

Neighbourhood-based evidence of tree diversity promotion by beech in an old-growth deciduous-coniferous mixed forest (Eastern Carpathians)

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Abstract Neighbourhood models are useful tools for understanding the role of positive and negative interactions in maintaining the tree species diversity in mixed forests. Under such a presumption, we aimed at testing several hypotheses concerning the mechanisms of autogenic species coexistence in an old-growth, beech-fir-spruce stand, which is part of the Slătioara forest reserve (Eastern Carpathians). Univariate/bivariate spatial point pattern analyses, the individual tree species-area relationship, the species mingling analysis and generalised linear mixed models of neighbour interference were applied on data concerning the position and allometry of all saplings and trees occurring within a 0.24 ha plot.

The monospecific distribution of either beech or spruce saplings did not support the spatial segregation hypothesis. There was no evidence of conspecific negative distance dependence, as no spatial segregation was detected between the saplings and trees of any species. Within 4 m-neighbourhood, the beech saplings appeared as diversity accumulators, which might be indicative of indirect facilitation (e.g., herd protection hypothesis). At tree stage, none of the three species showed either accumulator or repeller patterns in their neighbourhood with respect to sapling species richness. Signals of positive and negative interspecific association were found in tree-sized beech (at scales of 10 to 20 m) and spruce (at scales of 4 to 17 m), respectively. The former, highly interspersed pattern is in accordance with the hypothesis of positive complementary effects, whereas the latter, poorly intermingled pattern is probably linked to the unexpected, positive neighbouring effect of spruce trees on the stem growth of their conspecific saplings. Such self-favouring process might be due to a facilitative below-ground mechanism. Conversely, the beech saplings were suppressed through interference from the neighbouring conspecific trees.

The beech appears to be the key promoter of tree species coexistence in the study forest stand, in contrast to the low interspersed of spruce in the overstorey leading to lower local tree diversity.

Keywords: auto-facilitation, beech-fir-spruce mixed forest, diversity accumulator, neighbourhood effect, null models, self-competitor, spatial point pattern, tree species mingling.

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Introduction

Along with propagule availability and environmental filters, niche-based interactions have been widely considered as the main drivers of species coexistence and community assembly (Wilson 2011, Kraft et al. 2015). In forest communities, a number of mechanisms have been proposed to explain the local scale-coexistence of tree species: different patterns in seed dispersal and persistence (Harms et al. 2001, Wright 2002, Hou et al. 2004, Punchi-Manage et al. 2015); habitat heterogeneity (Koukoulas & Blackburn 2005, King et al. 2006, Getzin et al. 2008, Chen et al. 2010, Piao et al. 2013); autogenic alternation (reciprocal replacement) of species between ontogenetic cycles (Fox 1977, Woods 1979); allogenic formation of canopy gaps by natural disturbance (Canham 1988, Poulson & Platt 1996) and demographic stochasticity (Gravel et al. 2008). Recent studies have suggested that niche structuring is a major determinant of species diversity in temperate mixed forests (Gilbert & Lechowicz 2004, Laliberté et al. 2009, Zhang et al. 2010). Two different classes of biotic mechanisms mediate coexistence by preventing competitive exclusion (Chesson 2000): equalising mechanisms, which reduce the relative fitness difference between species (e.g., facilitation or symmetric competition) and stabilising mechanisms, which reduce niche overlap (e.g., specialisation or self-inhibition).

The niche-based mechanisms related to spatial processes are especially important for plant species coexistence because they are sessile organisms that interact mainly with

their close neighbours. Such interactions may lead to either negative or positive net effects, mainly depending on the balance between asymmetric competition for limiting resources (light, nutrients) and facilitation (nursing), i.e. either resource limitation or diversification (Chi et al. 2015, Bulleri et al. 2016). Other possible mechanisms underlying the negative and positive interactions between neighbouring plants may include shared pests (e.g., pathogens, herbivores) and respectively, shared mutualists - like mycorrhizae and seed dispersers (Punchi-Manage et al. 2015).

In temperate mixed forests composed of more or less shade-tolerant tree species, dominance can easily change from one species to another between consecutive generations (Woods 1984, Ariei & Lechowicz 2002). Negative spatial association between conspecifics by means of reciprocal replacement were reported in mixed deciduous-coniferous forests from different geographic regions (Bândiu 1977, Nakashizuka & Kohyama 1995, Akashi 1996, Kuninaga et al. 2015). The autogenic coexistence through reciprocal replacement of tree species can originate from various processes like, direct facilitation (e.g., light spectral filtering), intraspecific inhibition (e.g., auto-allelopathy) or indirect facilitation (e.g., ‘escape’ and ‘herd immunity’ hypotheses). As a necessary but not sufficient condition, it seems that coexistence requires interspecific differences in light transmissivity through the crowns of adult trees (Cammarano 2011). For instance, fir regenerates better under beech canopy due to the greater transmission of blue and red light (Bândiu 1977, Dobrowolska 1998). On the contrary, the self-inhibition of

fir saplings through auto-intoxication has been documented in pure silver fir stands (Becker & Drapier 1984, 1985).

The ‘escape hypothesis’ or ‘conspicuous negative density/distance-dependence’ (CNDD) assumes that, because the dispersed seed density is typically highest near the parent tree, specialised enemies (pathogens, herbivores) accumulate and reduce seedling establishment near conspecific trees, resulting in lower intraspecific aggregation (Comita et al. 2014). Recent studies brought evidence of CNDD as being an important driver of species coexistence in temperate old-growth forests (Getzin et al. 2008, Johnson et al. 2014, Kuang et al. 2017), including mixed coniferous-deciduous forests (Nakashizuka & Kohyama 1995, Hiura & Fujiwara 1999, Kotanen 2007, Bai et al. 2012, Piao et al. 2013). The ‘herd immunity hypothesis’ gives a similar explanation of the reciprocal replacement of trees species but from a different angle: it predicts that high local species diversity confers protection from natural enemies by rendering it more difficult for specialist natural enemies to locate the target plants (Wills et al. 1997). If both the escape and herd immunity theories hold, there should be a tendency toward high spatial mingling of tree species and ultimately, a high local species diversity (Blundell & Peart 2004, Volkov et al. 2005, Swamy et al. 2011, Pommerening & Uria-Diez 2017).

The approach based on distance-dependent analyses can be also employed to assess the performance of a focal tree based on the characteristics of its nearest neighbours. Usually, the target tree growth and/or survival is analysed as a function of the size and distance from the neighbours (Wagner & Radosevich 1998, Canham et al. 2004, Kunstler et al. 2016), but the taxonomic identity of the latter has been shown to be equally important (Uriarte et al. 2004). If the net effect of the nearest neighbours on the focal trees is not null, then spatial structure in local species richness may emerge (Lieberman & Lieberman 2007). Since positive and negative interspecific

interactions can cause local maxima and respectively, minima in species richness, the analysis of individual species-area relationship (ISAR) may reveal the taxonomic identity of the so-called diversity ‘accumulators’ and respectively, ‘repellers’ (Wiegand et al. 2009). Finally, the third category includes the so-called ‘neutral species’, which do not display patterns (peaks or saddles) in neighbourhood species richness and are presumably related to stochastic assorting (Wiegand et al. 2007). Species displaying high-diversity neighbourhoods may indicate a preponderance of positive interspecific interactions or strong CNDD, while species with low-diversity neighbourhoods may indicate dominance of inhibitory effects on heterospecific neighbours or strong conspecific positive density-dependence. As a consequence, the proportion of diversity ‘repellers’ and ‘accumulators’ within a community could shed light on the mechanisms ruling coexistence in tree communities (Espinosa et al. 2015).

The ‘spatial segregation hypothesis’, which involves negative spatial association between heterospecific individuals, can also be related to species coexistence (Pacala & Levin 1997). Intraspecific aggregation of juveniles (due to limited seed dispersal or gap-based regeneration niche) leads to interspecific segregation, which in turn prevents the exclusion of competitively inferior species (Stoll & Prati 2001), thereby promoting species diversity. At later life stages, stable coexistence of tree species can be achieved by ‘positive complementary effects’ that arise owing to great niche differentiation (Cavard et al. 2011, Lasky et al. 2014, Forrester & Bauhus 2016). Several mechanisms may be responsible for such effects, like reduction in crown interference due to spatial stratification (Pretzsch 2014) or improved nutrient availability by virtue of more efficient exploitation of soil resources (Rothe & Binkley 2001).

The main goal of this study was to search for spatial dependence and neighbourhood

patterns across/within tree species and size classes in an old-growth, mixed beech-fir-spruce forest, in order to test hypotheses about the underlying mechanisms of autogenic species coexistence. We hypothesized that local tree species diversity could be promoted and maintained by: i) facilitative interactions between heterospecific saplings in the shaded understorey; ii) effects of conspecific negative distance-dependence, self-inhibition and positive interspecific interactions between trees and saplings; iii) positive complementarity effects between canopy trees.

Assuming that such deterministic mechanisms of autogenic species coexistence exert stronger effects than negative interspecific interactions in self-regenerating, stable, old-growth mixed forests, we expected to observe (at small spatial scales) patterns of aggregation/segregation or positive/negative association between heterospecific/conspecific individuals, and negative neighbourhood effects of trees on the growth of conspecific saplings. By reference to appropriate null models of spatial point pattern, we analysed: i) the distribution of conspecific saplings for testing the spatial segregation hypothesis; ii) the distribution of saplings of each species with respect to their conspecific/heterospecific trees for testing the reciprocal replacement hypothesis, and iii) the individual tree species-area relationship and tree species mingling for testing the diversity accumulator/repeller hypothesis and respectively, the positive complementarity effects. In addition, we estimated the effect of the nearest conspecific/heterospecific tree size on the height of focal saplings for testing the hypothesis of asymmetric competition.

Materials and Methods

Study area

The Codrul Secular Slătioara forest reserve (47°27'N; 25°37'E) lies in the Rarău Mountains

(Eastern Carpathians, Romania) between 800 and 1510 m above sea level (Fig. 1). The climate is temperate-continental with mean annual temperatures between 3.9 and 5.8°C and mean annual precipitation ranging from 700 to 810 mm (Duduman et al. 2014). The forest reserve was created in 1941 and covered an area of 854.3 ha until in 2006, when it was extended to 1064.2 ha. The mixed forest canopy is formed of European beech (*Fagus sylvatica*), silver-fir (*Abies alba*) and Norway spruce (*Picea abies*), except in the upper montane stands (over 1350 m of elevation) that are beyond the beech altitudinal range.

The investigations were undertaken on a mild (25%) north-western slope covered by rendzina soils, at an elevation of about 830 m a.s.l. By reference to living plants only, the beech was by far the most abundant tree species in both over- and under-storey (67%), followed by spruce (24%) that rarely reached the uppermost level of the forest canopy (Table 1). The fir had a modest share of 9% and was poorly represented in the understorey, in spite of the fir trees having cumulated the largest basal area and being on average the tallest among the three species (Table 1). In terms of proportion of dead standing individuals in each species population, spruce was ranked first (22.7%), followed by fir (9.8%) and beech (only 4.8%). Overall, the tree population structure was uneven but also heterogeneous throughout the Slătioara forest (Cenușă et al. 2002), and in particular, the study stand featured a low number of trees in the middle size classes (Schnitzler et al. 2004). According to the forest classification on ecosystemic bases by Doniță et al. (1990), the study stand can be assigned to the forest ecosystem type 2316, characterised by highly to moderately productive spruce-beech-fir stands, developed on eu-mesobasic brown or rendzinic soils, well balanced in terms of water supply, featuring a mull-moder humus type and a herbaceous layer of *Oxalis-Dentaria-Asperula* type.

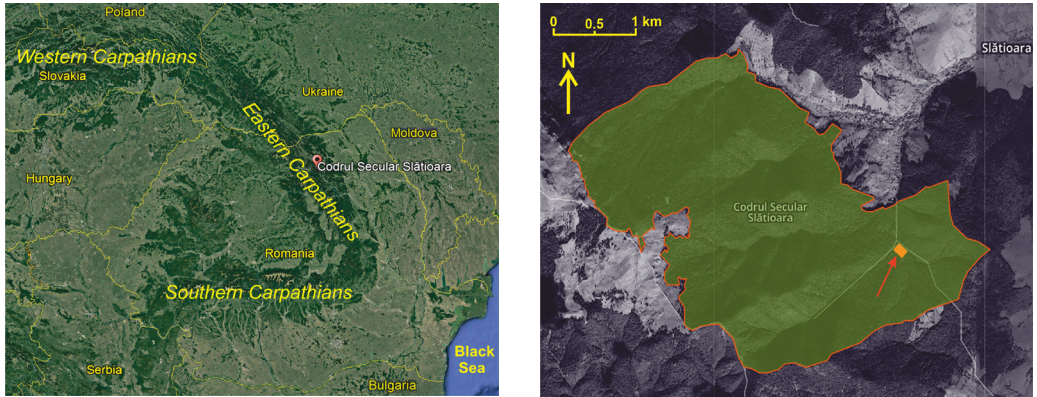


Figure 1 Geographic location of the Codrul Secular Slătioara forest reserve (left) and the approximative placement of the inventoried plot within the protected area (right).

Table 1 Summary statistics of the population size and allometry of the living plants (seedlings excluded) by tree species in the study forest stand.

Variable	Statistics	Fir	Beech	Spruce
Density (N/ha)	Sum	154	1154	413
Basal area (m ² /ha)	Sum	31.9	17.8	8.2
	Range (min - max)	3.2 - 114.5	3.2 - 79.3	3.2 - 116.8
Diameter (cm)	Median	28.1	4.8	6.3
	Mean ± SD	42.9 ± 38.2	13.5 ± 16.9	10.3 ± 17.4
	Range (min - max)	1.0 - 48.0	0.1 - 38.0	0.9 - 51.5
Height (m)	Median	12.5	3.7	2.9
	Mean ± SD	18.0 ± 16.9	6.4 ± 8.3	4.4 ± 7.2

Data collection

The field work was carried out in 2001 within a 40 x 60 m rectangular plot circumscribed to a relatively homogeneous area in terms of site conditions and stand physiognomy, and located (at that time) within the buffer zone of the forest reserve. The long sides of the plot were placed along the steepest slope path, i.e. perpendicular to the contour lines.

The height and Cartesian coordinates (with respect to one plot corner) of all living and dead standing tree species individuals (except seedlings) were measured using a

clinometer and respectively, a tape ruler. In addition, the stem girth at breast height (1.30 m) was measured on all individuals that were at least 1.50 m tall. Two size classes were distinguished based on trunk thickness, i.e. individuals displaying a stem girth of at least 10 cm (DBH ≥ 3.2 cm) were considered trees, whereas all others were included in the category of saplings.

Data analysis

We used point pattern analyses of fully mapped plant locations to explore the

univariate and bivariate spatial patterns in the distribution of individuals (Wiegand & Moloney 2014). The univariate analysis was employed on conspecific saplings to test the spatial segregation hypothesis. The bivariate analysis was performed on saplings relative to their conspecific or heterospecific trees, in order to test the auto-inhibition or the CNDD hypothesis, respectively. In the spatial point pattern analysis we used the pair-correlation function $g(r)$, which is a second-order statistic that employs the probability of observing a pair of points separated by a distance r (Illian et al. 2008). We computed the $g(r)$ distributions applying a lag distance of 0.5 m over a maximum range of 20 m (i.e., half the minimum side of the plot).

Neighbourhood effects on tree species richness and mingling were tested using species-by-all-species analyses, which integrate across all species around a focal species and are more likely to detect effects of biotic interactions than species-by-species analyses (Punchi-Manage et al. 2015). The individual species-area relationship (ISAR) estimates the change in species richness with increasing area and distance from heterospecific neighbours to target species individuals by integrating the spatial structure of individuals (Wiegand et al. 2007, Wiegand & Moloney 2014). Depending on the occurrence or absence of local minima or maxima of species richness with respect to a null model, the ISAR approach allows the grouping of target species in (diversity) accumulators, repellers and neutrals (Wiegand et al. 2007). The mingling index (M) is a measure of interspersions of trees of different species and is defined as the proportion of the n nearest neighbours that do not belong to the same species as the reference tree (Pommerening & Grabarnik 2019). If the nearest neighbours and the target tree always share the same species, then $M = 0$ (minimum intermingling), else if all neighbours are always taxonomically different from the target tree species, then $M = 1$ (maximum intermingling).

The significance of all previously mentioned

distributions or statistics (i.e., $g(r)$, ISAR and M) was assessed through simulations of (density constrained) random distribution of trees or saplings, in order to account for possible (undesirable) effects of habitat patchiness, stand history and dispersal limitation that can induce non-random patterns in the spatial disposal of individuals, irrespective of biotic interactions (Wiegand et al. 2007, Rayburn & Wiegand 2012, Baddeley et al. 2014, Espinosa et al. 2015, Tsai et al. 2015). To account for large variation in tree density within the plot, we only used inhomogeneous Poisson processes along with the Ripley's isotropic edge correction in simulating the null models of spatial independence. The tree or sapling density throughout the plot was computed non-parametrically by employing the Epanechnikov kernel estimators of the intensity function with the option for Jones-Diggle improved edge correction (Diggle 2010, Wiegand & Moloney 2014).

In the univariate $g(r)$ analysis, the null hypothesis was simulated through the random (but density-constrained) spatial disposal of conspecific saplings (Baddeley et al. 2015). The null model used for testing the significance of the bivariate $g(r)$ and ISAR was the independence of the two spatial point pattern types (across size classes and/or species), i.e. no spatial interaction between them (Baddeley et al. 2015). The simulations corresponding to the last null model were performed by randomly reallocating the spatial position of neighbouring saplings with punctual probabilities derived from the estimated density (intensity), while keeping the spatial arrangement of saplings or trees of focal species fixed (Wiegand & Moloney 2014). Finally, the significance of the observed M index values was tested through the null model of random labelling (independence between marks and points), that is by shuffling the taxonomic identity of trees while keeping the number and spatial position of trees in each species constant (Baddeley et al. 2015).

Two-sided, pointwise envelopes for the observed $g(r)$, ISAR and M distributions were generated from 999 Monte Carlo simulations and an overall goodness-of-fit (GoF) test was performed (Loosmore & Ford 2006).

To describe the neighbourhood interference of trees on the target sapling, we employed the Weiner's (1984) measure (W):

$$W = \sum_{i=1}^n \frac{s_i}{d_i^2}$$

where n is the total number of neighbours, d_i is the distance from the target sapling to the i -th neighbouring tree and s_i is the size of the i -th neighbouring tree. The size of trees was roughly estimated by reference to the volume of a cone whose dimensions were equal to the tree's diameter and height. We calculated the W values for each neighbouring tree species separately by considering only the nearest conspecific and heterospecific trees ($n=1$). In the rare cases in which the focal sapling was taller than one of the neighbouring tree, the corresponding W measure was equalled to zero.

Generalised linear mixed models (GLMMs) were employed to analyse the sapling height in each species as a function of the interference from each of the nearest neighbouring, conspecific and heterospecific trees, while controlling the influence of spatial autocorrelation (Bolker et al. 2009). The latter was handled through a residual random component with an anisotropic power covariance structure, which provided the best fitting results and could account for possible differences induced by the terrain slope. The negative binomial distribution along with a log-link was employed in GLMMs for adjusting the conditional probability distribution of the response variable (i.e., sapling height). The goodness-of-fit of each model was assessed through the generalised chi-square divided by the degrees of freedom (Gen. Chi-sq/DF).

Both living and dead individuals were considered in $g(r)$, ISAR and species mingling

analyses, as the allometric measures were not involved in computations. On the contrary, only living individuals were considered in the neighbourhood interference analysis through GLMMs.

Because the total number of fir saplings was too low (seven living and one dead), the results of analyses involving their spatial point pattern exclusively or their allometric characteristics were either incomplete or biased, and hence were not reported.

All numerical analyses were performed in R v3.6.3 environment (R Core Team 2020) using the packages 'spatstat' (Baddeley et al. 2020), 'idar' (de la Cruz 2019) and 'spatialsegregation' (Rajala 2019), except for GLMMs that were run in SAS/STAT 9.4 (SAS Institute Inc. 2014).

Results

A weak but significant aggregation of beech saplings was detected only at 1 m-scale (Fig. 2a). At larger scales, the distribution of beech saplings was not significantly different from the null model. The spruce saplings were randomly distributed at all scales (Fig. 2b).

Saplings of any species did not show significant spatial patterns with respect to their conspecific (Fig. 3a-c) or heterospecific trees (Fig. 3d-i).

Within 4 m-neighbourhood of beech saplings, a higher taxonomic sapling richness than expected under the null hypothesis was detected (Fig. 4a). Instead, the individual species-area relationships (ISARs) corresponding to the fir and spruce saplings were not significantly different from their simulated counterparts (Fig. 4b-c). When the trees and saplings were considered as focal and respectively, target individuals, the ISARs built for the three species (beech, fir and spruce) were all fully embedded within the corresponding simulation envelopes (Fig. 4d-f).

A significant, positive, spatial association between trees species was detected at scales larger than 10 m around the beech trees, as indicated

by the large observed values of the mingling index compared to the simulated values (Fig. 5a). An opposite pattern was detected within a radius of 4 to 17 m around the spruce trees, that is a significant, negative, spatial association between the three species (Fig. 5b). Finally, no significant spatial association between the three species was observed in the neighbourhood of fir trees (Fig. 5c).

The height of beech saplings was significantly, negatively affected by the interference from the nearest conspecific tree, whereas the negative effects of the nearest fir and spruce tree were not significant (Table 2). On the contrary, the nearest spruce tree displayed a significant, positive effect on the height of conspecific saplings (Table 2). The nearest beech exerted a non-significant, negative effect on the spruce sapling height, whereas the neighbourhood effect of the nearest fir tree was almost null (Table 2).

Table 2 Standardised coefficients associated with the (fixed) interference effects (W) of the nearest neighbour beech, fir and spruce tree on the height of beech ($n=156$) and spruce ($n=37$) saplings. The goodness-of-fit of each GLMM is reported in the last row

Response	Sapling height	
	Beech	Spruce
W (beech trees)	-1.282 **	-0.372 ^{ns}
W (fir trees)	-0.522 ^{ns}	-0.006 ^{ns}
W (spruce trees)	0.084 ^{ns}	0.494 *
Intercept	0.992	0.446
Gen. Chi-sq/DF	1.00	1.10

** 0.001 < p < 0.01; * 0.01 < p < 0.05; ^{ns} non-significant

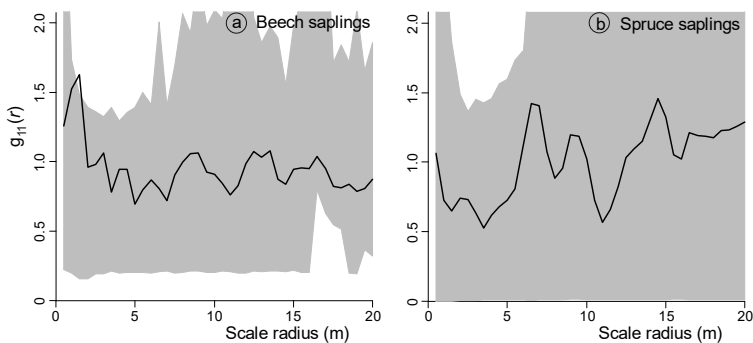


Figure 2 Empirical distribution of the univariate pair-correlation function $g_{11}(r)$ associated with the spatial distribution of beech **(a)** and spruce **(b)** saplings. The grey area represents a 99.9% simulation envelope based on a heterogeneous Poisson null model.

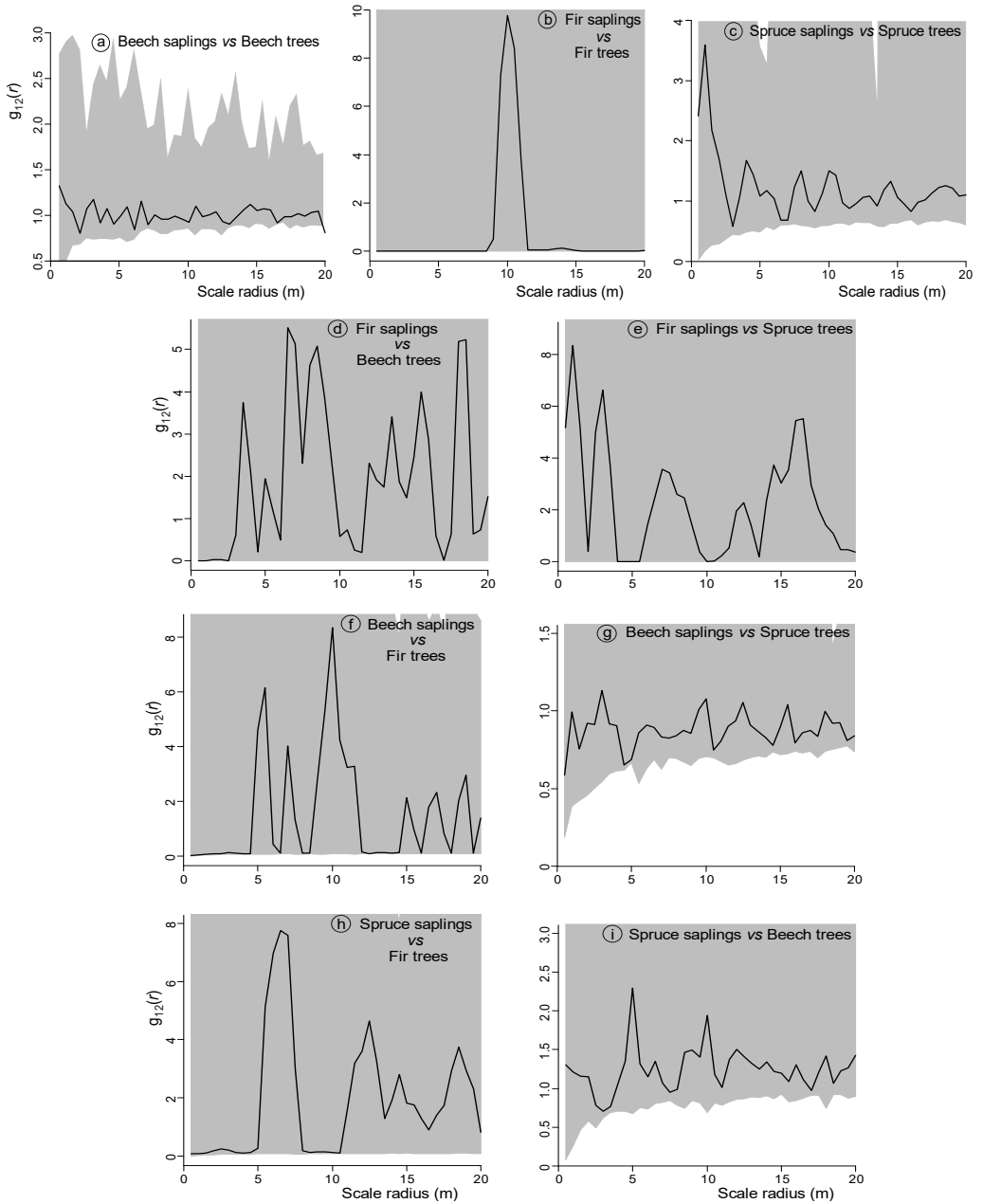


Figure 3 Empirical distribution of the bivariate pair-correlation function $g_{12}(r)$ associated with the spatial distribution of beech, fir and spruce saplings with respect to their conspecific (**a-c**) and respectively, heterospecific (**d-i**) trees. Simulation envelopes (in grey) as in Fig. 1.

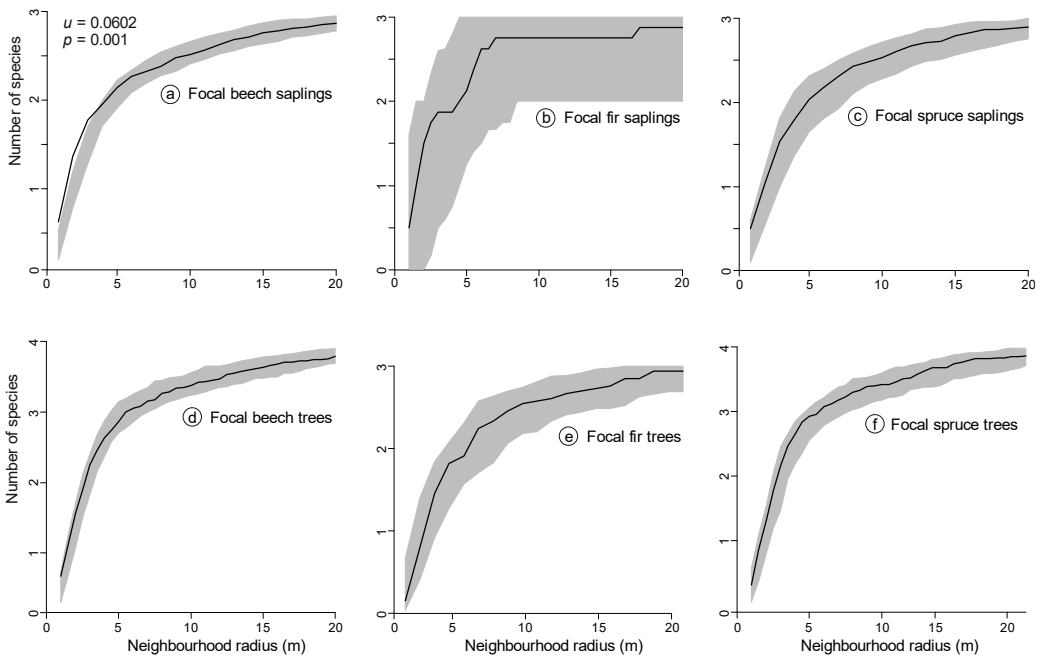


Figure 4 Observed individual species-area relationships (ISARs) built within-saplings (**a-c**) and across-size classes (**d-f**) by using every possible focal species. The number of species on the Y axis includes the focal species (size class). The statistics (u) of the goodness-of-fit test is displayed for significance validation. Simulation envelopes (in grey) as in Fig. 1.

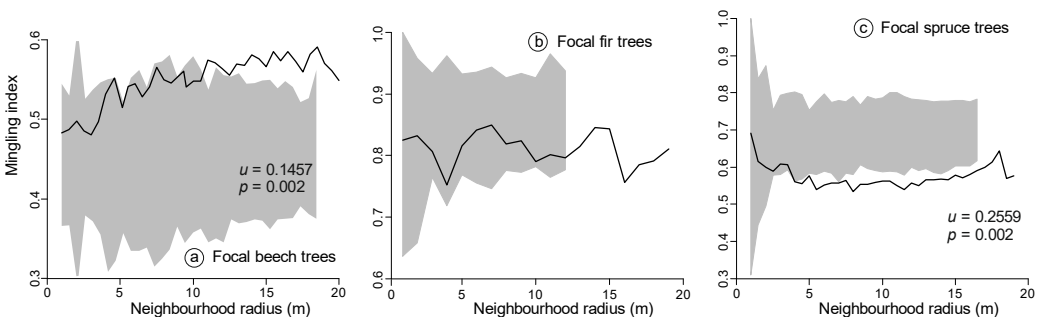


Figure 5 Empirical distribution of the mingling index (M) by neighbourhood radius built for trees only by using the beech (**a**), fir (**b**) and spruce (**c**) as focal species. The statistics (u) of the goodness-of-fit test is displayed for significance validation. The grey area represents a 99.9% simulation envelope based on the null model of random labelling. The envelopes are truncated at large scales because of the null variance (equal observed and simulated values of the mingling index).

Discussion

The monospecific distribution of either beech or spruce saplings did not support the spatial segregation hypothesis, which was found to explain the tree species coexistence in other temperate mixed forests (e.g., Wang et al. 2010, Zhou et al. 2019). Our results are, to some extent, unexpected as both beech and spruce are known to regenerate regularly within canopy gaps (Nagel et al. 2006, Paluch et al. 2019). Beech is a typical gap-filler capable of rapid crown enlargement (Nagel et al. 2010, Janík et al. 2016), whereas spruce is an early and competitive coloniser of canopy openings (Jonášová & Prach 2004).

We did not find evidence of conspecific negative distance/density dependence (CNDD) as no spatial segregation was detected between saplings and trees of any species. However, Janík et al. (2014) and Petriřan et al. (2015) reported spatial segregation between juvenile and mature beech individuals in old-growth beech-fir forests in western and southern Carpathians, respectively. Likewise, Kuninaga et al. (2015) and Ramage & Mangana (2017) found evidence of CNDD in *Fagus crenata* growing in mixed conifer-hardwood forests and respectively, in *Fagus grandifolia*-dominated, mixed hardwoods. Unfortunately, we could not test for CNDD in fir distribution because of the low number of saplings. Many studies reported the decline of fir populations in mixed stands due to poor seedling recruitment and sapling survival (Diaci et al. 2011, Szwagrzyk et al. 2012, Paluch & Jastrzębski 2013, Janík et al. 2014, Keren et al. 2014, Parobeková et al. 2018). It seems that not plant-plant interactions are responsible for the regression of fir in mixed stands, but rather a series of other factors among which high accumulation of beech litter (Simon et al. 2011, Janík et al. 2014) and damage by ungulates (Vrřka et al. 2009, Klopčic et al. 2010). However, none of these factors seemed to have been acting in the study forest area.

In spite of the well-documented process of reciprocal replacement between beech and fir in mixed forests (Bândiu 1977, Heiri et al. 2009, Vrřka et al. 2009, Diaci et al. 2010, Nagel et al. 2010), we did not observe advance regeneration of beech/fir saplings in the neighbourhood of fir/beech trees, which is in accordance with the findings from southern Carpathians (Petriřan et al. 2015). Similar independent spatial distributions between trees and saplings were also revealed at the other two pairs of species: spruce/beech and fir/spruce. Possibly, the demographic heterogeneity and stochasticity may have distorted the ecological response at species level (Hurtt & Pacala 1995) and may have diluted the spatial patterns in tree species distribution making them weak or undetectable (Gravel et al. 2008). On the other hand, a number of studies documented the positive effects of beech trees on fir regeneration (Dobrowolska & Veblen 2008, Vrřka et al. 2009, Paluch et al. 2016, Paluch et al. 2019).

At sapling stage, only beech displayed significant diversity patterns in its neighbourhood. The apparent role of diversity accumulator of beech saplings cannot be attributable to segregation as such a pattern was not revealed in the distribution of beech recruits. Higher than expected tree species richness in the neighbourhood of beech saplings is in accordance with the positive, although weak, correlations between seedling densities in the beech-fir and beech-spruce mixtures, as reported by Paluch et al. (2019), and might be indicative of net positive interactions or favourable microsites (e.g., gaps) for multiple species regeneration (Wiegand et al. 2007, Espinosa et al. 2015). Due to their relatively small size, it is unlikely that the beech saplings have acted as nurse plants (direct facilitation) with respect to fir and spruce saplings, but some sort of indirect facilitation cannot be excluded. For instance, a plausible explanation could be the herd protection (immunity) theory, i.e. enhanced survival linked to a reduced risk

of transmission of species-specific pests and pathogens because of the reduced intraspecific density in more diverse assemblages (Peters 2003, Comita et al. 2010).

At tree stage, none of the three species showed either accumulator or repeller patterns in their neighbourhood with respect to sapling species richness. The fact that beech trees do not act as diversity accumulators, like their juveniles, may be caused by the shift in habitat preferences during their ontogenetic development (e.g., large individuals require more resources and are more competitive) and/or by the different environmental conditions under which the recruitment of trees and saplings occurred (Espinosa et al. 2015). The predominance of neutral diversity patterns in the ISAR analyses points to several possible explanations: existence of environmental filters, i.e. species responding to some kind of environmental heterogeneity (Espinosa et al. 2015); contrasting interactions that average each other out, i.e. null balance of positive and negative interactions (Wiegand et al. 2007, Punchi-Manage et al. 2015); demographic stochasticity due to local disturbance, like those produced by herbivores, pathogens or weather extremes (Wiegand et al. 2007, Gravel et al. 2008). Various authors claimed that, in accordance with the neutral theory (no species interactions), the ecological drift, dispersal limitation and speciation alone can explain the maintenance of tree diversity at local scales, independent of species functional traits (Chave et al. 2002, Hubbell 2006).

Signals of positive and negative interspecific association were found in tree-sized beech and spruce, respectively. The relatively high values of mingling index observed in overstorey beech trees is very likely linked to the status of diversity accumulator revealed in beech saplings. Niche complementarity in root foraging, shade-tolerance, leaf persistence and crown growth architecture may also explain the positive association between beech and the two conifer species in the forest canopy.

Bolte et al. (2013) demonstrated that beech can adopt a flexible root foraging strategy to access soil resources less exploited by spruce, which instead maintains a conservative strategy by keeping a shallow vertical fine root distribution. Such positive complementary effects are partly responsible for the tendency of large trees towards high species mingling, as revealed in several mixed forests across Europe (Pommerening & Uria-Diez 2017). Nevertheless, we found evidence of avoidance effects in spruce trees due to negative association patterns with respect to the other two species. Several mechanisms may have led to such a poor species interspersion. First, the spruce trees displayed a positive effect on the growth of their conspecific saplings (see the next paragraph). Second, the spruce roots and litter deteriorate the edaphic conditions under which the beech and fir saplings could grow sustainably, i.e. by water and base cation depletion, and raw humus accumulation from and respectively, in the topsoil (Thelin et al. 2002, Paluch & Gruba 2012, Paluch et al. 2016). Third, despite being less shade-tolerant, spruce possesses some eco-physiological traits that translate in competitive advantages with respect to beech and fir: priority effects gained by the early colonisation of canopy openings (Jonášová & Prach 2004); best establishment on thick humus layers and coarse woody debris (Szewczyk & Szwagrzyk 1996, Orman & Szewczyk 2015); highest rates of height growth (Stăncioiu & O'Hara 2006).

Only neutral neighbouring effects of trees on the vertical growth of heterospecific saplings were detected in the study stand. On the contrary, significant interactions were revealed between saplings and their nearest parent trees. Like other studies performed in similar mixed forests from central Europe (Bosela et al. 2015, Mina et al. 2018), we observed a suppression in vertical growth of beech saplings in the neighbourhood of conspecific trees. Many studies demonstrated the low self-tolerance of beech (being a strong self-

competitor for both above-ground and below-ground resources) and its severe intraspecific asymmetric competition due to high lateral expansion (Pretzsch 2014, Pretzsch & Schütze 2016). Besides, beech performs better when growing in mixtures with conifers thanks to reduced intraspecific competition (Bosela et al. 2015, Pretzsch et al. 2010, Mina et al. 2018). On the other side, the unexpected positive effect (instead of interference) of the nearest spruce trees on conspecific saplings could only arise by the greater benefit from parent nursing than the energetic loss due to the asymmetric intraspecific competition. A possible explanation for this self-favouring process could be a facilitative below-ground mechanism, like mutualist soil organisms (e.g., mycorrhizae) that enhance the growth of saplings (Das et al. 2008, Bennett et al. 2017). As mentioned above, such a process may be also responsible for the observed negative spatial association between spruce and the other two species in the tree-size class. The detected auto-facilitation is not necessary in contradiction with the findings reported from the same forest reserve by Duduman et al. (2010), who revealed an opposite effect (interference) on spruce saplings but in terms of their radial growth and considering neighbouring trees of any species. A similar example of auto-facilitation was documented in hemlock trees (*Tsuga canadensis*) growing in mixed coniferous-deciduous forests in eastern North America (Woods 1984, Catovsky & Bazzaz 2002).

Limitations and concluding remarks

Our findings are circumscribed to a (relatively small) extent of 0.24 ha and the distance range of 20 m (i.e., half of the smallest side of the plot), which might have prevented the detection of spatial patterns beyond that scale, namely signals of interactions between the large trees. Also, the spatial-related patterns that we attributed to biotic interactions could have

been induced by habitat microheterogeneity and/or small-scale disturbance, if the latter two factors had acted at the same spatial scales. The ecological response of tree species revealed in this study are only valid in the range of submontane-lower montane belt (800-1200 m) where the climatic conditions are optimal for the growth of beech and fir. Therefore, our findings should be further validated through replicated studies in similar old-growth, (sub) montane mixed forests.

Both as juvenile and adult, the beech seems to be the main player in the equalising and stabilising mechanisms of coexistence and diversity maintenance in the study forest stand. The dominant role of beech in mixture with fir and spruce is also sustained by the unbalanced pair-wise competitive interactions, since the negative effects of beech size-symmetric competition on the growth of fir and spruce is much stronger than the effect of fir and spruce size-symmetric competition on beech growth (Mina et al. 2018). Conversely, the low intermingling of spruce in the overstorey leads to lower local tree diversity. This poor interspersed regeneration niche of spruce (e.g., on deadwood) relative to beech and fir (Šebková et al. 2012, Orman & Szewczyk 2015). The fir seems to occupy an intermediate rank between beech and spruce in terms of its contribution to maintaining the local tree diversity, but this outcome might be partly influenced by the low numeric share of fir, given the strong dependency of association strength on abundance (Vázquez et al. 2007). Based on similar processes observed in many similar forest stands from western Carpathians (Paluch et al. 2019), we suppose that strong reduction in stand density due to intensive exploitations prior to reserve foundation has promoted the establishment of spruce regeneration (even at the lower limit of its altitudinal range) and has decreased the recruitment of fir saplings.

References

- Akashi N., 1996. The spatial pattern and canopy-understorey association of trees in a cool temperate, mixed forest in western Japan. *Ecological Research* 11: 311-319. <https://doi.org/10.1007/BF02347788>
- Arii K., Lechowicz M.J., 2002. The influence of overstorey trees and abiotic factors on the sapling community in an old-growth *Fagus-Acer* forest. *Ecoscience* 9: 386-396. <https://doi.org/10.1080/11956860.2002.11682726>
- Baddeley A., Diggle P.J., Hardegen A., Lawrence T., Milne R.K., Nair G., 2014. On tests of spatial pattern based on simulation envelopes. *Ecological Monographs* 84: 477-489. <https://doi.org/10.1890/13-2042.1>
- Baddeley A., Rubak E., Turner R., 2015. Spatial point patterns: methodology and applications with R. Chapman and Hall/CRC Press, Boca Raton.
- Baddeley A., Rubak E., Turner R., 2020. Spatial point pattern analysis, model-fitting, simulation, tests. R package 'spatstat' v1.64-1. <https://cran.r-project.org/web/packages/spatstat/spatstat.pdf>
- Bai X., Queenborough S.A., Wang X., Zhang J., Li B., Yuan Z., Xing D., Lin F., Ye J., Hao Z., 2012. Effects of local biotic neighbors and habitat heterogeneity on tree and shrub seedling survival in an old-growth temperate forest. *Oecologia* 170: 755-765. <https://doi.org/10.1007/s00442-012-2348-2>
- Bândiu C., 1977. Lumina ca factor stabilizator al compoziției ecosistemelor de amestec de brad cu fag. In: Preda V. (ed.), Pădurea și spațiile verzi în actualitate și perspectivă. Academia RSR, Cluj-Napoca, pp. 73-82.
- Becker M., Drapier J., 1984. Rôle de l'allélopathie dans les difficultés de régénération du sapin (*Abies alba* Mill.). I Propriétés phytotoxiques des hydrosolubles d'aiguilles de sapin. *Acta Oecologica* 5: 347-356.
- Becker M., Drapier J., 1985. Rôle de l'allélopathie dans les difficultés de régénération du sapin (*Abies alba* Mill.). II Étude des lessivats naturels de feuillage, de litière et d'humus. *Acta Oecologica* 6: 31-40.
- Bennett J.A., Maherali H., Reinhart K.O., Lekberg Y., Hart M.M., Klironomos J., 2017. Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* 355: 181-184. <https://doi.org/10.1126/science.aai8212>
- Blundell A.G., Peart D.R., 2004. Density-dependent population dynamics of a dominant rain forest canopy tree. *Ecology* 85: 704-715. <https://doi.org/10.1890/01-4101>
- Bolker B.M., Brooks M.E., Clark C.J., Geange S.W., Poulsen J.R., Stevens M.H.H., White J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127-135. <https://doi.org/10.1016/j.tree.2008.10.008>
- Bolte A., Kampf F., Hilbrig L., 2013. Space sequestration below ground in old-growth spruce-beech forests – signs for facilitation? *Frontiers in Plant Science* 4: 322. <https://doi.org/10.3389/fpls.2013.00322>
- Bosela M., Tobin B., Seben V., Petras R., Larocque G.R., 2015. Different mixtures of Norway spruce, silver fir, and European beech modify competitive interactions in central European mature mixed forests. *Canadian Journal of Forest Research* 45: 1577-1586. <https://doi.org/10.1139/cjfr-2015-0219>
- Bulleri F., Bruno J., Silliman B.R., Stachowicz J.J., 2016. Facilitation and the niche: implications for coexistence, range shifts, and ecosystem functioning. *Functional Ecology* 30: 70-78. <https://doi.org/10.1111/1365-2435.12528>
- Cammarano M., 2011. Co-dominance and succession in forest dynamics: the role of interspecific differences in crown transmissivity. *Journal of Theoretical Biology* 285: 46-57. <https://doi.org/10.1016/j.jtbi.2011.06.031>
- Canham C.D., 1988. Growth and canopy architecture of shade-tolerant trees: the response of *Acer saccharum* and *Fagus grandifolia* to canopy gaps. *Ecology* 69: 786-795. <https://doi.org/10.2307/1941027>
- Canham C.D., Le Page P.T., Dave C.K., 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34: 778-787. <https://doi.org/10.1139/x03-232>
- Catovsky S., Bazzaz F.A., 2002. Feedbacks between canopy composition and seedling regeneration in mixed conifer broad-leaved forests. *Oikos* 98: 403-420. <https://doi.org/10.1034/j.1600-0706.2002.980305.x>
- Cavard X., Bergeron Y., Chen H.Y.H., Pare D., Laganier J., Brassard B., 2011. Competition and facilitation between tree species change with stand development. *Oikos* 120: 1683-1695. <https://doi.org/10.1111/j.1600-0706.2011.19294.x>
- Cenușă R., Popa C., Teodosiu M., 2002. Cercetări privind relația structură-funcție și evoluția ecosistemelor forestiere naturale din nordul țării. *Analele ICAS* 45: 9-19.
- Chave J., Muller-Landau H.C., Levin S.A., 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *American Naturalist* 159: 1-23. <https://doi.org/10.1086/324112>
- Chen L., Mi X.C., Comita L.S., Zhang L.W., Ren H.B., Ma K.P., 2010. Community-level consequences of density dependence and habitat heterogeneity in a subtropical broad-leaved forest. *Ecology Letters* 13: 695-704. <https://doi.org/10.1111/j.1461-0248.2010.01468.x>
- Chesson P., 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-366.
- Chi X., Tang Z., Xie Z., Guo Q., Zhang M., Ge J., Xiong G., Fang J., 2015. Effects of size, neighbors, and site condition on tree growth in a subtropical evergreen and deciduous broadleaved mixed forest, China. *Ecology and Evolution* 5: 5149-5161. <https://doi.org/10.1002/ece3.1665>
- Comita L.S., Muller-Landau H.C., Aguilar S., Hubbell S.P., 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329:

- 330-332. <https://doi.org/10.1126/science.1190772>
- Comita L.S., Queenborough S.A., Murphy S.J., Eck J.L., Xu K.Y., Krishnadas M., Beckman N., Zhu Y., 2014. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. *Journal of Ecology* 102: 845-856. <https://doi.org/10.1111/1365-2745.12232>
- Das A.J., Battles J.J., van Mantgem P.J., Stephenson N.L., 2008. Spatial elements of mortality risk in old-growth forests. *Ecology* 89: 1744-1756. <https://doi.org/10.1890/07-0524.1>
- de la Cruz M., 2020. Individual diversity-area relationships. R package 'idar' v1.1. <https://cran.r-project.org/web/packages/idar/idar.pdf>
- Diaci J., Rozenbergar D., Anic I., Mikac S., Saniga M., Kucbel S., Visnjic C., Ballian D., 2011. Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe. *Forestry* 84: 479-491. <https://doi.org/10.1093/forestry/cpr030>
- Diaci J., Rozenbergar D., Boncina A., 2010. Stand dynamics of Dinaric old-growth forest in Slovenia: are indirect human influences relevant? *Plant Biosystems* 144: 194-201. <https://doi.org/10.1080/11263500903560785>
- Diggle P.J., 2010. Nonparametric methods. In: Gelfand A.E., Diggle P.J., Fuentes M., Guttorp P. (eds.), *Handbook of spatial statistics*. CRC Press, Boca Raton, pp. 299-316.
- Dobrowolska D., 1998. Structure of silver fir (*Abies alba* Mill.) natural regeneration in the 'Jata' reserve in Poland. *Forest Ecology and Management* 110: 237-247. [https://doi.org/10.1016/S0378-1127\(98\)00286-2](https://doi.org/10.1016/S0378-1127(98)00286-2)
- Dobrowolska D., Veblen T.T., 2008. Treefall-gap structure and regeneration in mixed *Abies alba* stands in central Poland. *Forest Ecology and Management* 255: 34-69. <https://doi.org/10.1016/j.foreco.2008.02.025>
- Doniță N., Chiriță C., Stănescu V. (eds.), 1990. *Tipuri de ecosisteme forestiere din România. Centrul de Material Didactic și Propagandă Agricolă*, București.
- Duduman G., Roibu C.C., Duduman M.L., Miron-Onciul M., 2010. The influence of competition and dimensional-spatial characteristics of trees on their radial growth in old-growth Slătioara forest, Romania. *AES Bioflux* 2: 215-230.
- Duduman G., Tomescu C., Drăgoi M., Palaghianu C., 2014. Variabilitatea dimensională a arborilor și diversitatea florei vasculare în amestecuri de rășinoase cu fag din rezervația Codrul secular Slătioara. *Bucovina Forestieră* 14: 135-147.
- Espinosa C., Cruz M., Jara-Guerrero A., Gusmán E., Escudero A., 2015. The effects of individual tree species on species diversity in a tropical dry forest change throughout ontogeny. *Ecography* 39: 329-337. <https://doi.org/10.1111/ecog.01328>
- Forrester D.I., Bauhus J., 2016. A review of processes behind diversity-productivity relationships in forests. *Current Forestry Reports* 2: 45-61. <https://doi.org/10.1007/s40725-016-0031-2>
- Fox J.F., 1977. Alternation and coexistence of tree species. *American Naturalist* 111: 69-89. <https://doi.org/10.1086/283138>
- Getzin S., Wiegand T., Wiegand K., He F.L., 2008. Heterogeneity influences spatial patterns and demographics in forest stands. *Journal of Ecology* 96: 807-820. <https://doi.org/10.1111/j.1365-2745.2008.01377.x>
- Gilbert B., Lechowicz M.J., 2004. Neutrality, niches, and dispersal in a temperate forest understory. *Proceedings of the National Academy of Sciences USA* 101: 7651-7656. <https://doi.org/10.1073/pnas.0400814101>
- Gravel D., Beaudet M., Messier C., 2008. Partitioning the factors of spatial variation in regeneration density of shade-tolerant tree species. *Ecology* 89: 2879-2888. <https://doi.org/10.1890/07-1596.1>
- Harms K.E., Condit R., Hubbell S.P., Foster R.B., 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89: 947-959. <https://doi.org/10.1111/j.1365-2745.2001.00615.x>
- Heiri C., Wolf A., Rohrer L., Bugmann H., 2009. Forty years of natural dynamics in Swiss beech forests: structure, composition, and the influence of former management. *Ecological Applications* 19: 1920-1934. <https://doi.org/10.1890/08-0516.1>
- Hiura T., Fujiwara K., 1999. Density-dependence and co-existence of conifer and broad-leaved trees in a Japanese northern mixed forest. *Journal of Vegetation Science* 10: 843-850. <https://doi.org/10.2307/3237309>
- Hou J., Mi X., Liu C., Ma K., 2004. Spatial patterns and associations in a *Quercus-Betula* forest in northern China. *Journal of Vegetation Science* 15: 407-414. <https://doi.org/10.1111/j.1654-1103.2004.tb02278.x>
- Hubbell S.P., 2006. Neutral theory and the evolution of ecological equivalence. *Ecology* 87: 1387-1398. [https://doi.org/10.1890/0012-9658\(2006\)87\[1387:NTATEO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1387:NTATEO]2.0.CO;2)
- Hurt G.C., Pacala S.W., 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology* 176: 1-12. <https://doi.org/10.1006/jtbi.1995.0170>
- Illian J.B., Penttinen A., Stoyan H., Stoyan D., 2008. *Statistical analysis and modelling of spatial point patterns*. John Wiley & Sons, Chichester.
- Janík D., Adam D., Hort L., Král K., Šamonil P., Unar P., Vrška T., 2014. Tree spatial patterns of *Abies alba* and *Fagus sylvatica* in the Western Carpathians over 30 years. *European Journal of Forest Research* 133: 1015-1028. <https://doi.org/10.1007/s10342-014-0819-1>
- Janík D., Král K., Adam D., Hort L., Šamonil P., Unar P., Vrška T., McMahon S., 2016. Tree spatial patterns of *Fagus sylvatica* expansion over 37 years. *Forest Ecology and Management* 375: 134-145. <https://doi.org/10.1016/j.foreco.2016.05.017>
- Johnson D.J., Bourg N.A., Howe R., McShea W.J., Wolf A., Clay K., 2014. Conspecific negative density-dependent

- mortality and the structure of temperate forests. *Ecology* 95: 2493-2503. <https://doi.org/10.1890/13-2098.1>
- Jonašová M., Prach K., 2004. Central-European mountain spruce (*Picea abies* (L.) Karst.) forests: regeneration of tree species after a bark beetle outbreak. *Ecological Engineering* 23: 15-27. <https://doi.org/10.1016/j.ecoeng.2004.06.010>
- Keren S., Motta R., Govedar Z., Lucic R., Medarevic M., Diaci J., 2014. Comparative structural dynamics of the Janj mixed old-growth mountain forest in Bosnia and Herzegovina: are conifers in a long-term decline? *Forests* 5: 1243-1266. <https://doi.org/10.3390/f5061243>
- King D.A., Wright S.J., Connell J.H., 2006. The contribution of interspecific variation in maximum tree height to tropical and temperate diversity. *Journal of Tropical Ecology* 22: 11-24. <https://doi.org/10.1017/S0266467405002774>
- Klopčic M., Jerina K., Boncina A., 2010. Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: are red deer an important factor? *European Journal of Forest Research* 129: 277-288. <https://doi.org/10.1007/s10342-009-0325-z>
- Kotanen P.M., 2007. Effects of fungal seed pathogens under conspecific and heterospecific trees in a temperate forest. *Canadian Journal of Botany* 85: 918-925. <https://doi.org/10.1139/B07-088>
- Koukoulas S., Blackburn G.A., 2005. Spatial relationships between tree species and gap characteristics in broad-leaved deciduous woodland. *Journal of Vegetation Science* 16: 587-596.
- Kraft N., Adler P., Godoy O., James E., Fuller S., Levine J.M., 2015. Community assembly, coexistence, and the environmental filtering metaphor. *Functional Ecology* 29: 592-599. <https://doi.org/10.1111/1365-2435.12345>
- Kuang X., Yuan Z., Lin F., Ye J., Wang X., Wang Y., Hao Z., 2017. Conspecific density dependence and community structure: insights from 11 years of monitoring in an old-growth temperate forest in Northeast China. *Ecology and Evolution* 7: 5191-5200. <https://doi.org/10.1002/ece3.3050>
- Kuninaga T., Hirayama K., Sakimoto M., 2015. Negative canopy-understorey interaction shapes the sapling bank of *Fagus crenata* in a cool-temperate, conifer-hardwood mixed forest. *Plant Ecology* 216: 1191-1202. <https://doi.org/10.1007/s11258-015-0501-9>
- Kunstler G., Falster D., Coomes D.A., Hui F., Kooyman R.M., Laughlin D.C., Poorter L., Vanderwel M., Vieilledent G., Wright S.J., Aiba M., Baraloto C., Caspersen J., Cornelissen J.H.C., Gourlet-Fleury S., Hanewinkel M., Herault B., Kattge J., Kurokawa H., Onoda Y., Peñuelas J., Poorter H., Uriarte M., Richardson S., Ruiz-Benito P., Sun I.-F., Ståhl G., Swenson N.G., Thompson J., Westerlund B., Wirth C., Zavala M.A., Zeng H., Zimmerman J.K., Zimmermann N.E., Westoby M., 2016. Plant functional traits have globally consistent effects on competition. *Nature* 529: 204-207. <https://doi.org/10.1038/nature16476>
- Laliberté E., Paquette A., Legendre P., Bouchard A., 2009. Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. *Oecologia* 159: 377-388. <https://doi.org/10.1007/s00442-008-1214-8>
- Lasky J.R., Uriarte M., Boukili V.K., Chazdon R.L., 2014. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proceedings of the National Academy of Sciences USA* 111: 5616-5621. <https://doi.org/10.1073/pnas.1319342111>
- Lieberman M., Lieberman D., 2007. Nearest-neighbor tree species combinations in tropical forest: the role of chance, and some consequences of high diversity. *Oikos* 116: 377-386. <https://doi.org/10.1111/j.2006.0030-1299.15370.x>
- Loomore N.B., Ford E.D., 2006. Statistical inference using the G or K point pattern spatial statistics. *Ecology* 87: 1925-1931. [https://doi.org/10.1890/0012-9658\(2006\)87\[1925:SIUTGO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1925:SIUTGO]2.0.CO;2)
- Mina M., del Río M., Huber M.O., Thüring E., Rohrer B., 2018. The symmetry of competitive interactions in mixed Norway spruce, silver fir and European beech forests. *Journal of Vegetation Science* 29: 775-787. <https://doi.org/10.1111/jvs.12664>
- Nagel T., Svoboda M., Diaci J., 2006. Regeneration patterns after intermediate wind disturbance in an old-growth *Fagus-Abies* forest in southeastern Slovenia. *Forest Ecology and Management* 226: 268-278. <https://doi.org/10.1016/j.foreco.2006.01.039>
- Nagel T.A., Svoboda M., Rugani T., Diaci J., 2010. Gap regeneration and replacement patterns in an old-growth *Fagus-Abies* forest of Bosnia-Herzegovina. *Plant Ecology* 208: 307-318. <https://doi.org/10.1007/s11258-009-9707-z>
- Nakashizuka T., Kohyama T., 1995. The significance of the asymmetric effect of crowding for coexistence in a mixed temperate forest. *Journal of Vegetation Science* 6: 509-516. <https://doi.org/10.2307/3236349>
- Orman O., Szewczyk J., 2015. European beech, silver fir, and Norway spruce differ in establishment, height growth, and mortality rates on coarse woody debris and forest floor - a study from a mixed beech forest in the Western Carpathians. *Annals of Forest Science* 72: 955-965. <https://doi.org/10.1007/s13595-015-0492-7>
- Pacala S.W., Levin S.A., 1997. Biologically generated spatial pattern and the coexistence of competing species. In: Tilman D., Kareiva P. (eds.), *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, pp. 204-232.
- Paluch J., Bartkowiak L., Moser W.K., 2019. Interspecific effects between overstorey and regeneration in small-scale mixtures of three late-successional species in the Western Carpathians (southern Poland). *European Journal of Forest Research* 138: 889-905. <https://doi.org/10.1007/s10342-019-01209-y>
- Paluch J., Gruba P., 2012. Effect of local species composition on topsoil properties in mixed stands

- with silver fir (*Abies alba* Mill.). *Forestry* 85: 413-426. <https://doi.org/10.1093/forestry/cps040>
- Paluch J., Kolodziej Z., Skrzyszewski J., Bartkowiak L., Gruba P., 2016. Regeneration patterns of the late-successional *Abies alba* Mill.: inhibition in monospecific stands and colonization in mixed stands. *Annals of Forest Science* 73: 1015-1024. <https://doi.org/10.1007/s13595-016-0573-2>
- Paluch J.G., Jastrzębski R., 2013. Natural regeneration of shade-tolerant *Abies alba* Mill. in gradients of stand species compositions: limitation by seed availability or safe microsites? *Forest Ecology and Management* 307: 322-332. <https://doi.org/10.1016/j.foreco.2013.06.035>
- Parobeková Z., Pittner J., Kucbel S., Saniga M., Filípek M., Sedmáková D., Vencurik J., Jaloviari P., 2018. Structural diversity in a mixed spruce-fir-beech old-growth forest remnant of the Western Carpathians. *Forests* 9: 379. <https://doi.org/10.3390/f9070379>
- Peters H.A., 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters* 6: 757-765. <https://doi.org/10.1046/j.1461-0248.2003.00492.x>
- Petrișan I.C., Commarmot B., Hobi M.L., Petrișan A.M., Bigler C.H., Abrudan I.V., Rigling A., 2015. Structural patterns of beech and silver fir suggest stability and resilience of the virgin forest Șinca in the Southern Carpathians, Romania. *Forest Ecology and Management* 356: 184-195. <https://doi.org/10.1016/j.foreco.2015.07.015>
- Piao T., Comita L.S., Jin G., Kim J.H., 2013. Density dependence across multiple life stages in a temperate old-growth forest of northeast China. *Oecologia* 172: 207-217. <https://doi.org/10.1007/s00442-012-2481-y>
- Pommerening A., Grabarnik P., 2019. Individual-based methods in forest ecology and management. Springer, Cham.
- Pommerening A., Uria-Diez J., 2017. Do large forest trees tend towards high species mingling? *Ecological Informatics* 42: 139-147. <https://doi.org/10.1016/j.ecoinf.2017.10.009>
- Poulson T.L., Platt W.J., 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. *Ecology* 77: 1234-1253. <https://doi.org/10.2307/2265592>
- Pretzsch H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *Forest Ecology and Management* 327: 251-264. <https://doi.org/10.1016/j.foreco.2014.04.027>
- Pretzsch H., Block J., Dieler J., Dong P.H., Kohnle U., Nagel J., Spellmann H., Zingg A., 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Annals of Forest Science* 67: 712. <https://doi.org/10.1051/forest/2010037>
- Pretzsch H., Schütze G., 2016. Effect of tree species mixing on the size structure, density, and yield of forest stands. *European Journal of Forest Research* 135: 1-22. <https://doi.org/10.1007/s10342-015-0913-z>
- Punchi-Manage R., Wiegand T., Wiegand K., Getzin S., Huth A., Gunatilleke C., Gunatilleke I., 2015. Neighborhood diversity of large trees shows independent species patterns in a mixed dipterocarp forest in Sri Lanka. *Ecology* 96: 1823-1834. <https://doi.org/10.1890/14-1477.1>
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Rajala T., 2019. Segregation measures for multitype spatial point patterns. R package 'spatialegregation' v2.45. <https://cran.r-project.org/web/packages/spatialegregation/spatialegregation.pdf>
- Ramage B.S., Mangana I.J., 2017. Conspecific negative density dependence in American beech. *Forest Ecosystems* 4: 8. <https://doi.org/10.1186/s40663-017-0094-y>
- Rayburn A., Wiegand T., 2012. Individual species-area relationships and spatial patterns of species diversity in a Great Basin, semi-arid shrubland. *Ecography* 35: 341-347. <https://doi.org/10.1111/j.1600-0587.2011.07058.x>
- Rothe A., Binkley D., 2001. Nutritional interactions in mixed species forests: a synthesis. *Canadian Journal of Forest Research* 31: 1855-1870. <https://doi.org/10.1139/x01-120>
- SAS Institute Inc., 2014. SAS/STAT® 13.2 User's Guide. SAS Institute, Cary.
- Schnitzler A., Closset D., Gafta D., Cristea V., Schwoehrer C., 2004. Dynamique des populations et mosaïque forestière en hêtre-sapinière naturelle préservée. Une comparaison entre Vosges et Carpates. *Revue d'Écologie (Terre et Vie)* 59: 213-229.
- Šebková B., Šamonil P., Valtera M., Adam D., Janík D., 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. *Forest Ecology and Management* 280: 9-19. <https://doi.org/10.1016/j.foreco.2012.05.030>
- Simon A., Gratzner G., Sieghardt M., 2011. The influence of windthrow microsites on tree regeneration and establishment in an old growth mountain forest. *Forest Ecology and Management* 262: 1289-1297. <https://doi.org/10.1016/j.foreco.2011.06.028>
- Stăncioiu P.T., O'Hara K.L., 2006. Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. *European Journal of Forest Research* 125: 151-162. <https://doi.org/10.1007/s10342-005-0069-3>
- Stoll P., Prati D., 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* 82: 319-327. [https://doi.org/10.1890/0012-9658\(2001\)082\[0319:IAACII\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[0319:IAACII]2.0.CO;2)
- Swamy V., Terborgh J., Dexter K.G., Best B.D., Alvarez P., Cornejo F., 2011. Are all seeds equal? Spatially explicit comparisons of seed fall and sapling recruitment in a

- tropical forest. *Ecology Letters* 14: 195-201. <https://doi.org/10.1111/j.1461-0248.2010.01571.x>
- Szewczyk J., Szwagrzyk J., 1996. Tree regeneration on rotten wood and on soil in old-growth stand. *Plant Ecology* 122: 37-46. <https://doi.org/10.1007/BF00052814>
- Szwagrzyk J., Szewczyk J., Maciejewski Z., 2012. Shade-tolerant tree species from temperate forests differ in their competitive abilities: a case study from Raztocze, south-eastern Poland. *Forest Ecology and Management* 282: 28-35. <https://doi.org/10.1016/j.foreco.2012.06.031>
- Thelin G., Rosengren U., Callesen I., Ingerslev M., 2002. The nutrient status of Norway spruce in pure and in mixed-species stands. *Forest Ecology and Management* 160: 115-125. [https://doi.org/10.1016/S0378-1127\(01\)00464-9](https://doi.org/10.1016/S0378-1127(01)00464-9)
- Tsai C.H., Lin Y.C., Wiegand T., Nakazawa T., Su S.H., Hsieh C.H., Ding T.S., 2015. Individual species-area relationship of woody plant communities in a heterogeneous subtropical monsoon rainforest. *PLoS One* 10: e0124539. <https://doi.org/10.1371/journal.pone.0124539>
- Uriarte M., Condit R., Canham C.D., Hubbell S.P., 2004. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology* 92: 348-360. <https://doi.org/10.1111/j.0022-0477.2004.00867.x>
- Vázquez D.P., Melián C.J., Williams N.M., Blüthgen N., Krasnov B.R., Poulin R., 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116: 1120-1127. <https://doi.org/10.1111/j.0030-1299.2007.15828.x>
- Volkov I., Banavar J.R., He F., Hubbell S.P., Maritan A., 2005. Density dependence explains tree species abundance and diversity in tropical forests. *Nature* 438: 658-661. <https://doi.org/10.1038/nature04030>
- Vrška T., Adam D., Hort L., Kolář T., Janík D., 2009. European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) rotation in the Carpathians - a developmental cycle or a linear trend induced by man? *Forest Ecology and Management* 258: 347-356. <https://doi.org/10.1016/j.foreco.2009.03.007>
- Wagner R.G., Radosevich S.R., 1998. Neighborhood approach for quantifying interspecific competition in coastal Oregon forests. *Ecological Applications* 8: 779-794. [https://doi.org/10.1890/1051-0761\(1998\)008\[0779:NAFQIC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1998)008[0779:NAFQIC]2.0.CO;2)
- Wang X., Wiegand T., Hao Z., Li B., Ye J., Lin F., 2010. Species associations in an old-growth temperate forest in north-eastern China. *Journal of Ecology* 98: 674-686. <http://doi.org/10.1111/j.1365-2745.2010.01644.x>
- Weiner J., 1984. Neighbourhood interference amongst *Pinus rigida* individuals. *Journal of Ecology* 72: 183-195. <https://doi.org/10.1111/j.1365-2745.2010.01644.x>
- Wiegand T., Gunatilleke C.V.S., Gunatilleke I.A.U.N., Huth A., 2007. How individual species structure diversity in tropical forests. *Proceedings of the National Academy of Sciences USA* 104: 19029-19033. <https://doi.org/10.1073/pnas.0705621104>
- Wiegand T., Martinez I., Huth A., 2009. Recruitment in tropical tree species: revealing complex spatial patterns. *American Naturalist* 174: 106-140. <https://doi.org/10.1086/605368>
- Wiegand T., Moloney K.A., 2014. *Handbook of spatial point-pattern analysis in ecology*. CRC Press, Boca Raton.
- Wills C., Condit R., Foster R.B., Hubbell S.P., 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences USA* 94: 1252-1257. <https://doi.org/10.1073/pnas.94.4.1252>
- Wilson J.B., 2011. The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored. *Journal of Vegetation Science* 22: 184-195. <https://doi.org/10.1111/j.1654-1103.2010.01226.x>
- Woods K.D., 1979. Reciprocal replacement and the maintenance of codominance in a beech-maple forest. *Oikos* 33: 31-39. <https://doi.org/10.2307/3544508>
- Woods K.D., 1984. Patterns of tree replacement: canopy effects on understory pattern in hemlock-northern hardwood forests. *Vegetatio* 56: 87-107. <https://doi.org/10.1007/BF00033051>
- Wright S.J., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1-14. <https://doi.org/10.1007/s004420100809>
- Zhang C., Zhao X., Gadow K., 2010. Partitioning temperate plant community structure at different scales. *Acta Oecologica* 36: 306-313. <https://doi.org/10.1016/j.actao.2010.02.003>
- Zhou Q., Shi H., Shu X., Xie F., Zhang K., Zhang Q., Dang H., 2019. Spatial distribution and interspecific associations in a deciduous broad-leaved forest in north-central China. *Journal of Vegetation Science* 30: 1153-1163. <https://doi.org/10.1111/jvs.12805>