# What do we mean by 'refugia'?

K.D. Bennett [a,*], J. Provan [b]

[a] School of Geography, Archaeology and Palaeoecology, Queen's University, 42 Fitzwilliam Street, Belfast BT7 1NN, UK
[b] School of Biological Sciences, Queen's University, Belfast BT7 1NN, UK

## ARTICLE INFO

## ABSTRACT

The term 'refugia' was originally used to describe the restricted full-glacial locations of modern mid- and high-latitude taxa, especially trees and shrubs. We discuss the extension of this original use to other situations, including its widening to encompass 'interglacial refugia'. Recent genetic work with modern populations suggests that, at the glacial–interglacial transition, those taxa that did vastly increase their ranges and abundances did so from a small subset of their full-glacial populations. We suggest that 'bottleneck' might be a more appropriate term to use for temporarily reduced populations, to indicate continuity of the populations, and that individualistic response of taxa to climate change appears to extend to intra-specific levels. The extent to which expanded populations contribute to long-term genetic pools remains uncertain.

© 2008 Elsevier Ltd. All rights reserved.

## 1. Introduction

The concept of 'refugia', and derivatives, has been important in thinking about the changing distributions and abundances of organisms, especially in response to the climatic changes of the late Quaternary. However, as our understanding of these changes has increased, it is becoming apparent that the term may be widening while its usefulness is diminishing. Here, we review the history and uses of the term in late Quaternary biogeography, and consider whether the term is still useful and appropriate. We suggest that a more precise language would improve understanding, especially between palaeoecologists and geneticists, about what is actually happening to organisms' distributions and abundances on these timescales, and also help in identifying cause and effect for these changes.

Distribution and abundance are used here in the sense that 'distribution' refers to the overall geographical spread of a taxon, measured in two (occasionally three) dimensions. Abundance refers to the total numbers of individuals of a taxon, which might be spread evenly or (more often) unevenly over the distribution. The two can be combined as density (individuals per unit area), and which would also likely vary over the distribution. Distribution and abundance thus refer to attributes of the whole range of a taxon, whereas density is necessarily local. Distribution and abundance are regarded as independent, although towards the limits of possible values they will have some relationship (extremely high abundances will normally occupy wider distributions, and as abundances fall towards zero, distribution will inevitably contract). The refugial concept usually involves contractions in range (often to a particular place), as well as, implicitly or explicitly, reductions in abundance. It thus involves an element of the genetic usage of 'bottlenecks' as 'reductions in population size followed by population size increases' (Hawks et al., 2000).

The dual considerations of distribution and abundance are significant in population genetic terms. The effect of genetic drift, or the stochastic loss of overall genetic variation, is a function of effective population size, which is balanced in natural populations by incoming gene flow of new genotypes. Thus, the effects of drift would be more pronounced under the 'classical' scenario of glacial refugia, where populations are isolated from each other and are characterized by small effective population sizes. Where populations are more continuous, gene flow may ameliorate the negative effects of genetic drift.

## 2. Historical background

It has long been recognized that large-scale shifts of distributions must have taken place in response to development of Quaternary continental ice-sheets. Darwin (1859) used the phenomenon as part of an argument for why there should not have been much evolution as a result of these movements (by moving together, species keep their biotic environments constant). Scandinavian botanists argued early in the twentieth century that a portion of the modern Scandinavian arctic flora must have had

'refuges' in Scandinavia during glacial periods, perhaps along the coast (Dahl, 1946). The first use of the latinized form 'refugia' seems to have been by Heusser (1955), in his discussion of late Quaternary pollen data from the Queen Charlotte Islands (western Canada), in which he concluded that "The number and kinds of pollen in the basal peat favor the interpretation that vegetation persisted in refugia through at least the last glaciation" (Heusser, 1955, p. 429). From then on, the term has been used increasingly in scientific literature (Table 1) to refer to regions where elements of the modern flora and fauna might have survived glacial periods with greatly reduced numbers and distributions. Early uses were based on recognition of this situation from palaeoecological data (especially for north temperate trees), but after about 1990 the term has increasingly been used in genetics to refer to regions from which genetic data suggest that more widespread modern populations have originated. A significant early use was extension of the concept to Amazonian forests (Haffer, 1969), which initiated a long (and continuing: Wüster et al., 2005) discussion of the nature of tropical species range shifts between glacial and interglacial periods. Genetic work with population sizes of marine species on Quaternary timescales has added recognition that the effect of Quaternary climatic changes may have been to act as a ratchet on increasing populations, forcing a stepwise increase across multiple glacial–interglacial oscillations, rather than forcing populations to oscillate in a similar manner to climate (Chevolot et al., 2006; Hoarau et al., 2007).

While the existence of 'glacial refugia' for taxa now more widely distributed continues to attract attention (e.g. Sommer and Nadachowski, 2006; Bhagwat and Willis, 2008; Provan and Bennett, 2008), the reverse phenomenon, or 'interglacial refugia', has been relatively ignored. The term was used by Billings (1974) and MacVean and Schuster (1981), but to date (February 2008) the expressions 'interglacial refugia' and 'postglacial refugia' have occurred only 11 times in literature surveyed by ISI Web of Science (http://www.isiknowledge.com), although there are other articles that have clear reference to the concept (e.g. Stewart and Lister, 2001; Dalén et al., 2007; Bhagwat and Willis, 2008). In comparison, there are 578 occurrences of 'glacial refugia' in the same literature. The term 'refugia' is thus, in reality, synonymous with 'glacial refugia', which is how it was first used.

## 3. Responses to glacial–interglacial climatic oscillations

Palaeoecological records can give detailed and precise information about locations of past distributions, and abundances may be inferred, by working with *in situ* fossils. The time scale is often accurate and precise, based on radiometric dating. Genetic data differs from palaeoecological data in that inferences on past population sizes and locations are typically reached from analysis of modern populations at current locations. The nature and distribution of genetic diversity within modern populations may suggest that there have been past bottlenecks, and a molecular clock

**Table 1**
Growth in the use of the term 'refugi*' in scientific literature

| Years | Title | Topic |
|---|---|---|
| 1970–1974 | 4 | |
| 1975–1979 | 17 | |
| 1980–1984 | 25 | |
| 1985–1989 | 25 | |
| 1990–1994 | 40 | 253 |
| 1995–1999 | 75 | 545 |
| 2000–2004 | 133 | 1002 |
| *2005–2007* | *122* | *863* |

Source: ISI Web of Knowledge (http://www.isiknowledge.com). Note that the current period (2005–2007) is incomplete.

approach may be used to date this, but this approach cannot itself identify the location of past populations. However, it is often assumed that populations with greatest diversity must be ancestral, and their locations assumed to be the place of origin of the divergences to other, less diverse, modern populations. Contact zones, where recolonizing populations meet, may also exhibit high levels of diversity, but they tend to lack the unique haplotypes that characterize populations that have been isolated from each other throughout glacial maxima (Petit et al., 2003). Relative to palaeoecological data, genetic data are probably more accurate and precise about population sizes, and can indicate lines of ancestry, but less accurate (however precise) about timing and location. Recognizing this, there is a potential for confusion if imprecise genetically-inferred bottlenecks and the location of the populations concerned are equated with more precisely palaeoecologically-located and radiometrically-dated 'refugia', a phenomenon recognized as 'suck-in' by Baillie (1991).

Responses to glacial–interglacial climatic oscillations have taken various forms as inferred from both palaeoecological and genetic data. Some of these are described below, and illustrated diagrammatically in Fig. 1.

### 3.1. Classical refugia (Fig. 1a)

The dominant palaeoecological approach to refugia has been to use the pollen record to establish regions from which modern taxa have originated. Thus, Huntley and Birks (1983) mapped the distributions of pollen from, mostly, forest trees, over the whole of Europe for the period since 13,000 years ago and showed that these trees spread, typically, from areas around the margins of Europe, and argued that these regions were glacial refugia for forest trees. Bennett et al. (1991) suggested that mountainous areas of southern Europe were especially significant for the long-term survival of trees in Europe through multiple glacial–interglacial oscillations because their height offered sufficient scope for altitudinal shifts as climates changed. No evidence has been forthcoming to suggest that European temperate trees might have survived glacial periods beyond Europe, but little or no direct evidence (such as dated fossils) has been forthcoming to support the notion of survival exactly within the proposed refugial areas, although it is commonly assumed that this is what happened for many taxa of widely disparate types (e.g. Hewitt, 2000). Similar arguments have also been presented from other regions (e.g. Queen Charlotte Islands (western Canada): cf. Heusser, 1955; Lacourse et al., 2005).

Genetic work has contributed to understanding the glacial–interglacial behaviour of north temperate trees in several respects. It appears that the modern, expanded ranges of these trees originate from a subset of the populations present at the Last Glacial Maximum (LGM) (Heuertz et al., 2004; McLachlan et al., 2005; Magri et al., 2006). A large part of the total LGM population may have remained in more or less the same regions throughout the climatic oscillation. We still do not know, however, whether the expanding genotypes expand during every interglacial, or whether expanding populations can come from different genotypes. West (1980), for example, suggested that the strikingly different behaviour of *Corylus* between different interglacials was because of the evolution of different 'biotypes'. Also, we still do not know whether there is a return movement at the end of an interglacial, or whether the expanded population becomes extinct, as suggested by Bennett et al. (1991).

As with trees, genetic work on modern animal populations on northern continents is showing that populations that became extensive during the Holocene are drawn from a subset of the populations present in southern parts of northern continents, which are presumed to reflect the genetic diversity of the LGM.
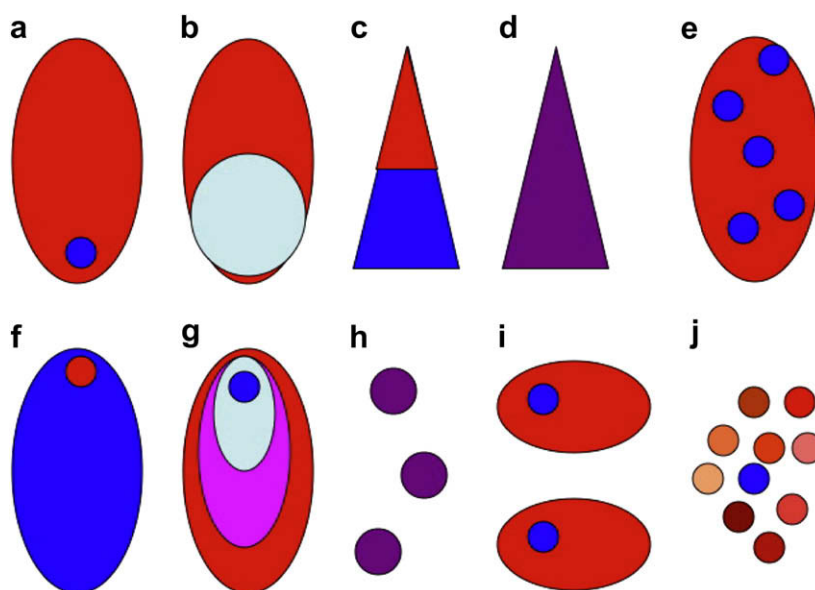
**Fig. 1.** Diagrammatic representation of selected species responses to glacial–interglacial climatic changes, in terms of distribution and abundance. Distributions (except where otherwise indicated): blue, glacial; red, interglacial. (a) Classical refugia. (b) Cryptic refugia. Distributions: pale blue, glacial (low abundance, not necessarily continuous). (c, d) Altitudinal shift. Purple: continuous. (e) Tropical refugia. Early-Holocene refugia have a similar pattern, but within the Holocene. (f) Interglacial refugia. (g) Stepwise expansions through successive glacial–interglacial oscillations. Four stages indicated: blue, to light blue, to pink, to red. (h) Stasis, with separated populations. Purple: continuous. (i) Separated into two disjunct populations by ancient vicariance, each of which expands after the LGM. (j) Speciation from one LGM species (blue) into multiple Holocene species (other colours).

Examples range from slugs (Pinceel et al., 2005) to newts (Babik et al., 2005) and mammals (Lessa et al., 2003).

### 3.2. Cryptic refugia (Fig. 1b)

A number of studies (e.g. Willis et al., 2000; Stewart and Lister, 2001; Willis and van Andel, 2004), based on dated fossils, now indicate that a range of mammal and tree taxa may well have survived glacial periods in central Europe, possibly scattered or at low densities, but nevertheless present. McGlone (1983) argued that New Zealand temperate forest trees were widespread but scarce during the LGM. This type of distribution was termed 'cryptic refugia' by Stewart and Lister (2001), because of the less obvious presence of taxa at low densities.

Other studies have also highlighted the possible existence of cryptic refugia as populations in 'pockets' of favourable microclimates within areas at higher latitudes previously regarded as being inhospitable (Fedorov and Stenseth, 2002; Kotlík et al., 2006). 'Cryptic' refugia need not, therefore, be continuous.

### 3.3. Altitudinal movements (Fig. 1c,d)

The late-Quaternary record of trees and shrubs in southwestern North America is based largely on macrofossil remain in packrat middens (Elias, 2007). These records lack the continuity at any one site of pollen records, but collectively offer an impressive volume of data through time and space that can be analysed at finer spatial scales than most pollen data. Spaulding et al. (1983) summarized records from southern Nevada (USA) and showed that, relative to the late Holocene, most trees and shrubs had altitudinally lower distributions during the LGM, but by varying amounts. For example, the LGM range of *Pinus flexilis* is completely lower than its modern altitudinal range, but the LGM range of *Pinus monophylla* overlaps its modern range. There are also taxa whose ranges have shifted only slightly, and at least one (*Atriplex confertifolia*) whose LGM range is slightly higher (with overlap) than its modern range. There is thus no simple movement of trees in shrubs down slopes or into areas of restricted range. The taxa concerned have shifted their

ranges individualistically in response to climate change, and have not necessarily even moved in the same direction (altitudinally).

### 3.4. Tropical refugia (Fig. 1e)

Possibly the greatest controversy surrounding the notion of 'refugia' in Quaternary literature has centred around the postulation (Haffer, 1969) that Amazonian lowland forest was, during dry climatic periods (broadly equivalent to glacials at high latitudes), divided into a number of isolated smaller forests which acted as refuges for the forest fauna, and from which they expanded during wetter periods. This hypothesis is clearly testable palaeoecologically, and has been shown to be wanting (Colinvaux et al., 1996; Haberle and Maslin, 1999; Colinvaux et al., 2000; Colinvaux et al., 2001; Kastner and Goñi, 2003; Bush et al., 2004): lowland Amazonia remained forested throughout the last glacial–interglacial oscillation and presumably previous oscillations, although discussion continues (Wüster et al., 2005). But how did these forests respond during these climatic oscillations? The available pollen record from lowland Amazonia (Colinvaux et al., 1996; Bush et al., 2004) suggests that the main elements of the lowland forest remained in place, but that montane elements moved to lower altitudes, resulting in forests that were a mixture of current montane and lowland forests. The abundances of lowland forest elements thus contracted during glacial periods, but possibly not their overall distribution, while the abundances and distributions of montane forest elements may have been considerably greater, having expanded out of relatively restricted regions, typified by modern ranges in the Andes (Colinvaux et al., 2000) and in the mountains of eastern Brazil (Ledru et al., 2007).

### 3.5. Early-Holocene refugia (Fig. 1e)

The seminal article of Pigott and Walters (1954) pointed out that the flora of the British Isles includes many widespread and abundant species that do not appear to occur readily within forests, and they asked how these species of 'discontinuous habitats' maintained themselves during periods, such as the Holocene, when the

landscape of most of the British Isles was probably completely forested. The compilation of Godwin (1975) supports their argument in showing that there are indeed many taxa with a substantial fossil record for the late Holocene, but a poor or absent record for the early Holocene. Some of these taxa are abundant as fossils in the lateglacial, others not. Thus, the herbs *Centaurea nigra* and *Plantago lanceolata* are now widespread taxa of disturbed ground in the British Isles, but are abundant as fossils only in the late Holocene, and scarce or absent in the early Holocene and lateglacial (Godwin, 1975). The herb *Eriophorum vaginatum* is currently a widespread plant of blanket peats in the uplands of the British Isles, but is abundant as fossils only in the late Holocene, and also scarce or absent in the early Holocene and lateglacial (Godwin, 1975). These are all examples of taxa that have been present but scarce throughout the Quaternary, but have increased to be common after human activity caused reduction of forests and modified upland habitats.

### 3.6. Interglacial refugia (Fig. 1f)

The Holocene extension of forest into the highest latitudes seen since the last interglacial (125 ka) has substantially reduced the area of land occupied by tundra and steppe flora and fauna. Consequently, the distributions and abundances of taxa from these environments must be a minimum during the current interglacial. Examples include plants such as the arctic-alpine herb *Dryas octopetala* and the arctic fox *Alopex lagopus*. *Dryas octopetala* was so abundant in northern and central Europe during the later stages of the last glaciation that geological stages have been named after it, but it is now a plant of restricted, disjunct, arctic and alpine distribution (Godwin, 1975). Disjunct distributions of this type have often been considered as 'glacial relict' (e.g. Reisch et al., 2003). The herb *Helianthemum* was a widespread and common fossil in British lateglacial deposits, but is now confined to the north and mountains. The shrub *Hippophae rhamnoides* was similarly widespread and common as a lateglacial fossil in Britain and Ireland, but is now confined to coasts (Godwin, 1975). The arctic fox is now a characteristic mammalian predator of tundra and northern mountains of northern North America and Eurasia, but during the last glacial fossils show that it occurred as far south as central Europe (Dalén et al., 2007), where it would have been much more widespread than now. In both cases, glacial periods represent times of range expansion, and interglacials times of contraction.

Disjunct seasonally dry forests of eastern South America have been treated as remnants of a more extensive seasonal formation that was at its maximum extent during the LGM (Prado and Gibbs, 1993; Pennington et al., 2000). For several of the component tree species, the present interglacial might thus be considered as a period of range contraction (and range splitting). However, Mayle (2004, 2006) has suggested that the dry forests of the LGM would have had a different composition than the present dry forests, so the present forests were assembled by means of population spread and long-distance dispersal. This example may well contain at least two types of behaviour: taxa that form LGM dry forests, which contracted in range or abundance at the glacial–interglacial transition; and taxa that form the present dry forests which presumably had more restricted ranges during the LGM, and are thus following more classic refugial behaviour.

### 3.7. Increasing populations (Fig. 1g)

Climatic changes of the late Quaternary have affected marine environments through sea temperatures and salinities as well as other properties. Additionally, the global reduction of sea level by about 120 m at LGM have had the consequence of shifting tidal and shallow marine environments by distances of, locally, hundreds of kilometres across shallow shelves (such as the Sunda shelf [SE Asia], the North Sea [NW Europe] and the Bering Straits [between Alaska and NE Asia]). The fossil record of these tidal and shallow water organisms is not strong, but their behaviour on Quaternary timescales has been investigated by genetic work on modern populations. For example, Provan et al. (2005) and Hoarau et al. (2007) show that common seaweeds of NW Europe, *Palmaria palmata* and *Fucus serratus* probably persisted during the LGM in a small number of refugia along the edge of the continental shelf near NW Spain and SW Ireland, and possibly also in the Hurd Deep, an extensive enclosed channel in the centre of the English Channel that may well have formed a saline lake during the LGM (Lericolais et al., 2003). Hoarau et al. (2007) infer from their genetic data that the total population of *Fucus serratus* has been increasing over the last few hundred thousand years, and that the effect of glacial–interglacial transitions has been to cause a stepwise increase: rapidly increasing populations during interglacial periods, static population size during glacial periods.

Wüster et al. (2005) investigated the molecular phylogeny of the neotropical rattlesnake (*Crotalus durissus* complex) and showed a gradual spread from central America at 1.85 Ma to northern Venezuela at 1.54 Ma and eastern Brazil at 1.08 Ma. No direct response to glacial–interglacial oscillations is resolvable from these data but the gradual spread at longer timescales is clear. The northern trees *Alnus* and *Quercus* also spread into South America following the uplift of the Panama isthmus, and these show oscillating local expansions and contractions superimposed on the overall spread (Hooghiemstra, 1984, 1989).

### 3.8. Stasis (Fig. 1h)

Where populations and species change radically in abundance or distribution, there are clear signals in fossil and genetic records that attract attention. Reality for the bulk of species may be more prosaic, but less often visible. On oceanic islands, opportunity for spread to or from the island may be rare and unrelated to climatic change. Climatic changes on islands may be small because of buffering of climate by the surrounding ocean, and climatically-forced competitive effects may be small.

In the South American tropics, genetic studies of populations of the tree *Caesalpinia echinata* with three major isolated populations along the coast of eastern Brazil, show that these populations have remained isolated through multiple glacial–interglacial oscillations (Lira et al., 2003). Lessa et al. (2003) found that several species of small mammal from western Amazonia appear to have experienced limited or no population expansion after the LGM, indicating stasis in, at least, abundance.

Species with very large population sizes may not exhibit the possible effects of genetic drift. North Atlantic copepods, for example, show no evidence of a genetic bottleneck despite a recorded abundance decrease of 70% attributed to global warming (J. Provan et al., unpublished data).

### 3.9. Ancient vicariance (Fig. 1i)

Three amphibian lineages in the Pacific northwest of North America have disjunct distributions that have been shown by genetic data to be best explained by pre-Quaternary vicariance (Carstens et al., 2005). Expansions since the LGM are superimposed on this older pattern, but the main separation into lineages is much older.

### 3.10. Speciation (Fig. 1j)

One of the most rapid bursts of speciation known occurred among cichlid fishes in Lake Victoria after the LGM. The lake dried

out completely at the LGM (Stager and Johnson, 2008), and since refilling has been recolonized by cichlids that have diversified into more than 500 species (Verheyen et al., 2003). This is a spectacular example, but shifting distributions near the LGM may be leading to speciation among gulls (e.g. Liebers and Helbig, 2002), and possibly other groups.

## 4. Discussion

As the above examples make clear, movements of taxa in response to climate changes have been complex. The behaviour of some taxa does correspond to the classical model of 'glacial refugia', but the behaviour of many others does not. There are many examples of taxa that show constrictions of range and reductions of abundance, but in response to factors that are other than climatic. Additionally, our understanding now of the nature of climate change provides a much more complex model than that available when the term 'glacial refugium' was first used, 50 or more years ago.

What is the alternative? Our understanding of range and abundance changes is also now much more sophisticated than it was 50 years ago, and it should be possible to discuss and present changes of distribution and abundance in a more sophisticated way than simply in terms of 'refugial' or otherwise. Three key elements are distribution, abundance and time, which will be discussed individually below. The basic model is that distribution and abundance will (i) change over time in a way that is at least as complex as the record of changing global temperatures (or ice-volumes), and (ii) that distribution and abundance do not necessarily change together.

### 4.1. Distribution

Species shift their distributions across landscapes in response to climatic and other environmental changes, but how large are these changes? In some cases, there is reason to think that distributions have changed radically. Many European north temperate trees are conspicuous largely by their absence during the LGM, and can be presumed to have had extremely restricted ranges at that time, followed by an enormous range expansion over several orders of magnitude during the early Holocene. Examples include *Tilia* and *Ulmus*, among others. On the other hand, some trees, notably conifers, but also *Betula*, may well have persisted through the LGM on the central European plains (Willis et al., 2000). If so, how do their ranges at this period compare with modern ranges? It is likely that the overall magnitude of changes in distribution for these taxa has been much smaller than for *Ulmus* or *Tilia*.

For most species, limited distributions are the norm (Gaston, 2008). Orme et al. (2006) show that 28% of bird species, globally, have distribution areas that are less than 0.15% of the Earth's land surface (or smaller than Great Britain), and the median range size for bird species is only about 0.58% of the Earth's land surface. The proportion of species which have extensive distributions is thus small and the proportion of organisms that are part of widespread species is also small. If most species are rare most of the time, it follows that the interesting behaviour is why some species become abundant, at least some of the time, rather than why species that happen to be abundant now were rare at some previous point in time.

The analysis of genetic diversity among European tree taxa by Petit et al. (2003) shows that much diversity is concentrated in middle latitudes, and higher latitudes are depauperate by comparison. It thus appears that the range of genotypes involved in the major distribution shifts is low.

### 4.2. Abundance

Abundances change, and not necessarily synchronously with distribution. For example, American beech (*Fagus grandifolia*) was scarce during the LGM, increased in south-east USA for a short-lived period around 12 ka, then decreased in abundance while spreading north at low density, and finally becoming abundant again in the area around the Great Lakes in the mid to late Holocene (Bennett, 1985; Pollen Viewer 3.2, 2008). This taxon shows a double peak in abundance between the LGM and present, in two widely separated regions. Before and between the peaks it was widespread in eastern North America, but abundant nowhere. Abundances of *Tilia* and *Ulmus* during the LGM are unknown, but are presumed to have been lower (by orders of magnitude) than abundances during the Holocene. Their local densities might, however, have been low or, in principle, even higher than anything seen in the Holocene.

### 4.3. Timing

Although climate seems to have been the main driving force behind distribution and abundance changes of the glacial–interglacial transition, it is not the only factor driving change on these time-scales. If climate were solely responsible, we should see distribution and abundance values that are at maxima and minima synchronously with maxima and minima of climate (or vice versa). Other factors, however, cause timings for distribution maxima and minima that differ from those of climate parameters. Some, mentioned above, are organisms that have achieved maxima during the late Holocene through association with human activity. Although temperate trees increase in abundance during interglacials, it is not always the same taxa that increase. European beech (*Fagus sylvatica*) has generally been scarce during interglacials and glacials alike, but was abundant in the stadials at the beginning of the last glacial, and has become abundant during the late Holocene (Magri et al., 2006). The separation of European bears into distinct lineages has been presumed to have occurred in response to range contractions of the LGM (Hewitt, 2000), but actually lineage splits seem to have occurred two or three times within the last 200 ka, only the last of which may have been coincident with the LGM (Saarma et al., 2007).

### 4.4. An alternative

The term 'bottleneck', in common use among geneticists, may provide a convenient replacement word for 'refugium' in contexts where only abundance is being discussed. It has the considerable advantage of indicating a continuity (populations go through bottlenecks, but come from refugia), and nearly all the taxa under consideration have a much longer history than the LGM. The usual system of geographic names (or, to be really precise, co-ordinates) can be used to define space, and dates (identified as radiometric or molecular) identify time.

The recent work by Magri et al. (2006) and Magri (2008) on the late Quaternary history of European beech points the way forward. Using palaeoecological data of dated pollen and macrofossil finds, and mitochondrial and nuclear DNA analyses, they have shown that this tree persisted through the LGM in several different regions of southern and central Europe, and also that only a few of these regions contributed significantly to the Holocene expansion of beech into northern Europe. Their conclusions are as specific and detailed as possible with respect to locations, areas, abundances and timings. Some beech populations (e.g. those in the Pyrenees) appear to expand little, if at all, between the LGM and the Holocene. For these, it would appear that a limited distribution in a physiographically well-defined region has been viable for at least one, and probably more, glacial–interglacial oscillation, and it is thus

doubtful whether occurrence there should be regarded as 'refugial' in either glacial or interglacial times. Similar features are seen in the haplotype distributions of red maple (*Acer rubrum*) and American beech in eastern North America (McLachlan et al., 2005). The main north European expansion of beech originated from LGM populations located in the region of Slovenia, and these have clearly expanded several orders of magnitude in area and abundance since the LGM. However, we do not know whether the ancestors of these populations were also widespread, and then became reduced to the LGM Slovenian populations. The history of beech before the LGM indicates that it was more widespread at certain periods, but not as extensively as during the Holocene. It is therefore possible to assume that beech, as a whole, has been through a bottleneck, but it is not clear whether this is also true for any of its subpopulations (since those that declined before the LGM are not necessarily those that expanded after the LGM).

Thus, while species may pass through bottlenecks in terms of expansion and contraction of abundance, this may arise through the summing of the behaviour of the various subpopulations that make up the species. However, if the expansion in each interglacial is due to a different subpopulation, we may have a situation where nothing passes through a bottleneck: we have a series of subpopulations, most of which are small and more or less uniform in size over long periods of time, and a small number of which increase substantially but briefly, and leave no genetic trace afterwards from having done so. The extraordinary expansions into higher latitudes seen in some taxa become even more extraordinary if the ancestors are a subset (possibly a small subset) of the LGM population, and not all of the LGM population. Other variants are possible, of course, but this extreme model could perhaps provide a convenient null hypothesis for testing.

It has recently been argued that palaeoclimatic models can be incorporated with phylogenetic reconstructions to help restrict these reconstructions to those that are likely under given realistic scenarios for past environments (Richards et al., 2007; Knowles et al., 2007). These offer potential for improvement of understanding of the distribution and abundance changes at the LGM and previous glacial–interglacial transitions. They are dependent, however, on the assumption that species population niches have not changed through time, which has long been a problem in palaeoenvironmental reconstructions (Birks, 1981). Taken to the extreme, this would also imply that species do not evolve over time, which is known to be untrue, even if it is not yet clear on what time scale it is untrue (Knowles, 2001; Bennett, 2004).

We have become accustomed to thinking that taxa respond individualistically in response to glacial–interglacial climatic changes. Genetic work is now showing that this applies at taxonomic levels below species: the range of behaviours seen at the glacial–interglacial transition is as high among subpopulations of a species as it is between species (or higher taxa).

## 5. Conclusion

The responses of organisms to climatic and other environmental changes through time have been complex and varied. Using a term such as 'glacial refugia' does not do justice to this rich behaviour, and is only rarely a reasonable description of what actually happened. It is therefore recommended that the term be replaced by a terminology that allows more precise specification of distribution and abundance through time, with especial focus on timing of key features such as maxima, minima of distribution or abundance, and maxima and minima of rates of change of these values. This practice makes it possible to distinguish clearly and naturally between different types of behaviour in terms of rates, direction and timing, and a focus on timing should facilitate comparison of records with different chronological bases (as different as radiometric and molecular clocks).

The identity of populations that change in distribution or area needs to be specified as precisely as possible at the lowest distinguishable taxonomic level possible. Following the discovery that only a small proportion of total genetic diversity is involved in major expansions, it becomes increasingly more interesting to determine which populations are involved, and why, following the type of analysis already carried out at species level (Bhagwat and Willis, 2008).

Consideration of changing populations in terms of continuity through bottlenecks and expansions is helpful for understanding the overall picture, as the work of Magri et al. (2006) and Magri (2008) clearly shows, even though they did not use the terms. Consideration of the same phenomena as 'refugia' places too much focus on origins of modern populations and inhibits thinking of the longer term. Ultimately, we need to push further back to see the lineage splits that gave rise to modern species such as beech, and the environmental context in which those took place. On that perspective, the fluctuations of the late Quaternary might be better treated as noise than as signal.

Arguably, the phenomenon of most interest in the complex shifting of populations since the LGM is why a few populations of a few species are able to become abundant, and the ecological and genetic consequences of expansions by several orders of magnitude in distribution and abundance. Genetic data is revealing that these expansions originate from subpopulations of species, not the whole species, while the remainder of the species persists as local populations of limited size and distribution. Do these expansions contribute to the overall history and evolution of species in the long term? Or are they the lemmings of popular myth, rushing off to inevitable doom? Consideration of 'refugia' has begun the process of generating data that will eventually help us answer this, so the term can be said to have served its purpose.

## Acknowledgements

## References

Babik, W., Branicki, W., Crnobrnja-Isailović, J., Cogălniceanu, D., Sas, I., Olgun, K., Poyarkov, N.A., Garcia-París, M., Arntzen, J.W., 2005. Phylogeography of two European newt species—discordance between mtDNA and morphology. Molecular Ecology 14, 2475–2491.

Baillie, M.G.L., 1991. Suck-in and smear: two related chronological problems for the 90s. Journal of Theoretical Archaeology 2, 12–16.

Bennett, K.D., 1985. The spread of *Fagus grandifolia* across eastern North America during the last 18,000 years. Journal of Biogeography 12, 147–164.

Bennett, K.D., 2004. Continuing the debate on the role of Quaternary environmental change for macroevolution. Philosophical Transactions of the Royal Society B 359, 295–303.

Bennett, K.D., Tzedakis, P.C., Willis, K.J., 1991. Quaternary refugia of north European trees. Journal of Biogeography 18, 103–115.

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.

Billings, W.D., 1974. Adaptations and origins of alpine plants. Arctic and Alpine Research 6, 129–142.

Birks, H.J.B., 1981. The use of pollen analysis in the reconstruction of past climates: a review. In: Wigley, T.M.L., Ingram, M.J., Farmer, G. (Eds.), Climate and History: Studies in Past Climates and Their Impact on Man. Cambridge University Press, Cambridge, pp. 111–138.

Bush, M.B., De Oliveira, P.E., Colinvaux, P.A., Miller, M.C., Moreno, J.E., 2004. Amazonian paleoecological histories: one hill, three watersheds. Palaeogeography, Palaeoclimatology, Palaeoecology 214, 359–393.

Carstens, B.C., Brunsfeld, S.J., Demboski, J.R., Good, J.M., Sullivan, J., 2005. Investigating the evolutionary history of the Pacific Northwest mesic forest

ecosystem: hypothesis testing within a comparative phylogeographic framework. Evolution 59, 1639–1652.

Chevolot, M., Hoarau, G., Rijnsdorp, A.D., Stam, W.T., Olsen, J.L., 2006. Phylogeography and population structure of thornback rays (*Raja clavata* L., Rajidae). Molecular Ecology 15, 3693–3705.

Colinvaux, P.A., De Oliveira, P.E., Bush, M.B., 2000. Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. Quaternary Science Reviews 19, 141–169.

Colinvaux, P.A., De Oliveira, P.E., Moreno, J.E., Miller, M.C., Bush, M.B., 1996. A long pollen record from lowland Amazonia: forest and cooling in glacial times. Science 274, 85–88.

Colinvaux, P.A., Irion, G., Räsänen, M.E., Bush, M.B., Nunes de Mello, J.A.S., 2001. A paradigm to be discarded: geological and paleoecological data falsify the HAFFER & PRANCE refuge hypothesis of Amazonian speciation. Amazoniana 16, 609–646.

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 of the USA 104, 6726–6729.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

Elias, S.A., 2007. Rodent middens. In: Elias, S.A. (Ed.), Encyclopaedia of Quaternary Science. Elsevier, Oxford, pp. 2356–2367.

Fedorov, V.B., Stenseth, N.C., 2002. Multiple glacial refugia in the North American Arctic: inference from phylogeography of the collared lemming (*Dicrostonyx groenlandicus*). Proceedings of the Royal Society B 269, 2071–2077.

Gaston, K.J., 2008. Biodiversity and extinction: the importance of being common. Progress in Physical Geography 32, 73–79.

Godwin, H., 1975. History of the British Flora. Cambridge University Press, Cambridge.

Haberle, S.G., Maslin, M.A., 1999. Late Quaternary vegetation and climate change in the Amazon Basin based on a 50,000 year pollen record from the Amazon Fan, ODP Site 932. Quaternary Research 51, 27–38.

Haffer, J., 1969. Speciation in Amazonian forest birds. Science 165, 131–137.

Hawks, J., Hunley, K., Lee, S.-H., Wolpoff, M., 2000. Population bottlenecks and Pleistocene human evolution. Molecular Biology and Evolution 17, 2–22.

Heuertz, M., Fineschi, S., Anzidei, M., Pastorelli, R., Salvini, D., Paule, L., Frascaria-Lacoste, N., Hardy, O.J., Vekemans, X., Vendramin, G.G., 2004. Chloroplast DNA variation and postglacial recolonization of common ash (*Fraxinus excelsior* L.) in Europe. Molecular Ecology 13, 3437–3452.

Heusser, C.J., 1955. Pollen profiles from the Queen Charlotte Islands, British Columbia. Canadian Journal of Botany 33, 429–449.

Hewitt, G., 2000. The genetic legacy of the Quaternary ice ages. Nature 405, 907–913.

Hoarau, G., Coyer, J.A., Veldsink, J.H., Stam, W.T., Olsen, J.L., 2007. Glacial refugia and recolonization pathways in the brown seaweed *Fucus serratus*. Molecular Ecology 16, 3606–3616.

Hooghiemstra, H., 1984. Vegetational and climatic history of the High Plains of Bogotá, Colombia: a continuous record of the last 3.5 million years. Dissertationes Botanicae 79, 368.

Hooghiemstra, H., 1989. Quaternary and upper-Pliocene glaciations and forest development in the tropical Andes: evidence from a long high-resolution pollen record from the sedimentary basin of Bogotá, Colombia. Palaeogeography, Palaeoclimatology, Palaeoecology 72, 11–26.

Huntley, B., Birks, H.J.B., 1983. An Atlas of Past and Present Pollen Maps for Europe 0–13,000 Years Ago. Cambridge University Press, Cambridge.

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.

Knowles, L.L., 2001. Did the Pleistocene glaciations promote divergence? Tests of explicit refugial models in montane grasshoppers. Molecular Ecology 10, 691–701.

Knowles, L.L., Carstens, B.C., Keat, M.L., 2007. Coupling genetic and ecological-niche models to examine how past population distributions contribute to divergence. Current Biology 17, 940–946.

Kotlík, P., Deffontaine, V., Mascheretti, S., Zima, J., Michaux, J.R., Searle, J.B., 2006. A northern glacial refugium for bank voles (*Clethrionomys glareolus*). Proceedings of the National Academy of Sciences of the USA 103, 14860–14864.

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. Palaeogeography, Palaeoclimatology, Palaeoecology 226, 36–57.

Ledru, M.-P., Salatino, M.L.F., Ceccantini, G., Salatino, A., Pinheiro, F., Pintaud, J.-C., 2007. Regional assessment of the impact of climatic change on the distribution of a tropical conifer in the lowlands of South America. Diversity and Distributions 13, 761–771.

Lericolais, G., Auffret, J.-P., Bourillet, J.-F., 2003. The Quaternary Channel River: seismic stratigraphy of its palaeo-valleys and deeps. Journal of Quaternary Science 18, 245–260.

Lessa, E.P., Cook, J.A., Patton, J.L., 2003. Genetic footprints of demographic expansion in North America, but not Amazonia, during the Late Quaternary. Proceedings of the National Academy of Sciences of the USA 100, 10331–10334.

Liebers, D., Helbig, A.J., 2002. Phylogeography and colonization history of lesser black-backed gulls (*Larus fuscus*) as revealed by mtDNA sequences. Journal of Evolutionary Biology 15, 1021–1033.

Lira, C.F., Cardoso, S.R.S., Ferreira, P.C.G., Cardoso, M.A., Provan, J., 2003. Long-term population isolation in the endangered tropical tree species *Caesalpinia echinata* Lam. revealed by chloroplast microsatellites. Molecular Ecology 12, 3219–3225.

MacVean, C., Schuster, J.C., 1981. Altitudinal distribution of passalid beetles (Coleoptera, Passalidae) and Pleistocene dispersal on the volcanic chain of northern central America. Biotropica 13, 29–38.

Magri, D., 2008. Patterns of post-glacial spread and the extent of glacial refugia of european beech (*Fagus sylvatica*). Journal of Biogeography 35, 450–463.

Magri, D., Vendramin, G.G., Comps, B., Dupanloup, I., Geburek, T., Gömöry, D., Latalowa, M., Litt, T., Paule, L., Roure, J.M., Tantau, I., vander Knaap, W.O., Petit, R.J., deBeaulieu, J.-L., 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. New Phytologist 171, 199–221.

Mayle, F.E., 2004. Assessment of the Neotropical dry forest refugia hypothesis in the light of palaeoecological data and vegetation model simulations. Journal of Quaternary Science 19, 713–720.

Mayle, F.E., 2006. The Late Quaternary biogeographical history of South American seasonally dry tropical forests: insights from palaeo-ecological data. In: Pennington, R.T., Lewis, G.P., Ratter, J.A. (Eds.), Neotropical Savannas and Dry Forests: Plant Diversity, Biogeography and Conservation. CRC Press, London, pp. 395–416.

McGlone, M.S., 1983. The history of New Zealand lowland forest since the last glaciation. In: Thompson, K., Hodder, A.P.H., Edmonds, A.S. (Eds.), Lowland Forests in New Zealand. University of Waikato, pp. 1–17.

McLachlan, J.S., Clark, J.S., Manos, P.S., 2005. Molecular indicators of tree migration capacity under rapid climate change. Ecology 86, 2088–2098.

Orme, C.D.L., Davies, R.G., Olson, V.A., Thomas, G.H., Ding, T.-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Owens, I.P.F., Blackburn, T.M., Gaston, K.J., 2006. Global patterns of geographic range size in birds. PLoS Biology 4 (7), e208.

Pennington, R.T., Prado, D.E., Pendry, C.A., 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography 27, 261–273.

Petit, R.J., Aguinagalde, I., deBeaulieu, 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.

Pigott, C.D., Walters, S.M., 1954. On the interpretation of the discontinuous distributions shown by certain British species of open habitats. Journal of Ecology 42, 95–116.

Pinceel, J., Jordaens, K., Pfenninger, M., Backeljau, T., 2005. Rangewide phylogeography of a terrestrial slug in Europe: evidence for Alpine refugia and rapid colonization after the Pleistocene glaciations. Molecular Ecology 14, 1133–1150.

Pollen Viewer 3.2, 2008. Animated Maps of Vegetation Change. Available online at URL. http://www.geo.brown.edu/georesearch/esh/QE/Research/VegDynam/VegAnima/VegAnima.htm.

Prado, D.E., Gibbs, P.E., 1993. Patterns of species distributions in the dry seasonal forests of South America. Annals of the Missouri Botanical Garden 80, 902–927.

Provan, J., Bennett, K.D., 2008. Phylogeographical insights into cryptic glacial refugia. Trends in Ecology and Evolution 23, 564–571.

Provan, J., Wattier, R.A., Maggs, C.A., 2005. Phylogeographic analysis of the red seaweed *Palmaria palmata* reveals a Pleistocene marine glacial refugium in the English Channel. Molecular Ecology 14, 793–803.

Reisch, C., Poschlod, P., Wingender, R., 2003. Genetic variation of *Saxifraga paniculata* Mill. (Saxifragaceae): molecular evidence for glacial relict endemism in central Europe. Biological Journal of the Linnean Society 80, 11–21.

Richards, C.L., Carstens, B.C., Knowles, L.L., 2007. Distribution modelling and statistical phylogeography: an integrative framework for generating and testing alternative biogeographical hypotheses. Journal of Biogeography 34, 1833–1845.

Saarma, U., Ho, S.Y.W., Pybus, O.G., Kaljuste, M., Tumanov, I.L., Kojola, I., Vorobiev, A.A., Markov, N.I., Saveljev, A.P., Valdmann, H., Lyapunova, E.A., Abramov, A.V., Männil, P., Korsten, M., Vulla, E., Pazetnov, S.V., Pazetnov, V.S., Putchkovskiy, S.V., Rökov, A.M., 2007. Mitogenetic structure of brown bears (*Ursus arctos* L.) in northeastern Europe and a new time frame for the formation of European brown bear lineages. Molecular Ecology 16, 401–413.

Sommer, R.S., Nadachowski, A., 2006. Glacial refugia of mammals in Europe: evidence from fossil records. Mammal Review 36, 251–265.

Spaulding, W.G., Leopold, E.B., van Devender, T.R., 1983. Late Wisconsin paleoecology of the American southwest. In: Porter, S.C. (Ed.), Late-Quaternary Environments of the United States. The Late Pleistocene, Vol. 1. Longman, London, pp. 259–293.

Stager, J.C., Johnson, T.C., 2008. The late Pleistocene desiccation of Lake Victoria and the origin of its endemic biota. Hydrobiologia 596, 5–16.

Stewart, J.R., Lister, A.M., 2001. Cryptic northern refugia and the origins of the modern biota. Trends in Ecology and Evolution 16, 608–613.

Verheyen, E., Salzburger, W., Snoeks, J., Meyer, A., 2003. Origin of the superflock of Cichlid fishes from Lake Victoria, East Africa. Science 300, 325–329.

West, R.G., 1980. Pleistocene forest history in East Anglia. New Phytologist 85, 571–622.

Willis, K.J., Rudner, E., Sümegi, P., 2000. The full-glacial forests of central and southeastern Europe. Quaternary Research 53, 203–213.

Willis, K.J., van Andel, T.H., 2004. Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. Quaternary Science Reviews 23, 2369–2387.

Wüster, W., Ferguson, J.E., Quijada-Mascareñas, J.A., Pook, C.E., daGraçaSalomão, M., Thorpe, R.S., 2005. Tracing an invasion: landbridges, refugia, and the phylogeography of the Neotropical rattlesnake (Serpentes: Viperidae: *Crotalus durissus*). Molecular Ecology 14, 1095–1108.