Overstory succession in a mixed *Quercus petraea–Fagus sylvatica* old growth forest revealed through the spatial pattern of competition and mortality

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ABSTRACT

Old-growth forests are often looked at as a reference for naturalness. Analyzing their successional pathways can provide valuable information on the main drivers of succession in the absence of anthropogenic influence. This knowledge could then prove particularly useful for the maintenance of mixed species stands as a management option to counteract potential changes in forest functions under foreseen climate scenarios. The study was conducted in an old growth *Quercus petraea–Fagus sylvatica* forest in the Runcu Grosi Natural Reserve, western Romania. Main goals of the research were to assess the structure of the old growth forest and understand how the spatial pattern of the two species is shaped by their competitive relationship. We wanted to figure out if the spatial relationship between *Q. petraea* and *F. sylvatica* is different between trees belonging to different layers, and how a possible difference can influence their successional dynamics. To accomplish these tasks, living and dead (both standing and lying) trees were mapped in four 0.56 ha plots. The relationship between trees, considering species, vegetative and social status, was analysed through univariate and bivariate point pattern analyses. Spatial structure based on tree size was investigated with Moran's correlograms and a local indicator of spatial association. The spatial relationship between understory and canopy trees was also assessed using crown cover data to test for differences among the species.

The upper layer is dominated by *Q. petraea*, whereas *F. sylvatica* was the only species in the suppressed one. The high amount of deadwood was mostly due to oak contribution. *F. sylvatica* living trees presented a clumped structure, while *Q. petraea* exhibited a random pattern. *F. sylvatica* dead trees showed instead repulsion to living ones. Suppressed trees were clumped at all distances, whereas trees belonging to dominant and intermediate strata were randomly distributed. Repulsion was found between the two species in the dominant layer. Beech recruitment occurred more frequently outside the canopy of dominant trees. Those beeches established under dominant tree showed a preference for oak cover.

The succession from oak-dominated to beech-dominated stands has already reached an advanced stage in this old growth forest. The two species competitive interactions are mostly driven by their different shade tolerance and crown plasticity. *Quercus–Fagus* mixed stands like the Runcu-Grosi one should be preserved to maintain forest diversity and enhance forest resilience. Oak decline could be reduced by the occurrence of natural disturbances, together with active management that should be promoted to reduce beech competitive pressure.

1. Introduction

Old-growth forests can represent an important source of information to understand the processes that drive successional pathways. In Europe very few examples of natural, temperate, lowland forests are still existing (Petritan et al., 2012). These

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remnant stands are usually located inside protected reserves where human intervention has been excluded over several decades.

Due to intensive management of the oak stands in Europe in the past, pure or mixed sessile oak (*Quercus petraea* (Matt.) Liebl.) forests without human impact are very rare and furthermore have been poorly studied (Korpel', 1995; Smejkal et al., 1995; Petritan et al., 2012). These ecosystems are considered highly valuable for biodiversity and their successional patterns are receiving considerable attention (Rohner et al., 2012), particularly under foreseen climate change scenarios suggesting potential shifts in succession, modifications in species ranges, mortality processes and disturbance regimes.

Sessile oak and European beech (*Fagus sylvatica* L.) are the most common late-successional native broadleaved species of European temperate forests and they usually coexist in mixed stands as a consequence of historical forest management (Bontemps et al., 2012; Ligot et al., 2013). Competitive pressure for growing space among the two species is generally high (Rohner et al., 2012). In the absence of human intervention (Ellenberg and Leuschner, 2010), competition is usually mediated by the higher shade tolerance of beech juveniles as opposed to the greater light requirements of oak juveniles (Collet et al., 1997, 2001; Stancioiu and O'Hara, 2006; Petritan et al., 2007, 2009; Wagner et al., 2010). A decline in oak abundance has been observed in the last decades in several European countries (Thomas et al., 2002). Mixed-species stands are anyway considered as extremely valuable given their presumed higher resilience and stability under most climate change scenarios (Lüpke, 2004, 2009; Knoke et al., 2008) and should thus be preserved. Species coexistence is often explained by interspecific variation in shade tolerance, which also plays a key role in driving forest succession (Pacala et al., 1996; Nakashizuka, 2001). Tree mortality is in turn a fundamental process in forest dynamics shaping successional trajectories through its spatial pattern which affects species composition and stand structure (Franklin et al., 1987).

Natural mortality in oak–beech forests still have to be deeply investigated (Rohner et al., 2012) and a particular focus should be devoted to analyzing the spatial distribution of tree mortality, especially within old-growth stands (Aakala et al., 2012), given their importance as a reference for naturalness.

Spatial pattern analysis has been widely used to assess tree distribution, species spatial interaction, and to detect evidence of biological processes. It is based on the pattern–process relationship which can be used to infer ongoing dynamics in a forest (Franklin et al., 1985; Chen and Bradshaw, 1999; Stoyan and Penttinen, 2000). Competition and facilitation, recruitment and mortality, are all ecological mechanisms that can leave footprints on forest structure which are detectable through spatial pattern analyses. The spatial pattern of trees is strictly related to demographic processes (He and Duncan, 2000) and this relationship can provide useful insights into competition mortality in a stand (Kenkel, 1988; Getzin et al., 2006; Das et al., 2011). However, few studies in European old-growth forests have used spatial pattern analysis to describe forest structure or to explain different ecological processes or mechanisms (Lingua et al., 2011; Lamedica et al., 2011; Garbarino et al., 2012).

The paper investigates oak–beech interactions and mortality processes through spatial analyses under old-growth conditions to infer forest succession dynamics in a temperate forest of Eastern Europe. We expect the spatial pattern of the two species to be different, given their differences in terms of shade tolerance and their role in the succession. Our hypothesis is in particular that a deviation from random mortality towards a more aggregate pattern should be found due to inter- and intra-specific competition and that a spatial relationship between trees in different layers should be useful in explaining recruitment processes.

2. Material and methods

2.1. Study site

The study was carried out in the Runcu Grosi Natural Reserve, located in western Romania (46°11′N and 22°07′E). The climate is temperate continental with a mean annual precipitation of 687 mm and a mean annual temperature of 9.8 °C (Monorostia meteorological station, 150 m a.s.l.). The natural reserve covers an area of 261.8 ha and is dominated by sessile oak and European beech. The soils are cambisols and luvisols, with a good water and nutrient supply.

2.2. Field sampling

In Spring 2012, four 0.56 ha intensive sampling plots (75 × 75 m) were established in the best preserved part (32.3 ha) of the Natural Reserve (Petritan et al., 2013). Plots were subjectively located in order to minimize topographic variation within the plots avoiding areas where forest structure was influenced by edaphic constraints (Larson and Franklin, 2006). All trees with a height >1.5 m were stem-mapped using Field Map® digital forest mapping systems (IFER Ltd., Czech Republic). Their x,y-location, dbh, total height and height of the crown base, and the crown projection (x,y-locations of 4–6 points, depending on crown shape) were measured and species and vitality attributes (dead/alive) were recorded. In order to analyse mortality patterns, we additionally recorded the former location of currently lying dead trees (stump or root plate for the uprooted trees). For logs, species, diameter at both ends and total length were recorded.

2.3. Data analysis

The volume of living and standing deadwood was determined consistent with Petritan et al. (2012) applying a double-logarithmic regression equation (Giurgiu and Drăghiciu, 2004). For lying deadwood we used the formula to compute the volume of a frustum of cone, considering only the portion lying within plot boundaries.

We used point pattern analysis and surface pattern analysis to investigate species and plant–plant interactions. Different hypotheses were tested applying different null models in order to avoid misinterpretation of the results (Aakala et al., 2007; Goreaud and Pélissier, 2003; Marzano et al., 2012).

All individuals in each plot were sorted into three canopy strata, representing different crown classes (dominant, intermediate and suppressed). In order to better capture local competition dynamics, and considering that some differences in site fertility could occur, the vertical stratification was defined separately in each plot following Latham et al. (1998).

To assess the spatial pattern of the overall tree population, individual species, and within each stratum, we utilized the univariate pair correlation function $g(r)$ (Stoyan and Stoyan, 1994; Wiegand and Moloney, 2004), under a homogeneous Poisson null model. We adopted the homogenous Poisson processes (CSR – Complete Spatial Randomness) since the exploratory analysis run for overstory trees showed a CSR distribution at all distances revealing that environmental heterogeneity was limited (Getzin et al., 2008) and confirming what was already observed in the field as a prerequisite for plot establishment.

To detect spatial relationships between species and between trees in different strata the bivariate $g_{12}(r)$ was used applying the toroidal shift null model (Palmer and Van der Maarel, 1995).

We tested the hypothesis of random tree mortality by using the bivariate $g_{12}(r)$ applying the random labelling null model (Aakala et al., 2007; Marzano et al., 2012). For this analysis we pooled the position data of both standing and lying dead trees.

For all the analyses, significant departure from the null models was evaluated based on 95% simulation envelopes, which were calculated from the 5th-lowest and 5th-highest values of 99 Monte Carlo simulations. When we could not determine an appropiate interval where the null model could be rejected (using the goodnees-of-fit (GoF) test for null hyphothesis; Diggle, 2003) we performed new simulations with sufficient repetitions (199 – in the case of intermediate stratum and dominant beech vs. dominant sessile oak or 999 – dominant beech vs. suppressed beech). The analysis was performed up to 25 m (1 m lag distance), not exceeding half the length of the 75 m plot side, to limit the influence of the margin effects. A distribution is classified as clumped, random or regular for univariate analysis, when the value is located above, inside or below the 95% confidence intervals, respectively. Similarly, for bivariate analysis, two populations are significantly positively correlated (attraction), spatially independent or significantly negatively correlated (repulsion), when the value is located above, inside or under the 95% confidence intervals, respectively.

All univariate and bivariate point pattern analyses were performed using the grid-based software Programita (Wiegand and Moloney, 2004). We conducted the spatial analyses considering the 4 plots as pseudo-replications since we were interested in the average spatial pattern (Raventós et al., 2010). Results of the four plots have been thus combined in one average graphic function, using the 'combine replicates tool' included in the Programita software (Wiegand and Moloney, 2004).

A limitation in the point pattern analyses is that trees are reduced to the stem point location. This issue becomes more important when trees are large. In order to better interpret spatial relationships between understory trees (characterized by limited size) and the canopy trees, we compared observed-to-expected occurrence under and outside the canopy cover applying the χ^2 test. Furthermore, the effects of different species crown cover were considered (under beech or under oak). Cover data were derived from GIS layers not considering overlapping area (cover of both beech and oak).

To evaluate if spatial patterns were correlated with tree size (DBH), we calculated spatial correlograms based on Moran's I (Legendre and Fortin, 1989). Each individual autocorrelation coefficient of the correlogram was tested to check if it was significantly different from zero. In addition, the correlogram was tested for significance ($\alpha = 0.05$) using a Bonferroni progressive correction (Legendre and Fortin, 1989; Fortin and Dale, 2005). We analysed neighbouring points applying 2 m distance lags, starting from each

tree position up to 26 m, consistently with the pair correlation function analyses.

A local indicator of spatial association (LISA, Anselin, 1995), the Getis-Ord $G_i^*(d)$ (Getis and Ord, 1992), adopting tree size (DBH) as a quantitative variable, was used to describe the spatio-temporal patterns of tree recruitment. We adopted a 10 m distance class to assess the medium-scale structure more linked to the processes at stand level (Carrer et al., 2013). All Moran's I and local $G_i^*(d)$ analyses were computed using the Excel add-in Rookcase (Sawada, 1999).

3. Results

Average basal area was 47.3 m² ha⁻¹, with a greater contribution from oak trees (Table 1). The average beech density was 712 trees ha⁻¹, whereas its density in the dominant stratum was very low (30.25 trees ha⁻¹) (Table 1). On the contrary, the average sessile oak density was 106.75 trees ha⁻¹, most of them being located in the dominant stratum.

Average density of dead trees was 167.25 trees ha⁻¹, with a slight majority of lying dead trees (53.5%). Average density of oak dead trees (112.25 trees ha⁻¹) was more than twice the beech one (55 trees ha⁻¹).

Mean volume per ha was quite high (769.38 m³ ha⁻¹), ranging from 634.15 to 874.9 m³ ha⁻¹ (Table 1). Oak always accounted for the majority of the biomass. Deadwood amount reached 240.67 m³ ha⁻¹ (91.8% oak).

The overall living tree spatial distribution assessed by g(r) is consistent with a clustered pattern (GoF; $p \leqslant 0.01$) at all distance classes (0–25 m) (Fig. 1). The two species had different spatial patterns: beech showed a clumped distribution ($p \leqslant 0.01$) with a maximum level of clustering at shorter distances (around 2 m; Fig. 1), while sessile oak exhibited a random pattern (Fig. 1). No evidence of a significant spatial interaction between living beech and sessile oak trees was found (Fig. 1).

Dead trees showed a random distribution for both the whole population and the individual species (Fig. 2). No significant spatial relationship was found between dead and living oaks. Beech mortality was located farther away from living beech trees than expected up to 7 m, conditioning the overall pattern (Fig. 2). The overall dead trees population showed repulsion to the living beech trees up to 11 m (Fig. 2, $p \leqslant 0.01$); however, not significant spatial relationship was found with living sessile oak trees at any distance (Fig. 2). Dead beech trees were randomly distributed around living

Table 1
Main stand characteristics of the sampled plots for *Q. petraea* and *F. sylvatica*. Average values and totals are calculated based on these two species only, without including sporadic species (less than 2.5% in basal area).

|	Plot 1 670 m a.s.l.		Plot 2 540 m a.s.l.		Plot 3 555 m a.s.l.		Plot 4 655 m a.s.l.		Average		
	F. sylvatica	*Q. petraea*	*F. sylvatica*	*Q. petraea*	*F. sylvatica*	*Q. petraea*	*F. sylvatica*	*Q. petraea*	*F. sylvatica*	*Q. petraea*	*Total*
Living trees (# ha⁻¹)	484	144	846	101	786	91	732	91	712	106.75	818.75
Dominant (# ha⁻¹)	20	123	34	76	21	80	46	89	30.25	92	122.25
Intermediate (# ha⁻¹)	66	21	39	25	68	11	57	2	57.5	14.75	72.25
Suppressed (# ha⁻¹)	398	–	773	–	697	–	629	–	624.25	–	624.25
Mean diameter (SD) (cm)	14.1 (14.4)	58.5 (11.4)	10.3 (12.6)	55.6 (9.7)	11.1 (13.9)	52.8 (9.8)	10.8 (17.7)	59.1 (9.8)	11.3 (14.8)	56.8 (10.6)	
Mean height (SD) (m)	10.8 (8.4)	33.1 (3.6)	10.2 (8.8)	32.8 (3.3)	9.9 (8.0)	32.7 (3.5)	8.3 (10.0)	35.3 (2.5)	9.8 (8.8)	33.4 (3.4)	
Basal area (m² ha⁻¹)	15.4	40.2	17.7	25.4	19.7	20.5	24.8	25.5	19.4	27.9	47.3
Percent of total basal area (%)	27.3	72.2	39.6	59.3	47.6	51.8	48.2	49.6	40.0	58.9	98.9
Volume (m³ ha⁻¹)	189.71	685.19	255.41	442.61	286.93	347.22	411.42	459.05	285.87	483.52	769.38
Standing dead trees (# ha⁻¹)	20	52	21	27	98	34	48	11	55	112.25	167.25
Standing dead trees volume (m³ ha⁻¹)	4.5	152.38	1.0	71.62	11.93	77.07	2.98	42.05	5.1	85.78	90.88
Lying dead tree (# ha⁻¹)	7	80	12	110	7	80	7	55	8.25	81.25	89.5
Lying dead trees volume (m³ ha⁻¹)	3.64	117.83	6.99	178.77	24.5	121.44	23.52	122.45	14.66	135.12	149.79
Deadwood volume (m³ ha⁻¹)	8.14	270.21	7.99	250.39	36.43	198.51	26.5	164.5	19.77	220.9	240.67
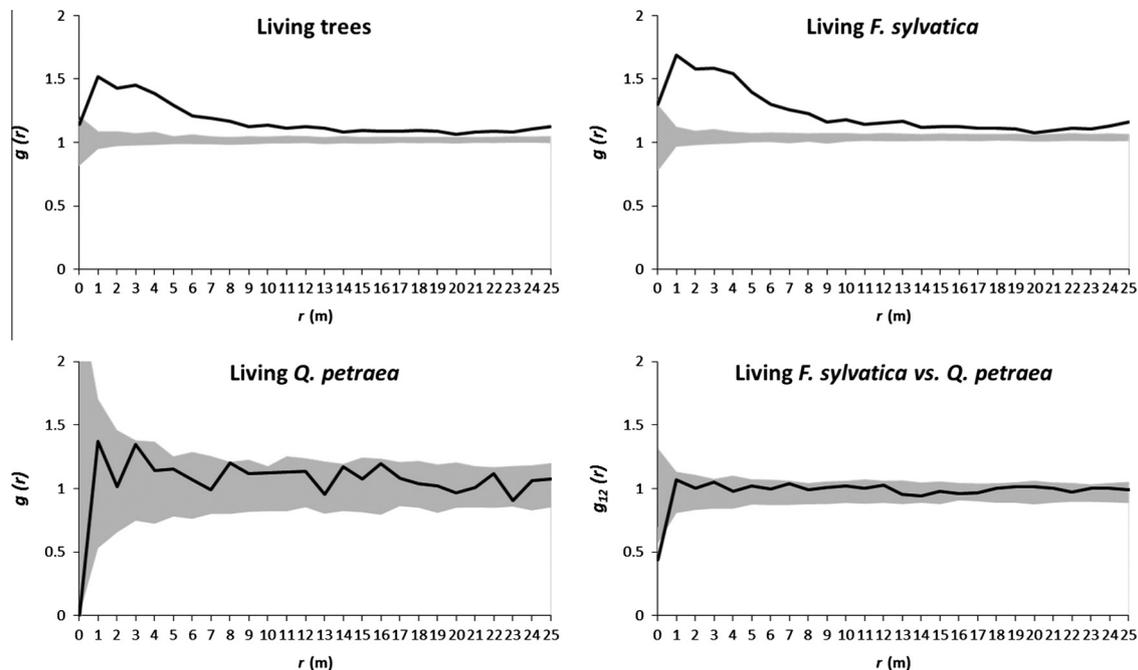
Fig. 1. Tree spatial patterns quantified with the pair correlation function $g(r)$ for the overall living tree population and for each species separately. In the lower right graph, bivariate pair-correlation function $g_{12}(r)$ between the two species. Critical bands from the Monte Carlo simulations are shaded ($p < 0.01$).

oak trees (Fig. 2), but they were negatively associated to the overall living tree population at short distance (1–6 m; Fig. 2, $p \leqslant 0.01$).

At short to medium distances (1–8 m) dead sessile oak trees were negatively associated to living beech trees ($p \leqslant 0.01$) and consequently to all living trees (Fig. 2).

As expected suppressed trees were significantly clumped ($p \leqslant 0.01$) at all distances (0–25 m; Fig. 3), whereas trees belonging to dominant and intermediate strata were randomly distributed, with the exception of the distance interval between 7 and 9 m where trees of the intermediate stratum were clumped ($p \leqslant 0.01$, 199 Monte Carlo simulations; Fig. 3). Both beech and sessile oak dominant strata showed a random spatial distribution over all distances (Fig. 3).

Suppressed trees showed attraction to the dominant trees at 5–7 m (Fig. 4, $p \leqslant 0.01$). Repulsion was found between dominant sessile oak and dominant beech from 3 to 8 m (Fig. 4, $p \leqslant 0.01$, 199 Monte Carlo simulations), while suppressed beech trees were negatively associated to dominant beech up to 2 m (Fig. 4, $p \leqslant 0.01$, 999 Monte Carlo simulations). No interaction was found between dominant oaks and suppressed beech trees.

Suppressed trees occurred more frequently outside the canopy of dominant trees than expected ($p < 0.01$; χ^2 test). Considering only beech trees occurring under the canopy, they occurred more frequently under oak cover than expected ($p < 0.01$; χ^2 test).

All Moran's I spatial correlograms for the overall population were globally significant at $p < 0.05$ (Bonferroni corrected test), revealing the existence of a tree size spatial structure (Table 2). However considering species separately, correlograms for beech were globally significant at $p < 0.05$ (Bonferroni corrected test), suggesting the existence of a tree size spatial structure for this species only, while oak correlograms were never significant (Table 2). These results were confirmed by the local $G_i^*(d)$ statistic rasterized in the plot maps (Appendix A), showing the localization of significant clusters for beech and the overall population and only a few clusters (and lying on the edge) for oak.

4. Discussion

Sessile oak was the dominant species mainly contributing to the remarkable basal area and volume of the forest, whereas beech was represented by a larger number of individuals. The amount of deadwood in the Reserve was quite high, averaging 240.67 m^3 ha^{-1}, placing the forest above the median of temperate deciduous broadleaved old growth forests (Burrascano et al., 2013). The more shade tolerant beech was the only species in the suppressed stratum, with few individuals in the intermediate and dominant ones. Sessile oak, in contrast, was scarcely represented in the intermediate stratum and no trees were found in the suppressed stratum. The presence of seedlings and saplings of sessile oak (1–3 years old) across the forest floor (visual observations) suggested that neither seed limitation nor a lack of germination sites were responsible for the absence of oak saplings taller than 1.5 m. Oak recruitment limitation (sensu Hurtt and Pacala, 1995), whose consequences can deeply affect composition, structure and diversity of forests (McEuen and Curran, 2004), is thus probably due to factors affecting seedling survival rather than seed germination.

Oak stands are generally not characterized by the presence of advanced regeneration, even if sessile oak may persist for many years as low, bushy saplings in small gaps; extremely dense canopy covers are tolerated only for the very first years (Diaci and Roženbergar, 2001). Lüpke and Hauskeller-Bullerjahn (2004) found that under low light conditions in the first years after planting the mortality of sessile oak was nearly double that of beech seedlings. Given their greater light requirements compared to beech, oak saplings can hardly compete and survive without good light conditions. Sessile oak seedlings have been shown to have a preference for light levels higher than 15–20% of full sunlight, meaning that gaps of at least 17–20 m diameter or beneath a broken to open canopy are suitable regeneration sites (Lüpke, 1995, 1998).
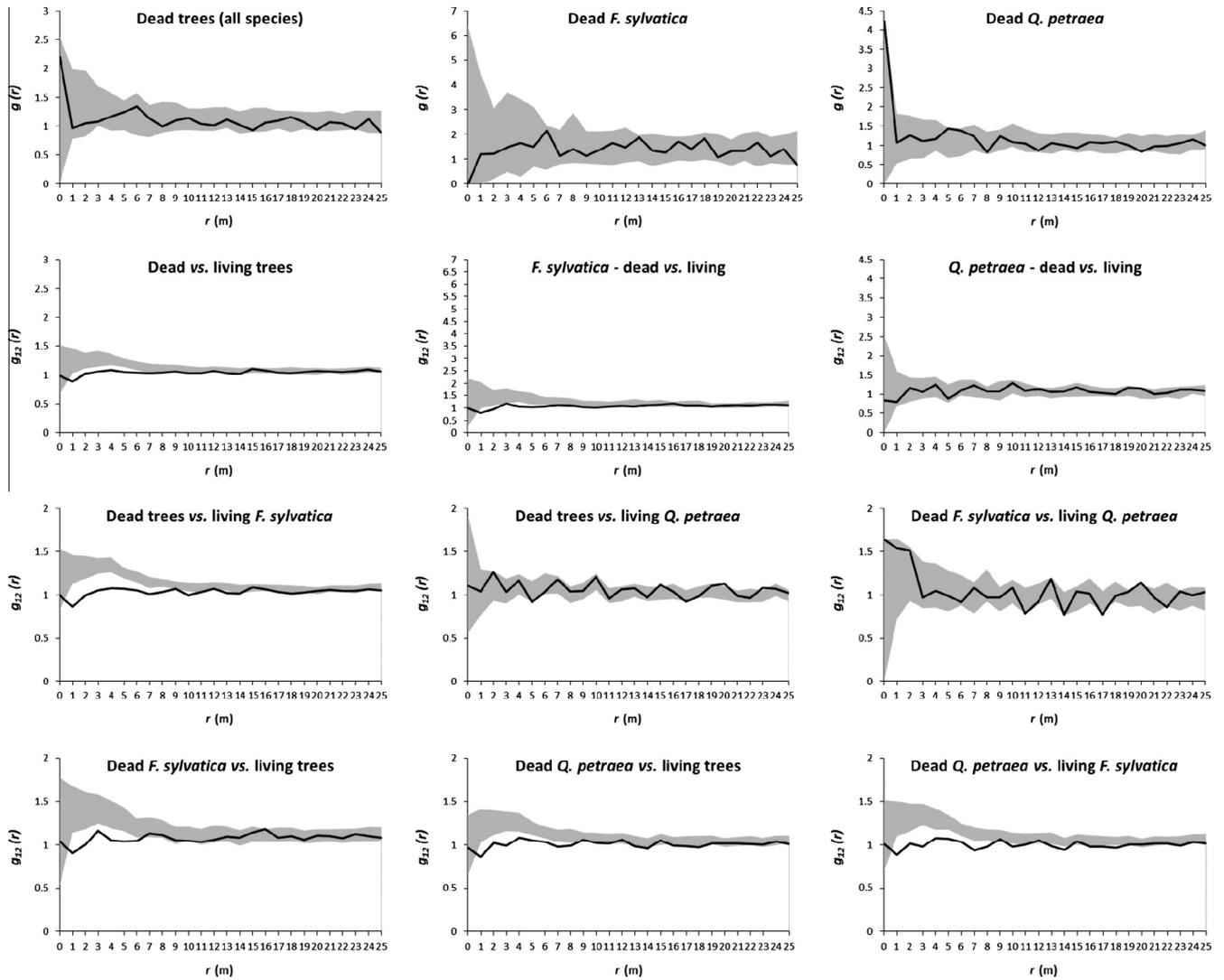
Fig. 2. Univariate analyses ($g(r)$) on the spatial patterns of dead trees and bivariate analysis ($g_{12}(r)$) of their spatial interaction with living trees under the random mortality null model. Critical bands from the Monte Carlo simulations are shaded ($p < 0.01$).
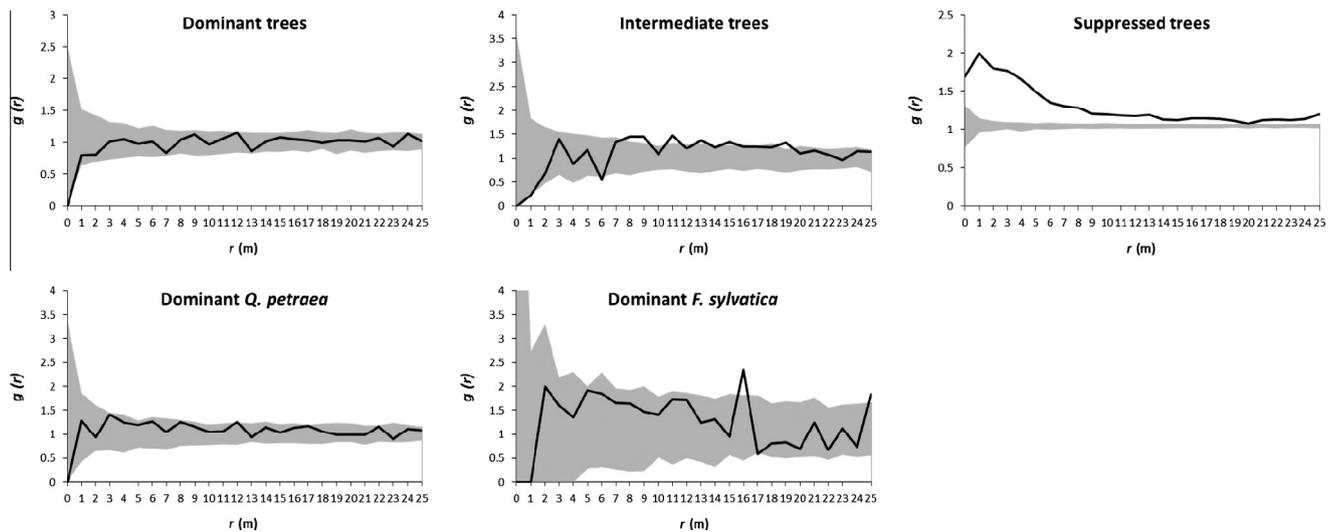

Fig. 3. Univariate analyses of the spatial pattern of trees belonging to different layers, considering all the species together and separately, using the pair-correlation function $g(r)$. Critical bands from the Monte Carlo simulations are shaded ($p < 0.01$).
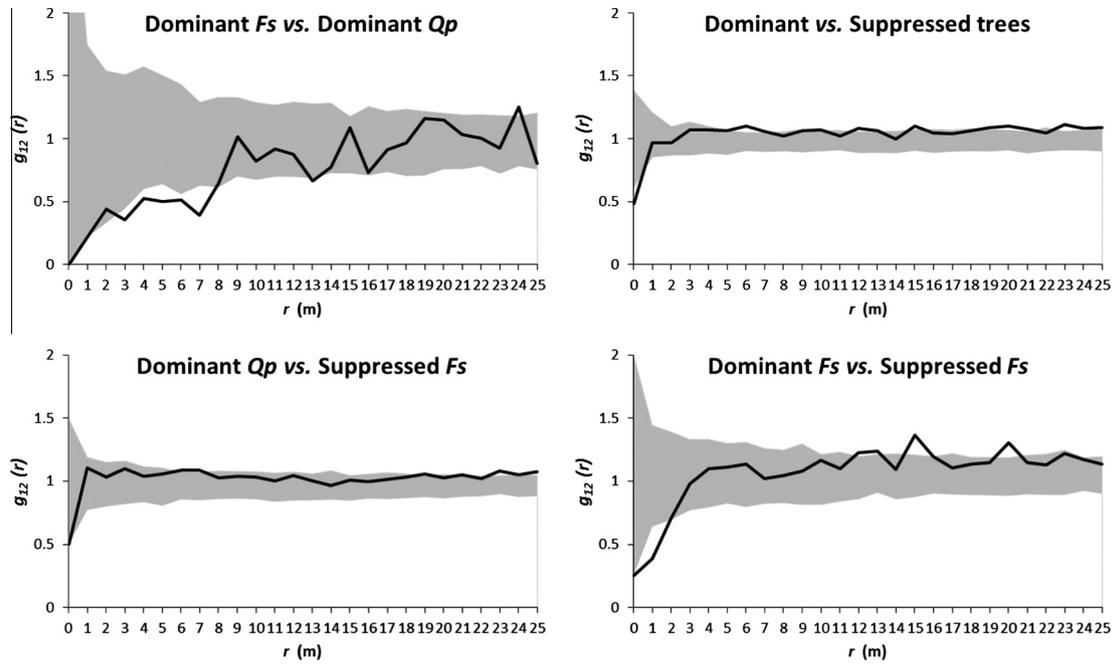
Fig. 4. Bivariate analyses of the spatial interaction between trees belonging to different layers, considering all the species together and separately, using the pair-correlation function $g_{12}(r)$. Critical bands from the Monte Carlo simulations are shaded ($p < 0.01$).

Table 2
Moran's $I(d)$ analyses for tree size (DBH).

	Distance (m)													Sig.
	2	4	6	8	10	12	14	16	18	20	22	24	26	
Plot 1- Overall tree population		▨				▨					▨			*
Plot 1- *Q. petraea*								▨						n.s.
Plot 1- *F. sylvatica*						▨								*
Plot 2- Overall tree population	▨	▨		▨								▨		*
Plot 2- *Q. petraea*														n.s.
Plot 2- *F. sylvatica*	▨													*
Plot 3- Overall tree population	▨													*
Plot 3- *Q. petraea*								▨						n.s.
Plot 3- *F. sylvatica*		▨												*
Plot 4- Overall tree population	▨	▨	▨								■	■		*
Plot 4- *Q. petraea*														n.s.
Plot 4- *F. sylvatica*	▨	▨	▨	▨	▨						■	■		*

Grey indicates significant positive values, black significant negative ones. The (*) symbol indicates global correlogram significance ($p < 0.05$).

It has been demonstrated that in European forests beech capability to grow and survive under low light levels is higher than that of oak, while high or intermediate light levels reverse the relationship (e.g. Newbold and Goldsmith, 1981; Diaci and Roženbergar, 2001; Kunstler et al., 2005). However, some studies have shown that even when light condition increases, oak saplings often show lower height increments than beech (Ligot et al., 2013), probably suffering from the lower morphological plasticity of their foliage and crown structures (Farque et al., 2001; Dieler and Pretzsch, 2013). Beech tolerance to slow growth and reduced

mortality at low light enable beech saplings to establish on a long term basis in the understorey, at the expenses of oak (Kunstler et al., 2005). The advanced beech regeneration is thus positioned to take advantage of more favourable light conditions (i.e. by an opening in the dominant canopy) and easily out compete oak seedlings, reaching the upper layers.

In the core area forest of the Runcu Grosi Reserve, trees in the dominant stratum, both beech and oak, were randomly distributed at all distances. The degree of aggregation tended to rise at lower levels in the canopy profile. In the intermediate layer some evidence of aggregation was found at medium distance (between 8 and 11 m), while the suppressed stratum was highly aggregated at all distances. This pattern has been reported in some other studies where it was explained by habitat heterogeneity (Chapin et al., 1994; Getzin et al., 2006, 2008) or limited seed dispersal (Grubb, 1977; Harms et al., 2000). Gravity is one of the most important factors affecting big seed dispersal, and for this reason most seeds of sessile oak and beech are dispersed within the crown projection of parental trees. Predation and dispersal by animals (Kollmann and Schill, 1996; Mosandl and Kleinert, 1998; Packham et al., 2012), germination rate, and seedlings survival could have further shaped the saplings demography, including spatial distributions.

We found a negative interaction between dominant trees and suppressed beech trees at shorter distances, which is more evident considering only beech dominant trees. As suggested by Hamill and Wright (1986) the negative relationship between juvenile and big trees is caused by the dependence of tree regeneration on light availability. Beech tendency not to establish close to mature conspecifics (Rozas, 2003) was confirmed in our study, together with its preferential recruitment under oak canopy cover. Beech suppressed trees could also take advantage of the ongoing reduction in oak cover since a decline of mature oak trees has already been observed in the area (Petritan et al., 2012), like in other sites in central Europe (e.g. Rohner et al., 2012). The positive spatial interaction found between dominant and suppressed trees at the distances of 5–7 m, corresponds to the area immediately outside the canopy of overstorey trees (mean radius 3.6 m), a pattern also found in other forest ecosystems (Getzin et al., 2011). Recruitment and survival are greater in this interspace between large tree crowns where canopy closure was more recent or small gaps could still be present.

A negative spatial interaction (repulsion) was found between the two species in the dominant layer up to 8 m corresponding to the average crown diameter and highlighting the ongoing competition dynamics in the canopy for space occupancy. Competition in the other canopy layers was harder to detect. Several different processes can lead to a net facilitative or competitive effect in a given species combination (Forrester, 2014). The balance between positive and negative interactions can vary over time and space (Lingua et al., 2008; Farrer et al., 2010; del Rio et al., 2014). Pretzsch et al. (2013) found that during drought periods growth of beech in mixture with oak can be superior to its growth in pure stands, showing that facilitation prevails under stress conditions. With its deep-root system, oak facilitates the more shallow-rooting beech through hydraulic lift of water, increasing resistance of the latter during drought years (Zapater et al., 2011).

Contrary to our hypothesis, in the forest reserve mortality was not spatially aggregated, even considering each species separately. The presence of allogenic mortality agents (e.g. disturbances) acting in a stand is usually manifested by a specific spatial pattern (Davis et al., 2005; Nagel and Diaci, 2006; Marzano et al., 2012). Spatial pattern analyses thus suggest that no factors in addition to background mortality (sensu Franklin et al., 1987) are likely playing a substantial role in mortality processes. Competition dynamics, and other endemic factors of background mortality,

are not easily detectable unless they are strong enough to cause substantial mortality (Getzin et al., 2006). Available growing space (sensu Oliver and Larson, 1996) is still allowing a high rate of survival within beech clusters. Moreover beech predominance in the suppressed layers is not affecting the mortality pattern which is currently prevailing in the dominant layer. The segregation of both dead beeches and oaks with living beeches, up to a distance corresponding to the average crown diameter in the dominant layer, again suggests that relatively recent beech in-growth processes are prevailing in determining current spatial patterns in the reserve.

The succession from oak-dominated to beech-dominated stands can be a process of natural restoration of the original forest, modified by past anthropogenic activities, which promoted oaks. Mixed-species stands should be preserved in order to maintain forest diversity and enhance resilience, particularly in the light of predicted climate change (Lüpke, 2004, 2009; Knoke et al., 2008). The adaptation potential to climate warming of pure beech forests has been questioned (Ligot et al., 2013). According to some studies, beech may lose its dominance towards more drought-tolerant tree species like oak, especially on soils with low water availability (Rennenberg et al., 2004; Geßler et al., 2007), and experience a decline in productivity in temperate climates (Ciais et al., 2005). Concerning oak species, whose presence is usually associated with a high degree of biodiversity, several authors are currently debating their potential ability to benefit from climate change, particularly in Central Europe and compared to beech (Rohner et al., 2012). To maintain an oak presence active management is necessary, mostly to reduce the competitive pressure (Rohner et al., 2012). Considering that beech is generally less browsed by deer (Cervus elaphus L.) and roe deer (Capreolus capreolus L.) than oak (Packham et al., 2012), control measures on ungulate population could also be adopted (Ligot et al., 2013) to favour oak recruitment and enhance oak presence in the regeneration layer. Natural disturbances, in the absence of anthropogenic ones, can contribute to the maintenance in the landscape of some oak-dominated stands if their spatial extent is big enough to allow oak recruitment. The natural disturbance regime in the Runcu-Grosi Natural Reserve is characterized by small scale disturbances generating small canopy gaps (mean size 79.7 m^2) with beech as the main gap filler species (Petritan et al., 2013). The persistence of oak stands in small forest preserves can thus be problematic since the spatial and temporal scales of disturbances do not favour the maintenance of oak-dominated forests.

Appendix A

Interpolated and z-transformed local $G_i^*(d)$ values computed for tree size for 10 m distance intervals. Red and blue colours depict respectively hot-spot (i.e. groups of trees bigger than the mean size within the plot) and cold-spot (i.e. groups of trees smaller than the mean size within the plot) areas, with the intensity of the colours being proportional to the value of the local $G_i^*(d)$ index. Bold contour lines indicate significant clusters.

	Plot 1	Plot 2	Plot 3	Plot 4
Overall tree population				
Q. petraea				
F. sylvatica				
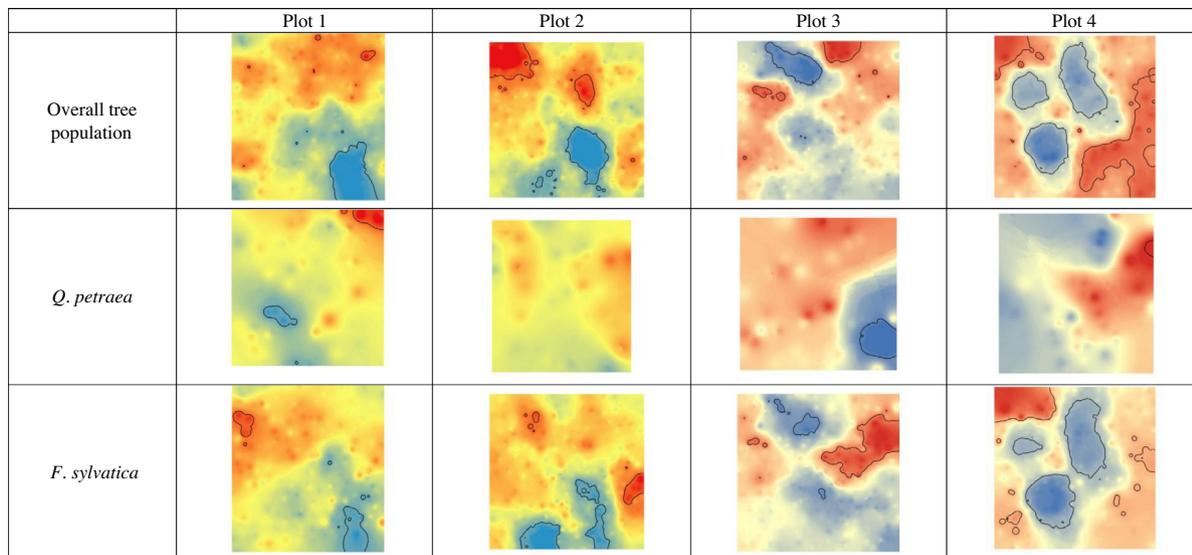
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