

The role of Quaternary environmental change in plant macroevolution: the exception or the rule?

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The Quaternary has been described as an important time for genetic diversification and speciation. This is based on the premise that Quaternary climatic conditions fostered the isolation of populations and, in some instances, allopatric speciation. However, the 'Quaternary Ice-Age speciation model' rests on two key assumptions: (i) that biotic responses to climate change during the Quaternary were significantly different from those of other periods in Earth's history; and (ii) that the mechanisms of isolation during the Quaternary were sufficient in time and space for genetic diversification to foster speciation. These assumptions are addressed by examining the plant fossil record for the Quaternary (in detail) and for the past 410 Myr, which encompasses previous intervals of icehouse Earth. Our examination of the Quaternary record indicates that floristic responses to climate changes during the past 1.8 Myr were complex and that a distinction has to be made between those plants that were able to withstand the extremes of glacial conditions and those that could not. Generation times are also important as are different growth forms (e.g. herbaceous annuals and arborescent perennials), resulting in different responses in terms of genetic divergence rates during isolation. Because of these variations in the duration of isolation of populations and genomic diversification rates, no canonical statement about the predominant floristic response to climatic changes during the Quaternary (i.e. elevated rates of speciation or extinction, or stasis) is currently possible. This is especially true because of a sampling bias in terms of the fossil record of tree species over that of species with non-arborescent growth forms. Nevertheless, based on the available information, it appears that the dominant response of arborescent species during the Quaternary was extinction rather than speciation or stasis. By contrast, our examination of the fossil record of vascular plants for the past 410 Myr indicates that speciation rates often increased during long intervals of icehouse Earth (spanning up to 50 Myr). Therefore, longer periods of icehouse Earth than those occurring during the Quaternary may have isolated plant populations for sufficiently long periods of time to foster genomic diversification and allopatric speciation. Our results highlight the need for more detailed study of the fossil record in terms of finer temporal and spatial resolution than is currently available to examine the significance of intervals of icehouse Earth. It is equally clear that additional and detailed molecular studies of extant populations of Quaternary species are required in order to determine the extent to which these 'relic' species have genomically diversified across their current populations.

Keywords: Quaternary; Ice Ages; speciation; isolation; refugia; plant macroevolution

1. INTRODUCTION

The Quaternary period spans the past 1.8 Myr and has been aptly described as 'a time of crisis and restructuring' (Brett *et al.* 1996). Large terrestrial ice-caps started to develop in the Northern Hemisphere *ca.* 2.75 Ma (Maslin *et al.* 1996; Jansen *et al.* 2000) resulting in multiple glacial-interglacial cycles driven by variations in orbital insolation on Milankovitch time-scales (Hays *et al.* 1976; Imbrie & Imbrie 1979). Glacial conditions accounted for up to 80% of the Quaternary. The remaining 20% was composed of interspersed shorter interglacial periods during which conditions were similar to, or warmer than, present (Frogley *et al.* 1999). During the Ice Ages, large

terrestrial ice sheets and permafrost attended by temperatures between 10–25 °C lower than present (Peltier 1994; Pollard & Thompson 1997) rendered much of the high- to mid-latitude regions uninhabitable for most communities. Aridity and temperatures between 2 and 5 °C lower than present also had a significant effect on biotic communities in lower latitudes (Hooghiemstra 1995; Colinvaux *et al.* 2000). Additionally, global atmospheric CO₂ was significantly lower than it is today, e.g. evidence from the Vostok ice core suggests that CO₂ concentrations during glacials were as low as 180 p.p.m.v., rising to pre-industrial 280 p.p.m.v. levels in the intervening interglacials (Petit *et al.* 1999).

The Quaternary Ice Ages were therefore environmentally distinctive and presumably engendered unusual biotic patterns that many would argue are uncharacteristic of most of the Earth's history. In particular, it is suggested that the repeated redistribution and isolation of plants and animals in micro-environmentally favourable locations

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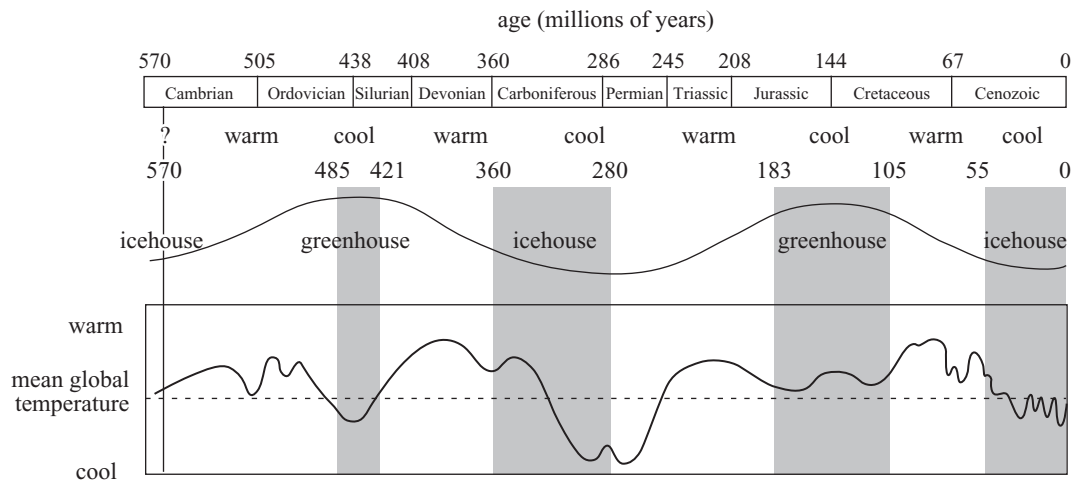


Figure 1. Climatic megacycles during the past 570 Myr (Huggett 1997; Willis & McElwain 2002). Sources for greenhouse/icehouse data from Fischer (1984), Crowley & North (1991) and Crowley (1998); warm and cold modes from Frakes *et al.* (1992); generalized temperature curve from Martin (1998).

during intervals of adverse climatic conditions (refugia) had important evolutionary implications (Vrba 1985, 1992, 1993; Bennett 1990, 1997). Three potential evolutionary scenarios have been suggested for these cycles of fragmentation and re-expansion of species ranges. The first is species persistence. According to this view, species underwent range fragmentation and re-expansion with each contraction–expansion cycle but this either failed to evoke genetic differentiation, or subsequent re-expansion and mixing of populations eliminated incipient speciation. The result is the appearance of evolutionary stasis. The second scenario is extinction. Isolation resulted in populations too small to survive and the affected species died out. The third possibility is classic allopatric speciation wherein geographical isolation engendered genetic differentiation among populations such that they were incapable of interbreeding on re-expansion.

Until recently, many workers believed that the predominant response of species to habitat fragmentation and loss during the Quaternary Ice Ages was stasis and extinction, with speciation taking place ‘occasionally’ in populations isolated because of perpetual environmental change at Milankovitch time-scales (Bennett 1990, 1997). However, during the past decade, the hypothesis that ‘the Quaternary Ice Ages are an important time for genetic diversification and speciation’ has become the focus of continued research (Jackson 2000), ranging from the level of the whole organism (both extant and extinct) to that of the molecular organization of the genome. Underlying much of this research and speculation are two key assumptions. The first assumption is that there was a redistribution and recombination of biotic communities during the Quaternary Ice Ages that was significantly different from that of most previous times in the Earth’s history. The second assumption is that, during the Ice Ages, communities were sufficiently isolated in time and space for genetic diversification and speciation to have occurred. Nevertheless, these assumptions remain largely unexplored empirically and they raise a variety of important questions. For example, how do biotic patterns during the Quaternary compare with those of previous times in the Earth’s history? Is there evidence to suggest that the mechanisms and

duration of Quaternary isolations were sufficiently long for genetic diversification and speciation to occur? Is there evidence in the fossil record for increased speciation rates during the Quaternary? Also are there any obvious differences in the fossil record between speciation rates of icehouse and greenhouse Earth? Over the past 600 Myr, there have been at least three intervals of icehouse Earth (figure 1) when there was widespread continental glaciation, global cooling and increased aridity. So, are speciation rates during these intervals significantly different to intervening greenhouse periods?

This paper aims to present an overview of the evidence from the plant fossil record to examine these assumptions and questions. The pivotal issue is whether the environmental changes observed for the Quaternary were the exception or the rule in plant macroevolution. From a purely logical perspective, stasis, extinction and speciation are all potential responses to habitat fragmentation and loss, and each must have occurred during the Quaternary Ice Ages, depending on the biology and history of a particular species. Thus, the issue is not whether one or all three occurred during the Quaternary, but which, if any, was more frequent than the other.

2. HOW DO BIOTIC PATTERNS DURING THE QUATERNARY COMPARE WITH PREVIOUS TIMES IN THE EARTH’S HISTORY?

Orbital variations related to changes in the Earth’s axial tilt, precession and eccentricity of the elliptical orbit around the sun (Milankovitch cycles) have undoubtedly occurred throughout geological time (Shackleton & Opdyke 1976; Herbert & Fischer 1986; Herbert & D’Hondt 1990). These variations also probably resulted in large and significant astronomical forcing of the climate at 400, 100, 41 and 19–23 kyr intervals (Imbrie & Imbrie 1979) throughout the Earth’s history, such that global biota have undergone constant redistribution and recombination of species at Milankovitch time-scales (Bennett 1990, 1997). For example, fossil pollen evidence from an annually laminated lake sequence from Pula Maar in Hungary, spanning *ca.* 330 kyr between 3–2.6 Ma (Late

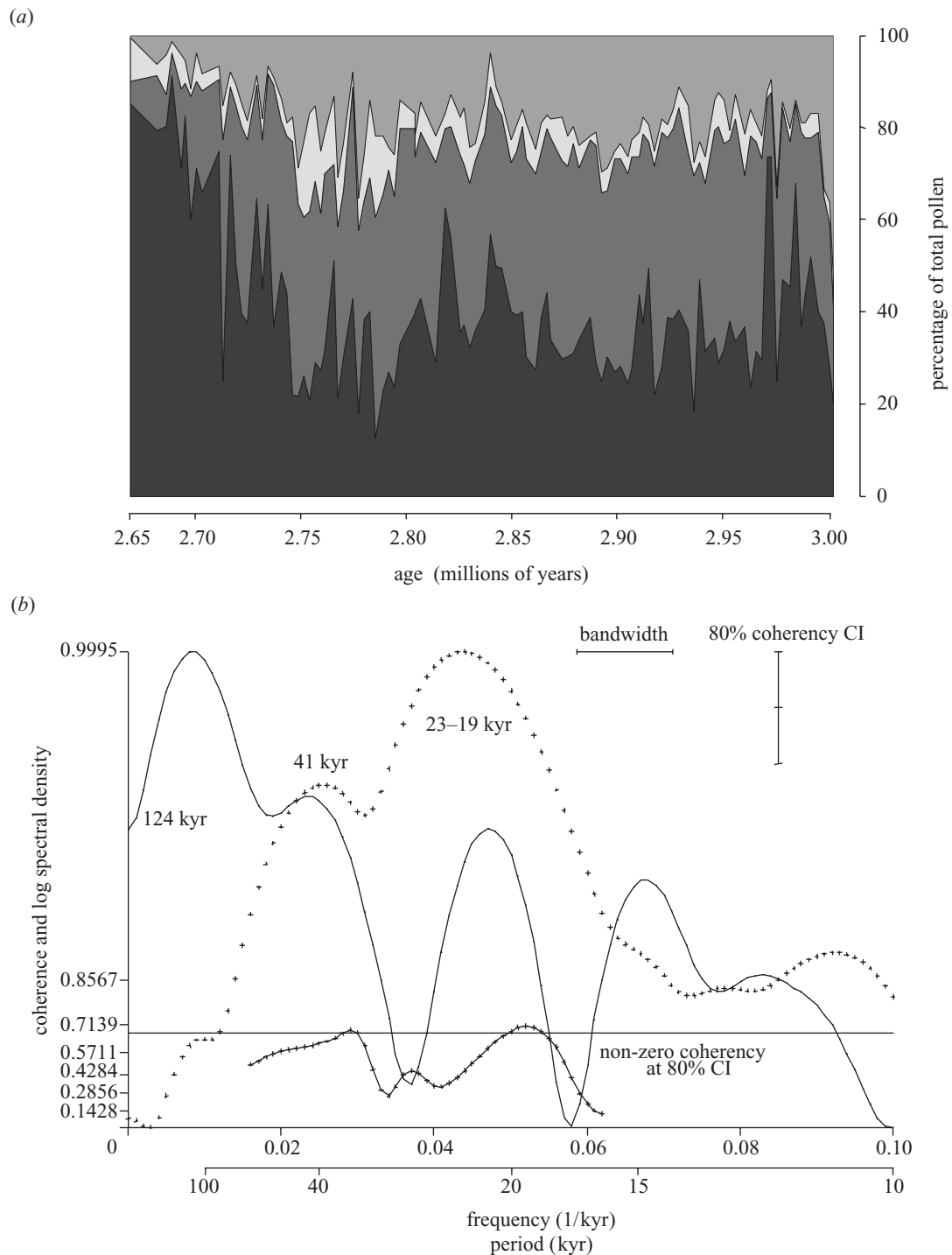


Figure 2. (a) Summary pollen diagram from Pula Maar crater, Hungary, spanning the interval 3.0–2.67 Ma. Four predominant vegetation formations can be recognized in the dataset, namely boreal forest (very dark grey: e.g. *Pinus*, *Picea*, *Larix*, *Abies*, *Tsuga*), temperate woodland (dark grey: e.g. *Quercus*, *Corylus*, *Fagus*, *Carpinus orientalis*, *Ulmus*), sub-tropical forest (mid-grey: e.g. *Sequoia*, *Nyssa*, *Eucommia*, *Pterocarya*, *Sciadopitys*) and herbaceous vegetation (light grey: e.g. *Poacea*, *Artemisia*, *Chenopodiaceae*). Throughout the 320 kyr forested vegetation was dominant. (b) Cross-spectral comparison of boreal pollen percentage data (solid line) with calculated summer insolation (crosses line) (July at 47° N (Laskar *et al.* 1993)) for the interval 3.0–2.67 Ma. Results demonstrate that during 3.0–2.67 Ma, a switch between a forest dominated by boreal species to subtropical/temperate species occurred at a periodicity of ca. 124, 41 and 21–19 kyr, corresponding closely to climatic change at Milankovitch frequencies (Willis *et al.* 1999a,b). The two records (insolation and boreal pollen percentage) are coherent (crosses and solid line) both at the 41 kyr and 23–19 kyr periodicities, adding further support to the suggestion that the changes seen in the vegetation are driven by changes in incoming orbital insolation.

Pliocene) indicates clear change in the dominance of forest types from predominantly boreal to sub-tropical/temperate at Milankovitch time-scales (Willis *et al.* 1999a,b; figure 2). Thus there is unequivocal evidence

that vegetation has been responding to climate change at Milankovitch frequencies well before the Quaternary. So what makes the Quaternary so biogeographically distinctive from other periods in the Earth's history? How do the

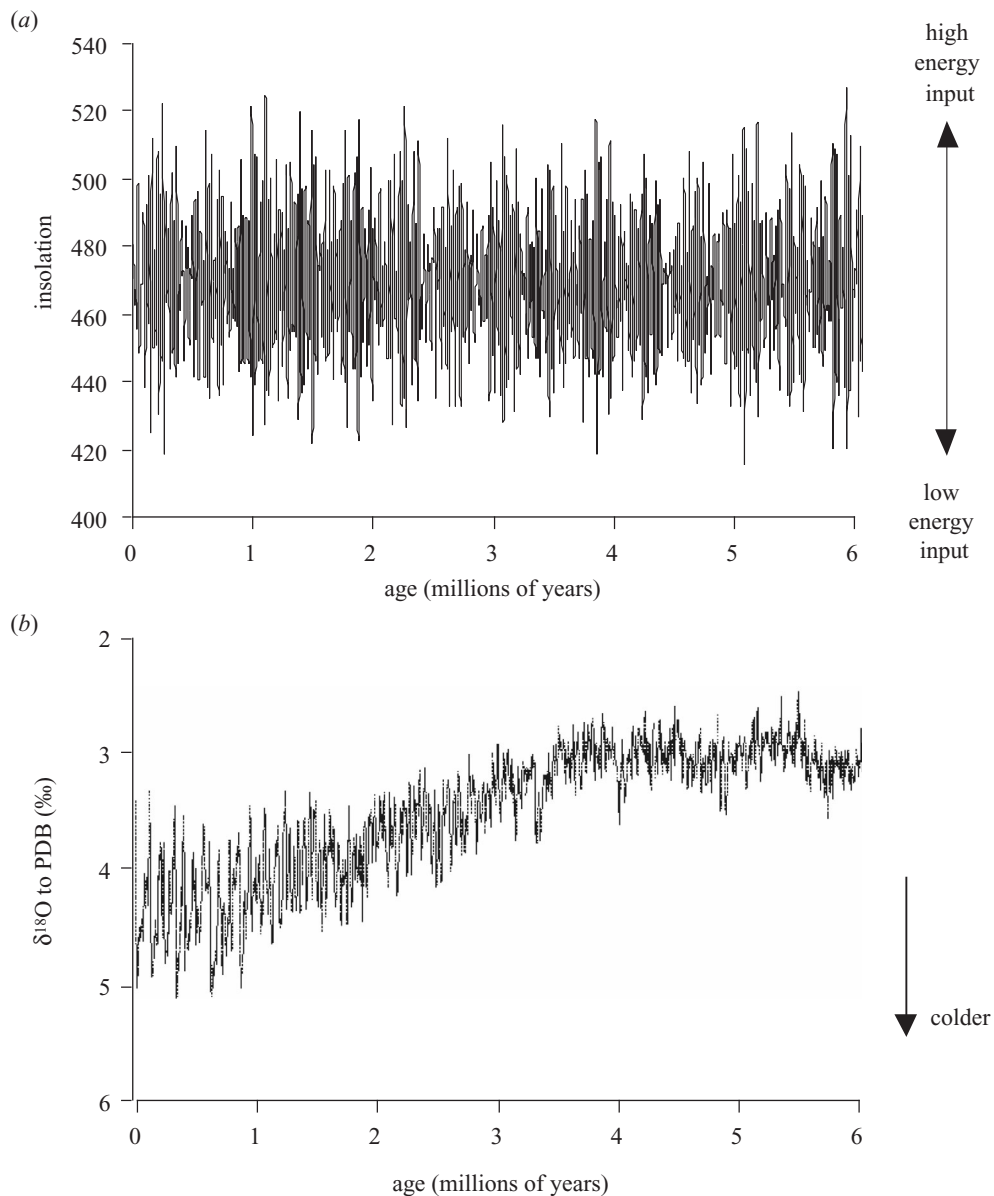


Figure 3. (a) Calculated Northern Hemisphere summer insolation (Wm^{-2}) at 45°N over the past 6 Myr based on the astronomical solutions of Laskar *et al.* (1993). (b) High resolution 6 Myr long composite diagram of $\delta^{18}\text{O}$ isotope record of benthic foraminifers from the ocean drilling programme sites 846 (Shackleton *et al.* 1995), V19-30 (Shackleton & Pisias 1985) and 677 (Shackleton *et al.* 1990) where the $\delta^{18}\text{O}$ record is expressed as a ratio to PeeDee Belemnite (PDB) measured in parts per mil (‰).

biotic patterns over the past 1.8 Myr differ in tempo or mode from those of previous times in the Earth's history?

Calculations of incoming solar radiation associated with orbital variations on Milankovitch time-scales now extend back to at least 50 Ma and indicate that there has been little change in the amplitude and frequency of oscillations through this time interval. In particular, there is no obvious increase of incoming solar radiation during the past 1.8 Myr (Laskar *et al.* 1993; figure 3a). This is in direct contrast to evidence from the geological record, especially the $\delta^{18}\text{O}$ record from ocean cores, which indicates that the Quaternary was a time of increasing amplitude of climate change resulting in progressive cooling with the build-up of large polar terrestrial ice-caps (Shackleton *et al.* 1995; figure 3b). Nonlinear dynamics in the Earth's climate system and atmosphere (including long-term reduction in atmospheric CO_2 , uplift of the Tibetan plateau and

internal ice-sheet dynamics; see Ruddiman 2001) are therefore thought to have triggered the Quaternary Ice Ages. Thus the significant difference between the Quaternary and other times in the Earth's history (with the exception of the Carboniferous: as discussed below) is that the variations in incoming solar radiation on Milankovitch time-scales were occurring against a background of increasing global cooling and uniquely low atmospheric CO_2 concentrations (Berner 1991; Maslin *et al.* 1996).

There are several long-term pollen sequences documenting the responses of terrestrial plants to the climatic fluctuations of the Quaternary in the Northern Hemisphere mid-latitude regions (e.g. Magri 1989; Reille & de Beaulieu 1990, 1995; Tzedakis 1993; Watts *et al.* 1996; Follieri *et al.* 1998; Okuda *et al.* 2001). In all of these, the predominant response to the glacial–interglacial cycles of the Quaternary appears to have been a transition from



Figure 4. Schematic diagram to indicate proposed areas of refugia for temperate tree taxa in the three southern peninsulas of Europe during the last full glacial (ca. 100–16 ka). Evidence to support this model comes from numerous fossil pollen and plant macrofossil assemblages. (Redrawn from Willis & McElwain (2002) and references cited therein.)

forested to non-forested vegetation (e.g. Tzedakis *et al.* 1997). Such pronounced changes (i.e. forest to grassland/parkland) during the Quaternary are therefore in direct contrast to the events immediately preceding 2 Myr when vegetation changes were mainly from one forest type to another at similar latitudinal locations (Willis *et al.* 1999b; figure 2).

In addition, studies on taxonomic richness through the Late Pliocene sequence indicate that, with low amplitude climatic fluctuations at Milankovitch time-scales, there was a change in the dominants in the community rather than a change in total number of species (Willis *et al.* 2004). This observation suggests that the predominant effect of the climate changes at Milankovitch frequencies before the Quaternary was interspecific competition, which altered the composition of existing biomes. In comparison, the significant reduction in taxonomic richness associated with orbital variations at Milankovitch time-scales during the Quaternary may reflect more pronounced migration, local extinction and the isolation of small populations.

In summary, the available data indicate that Quaternary climatic variations at Milankovitch time-scales resulted in a much more pronounced geographical response at mid to high latitudes, taking the form of extensive species redistributions and recombinations that resulted in some populations undergoing long periods of isolation in refugia during periods of climate extremes. However, the issue of the 'relative frequency' of Quaternary stasis, extinction and allopatric speciation remains, as does the issue of

whether the Quaternary is evolutionarily 'special' regarding the frequencies of these three possible responses to climatic crisis.

3. IS THERE EVIDENCE TO SUGGEST THAT THE MECHANISMS OF ISOLATION DURING THE QUATERNARY WERE SUFFICIENT FOR GENETIC DIVERSIFICATION AND SPECIATION TO OCCUR?

The second assumption of the Quaternary Ice-Age speciation model is directly related to the foregoing discussion, because the supposition that allopatric speciation was frequent during the Quaternary requires that the duration of isolation was sufficient for genetic diversification and speciation to occur. The location of these refugia is equally important. For example, it was originally suggested that refugia in Europe and the United States were located well beyond the ice sheets and permafrost, in regions where climatic extremes were not beyond the physiological capabilities of indigenous species (Whitehead 1973; Watts 1980; Wright 1981; Huntley & Birks 1983; Davis 1983; Bennett *et al.* 1991).

The European refugia, for example, were posited to be in the Near East and the three southern peninsulas of Europe (Balkan, Italian and Iberian). Indeed, pollen records for these regions are sufficiently robust to suggest that trees did survive in the southern European locations during the full-glacial period (Bennett *et al.* 1991; Tzedakis 1993; Willis 1996; Willis & Whittaker 2000). For

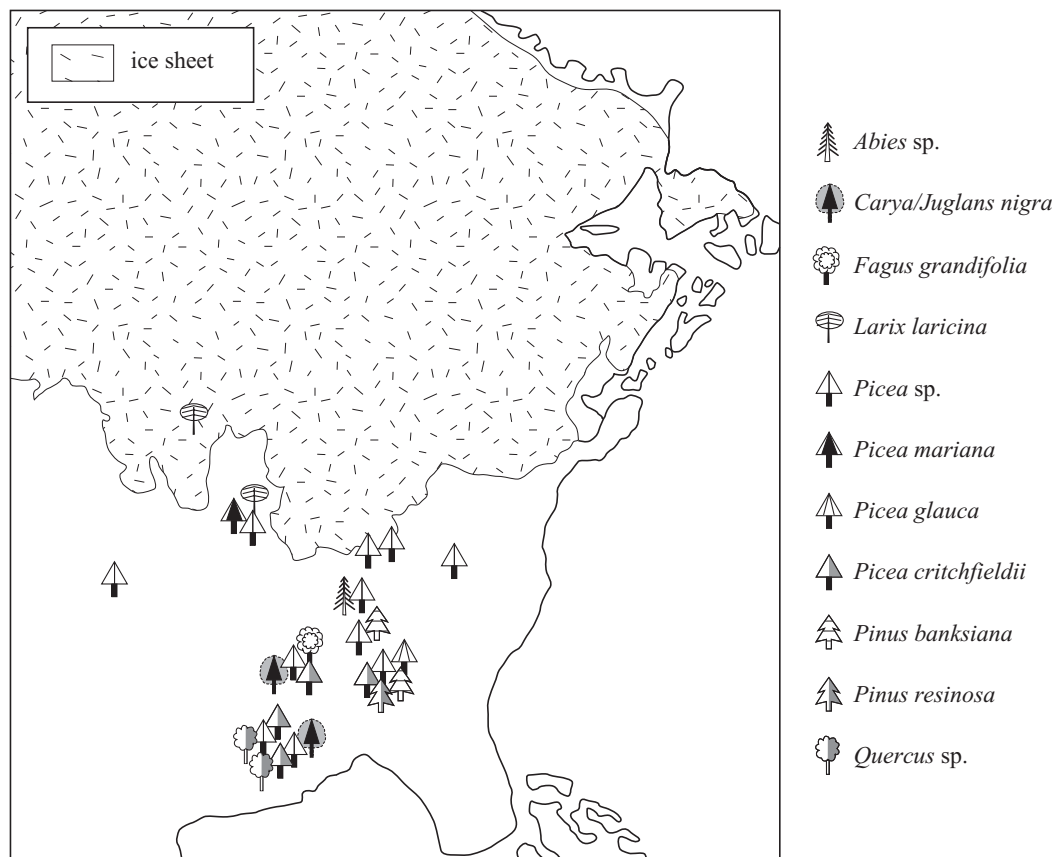


Figure 5. Schematic diagram to indicate location and species of trees identified through macrofossil evidence growing in eastern North America during the LGM (ca. 23–20 ka) (Jackson *et al.* 2000). The most northerly find of *Larix laricina* occurs at a site, which is within the reconstructed margin of the LGM ice sheet.

example, evidence from the long pollen sequence of Ioannina in Greece indicates a small but continuous presence of trees including *Quercus*, *Ulmus*, *Tilia*, *Corylus*, *Fagus*, *Abies*, *Carpinus betulus* and *Ostrya carpinifolia*/*Carpinus orientalis* throughout the last full glacial (Tzedakis *et al.* 2002). In this and many other shorter sequences extending back into the LGM, the low amounts of tree pollen are taken as evidence of local populations situated in small pockets of microenvironmentally favourable locations, i.e. refugia (Bennett *et al.* 1991; Willis 1996; Willis & Whittaker 2000). Evidence such as this has led to a well-established model that the three southern European peninsulas harboured small isolated populations of plants during the full glacial, which expanded and migrated into northern Europe with the onset of interglacial warming (figure 4).

The fossil evidence for southerly tree populations during the Quaternary glacials in both Europe and the United States appears to be unequivocal. What is not clear, however, is their northerly extent. How close did tree populations grow to the ice-caps, and were these southerly populations truly isolated? Answering these questions is critical to determining whether allopatric speciation could occur. The first evidence that full-glacial tree refugia might not be so tightly constrained as previously thought comes from the United States, where pollen and macrofossil evidence indicates that, at least in the eastern United States, many boreal taxa, including *Picea glauca*, *Pinus mariana* and *Pinus banksiana*, grew at the edge of the Laurentide ice sheet during the LGM (Jackson *et al.* 1997,

2000; figure 5). Similarly, in central and eastern Europe, there is increasing evidence for full-glacial tree growth in these regions from pollen, plant macrofossils and macrofossil charcoal assemblages. Indeed, there are now at least 35 localities in central and eastern Europe containing evidence from macrofossil wood charcoal assemblages indicative of at least 17 different tree taxa (Willis & Van Andel 2004). Most of this wood is from trees currently found in the boreal forest with a predominance of gymnosperms, including species of *Pinus*, *Picea*, *Larix* and several angiosperms such as *Salix* and *Betula*. Over 200 radiocarbon dates have been obtained from these assemblages, temporally constraining them to 37–16 ka, which is one of the coldest intervals of the last full glacial.

Evidence for the full-glacial survival of northerly populations (in some cases to the edge of the ice-caps) implies a more diffuse distribution of trees during cold stages than previously thought. Importantly, it is reasonable to speculate that some species were insufficiently isolated in space or time for allopatry to have occurred (Stewart & Lister 2001; Stewart 2003). This is not to say that some populations were not isolated, only that isolation cannot be invoked for all species. With the current evidence from the plant fossil record it is therefore fair to say that, with one or two exceptions, isolation in southerly refugia occurred for most temperate deciduous trees (angiosperms) but not for several boreal species (mainly gymnosperms). There is little fossil evidence for temperate deciduous trees growing close to the ice-caps, for example, and refugial localities for some appear, on the whole, to have been in the more

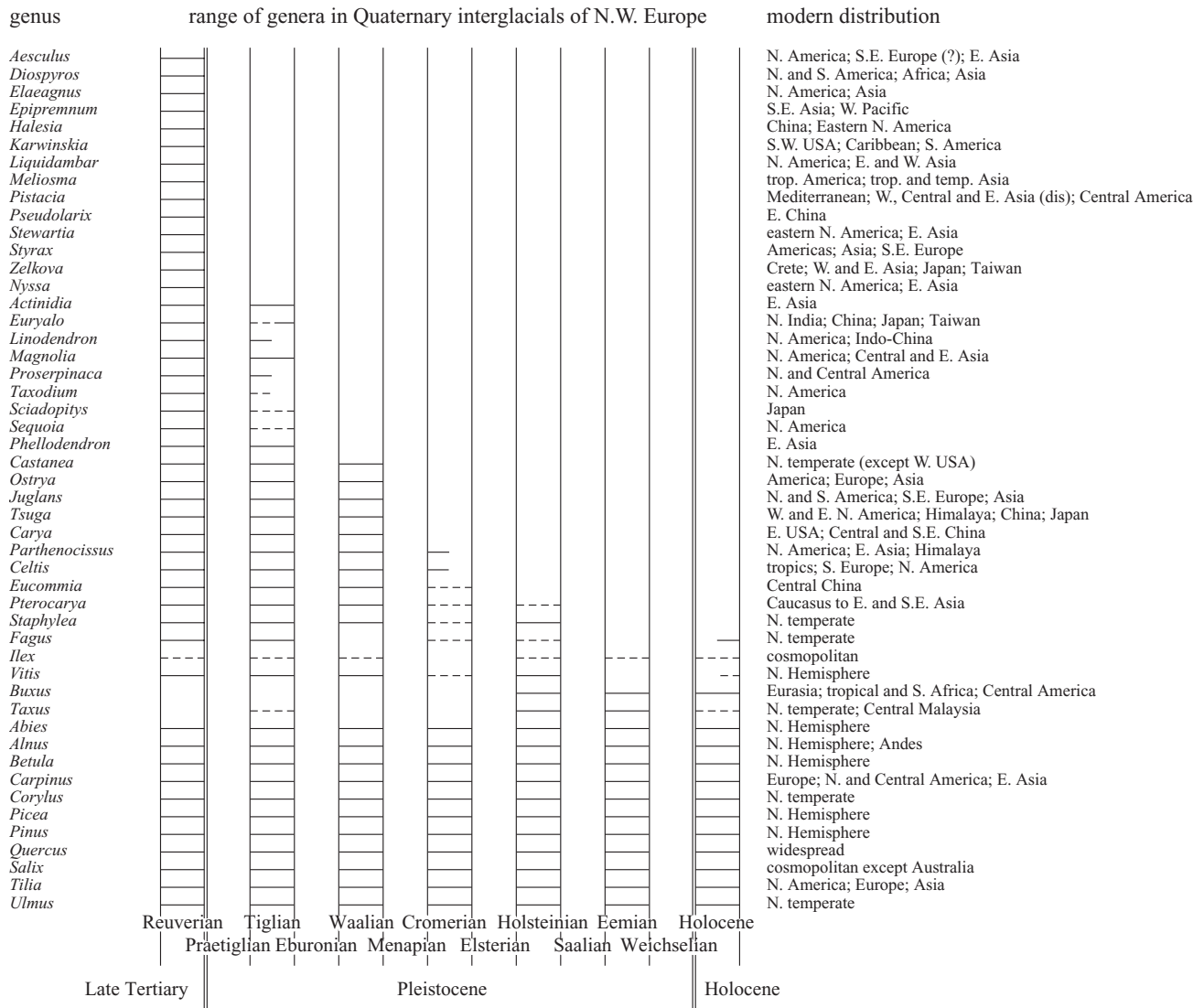


Figure 6. Tree taxa that disappeared from northwestern Europe during the Quaternary. The present-day distribution of these species is also indicated in the right-hand column. Dashed lines indicate a discontinuous presence during the interglacial (redrawn from Willis & McElwain (2002) after Van der Hammen 1983; Tallis 1991; Coxon & Waldren 1997).

southerly locations, possibly leading to geographical isolation. In comparison, those tree types that currently grow in the boreal forest, such as *Picea*, *Pinus* and some deciduous taxa including *Salix* and *Betula*, appear to have survived much closer to the ice-caps and therefore were probably never fully isolated during the cold stages of the Quaternary.

In summary, all of the available evidence indicates that the geographical responses of plant species to the climatic fluctuations during the Ice Ages in mid- to high-latitude regions were individualistic and undoubtedly complex (Jackson *et al.* 1997, 2000; Jackson & Overpeck 2000). When considering the role of the Quaternary Ice Ages in terms of genetic diversification and speciation, it is therefore important to differentiate between two general plant groups, namely those that were able to continue growing in northerly locations and those that were not. This distinction has important implications not only for the isolation, genetic diversification and speciation of plants, but also for the animals and early modern humans that relied upon these plants for food and shelter.

4. IS THERE EVIDENCE IN THE FOSSIL RECORD FOR INCREASED SPECIATION RATES DURING THE QUATERNARY?

Given that the fossil evidence suggests that at least some species were isolated in refugia on Milankovitch time-scales during the Quaternary Ice Ages, the next issue is the effect of this isolation. Is there evidence in the fossil record to support the idea that constant isolation and subsequent recombination of isolated populations resulted in increased genetic diversification and speciation, or were other mechanisms (i.e. stasis and extinction) more prevalent during the Quaternary?

Fossil evidence from mid- to high-latitude sites appears to be fairly unambiguous in suggesting that the predominant mode for the Quaternary was one of extinction (Van der Hammen *et al.* 1971; Tallis 1991; Coxon & Waldren 1997). In northwestern Europe, for example, there was a step-like disappearance of tree taxa with each subsequent glacial-interglacial cycle. However, in most cases, these extinctions were local, because these taxa have modern

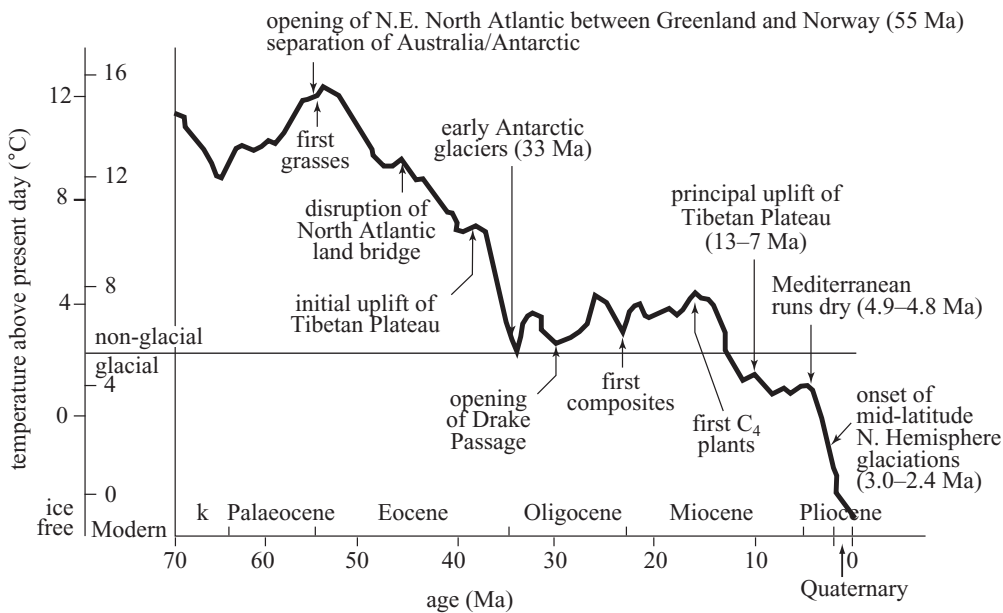


Figure 7. Temperature trends in the Tertiary, provided from oxygen isotope analysis of composite benthic foraminiferal records from Atlantic Deep Sea Drilling Program sites (Miller *et al.* 1987), where temperature is shown as degrees Celsius above present-day values. Note that the temperature scale determined from oxygen isotope analysis varies for an ice-free/modern world and that the transition between the two scales should be applied at the Eocene–Oligocene boundary (*ca.* 35 Ma). Against this temperature record are indicated major geological and botanical events during the Tertiary (from Graham (1999) and Willis & McElwain (2002)).

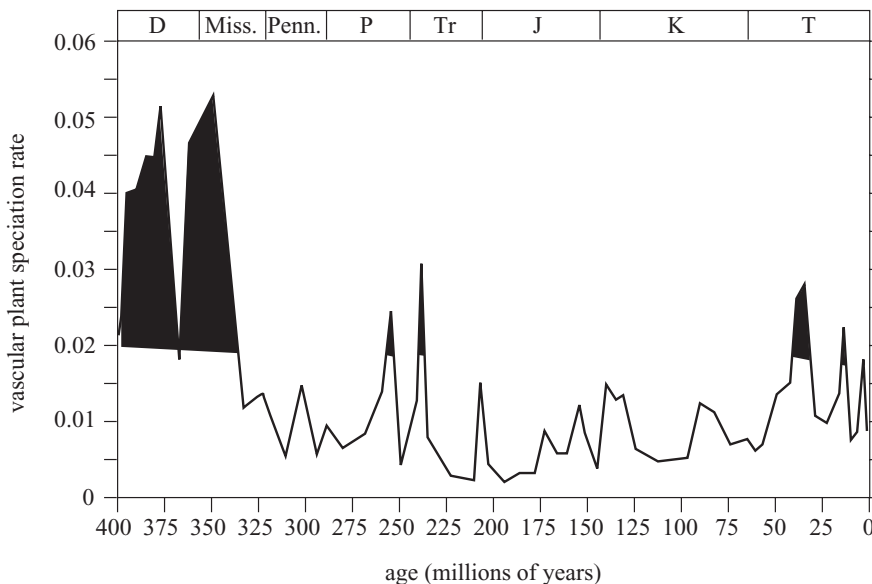


Figure 8. Speciation rate of vascular land plants over the past 400 Myr (Niklas 1997), where speciation rate is calculated as the number of new species appearing per geological stage time period per standing species diversity in each stage.

distributions in other parts of the world (figure 6). There are only a few examples where total extinction has been demonstrated, e.g. the Late Quaternary extinction of *Picea critchfieldii* in eastern North America (Jackson & Weng 1999).

So why is there no evidence for increased genetic diversification and speciation during the Quaternary? There are several possible explanations that can be broadly divided into two categories, one dealing with the nature of the fossil record, and the other with the length of time being examined. Both are important because speciation events may go undetected when the fossil record is too

fragmentary or when its temporal and spatial resolution is too crude. Most of the pollen record is biased in favour of wind-pollinated species and much of the plant macrofossil record in wetland or peatland species (Comes & Kadereit 1998). Levels of identification of fossil material are also poor, and in many circumstances it is only possible to identify fossils to their genera. Thus, pulses of genetic differentiation and ultimately speciation may have occurred but gone unrecorded in the fossil record. If so, the potential of molecular techniques to identify the ancestry of current populations needs to be explored to full effect. This approach has already substantially illuminated our

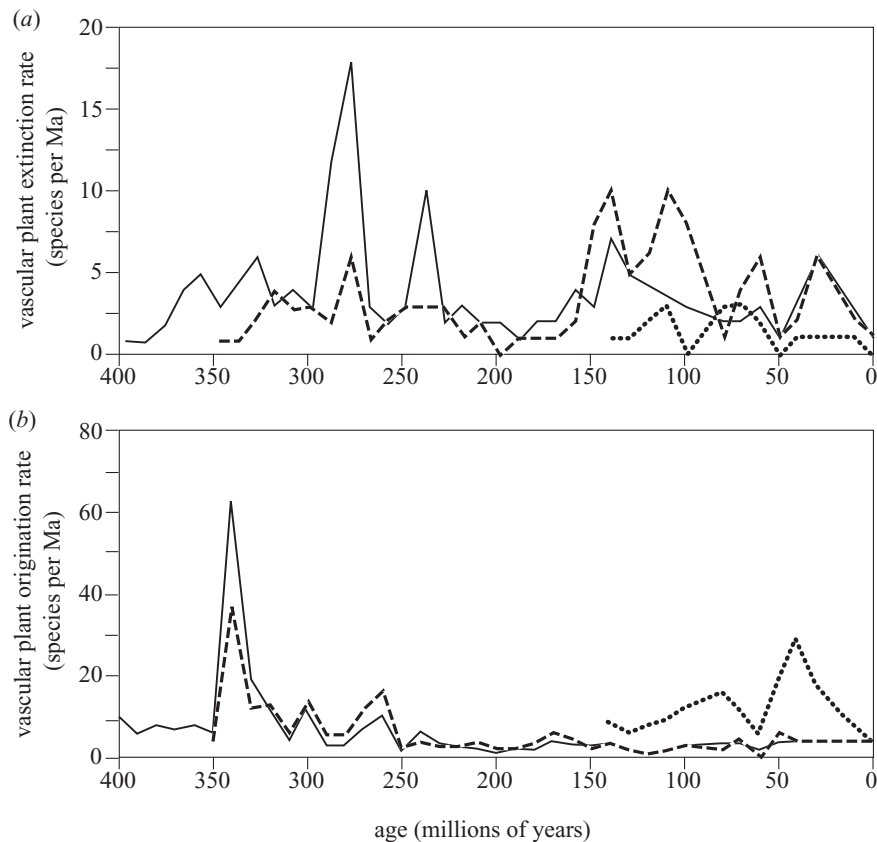


Figure 9. (a) Vascular plant extinction and (b) origination rate, over the past 400 Myr for the three plant reproductive clades (angiosperms (dotted lines); gymnosperms (dashed lines); and pteridophyte (solid lines)).

understanding of divergence times of plant lineages in the Ice Ages (Comes & Kadereit 1998; Hewitt 2000; see also Hewitt 2004; Kadereit *et al.* 2004; Lascoux *et al.* 2004) and, in the future, may show whether the lack of evidence for speciation during the Quaternary Ice Ages is an artefact of the fossil record.

A second explanation for a lack of evidence for increased speciation in the Quaternary fossil record revolves around the duration of isolation during the cold stages of the Quaternary with respect to the total length of Quaternary time (i.e. 1.8 Myr). Is it the case that isolation was simply too brief for speciation events to have occurred in refugial populations? Although calculations indicate that up to 80% of the Quaternary imposed glacial conditions, these periods were interspersed with interglacial warming. Indeed, estimates suggest that the longest periods of isolation for plants before the geographical expansion and mixing of populations in the intervening interglacials would have been *ca.* 100 kyr. Is this long enough for genetic variation to have become expressed phenotypically as to engender new species and record them as fossils? Or is it the case that intermixing in subsequent interglacials removed the accumulated genetic differentiation thus effectively resulting in stasis? Again the molecular record has much to offer through the identification of divergence times. So too does an examination of the longer-term geological record.

Such an examination indicates that the major radiations in the plant fossil record occurred over many millions of years, whereas the Quaternary glaciations barely afforded isolation through 2 million years (Niklas 1997; Willis &

McElwain 2002). In this regard, timing is everything. For example, based on an extensive analysis of the Phanerozoic record for plant life (410 Ma) (Niklas *et al.* 1983), the average duration of a fossil angiosperm species is *ca.* 3.5 Myr and new species appear about every 0.38 Myr (Niklas 1997). Taking these first estimates, therefore the average speciation rate that can be adduced from the fossil record is roughly one new species every 10% of the average species lifetime. If we assume that the average generation time of an individual (from seed to sexual maturity) is *ca.* 5 years, a speciation event occurs roughly once in every 76 000 generations (Niklas 1997), which is an ample number of sexual reproductive cycles for genetic divergence to have occurred in isolated plant populations during the Quaternary. An important caveat, however, is that 'averages' can be very misleading. The generation times for tree-sized species are, on average, much longer than 5 years, whereas those of annuals are 1 year. Therefore, different 'growth forms' (e.g. annual versus perennial, particularly arborescent, plants) are expected to respond differently in terms of genetic divergence during equivalent periods of isolation. Indeed, there are examples of tree species that have been isolated for up to 20 Myr through continental plate movements that nevertheless still interbreed and so remain classified as a single species (Raven *et al.* 1992). By contrast, there are herbaceous species where molecular and morphological evidence indicate genetic divergence leading to speciation in the past 100 kyr (see Kadereit *et al.* 2004). Therefore, all that can be said is that it is possible that increased speciation rates are not apparent during the Quaternary because the duration of

isolation was simply too brief, especially for arborescent species. Under these circumstances, it is desirable to examine speciation and extinction patterns during the past 40 Myr, rather than during only the past 1.8 Myr, because the former spans the whole period from the first development of ice sheets on the Antarctica continent heralding the transition to an 'icehouse' Earth (figure 1).

5. ARE THERE OBVIOUS DIFFERENCES BETWEEN SPECIATION RATES OF ICEHOUSE AND GREENHOUSE EARTH?

The factors responsible for the build-up of ice in the Southern Hemisphere from *ca.* 40 Ma are complex. It is now generally accepted that it was caused by a combination of factors, including continental plate movements, associated changes in patterns of oceanic and atmospheric circulation and rates of weathering, and a long-term decline in atmospheric CO₂ (Bernier 1995; Condie & Sloan 1998; Ruddiman 2001; Zachos *et al.* 2001). The details of these changes are not significant here. What is important is that the climatic conditions that these changes brought about (including global cooling, increased aridity and a lowering of atmospheric CO₂) started *ca.* 55 Ma as evidenced by reconstructions obtained from various proxies, including temperature records from δ¹⁸O measurements in ocean cores (Zachos *et al.* 2001; figure 7). These longer-term climate trends were superimposed on the variations in insolation at Milankovitch time-scales, resulting in increased amplitude of climate variability and, closely associated with this, the mechanisms forcing isolation of populations.

If the speciation rates of vascular land plants, calculated as the number of new species appearing per geological stage time period per standing species diversity in each stage (Niklas 1997), are plotted against geological age, some interesting patterns emerge (figure 8). Even though the first angiosperms (flowering plants) appeared in the fossil record from *ca.* 140 Ma followed by their radiation in the Mid-Cretaceous (*ca.* 100 Ma) (Niklas 1997; Willis & McElwain 2002; figure 9), the highest speciation rates of vascular plants over the past 150 Myr occurred between 40 and 35 Ma. In addition, if these rates are examined as origination and extinction rates (species per million years) and separated into the three higher-order groups of angiosperms, gymnosperms and pteridophytes, the high origination rate is due to angiosperm speciation, whereas gymnosperms and pteridophytes undergo relatively high extinction rates (figure 9).

These patterns suggest that the redistribution, recombination and isolating mechanisms associated with increasing extremes of climate during Milankovitch time-scales may typically increase genetic diversification and speciation rates. Therefore, although we do not see changes in the fossil record during the past 1.8 Myr (*i.e.* the Quaternary), increased speciation rates are apparent during the longer time interval known to have climatic features of an icehouse Earth (*i.e.* the past 55 Myr). However, as noted, several large-scale events occurred during the past 55 Myr and it could be argued that global environmental change associated with any of these may have provided the necessary triggering mechanism for speciation. Ideally, we need much finer-resolution and long-

term terrestrial records over this time interval to discern pulses of speciation and whether these accord with Milankovitch frequencies. Until these are forthcoming, another approach is to consider previous intervals in the geological record of icehouse Earth and to compare the vascular plant speciation rates with intervening periods of greenhouse Earth.

The geological evidence indicates that one of the longest and most extensive intervals of icehouse Earth in terms of its latitudinal extent was the Carboniferous–Permian Ice Age which occurred between *ca.* 360 and 286 Ma (Crowley *et al.* 1987; Crowley & North 1991; Crowley 1998). This interval saw widespread continental glaciation in the Southern Hemisphere, and global cooling and increased aridity in mid to high latitudes. Speciation rates of vascular land plants during this time interval (figure 8) appear to have increased, at least for about the first 30 Myr of glacial conditions (360–330 Ma). This interval probably experienced the greatest amount of speciation in the Earth's history, given that the high apparent speciation rate during the Devonian is probably inflated as the result of low standing diversity and extinction rates. Pteridophytes and gymnosperms both had high rates of origination during this interval of time against a backdrop of relatively low extinction rates (figure 9). Similar to the Tertiary, however, the period between 360–280 Ma was also one of active continental plate movement (Condie & Sloan 1998). It is therefore once again debatable whether the apparent increased speciation rates during the Carboniferous resulted from climatic changes occurring at Milankovitch time-scales or whether they reflect longer-term trends. Examination of more detailed temporal records (both fossil and molecular) from these two periods of icehouse Earth is essential to addressing this question adequately and should be the focus of future research to examine the significance of the Ice Ages in plant diversification and speciation.

6. CONCLUSIONS

Four conclusions can be drawn from our examination of the fossil record about the effect of the Quaternary Ice Ages on plant macroevolution.

- (i) The increasing amplitude of climatic variation and uniquely low atmospheric CO₂ concentrations occurring during the Quaternary were attended by significant floristic responses to environmental changes at Milankovitch time-scales. These changes were more pronounced and of a different kind than in many other previous time intervals. For example, during the Late Pliocene, the effect of climate changes at Milankovitch time-scales was predominantly changes in the dominant species in plant communities. By contrast, climatic changes at Milankovitch time-scales of the very same kind during the Quaternary were predominantly attended by migration, isolation and local extinction, which are traditionally thought to foster speciation.
- (ii) The responses of plant species to the Quaternary Ice Ages were individualistic and complex. Although some species experienced extensive isolation in time and space and survived in predominantly southern

Table 1. Factors favouring speciation, extinction or stasis of plant populations in an allopatric speciation model.

factors	favouring speciation	favouring extinction	favouring stasis	explanation
small isolated populations	✓	✓	×	low genetic variance and the potential for rapidly fixed allelic variants or mutations would favour speciation. The imposition of ecological stress or inbreeding depression (because of the rapid accumulation of recessive deleterious genes, i.e. increase in homozygosity) would favour extinction
large or contiguous populations	×	×	✓	
fluctuating population size (owing to founder effects)	✓	✓	×	founder effects could provide novel adaptive allelic combinations that would favour speciation, whereas maladaptive combinations would favour extinction
stable population size	×	×	✓	
self-pollination	✓	×	✓	severely restricts gene flow among populations; favours the emergence of adaptive mutations, but also favours stasis in the absence of adaptive mutations
self-incompatibility in pollination	×	×	✓	necessitates out-breeding, thereby increasing gene flow among neighbouring individuals or populations and decreasing the probability of reproductive isolation (and thus allopatric speciation)
unequal males and females (in dioecious systems)	✓	✓	×	a redundancy of ovulate flowers in a population can either result in extinction or genetic diversity, which in turn favours speciation with the appearance of adaptively functional mutations or chromosomal variants
equal males and females (in dioecious systems)	✓	×	×	favours high genetic diversity
short-lived seed banks	×	✓	×	if environmental conditions become too extreme, they are likely to exceed the tolerance limits of most or all variants left behind by a population
long-lived seed-banks	×	×	✓	populations can be recruited when environmental conditions return to normal
ecological specialists	×	✓	×	if an organism is a specialist and if the environment changes rapidly, it is likely that the niche of the organism will disappear, so speciation and stasis are not favoured
ecological generalists	×	×	✓	adaptation to many habitat types increases the probability of surviving rapid environmental changes or local disturbance

refugia, other species survived near the edges of icecaps (Jackson *et al.* 1997, 2000; Willis *et al.* 2000; Willis & Van Andel 2004). Thus, the 'southerly refugial' model for mid-latitude regions, as originally envisaged, probably requires significant modification. Plant species (and perhaps different growth forms) appear to have responded individually to the extremes of climate change, with southerly isolation occurring in only some species. The fossil evidence also indicates that isolation in southerly refugia was more common for angiosperms than for gymnosperms, possibly because the latter are, on the whole, more plastic in their response to environmental change compared with angiosperms.

- (iii) There is no evidence from the fossil record for increased speciation rates over the past 1.8 Myr. Indeed, in mid-latitude regions, the Quaternary appears to have been a time of extinction rather than speciation, which in most cases appears to have been localized. For example, all of the tree species that went extinct in northwest Europe continue to survive elsewhere in the world (Coxon & Waldren 1997). There are three possible explanations for this apparent 'lack of speciation'. First, barriers to gene

flow established during the comparatively brief duration of the Quaternary Ice Ages may have subsequently broken down during the intervening interglacials. If so, previously isolated populations may have interbred such that the fossil record gives the appearance of species stasis. Second, the resolution of the fossil record may be insufficient to detect genomic and long-lasting diversification. This possibility may be resolved by molecular studies in tandem with biogeographic analyses of extant taxa. Third, the length of time considered (i.e. the past 1.8 Myr) may be too short for high speciation rates to have occurred. The trend in global cooling resulting from continental plate movement and reduction in atmospheric CO₂ had already begun 55 Ma and, from *ca.* 40 Myr onwards, terrestrial ice sheets began to build in the Southern Hemisphere.

- (iv) An examination of speciation rates over the past 410 Myr, which spans several periods of icehouse and greenhouse Earth, indicates that unusually high vascular plant speciation rates occurred during intervals of icehouse Earth (e.g. Carboniferous and Tertiary) compared with intervening greenhouse intervals. The single exception is that of the Late

Permian–Early Triassic time interval. However, these high icehouse speciation rates may have resulted from environmental changes at time-scales longer than those of Milankovitch oscillations. If so, comparisons of the speciation rates of the Quaternary with those of other time periods are problematic at best, until such time that the Phanerozoic plant fossil record is resolved at a finer temporal and spatial level.

Overall, we conclude that the evolutionary responses of different groups of plants to the same environmental change are complex (table 1). In particular, a distinction has to be made between those plants that are able to withstand the extremes of glacial conditions and those that cannot. Generation times are also important as are different ‘growth forms’, which may respond differently in terms of genetic divergence rates during isolation regardless of differences in the duration of isolation. We caution not to place too much emphasis on tree species (in particular angiosperms) because this excludes a pluralistic and comprehensive understanding of the effects of the Ice Ages on biotic composition as a whole. Given the fact that some of the highest speciation rates of vascular land plants in the Earth’s history have occurred during Earth icehouse intervals, these rates might indeed have been considerable during the Quaternary.

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Discussion

W. G. Chaloner (*Geology Department, Royal Holloway, University of London, Egham, UK*). If we accept that the evidence for accelerated plant evolution through the Quaternary is not apparent in the fossil plant record, is it not possible that there were at least significant changes in ecological characteristics such as the range of climatic tolerance, without those changes being linked to recognizable speciation? How confident can we be that the range of climatic tolerance of a living species can be attributed to that species, when seen in a Quaternary pollen record? So much of our interpretation of Quaternary palaeoecology is based in effect on that type of extrapolation that I believe this question deserves serious consideration.

K. J. Willis. We agree that significant ecological, physiological or reproductive changes in heritable traits can occur in the absence of recognizable (morphological) speciation. Indeed, a change in a species range brought on by a physiological adaptation may represent a true speciation event even in the absence of a morphological change. Importantly, the whole question of the magnitude and type of genetic change required to call a particular organ-

ism a ‘new species’ is opened by your question. Clearly, when addressing rates of speciation (or extinction) in the fossil record, we are really using the morpho-species concept. However, we know from present-day examples that reproductive barriers exist between morphologically otherwise identical organisms (sibling species). So, many speciation (and pseudo-extinction) events may go undetected in the fossil record. Under these circumstances, we can only rely on the systematist to identify ‘species’ in the fossil record and we have to be wary of the limitations of the fossil record.

S. Knapp (*The Natural History Museum, London, UK*). The Ice-Ages model is based on allopatry. How do you think other modes of speciation were affected by the Ice Ages?

K. J. Willis. Allopatric speciation is clearly the model in the mind of most authors speculating on how organisms might have responded to the Ice Ages. We agree, however, that this is a particularly zoocentric perspective that ignores the high frequency of sympatric speciation observed for plants. Sympatric speciation appears not to be profoundly affected by population size (large or small), but rather appears to occur at a comparatively uniform rate within lineages but not across lineages (e.g. ferns and angiosperms). In this regard, the null hypothesis is that sympatric speciation is largely unaffected by Ice-Age events, a sort of *baso profundo*.

GLOSSARY

LGM: last glacial maximum