

IDEA AND  
PERSPECTIVE

## Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation?

Jens-Christian Svenning<sup>1\*</sup> and  
Flemming Skov<sup>2</sup>

<sup>1</sup>Department of Biological  
Sciences, University of Aarhus,  
Ny Munkegade 1540, DK-8000  
Aarhus C, Denmark

<sup>2</sup>Department of Wildlife  
Ecology and Biodiversity,  
National Environmental  
Research Institute, University of  
Aarhus, Grenaaavej 14, DK-8410  
Rønde, Denmark

\*Correspondence: E-mail:  
svenning@biology.au.dk

**Abstract**

The relative importance of contemporary climate and history as controls of geographical diversity patterns is intensely debated. A key example is the controversy over the extent to which temperate tree distributions and diversity patterns reflect postglacial dispersal limitation. Here, we focus on Central and Northern Europe, and show that recent estimates of tree migration rates  $< 100 \text{ m year}^{-1}$  imply that many species have probably not reached equilibrium with climate in this region. We then demonstrate that geographical accessibility from glacial refuges explains 78% of the geographical variation in the region's tree diversity and is a much stronger diversity predictor than climate. Finally, we show that realistic estimates of migration rates can be derived from the observed tree diversity pattern by assuming it to be purely dispersal driven. In conclusion, the tree diversity pattern in Central and Northern Europe could, to a large extent, be a result of postglacial dispersal limitation.

**Keywords**

History, macroecology, migration rate, non-equilibrium, postglacial recolonization, species richness, temperate trees

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**INTRODUCTION**

It is widely argued in ecology that large-scale patterns in diversity are predominantly a product of contemporary environmental conditions, notably climate, at least within continents (e.g. Currie 1991; Hawkins *et al.* 2003). However, this view has repeatedly been challenged by authors emphasizing non-equilibrium historical mechanisms (e.g. McGlone 1996; Graham *et al.* 2006). The debate has often focused on tree species distribution and diversity patterns in Europe and North America, two regions that were strongly affected by the Pleistocene ice ages. In both regions, most tree species have traditionally been assumed to have been restricted to southern refugia during cold periods, such as the Last Glacial Maximum (LGM) 21 000 years ago (Bennett *et al.* 1991). While recent studies have shown trees to have been widespread in eastern North America during the LGM (Jackson *et al.* 2000; McLachlan *et al.* 2005), and to a much more limited extent also in Europe (Willis & van Andel 2004), it remains clear that glacial climate had strong impact on tree species distributions in these regions. In the 1970s and early 1980s, the dispersal limitation was proposed to have caused strong time lags in the range responses of

temperate trees to postglacial warming in North America and Europe (Davis 1976; Huntley & Birks 1983). However, subsequently this view was abandoned and tree species distributions were argued to be largely in equilibrium with climate (Webb 1986; Huntley *et al.* 1989; Sykes *et al.* 1996). In the 1990s, this equilibrium view was bolstered by theoretical studies that emphasized the potential for extremely rapid tree migration rates (Pitelka & Plant Migration Workshop Group 1997; Clark *et al.* 1998). Recently, however, the pendulum has begun to swing back: the earlier theoretical arguments for very fast migration rates have been shown to be based on ecologically unrealistic modelling assumptions (Clark *et al.* 2001). Palaeoecological and phylogeographical studies have found evidence for more widespread and more northern refugia for a number of species, implying that postglacial migration rates have been overestimated in the earlier studies (McLachlan *et al.* 2005; Anderson *et al.* 2006; Yansa 2006). Some recent studies of tree distributions and diversity patterns have concluded that many species are still strongly dispersal limited in Europe (Svenning & Skov 2004, 2005), and that small-range species remain associated with their LGM refugia (Svenning & Skov 2007). Nonetheless, other studies

continue to favour the opposite conclusion and argue that tree distributions are largely in equilibrium with climate (Chaine & Beaubien 2001; Pearson & Dawson 2003; Tinner & Lotter 2006). The argument over the extent to which tree species ranges have been able to track the postglacial climate changes is not only of theoretical importance, but also crucial for assessing the potential impact of future climate changes. Modelling results based on no migration have consistently predicted much greater losses of species than if unlimited migration is assumed (Thomas *et al.* 2004; Thuiller *et al.* 2005).

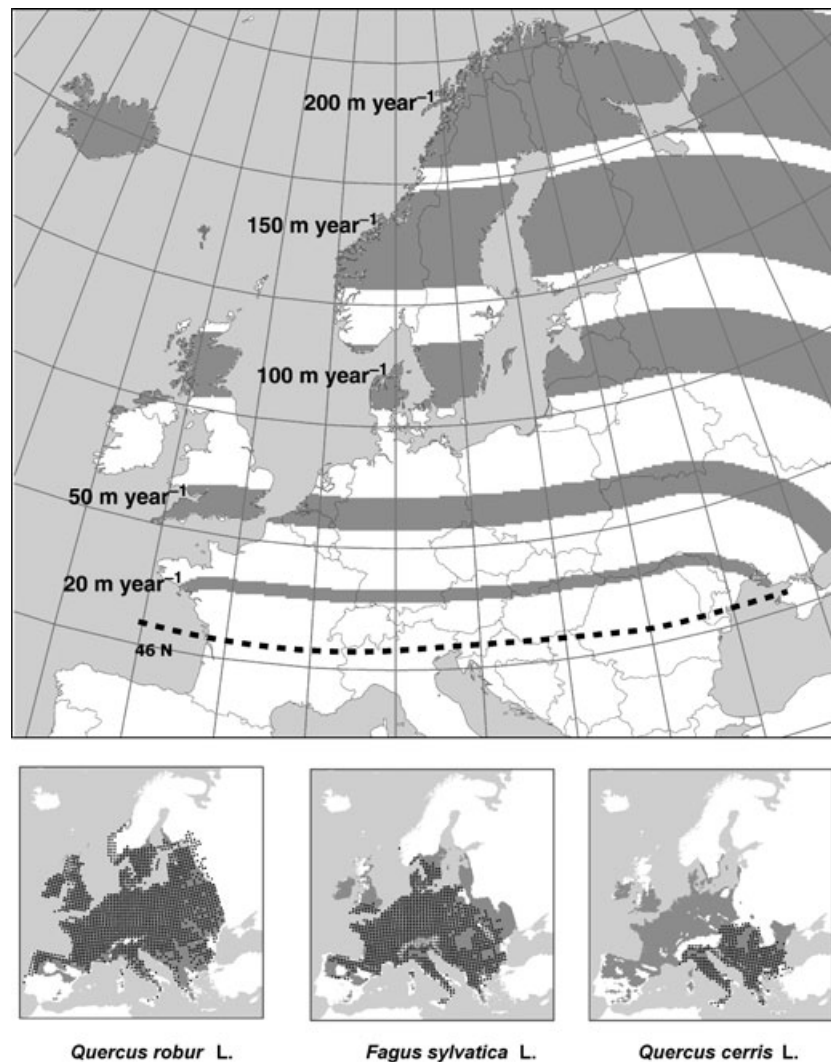
Here, we use geographically explicit modelling to investigate the extent to which the observed tree diversity and distribution patterns in Europe could be driven by limited dispersal out of the glacial refugia. Dispersal limitation here refers to range limitation caused by the migration process *per se*, notably lacking or slow seed arrival due to barriers to dispersal, localized dispersal, or low fecundity, as well as slow establishment once arrived, and not by limiting environmental conditions at the range margin. As our aim is to investigate the potential role of postglacial dispersal limitation, given only simple assumptions, other factors such as climate, landscape environmental permeability to migration, and species life history are largely ignored. We use data on tree species distributions from Atlas Florae Europaeae (AFE), which uses a mapping unit of  $\approx 50 \times 50$  km (Jalas & Suominen 1972–94). Russia, Belorussia, Ukraine and Moldova were excluded due to incomplete AFE coverage. Trees were defined as in Svenning & Skov (2004). Our results show that recent estimates of postglacial migration rates imply that many European tree species have probably not reached equilibrium with climate, that a simple measure of geographical accessibility from glacial refuges explains most of the variation in tree diversity in Central and Northern Europe, and that realistic estimates of migration rates and glacial refuge locations can be derived from the observed tree diversity pattern by assuming it to be purely dispersal driven.

#### HOW FAR COULD TREES HAVE MIGRATED GIVEN REALISTIC MIGRATION RATES?

Traditional palynology-based estimates of postglacial tree migration rates in Europe range from 25 to 2000 m year<sup>-1</sup>, with nearly two-thirds of the taxa investigated migrating no faster than 500 m year<sup>-1</sup> (Huntley & Birks 1983). However, these estimates are not representative of average postglacial tree migration rates for a number of reasons: perhaps most importantly, they were not estimated for taxa that failed to expand broadly (Huntley & Birks 1983) and hence are biased towards species with large postglacial range expansions. The importance of this bias is especially clear

when one considers that most European tree species have small southern ranges. Additionally, for many taxa the migration rates were computed for groups of species with similar pollen, e.g. deciduous *Quercus*, and not for single species (Huntley & Birks 1983), something that will also bias estimates upwards and hide slowly expanding species within the groups. Finally, as mentioned above rates have been overestimated for at least some taxa due to their more northern and widespread refuges than traditionally thought of (McLachlan *et al.* 2005; Anderson *et al.* 2006; Yansa 2006). Hence, typical postglacial migration rates for the North American *Acer rubrum* L. and *Fagus grandifolia* Ehrh. are <100 m year<sup>-1</sup> instead of 150–200 m year<sup>-1</sup>, and 300 m year<sup>-1</sup> instead of >1000 m year<sup>-1</sup> for *Picea glauca* (Moench) Voss (McLachlan *et al.* 2005; Yansa 2006). In Europe there is only clear evidence to suggest full-glacial refuges for temperate (non-boreal) trees as far north as southernmost Central Europe (Krebs *et al.* 2004; Willis & van Andel 2004; Magri *et al.* 2006), but such refuges are also substantially farther north than the extreme southern refuge locations sometimes proposed (Petit *et al.* 2002). Overall, most species probably migrated at average rates much lower than 500 m year<sup>-1</sup>. New mechanistic modelling similarly suggests that tree species migration rates will often be < 100 m year<sup>-1</sup> and that rates < 10 m year<sup>-1</sup> are not unrealistic (Clark *et al.* 2001). Figure 1 shows how far tree species could have expanded from the general southern refuge regions given more realistic migration rates. From this it is clear that migration rates of < 100 m year<sup>-1</sup> would be likely to cause many temperate tree species ranges to have failed to reach approximate equilibrium with present climate despite >10 000 years of relatively warm climate. Hence, the low range filling estimated for many European tree species by Svenning & Skov (2004) using bioclimatic envelope modelling is expected if such low migration rates apply (Fig. 1; also cf. Welk & Bruehlheide 2006; Svenning *et al.* 2006): a limited set of early, fast expanders like *Quercus robur* L. are probably largely in equilibrium with climate (Fig. 1). In contrast, many other species like *Fagus sylvatica* L. and *Quercus cerris* L. clearly are not (Fig. 1; Svenning & Skov 2004). Climatic analyses suggest that *Fagus sylvatica* has not yet reached its potential northern range limit in Britain (Fang & Lechowicz 2006), a result that is confirmed by its strong invasiveness beyond its native range throughout the British Isles (Watt 1931; Peterken 1996). It also appears to still be expanding in Scandinavia (Björkman 1999). *Quercus cerris* is naturalized and invasive as far north-west of its native south-eastern European range as England (Peterken 1996).

The above considerations are also relevant for other groups of organisms with similar LGM refuge locations, e.g. forest herbs, which are known to migrate very slowly, at 20 m year<sup>-1</sup> or less (Honnay *et al.* 2002). Hence, there is

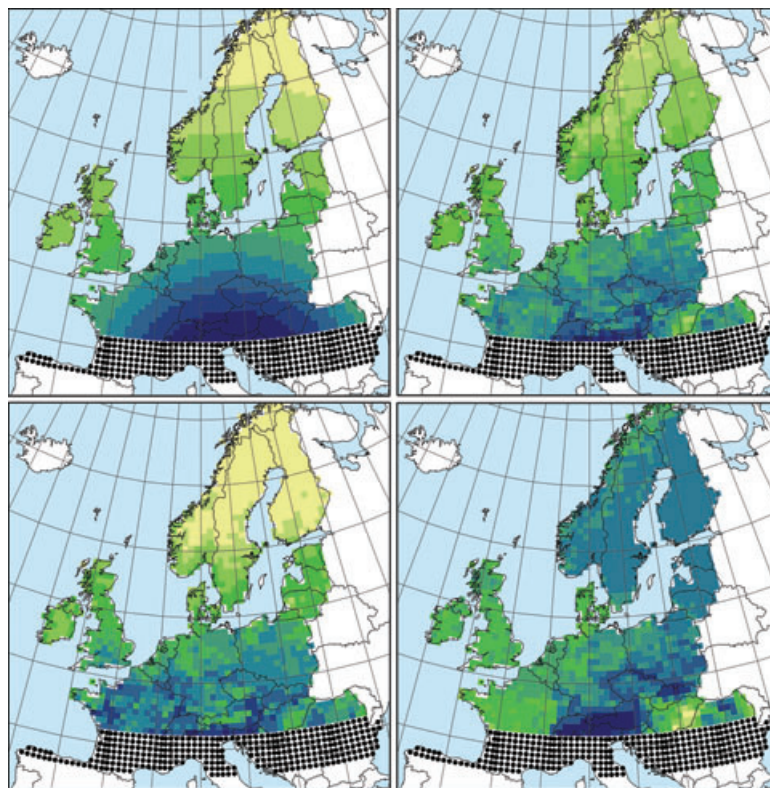


**Figure 1** Top: The northern range limit that a tree species could have reached from 46° N, the maximum northern limit of temperate tree full-glacial refugia (Petit *et al.* 2002; Krebs *et al.* 2004; Willis & van Andel 2004; Magri *et al.* 2006) under various migration rates assuming 11 000–14 000 years for dispersal (i.e. the southern and northern limit of the band for each migration rate, respectively) are shown. Crimea and regions further east are not considered as refugia. Bottom: Current native distribution of three temperate tree species (dots) and their climatic potential range (shading), estimated using bioclimatic envelope modelling as in Svenning & Skov (2004).

good reason to believe that the herbaceous forest flora is also experiencing strong postglacial dispersal limitation and that many species have yet to reach the northern parts of their potential distributions within Europe, as also indicated by bioclimatic envelope modelling (Skov & Svenning 2004).

Can tree migration rates and hence the degree to which they fill their climatic potential range be predicted from the autecological characteristics? It might be expected that tree migration rates would reflect species' dispersal ability and therefore seed dispersal syndromes (Higgins *et al.* 2003). However, no relationship has been found between postglacial tree migration rates and dispersal syndrome, probably

reflecting the poor link between dispersal syndrome and long-distance dispersal in plants (Higgins *et al.* 2003), as well as the impact of external factors such as the landscape environmental structure on migration rates (Collingham & Huntley 2000). Hence, it is not surprising that two oaks such as *Q. robur* and *Q. cerris* with similar propagules (1–4 cm acorns) fill their climatic potential range to widely different degrees (Fig. 1). We suggest that the degree of dispersal limitation in European trees may mainly be determined by the number and location of the glacial refugia and the environmental permeability of the areas between the refugia and the main areas with suitable climatic conditions at the



**Figure 2** Top-left: The accessibility of each  $50 \times 50$  m grid cell in Central and Northern Europe to postglacial immigration from the ice age tree refugia, computed as the inverse of the summed distances to all grid cell in the source area (Southern Europe at  $43\text{--}46^\circ$  N). Top-right: The current native species richness of tree species (60 species in total, 2–31 species per cell) in Europe. Right: Bottom-left: The current native species richness of temperate tree species (45 species in total, 0–22 species per cell). Bottom-right: The current native species richness of boreal tree species (15 species in total, 0–10 species per cell). Colour coding corresponds to 10 equal frequency categories, with yellow over green to blue representing low to high accessibility and few to many species, respectively.

present time, i.e. extrinsic ecogeographical factors. Notably, it is easy to imagine that the cold-hardy *Quercus robur* had more and more northerly located refugia than *Q. cerris* and for this reason could achieve an earlier and faster postglacial spread. The first tree species to spread would have met much less competition from other tree species than late-spreading species, which would have had to spread through well-established late-successional forest communities. Svenning & Skov (2004) did in fact find a relatively strong positive correlation between range filling and cold hardness in European trees.

#### CAN CURRENT PATTERNS OF TREE DIVERSITY BE PREDICTED FROM A SIMPLE MEASURE OF ACCESSIBILITY FROM GLACIAL REFUGIA?

While it is evident that climate and to a lesser extent other environmental factors such as soil do constrain Europe-wide tree species diversity and distribution patterns (Walter & Breckle 1986; Pigott 1991; Sykes *et al.* 1996; Svenning &

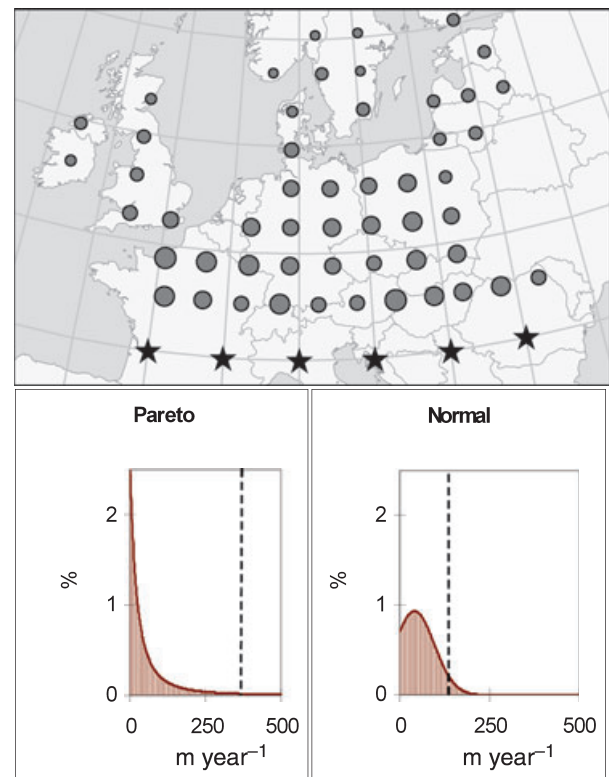
Skov 2005), we will now consider the extent to which these patterns could entirely be caused by dispersal.

If diversity patterns were entirely driven by limited dispersal out of the glacial refugia, we expect that the areas that are most accessible from the refugia, i.e. located closest to the greatest number of refugia, would harbour the greatest number of species. Figure 2 shows the pattern of accessibility across Central and Northern Europe as well as the observed pattern of tree species richness. The accessibility (ACC) of each grid cell in the receiving area (Central and Northern Europe) was computed as the inverse of the summed distances to all grid cells in the source area. Hence, the more distant a receiving grid cell on average is located from any one source cell the lower its accessibility. The source area was set to be Southern Europe at  $43\text{--}46^\circ$  N, as postglacial expansions into Central and Northern Europe primarily took place from or via this region (e.g. Petit *et al.* 2002; Magri *et al.* 2006). Albeit some of the most cold-tolerant tree species had LGM refugia somewhat further north, especially in eastern Europe (Willis & van Andel

**Table 1** Ordinary least-squares (OLS) and conditional autoregressive (CAR) multiple regressions of tree species richness in Central and Northern Europe ( $n = 1267$  cells; see Fig. 2) as a function of postglacial immigration accessibility (ACC), growing-degree-days (GDD), minimum winter temperature (TMIN) and water balance (WATB). Species richness is based on either all 60 tree species (Total), the 45 temperate (nemoral or Mediterranean), or the 15 boreal or alpine tree species (referred to as Total, Temperate, or Boreal, respectively) in Atlas Florae Europaeae. The connectivity distance parameter alpha was set to 3, as this caused spatial autocorrelation in the model errors to be reduced to negligible levels: Moran's  $i < 0.10$  (Total<sub>CAR</sub> and Temperate<sub>CAR</sub> models) or  $< 0.16$  (Boreal<sub>CAR</sub> model) for all 20 equal frequency distance classes). The standardized regression coefficients are given; n.s.,  $P \geq 0.05$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ . CAR models were fit in SAM 2.0 (Rangel *et al.* 2006)

	Total <sub>OLS</sub>	Total <sub>CAR</sub>	Temperate <sub>CAR</sub>	Boreal <sub>CAR</sub>
ACC	0.825***	0.811***	0.647***	0.625***
GDD	0.065 <sup>n.s.</sup>	0.009 <sup>n.s.</sup>	0.167***	-0.510***
TMIN	0.031 <sup>n.s.</sup>	0.069 <sup>n.s.</sup>	0.174***	-0.392***
WATB	0.012 <sup>n.s.</sup>	0.031 <sup>n.s.</sup>	0.004 <sup>n.s.</sup>	0.093*
$F(P)$	1153***	178.7***	257.9***	58.8***
$R^2$	0.785	0.815	0.871	0.544

2004), most tree species were probably restricted to areas south of 46° N (Bennett *et al.* 1991; Petit *et al.* 2002; Krebs *et al.* 2004; also cf. Magri *et al.* 2006). We note that the pattern of accessibility nicely predicts the peak in tree species richness in south-central Europe as well as the low tree species richness in marginal areas such as Ireland, Scotland, Fennoscandia, and north-eastern Europe (Fig. 2). Quantitatively, accessibility explained 78.1% of the geographical variation in richness in the study area ( $r^2$  from linear regression,  $P < 0.0001$ ,  $n = 1267$  cells). The relationship remained significant ( $P < 0.05$ ) if assessed as a correlation using Dutilleul's method to estimate the number of degrees of freedom corrected for spatial autocorrelation (computed using SAM 2.0: Rangel *et al.* 2006). For comparison, the key bioclimatic variables growing-degree-days (5° base; GDD), minimum winter temperature (TMIN) and water balance (WATB) together only explained 46.5% of the richness variation ( $R^2$  from multiple linear regression,  $P < 0.0001$ ,  $n = 1267$ ; climate data as in Svenning & Skov 2004, 2005). In a multiple linear regression with all the four factors, the standardized regression coefficient for ACC was the only significant coefficient and much greater than those for GDD, TMIN and WATB (Table 1). These results were robust to the influence of spatial autocorrelation as the corresponding conditional autoregressive (CAR) model produced identical results (Table 1). Hence, while ACC had a strong relationship to richness, the influence of climate on total tree species richness appeared negligible. The strong



**Figure 3** Top: Model layout for the stochastic optimization estimation of migration rates using six source refugia cells (asterisks) and 52 sink cells (circles). Circle size corresponds to the observed temperate tree species richness of the 50 × 50 km cell (range 3–18 species). Migration rates were estimated assuming the diversity pattern to be purely resulting from postglacial dispersal and assuming various probability distribution functions (see text for further details). Bottom: Optimized migration rate probability distribution functions: best Pareto distribution (left) and best normal distribution (right). Hatched lines show 95th percentile. See Table 2 for further results.

explanatory power of ACC, a simplistic measure of postglacial immigration opportunity, which ignores, for example, geographical biases in refuge locations and migration barriers, provides further support to the idea that postglacial dispersal limitation might be a strong determinant of current tree diversity and distribution patterns in Europe.

This interpretation is further supported when the richness of temperate (nemoral or Mediterranean) and boreal (including alpine) tree species ( $n = 45$  and 15, respectively) are considered separately. If the richness–accessibility relationship reflects postglacial dispersal limitation, we expect it to be positive for both groups, despite their opposite climatic preferences, as most of northern Central and Northern Europe was probably completely devoid of trees during the LGM and had to be recolonized

**Table 2** A summary of the results of the 10 best optimized solutions for each migration rate probability distribution function type. Model deviation is represented by the root-sum-of-squares (RSS) and the root-mean-square-error (RMSE). The parameter values and the median and 95th percentile limits for the migration rate probability distribution function are given as averages for the 10 best optimized solutions. The parameters defining the probability distribution functions were allowed to vary within the following limits: Pareto distribution [scale and shift parameter ( $a$ ): 1–100 m year<sup>-1</sup>, shape parameter ( $\theta$ ): 1–5], normal distribution [mean ( $m$ ): 5–500 m year<sup>-1</sup>, variance ( $s^2$ ): 5–500 m year<sup>-1</sup>], and uniform distribution [minimum (min): 0–25 m year<sup>-1</sup>; maximum (max): 25–2000 m year<sup>-1</sup>]. The time ( $t$ ) for migration was allowed to vary between 11 500 and 14 500 years, i.e. recolonization started some time during the Late Glacial.

Distribution	Deviation (RSS; RMSE)	Parameter values	Migration rate (median; 95th percentile) [m year <sup>-1</sup> ]
Pareto	15.8–15.9; 2.19–2.20	$a = 54.5$ ; $\theta = 1.44$ ; $t = 12\,405$	34; 382
Normal	27.4–27.8; 3.80–3.86	$m = 41.2$ ; $s^2 = 55.2$ ; $t = 11\,576$	57; 139
Uniform	32.7–32.9; 4.53–4.56	min = 3.9; max = 119.6; $t = 11\,565$	62; 114

subsequently. However, as boreal trees had more wide-spread and northerly refuges in Central Europe (Willis & van Andel 2004), we expect the relationship to be somewhat weaker for this group. These expectations were completely fulfilled by the autoregressive modelling results (Table 1).

#### CAN REALISTIC MIGRATION RATES BE INFERRED FROM THE OBSERVED DIVERSITY PATTERN?

In the following, we estimate probability distribution functions for species' postglacial migration rates from the observed geographical diversity pattern, assuming it to be driven purely by dispersal, and compare the resulting estimates to the revised migration rates discussed above. We used RISKOptimizer in the DecisionTools Suite (Palisade Corporation 2000) to estimate migration rate probability distribution functions that provide richness estimates that fit optimally to the observed pattern. The distribution of tree species across source LGM refugia and the time for recolonization were also optimized during the modelling. RISKOptimizer attempts to find optimal solutions to complex problems using stochastic simulation optimization with a genetic algorithm-based search strategy (Palisade Corporation 2000). See Fu *et al.* (2005) for a brief review of simulation optimization. Genetic algorithms and related simulation optimization procedures are often applied to find solutions to complex optimization problems in geography, economics and other areas (Openshaw & Openshaw 1997; Fu *et al.* 2005; Wilson & Dahl 2006). Genetic algorithms are inspired by evolutionary biology and iteratively apply operators such as inheritance, mutation and recombination in combination with selection of the best fit solutions to gradually develop a set of optimized candidate solutions (Openshaw & Openshaw 1997).

The model was set up as follows: six source refuge areas and 52 'sink' areas to be recolonized, each area corresponding to one AFE cell, were selected (Fig. 3). The source areas

were regularly placed close to the northern margin (45° N) of the main southern refuge areas (see above; Fig. 3). Sink cells were selected to systematically cover the part of the study area suited for temperate tree species today (defined by the combined present distribution of *Quercus robur* and *Corylus avellana* L.). We calculated a distance matrix between all source cells and all sink cells and calculated present-day temperate tree species richness for all sink cells. We focused on temperate tree species ( $n = 45$ ) to avoid the issue that some boreal species were relatively widely distributed in Eastern and Central Europe during the LGM (Willis & van Andel 2004). As we have no firm *a priori* knowledge of the type of the probability distribution function that characterizes species' migration rates, we ran the simulations using three types of distributions: the Pareto distribution implies that there are many species with relatively low rates and few species with high rates, the normal distribution allows for a unimodal distribution of rates (but truncated to avoid negative rates), while the uniform distribution assumes that all rates within the estimated limits are equally probable.

RISKOptimizer initially generated a set of 50 random solutions, where each solution consisted of a distribution of 45 species among the six source areas, the parameters for the given probability distribution of migration rates, and the time allowed for migration. Certain *a priori* constraints were placed on the allowable parameter and time values (Table 2), and each species had to be present in at least one of the source areas. RISKOptimizer gradually increased the fit of the set of solutions to the observed richness pattern by the following procedure: for each solution, a migration rate for each species was drawn from the selected probability distribution function and it was computed which sink cells the species could have reached given its refuge source locations and the time for recolonization. This procedure was repeated 100 times and the mean number of species reaching a given sink cell calculated to represent the



predicted values of the model solution. The fit of the solution was then represented by its deviation, computed as the root-sum-of-squares. The genetic algorithm repeatedly selected the solutions with the smallest deviation and based on these stochastically generated new solutions by operations such as recombination and mutation (Palisade Corporation 2000). The optimization was run until the general fit of the set of solutions was stable.

Table 2 shows the results from the 10 best solutions for each distribution type: a Pareto distribution of dispersal rates gave the best fit to the observed richness pattern (see also Fig. 3). Hence, assuming that the observed diversity patterns have arisen entirely through postglacial dispersal produced estimated migration rates ( $<100 \text{ m year}^{-1}$  for the majority of species) that are in line with the revised migration rates discussed above.

## CONCLUSION

A conservative interpretation of the presented results is that the major features of the geographical tree diversity observed in Central and Northern Europe could mainly be the result of postglacial dispersal limitation. While we acknowledge that our modelling is simplistic and that climate probably also constrains the observed patterns, our results raise the possibility that the importance of climate has been overestimated, and that of dispersal underestimated. The degree to which large-scale distribution and diversity patterns are limited by dispersal rather than climate should clearly remain an important research focus, being not only theoretically important, but also of crucial importance for developing credible estimates of the potential biodiversity impacts of future climate changes (Thomas *et al.* 2004; Thuiller *et al.* 2005). We suggest that progress is likely to come from an increased theoretical and empirical understanding of range dynamics and range limits, especially of the majority of species that have small ranges. Albeit dispersal limitation possibly play a stronger role in regions such as Europe that have been strongly impacted by Quaternary climatic changes, dispersal may well pose an important constraint in more stable regions, too (Tuomisto *et al.* 2003; Vormisto *et al.* 2004), for example due to relaxed selection against poor dispersal and little time for dispersal in the many young taxa produced by increased speciation (Dynesius & Jansson 2000). It will be an important challenge for future research to provide an understanding of the geographical variation in the importance of dispersal limitation as a control of diversity patterns.

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## REFERENCES

- Anderson, L.L., Hu, F.S., Nelson, D.M., Petit, R.J. & Paige, K.N. (2006). Ice-age endurance: DNA evidence of a white spruce refugium in Alaska. *Proc. Natl. Acad. Sci. USA*, 103, 12447–12450.
- Bennett, K.D., Tzedakis, P.C. & Willis, K.J. (1991). Quaternary refugia of north European trees. *J. Biogeogr.*, 18, 103–115.
- Björkman, L. (1999). The establishment of *Fagus sylvatica* at the stand-scale in southern Sweden. *Holocene*, 9, 237–245.
- Chaine, I. & Beaubien, E.G. (2001). Phenology is a major determinant of tree species range. *Ecol. Lett.*, 4, 500–510.
- Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G.A. *et al.* (1998). Reid's paradox of rapid plant migration: dispersal theory and interpretation of paleoecological records. *BioScience*, 48, 13–24.
- Clark, J.S., Lewis, M. & Horvath, L. (2001). Invasion by extremes: population spread with variation in dispersal and reproduction. *Am. Nat.*, 157, 537–554.
- Collingham, Y.C. & Huntley, B. (2000). Impacts of habitat fragmentation and patch size upon migration rates. *Ecol. Appl.*, 10, 131–144.
- Currie, D.J. (1991). Energy and large-scale patterns of animal- and plant-species richness. *Am. Nat.*, 137, 27–49.
- Davis, M.B. (1976). Pleistocene biogeography of temperate deciduous forests. *Geosci. Man*, 13, 13–26.
- Dynesius, M. & Jansson, R. (2000). Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proc. Natl. Acad. Sci. USA*, 97, 9115–9120.
- Fang, J. & Lechowicz, M.J. (2006). Climatic limits for the present distribution of beech (*Fagus* L.) species in the world. *J. Biogeogr.*, 33, 1804–1819.
- Fu, M.C., Glover, F.W. & April, J. (2005). Simulation optimization: a review, new developments, and applications. In: *Proceedings of the 2005 Winter Simulation Conference* (eds Kuhl, M.E., Steiger, N.M., Armstrong, F.B. & Joines, J.A.). Institute of Electrical and Electronics Engineers, Piscataway, New Jersey, pp. 83–85.
- Graham, C.H., Moritz, C. & Williams, S.E. (2006). Habitat history improves prediction of biodiversity in rainforest fauna. *Proc. Natl. Acad. Sci. USA*, 103, 632–636.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M. *et al.* (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117.
- Higgins, S.I., Nathan, R. & Cain, M.L. (2003). Are long-distance dispersal events in plants usually caused by non-standard means of dispersal? *Ecology*, 84, 1945–1956.
- Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B. & Hermy, M. (2002). Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecol. Lett.*, 5, 525–530.
- Huntley, B. & Birks, H.J.B. (1983). *An Atlas of Past and Present Pollen Maps for Europe: 0–13000 years ago*. Cambridge University Press, Cambridge.

- Huntley, B., Bartlein, P.J. & Prentice, I.C. (1989). Climatic control of the distribution and abundance of beech (*Fagus* L.) in Europe and North America. *J. Biogeogr.*, 16, 551–560.
- Jackson, S.T., Webb, R.S., Anderson, K.H., Overpeck, J.T., Webb, T., III, Williams, J.W. *et al.* (2000). Vegetation and environment in Eastern North America during the Last Glacial Maximum. *Q. Sci. Rev.*, 19, 489–508.
- Jalas, J. & Suominen, J. (eds) (1972–94). *Atlas Florae Europaeae: Distribution of Vascular Plants in Europe*, Vols 1–10. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki.
- Krebs, P., Conedera, M., Pradella, M., Torriani, D., Felber, M. & Tinner, W. (2004). Quaternary refugia of the sweet chestnut (*Castanea sativa* Mill.): an extended palynological approach. *Veg. Hist. Archaeobot.*, 13, 145–160+285.
- Magri, D., Vendramin, G.G., Comps, B., Dupanloup, I., Geburek, T., Gömöry, D. *et al.* (2006). A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. *New Phytol.*, 171, 199–221.
- McGlone, M.S. (1996). When history matters: scale, time, climate and tree diversity. *Glob. Ecol. Biogeogr. Lett.*, 5, 309–314.
- McLachlan, J.S., Clark, J.S. & Manos, P.S. (2005). Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, 86, 2088–2098.
- Openshaw, S. & Openshaw, C. (1997). *Artificial Intelligence in Geography*. John Wiley & Sons, New York.
- Palisade Corporation (2000). *Guide to RISKOptimizer*. Simulation Optimization for Microsoft® Excel. Palisade Corporation, Ithaca, NY.
- Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.*, 12, 361–371.
- Peterken, G.F. (1996). *Natural Woodland: Ecology and Conservation in Northern Temperate Regions*. Cambridge University Press, Cambridge.
- Petit, R.J., Brewer, S., Bordács, S., Burg, K., Cheddadi, R., Coart, E. *et al.* (2002). Identification of refugia and post-glacial recolonisation routes of European white oaks based on chloroplast DNA and fossil pollen evidence. *For. Ecol. Manage.*, 156, 49–74.
- Pigott, C.D. (1991). *Tilia cordata* Miller. *J. Ecol.*, 79, 1147–1207.
- Pitelka, L.F. & Plant Migration Workshop Group (1997). Plant migration and climate change. *Am. Sci.*, 85, 464–473.
- Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2006). Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Glob. Ecol. Biogeogr.*, 15, 321–327.
- Skov, F. & Svenning, J.-C. (2004). Potential impact of climatic change on the distribution of forest herbs in Europe. *Ecography*, 27, 366–380, 827–828.
- Svenning, J.-C. & Skov, F. (2004). Limited filling of the potential range in European tree species. *Ecol. Lett.*, 7, 565–573.
- Svenning, J.-C. & Skov, F. (2005). The relative roles of environment and history as controls of tree species composition and richness in Europe. *J. Biogeogr.*, 32, 1019–1033.
- Svenning, J.-C. & Skov, F. (2007). Ice age legacies in the geographic distribution of tree species richness in Europe. *Glob. Ecol. Biogeogr.*, 16, 234–245.
- Svenning, J.C., Normand, S. & Skov, F. (2006). Range filling in European trees. *J. Biogeogr.*, 33, 2018–2021.
- Sykes, M.T., Prentice, I.C. & Cramer, W. (1996). A bioclimatic model for the potential distributions of north European tree species under present and future climates. *J. Biogeogr.*, 23, 203–233.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C. *et al.* (2004). Extinction risk from climate change. *Nature*, 427, 145–148.
- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005). Climate change threats to plant diversity in Europe. *Proc. Natl. Acad. Sci. USA*, 102, 8245–8250.
- Tinner, W. & Lotter, A.F. (2006). Holocene expansions of *Fagus silvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? *Q. Sci. Rev.*, 25, 526–549.
- Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, 299, 241–244.
- Vormisto, J., Svenning, J.-C., Hall, P. & Balslev, H. (2004). Diversity and dominance in palm (Arecaceae) communities in terra firme forests in the western Amazon basin. *J. Ecol.*, 92, 577–588.
- Walter, H. & Breckle, S.-W. (1986). *Ecological Systems of the Geobiosphere 3: Temperate and Polar Zonobioses of Northern Eurasia*. Springer-Verlag, Berlin.
- Watt, A.S. (1931). Preliminary observations on Scottish beechwoods. *J. Ecol.*, 19, 137–157.
- Webb, T., III (1986). Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. *Vegetatio*, 67, 75–91.
- Welk, E. & Bruehlheide, H. (2006). There may be bias in R/P ratios (realized vs. potential range) calculated for European tree species – an illustrated comment on Svenning & Skov (2004). *J. Biogeogr.*, 33, 2013–2018.
- Willis, K.J. & van Andel, T.H. (2004). Trees or no trees? The environments of central and eastern Europe during the Last Glaciation. *Q. Sci. Rev.*, 23, 2369–2387.
- Wilson, W.W. & Dahl, B. (2006). Costs and risks of segregating GM wheat in Canada. *Can. J. Agric. Econ.*, 54, 341–359.
- Yansa, C.H. (2006). The timing and nature of Late Quaternary vegetation changes in the northern Great Plains, USA and Canada: a re-assessment of the spruce phase. *Q. Sci. Rev.*, 25, 263–281.

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