PROCEEDINGS OF THE ROYAL SOCIETY B | BIOLOGICAL SCIENCES

Refugia revisited: individualistic responses of species in space and time

John R. Stewart, Adrian M. Lister, Ian Barnes and Love Dalén

References	**This article cites 77 articles, 13 of which can be accessed free** http://rspb.royalsocietypublishing.org/content/277/1682/661.full.html#ref-list-1 **Article cited in:** http://rspb.royalsocietypublishing.org/content/277/1682/661.full.html#related-urls
Subject collections	Articles on similar topics can be found in the following collections ecology (1306 articles) evolution (1430 articles) molecular biology (121 articles)
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

Review

Refugia revisited: individualistic responses of species in space and time

John R. Stewart[1], Adrian M. Lister[1], Ian Barnes[2] and Love Dalén[2,*,†]

[1]*Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK*
[2]*School of Biological Sciences, Royal Holloway University of London, Egham, Surrey TW20 0EX, UK*

Climate change in the past has led to significant changes in species' distributions. However, how individual species respond to climate change depends largely on their adaptations and environmental tolerances. In the Quaternary, temperate-adapted taxa are in general confined to refugia during glacials while cold-adapted taxa are in refugia during interglacials. In the Northern Hemisphere, evidence appears to be mounting that in addition to traditional southern refugia for temperate species, cryptic refugia existed in the North during glacials. Equivalent cryptic southern refugia, to the south of the more conventional high-latitude polar refugia, exist in montane areas during periods of warm climate, such as the current interglacial. There is also a continental/oceanic longitudinal gradient, which should be included in a more complete consideration of the interaction between species ranges and climates. Overall, it seems clear that there is large variation in both the size of refugia and the duration during which species are confined to them. This has implications for the role of refugia in the evolution of species and their genetic diversity.

Keywords: cryptic refugia; Quaternary; climate change; speciation; geographical distribution

1. INTRODUCTION

It has long been recognized that the geographical ranges of species have expanded and contracted in a cyclical manner according to the climatic changes of the Quaternary (Darwin 1859, pp. 364–382; Hewitt 1996; Bennett & Provan 2008). The places where species persist during glaciations have generally been described as refugia. Isolation within such glacial refugia, and the timing and mode of expansion from them, have become topics of increasing importance in our understanding of evolutionary processes such as adaptation, speciation and extinction. Understanding how species have responded to past climate changes, and where they endured periods of adverse climates, also has relevance for models forecasting how current climate change may affect species. The subject of Quaternary refugia is therefore of interest to a variety of researchers including palaeoecologists, population geneticists and conservation biologists. Owing to the breadth of this array of interested scientists, however, there is confusion about the meaning of the refugium concept.

We propose here that Quaternary refugia should be defined as the geographical region or regions that a species inhabits during the period of a glacial/interglacial cycle that represents the species' maximum contraction in geographical range. This is a flexible definition that accommodates species that are adapted to different climatic conditions, while at the same time highlighting the idea that species in general respond to climatic changes independently of each other (Taberlet *et al.* 1998; Stewart 2008; see also the literature on vegetational change reviewed by Hewitt 1996). We nonetheless consider it useful to identify and discuss different categories of refugium, based both on general geographical location and whether the refugium is inhabited by a temperate or a cold-adapted species. The oceanic–continental gradient, with its corresponding variation in key parameters, will be considered in greater detail owing to its relevance to organisms of the last cold stage of the Pleistocene. Furthermore, we discuss the effects of differing refugial sizes and varying lengths of time during which populations are restricted to refugia. We also consider the degree to which different species have the same refugia and the fate of populations outside refugia during the contraction phase. Finally, the role of refugia in species evolution is discussed, with examples illustrating different possible scenarios. We have concentrated on the mid- to high-latitude Palaearctic as this area has a relatively well-documented history and has been the locus of pioneering studies on the biotic effects of glacial/interglacial cycles (e.g. Hewitt 1996, 1999, 2000), while recognizing that many analogous studies have been made in North America (Avise 2000; Swenson & Howard 2005).

2. PREVIOUS USE OF THE REFUGIUM CONCEPT

The glacial refugium hypothesis has dominated studies of ice age biogeography for some time (e.g. Holder *et al.* 1999). This concept sees the cold, glacial, phases of Earth's recent history as being the primary forcers of population divergence and, in some cases, speciation (Hewitt 1996). This emphasis on the cold phases comes partly from the origin of the refugium concept, which

* Author for correspondence (love.dalen@nrm.se).
† Present address: Molecular Systematics Laboratory, Swedish Museum of Natural History, 104 05 Stockholm, Sweden.

arose from a consideration of the contraction phase of vegetation during glacial stages (Bennett & Provan 2008). It has also led to a general assumption that many organisms are pushed southwards as the glaciated north becomes inhospitable to many life forms. In recent phylogeographic studies, different organisms have been shown to expand out of various European peninsulae and other southern refugia at the end of the last ice age (Taberlet *et al.* 1998; Hewitt 1999, 2000, 2004). This picture was, however, complicated by the suggestion that cryptic northern refugia had existed in the Late Pleistocene for some temperate organisms (Bilton *et al.* 1998; Willis *et al.* 2000; Stewart & Lister 2001; Stewart 2003). In addition, it has been argued that some, or most, peninsular populations were areas of endemism rather than refugia (Bilton *et al.* 1998; Stewart 2003; Bennett & Provan 2008; Bhagwat & Willis 2008; Provan & Bennett 2008).

Over recent years, the use of the glacial refugium concept has broadened, and has frequently been applied to cold-adapted species such as lemmings (Fedorov & Stenseth 2001, 2002), rock ptarmigan (*Lagopus muta*; Holder *et al.* 1999), mountain sheep (Loehr *et al.* 2005), mountain avens (*Dryas integrifolia*; Tremblay & Schoen 1999) and white spruce (*Picea glauca*; Anderson *et al.* 2006). The problem, in our view, with assigning glacial refugia to cold-adapted species is that they generally have a larger distribution during cold stages than during periods of warm climate (e.g. Stewart & Lister 2001; Dalén *et al.* 2005; Stewart & Dalén 2008). Although vicariance events may have resulted from the growth of ice sheets during cold stages, or rising sea levels during warm periods, such isolated populations can hardly be viewed as refugial, since the species would have had large distributions elsewhere (Musil 1985; Tyrberg 1991; Stewart *et al.* 2003, etc.). Instead, we argue that since the range of cold-adapted species is at its minimum during periods of warm climate, such species are in refugia during interglacials. Our refugial concept also excludes 'range shifts' that do not entail a significant contraction of area; population or genetic 'bottlenecks', which imply reduced population size and will often result from refugial contraction but do not entail it; populations left in isolation as the species range contracts but that rapidly extirpate as climate worsens; and species that permanently occupy a small range. We also do not treat an area *per se* as a refugium except insofar as it contains refugial populations of one or more species.

An important category of refugia are the cryptic refugia as defined by Stewart & Lister (2001). Cryptic refugia are refugia situated at different latitudes or longitudes than would normally be expected, and often resemble climatic islands in which conditions differ favourably from the surrounding areas. Rull (2009) has revived his concept of 'macrorefugia' and 'microrefugia' for larger and smaller refugial areas, subsuming cryptic refugia within microrefugia. However, his concept of microrefugia covers a broader range of phenomena, including widespread but low-density populations, and hypothesized large numbers of small, isolated populations, than we consider here; and his definition of microrefugia would include any area with a small, isolated population, whereas we limit the refugial concept to the contraction phase of a species' expansion–contraction cycle. Finally, although (as discussed below) cryptic refugia will often be smaller

than conventional refugia, small size is not integral to their definition.

Recently, the value of continuing to use the refugium concept has been challenged by Bennett & Provan (2008), who point out that there are many and complex ways in which species respond to climatic and environmental change, and that the refugial concept has lacked clear definition and has been used in confusingly different ways. While we agree with those points, we believe that the refugial concept, as we have defined and limited it, remains important for a variety of reasons. The cycle of expansion and contraction into refugia (as we define them) has a particular importance in species-level evolution, including its significance in determining the pattern of genetic variation in a species. Issues of refugium size are also important, both because they lead to testable predictions of the effects of refugial contraction across taxa and because of their relevance to extinction risk, both in the past and in the conservation biology of today. Finally, refugia remain important as the source populations from which species expand their ranges at the onset of more favourable conditions.

3. SPATIAL AND TEMPORAL CATEGORIES OF REFUGIA

The concept of refugium used here is the area occupied by an individual species, not the area occupied by a whole community of species as in some studies (e.g. Whittington-Jones *et al.* 2008). We propose to classify refugia first from a temporal perspective, where species can be broadly viewed as having either glacial or interglacial refugia. Second, we divide refugia into further categories based on their geographical location. The categories of refugia, therefore, include the traditional southern refugia and the equivalent polar refugia for cold-adapted species, as well as cryptic refugia to the north or south of the main areas into which populations contract (figure 1). This classification is reminiscent of that used by Thienemann (1950). We also introduce a new dimension, the continental/oceanic gradient, and discuss refugia for organisms adapted to these respective conditions.

Examples of each type of refugium are given below and are listed in table 1. It is acknowledged that for some species it may be difficult to determine whether they had larger or smaller ranges during glacials or interglacials. This would be particularly the case for taxa with broad ecological ranges (e.g. the wolf *Canis lupus*), and for species with meagre fossil records (e.g. many insects). It should also be noted that the definitions given here are for the Northern Hemisphere and that these would have their mirror image in the Southern Hemisphere.

(a) Glacial refugia
(i) Southern refugia
These are the traditionally accepted refugia for temperate species during glacial phases, which in general comprise the southern portion of the species' distribution during warm climatic phases such as the current interglacial. In Europe, southern refugia are generally located within the Iberian, Italian and Balkan peninsulas. The identification of these refugia was initially based on palaeoecological evidence (Huntley & Birks 1983; Bennett *et al.* 1991) and was later confirmed through
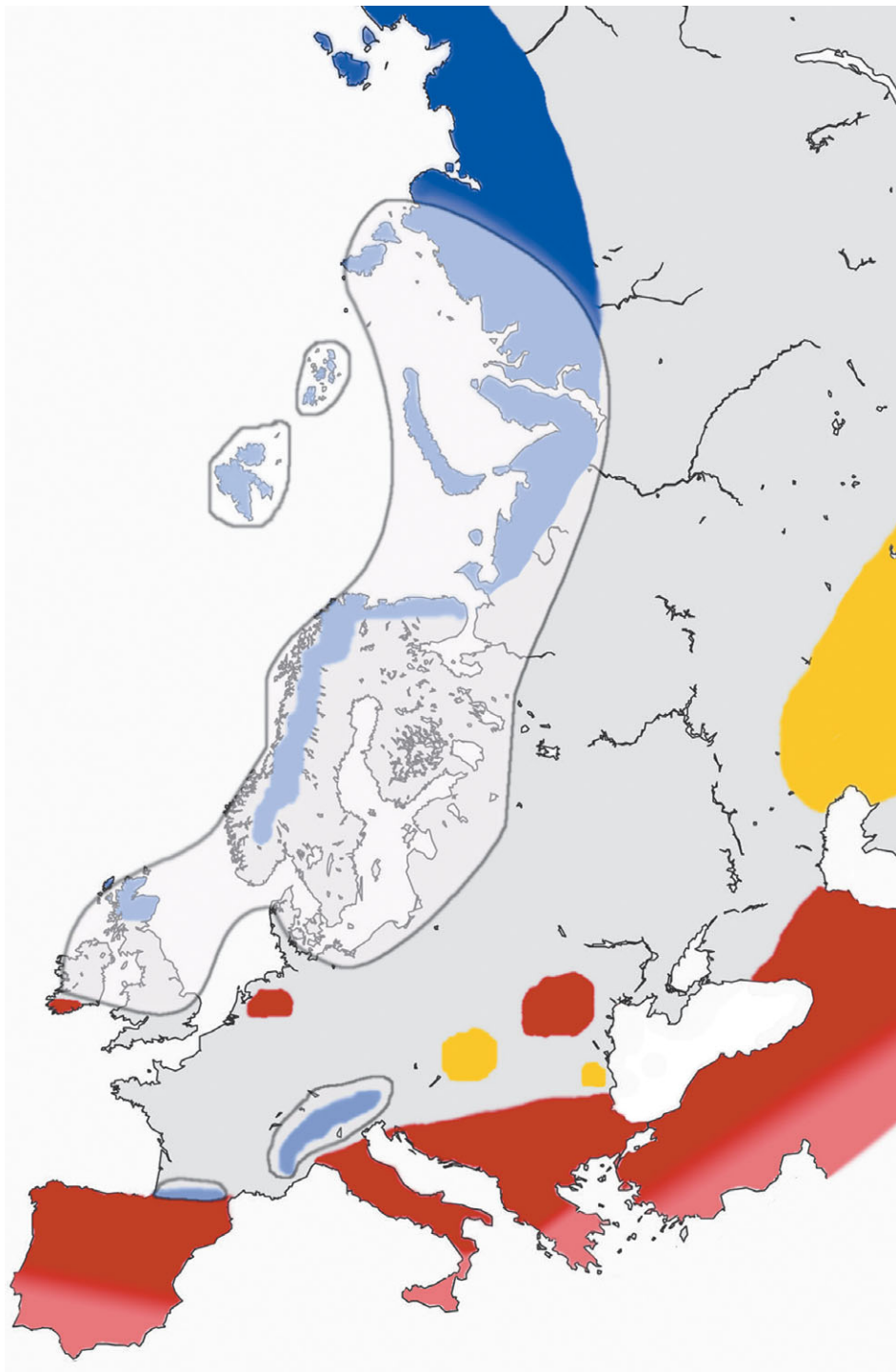
Figure 1. Schematic map showing some types of refugia for Europe and western Asia. Interglacial refugia for cold-adapted species are shown in blue, glacial refugia for temperate species in red. Long-term refugia, indicated by dark blue/red, are a subset of all refugia that are inhabited throughout at least one full glacial/interglacial cycle. The areas shown in paler colour are refugia in the sense that they are inhabited during the contraction phase, but are not inhabited during the expansion phase owing to the spread of ice sheets during glacials (cold-adapted species), or excessive temperatures and/or too high aridity during interglacials (temperate species). Also shown, in yellow, are interglacial refugia along the oceanic/continental gradient, with a continental refugium in the east and cryptic refugia further west. The ice sheet for the Last Glacial Maximum is taken from Ehlers & Gibbard (2004). The diagram is schematic; not all of the refugia would have been occupied simultaneously, but the ranges are based on real examples taken from table 1.

phylogeographic studies, which showed that many extant populations further north are derived from southern regions (Hewitt 1996, 1999, 2000). This pattern of glacial survival in the South, followed by post-glacial recolonization of northern regions, seems to be a general

pattern among a variety of temperate taxa, including plants, insects and vertebrates (Hewitt 2001). However, different species' expanded populations seem to be derived from different southern refugia, suggesting that species have responded individualistically to the increases

Table 1. Classification of refugia together with examples identified by phylogeographic and other studies.

refugium type	taxon	study
temperate taxa in glacials		
southern refugia	*U. arctos, Erinaceus* sp., *Chorthippus parallelus, Quercus* spp., *Arvicola* spp., *Crocidura suaveolens, Triturus* spp., *Apodemus sylvaticus*	Hewitt (1996, 1999, 2000), Taberlet *et al.* (1998).
cryptic northern refugia	*Clethrionomys glareolus, Sorex araneus, Microtus araneus, Asplenum ceterah, Carex digitata*	Wójcik *et al.* (2002), Trewick *et al.* (2002), Tyler (2002*a,b*), Jaarola & Searle (2003), Deffontaine *et al.* (2005) and Teacher *et al.* (2009).
cold taxa in interglacials (e.g. present day)		
polar refugia	*R. tarandus, A. lagopus, Dicrostonyx* spp., *Lagopus* spp.	Fedorov *et al.* (1999), Flagstad & Røed (2003), Dalén *et al.* (2005) and Stewart & Dalén (2008).
cryptic southern refugia	*L. muta, D. octopetala, B. nana, H. lapponicus*	Angus (1983) and Stewart & Lister (2001).
continental-adapted taxa in interglacials (e.g. present day)		
continental refugia	*Spermophilus* spp., *S. tatarica* and *Ochotona* spp.	no study but apparent from comparison between fossil record and modern distribution, e.g. Musil (1985).
cryptic refugia for continental-adapted taxa (in more oceanic areas)	*S. subtilis, H. rhamnoides.*	no study but apparent from fossil record and modern distribution, e.g. Macdonald & Barrett (1993) and Iversen (1973).

in habitat availability brought on by the climatic changes at the end of the last glaciation (Taberlet *et al.* 1998).

In the last decade, several studies have confirmed the existence of similar southern refugia in North America (e.g. Lacourse *et al.* 2005; Soltis *et al.* 2006), as well as analogous northern refugia in the Southern Hemisphere (Byrne 2008).

(ii) *Cryptic northern refugia*

Cryptic northern refugia are glacial refugia for temperate taxa situated at higher latitudes than the expected areas of suitable habitat to the South. The concept, as originally conceived by Stewart & Lister (2001) was applied to taxa that were not generally accepted as living in central or northern Europe during the last glaciation. However, the concept is in need of refinement as it has subsequently been applied to non-temperate taxa (e.g. Pruett & Winker 2005). In fact, the original inclusion of pine (*Pinus sylvestris*) living on the Norwegian coast during the last glaciation (Stewart & Lister 2001), was already stretching the definition of a cryptic northern refugium as this taxon is not strictly temperate and is relatively cold-tolerant.

The cryptic northern refugium hypothesis has received significant support since its publication, with phylogeographic studies finding evidence for northern refugia in various temperate organisms, including small mammals (Wójcik *et al.* 2002; Jaarola & Searle 2003; Deffontaine *et al.* 2005; Kotlik *et al.* 2006), ferns (Trewick *et al.* 2002), sedges (Tyler 2002*a,b*), snails (Haase & Bisenberger 2003; Pfenninger *et al.* 2003; Benke *et al.* 2009), freshwater fishes (Hänfling *et al.* 2002; Volckaert *et al.* 2002), amphibians (Teacher *et al.* 2009) and reptiles (Carlsson 2003). Further evidence in support of the hypothesis has come from the study of fossil pollen, plant macros including wood charcoal, and mammals (Birks 2003; Willis & van Andel 2004; Sommer & Nadachowski 2006; Caseldine *et al.* 2008).

(**b**) *Interglacial refugia*

(i) *Polar refugia*

Polar refugia are the high-latitude regions where cold-adapted species persist through interglacials. In the Northern Hemisphere, polar refugia are located in the northernmost parts of continental Eurasia and North America, as well as in several islands in the Arctic Ocean, for example Greenland, Svalbard, Wrangel Island and the New Siberian Islands.

During the last glaciation, many cold-adapted species had a larger distribution than they have today. Furthermore, several studies on cold-adapted species have identified genetic signatures of increase in population size during the early stages of the last glaciation, suggesting that these species had small population sizes also during the last interglacial (Fedorov *et al.* 1999; Flagstad & Røed 2003; Shapiro *et al.* 2004; Dalén *et al.* 2005). It therefore seems likely that glacial expansions and interglacial contractions were a recurrent pattern for cold-adapted species during the Late Quaternary. This supports the idea that cold-adapted species are in refugia during interglacials, and thus respond to climatic changes in the opposite way to temperate species. Several Arctic species are at present confined exclusively to polar refugia, for example Arctic fox (*Alopex lagopus*), lemmings (*Lemmus* spp. and *Dicrostonyx* spp.), reindeer (*Rangifer tarandus*) and muskox (*Ovibos moschatus*). The present ranges of some of these species are large, but they are still significantly reduced compared with their size during the last glaciation.

(ii) *Cryptic southern refugia*

Cryptic southern refugia are interglacial refugia for cold-adapted species situated at lower latitudes. Today, and presumably also during previous interglacials, these refugia accommodate relict populations of formerly widespread cold-adapted Pleistocene taxa such as mountain

avens *Dryas octopetala*, dwarf birch *Betula nana*, rock ptarmigan *Lagopus mutus*, Arctic hare *Lepus timidus* and the water beetle *Helophorus lapponicus* (Angus 1983). Although not 'cryptic' in the original sense (since their present ranges are well known), we nonetheless retain the term to emphasize the parallel to cryptic northern refugia. Refugial areas for these taxa generally have a montane topography such as the Alps and Pyrenees, although when situated at higher latitudes the altitude can be lower. The Scottish highlands are therefore included as a cryptic southern refugium for rock ptarmigan *L. mutus* and red/willow grouse *Lagopus lagopus*. Populations of cold-adapted species in cryptic southern refugia are often surrounded during interglacials by populations of temperate species that have expanded from their glacial refugia. Most of the species in these refugia also have disjunct distributions (polar refugia) to the north (e.g. rock ptarmigan, mountain avens, Arctic hare and *H. lapponicus*). Some, however, are only known in the southern montane refugia (e.g. ibex *Capra ibex* and chamois *Rupicapra rupicapra*) in southern Europe, although they were also found in more northerly rocky lowland areas, such as southern Belgium (Stewart *et al.* 2003), during the Late Pleistocene.

(c) The oceanic–continental gradient

One biogeographic dimension that is often ignored in discussions on species' response to the glacial/interglacial cycle is the oceanic–continental axis. 'Oceanic' adaptation implies more humid, less seasonably variable climate; 'continental' adaptation, drier climate with greater seasonal variation. This is often a longitudinal perspective as opposed to the latitudinal aspect of northern and southern refugia. We are unaware of any phylogeographic studies explicitly dealing with this perspective in detail. However, Eurasian mammal species such as the ground squirrel *Spermophilus* spp., saiga antelope *Saiga tatarica* and pika *Ochotona* spp. have more restricted continental distributions in the Palaearctic today, having had more extensive distributions, extending to the British Isles, during parts of the last glaciation (Musil 1985). In fact, it is this longitudinal gradient that explains the expansion of steppic species and their inclusion in the Late Pleistocene 'steppe–tundra' biome. We therefore propose that some species have continental interglacial refugia.

Based on the existence of cryptic northern refugia for temperate species and cryptic southern refugia for cold species, it seems possible that a similar phenomenon could exist along the longitudinal axis. For example, one could expect species currently in eastern continental refugia also to occur in cryptic refugia along the west of Eurasia today. Possible examples are the southern birch mouse (*Sicista subtilis*) in Hungary and Romania (Macdonald & Barrett 1993) and some of the halophytic plant species, such as sea buckthorn (*Hippophaë rhamnoides*), found along the Atlantic seaboard as well as in the Asiatic steppe (Iversen 1973). Identifying currently isolated populations as cryptic refugia requires care, however, as in some cases their separation or even existence may be the result of historical human impact on the landscape. In theory, one might speculate that

these refugia would have a counterpart in refugia, and cryptic refugia, for 'oceanic-adapted' species during glacials, since the extension of arid climates during the Late Pleistocene would have been as much of an impediment to some taxa as the cold itself. However, we know of no good example of a species that follows such a pattern. The hippopotamus *Hippopotamus amphibius*, for example, shows an oceanic distribution in the Palearctic during the last interglacial, in that it spread no further east than central Europe because of its intolerance of cold winters. Its range contraction during the last glaciation, however, was southward rather than westward, in this respect similar to other temperate species occupying southern refugia.

The longitudinal and traditional latitudinal gradients would thus work in tandem in defining the precise location of a species' refugium, depending on the species' ecology. This agrees with the expectation that species will respond individualistically, and not in concert, to climatic changes (Taberlet *et al.* 1998).

4. OTHER CATEGORIES OF REFUGIUM

The question arises whether some temperate species could be in refugia during warm periods such as interglacials, and cold-adapted species during cold periods. As discussed above, mere isolation is not enough to justify describing a population as refugial. Hence, populations of temperate species isolated on islands during interglacials, or of cold-adapted species isolated through glacial vicariance, for example along the coasts and on nunataks, would not alone constitute refugial populations, as long as total species range remained large. However, following the definition of a refugium proposed in this paper, some cold-adapted species may actually have a smaller distribution during parts of glacials compared with interglacials owing to the advance and retreat of glaciers and continental ice sheets. In periglacial areas, habitat restriction evidently contracted the ranges of even cold-adapted species into refugia during the maximally severe phases of glacial climate (e.g. woolly mammoths; Stuart *et al.* 2004).

Some cold-adapted species endemic to mountainous regions might constitute a further category. Montane species generally have larger ranges during glacials when they spread to lowland areas (Stewart *et al.* 2003). However, some alpine species may be explicitly adapted to a montane environment, and would thus not have expanded into the surrounding lowlands during glacials. Such alpine-adapted species could thus have larger distributions during interglacials owing the expansion of mountain glaciers during cold stages, and would instead have been confined to nunataks or peripheral refugia during glaciations (Holderegger & Thiel-Egenter 2008).

5. THE SIZE OF REFUGIA AND DURATION OF OCCUPATION

Cryptic refugia are generally expected to be smaller than the more traditional southern and polar refugia because they are peripheral and are surrounded by unsuitable habitats. Cryptic northern refugia may often comprise sheltered habitats located in deeply incised valleys that provided microclimates for temperate species, allowing them to survive at latitudes where they would normally

have perished (Stewart & Lister 2001). Nonetheless, recent work using back-casted species distribution models has suggested relatively widespread distributions for some small mammal species to the north of the traditional southern refugia during the Last Glacial Maximum (Fløjgaard *et al.* 2009).

Cryptic southern refugia are generally located in mountainous regions, where the high altitude provides cooler climates than the surrounding landscape, thus permitting the local survival of cold-adapted species at relatively low latitudes during interglacials. Most such refugia will be smaller than the regions comprising polar refugia, at least in the Northern Hemisphere, although this is not always clear-cut since high-altitude plateaus and mountain ranges can be quite large.

The Quaternary encompassed climatic cycles of differing amplitudes and durations. This affected the length of time temperate and cold-adapted species were confined to refugia, which in turn can be expected to have had important ecological and evolutionary consequences. One of the major features of the Quaternary is the long-term climatic cycling of the last 700 kyr. These cycles, with long glaciations lasting up to 100 kyr and shorter interglacials lasting 10–15 kyr, are thought to have been a major driving force for population divergence in temperate species (Hewitt 1996). However, embedded within these long-scale cycles are short-term climatic events that took place on a millennial scale. These include warm interstadials and particularly cold stadials during glacials, as well as cool episodes during interglacials. These were first documented through terrestrial pollen analyses and subsequently correlated with detailed marine records (Shackleton & Opdyke 1973; Tzedakis 1993). Since then, further complexity has been detected in the cold Heinrich events seen in marine sediments and the warm Dansgaard–Oeschger events (Greenland interstadials) identified in ice cores (Svensson *et al.* 2006).

The general expectation from the broad-scale pattern, with long glacials and shorter interglacials, is that temperate species spend much longer in refugia than cold-adapted species. The effect of the shorter millennial-scale fluctuations in climate is less clear, since these are difficult to identify with precision in the terrestrial record. However, it is probable that they also caused ecological disturbances and gave rise to shorter term episodes of refugial isolation and range expansions of temperate and cold-adapted species during stadials and interstadials. On the other hand, the duration of these fluctuations may in some cases have been so short that, even when climatically favourable, many species did not expand their range fully. For example, slow-moving temperate species in the Northern Hemisphere were probably not able to expand as far north during interstadials as expected, and vice versa for cold-adapted species during stadials.

From an evolutionary perspective, the most important refugial areas are geographical regions where a species has persisted throughout a series of full glacial/interglacial cycles (each 100–120 kyr in duration), since each full cycle will usually have included a species' maximum and minimum distributions. The locations that a species inhabits continuously for at least one full glacial/interglacial cycle can be viewed as constituting 'long-term refugia' (Stewart & Dalén 2008), and we expect

that they will tend to harbour the greatest level of genetic diversity within the species' range. However, it is important to note that not all refugia, as defined earlier, will constitute long-term refugia. For example, many Arctic regions that are inhabited by cold-adapted species during interglacials, and thus are refugia by our definition, are made uninhabitable during glacials by advancing ice sheets (see earlier). In the same way, some southern glacial refugia may become too hot or arid for a temperate species to persist there during interglacials. In the case of cryptic refugia, some may operate over several climatic cycles, others only for one. This will vary with the niche of the particular species and the geographical and climatic characteristics of the area that formed the refugium. Consequently, what we here define as long-term refugia will represent a subset of all refugia, and will include both polar and southern refugia, as well as some cryptic refugia.

The combination of refugial size and duration has implications for species persistence. The reason for this is that a population's ability to persist throughout a period of adverse climate (cold or warm depending on the species' ecology), without becoming extinct owing to demographic stochasticity or inbreeding (Lande 1988), depends on the putative refugium's carrying capacity as well as the duration of the climatic stage. The probability that a population will survive throughout a period of adverse climate is therefore inversely related to the duration of confinement, and positively related to the size of the potential refugium. This suggests that it could be possible to define a 'minimum refugium size' required for species persistence, which would be dependent on the climatic interval (100 kyr glaciations, 10–15 kyr interglacials or millennial-scale stadials/interstadials), as well as the space requirements of the species in question (figure 2). Some general predictions arise from this concept, particularly for animals. First, one would expect cryptic refugia, owing to their relatively small size, to be less common for large-bodied species since the carrying capacity is generally lower for such species. Second, species with a large body size would be less likely to persist in cryptic northern refugia compared with those in cryptic southern refugia, since glaciations are normally an order of magnitude longer than interglacials. Third, one would expect a trophic effect, where species with a high trophic level (e.g. carnivores), regardless of their body size, would be less likely to survive through 'adverse' climatic periods in small patches of suitable habitat (figure 2), because of low population size and limited food base, a concept familiar from island biogeography (MacArthur & Wilson 1967).

6. THE ROLE OF SPECIES INDEPENDENCE AND THE CONGRUENCE OF REFUGIA

Recently, the individualistic (or independent) response of species to climate change over several glacial cycles has been discussed (Stewart 2008). This independence has implications for the congruence of refugia for different species. Clearly, refugia will often be congruent owing to their similar climatic and environmental requirements, rather than any species-specific interdependence. Congruence can also occur when species have similar discontinuous ranges resulting from different histories
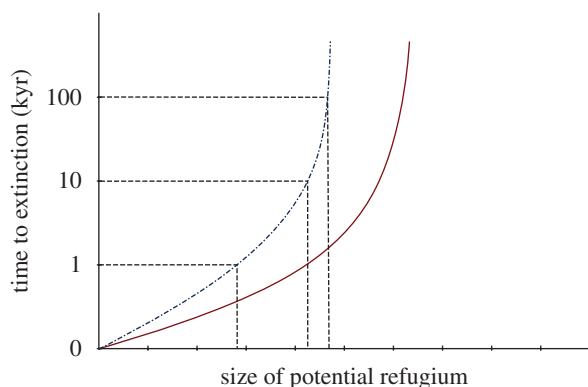
Figure 2. Conceptual figure showing the relationship between size of a potential refugium and time to extinction of the population (caused by demographic or genetic stochasticity). Each line represents a range of areas occupied by populations of a given species. The time required for population extirpation is dependent on the size of the habitat patch, and the horizontal dashed lines indicate the minimum viable refugium size, i.e. the relative sizes required to survive millennial-scale events, 10 kyr interglacials and 100 kyr glaciations. The slope of the curve depends on several factors such as body size, generation length and, as illustrated here, trophic level. Dash-dotted curve, trophic level 0; solid curve, trophic level 1.

(Soltis *et al.* 2006). Coevolved relationships may lead to stronger congruence of distributional history, for example between some insects and their food plants, or parasites and their hosts. In many cases, however, species are believed not to be highly interdependent. This suggests, for instance, that the existence of trees need not be accompanied by the herbivores often associated with them. A small stand of deciduous trees in the north of Europe during a glacial is unlikely to be accompanied by the whole ecosystem associated with a deciduous forest biome in the area today. However, if it is associated with some species, it needs to satisfy their habitat tolerances as well as being large enough, with an adequate carrying capacity for the species. This variation in community composition, together with the geographically isolated nature of cryptic refugia, again recalls island biogeography and can be expected to promote ecologically adaptive evolution (Hewitt 1996, 1999; Stewart 2008).

7. THE FATE OF POPULATIONS OUTSIDE REFUGIA

There is an outstanding question about the fate of populations outside refugia when climatic changes lead to refugial confinement. Bennett *et al.* (1991) used data from the pollen record to show that many tree populations in northern Europe became extinct at the onset of the last glaciation. Correspondingly, a recent study by Dalén *et al.* (2007) showed that southern populations of the Arctic fox (*A. lagopus*) did not contribute genetically to present-day populations when temperatures increased at the end of the last glaciation. The results from these studies suggest that expanded populations become extinct instead of tracking retreating habitats by physically moving into the refugium

(Hewitt 1993, 1996; Lister 1997; Stewart *et al.* 2003; Dalén *et al.* 2007). This implies that populations in long-term refugia are descended from individuals that are already in place during the expansion phase, and consequently that populations outside refugia make little or no contribution to the long-term evolution of the species. It should, however, be noted that the fate of extra-refugial populations has only been investigated in a limited number of taxa (Bennett *et al.* 1991; Dalén *et al.* 2007), and thus would benefit from further study. Nonetheless, we note that rarity of habitat tracking has the potential to explain the high degree of population turnover described in several recent ancient DNA studies (Barnes *et al.* 2002; Hofreiter *et al.* 2007; Leonard *et al.* 2007). It also limits the value of phylogeographic studies of taxa currently in refugia (i.e. Arctic taxa). This is because it is not possible to analyse the previously expanded populations without using ancient DNA. A failure to take account of recently extirpated populations may lead to erroneous conclusions.

The ultimate fate of a species in a contraction phase may be complete extinction, and because species' ranges tend to contract in the direction of their refugia, the long-term refugial areas will often be the eventual location of the terminal populations (von Koenigswald 1999; Lister & Stuart 2008).

8. EVOLUTION AND SPECIATION

It is clear that refugial phases are times when populations will be in isolation and hence more prone to evolutionary divergence. As discussed earlier, different types of refugia have different characteristics that lend themselves to hypotheses of population differentiation and even speciation. These factors will be discussed in turn.

The first factor to consider is that glacials—considered broadly as even-numbered marine oxygen isotopic stages—are longer than interglacials, so that cold-adapted and temperate species have been restricted to refugia for different lengths of time. In addition, polar refugia, being situated near the poles, will tend to be geographically much closer together compared with southern refugia. These two factors lead to an expectation of less population divergence between populations in polar refugia than those in southern refugia, in turn suggesting that the opportunity for population differentiation is greater in temperate species.

The question then arises whether refugial isolation can lead to speciation. Lister (2004) concluded that several hundred thousand years of isolation are normally required for speciation to occur among mammals, although exceptions exist in other groups (e.g. cichlid fishes; Johnson *et al.* 1996). This implies that refugial isolation during one glacial cycle would often be insufficient for speciation to take place. However, it is tempting to speculate that isolation in cryptic refugia could occasionally lead to this kind of rapid evolution, as these populations fulfil several of the requirements for allopatric speciation (Mayr 1954; Eldredge & Gould 1972), particularly 'ecological' speciation under strong adaptive selection (Hendry *et al.* 2007; Nosil *et al.* 2009). First, populations in glacial cryptic northern and interglacial cryptic southern refugia, occupying 'pockets' of suitable habitat in otherwise unfavourable regions, are likely often to be smaller than

their counterparts in southern/polar refugia. Second, it is likely that the populations in these cryptic refugia are subjected to different selective pressures than the populations inhabiting the more traditional refugia, especially when the refugial isolation is accompanied by a change in climate. Third, extinction of predators and competitors owing to environmental change and small patch size could change community structure and thus alter the species' realized niche and hence the selective pressures on species—the 'New Neighbour' hypothesis of Hewitt (1996, 2000, 2001) and (Stewart 2008, in press). These processes could lead to rapid adaptive divergence and, if reproductive isolation were underway before refugial populations expanded and met on climatic amelioration, constitute the first steps towards speciation.

The potential for speciation would be higher for populations in cryptic northern refugia during the longer glacials than for cryptic southern refugial populations during the shorter interglacials. It is therefore interesting to consider the role of cryptic northern refugia for the evolution of Arctic species, such as polar bear from brown bear and the Arctic fox from swift fox. The phylogenetic evidence clearly shows that the polar bear (*Ursus maritimus*) evolved from the brown bear (*Ursus arctos*) and that this probably happened within the last 200–300 kyr (Talbot & Shields 1996; Ho *et al.* 2008). For the polar bear to have evolved its unique adaptations, a brown bear population must have become exposed to northern climates and oceanic habitats. We suggest that such a population is likely to have lived in a cryptic northern refugium as this would have provided an opportunity for allopatric speciation in isolation from other brown bears. Similarly, the origin of the Arctic fox (*A. lagopus*) from the temperate swift fox (*Vulpes velox*) is thought to have happened at approximately the same time as (Geffen *et al.* 1992), or slightly earlier than (Sher 1986), the polar bear evolved from the brown bear.

Similar evolution is presumably ongoing in the cryptic southern refugia of the Alps and Pyrenees today where, for example, distinct subspecies of rock ptarmigan have evolved (*L. m. helvetica* and *L. m. pyrenaicus*). It is less likely, however, that temperate species (rather than just subspecies) have evolved from arctic ancestors in cryptic southern refugia, both because interglacials are shorter than glacials and because there is greater niche occupancy in the species-rich, long-held temperate regions compared with the relatively recently originated arctic zone.

Another speciation scenario that has been invoked is the differentiation within temperate species while in different southern refugia (Hewitt 1996; Lister 2004). Quaternary glacial cycles are believed to have promoted population divergence, and sometimes even speciation, among populations in the Mediterranean peninsulae, for example, although this seems to have required isolation on time scales exceeding a single glaciation (Hewitt 1996). Such isolation between southern refugia, despite mixing of lineages further north during interglacials, is thought to have been made possible by a lack of habitat tracking at the onset of glaciations (Hewitt 1999). It has also been pointed out that many species never expanded from their southern ranges, which allowed for long-term isolation between populations (Bilton *et al.* 1998), although by our definition these are not refugia. Speciation among populations in southern refugia might generally be slower than in cryptic northern refugia, as their population sizes are likely to be larger because of the broader geographical area, which could have a tempering effect on the rate of adaptive divergence (Mayr 1954). The importance of small population size in evolution is, however, a topic of debate (Barton & Charlesworth 1984; Coyne & Orr 2004). Furthermore, since different southern refugia lie on approximately the same latitude, their populations may have been subject to similar selection pressures, especially given the additional buffering effect provided by the complex topography of many southern refugia (Tzedakis *et al.* 2002).

9. CONCLUSION

The subject of refugia is relevant to many areas of ecology and evolutionary biology. Furthermore, the individualistic nature of species' responses to climate change implies that the location of refugia varies according to the climate as well as to the adaptations of individual species or populations. We therefore suggest that, in general, refugia can be classified as either glacial or interglacial refugia. Glacial southern refugia are the traditional low-latitude refugia for temperate taxa best known from the work of Hewitt (1996, 1999, 2000), whereas interglacial polar refugia harbour cold-adapted taxa at high latitudes during warm periods, such as the interglacial we are in today. However, owing to the complex structure of environments and habitats across space, it is also proposed that cryptic northern refugia exist during glacials and equivalent cryptic southern refugia during interglacials. The existence of the former has had increasing support from phylogeographic (including ancient DNA) studies of a wide range of organisms, while cryptic southern refugia can be seen in areas such as the Alps today. An additional dimension is the oceanic/continental gradient, with continental-adapted taxa in refugia during interglacials.

In general, cryptic refugia are smaller in size than southern glacial or polar interglacial refugia. Furthermore, the length of time during which organisms are isolated in refugia differs between cold and temperate taxa, since glacials are longer than interglacials. This disparity among different types of refugia, as well as the individualistic nature of species' responses to climate change, has several evolutionary implications. For example, individualism may lead to new ecological associations and interactions, which in themselves can impose novel selective pressures on populations (Hewitt 1996, 2000, 2001), Stewart (in press). Also, populations inhabiting small refugia, such as populations of temperate species in cryptic northern refugia, are more likely to become extinct. Such populations would not then act as sources of expansion on climatic amelioration (Sommer & Zachos in press). Paradoxically, however, long-term isolation of small populations can lead to rapid population divergence. Combined with the novel selection pressures in peripheral refugia, this could potentially lead to speciation. We therefore propose that isolation of temperate species in cryptic northern refugia may have played an important role in the origin of Arctic species.

REFERENCES

Anderson, L. L., Sheng Hu, F., Nelson, D. M., Petit, R. J. & Paige, K. N. 2006 Ice-age endurance: DNA evidence of a white spruce refugium in Alaska. *Proc. Natl Acad. Sci. USA* **13**, 12 447–12 450. (doi:10.1073/pnas.0605310103)

Angus, R. B. 1983 Evolutionary stability since the Pleistocene illustrated by reproductive compatibility between Swedish and Spanish *Helophorus lapponicus* Thomson (Coleoptera, Hydrophilidae). *Biol. J. Linn. Soc.* **19**, 17–25. (doi:10.1111/j.1095-8312.1983.tb00773.x)

Avise, J. C. 2000 *Phylogeography: the history and formation of species.* Cambridge, MA: Harvard University Press.

Barnes, I., Matheus, P., Shapiro, B., Jensen, D. & Cooper, A. 2002 Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science* **295**, 2267–2270. (doi:10.1126/science.1067814)

Barton, N. H. & Charlesworth, B. 1984 Genetic revolutions, founder effects, and speciation. *Annu. Rev. Ecol. Syst.* **15**, 133–164. (doi:10.1146/annurev.es.15.110184.001025)

Benke, M., Brändle, M., Albrecht, C. & Wilke, T. 2009 Pleistocene phylogeography and phylogenetic concordance in cold-adapted spring snails (*Bythinella* spp.). *Mol. Ecol.* **18**, 890–903. (doi:10.1111/j.1365-294X.2008.04073.x)

Bennett, K. D. & Provan, J. 2008 What do we mean by 'refugia'? *Quat. Sci. Rev.* **27**, 2449–2455. (doi:10.1016/j.quascirev.2008.08.019)

Bennett, K. D., Tzedakis, P. C. & Willis, K. J. 1991 Quaternary refugia of north European trees. *J. Biogeogr.* **18**, 103–115. (doi:10.2307/2845248)

Bhagwat, S. A. & Willis, K. J. 2008 Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? *J. Biogeogr.* **35**, 464–482. (doi:10.1111/j.1365–2699.2007.01861.x)

Bilton, D. T., Mirol, P. M., Mascheretti, S., Fredga, K., Zima, J. & Searle, J. B. 1998 Mediterranean Europe as an area of endemism for small mammals rather than a source for northwards postglacial colonization. *Proc. R. Soc. Lond. B* **265**, 1219–1226. (doi:10.1098/rspb.1998.0423)

Birks, H. H. 2003 The importance of plant macrofossils in the reconstruction of Lateglacial vegetation and climate: examples from Scotland, western Norway and Minnesota, USA. *Quat. Sci. Rev.* **22**, 453–473. (doi:10.1016/S0277-3791(02)00248-2)

Byrne, M. 2008 Evidence for the multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography. *Quat. Sci. Rev.* **27**, 2576–2585. (doi:10.1016/j.quascirev.2008.08.032)

Carlsson, M. 2003 Phylogeography of the adder, *Vipera berus*. In Comprehensive Summaries of Uppsala Dissertations from the Faculty of Sciences and Technology 849. Uppsala, Sweden: Acta Universitatis Upsaliensis.

Caseldine, C. J., McGarry, S. N. F., Baker, A., Hawksworth, C. & Smart, P. L. 2008 Late Quaternary speleothem pollen in the British Isles. *J. Quat. Sci.* **23**, 193–200. (doi:10.1002/jqs.1121)

Coyne, J. A. & Orr, H. A. 2004 *Speciation.* Sunderland, MA: Sinauer Associates.

Dalén, L., Fuglei, E., Hersteinsson, P., Kapel, C. M. O., Roth, J. D., Samelius, G., Tannerfeld, M. & Angerbjörn, A. 2005 Population history and genetic structure of a circumpolar species: the Arctic fox. *Biol. J. Linn. Soc.* **84**, 79–89. (doi:10.1111/j.1095-8312.2005.00415.x)

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. *Proc. Natl Acad. Sci. USA* **104**, 6726–6729. (doi:10.1073/pnas.0701341104)

Darwin, C. R. 1859 *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*, 1st edn. London, UK: John Murray.

Deffontaine, V., Libois, R., Kotlík, P., Sommer, R., Nieberding, C., Pradis, E., Searle, J. B. & Michaux, J. R. 2005 Beyond the Mediterranean peninsulas: evidence of central European glacial refugia for temperate forest mammal species, the bank vole (*Clethrionomys glareolus*). *Mol. Ecol.* **14**, 1727–1739. (doi:10.1111/j.1365-294X.2005.02506.x)

Ehlers, J. & Gibbard, P. 2004 *Quaternary glaciations—extent and chronology.* London, UK: Elsevier.

Eldredge, N. & Gould, S. J. 1972 Punctuated equilibria: an alternative to phyletic gradualism. In *Models in paleobiology* (ed. T. J. M. Schopf), pp. 82–115. New York, NY: Freeman, Cooper & Co.

Fedorov, V. B. & Stenseth, N. C. 2001 Glacial survival of the Norwegian lemming (*Lemmus lemmus*) in Scandinavia: inference from mitochondrial DNA variation. *Proc. R. Soc. Lond. B* **268**, 809–814. (doi:10.1098/rspb.2001.1584)

Fedorov, V. B. & Stenseth, N. C. 2002 Multiple glacial refugia in the North American Arctic: inference from phylogeography of the collared lemming (*Dicrostonyx groenlandicus*). *Proc. R. Soc. Lond. B* **269**, 2071–2077. (doi:10.1098/rspb.2002.2126)

Fedorov, V. B., Fredga, K. & Jarrell, G. H. 1999 Mitochondrial DNA variation and the evolutionary history of chromosome races of collared lemmings (*Dicrostonyx*) in the Eurasian Arctic. *J. Evol. Biol.* **12**, 134–145. (doi:10.1046/j.1420-9101.1999.00017.x)

Flagstad, Ø. & Røed, K. H. 2003 Refugial origins of reindeer (*Rangifer tarandus* L.) inferred from mitochondrial DNA sequences. *Evolution* **57**, 658–670. (doi:10.1554/0014-3820(2003)057[0658:ROORRT]2.0.CO;2)

Fløjgaard, C., Normand, S., Skov, F. & Svenning, C. 2009 Ice age distributions of European small mammals: insights from species distribution modelling. *J. Biogeogr.* **36**, 1152–1163. (doi:10.1111/j.1365-2699.2009.02089.x)

Geffen, E., Mercure, A., Girman, D. J., Macdonald, D. W. & Wayne, R. K. 1992 Phylogenetic relationships of the fox-like canids: mitochondrial DNA restriction fragment, site and cytochrome *b* sequence analyses. *J. Zool.* **228**, 27–39. (doi:10.1111/j.1469-7998.1992.tb04430.x)

Haase, M. & Bisenberger, A. 2003 Allozymic differentiation in the land snail *Arianta arbustorum* (Stylommatophora, Helicidae): historical inferences. *J. Zool. Syst. Evol. Res.* **41**, 175–185. (doi:10.1046/j.1439-0469.2003.00208.x)

Hänfling, B., Hellemans, B., Volckaert, F. A. M. & Carvallho, G. R. 2002 Late glacial history of the cold-adapted freshwater fish *Cottus gobio*, revealed by microsatellites. *Mol. Ecol.* **11**, 1717–1729. (doi:10.1046/j.1365-294X.2002.01563.x)

Hendry, A. P., Nosil, P. & Rieseberg, L. H. 2007 The speed of ecological speciation. *Funct. Ecol.* **21**, 455–464. (doi:10.1111/j.1365-2435.2006.01240.x)

Hewitt, G. 1993 Postglacial distribution and species substructure: lessons from pollen, insects and hybrid zones. In *Evolutionary patterns and processes* (eds D. R. Lees & D. Edwards), pp. 97–123. London, UK: Academic Press.

Hewitt, G. 1996 Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linn. Soc.* **58**, 247–276. (doi:10.1111/j.1095–8312.1996.tb01434.x)

Hewitt, G. 1999 Post-glacial recolonisation of European biota. *Biol. J. Linn. Soc.* **68**, 87–112. (doi:10.1111/j.1095-8312.1999.tb01160.x)

Hewitt, G. 2000 The genetic legacy of the Quaternary ice ages. *Nature* **405**, 907–913. (doi:10.1038/35016000)

Hewitt, G. M. 2001 Speciation, hybrid zones and phylogeography—or seeing genes in space and time. *Mol. Ecol.* **10**, 537–549. (doi:10.1111/j.1365–294X.2001.01202.x)

Hewitt, G. M. 2004 Genetic consequences of climatic oscillations in the Quaternary. *Phil. Trans. R. Soc. Lond. B* **359**, 183–195. (doi:10.1098/rstb.2003.1388)

Ho, S. Y. W., Saarma, U., Barnet, R., Haile, J. & Shapiro, B. 2008 The effect of inappropriate calibration: three case studies in molecular ecology. *PLoS One* **3**, e1615. (doi:10.1371/journal.pone.0001615)

Hofreiter, M., Münzel, S., Conard, N. J., Pollack, J., Slatkin, M., Weiss, G. & Pääbo, S. 2007 Sudden replacement of cave bear mitochondrial DNA in the Late Pleistocene. *Curr. Biol.* **17**, R122–R123. (doi:10.1016/j.cub.2007.01.026)

Holder, K., Montgomerie, R. & Friesen, V. L. 1999 A test of the glacial refugium hypothesis using patterns of mitochondrial and nuclear DNA variation in rock ptarmigan (*Lagopus mutus*). *Evolution* **53**, 1936–1950. (doi:10.2307/2640452)

Holderegger, R. & Thiel-Egenter, C. 2008 A discussion of different types of glacial refugia used in mountain biogeography and phylogeography. *J. Biogeogr.* **36**, 476–480. (doi:10.1111/j.1365-2699.2008.02027.x)

Huntley, B. & Birks, H. J. B. 1983 *An atlas of past and present pollen maps of Europe, 0–13,000 years ago.* Cambridge, UK: Cambridge University Press.

Iversen, J. 1973 *The development of Denmark's nature since the last glacial.* Danm. Geol. Unders. V **7C**, 1–126.

Jaarola, M. & Searle, J. B. 2003 Phylogeography of field voles (*Microtus agrestis*) in Eurasia inferred from mitochondrial DNA sequences. *Mol. Ecol.* **11**, 2613–2621. (doi:10.1046/j.1365–294X.2002.01639.x)

Johnson, T. C., Scholz, C. A., Talbot, M. R., Kelts, K., Ricketts, R. D., Gideon, N., Beuning, K., Ssemmanda, I. & McGill, J. W. 1996 Late Pleistocene desiccation of Lake Victoria and rapid evolution of cichlid fishes. *Science* **273**, 1091–1093. (doi:10.1126/science.273.5278.1091)

Kotlik, P., Deffontaine, V., Mascheretti, S., Zima, J., Michaux, J. R. & Searle, J. B. 2006 A northern glacial refugium for bank voles (*Clethrionomys glareolus*). *Proc. Natl Acad. Sci. USA* **103**, 14 860–14 864. (doi:10.1073/pnas.0603237103)

Lacourse, T., Mathewes, R. W. & Fedje, D. W. 2005 Late-glacial vegetation dynamics of the Queen Charlotte Islands and adjacent continental shelf, British Columbia, Canada. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **226**, 36–57. (doi:10.1016/j.palaeo.2005.05.003)

Lande, R. 1988 Genetics and demography in biological conservation. *Science* **241**, 1455–1460. (doi:10.1126/science.3420403)

Leonard, J. A., Vilá, C., Fox-Dobbs, K., Koch, P. L., Wayne, R. K. & Van Valkenberg, B. 2007 Megafaunal extinctions and the disappearance of a specialized wolf ecomorph. *Curr. Biol.* **17**, 1146–1150. (doi:10.1016/j.cub.2007.05.072)

Lister, A. M. 1997 The evolutionary response of vertebrates to Quaternary environmental change. In *Past and future rapid environmental changes: the spatial and evolutionary responses of terrestrial biota* (eds B. Huntley, W. Cramer, A. V. Morgan, H. C. Prentice & J. R. M. Allen), pp. 287–302. NATO ASI Series I, no. 47. Berlin, Germany: Springer.

Lister, A. M. 2004 The impact of Quaternary Ice Ages on mammalian evolution. *Phil. Trans. R. Soc. Lond. B* **359**, 221–241. (doi:10.1098/rstb.2003.1436)

Lister, A. M. & Stuart, A. J. 2008 The impact of climate change on large mammal distribution and extinction: evidence from the last glacial/interglacial transition. *C. R. Geosci.* **340**, 615–620. (doi:10.1016/j.crte.2008.04.001)

Loehr, J., Worley, K., Grapputo, A., Carey, J., Veitch, A. & Coltman, D. W. 2005 Evidence for cryptic glacial refugia from North American mountain sheep mitochondrial DNA. *J. Evol. Biol.* **19**, 419–430. (doi:10.1111/j.1420-9101.2005.01027.x)

MacArthur, R. H. & Wilson, E. O. 1967 *The Theory of island biogeography.* Princeton, NJ: Princeton University Press.

Macdonald, D. & Barrett, P. 1993 *Mammals of Britain and Europe.* London, UK: Harper Collins Publishers.

Mayr, E. 1954 Change of genetic environment and evolution. In *Evolution as a process* (eds J. Huxley, A. C. Hardy & E. B. Ford), pp. 157–180. London, UK: Allen & Unwin.

Musil, R. 1985 Paleobiogeography of terrestrial communities in Europe during the Last Glacial. *Acta Musei Nationalis Pragae* **XLI B**, pp. 1–2, 1–83.

Nosil, P., Harmon, L. J. & Seehausen, O. 2009 Ecological explanations for (incomplete) speciation. *Trends Ecol. Evol.* **24**, 145–156. (doi:10.1016/j.tree.2008.10.011)

Pfenninger, M., Posada, D. & Magnin, F. 2003 Evidence for the survival of the Pleistocene climatic change in Northern refugia by the land snail *Trochoidea geyeri* (Soós 1926) (Helicellinae, Stylommatophora. *BMC Evol. Biol.* **3**, 8. (doi:10.1186/1471-2148-3-8)

Provan, J. & Bennett, K. D. 2008 Phylogeographic insights into cryptic glacial refugia. *Trends Ecol. Evol.* **23**, 564–571. (doi:10.1016/j.tree.2008.06.010)

Pruett, C. L. & Winker, K. 2005 Biological impacts of climatic change on a Beringian endemic: cryptic refugia in the establishment and differentiation of the rock sandpiper (*Calidris ptilocnemis*). *Clim. Change* **68**, 219–240. (doi:10.1007/s10584-005-158-4)

Rull, V. 2009 Microrefugia. *J. Biogeogr.* **36**, 481–484. (doi:10.1111/j.1365–2699.2008.02023.x)

Shackleton, N. J. & Opdyke, N. D. 1973 Oxygen isotope and palaeomagnetic stratigraphy of Equatorial Pacific core V28–238: Oxygen isotope temperatures and ice volumes on a 10^5 year and 10^6 year scale. *Quat. Res.* **3**, 39–55. (doi:10.1016/0033-5894(73)90052-5)

Shapiro, E. *et al.* 2004 Rise and fall of the Beringian steppe bison. *Science* **306**, 1561–1565. (doi:10.1126/science.1101074)

Sher, A. V. 1986 Olyorian land mammal age of northeastern Siberia. *Paleontogr. Ital.* **74**, 97–112.

Soltis, D. E., Morris, A. B., McLachlan, J. S., Manos, P. S. & Soltis, P. S. 2006 Comparative phylogeography of unglaciated eastern North America. *Mol. Ecol.* **15**, 4261–4293. (doi:10.1111/j.1365-294X.2006.03061.x)

Sommer, R. S. & Nadachowski, A. 2006 Glacial refugia of mammals in Europe: evidence from fossil records. *Mammal Rev.* **36**, 251–265. (doi:10.1111/j.1365-2907.2006.00093.x)

Sommer, R. S. & Zachos, F. E. 2009 Fossil evidence and phylogeography of temperate species: 'glacial refugia' and post-glacial recolonization. *J. Biogeog.* **36**, 2013–2020. (doi:10.1111/j.1365-2699.2009.02187.x)

Stewart, J. R. 2003 Comment on 'Buffered tree population changes in a Quaternary refugium: Evolutionary implications'. *Science* **299**, 825a. (doi:10.1126/science.1079388)

Stewart, J. R. 2008 The progressive effect of the individualistic response of species to Quaternary climate change: an analysis of British mammalian faunas. *Quat. Sci. Rev.* **27**, 2499–2508. (doi:10.1016/j.quascirev.2008.08.003)

Stewart, J. R. In press. The evolutionary consequence of the individualistic response to climate change. *J. Evol. Biol.*

Stewart, J. R. & Dalén, L. 2008 Is the glacial refugium concept relevant for northern species? A comment on Pruett and Winker 2005. *Clim. Change* **86**, 1–2. (doi:10.1007/s10584-007-9366-9)

Stewart, J. R. & Lister, A. M. 2001 Cryptic northern refugia and the origins of modern biota. *Trends Ecol. Evol.* **16**, 608–613. (doi:10.1016/S0169-5347(01)02338-2)

Stewart, J. R., van Kolfschoten, M., Markova, A. & Musil, R. 2003 The mammalian faunas of Europe during oxygen isotope stage three. In *Neanderthals and modern humans in the European landscape during the last glaciation, 60,000 to 20,000 years ago: archaeological results of the stage 3 project* (eds T. H. van Andel & S. W. Davies), pp. 103–129. McDonald Institute Monograph Series. Cambridge, MA: McDonald Institute.

Stuart, A. J., Kosintsev, P. A., Higham, T. F. G. & Lister, A. M. 2004 Pleistocene and Holocene extinction dynamics in giant deer and woolly mammoth. *Nature* **431**, 684–689. (doi:10.1038/nature02890)

Svensson, A. *et al.* 2006 The Greenland Ice Core Chronology 2005, 15–42 ka. Part 2: comparison to other records. *Quat. Sci. Rev.* **25**, 3258–3267. (doi:10.1016/j.quascirev.2006.08.003)

Swenson, G. & Howard, D. J. 2005 Clustering of contact zones, hybrid zones, and phylogeographic breaks in North America. *Am. Nat.* **166**, 581–591. (doi:10.1086/491688)

Taberlet, P., Fumagalli, L., Wust-Saucy, A. G. & Cosson, J. F. 1998 Comparative phylogeography and postglacial colonization routes in Europe. *Mol. Ecol.* **7**, 453–464. (doi:10.1046/j.1365-294x.1998.00289.x)

Talbot, S. L. & Shields, G. F. 1996 Phylogeography of brown bears (*Ursus arctos*) of Alaska and paraphyly within the Ursidae. *Mol. Phylogenet. Evol.* **5**, 477–494. (doi:10.1006/mpev.1996.0044)

Teacher, A. G. F., Garner, T. W. J. & Nichols, R. A. 2009 European phylogeography of the common frog (*Rana temporaria*): routes of postglacial colonization into the British Isles, and evidence for an Irish glacial refugium. *Heredity* **102**, 490–496. (doi:10.1038/hdy.2008.133)

Thienemann, A. 1950 *Verbreitungsgeschichte der Süsswassertierwelt Europas*. Die Binnengewässer. Band XVIII. Stuttgart, Germany: Schweizerbart'sche Verlagsbuchhandlung.

Tremblay, N. O. & Schoen, D. J. 1999 Molecular phylogeography of *Dryas integrifolia*: glacial refugia and postglacial recolonization. *Mol. Ecol.* **8**, 1187–1198. (doi:10.1046/j.1365-294x.1999.00680.x)

Trewick, S. A., Morgan-Richards, M., Russell, S. J., Henderson, S., Rumsey, F. J., Pínter, I., Barrett, J. A., Gibby, M. & Vogel, J. C. 2002 Polyploidy, phylogeography and Pleistocene refugia of rockfern *Asplenum ceterah*: evidence from chloroplast DNA. *Mol. Ecol.* **11**, 2003–2012. (doi:10.1046/j.1365-294X.2002.01583.x)

Tyler, T. 2002a Geographical distribution of allozyme variation in relation to post-glacial history in *Carex digitata*, a widespread European woodland sedge. *J. Biogeogr.* **29**, 919–930. (doi:10.1046/j.1365-2699.2002.00698.x)

Tyler, T. 2002b Large-scale geographic patterns of genetic variation in *Melica nutans*, a widespread Eurasian woodland grass. *Plant Syst. Evol.* **236**, 73–87. (doi:10.1007/s00606-002-0235-8)

Tyrberg, T. 1991 Arctic, montane and steppe birds as glacial relicts in West Palearctic. *Orn. Verh.* **25**, 29–49.

Tzedakis, P. C. 1993 Long-term tree populations in northwest Greece through multiple Quaternary climatic cycles. *Nature* **364**, 437–440. (doi:10.1038/364437a0)

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. (doi:10.1126/science.1073083)

Volckaert, F. A. M., Hänfling, B., Hellemann, B. & Carvalho, G. R. 2002 Timing of the population dynamics of bullhead *Cottus cottus* (Teleostei: Cottidae) during the Pleistocene. *J. Evol. Biol.* **15**, 930–944. (doi:10.1046/j.1420-9101.2002.00469.x)

von Koenigswald, W. 1999 Hat der Mensch das Aussterben der grossen pleistozanen Pflanzenfresser verursacht? *Kaupia* **9**, 193–201.

Whittington-Jones, G. M., Bernard, R. T. F. & Parker, D. M. 2008 Bushclumps as refugia for small mammals in two Eastern Cape conservation areas. *Afr. Zool.* **43**, 273–276. (doi:10.3377/1562-7020-43.2.273)

Willis, K. J. & van Andel, T. H. 2004 Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Quat. Sci. Rev.* **23**, 2369–2387. (doi:10.1016/j.quascirev.2004.06.002)

Willis, K. J., Rudner, E. & Sümegi, P. 2000 The full-glacial forests of central and southeastern Europe. *Quat. Res.* **53**, 203–213. (doi:10.1006/qres.1999.2119)

Wójcik, J. M., Ratkiewicz, M. & Searle, J. B. 2002 Evolution of the common shrew *Sorex araneus*: chromosomal and molecular aspects. *Acta Theriol.* **47**(Suppl. 1), 139–167.