



# Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species

Wolfgang Willner, Romeo Di Pietro and Erwin Bergmeier

W. Willner (wolfgang.willner@vinca.at), Vienna Inst. for Nature Conservation and Analyses, Giessergasse 6/7, AT-1090 Vienna, Austria. – R. Di Pietro, Dept ITACA, Univ. of Rome “La Sapienza”, Via Flaminia 70, IT-00196 Rome, Italy. – E. Bergmeier, Dept of Vegetation and Phytodiversity Analysis, Albrecht von Haller Inst. of Plant Sciences, Univ. of Göttingen, Untere Karspüle 2, DE-37073 Göttingen, Germany.

The post-glacial migration of European beech *Fagus sylvatica* has been addressed by many studies using either genetic or fossil data or a combination of both. In contrast to this, only little is known about the migration history of beech forest understorey species. In a review of phytosociological literature, we identified 110 plant species which are closely associated with beech forest. We divided the distribution range of European beech forests into 40 geographical regions, and the presence or absence of each species was recorded for each region. We compared overall species numbers per region and numbers of narrow-range species (species present in <10 regions). A multiple regression model was used to test for the explanatory value of three potential diversity controls: range in elevation, soil type diversity, and distance to the nearest potential refuge area. A hierarchical cluster analysis of the narrow-range species was performed.

The frequency of range sizes shows a U-shaped distribution, with 42 species occurring in <10 regions. The highest number of beech forest species is found in the southern Alps and adjacent regions, and species numbers decrease with increasing distance from these regions. With only narrow-range species taken into consideration, secondary maxima are found in Spain, the southern Apennines, the Carpathians, and Greece. Distance to the nearest potential refuge area is the strongest predictor of beech forest species richness, while altitudinal range and soil type diversity had little or no predictive value. The clusters of narrow-range species are in good concordance with the glacial refuge areas of beech and other temperate tree species as estimated in recent studies. These findings support the hypothesis that the distribution of many beech forest species is limited by post-glacial dispersal rather than by their environmental requirements.

The flora and vegetation of Europe has been strongly affected by the climatic fluctuations of the Quaternary. Deciduous forests, which form the dominant natural vegetation of temperate and submediterranean Europe, were subjected to repeated range contractions and re-expansions following the cycle of glacial and interglacial periods. During the Last Glacial Maximum, deciduous forests were restricted to refuge areas in the southern part of Europe (Bennett et al. 1991, Prentice et al. 2000, Leroy and Arpe 2007). The postglacial recolonisation of the most important temperate tree species has been studied in recent papers using genetic and/or fossil data or species distribution modelling (Grivet and Petit 2003, Terhürne-Berson et al. 2004, Magri et al. 2006, Svenning et al. 2008a). In contrast to this, only little is known about the migration of herb and shrub species which grow in the understorey of these forests.

The most abundant deciduous tree species of the European temperate zone is the European beech *Fagus sylvatica*, hereafter: *Fagus*. Its distribution extends from the mountains of southern Europe (northern Spain, Italy, Greece) to the lowlands of southern England and southern Sweden (Jalas and Suominen 1976). The distribution limits

of *Fagus* can be explained mainly by its sensitivity to dry summers and extremely cold winters, although there is clear evidence that it has not yet recolonised its full potential range in northern Europe (Sykes et al. 1996, Bolte et al. 2007). Within its distribution range, *Fagus* is a highly competitive species, but it avoids waterlogged, saline, dry, and disturbed sites (Ellenberg 1996). Typically, it forms more or less monodominant stands, while in some mountain ranges European fir *Abies alba*, hereafter: *Abies* is codominant (Bohn et al. 2000/2003). In some types of deciduous forests (oak-hornbeam and ravine forests), *Fagus* is a constant, but minor companion species. The maximum altitudinal range of beech forests is reached in the Alps and Dinaric mountains, where *Fagus* is the dominant species between 400 and 1600 m a.s.l.

Given the wide geographical and ecological amplitude of *Fagus*, it is hardly surprising that the floristic composition of beech forest understorey is quite diverse. A good deal of this diversity can be explained by differences in altitude and soil conditions (Bergmeier and Dimopoulos 2001, Willner 2002, Di Pietro et al. 2004, Willner et al. 2004, Tzonev et al. 2006, Tsiripidis et al. 2007). Many of its understorey

species have a narrower ecological amplitude than beech itself and are therefore restricted to certain types of beech forest. However, an important part of the variation in beech forest composition appears to be rather difficult to explain by differences in ecological conditions. This kind of variation is usually related to geographical gradients (Dierschke 1990, Dierschke and Bohn 2004, Tsiripidis et al. 2007). Many understorey species occur only in a part of the distribution range of *Fagus*, some in wider areas, some only in a few mountain ranges. It has already for a long time repeatedly been suggested that this pattern might reflect the history of postglacial recolonisation from different refugia (Oberdorfer and Müller 1984, Dierschke and Bohn 2004). Recent studies showed that the distribution of many forest species may be limited by seed dispersal and colonisation capacity rather than by climate or other environmental factors (Honnay et al. 2002, Svenning and Skov 2007, Van der Veken et al. 2007, Svenning et al. 2008b). According to this dispersal limitation hypothesis, some species could fill their potential range to a large extent, while others have migrated only short distances from their refugia.

Species with their ecological optima in beech forests (in the following called “beech forest species”) are shade-tolerant and adapted to mesic conditions (Ellenberg 1996). Outside forest habitats, such species would not survive for a long time. Since these species are hardly represented in fossil-pollen and macrofossil sites, we have no direct evidence of their fate during the glacial period. Following the dispersal limitation hypothesis, their current distribution patterns should bear the imprint of postglacial migration history. Species numbers would be expected to be maximum close to refuge areas and to decrease with increasing distance from these areas. Regions where migration waves from two or more refugia met each other might exhibit equally high or even higher species numbers. The latter effect should be less pronounced if focusing on species which migrated only over short distances (“narrow-range species”). In this paper, we evaluate the explanatory power of historical versus environmental factors to explain the broad scale diversity patterns of European beech forest species. In addition to the analysis of species numbers we compare the geographical distribution of narrow-range beech forest species with the glacial refuge areas of European temperate trees, in particular *Fagus*, as estimated in recent genetic and paleobotanical studies.

## Data and methods

### Selection of beech forest species

The focus of the present study are the herb and shrub species that are closely associated with *Fagus* (i.e. those forest species which only rarely occur outside beech forest). For lack of a pan-European database of vegetation plot data, species selection was based on a review of phytosociological literature as well as on personal expert knowledge. We compiled all species given as “character species” of beech forests and closely related vegetation types (*Fagetalia sylvaticae* and *Luzulo-Fagetalia* sensu Rodwell et al. 2002) in phytosociological monographs. This preliminary list of beech forest species was slightly modified according to the

field expertise of the authors. Extremely rare and taxonomically problematic species were removed from the list if their presence or absence could not be verified for all regions. A potential problem is that the same species may have a different fidelity to beech forests in different regions, as in the case of *Orthilia secunda* and *Pyrola minor*, which are restricted to beech forests in the Italian Apennines and in the southern Balkans, but in the Alps occur more commonly in coniferous forests). However, we tried to select only species with high fidelity to beech forests throughout the species’ range. In the end, 110 species were selected for the analysis (Supplementary material 3). In contrast to many other studies on diversity patterns, our focus species represent a rather narrow spectrum of ecological niches. It is noteworthy that most of the species prefer base-rich beech forests, while none of them is exclusive to acidic beech forests: species that occur in acidic, but not in base-rich beech forests almost invariably also occur in acidic oak or coniferous forests (see Willner et al. 2004 for a historic interpretation of this observation). Species nomenclature follows Conti et al. (2005) for taxa occurring in Italy, and Tutin et al. (2001) for all other taxa.

### Delimitation of regions

To record the distribution of the selected species, the range of European beech forests was divided into 40 regions, serving as “operational geographic units” (Fig. 1). The decision to use irregularly delimited regions instead of a regular grid was based on the following considerations: 1) most data sources refer to geomorphological or political units. To assign these data to grid cells would be difficult even if the grid were very coarse. 2) The distribution of beech forests in southern Europe follows the main mountain ranges and would be quite inadequately covered by a regular grid unless the grid cells were very small. The

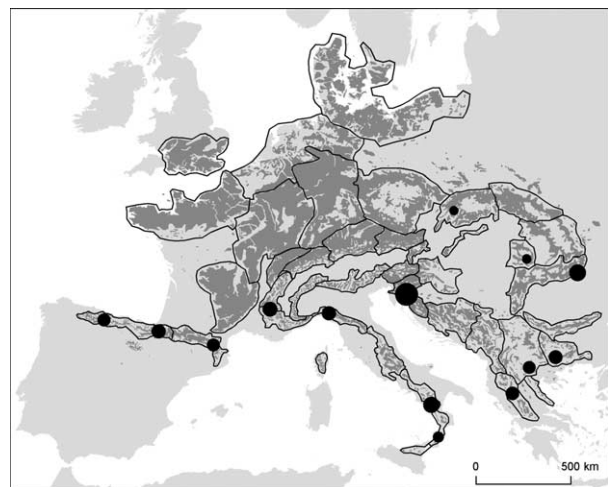


Figure 1. Location of potential glacial refuge areas of European beech forest species, defined as areas in which full-glacial populations of *Fagus*, *Carpinus*, and/or *Abies* most likely occurred according to paleobotanical evidence. Dot size roughly reflects refuge area size. The recent distribution of beech forests is given in dark grey. The black lines show the delimitation of regions used in this study.

delimitation of the regions was drawn as far as possible along obvious geomorphological structures. In the absence of clear geomorphological boundaries, the geographical classification of European beech forests by Bohn et al. (2000/2003) was followed. In the Balkans, political boundaries were also taken into account because most data from this part of Europe refer to certain countries. Regions tend to be larger in the north because the biogeographical patterns in the relatively flat landscapes north of the Alps are less complex than in the mountainous southern part of Europe. Small and isolated patches of beech forest outside the main ranges were not included.

## Data compilation

For each region, the presence or absence of each species was recorded. Data were preferably compiled from phytosociological data (mostly synoptic tables, but also single relevés where available). Additional information was derived from distribution maps and floras in order to avoid artificial absences in regions with scarce phytosociological records. Three degrees of species presence were distinguished: *r* (isolated occurrences covering <5% of the region's area), + (present in 5–20% of the region's area), 1 (present on >20% of the region's area). References of the data sources and the full species-by-region-matrix are given in the Supplementary material.

## Data analysis

A frequency distribution of range sizes of the selected 110 species, approximated by the number of regions in which a species is present, was calculated. To examine for possible effects of the unequal size of regions, we tried also an alternative approximation of range sizes: we transformed presence categories *r*, +, and 1 into 0.05, 0.2, and 1, respectively, multiplied with the area mapped as beech forest within each region (Bohn et al. 2000/2003), and calculated the sum over all regions. However, the form of the range size distribution was basically the same in both cases, so we preferred simple counts of regions. For this analysis as well as the following ones, presence-absence data were used, treating category *r* as absence in order to exclude isolated populations which might be the result of recent anthropogenic dispersal.

Overall species numbers and numbers of narrow-range species (species which are present in <10 regions) were calculated for each region, and species numbers were analysed using multiple linear regression. We generated three potential explanatory variables: range in elevation (calculated from a digital elevation model of 1 × 1 km grid size), soil type diversity (derived from the European Soil Database, <eusoiils.jrc.ec.europa.eu/ESDB\_Archive/ESDB/index.htm>), and postglacial dispersal history. Surface area was not used as explanatory variable, since it had a strong negative correlation with species richness, an obvious artifact of the larger size of regions towards the north. The first two variables represent spatial heterogeneity in ecological conditions within a region, a factor well known for explaining high species richness (Turner 2004). Only elevations and soil types within the area mapped as beech forests (Bohn et al.

2000/2003) were considered. Soil types that never occur under beech were excluded. All values were calculated using ArcView GIS 3.3.

For the third variable, postglacial dispersal history, we calculated for each region the minimum distance to the nearest potential refuge area of beech forest species (Fig. 1). Until recently only two refuge areas of European beech were generally accepted: the southern Apennines, and the Balkan peninsula (Huntley and Birks 1983, Taberlet et al. 1998). In contrast to this, Magri et al. (2006) confirmed additional refugia in northern Spain and the southwestern Alps and pointed out that the main source area for the colonisation of central and northern Europe was located in the northwestern Dinaric mountains (Slovenia, Croatia). In the southern Balkan peninsula (northwestern Greece, Macedonia, Pirin mountains), at least three different refugial populations could be distinguished, but they expanded only locally and did not contribute to the recolonisation of other parts of Europe. Still doubtful is the situation in the Carpathians where two putative refugia are indicated in the westernmost Carpathians ("southern Moravia") and in the Apuseni mountains in Romania (Magri et al. 2006). Of course, no understorey species is absolutely dependent on beech, many of them occur also in forests of hornbeam *Carpinus betulus*, hereafter: *Carpinus*, sycamore *Acer pseudoplatanus*, or even in coniferous forests dominated by *Abies*. For *Carpinus*, which arrived much later than *Fagus* in most parts of Europe, refugia have been located in Croatia, southern Italy, southeastern Romania, and northern Greece (Huntley and Birks 1983, Grivet and Petit 2003). *Abies* had refuge areas in southern Italy, the Pyrenees, the southwestern Alps, the northern Apennine, northeastern Romania, and northern Greece; an additional refuge area in the northeastern Dinaric mountains is rather doubtful (Terhürne-Berson et al. 2004, Feurdean and Willis 2008). Little is known of the Holocene expansion of *Acer pseudoplatanus*, but taking its current range and ecological position into account it is likely that this species shared at least some refugia with *Fagus* and migrated either as its companion or afterwards.

To synthesize the geographical pattern of narrow-range species, we performed a hierarchical cluster analysis (complete linkage algorithm, Jaccard similarity index) based on the geographical distribution of these species.

All statistical analyses were performed using SPSS software.

## Results

European beech forest species have a U-shaped frequency distribution of range sizes (Fig. 2): 42 species are present in <10 regions ("narrow-range species"), whereas 39 species are present in >30 regions. Only 29 species show an intermediate range extent, being present in ≥10 but <30 regions. All narrow-range species are restricted to regions in the Alps, Carpathians, and further south.

The highest number of beech forest species is found in the southeastern Alps (between Lombardia in the west and Slovenia in the east), the northern Apennines, and the northeastern Dinaric mountains. With increasing distance from these centres of diversity, species numbers are decreasing, reaching its minimum in northeastern and northern

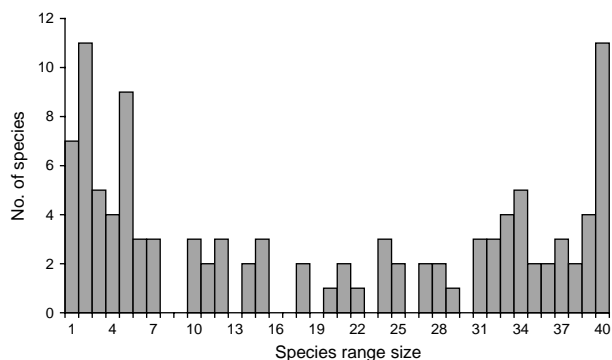


Figure 2. Frequency distribution of geographic range size of the 110 beech forest species. Range size is approximated by the number of regions in which the species is present.

European beech forests (Fig. 3). This picture changes when only narrow-range species are taken into consideration: in this case, the highest species diversity is observed in the southern Apennines, and although the southern Alps, northern Apennines, and northeastern Dinaric mountains still reach high species numbers, secondary maxima are found in northern Spain, the Carpathians, and northeastern Greece (Fig. 3). The multiple regression model identified distance to the nearest potential refuge area as the strongest predictor of species richness, both for the total number of beech forest species and (at  $p = 0.108$ ) for the number of narrow-range species. Range in elevation and soil type diversity had no significant effects (Table 1).

A 13-cluster solution for the hierarchical cluster analysis revealed a clear pattern in the geographical distribution of narrow-range species (Fig. 4–5). Cluster 1 included four species restricted to the Carpathians, and its distribution centre lies in the southern and eastern Carpathians where all four species are present. Cluster 2 included three species with a mainly Bulgarian distribution, although one species (*Pulmonaria rubra*) is distributed in the southern and eastern Carpathians as well. Cluster 3, consisting of six species, represented a group of so-called “Illyrian” species which have their centre of diversity in the northeastern Dinaric

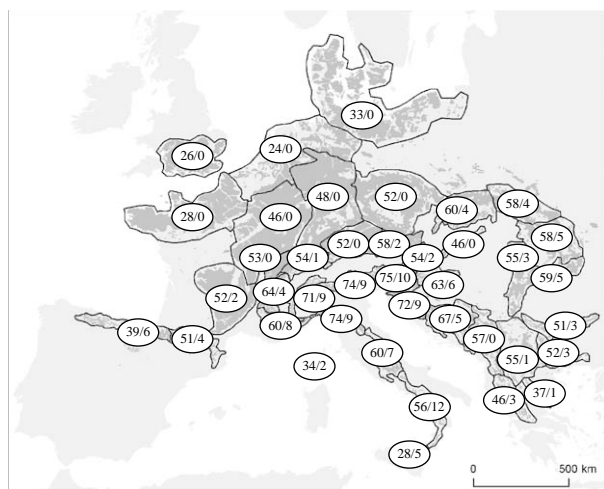


Figure 3. Total number of beech forest species (first value) and number of narrow-range beech forest species (i.e. species and subspecies present in <10 regions; second value) in each region.

mountains (Croatia, Slovenia). Cluster 4 included only one species (*Poa stiriaca*) from the southeastern Alps and the western Carpathians. Cluster 5 was composed of four species from the southwestern Alps and partly also reaching the northern Apennines. Cluster 6 comprised two species (*Pulmonaria apennina*, *Cardamine kitaibelii*) which are mainly distributed in the Apennines and adjacent parts of the southwestern Alps. Clusters 7 and 8 both included species of southern Italian distribution, while cluster 9 was restricted to southern Balkan beech forests and included only one species (*Lathyrus alpestris*). Cluster 10 includes three species with a similar Illyrian distribution as cluster 3, but with presences of two members each in the northern Apennines and in the northeastern Alps. Clusters 11 and 12 each consist of only one species, each being present in only one region (the Italian Alps between Trentino and Veneto, and the northeastern Carpathians, respectively). Finally, cluster 13 included six species with a centre in northern Spain, and with two species extending eastwards to the French Massif Central.

## Discussion

### Range size distribution of beech forest species

U-shaped or bimodal frequency distributions of geographic range sizes have been reported at regional or community scales, whereas range size distributions on continental or global scales are usually log-normal with many more narrow-range species than widespread ones (Gaston 1996, Gaston and Blackburn 2000, Arita and Rodriguez 2002). The U-shaped range size distribution found in this study (Fig. 2) may be related to the fact that we focused on a rather narrowly defined ecological species group. According to Gaston and Blackburn (2000), bimodality tends to be more pronounced when sites are more similar, and more species can occur at all sites. Thus, the form of the range size distribution may depend on the ecological heterogeneity of the species assemblage rather than on the scale of the study. Moreover, strong environmental change in the past is likely to influence range size distributions (Gaston 1998). Temperate deciduous forests have been subjected to severe range contractions during the Pleistocene (Prentice et al. 2000). The total area covered by beech forests at 15 000 cal. yr BP was estimated to have been of two orders of magnitude less extensive than at present, fragmented in multiple refugia which were isolated from each other

Table 1. Multiple linear regression models for (a) total number of beech forest species ( $R^2 = 0.416$ ), and (b) number of narrow-range beech forest species ( $R^2 = 0.27$ ). Standardized regression coefficients (B) and probabilities (p) are given. Bold values are significant ( $p < 0.05$ ).

	B	p
(a) All beech forest species		
Range in elevation	0.217	0.218
Soil type diversity	0.054	0.680
Distance from potential refugia	<b>-0.479</b>	<b>0.008</b>
(b) Narrow-range beech forest species		
Range in elevation	0.236	0.232
Soil type diversity	-0.104	0.478
Distance from potential refugia	-0.316	0.108

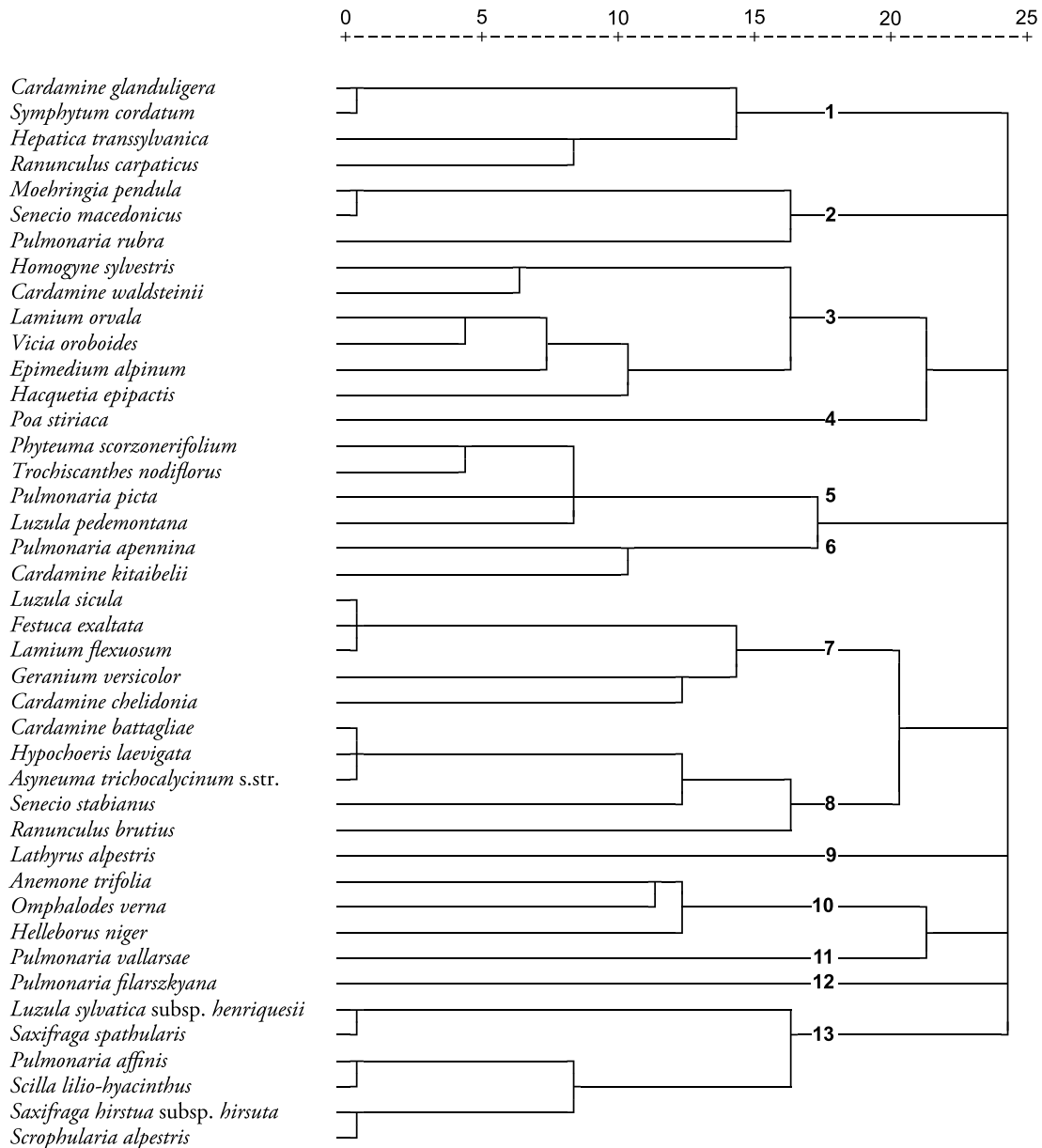


Figure 4. Dendrogram of cluster analysis of narrow-range species and subspecies. The bold numbers refer to the 13-cluster solution selected to visualise geographical patterns.

(Magri 2008). Species with low dispersal capacity bear a higher risk to lose some of their populations than species with high dispersal capacity. In consequence, the first might have become restricted to a few or even a single refuge area, unable to reach other potential refugia before the next glaciation. Repeated glacial isolation also have led to speciation, especially in the genera *Cardamine* and *Pulmonaria*, where several representatives clearly originate from rather recent speciation (Cesca and Peruzzi 2002, Kirchner 2004), probably in isolated beech forest environments.

### Species numbers, refuge areas and narrow-range beech forest species

It has long been known that regions with high topographic heterogeneity have more species than homogenous ones.

Mountain areas may increase the number of species in various ways: greater habitat diversity within a small surface area, better possibilities to respond to climate changes by small scale altitudinal range shifts, and higher speciation rate (Turner 2004). However, we found that range in elevation, which is a common measure of topographic heterogeneity, has only a weak predictive value (always nonsignificant) for the number of beech forest species within a region, while soil type diversity was an even weaker predictor (Table 1). Our findings are hence in good accordance with the predictions of the dispersal limitation hypothesis: the highest species richness was observed in areas close to potential glacial refuge areas. At first glance this seems to contradict earlier findings that species richness of beech forests on plot level is highly correlated with soil pH (Willner et al. 2004). However, this variation of alpha

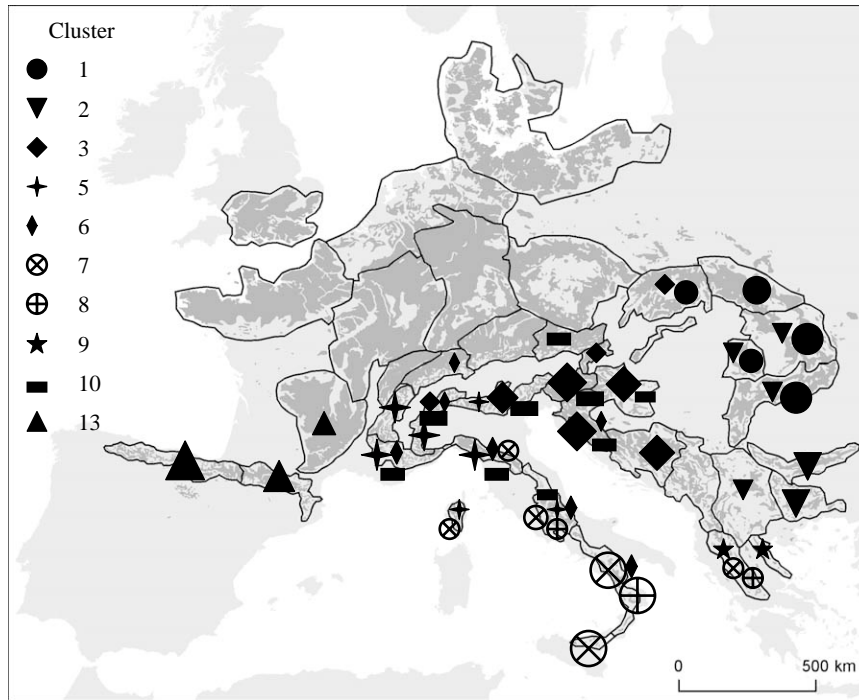


Figure 5. Geographical distribution of narrow-range beech forest species clusters. Symbol size represents the number of cluster members present in the region. Clusters 4, 11, and 12 are not shown.

diversity is mainly attributed to species with wider ecological range occurring in various types of forest and at their margins rather than being exclusive of beech forests. The focus species of this study, while displaying considerable altitudinal variation, prefer quite similar soil types (mostly cambisols). Acidic beech forests contribute little to the number of beech forest species in a region.

Particular high species numbers are found in the arch stretching from the northern Apennines, along the southern Alps, to the northeastern Dinaric mountains (Fig. 3). In this area, migration routes from at least three refugia (the Apennines, the southwestern Alps, and the northeastern Dinaric mountains) should have flown together. If only narrow-range species are taken into consideration, additional maxima are revealed which correspond with potential refugia in northern Spain, the southern Apennines, northeastern Greece, and Romania. The high number of narrow-range species in the northern Apennines may be explained by its central position close to three different beech refugia. Additionally, some species may have survived in the area associated with other mesophilous trees. According to pollen sequences and macrofossils records, the northern Apennines were colonised by *Fagus* only recently (4000 yr BP), while *Abies* had a long post-glacial history in this area (Lowe and Watson 1993).

Most clusters of narrow-range species can be attributed to one of the beech refuge areas (Fig. 5). Refugia in northern Spain and the southwestern Alps correspond with species clusters 13 and 5, respectively. The well-documented refuge area of southern Italy is reflected by species clusters 7 and 8. Both species groups are fully represented only in the southern Apennines. In contrast, neither Sicily nor the central Apennines have any exclusive species. These regions were apparently less important as refuge areas for beech forest

species compared to the southern Apennines. Cluster 6 comprises two species, *Pulmonaria apennina* and *Cardamine kitaibelii*, which probably have a different paleobotanical background. The first presumably started post-glacial migration from the southern Apennines and spread northwards throughout the entire Apennine range, similar to other species which occur in thermophilous beech forests such as *Cardamine chelidonia*, *Anemone apennina*, *Allium pendulinum*, and *Cyclamen hederifolium* (the latter two not included in the present list as they are also common in submontane mixed forests); *Cardamine kitaibelii*, on the other hand, had probably a more or less continuous pre-glacial pan-adriatic distribution which underwent fragmentation and reduction during the last glaciation, leaving isolated populations in the Apennines, the Alps, and the Dinaric mountains. The important glacial beech population in the northeastern Dinaric mountains corresponds with species cluster 3. There are also several species with intermediate range size which may be attributed to this refuge area, e.g. *Cardamine enneaphyllos*, *C. trifolia*, *Cyclamen purpurascens*, *Aposeris foetida*, and *Scopolia carniolica*. Some of these species may have survived the glacial period in the Carpathians as well. There is increasing paleobotanical evidence for a glacial population of beech in the western Carpathians, which would constitute the northernmost refuge area discovered so far (Magri et al. 2006, Jankovská and Pokorný 2008). This might explain the isolated occurrence of *Hacquetia epipactis* in the western Carpathians, where it occupies a relatively small area ca 400 km away from the main range of the species. In the same area, there is an outpost of *Aremonia agrimonoides*, a southeastern European beech forest species with an intermediate range size (present in 18 regions). The occurrence of two species of the southern Italian clusters in northeastern Greece represents a pattern

which is known for other vegetation types as well such as thermophilous woodlands and vegetation on rocks (Di Pietro and Wagensommer 2008). Especially in the latter case this was interpreted as an old amph-adriatic relationship dating back to Oligocene-Miocene when Apulia was connected with the southern Balkan by carbonate banks repeatedly exposed to subaerial conditions (Mazza and Rustioni 2008). The beech forest species, however, probably crossed the Adriatic Sea more recently, perhaps in the course of sea-level lowstands during glacial periods (Rohling et al. 1998). The narrow-ranged *Lathyrus alpestris* (cluster 9), which is present only in the mountains of northern Greece, coincides with the existence of ice-age beech forest refugia in this region whereas cluster 2 corresponds well with the refuge area located in the Pirin mountains in southern Bulgaria (Magri et al. 2006).

The only considerable discrepancy between the phylogeographical pattern of beech forest species and the recently estimated refuge areas of beech concerns the southern and eastern Carpathians. Magri et al. (2006) confirm the continuous pollen record of beech in the Apuseni mountains since 7000 cal. yr BP, but argue that the adjacent southern and eastern Carpathians were colonised 2000–3000 yr later. Apart from the fact that such a delay in migration seems quite unlikely, there is also some genetical and pollen evidence for a refuge area in that part of the Carpathians (Magyari 2002, Gömöry et al. 2003). Five beech forest species (cluster 1 and 12) are endemic to the Carpathians, but none of them reaches the westernmost part of the mountain chain. Several species have a similar distribution within the Carpathians (*Pulmonaria rubra*, *Scopolia carniolica*, *Aposeris foetida*), but are present in other regions as well, perhaps because they survived in more than one refuge area. Two species are restricted to the southern and eastern Carpathians, suggesting that the most important refuge area for the studied species should be located in one of these regions rather than in the Apuseni mountains. However, without further paleobotanical or genetical confirmation, the assumption of a glacial beech population in the southern or eastern Carpathians remains speculative. An alternative explanation could be that the Carpathian narrow-range species survived the glacial period in association with *Carpinus* for which a refuge area in this part of the Carpathians was confirmed by palynological and genetical data (Magyari 2002, Grivet and Petit 2003, Feurdean 2005).

## Conclusion

The distribution of many species is evidently limited by postglacial dispersal rather than by environmental requirements (Araujo et al. 2008, Svenning et al. 2008b). The hotspots of narrow-range beech forest species are in good concordance with the glacial refuge areas of *Fagus sylvatica* and other temperate tree species as estimated in recent studies. The geographical pattern of narrow-range species is also consistent with the recent classification of floristic elements of European vascular plants (Finnie et al. 2007), underlining the high proportion of European endemic species in the mountains of central and southern Europe. Our results show that this pattern is followed not only by above-timberline floras with their well-known richness in endemic taxa, but also for species assemblages of montane

forests. Moreover, our results suggest that most if not all of the studied species have been associated with beech for at least one glacial cycle, and that the current distribution of understorey species is a reasonable indicator for the localisation of glacial refuge areas of temperate forests. The possibility that some species may have survived the Last Glacial Maximum associated with *Abies* or *Carpinus* rather than with *Fagus* is in concordance with phytosociological evidence according to which forest communities dominated by these tree species are floristically and ecologically similar and that even today beech forest species may occur in such forests (Ellenberg 1996). This challenges a current paradigm in paleoecology that plant communities are ephemeral assemblages, and that the vegetation during the Last Glacial Maximum mostly consisted of vegetation types without present-day analogues (Huntley 1991, Prentice et al. 2000; but see Birks 2003). Further research should be focused on the phylogeography of forest herbs and shrubs in order to test our conclusions with molecular data. Considerable progress could be reached by establishing a pan-European database with vegetation plot data. Moreover, species traits analyses may help to understand why beech forest species differ so much in their colonisation capacity.

*Acknowledgements* – We thank Jens-Christian Svenning, Donatella Magri, and one anonymous referee for their valuable comments on a previous version of the manuscript, and Christoph Plutzer for technical assistance with GIS.

## References

- Araujo, M. B. et al. 2008. Quaternary climate changes explain diversity among reptiles and amphibians. – *Ecography* 31: 8–15.
- Arita, H. T. and Rodríguez, P. 2002. Geographic range, turnover rate and the scaling of species diversity. – *Ecography* 25: 541–550.
- Bennett, K. D. et al. 1991. Quaternary refugia of north European trees. – *J. Biogeogr.* 18: 103–115.
- Bergmeier, E. and Dimopoulos, P. 2001. *Fagus sylvatica* forest vegetation in Greece: syntaxonomy and gradient analysis. – *J. Veg. Sci.* 12: 109–126.
- Birks, H. H. 2003. The importance of plant macrofossils in the reconstruction of lateglacial vegetation and climate: examples from Scotland, western Norway, and Minnesota, USA. – *Quat. Sci. Rev.* 22: 453–473.
- Bohn, U. et al. 2000/2003. Karte der natürlichen Vegetation Europas/Map of the Natural Vegetation of Europe. Maßstab/Scale 1: 2 500 000. Teil 1: Erläuterungstext mit CD-ROM; Teil 2: Legende; Teil 3: Karten. – Landwirtschaftsverlag, Münster.
- Bolte, A. et al. 2007. The north-eastern distribution range of European beech – a review. – *Forestry* 80: 413–429.
- Cesca, G. and Peruzzi, L. 2002. A new species of *Cardamine* subgen. *Dentaria* (Cruciferae), apocendemic in Calabria (southern Italy). – *Plant Biosyst.* 136: 313–320.
- Conti, F. et al. (eds) 2005. An annotated checklist of the Italian vascular flora. – Ministero dell’Ambiente e della Tutela del Territorio, Roma.
- Dierschke, H. 1990. Species-rich beech woods in mesic habitats in central and western Europe: a regional classification into suballiances. – *Vegetatio* 87: 1–10.
- Dierschke, H. and Bohn, U. 2004. Eutraphente Rotbuchenwälder in Europa. – *Tuexenia* 24: 19–56.

- Di Pietro, R. and Wagensommer, R. P. 2008. Analisi fitosociologica su alcune specie rare e/o minacciate del Parco Nazionale del Gargano (Italia centro-meridionale) e considerazioni sintassonomiche sulle comunità casmofitiche della Puglia. – *Fitosociologia* 45: 177–200.
- Di Pietro, R. et al. 2004. Contribute to the nomenclatural knowledge of the beech-woodland communities of southern Italy. – *Plant Biosyst.* 138: 27–52.
- Ellenberg, H. 1996. Vegetation Mitteleuropas mit den Alpen. – Ulmer.
- Feurdean, A. 2005. Holocene forest dynamics in northwestern Romania. – *Holocene* 15: 435–446.
- Feurdean, A. and Willis, K. J. 2008. Long-term variability of *Abies alba* in NW Romania: implications for its conservation management. – *Divers. Distrib.* 14: 1004–1017.
- Finnie, T. J. R. et al. 2007. Floristic elements in European vascular plants: an analysis based on Atlas Florae Europaeae. – *J. Biogeogr.* 34: 1848–1872.
- Gaston, K. J. 1996. Species range size distributions: patterns, mechanisms and implications. – *Trends Ecol. Evol.* 11: 197–201.
- Gaston, K. J. 1998. Species-range size distributions: products of speciation, extinction and transformation. – *Phil. Trans. R. Soc. B* 353: 219–230.
- Gaston, K. J. and Blackburn, T. M. 2000. Patterns and process in macroecology. – Blackwell.
- Gömöry, D. et al. 2003. Spatial patterns of the genetic differentiation in European beech (*Fagus sylvatica* L.) at allozyme loci in the Carpathians and the adjacent regions. – *Silvae Genet.* 52: 78–83.
- Grivet, D. and Petit, R. J. 2003. Chloroplast DNA phylogeography of the hornbeam in Europe: evidence for a bottleneck at the outset of postglacial colonization. – *Conserv. Genet.* 4: 47–56.
- Honnay, O. et al. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. – *Ecol. Lett.* 5: 525–530.
- Huntley, B. 1991. How plants respond to climate change: migration rates, individualism and the consequences for plant communities. – *Ann. Bot.* 67 (Suppl. 1): 12–22.
- Huntley, B. and Birks, H. J. B. 1983. An atlas of past and present pollen maps for Europe: 0–13 000 years ago. – Cambridge Univ. Press.
- Jalas, J. and Suominen, J. (eds) 1976. Atlas Florae Europaeae 3. Salicaceae to Balanophoraceae. – Committee for Mapping the Flora of Europe, Helsinki.
- Jankovská, V. and Pokorný, P. 2008. Forest vegetation of the last full-glacial period in the western Carpathians (Slovakia and Czech Republic). – *Preslia* 80: 307–324.
- Kirchner, D. E. 2004. Molekulare Phylogenie und Biogeographie der Gattung *Pulmonaria* (Boraginaceae). – Verlagshaus Mainz, Aachen.
- Leroy, S. A. G. and Arpe, K. 2007. Glacial refugia for summer-green trees in Europe and south-west Asia as proposed by ECHAM3 time-slice atmospheric model simulations. – *J. Biogeogr.* 34: 2115–2128.
- Lowe, J. J. and Watson, C. 1993. Lateglacial and early Holocene pollen stratigraphy of the northern Apennines, Italy. – *Quat. Sci. Rev.* 12: 727–738.
- Magri, D. 2008. Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*). – *J. Biogeogr.* 35: 450–463.
- Magri, 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.
- Magyari, E. 2002. Holocene biogeography of *Fagus sylvatica* L. and *Carpinus betulus* L. in the Carpathian-Alpine Region. – *Folia Historico-Naturalia Musei Matraensis* 26: 15–35.
- Mazza, P. P. A. and Rustioni, M. 2008. Processes of island colonization by Oligo-Miocene land mammals in the central Mediterranean: new data from Scontrone (Abruzzo, central Italy) and Gargano (Apulia, southern Italy). – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 267: 208–215.
- Oberdorfer, E. and Müller, T. 1984. Zur Synsystematik artenreicher Buchenwälder, insbesondere im praealpinen Nordsaum der Alpen. – *Phytocoenologia* 12: 539–562.
- Prentice, I. C. et al. 2000. Mid-Holocene and glacial-maximum vegetation geography of the northern continents and Africa. – *J. Biogeogr.* 27: 507–519.
- Rodwell, J. S. et al. 2002. The diversity of European vegetation. An overview of phytosociological alliances and their relationships to EUNIS habitats. – Report EC-LNV nr. 2002/054, Wageningen.
- Rohling, E. J. et al. 1998. Magnitudes of sea-level lowstands of the past 500,000 years. – *Nature* 394: 162–165.
- Svenning, J.-C. and Skov, F. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? – *Ecol. Lett.* 10: 453–460.
- Svenning, J.-C. et al. 2008a. Glacial refugia of temperate trees in Europe: insights from species distribution modelling. – *J. Ecol.* 96: 1117–1127.
- Svenning, J.-C. et al. 2008b. Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. – *Ecography* 31: 316–326.
- Sykes, M. T. et al. 1996. A bioclimatic model for the potential distribution of north European tree species under present and future climates. – *J. Biogeogr.* 23: 203–233.
- Taberlet, P. et al. 1998. Comparative phylogeography and postglacial colonization routes in Europe. – *Mol. Ecol.* 7: 453–464.
- Terhürne-Berson, R. et al. 2004. The spread of *Abies* throughout Europe since the last glacial period: combined macrofossil and pollen data. – *Veg. Hist. Archaeobot.* 13: 257–268.
- Tsiripidis, I. et al. 2007. Geographical and ecological differentiation in Greek *Fagus* forest vegetation. – *J. Veg. Sci.* 18: 743–750.
- Turner, J. R. G. 2004. Explaining the global biodiversity gradient: energy, area, history and natural selection. – *Basic Appl. Ecol.* 5: 435–448.
- Tutin, T. G. et al. 2001. Flora Europaea (5 volume set and CD-ROM pack). – Cambridge Univ. Press.
- Tzonev, R. et al. 2006. Beech forest communities in Bulgaria. – *Phytocoenologia* 36: 247–279.
- Van der Veken, S. et al. 2007. Life-history traits are correlated with geographical distribution patterns of western European forest herb species. – *J. Biogeogr.* 34: 1723–1735.
- Willner, W. 2002. Syntaxonomische Revision der südmitteleuropäischen Buchenwälder. – *Phytocoenologia* 32: 337–453.
- Willner, W. et al. 2004. Alpha and beta diversity in central European beech forests. – *Fitosociologia* 41 (Suppl. 1): 15–20.

Download the Supplementary material as file E5957 from <[www.oikos.ekol.lu.se/appendix](http://www.oikos.ekol.lu.se/appendix)>.