

Faunal diversity of *Fagus sylvatica* forests: A regional and European perspective based on three indicator groups

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Abstract. While the postglacial history of European beech (*Fagus sylvatica*) and the plant species composition of beech forests in Central Europe are fairly well understood, the faunal biodiversity has been less well investigated. We studied three groups of mostly sedentary organisms in beech forest at regional and European scales by combining field studies with a compilation of existing literature and expert knowledge. Specifically, we examined the relationship between host tree genera and saproxylic beetles, and the diversity and composition of forest ground-dwelling molluscs and ground beetles in relation to the abundance of beech. At a West Central European scale (Germany), where beech has a “young” ecological and biogeographical history, we found 48 primeval forest relict species of saproxylic beetles associated with beech, 124 ground beetles and 91 molluscs inhabiting beech forest, yet none exclusive of West Central European beech forests. High levels of faunal similarity between beech and other woodland trees suggested that many of the beech forest dwelling species are euryoecious and likely to originate from mid-Holocene mixed broadleaf forests. Beech forests of the mountain ranges in Southern and East Central Europe, which are ecologically and biogeographically “old”, were found to harbour distinct species assemblages, including higher contingents of saproxylic beetles and carabids in the Carpathians and narrow-range endemic gastropods of Carpathian broadleaf forest. The observed biodiversity patterns suggest differentiated conservation priorities in “young” and “old” European beech forest regions. **Keywords** beech forests, faunal biodiversity, *Carabidae*, conservation priorities, ecological history, habitat continuity, Mollusca, primeval forest relicts, saproxylic beetles.

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Introduction

The biogeographic patterns we observe today are highly influenced by current and past environmental conditions, human impact, soil development and biological evolution (Fang and Lechowicz 2006). European beech (*Fagus sylvatica* L.) forest development in West, Central and Northern Europe has been very different, compared to South and South-Eastern Europe (Magri et al. 2006, Giesecke et al. 2007). For example, Illyric beech forests in the western part of the Balkan Peninsula occur at least since early postglacial times (10300–8800 years BP), and they are particularly diverse in forest plant species (Horvat et al. 1974). In contrast, North of the Alps beech appeared first approximately 8000 years BP (Tinner & Lotter 2006). In the period of Subboreal (4500–3000 years BP), the mixed mesophytic upland and lowland forests were subjected to several waves of beech invasion (Pott 1989, Pott 1997), but it was not until the Subatlantic period (3000–1000 years BP) that the composition finally shifted towards nearly pure beech forests.

Beech forests provide habitat conditions different from those of other broadleaf forest types, characterised by deep shade, leaf litter durability and accumulation, and a rather species-poor shrub and moss layer (Delagrangé et al. 2006, Valladares & Niinemets 2008, Brunet et al. 2010). The plant species composition of European beech forests and their geographical and ecological differentiation are well known (e.g., Dierschke 1990, Diekmann et al. 1999, Bohn et al. 2000/2003, Willner 2002, Dier-

schke & Bohn 2004). Regional monographs emphasise both abiotic factors and the role of humans in shaping beech woodlands and their distribution (e.g., Horvat et al. 1974, Dierßen 1996, Ellenberg & Leuschner 2010). Willner et al. (2009) showed that the distribution of many range-restricted beech forest understorey plants may be explained by dispersal limitations rather than by their environmental requirements. In contrast, the faunal species diversity and its development in European beech forests, beyond local studies, are far less well known.

In the past, animal species either followed beech from their refugia or were already present in the region and colonised the expanding beech forests. In the first case, at least some specialised beech forest dwellers may be expected, while in the second case, exclusive beech specialists may be lacking unless there is evidence of recent speciation. To test for potential mechanisms explaining faunal species composition of European beech forests, the distinctiveness of species pools rather than species numbers is to be analysed. Habitat-related species pools may comprise: (i) ubiquitous, (ii) range-restricted but euryoecious, (iii) stenoecious species. The proportion of each in a biotope or region may serve as an indicator of the ecological history and distinctiveness.

The aim of our study was to revealing patterns of ecological distinctiveness of European beech forest using three indicator animal groups with sufficient data available, saproxylic beetles, woodland ground beetles (*Carabidae*), and woodland molluscs. The selected groups differ in their association to specific

forest structures (e.g. deadwood), and they represent different trophic levels, feeding habits and dispersal potential.

Saproxylic beetles play an important role in wood decomposition and nutrient cycling in forest ecosystems (Nieto & Alexander 2010). They form a taxonomically and, apart from their dependence on dead or dying wood, ecologically heterogeneous group. Generally, many saproxylic beetles are associated with specific properties of old growth stands such as stand continuity and the occurrence of ancient trees (Nilsson & Baranowsky 1993, 1994; Müller et al. 2012).

Ground beetles (*Carabidae*) are important predators in forest ecosystems (Lovei & Sunderland 1996) and include poor, medium and well-dispersing species, with only the latter exhibiting flight capability (Riley & Browne 2011). Many species are restricted to particular habitats (Gutiérrez et al. 2003). Due to their species diversity and dispersal limitations, and due to their important role in ecosystems, ground beetle assemblages reflect well the ecological history and conservation value of forest habitats. Land snails (*Gastropoda*) and well preserved fossil snail shells from limestone and Holocene calcareous tufa sediments have been widely used as indicators for (palaeo-)environmental conditions and changes (Gedda 2001, Meyrick 2003, Gedda 2006, Mitrović 2007). A special feature of this group is its limited dispersal potential.

We hypothesise that in West Central Europe where beech forests are ecologically and biogeographically “young”, (i) the period of beech dominance has been too short to beget beech forest specialists and hence, if there are any in west central Europe, they most likely followed *Fagus* during its postglacial expansion; (ii) relict species of primeval forest are hardly beech forest specialists, but rather adapted to broadleaf forest in general; (iii) structural and tree species diversity of woodlands are crucial for tree and ground dwelling faunal diversity and more important than the presence of any

particular tree genus.

We considered mesoscale (Germany or part thereof) and macroscale (multiple European countries) faunal diversity patterns and infer that there are different implications for conservation management in ecologically and biogeographically “young” and “old” beech forest regions.

Materials and methods

Species groups investigated

(i) As the range of host trees of Germany’s 1378 saproxylic beetle species (Schmidl & Bußler 2004) is insufficiently known and even less so for Europe as a whole, we selected a subset of saproxylic beetle species for which reliable host tree data in Germany and Europe exists. Müller et al. (2005) provided a list of 115 central European saproxylic beetles of primeval forest (PFR hereafter, “Urwaldreliktarten” in germ.), among them some of the most endangered European species (Jansson 2009). We compiled the published tree genus records of the 115 PFR species from Germany, Austria, France, Finland, Sweden and Romania, supplemented by our additional field notes from Romania, Poland, Finland and Germany (see Supporting Information I for details on the underlying literature).

(ii) For ground beetles, we used a dataset comprising 622 plots, with 415 in Germany and 207 elsewhere in Central, South Eastern and Eastern Europe (see Table 1 and Supporting Information II for details about the studies included). A total of 381 plots (61%) were related to beech forests, while 241 sample plots were in ravine forests and in various mostly near-natural oak, lime, pine and spruce forests (Table 1). The dataset includes log transformed abundance data of ground beetle assemblages per plot and among other information, the abundance of beech in the tree layer scaled at $0 \leq 1\%$ cover, $1 \leq 30\%$, $2 \leq 50\%$, $3 \leq 70\%$, $4 \leq$

Table 1 Allocation of all 622 ground beetle (Carabidae) sample plots to habitat type and region. Beech forest plots are represented by 381 stands

Habitat type	Costal lowlands		Central European uplands		Northern (and Central) Alps		Southeastern Mountains (southern Alps, western Balkans)		Carpathian and Sudeten Mountains		Eastern Continental Plains		Total
	Atlantic region of Germany	North German Plain (if not Atlantic)	Baltic (Poland)	Western uplands and scarplands (Subatlantic)	Eastern uplands (Hercynian-Polonic)	Western Alps (incl. Swiss Jura and Alpine foreland)	Eastern Alps	Alpine-Adriatic region	Western Balkans (Illyric)	Not subdivided	Hungarian plain, Transylvanian plateau	Transcarpathian plains (Ukraine)	
Beech	3	1	15	73	170	9	30	4	6	61	9		381
Ravine				10	36		5	2	1		2		56
Mixed oak		1	9	39	9	4	1	5	1	2	34	5	110
Pine					26		2			15			43
Spruce			10	4	9		9						32
Total	4	1	34	126	250	13	47	11	8	78	45	5	622

90%, 5 > 90%.

(iii) In the absence of comprehensive mollusc data for Europe or any larger area (but see Čiliak & Šteffek 2011 for the Slovak Republic) we established a mollusc (land snails, slugs and freshwater molluscs) dataset of habitat-related species abundance data from 70 forest reserves in Bavaria, Southern Germany, representing most natural forest types of this area (Bohn 2000/2003, Walentowski et al. 2001, Walentowski et al. 2013). We combined that with environmental data made available through the Forest Reserve Database of the Bavarian State Institute of Forestry (see Supporting Information III for details). The mollusc dataset is considered representative of the Central European uplands including parts of the Northern Limestone Alps.

Studied forest habitat types (ground dwellers)

For the forest ground-dwelling groups (ground beetles and molluscs) we distinguished six forest habitat types: beech, mixed montane (*Fagus*, *Abies*, *Picea*), oak and oak-lime-hornbeam, mixed ravine and slope woods (*Tilia*, *Ulmus*, *Fraxinus*, *Acer*), (Semi)natural pine woods (*Pinus sylvestris*), (Semi)natural spruce forest (*Picea abies*). Regarding molluscs, riparian and other wetland forests (*Populus*, *Alnus*, *Fraxinus*) were included, and lowland to submontane beech forests (often co-dominated by beech and oak) were separated from montane forests (often co-dominated by beech, fir and spruce). In contrast, for the carabid data set, wetland forests were disregarded as they showed little relationship to beech forests at the European scale, and lowland beech forests were merged with montane mixed beech forests. Further, the carabid beetle data

were related to different levels of forest utilisation intensity: 0-virgin forest, 1- semi-virgin forests (cut in the past but virgin forest structures intact), 2-bordering virgin forest, 3-old reserve (not cut in more than 50 years, sizable), 4-young reserve (not cut in less than 50 years, mostly small), 5-managed forest or not cut in less than 20 years. All mollusc data fall into category 4.

Geographic range, spatial scales and data compilation

Data was analysed on two spatial levels, (i) mesoscale (Germany for saproxylic and ground beetles and Bavaria for molluscs), assumed to be representative for west central Europe and (ii) macroscale (considering saproxylic beetles and carabids), comprising European sites with short or long distances to glacial broadleaf forest refuge areas. To categorise the macroscale data biogeographically (and along with different degrees of forest use), we distinguished six regions: Atlantic and Baltic coastal lowlands, Central European uplands, Northern and Central Alps, Southern Alps and western Balkans, Carpathian and Sudeten Mountains, Eastern continental plains (Table 1).

Statistical analyses

We used cluster analysis (Ward's method with binary Bray-Curtis distances) to detect associations of saproxylic beetle assemblages (of species recorded at least once on beech) with host tree species. The appropriate number of clusters was identified using bootstrapping methods (Hennig 2010). Canonical Correspondence Analysis (CCA) with beech cover as the constraining factor linked ground beetle and mollusc communities to the abundance of European beech. Detrended Correspondence Analysis (DCA) was used to identify environmental factors related to the differences found in the mollusc and ground beetle datasets, respectively. Subsequently, we correlated the

DCA scores with environmental factors (for molluscs: mean annual precipitation and temperature, elevation, forest type, soil base status, in 3 classes - low, medium, high, surface water, rocks, proportion of beech, for ground beetles: forest type, land use intensity, in 4 classes - none to very intensive, the proportion of beech). To reveal differences between geographic ranges, analyses for saproxylic and ground beetles were performed separately for the entire dataset (Europe) and for selected regions. All statistical analyses were performed using R 2.14 (R Development Core Team 2011), with the additional packages *vegan* (Oksanen et al. 2011) and *fpc* (Hennig 2010).

Results

Mesoscale diversity

Forty-eight (42%) of the 115 PFR saproxylic beetle species recorded in Germany were found on beech at least once. For comparison, 66 PFR species (57%) were found on oak, much less on *Populus* (21; 18%), *Salix* (19; 17%), *Picea* (18; 16%), *Tilia* (15; 13%) and *Ulmus* (14; 12%). The cluster analysis revealed eight clusters of host trees associated with beetle assemblages (Fig. 1). Thirteen PFR species were found to characterise the various groups of host tree genera (Table 2).

Cluster 5 includes beech (*Fagus*) and the deciduous tree genera *Quercus* (most similar to beech), *Ulmus*, *Populus* and *Salix*. Together with *Carpinus* and *Acer* (cluster 4), being most similar in species composition to cluster 5, those tree genera are characteristic for lowland and lower upland forest, including both zonal and azonal pioneer woodlands. The next most similar clusters (6, 7 and 8) included a range of broadleaf trees that represent more or less warm sites in the nemoral forest and cultural landscape: cluster 6 - *Platanus* (introduced), *Pyrus* and *Malus* (native and cultivated), cluster 7 - *Aesculus* (introduced), *Fraxinus* and *Tilia*,

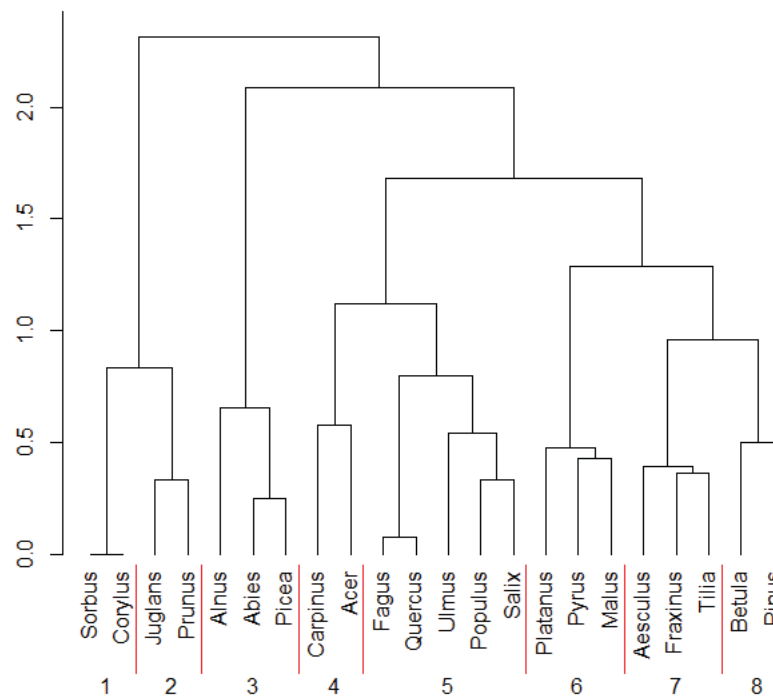


Figure 1 Clusters of host tree genera of 48 beech exploiting primeval forest relict species of saproxylic beetles at the mesoscale (Germany)

Table 2 Saproxylic beetle species indicating groups of host tree genera in Germany (threshold indicator value [IV] > 40%). Cluster numbers correspond to Fig. 1

	cluster	IV	<i>p</i> - value
<i>Ceruchus chrysomelinus</i>	3	41.1	0.010
<i>Nematodes filum</i>	4	71.4	0.011
<i>Dicerca berolinensis</i>	4	71.4	0.011
<i>Allecula rhenana</i>	4	62.5	0.005
<i>Euryusa coarctata</i>	5	80.0	0.003
<i>Ampedus elegantulus</i>	5	80.0	0.004
<i>Megapenthes lugens</i>	5	60.0	0.001
<i>Ischnodes sanguinicollis</i>	5	50.0	0.003
<i>Neatus picipes</i>	5	46.0	0.001
<i>Elater ferrugineus</i>	5	42.9	0.001
<i>Crepidiphorus mutilatus</i>	7	55.6	0.001
<i>Abraeus parvulus</i>	7	52.6	0.012
<i>Teretrius fabricii</i>	8	55.6	0.004

cluster 8 - *Betula* and *Pinus*. Less accordance in saproxylic beetle assemblages with beech and oak was observed for *Alnus*, *Abies* and *Pi-*

cea (cluster 3). The PFR species of these genera inhabit cool mountainous or wet forests. The most pronounced dissimilarities (clusters

1 and 2) to beech and oak were observed for *Corylus*, *Juglans* (introduced), *Prunus* (native and cultivated) and *Sorbus*, presumably due to their different, often shrubby habit, low maximum age, the resulting lack of deadwood and rarity of ancient trees. All saproxylic beetle PFR species found on beech wood occurred on a range of host tree species, although some prefer specific groups of host trees. While none is entirely restricted to beech, six out of 48 beech exploiting PFR species were exclusively associated with the host tree genera of cluster 5 (Table 2).

Among the 191 ground beetle (carabid) species sampled across the forest types of Germany, 124 species (66%) were observed in beech forests, but none of these species were exclusive of beech forests. While *Pterostichus burmeisteri* did show a significant preference for beech forests ($r = 0.60$, $t = 15.47$, $df = 426$, $p < 0.001$), it has been recorded in ravine forests, too. The carabid composition of semi-natural conifer forests (subalpine spruce forests, pine-woods) showed little similarity to that of de-

ciduous forest (Fig. 2). All carabid assemblages found in deciduous forest types overlapped to a large extent. Beech forest carabid fauna overlapped particularly with that of ravine forests and less so with that of oak forests.

A total of 181 mollusc species (five of them with data deficiencies and thus excluded from the DCA analysis) was observed in the 70 Bavarian forest nature reserves, including land snails (123 species), slugs (23), freshwater snails (26) and bivalves (9). The species composition was strongly depending on temperature (correlation with first axis: $r = 0.5$, $t = 4.79$, $df = 68$, $p < 0.001$) and correspondingly on elevation (correlation with first axis: $r = -0.43$, $t = -3.96$, $df = 68$, $p < 0.001$), further on base content (correlation with first axis: $r = -0.58$, $t = 5.83$, $df = 68$, $p < 0.001$; for second axis: $r = -0.8$, $t = 11.09$, $df = 68$, $p < 0.001$) (Fig. 3). The first axis of the DCA showed a gradient from warm floodplain sites to cool montane to subalpine levels of the Alps. The second axis showed a gradient from acid-oligotrophic sites to eutrophic sites. Assemblages

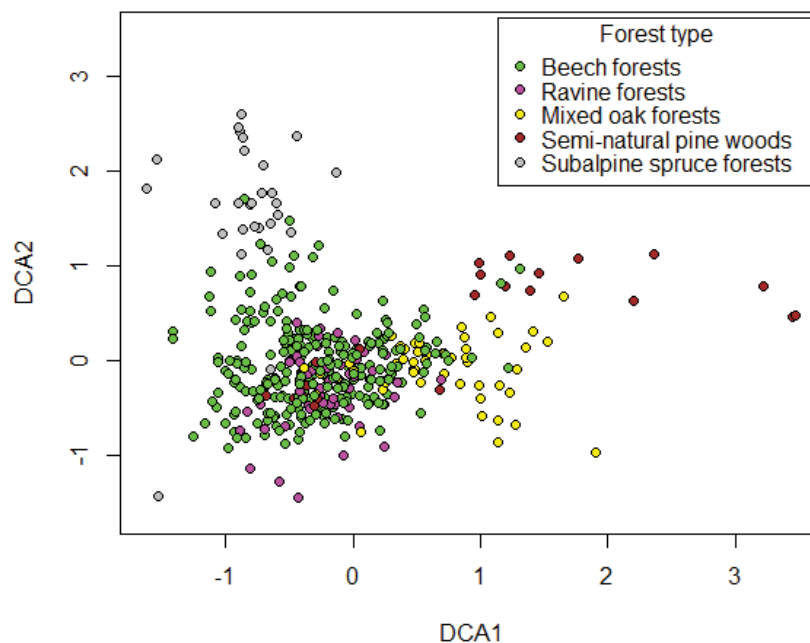


Figure 2 Ordination diagram (DCA) of the ground beetle assemblages of different forest types in Germany (from 428 sample plots and 191 species). Axis 1: eigenvalue 0.46, length of gradient 5.09. Axis 2: eigenvalue 0.29, length of gradient 4.05.

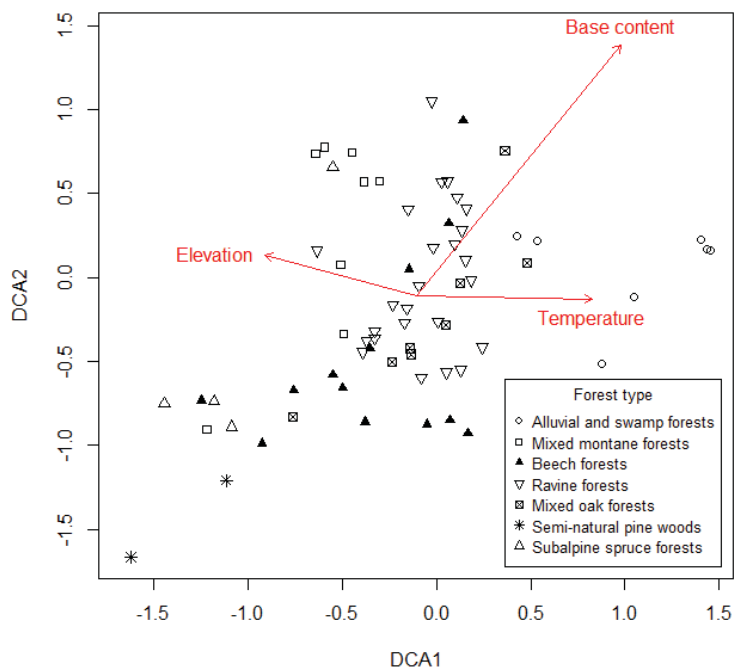


Figure 3 Ordination diagram (DCA) of the mollusc assemblages (176 species) of different forest types in 70 Bavarian forest reserves. Axis 1: eigenvalue 0.24, length of gradient 3.07. Axis 2: eigenvalue 0.19, length of gradient 2.71, environmental vectors passively plotted.

of molluscs inhabiting beech forests (91 species) showed a scattered distribution in the ordination plot with similarities to assemblages of various forest types, particularly of mixed oak woodlands and ravine forests. We did not find positive correlations of mollusc species specifically with beech. A negative correlation (not shown) between beech dominance and molluscs of wet forest (*Zonitoides*, *Oxyloma*, *Succinea*) and riparian forest (*Trochulus*) was to be expected.

Macroscale diversity

At a European scale, a total of 63 (55%) of the 115 PFR saproxylic beetles were found to be exploiters of beech wood, thus 15 more species than at a central European level. This was not merely an effect of the larger area, since also in a single region such as southern Romania a higher number of PFR saproxylic beetles associated with beech were observed (10 species). As for Germany, PFR on beech were outnumbered by those on oak (80 spe-

cies; 70%), while other host tree genera were less represented (*Populus*, 37 species; *Picea*, 29; *Abies*, 26; *Pinus*, 25; *Salix*, 24; *Tilia*, 24). All host tree genera had more associated PFR saproxylic beetle species at a European scale than at a west central European scale.

The similarities regarding beetle assemblages (Fig. 4) and the correlations between species occurrences and host tree clusters (Table 3) were similar to those observed at the mesoscale. Two high-level groupings were distinguished: the first group (combining clusters 1 to 5) mainly included tree genera of the southern-nemoral transition zone with a more southern (sub-Mediterranean) or lowland distribution. The second group (clusters 6 to 9) included tree genera associated with temperate and cool-temperate zones (nemoral, boreo-nemoral) as well as wetland, pioneer and montane-prealpine sites.

Beech forests carabid assemblages differed considerably among regions (Fig. 5). Distinct assemblages were identified in the Carpathian and Sudeten high mountain ranges and in the

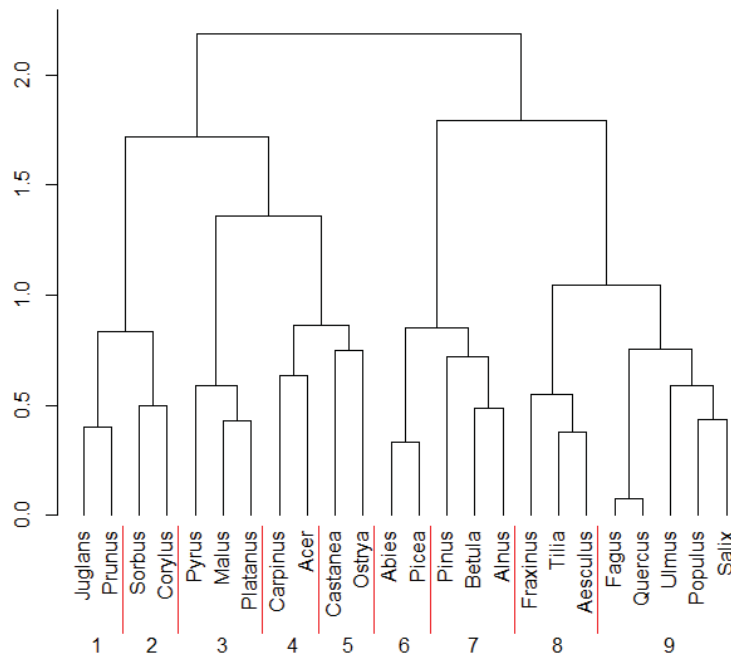


Figure 4 Clusters of host tree genera of 63 beech exploiting primeval forest relict species of saproxylic beetles at the European scale (Germany, Austria, France, Finland, Sweden and Romania)

Table 3 Saproxylic beetle species indicating groups of host tree genera in Europe (threshold indicator value $IV > 40\%$). Cluster numbers correspond to Fig. 4

	cluster	IV	<i>p</i> - value
<i>Allecula rhenana</i>	4	62.5	0.003
<i>Nematodes filum</i>	4	48.4	0.026
<i>Mycetoma suturale</i>	6	83.3	0.011
<i>Lacon lepidopterus</i>	6	71.4	0.009
<i>Ipedia binotata</i>	6	48.4	0.028
<i>Ampedus elegantulus</i>	6	43.5	0.017
<i>Abraeus parvulus</i>	8	57.7	0.005
<i>Crepidiphorus mutilatus</i>	8	55.6	0.002
<i>Euryusa coarctata</i>	9	80.0	0.005
<i>Triplax collaris</i>	9	80.0	0.004
<i>Epierus comptus</i>	9	60.0	0.049
<i>Megapenthes lugens</i>	9	60.0	0.001
<i>Ischnodes sanguinicollis</i>	9	54.6	0.001
<i>Neatus picipes</i>	9	46.2	0.002
<i>Elater ferrugineus</i>	9	42.9	0.001
<i>Thoracophorus corticinus</i>	9	40.0	0.001

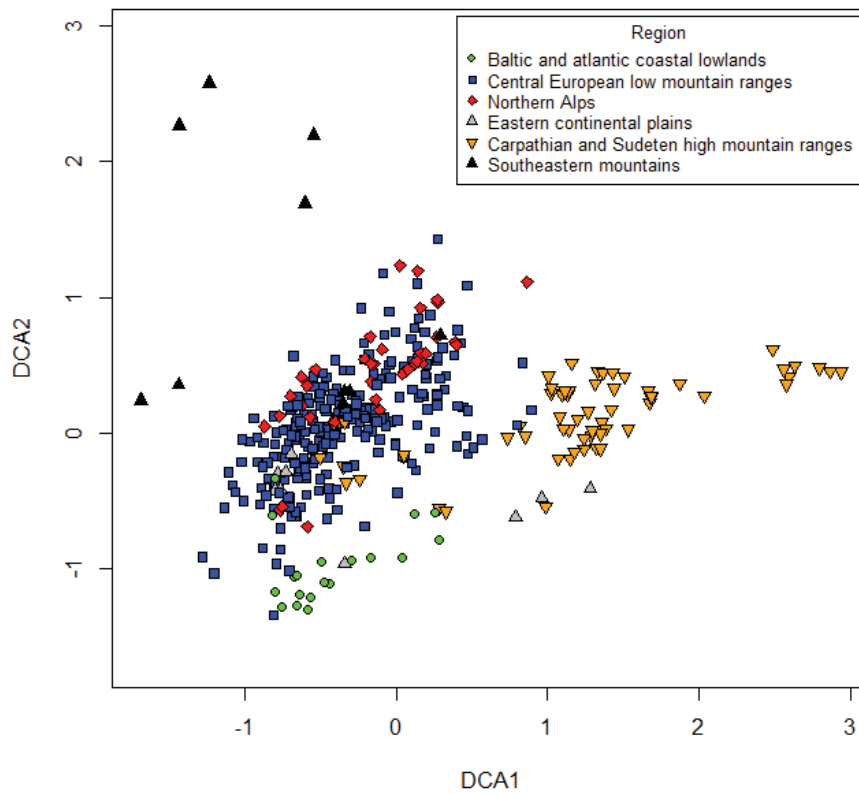


Figure 5 Ordination diagram (DCA) of the ground beetle assemblages of beech forests in various European regions derived from 381 sample plots and 199 species. Axis 1: eigenvalue 0.41, length of gradient 4.62. Axis 2: eigenvalue 0.26, length of gradient 3.31.

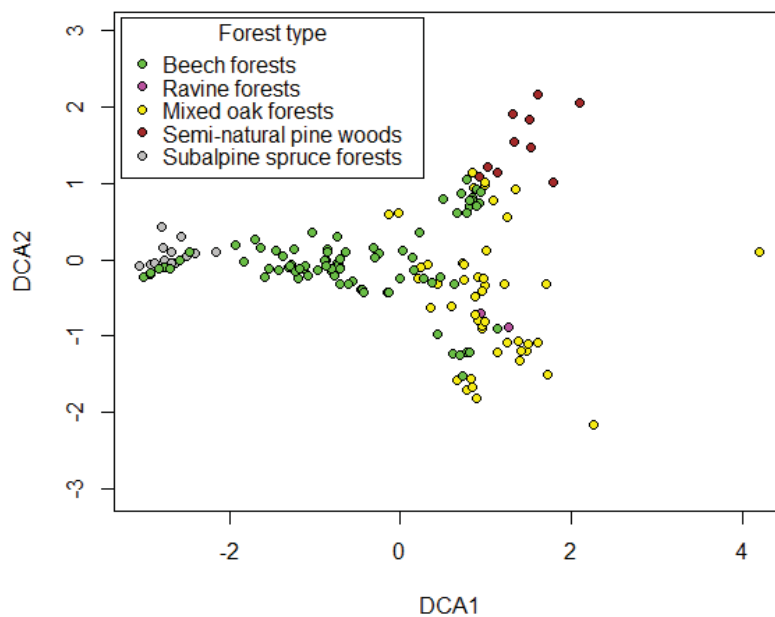


Figure 6 Ordination diagram (DCA) of the ground beetle species assemblages of the Carpathians and adjacent regions derived from 160 sample plots and 199 species. Axis 1: eigenvalue 0.64, length of gradient 7.25. Axis 2: eigenvalue 0.38, length of gradient 4.33.

South Alps and West Balkans. Some species occurred only in beech forests in the Carpathian and Illyric regions, respectively (Fig. 5, Table 4). Carabid assemblages in beech forests of the Carpathians and adjacent regions were more distinct, showing very little overlap with those of other habitat types (Fig. 6).

We found 10 carabid species positively correlated with beech cover in the Carpathians and adjacent regions (Table 4). Some are Carpathian endemics (*Carabus obsoletus* subsp. *carpathicus*, *Pterostichus foveolatus*, *P. pilosus*) or occur but very rarely in west central Europe (*Licinus hoffmannseggi*). Further species (*Abax parallelepipedus*, *Cychrus caraboides*) showed a positive correlation with beech abundance but are not beech forest specialists in West Central Europe. None of these species necessarily is tied to beech forests, let alone in all parts of its range. For example, even *P. pilosus* as a Carpathian endemic can be found in sub-alpine areas and high-elevation spruce forests, in our dataset it clearly favours beech forests in the way that it is positively correlated to the share of beech. Regionality of the habitat may play a major role, especially for those species whose range extends beyond one region, but possibly even within one region if it is large enough in longitudinal or latitudinal extension and if subspecific taxa are involved.

Discussion

Mesoscale diversity

Late Holocene mass expansion of beech and the spread of zonal beech forests to West Central Europa took place at the end of late Neolithic (Lang 1994) and Bronze ages. Hence, interactions between beech and broadleaf forest species date back to just about 20 tree generations (Walentowski & Winter 2013). The effective time of coexistence may have been even shorter due to simultaneous human impacts.

Among the 48 beechwood dwelling PFR species of saproxylic beetles and the beech forest ground-dwelling carabid and mollusc species observed in our study, neither exclusive beech forest specialists nor regional endemics were found. This is an indicative of a rather short period of joint evolution in beech ecosystems. Recent speciation, as observed in the land snails *Bulgarica vetusta* subsp. *festiva* and *Cochlodina costata* subsp. *franconica* on dolomite and limestone rocks and boulders (Hässlein 1960), seems to be restricted to more or less open habitats. This result is congruent with findings in forest systems regarding vascular plants (Walentowski & Zehm 2010) and woody plants (endemic *Sorbus* apomicts, Meyer et al. 2005), and also with the ground

Table 4 Ground beetle (carabid) species positively correlated with beech dominance as derived from a CCA of the macroscale dataset (threshold $r > 0.4$).

	<i>r</i> - value	<i>t</i> - value	df	<i>p</i> - value
<i>Carabus auronitens</i>	0.59	9.09	158	< 0.001
<i>Carabus obsoletus</i>	0.52	7.64	158	< 0.001
<i>Molops piceus</i>	0.50	7.19	158	< 0.001
<i>Carabus linnei</i>	0.49	6.99	158	< 0.001
<i>Abax parallelepipedus</i>	0.46	6.55	158	< 0.001
<i>Cychrus caraboides</i>	0.45	6.38	158	< 0.001
<i>Pterostichus foveolatus</i>	0.45	6.34	158	< 0.001
<i>Pterostichus burmeisteri</i>	0.44	6.13	158	< 0.001
<i>Pterostichus pilosus</i>	0.44	6.08	158	< 0.001
<i>Licinus hoffmannseggi</i>	0.40	5.45	158	< 0.001

beetles to be found in the canopy of European beech forests (Müller-Kroehling & Zehetmair 2014).

Specific habitat structures and habitat continuity seems to be more important for the species groups investigated than the presence or abundance of beech. Saproxyllic PFR beetles have survived on deadwood of various host tree genera, some confined to ancient trees in pasture landscapes and parks (Speight 1989, Warren & Key 1991), partly substituting for the loss of habitats in primeval forests. In fact, temporal scale as well as structure and surroundings matter for the survival of relict populations (Økland et al. 1996, Jonsson et al. 2005, Sverdrup-Thygeson et al. 2010, Buse 2012, Sverdrup-Thygeson et al. 2014), and many of the PFR xylobiont beetles in Europe are rather primeval forest structure specialists than primeval forest species. Even the cerambycid *Rosalia alpina* (EC Habitats Directive, Supporting Information II and IV), often cited as flagship species of old beech forests, is rather a specialist for sun-exposed trunks of various broad-leaved trees (*Fagus*, *Fraxinus*, *Tilia*, *Ulmus*, *Acer*) featuring dry decaying timber in ancient woods and grazed open forests (Russo et al. 2010).

Many forest specialists are poor dispersers due to the relative stability of their habitat and were therefore little likely to spread from their refuge areas to the establishing beech forests of Central Europe. A high degree of overlap in the invertebrate communities of different forest types in West Central Europe suggests that many species of beech forests observed today originate in other – adjacent – types of woodland such as oak forests and in particular tree species-rich ravine and boulder forests. Due to massive human impacts on woodlands such as historic overexploitation, an overall alteration and simplification of forest structures caused by post-war depletion and acquisitive forestry, especially in the past 60 years, PFR species that depend on habitat continuity and structural diversity including high amounts of

deadwood retreated to isolated locations or became extinct.

Our data reveal that the majority of the ground-dwelling carabids and molluscs of the beech forests in West Central Europe are indeed euryoecious, i.e. to be found in a variety of forest habitats. It can be assumed that they were already present prior to the immigration of beech in mid-Holocene mixed deciduous broadleaf forests of *Ulmus*, *Tilia*, *Fraxinus* and *Quercus*, as indicated by the large faunal similarities. Specifically, the more stenoecious taxa among the ground-dwelling mollusc and ground beetle species require deadwood and stand continuity, which may be provided by shady deciduous forest types in general (e.g., ravine forests), not exclusively by beech forests. Fossil evidence suggests that woodland snail diversity declined significantly during the late Holocene (Hässlein 1960, Ložek 1982 a, b, c, Gedda 2006). Beech expansion might have been a decisive factor for that, due to the unfavourable chemical composition of leaf litter, the production of acid stemflows and the lowering of soil pH values and microbial activity (Jacob et al. 2010, Thoms et al. 2010). The land snails *Azeca goodallii* and *Perforatella bidentata* were more common in the Atlantic period from about 7500 to 5000/4500 cal BP, and under present-day conditions in Bavaria occur only in few residual populations (Hässlein 1960). They are presently associated with moist boulder scree forest with *Tilia*, *Ulmus*, *Fraxinus* and *Acer*, under conditions that do not allow beech to become dominant.

Macroscale diversity

Pyrenees, Alps, Apennines and Carpathians are hotspots of beech forest endemics and stenoecious species (Pott 2000, Willner et al. 2009). While these mountain ranges form a massive East-West barrier inhibiting species migrations in the Quaternary, they also provided refuges in sheltered places such as in steep-sided valleys, and triggered speciation (Magri 2008). The

Balkan and the Rhodope Mountains facilitated species migrations between the biodiverse Illyric and Carpathian beech forests and the Mediterranean and Black Sea regions (Willner et al. 2009, Walentowski et al. 2010). Short distances to refuges allowed the expansion of broadleaf forests including beech during inter- and postglacial periods. Coherent forest areas with primeval beech forest remnants occurred throughout the Holocene. Intact predator-prey relationships ensured the processual integrity of forest.

Our results suggest a species-time or host-age dependent relationship (Southwood 1961, Birks 1980, Rosenzweig 1995) between invertebrate assemblages and beech ecosystems, as shown above for saproxylic beetles in southern Romania. The patterns of richness and endemism among the investigated beetle groups confirm the validity of the refuge distance model found for vascular plants (Willner et al. 2009). Ground beetle assemblages at short distance from potential refuge areas contain more species associated with beech forest (ascertained by our data for 10 carabids in the Carpathians) and narrow range species (three Carpathian endemics). None of these species is exclusive to beech forests, let alone in all parts of its range. For example, *Pterostichus pilosus*, a Carpathian endemic (Nitzu et al. 2008), occurs in sub-alpine areas and high-elevation spruce forests, but in our dataset is positively correlated to the proportion of beech. Regionality of the habitat does play a major role, especially for those species whose range extends beyond one region, but possibly even within one region if it is large enough in longitudinal or latitudinal extension and if subspecific taxa are involved.

Studies such as of Brandmayr (1983), Comandini & Vigna Taglianti (1990), Vigna Taglianti & De Felici (1994) and Rizun & Chumak (2003) showed that the Carpathians, but also the Pyrenees, Southern Alps, Apennines and Balkan ranges are home to a carabid fauna of high species diversity and endemic richness.

Italian montane forests have 159 ground beetle species endemic to Italy, corresponding to an endemism rate of 31% (Brandmayr et al. 2003).

An increase in endemism towards the southern and southeast European mountains is evident also for terrestrial molluscs (Cameron et al. 2011). Hotspots of mollusc endemism are found in the Mediterranean and Alpine biogeographic regions, especially on limestone substrates. These overall trends have been specified in a case study on forest ground-dwelling molluscs from the Slovak Carpathians (Čiliak & Šteffek 2011). The authors observed among others seven Carpathian endemic gastropods (*Bielzia coerulans*, *Cochlodina cerata*, *Faustina faustina*, *Monachoides vicinus*, *Perforatella dibothrion*, *Vitrea transsylvanica*, *Vestia gulo*), one Alps-Carpathian disjunction (*Eucoberesia nivalis*) and one land snail restricted to the Western Carpathians (*Petasina unidentata* subsp. *carpatica*), suggesting a glacial forest refuge that remains to be confirmed.

Conservation issues

Conservation status assessments based merely on species numbers may fall short if the distinctiveness of species pools goes unregarded (Andersson et al. 2013). Our study on European beech forest highlights the importance of studying macroscale biodiversity to see mesoscale biodiversity in perspective. On the one hand this perspective corroborates the necessity of international conservation strategies, on the other hand conservation responsibilities and priorities might differ at a regional level.

Macroscale responsibilities requiring national and international conservation efforts for European beech forest should focus on the preservation of sufficiently large and coherent areas in the core regions of European beech with special attention to the south, south central and southeast European mountains with glacial refuge areas. These eco-historically old

beech forest areas and, in particular, the unique primeval forests, are essential for most of the beech forest dwelling endemics and stenocious species, thus exhibiting a maximum evolutionary and ecological distinctiveness.

Mesoscale responsibilities requiring regional, national or binational efforts in ecologically young beech forest areas, e.g. in Germany, should, in the absence of narrow-range endemics and with only very few beech specialists, focus on maintaining and improving forests composed of native tree species in their natural habitats, by designing sizable forest reserves containing considerable proportions also of non-beech forest types.

In west central European beech forest ecosystems, being by far the most important broadleaf forest type, their local conditions, processes and functions have ever been much affected by human land use and forestry. Conservation focus should be on the faunal, fungal and floral diversity of old-growth forests in general. Saproxyllic beetles, woodland ground beetles and woodland molluscs of the young post-ice age temperate forests, that are presently labelled as beech forest species are in fact linked to an adequate frequency and habitat continuity of admixed secondary tree species (like *Quercus*, *Acer*, *Fraxinus*, *Ulmus*) within beech forest landscapes. For cool temperate mountain mixed forests with distinct boreal-montane species pools (e.g. related to Urwald relict species) and species which are old growth obligates (like the ground beetle *Licinus hoffmanseggi*), the admixture of indigenous softwoods (*Alnus incana*, *Abies alba*, *Picea abies*) and high deadwood amounts are of paramount relevance. The low levels of structural diversity and deadwood amounts in many stands should be substantially increased in sufficient areas, the natural development of initial as well as senescent stages allowed, the integrity of large forest areas be maintained and the connectivity between different forest habitats and sites maintained or restored. The latter gains particular importance in the light

of climate change pressure on cold-preferential species (Müller-Kroehling et al. 2014).

As PFR species occur in isolated sites and depend chiefly on wood amounts and tree structures and less on beech forest as such, their preservation also relies on local efforts in small areas, sometimes focussing on specific tree groups, sometimes on exposed wooded areas or on azonal formations. Ongoing management directed to keep old oaks free standing and sun exposed and to ensure the recruitment of young oaks, and the restoration of abandoned pasture woodlands should have a high priority in nature conservation (Jansson 2009). Also the beech forest natural ecotones require special attention as they may provide habitats for particular relict woodland invertebrate populations.

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Supporting Information

The online version of the article includes the Supp. Info.

Supp. Info. I: Saproxyllic beetle data sources

Supp. Info. II: Ground beetle (Carabidae) data sources

Supp. Info. III: Mollusc data collection