & Willis, K.J. (2009) How does spatial heterogeneity influence resilience to climatic changes? Ecological dynamics in southeast Madagascar. *Ecological Monographs*, **79**, 557–574.
- Waltari, E., Hijmans, R.J., Perterson, A.T., Nyári, Á., Perkins, S.L. & Guralnick, R.P. (2007) Locating Pleistocene refugia: comparing phylogeographic and ecological niche model predictions. *PLoS ONE*, **2**, e563.
- Wardell-Johnson, G. & Roberts, J.D. (1993) Biogeographic barriers in a subdued landscape: the distribution of the *Geocrinia rosea* (Anura: Myobatrachidae) complex in south-western Australia. *Journal of Biogeography*, **20**, 95–108.
- Weiss, S.B., Murphy, D.D. & White, R.R. (1988) Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology*, **69**, 1486–1496.
- Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.
- Willis, K.J. & Bhagwat, S.A. (2009) Biodiversity and climate change. *Science*, **326**, 806–807.
- Willner, W., Di Pietro, R. & Bergmeier, E. (2009) Phylogeographical evidence for post-glacial dispersal limitation of European beech forest species. *Ecography*, **32**, 1011–1018.
- Wulder, M.A. & Franklin, S.E. (2007) *Understanding forest disturbance and spatial pattern remote sensing and GIS approaches*. CRC Press, Boca Raton, FL.
- Yates, C.J., Elith, J., Latimer, A.M., Le Maitre, D., Midgley, G.F., Schurr, F.M. & West, A.G. (2010) Projecting climate change impacts on species distributions in megadiverse South African Cape and Southwest Australian Floristic Regions: opportunities and challenges. *Austral Ecology*, **35**, 374–391.
- Yesson, C. & Culham, A. (2006) Phyloclimatic modeling: combining phylogenetics and bioclimatic modeling. *Systematic Biology*, **55**, 785–802.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Fig. S1.** The number of *Web of Science* publications containing refugia and refuges in the title, abstract or keywords in the disciplines of ecology, evolution and conservation.

**Appendix S1** Methods used in the literature search.

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## BIOSKETCH

The authors are part of the Climate Change Refugia Research Group (<http://refugia.curtin.edu.au/>), which is composed of scientists from various organizations and affiliated with the Curtin Institute for Biodiversity and Climate. Members share a concern about the potential impacts of impending climate change on the biodiversity of our planet and believe that some of the predicted extinctions can be prevented by identifying and protecting refugia. All authors contributed to the development of ideas and concepts. G.K. led the literature review and writing.

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