Species richness influences the spatial distribution of trees in European forests

Cristina C. Bastias[1], Daniel A. Truchado[3], Fernando Valladares[1,2], Raquel Benavides[1], Olivier Bouriaud[4], Helge Bruelheide[5,6], Andrea Coppi[7], Leena Finér[8], Teresa E. Gimeno[9,10], Bogdan Jaroszewicz[11], Michael Scherer-Lorenzen[12], Federico Selvi[13] and Marcelino De la Cruz[2]

[1]LINCGlobal, Dept of Biogeography and Global Change, National Museum of Natural Sciences, MNCN, CSIC, ES-28006 Madrid, Spain
[2]Area of Biodiversity and Conservation, Dept of Biology and Geology, E.S.C.E.T., Univ. Rey Juan Carlos, Móstoles, Spain
[3]Dept of Biodiversity, Ecology and Evolution, Faculty of Biology, Complutense Univ. of Madrid, Madrid, Spain
[4]Faculty of Forestry, Stefan cel Mare Univ. of Suceava, Suceava, Romania
[5]Inst. of Biology / Geobotany and Botanical Garden, Martin Luther Univ. Halle-Wittenberg, Halle (Saale), Germany
[6]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
[7]Dept of Biology, Univ. of Firenze, Firenze, Italy
[8]Natural Resources Inst. Finland (Luke), Joensuu, Finland
[9]Basque Centre for Climate Change (BC3), Leioa, Spain
[10]IKERBASQUE, Basque Foundation for Science, Bilbao, Spain
[11]Białowieża Geobotanical Station, Faculty of Biology, Univ. of Warsaw, Białowieża, Poland
[12]Faculty of Biology, Geobotany, Univ. of Freiburg, Freiburg, Germany
[13]Dept of Agriculture, Food, Environment and Forestry Laboratories of Botany, Univ. of Firenze, Firenze, Italy

Corresponding author: Cristina C. Bastias, LINCGlobal, Dept of Biogeography and Global Change, National Museum of Natural Sciences, MNCN, CSIC, ES-28006 Madrid, Spain. E-mail: crbasc@gmail.com

Decision date: 21-Nov-2019

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: [10.1111/oik.06776].

ABSTRACT

The functioning of plant communities is strongly influenced by the number of species in the community and their spatial arrangement. This is because plants interact with their nearest neighbors and this interaction is expected to be stronger when the interacting individuals are ecologically similar in terms of resource use. Recent evidence shows that species richness alters the balance of intra- versus interspecific competition, but the effect of species richness, and phylogenetic and functional diversity on the spatial pattern of the plant communities remain less studied. Even far, how forest stand structure derived from past management practices can influence the relationship between species richness and spatial pattern is still unknown. Here, we evaluate the spatial distribution of woody individuals (DBH >7.5 cm) in 209 forest stands (i.e. plots) with an increasing level of species richness (from 1 up to 10 species) in six forest types along a latitudinal gradient in Europe. We used completely mapped plots to investigate the spatial pattern in each forest stand with point pattern techniques. We fitted linear models to analyze the effect of species richness (positively correlated with phylogenetic diversity) and functional diversity on tree spatial arrangements. We also controled this relationship by forest type and stand structure as a proxy of the management legacy. Our results showed a generalized positive effect of species richness and functional diversity on the degree of spatial clustering of trees, and on the spatial independence of tree sizes regardless of the forest type. Moreover, current tree spatial arrangements were still conditioned by its history of management; however its effect was independent of the number of species in the community. Our study showed that species richness and functional diversity are relevant attributes of forests influencing the spatial pattern of plant communities, and consequently forest functioning.

Keywords: spatial point pattern, intraspecific competition, plant-plant interactions, stand structure, functional diversity, mixed forests, FunDivEurope

INTRODUCTION

Anthropogenic actions have resulted in multiple changes at the global scale that have often caused biodiversity loss. Substantial theoretical and experimental evidence has demonstrated that the functioning of many forest ecosystems closely depends on its species diversity (Loreau 2001, Gamfeldt et al. 2013, van der Plas et al. 2016). As species often differ in their functional strategies deployed to exploit environmental resources (Hutchinson 1957, Silvertown 2004), the addition or loss of any species may impact the functioning of the entire community (Tilman et al. 1997). Moreover, it is often argued that forest multifunctionality occurs as a result of complementarity in resource use among functionally diverse species (Hooper et al. 2005). Thus, it is expected that two species with similar resource use strategies cannot stably coexist (MacArthur and Levins 1967). Still, modern coexistence theory also considers that two species will coexist if their niche differences overcome their fitness differences (Chesson 2000, Adler et al. 2007). Under this perspective, niche differences are estimated as the relative ratio between intra- and interspecific competition (Chesson 2012). Niche differences operate as a stabilizing factor promoting coexistence when species limit themselves more than they limit others (Chesson 2000), i.e., when intraspecific competition has stronger effects than interspecific competition. Although the source of such differences remains unknown in many cases (Godoy et al. 2018), efforts have been made to relate them to plant functional traits (Kraft et al. 2015), including differences in phenology or morphology, or even to relate them to spatial segregation (Chesson 2000, Adler et al. 2007).

In plant communities like forest systems, space availability is a key feature influencing community functioning and structure (Tirado and Pugnaire 2003, Maestre et al. 2005, 2012). Sessile organisms, such as trees, are forced to interact with their nearest neighbors, which results in forest stands with spatial patterns and tree size structures reflecting these interactions (Watt 1947, Stoll and Weiner 2000). The effects of plant-plant interactions on the spatial pattern of trees are well-known, with intraspecific competition leading to regular, self-thinned patterns (e.g. Kenkel 1988) and interspecific competition generating spatial segregation at larger scales (Kenkel 1994). These patterns agree with long-standing theory predicting that the processes of self-thinning in mixed stands (often termed “alien thinning”) are subtly different from those occurring in pure stands (Harper and McNaughton 1962). For example, Pretzsch et al. (2017) showed shifts in the slope of the stand self-thinning line due to packing density, which might be higher under mixed than monospecific conditions. The modern coexistence theory would explain this outcome as a consequence of indirect competition effects that only emerge in diverse systems (Saavedra et al. 2017). A reflection of the tree-tree interactions can be also observed in the spatial correlation of the tree sizes (DBH or basal area) within a tree community. Tree sizes in forests stands usually show negative spatial dependence, i.e., the sizes of two close trees is usually smaller than the sizes of two randomly chosen trees in the stand (Stoyan and Penttinen 2000). Translating it to a species diversity context, less spatial dependence in tree sizes should be expected in mixed communities in comparison to monospecific ones by minimizing the intraspecific interactions and increasing the interactions between individuals with different resource use strategies. Despite an increasing number of studies assessing the relationships between species richness, forest functioning and coexistence processes in the last decades (Jucker et al. 2014a, b, Liang et al. 2016, Bastias et al. 2017, Benavides et al. 2019) only few of them have studied it from an spatially explicit approach and addressed other aspects of biodiversity such as phylogenetic or functional diversity.

European forests are characterized by a low number of tree species in comparison with other forests at similar latitudes, which is mostly due to species extinctions during the glacial periods and high anthropogenic pressures for centuries

(Walter 1985). Over the last decades, a change in forest management policies encouraging mixed and structurally more diverse forest stands, has often caused relevant large-scale changes in tree spatial pattern as well as in species composition and forest structure (Johann 2007). Uneven-sized forest stands are usually considered stable in terms of structure and composition at long term (Larsen 1995, Schütz 2001). For old-growth forest systems, which have reached relative stability in terms of structure and composition, some authors have suggested that stabilizing niche differences (e.g. resource partitioning) override fitness differences among species (Chesson 2000, Adler et al. 2007, Barabás et al. 2016). Nevertheless, the relationship between forest structure derived from past management practices, species richness and the spatial pattern of trees has received little attention despite having relevant implications for ecosystem dynamics and functioning (Petritan et al. 2015).

In this paper, we examine the effect of species richness and phylogenetic and functional diversity on the spatial distribution of trees in 209 forest stands differing in species richness (ranging from 1 to 10 species). Forest stands were distributed in six regions along a latitudinal gradient in Europe, from Mediterranean to boreal forests. Assuming that in stable communities, such as mature European forests, the effects of intraspecific competition override those of interspecific interactions, we hypothesize that the frequency of intraspecific interactions decreases as species richness increases, resulting in less self-thinning and, therefore, less regular spatial patterns of trees in the community, and also less spatial dependence of tree sizes, regardless forest type and species identity. Our reasoning is that higher species richness promotes higher phylogenetic and also could raise thefunctional diversity, which would result in an increase of different resource use strategies. In other words, resource niches of adjacent individuals overlap less in mixed communities due to fewer intraspecific interactions and thus, the distance between neighboring individuals is reduced (i.e. tree clustering).

We also expect that the relationship between species richness and spatial pattern of trees is mediated by the stand structure, which in turn is derived from past management practices. In this line, we hypothesize higher tree clustering in stands structurally more diverse (i.e. uneven-sized stands), with higher species richness due to a different spatial resource utilisation and competition releases among co-occurring trees.

MATERIALS AND METHODS

Study design

We based our study on a network of permanent plots designed within the FunDivEUROPE project (*http://www.fundiveurope.eu*) to explore the effect of tree species richness on different ecosystem functions in European forests (Baeten et al. 2013). The plot network consists of 209 square plots of 30 m × 30 m distributed in six forest types, which span a wide bioclimatic European range: a boreal forest in Finland, a hemiboreal forest in Poland, a temperate forest in Germany, a sub-continental temperate forest in Romania, a temperate Mediterranean forest in Italy and a continental Mediterranean forest in Spain. In each forest type, plots were set up along a species richness gradient of the regional dominant tree species (Table A1). All sites are considered ancient forests, i.e., they have been continuously forested at least since the oldest available land-use maps (Baeten et al. 2013). Key features of the experimental design was the strict avoidance of a dilution gradient, special attention to community evenness and minimal covariation with other environmental factors. Therefore, plots were selected ensuring two criteria: (i) all species represented in all richness levels, maximize evenness of the dominant species, i.e. relative abundance of the dominant species was as balanced as possible in all mixed plots; and (ii) minimize the presence of non-dominant species within the plot (i.e. preferably the summed basal area of these species is below 5% of the total basal area, with a maximum of ca. 10%), which also have very low or low representation in the whole forest. This latter criterion was not exclusive to include non-dominant species in the spatial pattern analyzes as their presence may alter the spatial arrangement of the rest of individuals in the community. Thus, the richness gradient ranged from monospecific to mixed stands including up to 10 different tree species considering all species within a community, including non-dominant species (Table A1). Although some stands had been subject to management practices in the past (e.g. group cutting, coppicing, etc) depending on their species composition and forest type (an intense management in Finland whereas a low frecuency of management practices in Spain or Romania), they were selected based on their current condition showing minimal signs of recent management. See Baeten et al. (2013) for further details on the experimental design, selection criteria of the forest stands and forest location.

Data collection

In each forest stand (i.e. plot), all tree individuals (DBH > 7.5cm) were identified by species recorded their height and calculated their basal area. We also calculated the spatial coordinates (x, y) for each tree individual as the distance taken from each tree to a reference point (botton-left corner) in each plot using a measuring tape or a ultrasonic distance measurer (Haglöf, Långsele, Sweden). Multi-steemed trees were considered as a single individual by summing the basal area of all stems within each tree. Information on the number of trees per plot and forest type can be found in Table A2.

Additionally, we recorded trait data for each identified species in the six study forests in order to quantify the functional component of the tree diversity in each plot. We focused on five key traits, which are considered to capture the plant strategy schemes: specific leaf area, wood density, maximum height, seed mass and shade tolerance (Westoby 1998). Maximum height for all species and mean SLA for dominant species were obtained from field meassurements (Benavides et al. 2019). Mean trait values for wood density, seed mass, shade tolerance and SLA for non-dominant species were obtained from different databases such as TRY (Kattge et al. 2011), LEDA (Kleyer et al. 2008), KEW (“Royal Botanic Gardens Kew” 2019), BiolFlor (Kühn et al. 2004) and the literature (e.g. shade tolerance trait values from (Niinemets and Valladares 2006)), priorizing as much as possible those trait measures performed in similar latitudes where species were present. See Table A3 for mean trait values of each species.

We calculated two different multifunctional indexes at plot level taking into account the species relative abundance: (i) Rao’s quadratic entropy (RaoQ; (Botta-Dukát 2005), which measures the mean functional dissimilarity between two randomly chosen individuals and (ii), functional dispersion index (FDis; Laliberté and Legendre 2010) that calculates the mean distance in multidimensional trait space of individual species to the centroid of all species. Furthermore, we carried out the construction of the phylogenetic tree for all species identified in the field using the mega-tree implemented in the R package ‘V.PhyloMaker’ (i.e. GBOTB.extended.tre) (Jin and Quian 2019). Then, we calculated a phylogenetic diversity index (PD) at plot level (i.e. the total branch length spanned by the tree including all species in a local community; Faith (1992)), which is a biodiversity index that quantifies the combined genetic diversity across species. PD and FDis were strongly correlated with species richness and RaoQ, respectively (Figure A1). Thus, they were exluded from subsequent analyses to avoid collinearity problems (Dormann et al. 2013). Correlations among diversity indices were carried out using the R package ‘corrplot’ (Wei and Simko 2017), the phylogenetic and functional diversity indices were calculated using the R package ‘picante’ (Kembel et al. 2010) and R package ‘FD’ (Laliberté et al. 2014), respectively.

Finally, we classified each stand (plot) into three categories: even-sized, semi-sized and uneven-sized, according to the distribution of DBH size classes (Lähde et al. 1994). Forest stand structures have often been described by their diameter distributions (Goff and West 1975), which have also been used as a proxy of differences in the management history of each stand that underlie the current forest spatial distribution (Schütz 2001, Petritan et al. 2015). Even-sized stands generally have a nearly bell-shaped diameter distribution with most of the trees in the average diameter class. An even-sized stand is typically a result of a previous shelterwood cutting system for forest management (Powell 2013). In some cases, stands may be dominated by two well-defined size classes (i.e. semi-sized stands) differing in diameter. This is typically associated to group cutting systems and coppicing. On the contrary, uneven-sized stands are characterized by a high density of tiny individuals (i.e. small DBH), and this density declines as size classes increase to the point where the largest size classes can be quite scattered. These stands typically arise when stands are managed using selection or group selection cutting systems as regeneration quickly fills the frequent canopy gaps originated and then competition reduces the number of individuals (Powell 2013).

Analyses

Intraspecific interactions, species richness and functional diversity.

We calculated the mean number of intraspecific neighbors for each species in each plot from the average of the number of conspecific individuals around each tree within a circle of radius spanning from 3.5 to 15 m with increment of 0.5 m. Then, we fitted a generalized linear model (McCullagh and Nelder 1989) to test our initial assumption that the frequency of intraspecific interactions would decrease with increasing species richness and phylogenetic and functional diversity. We included forest type (and its interaction with species richness) to control other intrinsic factors affecting the relationship between species diversity and the frequency of intraspecific interactions in each forest type.

Spatial pattern of the communities

We employed two widely used summary statistics to characterize the spatial pattern of trees in each plot: Ripley's K-function (K) and the nearest-neighbors distance distribution G (Diggle 2003, Loosmore and Ford 2006). $K(r)$ estimates the expected number of points within a circle of radius r around a typical point of the pattern, weighted by the intensity (i.e., the density) of the plot (Diggle 2003). $G(r)$ estimates the proportion of points of the pattern which have their nearest-neighbor at a distance equal or inferior to r. Therefore, both statistics summarize different aspects of the spatial pattern, based on second-order properties and nearest-neighbour distances, respectively (Diggle 2003). In any case, for a given spatial scale r, both functions render smaller values as the stand is more regular, and larger values as the stand is more clustered.

To stabilize the variance of the estimated functions, we transformed K(r) into the L-function (Diggle 2003), i.e., $L(r) = \sqrt{K(r)/\pi} - r$, and used Fisher's arcsin transformation on $G(r)$, i.e., $\Phi\big(G(r)\big) = arcsin\sqrt{G(r)}$ (Baddeley et al. 2015).

As we were also interested in the spatial distribution of tree sizes (measured as basal area), we computed also the mark-correlation function. For a quantitative variable m (e.g., the DBH or basal area) which varies throughout the points of a spatial point pattern, the mark-correlation function is defined as $k_{mm}(r) = \frac{c_{mm}(r)}{\mu^2}$, where $c_{mm}(r)$ is the conditional mean of the product of the marks of all point-pairs (i, j) separated by a distance r, and μ is the mean of m (Illian et al. 2008). This measures the spatial dependence of the marks (Baddeley et al. 2015).

In order to get a "global" estimation of the spatial structure of the pattern in a range of scales (defined by r_0 and r_{max}); we reduced each transformed summary function to a single numerical value (Loosmore and Ford 2006). For this, we employed a statistic partially similar to the well-known goodness-of-fit (GoF) statistics u, which was defined as follows (Diggle 2003, Loosmore and Ford 2006, Wiegand and Moloney 2014, Baddeley et al. 2015):

$$DR_F = \sum_{r_0}^{r_{max}} (\hat{F}(r) - F(r)),$$

where $\hat{F}(r)$ is the observed value of either $L(r)$, $\Phi\big(G(r)\big)$ or $k_{mm}(r)$ and $F(r)$ their respective expected values under a null model of spatial randomness (complete spatial randomnes, i.e., CSR, for L an Φ and random labelling, i.e., random permutation of marks, for k_{mm}). In other words, we computed for each plot an estimation of how much its spatial pattern of trees or tree sizes deviated from an hypothetical completely random pattern. Note that, in comparison with the GoF statistics u, we did not square the difference of functions in the summation as we were not interested in the absolute difference from the expected value under CSR but in the net deviation and in its sign. On the other hand, we did not test the spatial patterns in the plots against CSR or random labelling, but simply used these null models as baseline, intermediate reference level between "aggregated" and "regular" patterns in the case of tree patterns or between positive and negative spatial dependence in the case of tree sizes.

Summary functions were computed with the package 'spatstat' (Baddeley et al. 2015) in R (R Developemnt Core Team 2018). Following the recomendations of Baddeley et al. (2015) for plot sizes similar to ours, we computed the summary functions between r_0 = 0.00 and r_{max} = 7.50 m, with the default intervals in spatstat (i.e., around 0.15 m for the size of our plots), applying Ripley's isotropic correction (Ripley 1977) for K and k_{mm}, and using the Kaplan-Meier estimator of G to avoid edge effects.

Species richness, functional diversity and spatial pattern of forest stands.

Using the DR_F statistics defined previously, we summarized the spatial pattern of the forest stands at two different scales: from r_0=0.0 to r_{max}=7.5 m (hereafer "medium scale") and from r=0.0 to r_{max}=3.5 m (hereafer "fine scale"). Note that the words "medium" and "fine" are relative, and we employed them to distinguish both scales in the context of the present study, without any further assumption.

We fitted linear models (Rao and Toutenburg 1995) for each statistics (DR_K and DR_G and $DR_{k_{mm}}$) and spatial scale (medium and fine scales) to test the effect of species richness and functional diversity on the spatial pattern of trees and tree sizes (as measured by DR_F). We used DR_F as the response variable and species richness and functional diversity (RaoQ) as predictors. We included the median value of the tree basal areas for each stand (plot) as a covariable to account for tree sizes among forest stands (only for DR_K and DR_G models) together with stand structure (three levels), forest type, and their interactions with species richness to control by different management histories at stand level and other potential intrinsic local processes at forest level. We compared the full models with all possible models including predictors and covariables for each statistics (DR_F for $K(r)$ and $G(r)$ and $k_{mm}(r)$), and scale. Specifically, we searched for the model that provided the best fit to the data using the Akaike Information Criteria corrected for finite sample sizes (AICc; Burnham and Anderson 2002, Johnson and Omland 2004). To evaluate the consistency of the best models, we selected the set of competing models with ΔAICc values < 2. We then calculated the weight for each effect in the full model, by summing the Akaike weights of the competing models in which they appear (Burnham and Anderson 2002). The weight for each effect ranged from 1 (present in the best model and all the competing models) to 0 (not present in any model), and was used to compare the importance of the effects appearing in the best model to those not included. When both forest type and stand structure were present in the best model (without interaction with species richness), Tukey *post-hoc* tests were performed to compare the relationship between spatial distribution and species richness among forests and stand structures.

Statistical analyses were carried out in R 3.5.0 (R Development Core Team 2013), using package ‘stats’, package ‘car’ (Fox and Weisberg 2011), package ‘multcomp’ (Hothorn et al. 2008) and package ‘MuMIn’ (Barton 2019).

RESULTS

We found an overall trend of decreasing mean number of intraspecific neighbors with increasing species richness (positively correlated with phylogenetic diversity) and functional diversity (Figure 1; Table A4). This trend with species richness became significant from ‘fine’ (3.5 m) to larger scales (15 m) (Table A5). Significant differences in the mean number of intraspecific neighbors were observed among forest types, but its interaction with species richness was not significant (Table A4).

From the model selection method, we found that species richness and functional diversity were included as predictors to explain the spatial aggregation of trees for both spatial functions (K, G) and at both fine (0.0 - 3.5 m) and medium spatial scale (0.0 - 7.5 m) (Table 1, Table A6), with the only exception of FD for $K(r)$ at medium scale. Particularly, we observed an overall positive trend of the spatial aggregation of trees with higher species richness and functional diversity in all cases where were included as predictors (Figure 2A-D, Table 1, Table A6). In other words, the tree distribution was less regular in plots with higher number of species and phylogenetically and functionally more diverse. In the same line, we also found that tree sizes (basal area) were more spatially independent as species richness and functional diversity increased at both fine and medium scale, i.e less negative values of $k_{mm}(r)$ function were observed in stands with higher number of species and more phylogenetically and functionally diverse (Figure 2E, Table 1, Table A6). We also obtained that plots with greater tree sizes (high median values of basal areas) showed much less tree clustering (Table A6). Furthermore, forest type and the stand structure were two important predictors to explain the spatial distribution of trees in all cases (Figure 3, Figure A2, Table 1, Table A6). Particularly, we found that uneven-sized stands presented more tree clustering than the even- and semi-sized stands, becoming significatively different at medium and fine scale with *K* function (Figure A2). However, there were no significant interactions between species richness and forest type and stand structure (Table 1, Table A6) for any function (*K*, *G* or k_{mm}) and for any of the study scales, with the only exception of *G* function at fine scale. In other words, the effect of species richness (and therefore, its correlated phylogenetic diversity) on the spatial pattern was similar, irrespective of the forest type and management legacy (Table A6).

DISCUSSION

Our study showed a generalized effect of species richness of the community (positively correlated with phylogenetic diversity) on the spatial distribution of trees at the spatial scales analysed, suggesting a less regular spatial distribution of tree individuals as species richness increased along the entire European bioclimatic gradient. Our results suggest that this pattern is partly due to a greater functional diversity which would allow individual trees to live closer together in space, independently of their size (basal area), as it promotes complementarity in the resource use. Moreover, our study pointed out that the current tree spatial arrangements are conditioned by stand management history, but its influence on tree spatial pattern was independent to the number of species of the community.

In forest systems, it is widely assumed that the spatial distribution of trees changes with the stand development. Thus, early recruits usually appear in clumped distributions as a consequence of limited dispersal when forest regenerates naturally (Wiegand et al. 2007, Lara-Romero et al. 2016). However, this clumped pattern becomes more regular with time as some individuals grow and others die due to negative density-dependent thinning (Getzin et al. 2008, Chacón-Labella et al. 2014) including competitive interaction effects (Kenkel 1988, Getzin et al. 2006). As we expected, our previous assumption on decreasing the probability of intraspecific encounters as species richness, phylogenetic and functional diversity increase was corfirmed. This result suggests that an increasing number of species in the community alters the balance between intra- and interspecific competition, and impacts on the community spatial pattern. The underlying mechanism is that plant-plant interactions in space become stronger as the interacting individuals are ecologically more similar in terms of resource use. In contrast, competitive interactions should be weaker when resource niches of adjacent individuals overlap less. An effect of reduced interspecific competition is that mixed stands usually outperform monospecific ones, at least in terms of growth (Vilà et al. 2007, Morin et al. 2011, Ruiz-Benito et al. 2014) and growth resistence in drough periods (Gazol and Camarero 2016). For example, analyzing combinations of pairs of European tree species, Pretzsch and Biber (2016) showed that mixed stands attained higher densities than monospecific ones. In this line, our study went further and included the spatial tree layout, suggesting that individuals in richer and more functionally diverse communities occur closer to each other (Figure 2).

The strength of plant-plant interactions, determined by how spatially close the individuals are, as well as their niche and fitness differences (sensu modern coexistence theory perspective; Chesson 2000, Adler et al. 2007), may affect the expression of ecological processes involved in species dynamics such as growth, regeneration, and mortality (Mokany et al. 2008). For instance, Chamagne et al. (2017) found that increasing tree species diversity enhanced individual growth in central European forest stands. Ngo Bieng et al. (2013) showed that intraspecific competition had a greater negative effect on growth of oak and pine species than interspecific competition in a mature mixed European forest. Further, these authors also found that the productivity of both pine and oak was affected by its spatial pattern, being higher when they grew in well-mixed stands than when they formed patchy mixtures. These examples suggest that complementarity in resource use is one of the primary mechanisms underlying increased performance of mixed stands over monocultures (Paquette and Messier 2011, Morin et al. 2011, Ratcliffe et al. 2017). As suggested by the positive effect of functional diversity both on tree clustering and on the independence of adjancet tree sizes, complementarity is also likely to underlie our observed spatial pattern affected by species richness regardless of the past sylvicultural practices. Niche differentiation and resource partitioning between individuals allows trees to grow closer to each other, and thus lead to clustering patterns. The presence of stabilising niche differences is a precondition of **complementarity** (Barry et al. 2019), which**, in turn favors** species coexistence and enhanced ecosystem functioning (Chesson 2000, Saavedra et al. 2017). In a modelling study of European temperate forests across a large climatic gradient similar to ours, Morin et al. (2011) found that the increase of productivity with species richness was mediated through functional complementarity in exploiting resources such as light. Particularly, Morin et al. (2011) found that higher species richness generated higher variation of shade tolerance and growing strategies, which in turn resulted in faster responses (i.e., re-colonization) to small-scale mortality events. Moreover, complementarity related to an increase of species richness in forests does not only enhance yield, i.e increased biomass production, but it may also affect the spatial distribution of biomass. So, for instance, species in mixed communities have showed complementarity in crown shapes, leading to increased canopy space filling which did not occur in monospecific stands (Jucker et al. 2014a, Pretzsch 2014). However, the complementarity effect in crown shapes found by Jucker et al. (2014a) in the same continental Mediterranean forest studied here, is partly due to past management practices. Certain management practices such as thinning often facilitate the vertical layering of species, which also give trees more space to expand their crowns, thereby changing their allometry (e.g. Pretzsch 2014). In our study, we have been able to isolate the effect of managament legacy from the effect of species interactions on tree spatial distribution, and our results still suggest complementarity as the mechanism partly explaining the positive relationship between the tree clustering and species richness in our European study forests.

Looking for the influence of species richness on the spatial distribution of trees in forests along a wide European bioclimatic gradient, special attention should be paid to past management of such forests. Our study showed that the current spatial distributions of the study forests are, at least in part, a reflection of their history in silvicultural practices. This means that stands structurally more diverse in terms of DBH showed higher tree aggregation in the same space than even-sized stands. This can be explained because the silvicultural practices generating uneven-sized stands promote higher variety in tree sizes as well as higher levels of vertical structure (Wolf 2005). Thus, individuals in uneven-sized stands make a better use of the resources in comparison to those in even-sized forests. On the contrary, planting and thinning regimes promoting even-sized stands (Mäkinen and Isomäki 2004, Bergh et al. 2014) lead to more regular spatial patterns when trees with similar resource demands compete strongly. Therefore, the influence of forest management practices on the spatial pattern of trees is straightforward, although it is expected that management signal fades throughout time as anthropogenic influence ceases (Rozas et al. 2009). In line with other studies, our work showed evidence of the importance of its consideration in spatial studies of plant communities for prediciting ecosystem functionality (Rozas and Prieto 2000, Wolf 2005). In a similar way, our analyses also confirmed the existence of region-specific differences in the spatial pattern of trees among the studied forests (Figure 3), but demonstrated that the effect of species richness was the same for all of them, independently of forest type, its species composition and management history (Table 1, Table A6).

CONCLUSIONS

Our study has demonstrated that species richness shapes the spatial pattern of plant communities, partly mediated through an increase in the number of resource use strategies. Our results showed an increase in tree aggregation with increasing species richness that prevailed along the entire European bioclimatic gradient. In other words, tree species richness had a similar effect on the spatial distribution of individual trees from boreal to Mediterranean forests. This finding points out to a neglected macroecological pattern in ecological research. Overall, our study provides empirical evidence of species richness is a relevant forest attribute that affects community structure and functioning given that certain key ecosystem processes (e.g. recruitment or seed dispersal) are strongly affected by tree spatial distribution. The knowledge gained through this study can help to formulate forest management guidelines supporting the maintainance and promotion of mixed forests and their ensuing ecosystem services and functions in the future.

ACKNOWLEDGMENTS

We greatly acknowledge all colleagues and technicians that participated in the establishment of plots and the collection of spatial data. We are grateful to the land owners who granted access to the forest sites. Moreover, we thank to Andrés Bravo-Oviedo for helping to improve the manuscript. CCB is beneficiary of a FPU grant funded by the Spanish Government (AP2010-5600). This research was supported by the FunDivEUROPE project, receiving funding from the European Union Seventh Framework Programme (FP7/2007–2013) under grant agreement no.265171, the Spanish-funded project REMEDINAL TE-CM S2018/EMT-4338 and COMEDIAS

FEDER/Ministerio de Ciencia, Innovación y Universidades – Agencia Estatal de Investigación/ _Proyecto CGL2017-83170-R. RB was funded by a Marie Skłodowska-Curie Intra-European fellowship (Grant Agreement No. 302445).

Author contributions: C.C.B, D.T, F.V, R.B and M.C. conceived the initial idea. All authors, except D.T and M.C, participated in the data collection; C.C.B, D.T, M.C. analysed the data; and C.C.B, D.T, M.C. wrote the first draft of the manuscript, with comments from all authors.

REFERENCES

Adler, P. B. et al. 2007. A niche for neutrality. - Ecol. Lett. 10: 95–104.

Baddeley, A. et al. 2015. Spatial Point Patterns: Methodology and Applications with R. - Chapman and Hall/CRC.

Baeten, L. et al. 2013. A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. - Perspect. Plant Ecol. Evol. Syst. 15: 281–291.

Barabás, G. et al. 2016. The Effect of Intra- and Interspecific Competition on Coexistence in Multispecies Communities. - Am. Nat. 188: E1–E12.

Barry, K. E. et al. 2019. The Future of Complementarity: Disentangling Causes from Consequences. - Trends Ecol. Evol. 34: 167–180.

Barton, K. 2019. MuMIn: Multi-Model Inference.

Bastias, C. C. et al. 2017. Intraspecific leaf trait variability along a boreal-to-tropical community diversity gradient. - PLoS ONE 12(2): e0172495.

Benavides, R. et al. 2019. The functional trait space of tree species is influenced by the species richness of the canopy and the type of forest. - Oikos 0: 1–11.

Bergh, J. et al. 2014. Long-term responses of Scots pine and Norway spruce stands in Sweden to repeated fertilization and thinning. - For. Ecol. Manag. 320: 118–128.

Botta- Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. - J. Veg. Sci. 16: 533–540.

Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. - Springer-Verlag.

Cardinale, B. J. et al. 2011. The functional role of producer diversity in ecosystems. - Am. J. Bot. 98: 572–592.

Chacón-Labella, J. et al. 2014. Negative density dependence and environmental heterogeneity effects on tree ferns across succession in a tropical montane forest. - Perspect. Plant Ecol. Evol. Syst. 16: 52–63.

Chamagne, J. et al. 2017. Forest diversity promotes individual tree growth in central European forest stands. - J. Appl. Ecol. 54: 71–79.

Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. - Annu. Rev. Ecol. Syst. 31: 343–366.

Chesson, P. 2012. Species competition and predation. In Encyclopedia of Sustainability Science and Technology (Leemans, R., ed.). - Springer Science & Business Media.

Diggle, P. J. 2003. Statistical Analysis of Spatial Point Patterns. - Hodder Arnold.

Dormann, C. F. et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. - Ecography 36: 27–46.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. - Biol. Conserv. 61: 1–10.

Fox, J. and Weisberg, H. S. 2011. An R Companion to Applied Regression. - SAGE Publications, Inc.

Gamfeldt, L. et al. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. - Nat. Commun. 4: 1340.

Gazol, A. and Camarero, J. J. 2016. Functional diversity enhances silver fir growth resilience to an extreme drought. - J. Ecol. 104: 1063–1075.

Getzin, S. et al. 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. - Ecography 29: 671–682.

Getzin, S. et al. 2008. Heterogeneity influences spatial patterns and demographics in forest stands. - J. Ecol. 96: 807–820.

Godoy, O. et al. 2018. Towards the Integration of Niche and Network Theories. - Trends Ecol. Evol. 33: 287–300.

Goff, F. G. and West, D. 1975. Canopy–understory interaction effects on forest population structure. - Forest Science 21: 98–108.

Harper, J. L. and McNaughton, I. H. 1962. The Comparative Biology of Closely Related Species Living in the Same Area. - New Phytol. 61: 175–188.

Hooper, D. U. et al. 2005. Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. - Ecol. Monogr. 75: 3–35.

Hothorn, T. et al. 2008. Simultaneous inference in general parametric models. - Biom. J. Biom. Z. 50: 346–363.

Hutchinson, G. E. 1957. Concluding remarks. - Cold Spring Harb. Symp. Quant. Biol. 22: 415–427.

Illian, J. B. et al. 2008. Statistical Analysis and Modelling of Spatial Point Patterns. - John Wiley & Sons.

Jin, Y. and Quian, H. 2019. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. - Ecography 42: 1353–1359.

Johann, E. 2007. Traditional forest management under the influence of science and industry: The story of the alpine cultural landscapes. - For. Ecol. Manag. 249: 54–62.

Johnson, J. B. and Omland, K. S. 2004. Model selection in ecology and evolution. - Trends Ecol. Evol. 19: 101–108.

Jucker, T. et al. 2014a. Competition for light and water play contrasting roles in driving diversity-productivity relationships in Iberian forests. - J. Ecol. 102: 1202–1213.

Jucker, T. et al. 2014b. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. - Ecol. Lett. 17: 1560–1569.

Kattge, J. et al. 2011. TRY – a global database of plant traits. - Glob. Change Biol. 17: 2905–2935.

Kembel, S. W. et al. 2010. Picante: R tools for integrating phylogenies and ecology. - Bioinformatics 26: 1463–1464.

Kenkel, N. C. 1988. Pattern of Self-Thinning in Jack Pine: Testing the Random Mortality Hypothesis. - Ecology 69: 1017–1024.

Kenkel, N. C. 1994. Bivariate pattern analysis of jack pine - trembling aspen interaction. - Abstr. Bot. 18: 49–55.

Kleyer, M. et al. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. - J. Ecol. 96: 1266–1274.

Kraft, N. J. B. et al. 2015. Plant functional traits and the multidimensional nature of species coexistence. - Proc. Natl. Acad. Sci. 112: 797–802.

Kühn, I. et al. 2004. BiolFlor – a new plant-trait database as a tool for plant invasion ecology. - Diversity and Distribution 10: 363–365.

Lähde, E. et al. 1994. Structure and yield of all-sized and even-sized conifer-dominated stands on fertile sites. - Ann. Sci. For. 51: 97–109.

Laliberté, E. and Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. - Ecology 91: 299–305.

Laliberté, E. et al. 2014. R package “FD”: Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R Package Version 1.0-12.

Lara- Romero, C. et al. 2016. What causes conspecific plant aggregation? Disentangling the role of dispersal, habitat heterogeneity and plant–plant interactions. - Oikos 125: 1304–1313.

Larsen, J. B. 1995. Ecological stability of forests and sustainable silviculture. - For. Ecol. Manag. 73: 85–96.

Liang, J. et al. 2016. Positive biodiversity-productivity relationship predominant in global forests. - Science 354: aaf8957.

Loosmore, N. B. and Ford, E. D. 2006. Statistical Inference Using the G or K Point Pattern Spatial Statistics. - Ecology 87: 1925–1931.

Loreau, M. 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. - Science 294: 804–808.

MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. - Am. Nat.: 377–385.

Maestre, F. T. et al. 2005. Does spatial pattern matter to ecosystem functioning? Insights from biological soil crusts. - Funct. Ecol. 19: 566–573.

Maestre, F. T. et al. 2012. Plant Species Richness and Ecosystem Multifunctionality in Global Drylands. - Science 335: 214–218.

Mäkinen, H. and Isomäki, A. 2004. Thinning intensity and growth of Scots pine stands in Finland. - For. Ecol. Manag. 201: 311–325.

McCullagh, P. and Nelder, J. A. 1989. Generalized Linear Models, Second Edition. - Chapman and Hall/CRC.

Mokany, K. et al. 2008. Effects of spatial aggregation on competition, complementarity and resource use. - Austral Ecol. 33: 261–270.

Morin, X. et al. 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species: Species richness promotes forest productivity. - Ecol. Lett. 14: 1211–1219.

Ngo Bieng, M. A. et al. 2013. Spatial pattern of trees influences species productivity in a mature oak–pine mixed forest. - Eur. J. For. Res. 132: 841–850.

Niinemets, Ü. and Valladares, F. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. - Ecol. Monogr. 76: 521–547.

Paquette, A. and Messier, C. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. - Glob. Ecol. Biogeogr. 20: 170–180.

Petritan, I. C. et al. 2015. Structural patterns of beech and silver fir suggest stability and resilience of the virgin forest Sinca in the Southern Carpathians, Romania. - For. Ecol. Manag. 356: 184–195.

Powell, D. C. 2013. Silvicultural Activities: Description and Terminology. - White Paper F14-SO-WP-Silv-34.

Pretzsch, H. et al. 2017. Mixed-species forests: ecology and management. - Springer.

Pretzsch, H. 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. - For. Ecol. Manag. 327: 251–264.

Pretzsch, H. and Biber, P. 2016. Tree species mixing can increase maximum stand density [1]. - Can. J. For. Res. 46: 1179–1193.

R Development Core Team 2013. R: A language and environment for statistical computing.

Rao, C. R. and Toutenburg, H. 1995. Linear Models: Least Squares and Alternatives. - Springer-Verlag.

Ratcliffe, S. et al. 2017. Biodiversity and ecosystem functioning relations in European forests depend on environmental context. - Ecol. Lett. 20: 1414-1426.

Ripley, B. D. 1977. Modelling spatial patterns. - J. R. Stat. Soc. Ser. B Methodol.: 172–212.

Royal Botanic Gardens Kew. (2019) Seed Information Database (SID). Version 7.1. Available from: http://data.kew.org/sid/

Rozas, V. and Prieto, J. A. 2000. Competition, mortality, and development of spatial patterns in two Cantabrian populations of Fagus sylvatica L. (Fagaceae). - An. Jardín Botánico Madr. 58: 117–131.

Rozas, V. et al. 2009. Spatial structure of deciduous forest stands with contrasting human influence in northwest Spain. - Eur. J. For. Res. 128: 273–285.

Ruiz-Benito, P. et al. 2014. Stand Structure and Recent Climate Change Constrain Stand Basal Area Change in European Forests: A Comparison Across Boreal, Temperate, and Mediterranean Biomes. - Ecosystems 17: 1439–1454.

Saavedra, S. et al. 2017. A structural approach for understanding multispecies coexistence. - Ecol. Monogr. 87: 470-486.

Schütz, J. P. 2001. Der Plenterwald und Weitere Formen Strukturierter und Gemischter Wälder. - Berlin Parey.

Silvertown, J. 2004. Plant coexistence and the niche. - Trends Ecol. Evol. 19: 605–611.

Stoll, P. and Weiner, J. 2000. A neighborhood view of interactions among individual plants. - Geom. Ecol. Interact. Simpl. Spat. Complex.: 11–27.

Stoyan, D. and Penttinen, A. 2000. Recent Applications of Point Process Methods in Forestry Statistics. - Stat. Sci. 15: 61–78.

Tilman, D. et al. 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. - Science 277: 1300–1302.

Tirado, R. and Pugnaire, F. I. 2003. Shrub spatial aggregation and consequences for reproductive success. - Oecologia 136: 296–301.

van der Plas, F. et al. 2016. Jack-of-all-trades effects drive biodiversity–ecosystem multifunctionality relationships in European forests. - Nat. Commun. 7: 11109.

Vilà, M. et al. 2007. Species richness and wood production: a positive association in Mediterranean forests. - Ecol. Lett. 10: 241–250.

Walter, H. 1985. Vegetation of the earth. - Springer-Verlag.

Watt, A. S. 1947. Pattern and process in the plant community. - J. Ecol. 35: 1–22.

Wei, T. and Simko, V. 2017. R package “corrplot”: Visualization of a Correlation Matrix (Version 0.84).

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. - Plant Soil 199: 213–227.

Wiegand, T. and Moloney, K. 2014. Handbook of Spatial Point-Pattern Analysis in Ecology. - CRC Press.

Wiegand, T. et al. 2007. Analyzing the Spatial Structure of a Sri Lankan Tree Species with Multiple Scales of Clustering. - Ecology 88: 3088–3102.

Wolf, A. 2005. Fifty year record of change in tree spatial patterns within a mixed deciduous forest. - For. Ecol. Manag. 215: 212–223.

Supporting information

Appendix A: Supplementary description of the study forests and additional analyses.

Figure Legends

Figure 1. Results from the linear model testing the effect of species richness and functional diversity of the community on the mean number of intraspecific neighbors, calculated for each species within 7.5 m of radius around each individual in the spatial pattern.

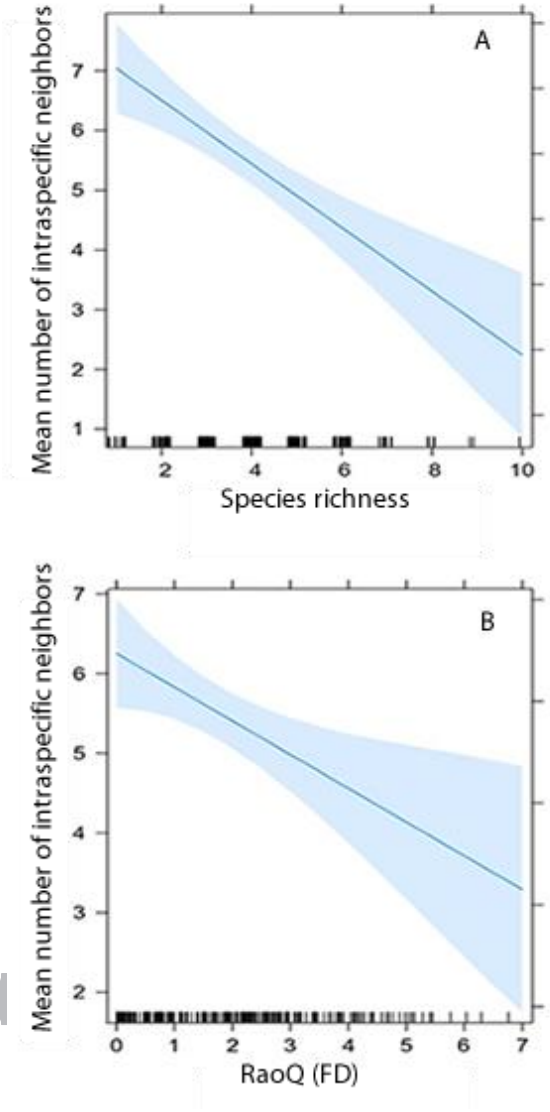

Figure 2. A-D) Changes in the stastistics DR_K (K-Ripley) and DR_G (nearest-neighbor) quantifying the net deviation of the observed spatial pattern from a random spatial pattern at medium (0-7.5m) and fine scale (0-3.5m) with increasing species richness and functional diversity of the community. E) Changes in the statistic $DR_{k_{mm}}$ quantifying the net deviation of the observed patern of basal area distribution from a random labelling null model with increasing functional diversity.

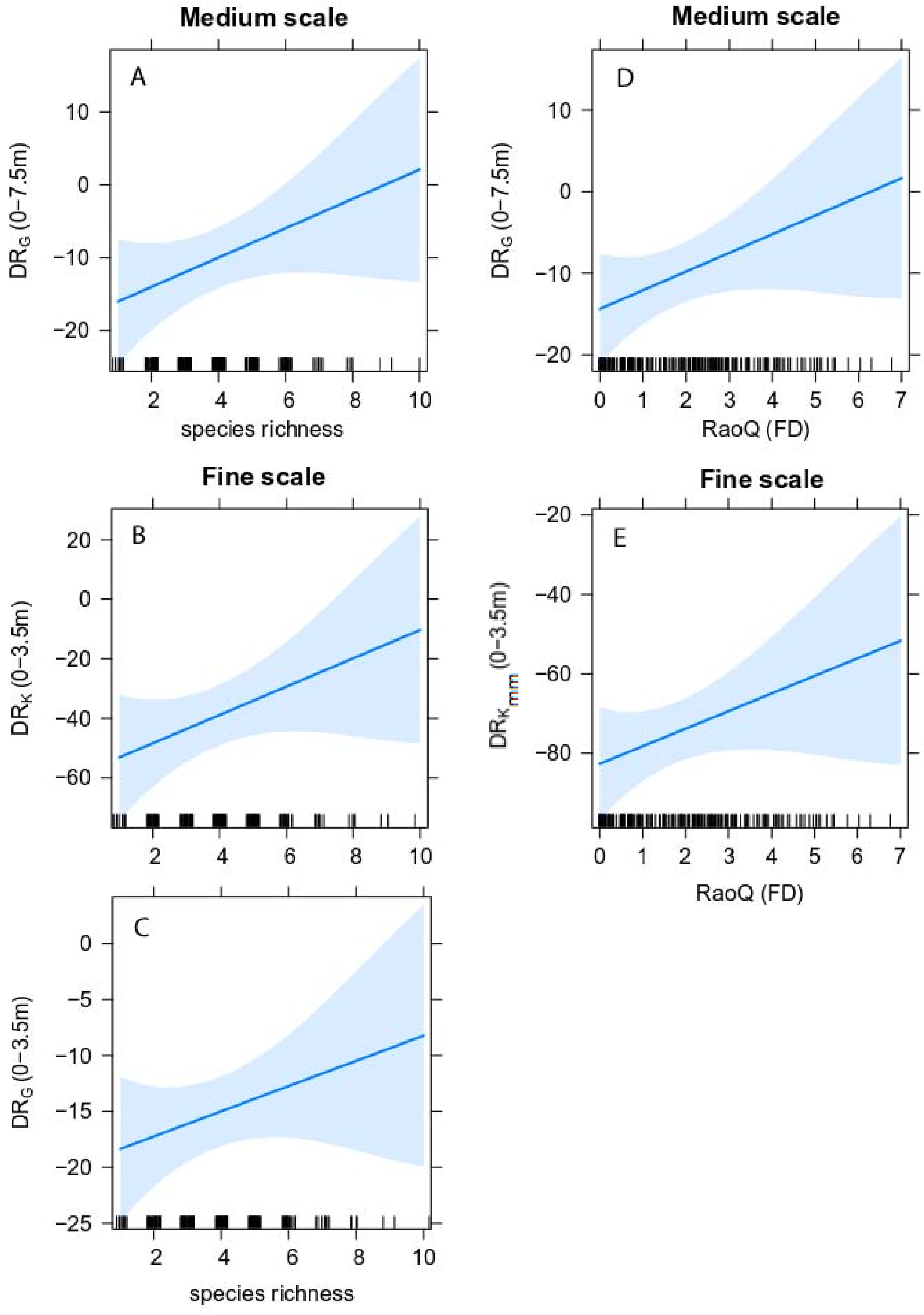

Figure 3. Stastistics DR_K (K-Ripley) and DR_G (nearest-neighbor) quantifying the net deviation of the observed spatial pattern from a random spatial pattern at two different scales [Fine:0-3.5m and medium: 0-7.5m] for each forest type. Letters indicate groups of forest types without significant differences in spatial pattern (Results of Tukey's posthoc-tests). Abbreviations of forest types are Hemib-. (hemiboreal), Sub-. T. (sub-continental temperate), Temp. (temperate), T. Medit. (temperate Mediteranean) and C. Medit. (continental Mediterranean).

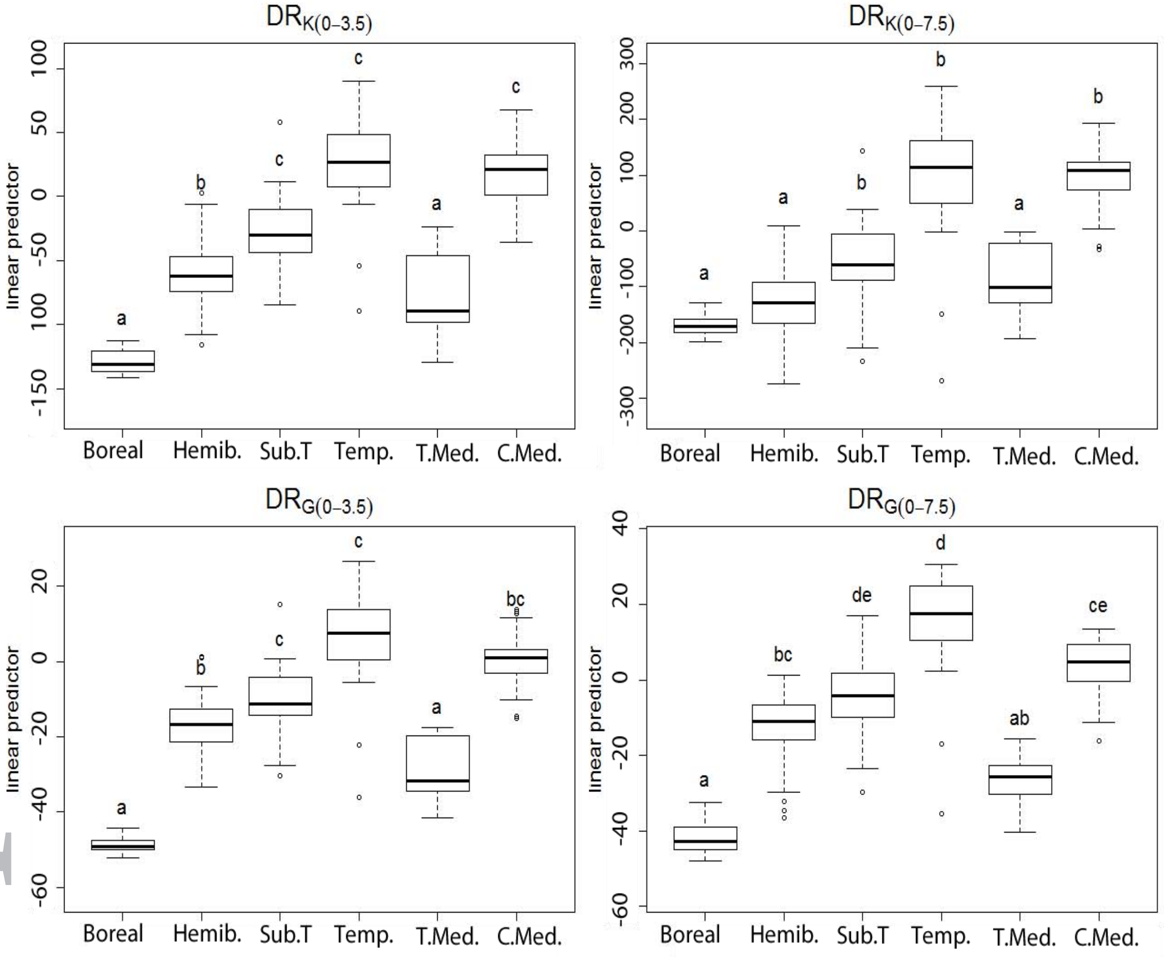

Table Legends

Table 1. Summary table of the set of competing linear models (ΔAICc < 2) selecting by model selection method. Effect of species richness, functional diversity, the median value of tree sizes measured as basal area (BA_median), stand structure (used as a proxy of the legacy of past management practices for each stand) and forest type on the spatial pattern of the forest stands (DR_F) DR_F: deviation from null model (complete spatial randomness or random labelling) estimated with Ripley's $K(r)$ function, nearest-neighbour distance distribution $G(r)$ function and mark correlation function $k_{mm}(r)$. Fine scale: differences estimated for the range beween $r_0 = 0.0$ and $r_{max} = 3.5$ m. Medium scale: differences estimated for the range beween $r_0 = 0.0$ and $r_{max} = 7.5$ m. In brackets is the relative weight of each predictor within the set of competing models, with its sign positive (+) or negative (-) for continuous variables. Df: degrees of freedom of the optimum model, AICc = average Akaike Information Criteria for limited sample sizes (AICc) of all competing models. Weight: mean Akaike weights can be interpreted as the mean probability that model is the best model for the observed data among all candidate set of models. R^2: coefficient of determination for the optimum model.

	DR_K		DR_G		$DR_{K_{mm}}$	
Predictors	*Medium*	*Fine*	*Medium*	*Fine*	*Medium*	*Fine*
Species Richness	+ (0.19)	+ (0.5)	+ (0.46)	+ (0.51)	+ (0.27)	+ (0.14)
Functional Diversity		+ (0.17)	+ (0.46)	+ (0.15)	+ (0.23)	+ (0.38)
BA_median	- (1)	- (1)	- (1)	- (1)	n.i	n.i
Stand structure	(0.71)	(0.86)		(0.84)	(0.84)	(0.69)
Forest type	(1)	(1)	(1)	(1)	(1)	(1)
Species richness*Forest type				+ (0.12)		
Species richness*Stand structure						
No. models (AICc <2)	4	3	4	5	4	5
Df	10	11	9	10	9	9
AICc	2665.3	2350.2	1981.1	1855.5	1194.2	2289.3
Weight	0.333	0.25	0.25	0.20	0.25	0.20
R^2	0.53	0.45	0.37	0.5	0.12	0.10