



Niche expansion after competitor extinction? A comparative assessment of habitat generalists and specialists in the tree floras of south-eastern North America and south-eastern Europe

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ABSTRACT

Aim The aim of this study was to test R.H. MacArthur's hypothesis that realized niche breadth is constrained by species pool size – the greater the number of species in a region, the more competition restricts the distribution of each species with respect to environmental tolerances and habitat characteristics.

Location The northern Balkan region in south-eastern Europe (Illyrian Floristic Province) and the southern Appalachian region of the USA.

Methods We compared co-occurrence-based distributions of habitat specialization of tree species in two geographic regions that are ecologically similar but differ in species pool size. We applied two methods. First, we used a rank-ordering of species along a gradient of estimated niche breadth that is based solely on species co-occurrence information derived from vegetation databases from each region. To compare niche-breadth distributions of different datasets we developed a procedure that standardizes expected values of species co-occurrences independently of the size of the species pool. Second, we calculated species turnover along an elevational gradient for both regions, estimated as the rate of decay of compositional similarity with elevation distance.

Results Despite a twofold larger species pool, and in contrast to our hypothesis, there was no greater specialization trend in the tree species of the southern Appalachian region, regardless of phylogenetic subgroupings or whether rare species were included. After correcting for differences in species pools, the similarity decay with elevation distance was marginally stronger in the southern Appalachian region.

Main conclusions MacArthur's hypothesis was not supported by our analysis. While the compositional distance decay with elevation revealed only a slight trend towards narrower realized niches in the tree flora of the southern Appalachian region, the co-occurrence approach suggested the opposite. Our results indicate that species distributions are largely constrained by environmental tolerances, and that biotic pressure in the form of competition from ecologically similar species plays a relatively minor role in the ability of species to establish mature individuals in different habitat types.

Keywords

Appalachians, Balkans, beta diversity, competition, distance decay, Jaccard similarity, niche breadth, species packing, temperate tree diversity.

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INTRODUCTION

The influence of regional biotic properties on local community assembly has been a primary research focus in community ecology at least since the work of Robert H. MacArthur (1955, 1972) and MacArthur & Levins (1967). MacArthur suggested that species niche breadths are constrained by the size of the species pool; that is, the greater the number of species, the more species behaviours are limited by competition with ecologically similar species and the smaller the realized niche (MacArthur, 1972). Such ‘species packing’ arguments are strongly associated with a niche-driven (*sensu* Hubbell, 2001) view of species coexistence (Tilman, 1982; Ricklefs, 1987; Rosenzweig, 1995; Chase & Leibold, 2003). However, the relationships between the expression of niche breadth and species pool size have been difficult to quantify (Lawesson & Oksanen, 2002; Peet *et al.*, 2003). One issue has been the absence of niche-breadth metrics that are able to encompass species performance along more than one or a few environmental gradients, thus precluding a general treatment of the extent of habitat specialization in any particular assemblage (Fridley *et al.*, 2007). Another problem is the difficulty in finding communities suitable for comparison, that is, communities in which the variable of interest – species pool size – varies independently of environmental conditions that may themselves influence species’ habitat associations. Although experimental studies have shed much light on the extent to which local species abundances are constrained by competition in the context of different species pools (Hooper, 1998; Weigelt *et al.*, 2007), the interpretation of such experiments is limited by a small array of habitat conditions, relatively small species pools, and a restrictive assessment of competition often based on short-term size suppression (Aarssen & Keogh, 2002).

An alternative approach to testing MacArthur’s hypothesis that realized niche breadth is constrained by species pool size is to compare species behaviours in two geographic regions that are ecologically similar but differ in species pool size for historical reasons. The floristic similarities between today’s temperate deciduous forest regions of Europe and eastern North America have been recognized since the time of Linnaeus (Boufford & Spongberg, 1983). Land bridges between North America and Europe existed at least until the late Eocene and provided migration routes for floral elements (Frederiksen, 1988). Different historical trajectories of repeated migrations since the late Pliocene, which were influenced by differences in both climate and topography between continents, are thought to be responsible for the higher extinction rate in Europe (Schroeder, 1998; Willis & Whittaker, 2000). As a result, the present-day tree species diversity is substantially lower in Europe than in eastern North America (Huntley, 1993).

What are the implications of a lower total species pool in Europe for contemporary species interactions? MacArthur’s hypothesis would suggest that fewer total species means that contemporary species experience less overall competition and have wider realized niches or habitat tolerances today than

they did before the Pleistocene; conversely, a larger species pool in America should reduce the average habitat tolerance of trees in the American flora. Another possibility is that taxa of narrow ecological specialization were more likely to go extinct in Europe, leaving a flora that is relatively enriched with generalists (Svenning, 2003; Manthey & Box, 2007). Both considerations suggest that the contemporary flora of large woody species in Europe (here defined as those of a maximum height of at least 5 m) should contain relatively more generalist species than that in eastern North America. Although a number of researchers have compared the floristic diversity of temperate regions (e.g. Latham & Ricklefs, 1993; Francis & Currie, 1998, 2003; Ricklefs *et al.*, 1999, 2004; Qian & Ricklefs, 2000), including comparative assessments of geographic ranges (Ricklefs & Latham, 1992; Qian & Ricklefs, 2004) and the extinction sensitivity of different taxa (Svenning, 2003; Manthey & Box, 2007), no study has yet investigated whether existing species pool differences are associated with differences in average niche breadth across regions.

We selected two regions, one in south-eastern Europe (SEE) and one in south-eastern North America (SENA) that strongly differ in total tree species richness but are otherwise comparable in geographic extent and ranges of environmental factors commonly cited as important controls of tree distribution, such as elevation, soil moisture and soil pH (Horvat *et al.*, 1974; Ellenberg, 1988; Monk *et al.*, 1989; Newell, 1997). We then compared the realized niche-breadth distributions of species from each region. Rather than measuring niche breadth along preselected environmental gradients from plot data (Whittaker, 1956; Austin & Meyers, 1996; Oksanen & Minchin, 2002; Pepler-Lisbach & Kleyer, 2009), we applied a new procedure for rank-ordering species along a gradient of estimated niche breadth that is solely based on species co-occurrence information derived from vegetation databases from each region (Fridley *et al.*, 2007; Manthey & Fridley, 2009). Our objective was to test MacArthur’s (1972) hypothesis that realized niche breadth contracts with a larger species pool – that is, the richer SENA tree flora is associated with a greater degree of habitat specialization than the more depauperate SEE tree flora. In order to apply the Fridley *et al.* (2007) generalist–specialist approach for the comparison of niche-breadth distributions of different datasets, we developed a new procedure that standardizes expected values of co-occurrences independently of the size of the species pool.

MATERIALS AND METHODS

Study areas and vegetation survey data

We selected the two model regions on the basis of the following criteria: availability of vegetation survey data, relatively similar climates, comparable elevational gradients and comparable geographic extent (Table 1). The two areas selected are located in the northern Balkan region in SEE (Fig. 1a) and in the southern Appalachian region of the United States (Fig. 1b). Both regions are considered to have been

Table 1 Ranges of elevation and climatic variables within the datasets of two model regions in south-eastern Europe and south-eastern North America. Climate data were assembled from the personal climate station archive of Elgene O. Box of the University of Georgia.

	South-eastern Europe	South-eastern North America
Elevation (m)	65 to 1620	25 to 1615
Mean temperature of the warmest month (°C)	13 to 23	17 to 27
Mean temperature of the coldest month (°C)	-7 to 3	-3 to 7
Mean annual precipitation (mm)	800 to > 2000	950 to 2000
Absolute minimum temperature (°C)	-30 to -15	-30 to -18

major refuge areas for temperate deciduous forest species during the Last Glacial Maximum (Huntley & Birks, 1983; Delcourt & Delcourt, 1993). Within each region, we selected only plots representing forest stands that were classified as mature, late-successional stands without signs of recent natural or anthropogenic disturbances. Vascular plant nomenclature follows Tutin *et al.* (2001) for SEE and Kartesz (1999) for SENA.

South-eastern Europe

The study area in SEE is confined to the Illyrian Floristic Province, as defined by Meusel *et al.* (1965). The Illyrian Province spans those parts of north-eastern Italy, Slovenia, Croatia, Bosnia-Herzegovina, Serbia and Montenegro with moderate to relatively high summer precipitation rates sufficient to support mesic deciduous forests (Fig. 1a). Excluded within these countries are the Mediterranean areas along the Adriatic Sea as well as the Pannonian Plain, with its more continental climate. Most of the area is covered by the

mountain ranges of the Dinaric Alps, but in the northwest it also includes parts of the Julian Alps and its foothills. The bedrock conditions of the Dinaric and the Julian Alps are dominated by calcareous substrates from the Triassic, Jurassic and Cretaceous periods. These are interspersed with crystalline rocks of Palaeozoic origin, alluvial sedimentary material and volcanic rock types. Consequently, the range of soil reaction conditions covered by the SEE vegetation plots spans from very acidic, siliceous to very base-rich, calcareous soils.

Within the Illyrian Floristic Province, various community types dominated by European beech (*Fagus sylvatica*) account for the majority of submontane and montane forests (Table 2). Beech forests are gradually replaced by mixed oak–hornbeam forests at lower elevations with higher temperatures and increasing drought stress. Outposts of submediterranean–subcontinental thermophilous oak forests have developed on dry ridges and south-facing slopes with shallow soils. Extensive hardwood alluvial forests, dominated by pedunculate oak (*Quercus robur*) and various ash species (*Fraxinus angustifolia*, *F. excelsior*) still exist in some of the large stream floodplains. Alder (*Alnus incana*) forests dominate along montane rivers. Species-rich mixed mesic forests can be found in coves and ravines and on north-facing slopes. Under montane and altimontane conditions, mixed beech–fir–spruce forests replace beech communities.

The SEE plots representing the Illyrian Floristic Province come from 30 sources, published between 1938 and 1996 (see Appendix S1 in the Supporting Information). All plots were sampled following the Braun–Blanquet approach (Mueller-Dombois & Ellenberg, 2002). The geographic positions of plots range from 42.50° N to 46.30° N latitude and from 11.10° E to 20.50° E longitude (Fig. 1a). All sources represent local or regional forest vegetation studies with a primary focus on community descriptions carried out by vegetation scientists. To keep the plot size distribution compatible with the SENA dataset we selected plots with a documented size of between 200 and 1000 m² (1075 in total, mean plot size SEE: 508 m²; SENA: 476 m²). Considering that the relative importance of

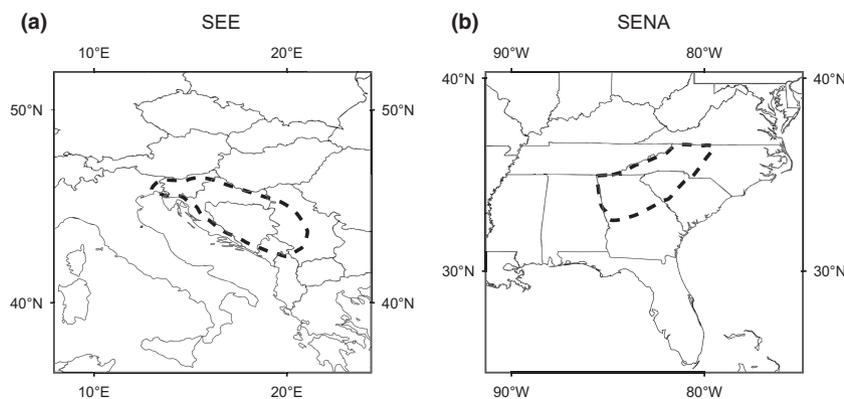


Figure 1 The model regions in (a) south-eastern Europe (SEE) and (b) south-eastern North America (SENA). SEE includes summer-humid regions of north-eastern Italy, Slovenia, Croatia, Bosnia & Herzegovina, Serbia and Montenegro. The delineation approximately corresponds to the Illyrian Floristic Province (Meusel *et al.*, 1965). SENA includes the mountain and Piedmont regions of North Carolina, South Carolina and Georgia.

Table 2 Some characteristics of forest community groups covered by the European dataset. The assemblage of forest communities is original and was derived from a preliminary clustering and subsequent ordination of the plot data.

Forest community types	Important tree species	Elevational range	Soil characteristics
Beech–fir–spruce forests	<i>Fagus sylvatica</i> , <i>Abies alba</i> , <i>Picea abies</i> , <i>Acer pseudoplatanus</i> , <i>Sorbus aucuparia</i>	Montane to altimontane (mainly above 1000 m)	Slightly acidic to base-rich
Mixed beech–oak–chestnut forests	<i>Fagus sylvatica</i> , <i>Quercus petraea</i> , <i>Picea abies</i> , <i>Castanea sativa</i> , <i>Abies alba</i>	Submontane to montane (mainly below 800 m)	Strongly acidic
Beech forests	<i>Fagus sylvatica</i> , <i>Acer pseudoplatanus</i> , <i>Fraxinus ornus</i> , <i>Acer campestre</i> , <i>Ostrya carpinifolia</i> , <i>Quercus petraea</i> , <i>Picea abies</i>	Submontane to montane	Base-rich (mainly on limestone)
Mixed mesophytic forests (mainly in coves and ravines)	<i>Carpinus betulus</i> , <i>Acer pseudoplatanus</i> , <i>Acer campestre</i> , <i>Fraxinus excelsior</i> , <i>Fagus sylvatica</i> , <i>Tilia cordata</i>	Submontane to montane (mainly below 800 m)	Base-rich
Mixed oak–hornbeam forests	<i>Quercus petraea</i> , <i>Carpinus betulus</i> , <i>Fagus sylvatica</i> , <i>Castanea sativa</i>	Foothills to submontane	Slightly acidic to base-rich, deep soils
Submediterranean–subcontinental thermophilous oak forests	<i>Quercus petraea</i> , <i>Q. cerris</i> , <i>Q. frainetto</i> , <i>Fraxinus ornus</i> , <i>Pinus nigra</i>	Foothills to submontane	Mainly base-rich, upper south- to west-facing slopes and ridges
Alluvial forests	<i>Quercus robur</i> , <i>Fraxinus angustifolia</i> , <i>F. excelsior</i> , <i>Ulmus minor</i> , <i>Carpinus betulus</i>	Mainly foothills	Base-rich, high groundwater level and regular flooding

niche processes for controlling beta diversity may shift across spatial scales (Holyoak & Loreau, 2006; Laliberté *et al.*, 2009) we expected that the selected plot size range should be well suited to reflect possible competitive effects between tree individuals in temperate forest stands.

Southern Appalachian region

The study area includes the southern Blue Ridge Mountains and Piedmont provinces of North Carolina, South Carolina and Georgia, ranging from about 33° N to 36.50° N latitude and from 85° W to 77° W longitude (Fig. 1b). The soils are derived largely from metamorphic gneiss, schist or quartzite and acidic metasedimentary rocks. Millions of years of weathering in combination with acidic substrates have formed predominantly infertile, acidic soils. Only small areas within the region are characterized by rich, circum-neutral soils.

We used data from survey plots from the Carolina Vegetation Survey (CVS), archived by the North Carolina Botanical Garden, Chapel Hill, NC, USA (see Appendix S1; for more details see Fridley *et al.*, 2005). All of the plots were surveyed as part of regional projects following the CVS protocol described in Peet *et al.* (1998). From the CVS archive we selected a set of 1075 plots from late-successional stands that closely match the distribution of the SEE set with regard to elevation and plot size (Fig. 2). Soil reaction information exists for 991 of the vegetation plots, with pH values ranging from 3.0 to 7.3 with a median of 4.4, representing generally more acidic substrate conditions than in SEE.

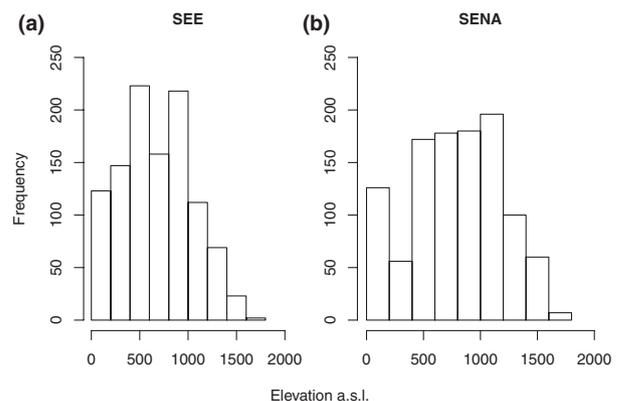


Figure 2 Distribution of plot elevation for (a) the south-eastern Europe (SEE) (mean = 688.1 m) and (b) the south-eastern North America (SENA) (mean = 791.2 m) vegetation plots.

Characteristic woody species and site conditions for the SENA forest community types are briefly described in Table 3. A comprehensive work on the vegetation ecology of the southern Appalachian Mountains was published by Newell (1997). Along an elevational gradient, forest types can roughly be divided into three groups: piedmont forests, montane forests and northern hardwood forests. Upland forests of the first two groups can further be classified into xeric/subxeric and mesic communities. In contrast to the dominant role of *Fagus sylvatica* in SEE forests, no single tree species in the SENA study area tends to dominate in a broad range of forest

Table 3 Some characteristics of forest community types of the southern Blue Ridge Mountain and Piedmont province. The assemblage of forest communities is original and was derived from a preliminary clustering and subsequent ordination of the plot data.

Forest community types	Characteristic large woody species	Elevational range (in m a.s.l.)	Site characteristics
Piedmont xeric forests	<i>Pinus echinata</i> , <i>P. virginiana</i> , <i>Carya pallida</i> , <i>Quercus montana</i> , <i>Q. falcata</i> , <i>Q. stellata</i> , <i>Q. marilandica</i> , <i>Vaccinium arboreum</i> , <i>Diospyros virginiana</i>	Foothills to submontane (75–500)	Upper south- to west-facing slopes and ridge tops with shallow, rocky soils
Piedmont subxeric forests	<i>Quercus alba</i> , <i>Q. coccinea</i> , <i>Q. velutina</i> , <i>Q. rubra</i> , <i>Carya glabra</i> , <i>C. alba</i> , <i>Oxydendrum arboretum</i> , <i>Cornus florida</i>	Foothills to submontane (75–500)	East-, south- and west-facing slopes with well-drained soils
Piedmont mesic forests	<i>Quercus rubra</i> , <i>Fraxinus americana</i> , <i>Fagus grandifolia</i> , <i>Cornus florida</i> , <i>Liriodendron tulipifera</i> , <i>Cercis canadensis</i> , <i>Acer leucoderme</i>	Foothills to submontane (75–500)	Lower north- to east-facing slopes with deep soils, coves and bottomlands without regular flooding
Alluvial forests	<i>Liquidambar styraciflua</i> , <i>Platanus occidentalis</i> , <i>Acer negundo</i> , <i>A. barbatum</i> , <i>Alnus serrulata</i> , <i>Betula nigra</i> , <i>Ilex decidua</i> , <i>Carpinus caroliniana</i> , <i>Ulmus alata</i> , <i>U. americana</i> , <i>Fraxinus pennsylvanica</i> , <i>Celtis occidentalis</i> , <i>Lindera benzoin</i>	Foothills to montane (25–1000)	Stream banks, moist deep soils in floodplains and bottomlands with regular flooding
Montane xeric forests	<i>Quercus montana</i> , <i>Q. coccinea</i> , <i>Pinus rigida</i> , <i>P. virginiana</i> , <i>P. pungens</i> , <i>Symplocos tinctoria</i>	Submontane to altimontane (500–1500)	Xeric, upper south- and west-facing slopes and ridgetops, shallow, rocky soils
Montane dry-mesic oak forests	<i>Quercus rubra</i> , <i>Q. montana</i> , <i>Q. alba</i> , <i>Tsuga canadensis</i> , <i>Castanea dentata</i> , <i>Pinus strobus</i> , <i>Kalmia latifolia</i> , <i>Oxydendrum arboretum</i>	Submontane to altimontane (500–1500)	Well-drained upland sites of different aspect and slope position
Montane (rich and acid) mesic forests	<i>Fraxinus americana</i> , <i>Liriodendron tulipifera</i> , <i>Carya cordiformis</i> , <i>Tilia americana</i> , <i>Acer saccharum</i> , <i>Halesia tetraptera</i> , <i>Aesculus flava</i> , <i>Cornus alternifolia</i> , <i>Juglans nigra</i> , <i>Asimina triloba</i> , <i>Lindera benzoin</i>	Submontane to altimontane (500–1500)	Coves and lower slopes with deep soils
Northern hardwood forests	<i>Acer pensylvanicum</i> , <i>A. spicatum</i> , <i>A. saccharum</i> , <i>Betula alleghaniensis</i> , <i>Prunus pensylvanica</i> , <i>Aesculus flava</i> , <i>Picea rubens</i> , <i>Abies fraseri</i> , <i>Sambucus racemosa</i> , <i>Sorbus americana</i>	Altimontane (> 1400)	Well-drained upland sites of different aspect and slope position

types. However, there are several trees that commonly co-occur in most upland forests in the southern Appalachian region (e.g. *Acer rubrum*, *Quercus alba*, *Carya glabra*, *Carya alba*, *Nyssa sylvatica*, *Cornus florida*, *Prunus serotina*). The maximum elevation of about 1615 m a.s.l. in the SENA data was set to be comparable to the respective maximum in SEE and led to the exclusion of sub-boreal forest communities, which occur mainly above 1600 m.

Data preparation

For each dataset we removed low-resolution taxa (i.e. determination to genus level or higher) and aggregated all subspecies to the species level. For the estimation of relative niche width we chose to limit the species pool of our analysis to mid- to large-sized woody species that reach a maximum height of at least 5 m, either with single or multiple stems. This selection provides an assemblage of species that generally exist within the same vertical strata and functional group and are expected to compete for the same resources (Clark, 2010).

It further comprises a group of taxa generally well distributed geographically within the study areas, but representing a wide variety of perceived habitat affinities. Under these constraints, the total species pools for the analysis consisted of 76 woody species for SEE and of 155 species for SENA. To restrict the co-occurrence information to those individuals that have been able to grow above the herb layer, a species was only considered present in a plot if it existed in the shrub or tree layers; thus, we did not include presences of seedlings or small saplings. All calculations are based on presence–absence data.

Estimation of relative niche width

We applied a modified version of the procedure of Fridley *et al.* (2007) that rank-orders species along a gradient of estimated niche breadth based on species co-occurrence information. The method requires information only on the relative degree to which focal species co-occur with other species within a given area. It is based on the assumption that,

all else being equal, habitat generalists co-occur with many species across their range. Consequently, the plots in which they occur are characterized by a relatively high rate of species turnover. Habitat specialists, regardless of their frequency, co-occur with relatively few species and will exhibit relatively low species turnover because they tend to occur with the same species. Consequently, co-occurrence information is used as a biological assay for ‘habitat diversity’ or ‘niche width’ that requires no assumptions about the definition of a habitat or the most critical environmental factors that control plant species distributions (Fridley *et al.*, 2007). The co-occurrence-based approach is fundamentally different from other approaches of measuring niche widths along environmental gradients because it considers plant communities – realized assemblages of species at a given plot location – as equivalents of habitats. Thus, a habitat specialist in the commonly used sense, for example a plant limited to very moist sites, may be regarded as a generalist in the co-occurrence approach if the variation in plant communities is much higher at very moist sites compared with the remaining moisture gradient.

The original approach described in Fridley *et al.* (2007) used an additive partitioning approach to quantify beta diversity (Veech *et al.*, 2002), but two recent papers have recommended alternative turnover indices (Manthey & Fridley, 2009; Zeleny, 2009), where the choice of the most appropriate beta diversity index depends on various dataset characteristics (Manthey & Fridley, 2009). It has been shown with simulated data that the approach is relatively robust against variation in the size of local species pools (Manthey & Fridley, 2009; Zeleny, 2009), habitat-sampling bias (Fridley *et al.*, 2007) and large variations in species frequency (Fridley *et al.*, 2007).

In our data some European species show a relatively large positive skewness of plot richness distributions; that is, they occur much more often in species-poor than in species-rich plots (e.g. *Larix decidua*, *Picea abies*, *Salix caprea*). Thus, we used the mean Jaccard dissimilarity of plot pairs as a measure of beta diversity (for more details on the behaviour of different beta diversity indices in the context of co-occurrence-based niche modelling see Manthey & Fridley, 2009). Pairwise Jaccard dissimilarity was favoured over the multiple plot dissimilarity approach proposed by Baselga *et al.* (2007), which was one of the alternative indices tested in Manthey & Fridley (2009), because we regard complete compositional nestedness as a potential reflection of ecological differences in the study regions. For example, with increasing elevation a forest community may regularly lose some species without gaining new species because of decreasing area towards a summit. This would be regarded as complete compositional nestedness and calculated as no species turnover using the multiple plot dissimilarity approach of Baselga *et al.* (2007).

We calculated the turnover for each species directly as the average of all pairwise Jaccard dissimilarities (\bar{D}_{Jacc}) of the plot subset containing a focal species. To obtain a stable maximum Jaccard dissimilarity of 1 (no shared species) we excluded the focal species from the calculation. We applied the estimation of relative niche widths for species sets with contrasting

minimum plot frequencies of 20 and 2. The restriction to more frequent species with a minimum occurrence of 20 takes into account that the total frequency of a species is influenced by a multitude of other, not necessarily niche-related, factors, such as fecundity, dispersal, or land use history. However, the share of species exceeding that cut-off level differs substantially between the two regions (SEE: 64.5%, SENA: 50.3%). This difference can potentially introduce bias in the cross-continental niche-width comparison away from finding more specialization in the SENA tree flora, because a larger proportion of the total SENA flora would be excluded on this basis. Therefore, we additionally considered all species with any turnover in the data, that is, with at least two occurrences, a proportion (89%) that is consistent across regions.

Standardization of generalist–specialist values across datasets

Absolute \bar{D}_{Jacc} values are potentially influenced by the total species pool and the respective plot-richness distribution of a given dataset. For example, the exclusion of the focal species has a stronger effect on \bar{D}_{Jacc} in the less species-rich SEE plots because on average about 17% of species are removed compared with only about 9% in the SENA data. Because our aim was to compare generalist–specialist patterns between two model regions that differ in the size of their respective species pools, it was necessary to standardize \bar{D}_{Jacc} values. We applied a standardization that combines a randomized species pool reduction with a weighting of \bar{D}_{Jacc} values according to the overall mean of beta diversity across all pairwise samples. First we randomly reduced the larger pool of the SENA dataset to the same size as the SEE species pool (76 species) before calculating \bar{D}_{Jacc} values as described above. To achieve this reduction we separated all occurrences of the focal species from the full data, conducted a random selection of 75 species out of the remaining 154 species, and combined the occurrences of the 75 selected species with the retained occurrences of the focal species. This procedure regularly led to the exclusion of a few plots without selected species (but always < 1%). Note that a random reduction of the species pool does not change the ratio between rare and common species, which would otherwise influence the dissimilarity structure of the data. Second, we calculated the overall mean of the Jaccard dissimilarity matrix (\bar{D}_{total}) of the respective reduced dataset and divided the \bar{D}_{Jacc} values by \bar{D}_{total} . For each focal species we repeated the procedure 100 times and took the average standardized \bar{D}_{Jacc} value. For the SEE data only the second step, namely division of \bar{D}_{Jacc} by \bar{D}_{total} , was applied. \bar{D}_{total} represents the overall dissimilarity of a given dataset. Thus, the standardized \bar{D}_{Jacc} metric relativizes the estimated niche breadth of each species by reference to the \bar{D}_{total} value of a given dataset. Note, however, that the standardized \bar{D}_{Jacc} values can be > 1, if the mean dissimilarity of a particular subset is higher than that of the whole dataset.

Figure 3 illustrates the need for standardization by \bar{D}_{total} . It shows two simplified scenarios with contrasting species pools

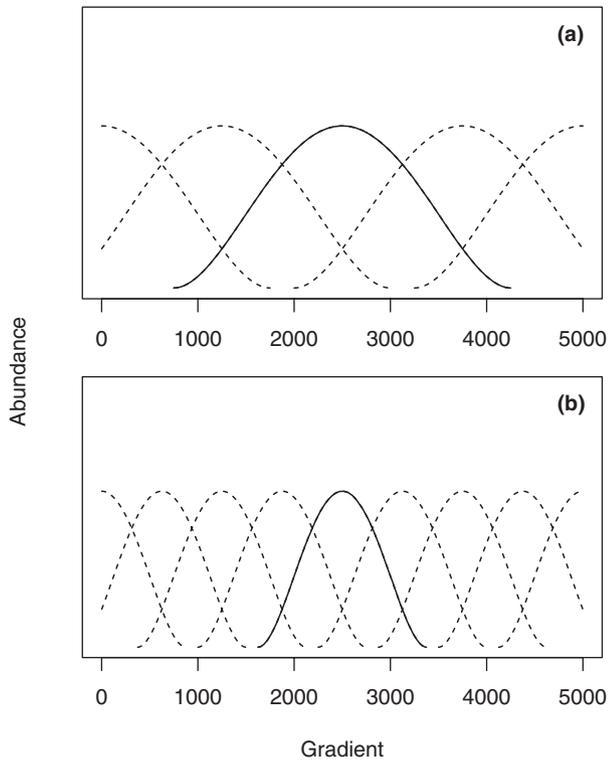


Figure 3 Simplified model of contrasting coenoclines with (a) five and (b) nine regularly distributed species niches along artificial environmental gradients of the same length. The focal species (in bold) differ in the absolute range along the gradient but have identical overlap patterns with neighbouring species. Without standardization by the total Jaccard dissimilarity \bar{D}_{total} , which is higher in the nine-species coenocline with more species turnover (b), the \bar{D}_{jacc} values of the focal species would not be different.

of five and nine species regularly distributed along artificial environmental gradients of the same length. With a random sampling of 1000 plots that contain all species present at a

given location of the gradient, in both scenarios the plots of the focal species (in bold) have a very similar structure in Jaccard dissimilarity (\bar{D}_{jacc} : 0.555 vs. 0.548), despite the different gradient ranges. Because in (a) the focal species co-occurs with all other species, which is not the case in (b), \bar{D}_{total} values differ between the scenarios (5 species: 0.552; 9 species: 0.7524) and allow for an effective comparison of niche widths that reflects actual differences in the relationships between species ranges and total gradient lengths (standardized \bar{D}_{jacc} values: 1.005 vs. 0.729).

Simulation to test the standardization

We analysed the effectiveness of this standardization approach with simulated data of randomly parameterized species distributions with known niche width along a single ‘environmental’ gradient, following the general approach of Fridley *et al.* (2007) and Mantley & Fridley (2009). For four scenarios that differed in species pool and average niche widths we created species niches using the beta function (Minchin, 1987) with random parameterizations of niche width, amplitude and location of optimum (Table 4).

For each simulation of niches along the one-dimensional gradient we created a dataset of 1000 plots by randomly assigning a plot to a gradient location. Assuming a linear local–regional relationship (Mantley & Fridley, 2009), we randomly sampled 66% of the species pool based on the simulated probability of species occurrences at each assigned plot location. In a first scenario we created a dataset containing 50 species with a mean niche width of 2427 gradient units. In the second scenario the dataset of 50 species was duplicated to obtain a total pool of 100 species, but with an identical niche-width pattern to in the first scenario. In two other scenarios containing 100 species, the mean niche widths were either narrower or wider than that of the first scenario (Table 4).

Table 4 Parameter values for niche simulations using the beta function (after Minchin, 1987), and characteristics of various standardization scenarios (note the differences between mean niche widths and mean species ranges owing to truncated niches at gradient ends). The four niche simulations represent coenoclines with differences in total species richness and mean niche widths.

Parameter	Description	Value			
S	Total number of species	50	100	100	100
Ao	Niche amplitude	Lognormal RV of mean = 2 and SD = 1 (log scale)			
m	Location of niche optimum	Uniform RV of gradient range 100–4900			
a, b	Niche shape left and right side	1.99	1.99	1.99	1.99
r	Niche width	Normal RV with mean = x and SD = 600			
x	Mean niche width	2900	2900	2400	3400
	Mean species range (as gradient units)	2427	2427	2135	2919
	Minimum species range (as gradient units)	1283	1283	833	1701
	Maximum species range (as gradient units)	3683	3683	3800	4691
	Total species occurrences	15,992	32,220	21,021	41,798
	\bar{D}_{total}	0.740	0.741	0.765	0.680
	Pearson correlation between actual range and standardized \bar{D}_{jacc}	0.886***	0.899***	0.890***	0.915***

RV, random variation.

***P < 0.001.

Calculation of similarity decay with elevation distance

To compare the results of the co-occurrence-based estimation of realized niche breadth with those of a gradient-based approach, we calculated species turnover along an elevational gradient for the full datasets of both regions, estimated as the rate of decay of compositional similarity (Nekola & White, 1999) with elevation distance. As in the co-occurrence approach, we used Jaccard's index but here expressed as a similarity measure. To calculate the similarity decay for both regions we followed the general procedure as described in Nekola & White (1999): (1) removal of all plot pairs that shared no species from the similarity matrix; (2) rescaling to a common mean by dividing each matrix of Jaccard similarities by the respective mean; (3) calculation of a linear regression to determine the slope and intercept of the vegetation similarity–elevation distance relationship. To correct for a possible influence of differences in species pool on the similarity decay independent of our niche-breadth focus, we randomly reduced the species pool of the SENA data to the size of the SEE pool (76 species) before calculating steps 1–3, and repeated this procedure 1000 times. We tested for a difference between the mean of the permuted SENA slope values ($n = 1000$) and the slope of the SEE data in the following way: in each permutation we calculated the slope, intercept and the variance–covariance matrix between slope and intercept from the respective linear model. Then we calculated the mean of the slope variances of all permutations S_{perm}^2 and the variance of slope values S_{slopes}^2 . The standard error SE_{SENA} of the mean slope value of the permutations is given in equation 1 as

$$SE_{SENA} = \sqrt{\frac{S_{perm}^2 + S_{slopes}^2}{n}}, \quad (1)$$

where n is the number of permutations. The standard error of the SEE slope SE_{SEE} is given in equation 2 as

$$SE_{SEE} = \sqrt{S^2}, \quad (2)$$

where S^2 is the variance of the SEE slope value. We estimated the 97.5% confidence intervals CI_{SENA} and CI_{SEE} of the two resulting standard errors of slopes by multiplying each standard error by the 97.5 quantile. We used 97.5% confidence intervals to accept or reject the null hypothesis of no differences between slopes with a probability level of 5% (Bonferroni correction).

For all analyses we used the statistical software R version 2.10.1 (R Development Core Team, 2009). In Appendix S2, the R code is provided for the calculation of the generalist–specialist metric, and for the elevation distance decay calculation including the slope comparison.

RESULTS

Effectiveness of the standardization approach

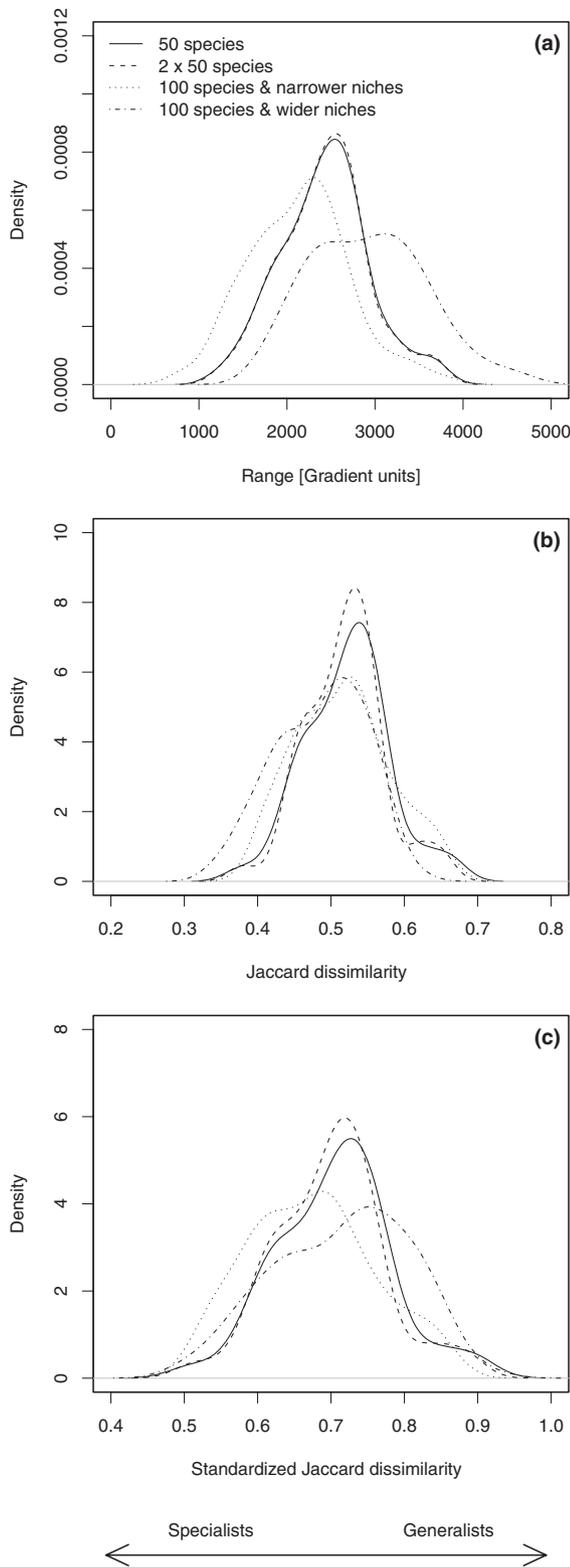
Figure 4(a) represents the distribution of the known niche breadths of the four one-dimensional coenoclines. Figure 4(b)

shows the distribution of estimated \bar{D}_{Jacc} values after random species pool reduction to 50 species for the three datasets containing 100 species, but without correction for \bar{D}_{total} . It shows that the symmetric shift of niche widths, simulated with normal variation and constant standard deviation (Table 4), cannot be detected by the co-occurrence approach without further standardization when using a dissimilarity index as the measure of beta diversity. Although the correlation between known and estimated niche ranges is high in all scenarios (Table 4, last row), and species are in general correctly ranked along the generalist–specialist gradient, the distributions do not reflect the underlying differences in mean niche widths between the scenarios. This is because with broader niches both local species densities and the average overlap of a focal species with other species increases, which prevents an increase in mean dissimilarity within a species' range (see Fig. 3). Only the introduction of the global measure of beta diversity \bar{D}_{total} allows for an effective comparison of niche widths between different datasets (Fig. 4c), provided that the datasets are stratified to comparable gradient lengths of important environmental factors.

Patterns of habitat specialization across regions

The mean alpha diversity of large woody plants is 5.8 species per plot (7.6% of the total species pool) in the SEE dataset and 11.4 species (7.4% of the total species pool) in the SENA dataset. On average, the species have a plot frequency of 81.7 in the SEE data and of 79.1 in the SENA data. The overall dissimilarity \bar{D}_{total} is also similar in the two datasets (SEE: 0.841, SENA: 0.853), and the value hardly changes for the SENA data after species pool reduction to 76 randomly selected species (mean \bar{D}_{total} after 1000 permutations: 0.850).

The values of \bar{D}_{Jacc} for large woody species from SEE and SENA that occur in a minimum of 20 plots are listed in Appendix S3. From the total of 76 large woody species that occur in the SEE plots, 49 (64.5%) were included in the analysis. In the SENA dataset, 78 of the 155 large woody species (50.3%) exceeded the cut level of 20 plots and were included in the analysis. The species are arranged according to the specialist–generalist gradient, from the most generalist species (SEE: *Fagus sylvatica* = 1.036, SENA: *Acer rubrum* = 1.011) to the most specialist species (SEE: *Larix decidua* = 0.522, SENA: *Pinus pungens* = 0.722; all values expressed as standardized \bar{D}_{Jacc}). When excluding the focal species, all possible plot pairs across late-successional forests in the Illyrian Floristic Province containing *Fagus sylvatica* have an average Jaccard dissimilarity of 0.871. This value slightly exceeds \bar{D}_{total} of the European data (0.841) and results in a standardized value of 1.036. In 758 plots the focal species co-occurs with 66 other large woody species from the total species pool of 76, with an average plot richness of 5.49. At the other extreme, all plot pairs containing *Larix decidua* have an average dissimilarity of 0.439. The focal species co-occurs in 40 plots with 26 other large woody species, with an average plot richness of 4.38.



While in SENA estimated niche widths are independent of total plot frequency (Spearman rank correlation, $\rho = 0.008$, $P = 0.94$), these variables are significantly correlated in SEE ($\rho = 0.491$, $P < 0.001$). \bar{D}_{jacc} values are predicted in both regions by the total number of co-occurring species (SEE: $\rho = 0.678$, $P < 0.001$; SENA: $\rho = 0.520$, $P < 0.001$). Absolute

Figure 4 Density distribution of niche widths of four simulation scenarios with differences in species pools and mean niche widths. (a) Distributions of known niche widths of simulated species in four scenarios; (b) distributions of estimated niche widths of four scenarios without standardization; and (c) distributions of estimated niche widths after standardization. Standardization of Jaccard dissimilarities of the scenarios with 100 species was achieved by 100 random reductions of the species pool to the size of the small pool (50 species). Within each random reduction the resulting dissimilarity values are divided by the total Jaccard dissimilarity (see text for details). Niches were modelled using the beta function with parameters described in Table 4.

elevation ranges of species are also correlated with the generalist–specialist patterns (Spearman rank correlation, SEE: $\rho = 0.431$, $P = 0.002$; SENA: $\rho = 0.233$, $P = 0.04$). There is no significant relationship between the mean richness of plots containing a focal species and \bar{D}_{jacc} values (Spearman rank correlation, SEE: $\rho = 0.123$, $P = 0.398$; SENA: $\rho = 0.173$, $P = 0.123$).

Within both regions, understorey and canopy species do not differ significantly in estimated niche widths. While in the SEE data the understorey species tend to have slightly broader niches than the canopy trees (mean standardized \bar{D}_{jacc} : canopy = 0.884, understorey = 0.914, $P = 0.388$), there are virtually no differences in the SENA data (mean standardized \bar{D}_{jacc} : canopy = 0.922, understorey = 0.923, $P = 0.809$).

Distributions of original and standardized \bar{D}_{jacc} values for species with a minimum plot frequency of 20 are shown in Fig. 5(a,b), and for all species with more than a single occurrence in Fig. 5(c). A phylogenetically stratified subset of species from Fig. 5(b) is presented in Fig. 5(d). This includes only species from those genera that occur in both sets of analysed species. Contrary to our main hypothesis, and regardless of the minimum occurrence level or phylogenetic similarity, the generalist–specialist distribution patterns show a trend towards broader realized niches in the SENA data. However, Wilcoxon rank sum tests revealed a significant difference between the regions only for the largest species selection (Fig. 5c).

Differences in similarity decay with elevation distance

Figure 6(a) shows a locally weighted regression of Jaccard similarities against elevation distance without pool reduction for both regions. The lines indicate relatively linear similarity decay in the two regions, with no obvious slope differences. Figure 6(b) represents the linear functions of similarity decay after correcting for richness differences using repeated random species pool reductions for the SENA dataset, removal of zero similarities and standardization to a common mean. Compared with the European species distribution along the elevational gradient, the similarity decay in the SENA region is slightly stronger, reflecting a slight but significant trend towards more specialized species along this gradient (Fig. 6b). The pattern is supported by the fact that the average

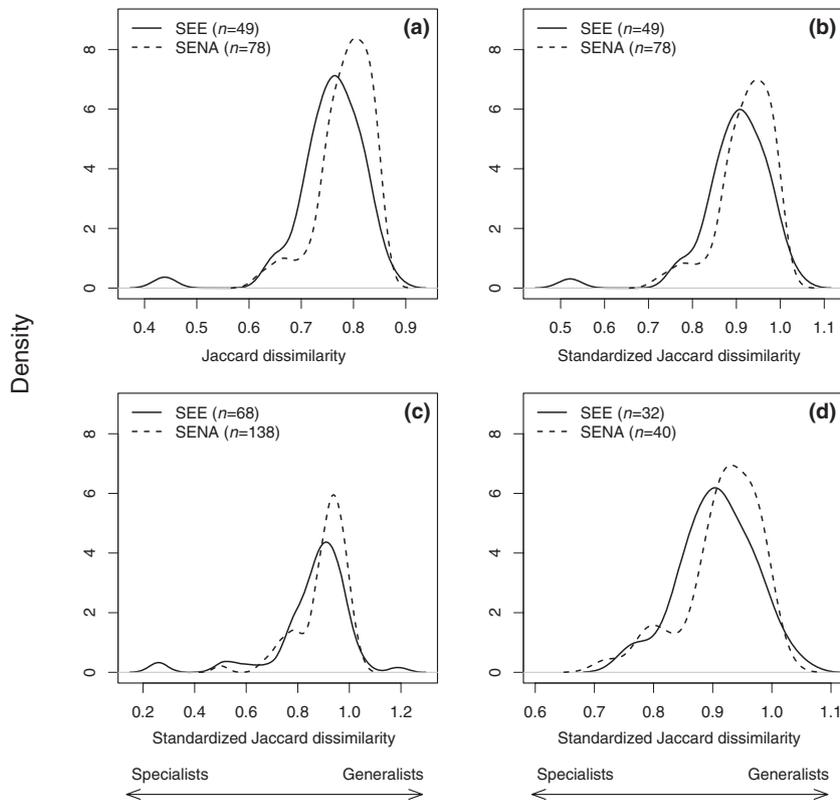


Figure 5 Density distributions of estimated niche widths, expressed as original or standardized Jaccard dissimilarity values of large woody species from south-eastern Europe (SEE) (solid lines) and south-eastern North America (SENA) (dashed lines). Panels (a) and (b) show the distribution of those species with a minimum plot frequency of 20, either (a) without or (b) after standardization. Panel (c) represents the distribution of all species that occur at least twice in the respective dataset, and panel (d) represents a phylogenetically stratified subset of species from (b) where the respective genera occur in both sets of analysed species (Wilcoxon rank sum test: Fig. 5b, $P = 0.054$; Fig. 5c, $P = 0.031$; Fig. 5d, $P = 0.266$). See text for details of calculation and standardization of Jaccard dissimilarity.

elevational range of species is slightly but not significantly larger in SEE than in SENA (741.8 m vs. 708.2 m, Wilcoxon rank sum test: $P = 0.851$).

DISCUSSION

The hypothesis that the twofold-higher species number in the SENA dataset compared with the SEE dataset is associated with a significantly greater tendency of SENA trees towards habitat specialization was not supported by our analyses. Only the elevation distance decay analysis revealed a slight trend towards narrower realized niches in the SENA flora, but the significance in slope differences is attributed mainly to the high number of permutations and is unlikely to be biologically meaningful. Rescaled to the original Jaccard similarity, the slope difference corresponds to a difference of < 0.001 units of Jaccard similarity per 100-m elevation distance. This can be translated to a mean turnover difference of the magnitude of 0.01 species per 100 m elevation distance in the SEE data or 0.02 species per 100 m within the SENA data.

In the co-occurrence-based niche-breadth analysis, a surprising trend towards narrower realized niches in European tree species was found in all three analysed subsets. While this trend was significant in the analysis that included all non-singleton species, there was little evidence overall to support major differences in realized niche breadths between the large woody species of the study regions.

At face value, these results suggest that species distributions are largely determined by (abiotic) environmental constraints,

and that biotic pressure in the form of competition from ecologically similar species plays a relatively minor role in the ability of species to establish mature individuals in different habitat types. Many other analyses of tree distributions in both regions have also asserted that contemporary environmental factors are the primary drivers of species occurrences. For example, Morin *et al.* (2007) linked SENA tree range limits to drought and freezing stresses associated with differences in leafing and foliar phenology among species, and posited only a minor role for interspecific competition in delimiting range boundaries. In studies of smaller spatial extent, Coudun *et al.* (2006) and Pinto & Gegout (2005) found a much better prediction of the distribution of European temperate trees when using soil variables as additional predictors compared with models using only climate variables.

Other aspects of our method must also be considered when interpreting our comparison of niche breadths among our focal regions. For example, our use of species occurrences from all selected plots where an individual is present in the shrub layer may include some locations where the species will not reproduce, and thus may not legitimately be within a species' niche (Pulliam, 2000). Furthermore, the use of presence-absence data instead of species abundances makes no distinction between dominant and subordinate species in a stand and thus estimates niches in a very broad sense. However, because these issues apply to both regions, we have no reason to suspect them of leading to a bias in niche-breadth estimation between focal regions.

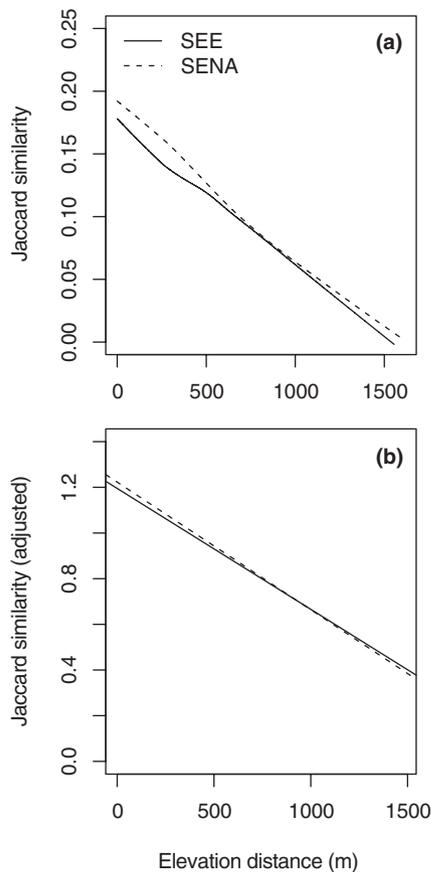


Figure 6 Decay of similarity in tree species composition with increasing elevation distance in the south-eastern Europe (SEE) and south-eastern North America (SENA) datasets. Similarities are measured with Jaccard's index. (a) Lowess smoother of the original similarity matrices without species pool reduction and no removal of plot pairs that share no species (zero similarity). (b) Linear regression curves after removal of zero dissimilarities and adjustment to a common mean. Intercept and slope values of the American data are means of 1000 replications with random reduction of the species pool to 76 species. Compared with the SEE data, similarity decay is only slightly, but significantly, stronger with increasing elevation distance in the SENA forest communities (slope SEE: -0.0529 , 97.5% confidence interval = -0.0538 to -0.0520 ; mean slope SENA: -0.0559 , 97.5% confidence interval = -0.0563 to -0.0555). Slope values are in units of adjusted community similarity per 100-m elevation distance.

Slight indications of a more specialized woody flora of SEE from our co-occurrence analysis may indicate differences in environmental variation within regions, despite our attempt at environmental standardization of the two regions. In particular, the geological bedrock and soil conditions are more diverse in SEE than in the Appalachian Mountains. Moreover, the younger and less weathered alpidic mountain ranges in SEE are characterized by a steeper and more rugged relief than are the older Appalachian Mountains with their Palaeozoic origin, which probably contributes to a greater heterogeneity of microclimatic conditions in SEE. Taking these abiotic differ-

ences into account it is possible that the large woody species in SEE are distributed across more habitat heterogeneity than are their American counterparts. As a result of a more diverse set of habitats, the overall environmental gradient sampled in the SEE data would be longer than in the SENA data. This in turn could have led to an overestimation of \bar{D}_{total} for the European data (see Fig. 3 for the importance of equal gradient lengths in the comparison). A lower \bar{D}_{total} value for Europe would lead to a shift of the density curves of European species in Fig. 5(b–d) towards broader niches and diminish the differences in niche-width pattern between the model regions.

Differences in bedrock geology and soil conditions also point to contrasting asymmetric distributions of soil reaction conditions in the two study regions. While in the SENA data the majority of plots have acidic soils, the opposite situation can be found in the SEE data, for which base-rich to calcareous soils prevail. Ewald (2003) and Peet *et al.* (2003) revealed a positive relationship between species pool sizes and soil pH in Europe and in the Southern Appalachians, respectively. In the SEE data, the combination of a higher proportion of base-rich plots and a larger species pool for base-rich sites might be responsible for a species turnover pattern that is higher than it would be under soil conditions comparable to those for the SENA data. However, herbaceous plants contribute much more to this positive pH–richness relationship, and these are excluded from our analysis. From the list of 49 analysed European species (Appendix S3), 19 are considered as indifferent against soil reaction and an additional 20 have Ellenberg *R*-values of 6, 7 or 8 (Ellenberg *et al.*, 1992), indicating relatively broad tolerances for weakly acidic to base-rich soils that do not help to explain the narrower realized niches of European trees.

In contrast, the slightly steeper slope of the SENA data in similarity decay rates with increasing elevation distance is weak support for the expectation of more specialized species in southern Appalachian forests, at least along this particular gradient. Indeed, the difference in distance decay may reflect more general differences in the tree floras of western Eurasia and eastern North America with regard to bioclimatic limitations. A recent cross-continental comparison revealed that three out of eight main bioclimatic range groups of deciduous trees from eastern North America have (almost) no counterparts in the European tree flora (Manthey & Box, 2007). These are: (1) the northern hardwood species that only occur at higher elevations in the southern Appalachians (e.g. *Acer spicatum*, *A. saccharum*, *Betula alleghaniensis*), (2) a group of trees with ranges more or less confined to the Appalachian Mountains (e.g. *Quercus montana*, *Magnolia acuminata*), and (3) a group of southern species with high warmth and moisture requirements that, within the American model region, are found mainly in the Piedmont region and other low-elevation sites (e.g. *Carya pallida*, *Quercus falcata*). While south-eastern European forests also have warmth-demanding southern species confined to lower elevations (e.g. *Acer monspessulanum*, *Quercus cerris*), there are only a few trees with particular preferences for higher elevations (e.g. *Larix*

decidua). However, Svenning (2003) and Manthey & Box (2007) show that these contemporary differences in the climatic requirements of tree floras are more likely to be the result of a deterministic sorting process triggered by past climatic differences than to result from different levels of current interspecific competition.

We conclude that the twofold difference in species pool size among the tree floras of south-eastern Europe and the south-east USA does not readily translate into obvious differences in realized niche breadths. Environmental differences not taken into account, such as substrate or microclimatic variation, may have contributed to the unexpected trend towards narrower estimated niche breadth in the SEE data. Our results suggest that competitive effects of co-occurring tree species are not strongly species-specific, or are at least weak compared with environmental drivers of fitness such as temperature and water regimes and substrate properties such as nutrient availability. Thus, realized niche properties may be more historically conserved than MacArthur (1972) envisioned.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of south-eastern Europe (SEE) and south-eastern North America (SENA) dataset sources.

Appendix S2 R code implementing the generalist–specialist metric and the elevation distance decay comparison.

Appendix S3 Habitat generalist–specialist tendencies for 49 large woody species of south-eastern Europe and for 78 large woody species of south-eastern USA.

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