

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/282562862>

Structural patterns of beech and silver fir suggest stability and resilience of the virgin forest Sinca in the Southern Carpathian....

Article in *Forest Ecology and Management* · July 2015

DOI: 10.1016/j.foreco.2015.07.015

CITATIONS

9

READS

472

7 authors, including:



Ion Catalin Petritan

Universitatea Transilvania Brasov

33 PUBLICATIONS 284 CITATIONS

[SEE PROFILE](#)



Brigitte Commarmot

Swiss Federal Institute for Forest, Snow and ...

19 PUBLICATIONS 212 CITATIONS

[SEE PROFILE](#)



Martina Hobi

Swiss Federal Institute for Forest, Snow and ...

14 PUBLICATIONS 219 CITATIONS

[SEE PROFILE](#)



Any Mary Petritan

National Research and Development Institut...

31 PUBLICATIONS 339 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Long-term Irrigation Experimental Platform Pfynwald [View project](#)



Predicting Ozone Fluxes, Impacts and Critical Levels on European Forests - PRO3FILE [View project](#)



Structural patterns of beech and silver fir suggest stability and resilience of the virgin forest Sinca in the Southern Carpathians, Romania



Ion Catalin Petritan^{a,b,*}, Brigitte Commarmot^a, Martina Lena Hobi^a, Any Mary Petritan^{a,c}, Christof Bigler^d, Ioan Vasile Abrudan^b, Andreas Rigling^a

^a Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

^b Transilvania University, Sirul Beethoven 1, ROU-500123 Brasov, Romania

^c National Institute for Research-Development in Forestry "Marin Drăcea", Eroilor 128, 077190 Voluntari, Romania

^d Forest Ecology, Department of Environmental Systems Science, ETH Zurich, Universitätsstrasse 16, CH-8092 Zürich, Switzerland

ARTICLE INFO

Article history:

Received 6 March 2015

Received in revised form 15 July 2015

Accepted 20 July 2015

Available online 29 July 2015

Keywords:

Primeval forest

Tree spatial pattern

Fagus sylvatica

Abies alba

Species coexistence

Small-scale disturbances

ABSTRACT

The structural patterns and dynamics of a primeval silver fir (*Abies alba*) – European beech (*Fagus sylvatica*) forest in the Southern Carpathians (Romania) were assessed to gain deeper insight into species interactions and mechanisms of coexistence, and to study the influence of species composition on forest structure. At 21 sample plots, each covering 0.123 ha within an area of 240 ha, all living and dead trees ≥ 6 cm dbh (diameter at breast height) were mapped and measured. Regeneration was assessed on four sub-plots per plot. Additionally, a 1-ha permanent plot established in 2003 was re-measured in 2013 to obtain information on stand dynamics. Point pattern analyses were conducted to study the spatial patterns and tree-to-tree interactions. The overall dbh distributions of beech and fir tended to indicate sustainable population structures. The share of beech varying from 24.8% to 95% (average 58%) in stand basal area did not influence stand parameters such as basal area or volume, nor the distribution of growing stock to different canopy layers. We found fir to dominate the lowest dbh classes in plots that were strongly dominated by beech in the top layer and vice versa, locally indicating species alternation. The regeneration density of fir was lower than of beech, although browsing by ungulates was negligible. In contrast to its share among living trees, fir contributed two-thirds to the deadwood volume. The 10-year changes in forest structure and mortality rate on the 1-ha plot were very small, suggesting the absence of recent intermediate or severe disturbances. The spatial patterns of the dead trees and of the living beech and fir in different canopy layers agreed with a disturbance regime dominated by stochastic small-scale events. Although the spatial patterns of beech and fir were similar, the tree-to-tree interactions indicated a higher intraspecific competition of beech than of fir and a higher shade tolerance of fir particularly in later stages of development. Both could be important factors for the coexistence of the two species. We conclude that the primeval fir–beech forest Sinca shows under the present small scale disturbance regime a high stability and structural resilience. Temporal changes in species composition only lead to small fluctuations in stand parameters and do not threaten the long-term coexistence of beech and fir. Forest managers may vary the species composition of fir–beech forests without substantially influencing the overall forest structure or productivity.

© 2015 Elsevier B.V. All rights reserved.

Abbreviation: PBBA, percentage of beech in the stand basal area.

* Corresponding author at: Transilvania University, Sirul Beethoven 1, ROU-500123 Brasov, Romania.

E-mail addresses: ion.petritan@wsl.ch, petritan@unitbv.ro (I.C. Petritan), brigitte.comarmot@wsl.ch (B. Commarmot), martina.hobi@wsl.ch (M.L. Hobi), any.petritan@wsl.ch (A.M. Petritan), christof.bigler@env.ethz.ch (C. Bigler), abrudan@unitbv.ro (I.V. Abrudan), andreas.rigling@wsl.ch (A. Rigling).

<http://dx.doi.org/10.1016/j.foreco.2015.07.015>

0378-1127/© 2015 Elsevier B.V. All rights reserved.

1. Introduction

The increasing demand for various forest ecosystem goods and services and the uncertainties caused by climate change associated with higher temperatures and more frequent and/or severe disturbances have increased the interest in uneven-aged and close-to-nature silviculture (Diaci et al., 2011). Pure and mixed European beech (*Fagus sylvatica* L.) forests are the most widespread forest types in Central Europe, but intensive forest management over the centuries has changed species composition and stand

structure. Old-growth forests which have never been subject to timber harvesting are rare and confined to few areas mainly in the Carpathian and Balkan regions (Leibundgut, 1982; Korpel, 1995). These forest remnants are important reference systems for forest management and unique research objects for understanding natural forest dynamics and ecosystem processes (Wirth et al., 2009; Višnjić et al., 2013).

Mixed mountain forests with shade-tolerant silver fir (*Abies alba* Mill.) and beech, and slightly less shade-tolerant Norway spruce (*Picea abies* Karst) (Niinemets and Valladeres, 2006; Ellenberg and Strutt, 2009) are considered the most suitable forest types for continuous cover forest management with single-tree selection (Schütz, 2001), although single-tree and group selection management is also possible e.g. in pure beech forests or beech mixed with other broadleaves (Dittmar, 1990, 1992). In conifer-beech plenter forests, beech is usually maintained with a share of less than 20% of the growing stock only, as it is assumed to have a negative effect on the typical plenter structure characterised by the vertical arrangement of tree crowns in space. Schütz (2001) recommends to admix beech in such plenter forests clustered in groups rather than as single trees interspersed with conifers. Little is known, however, about the spatial patterns of the different species in primeval fir-beech forests and the influence of beech on the vertical and horizontal structuring of these old-growth mixed mountain forests. It can be assumed that differences in crown architecture, growth rates under different light conditions and at different live stages, and growth response to improved light conditions influence the interactions and spatial distribution of the two species. While beech and fir can establish at low light levels (Stancioiu and O'Hara, 2006; Rozenbergar et al., 2007) and are both known to survive suppression periods of more than 100 years (Trotsiuk et al., 2012; Nagel et al., 2014), the studies of Nagel et al. (2014) in a primeval fir beech forest in the Dinaric Mountains suggested, that the shade tolerance of silver fir at later stages of development (pole stage) is higher than that of beech. Beech saplings grow faster than fir over a range of light conditions, particularly at higher light levels (Stancioiu and O'Hara, 2006), but its tendency to plagiotropic growth when suppressed for a long period (Rozenbergar et al., 2007) may make it more difficult for beech to respond to small-scale disturbances than for silver fir (Motta et al., 2011). Interspecific differences in shade tolerance have been used to explain species coexistence in various forest types (Pacala et al., 1996; Petritan et al., 2014), but it is not clear, whether it also plays a role in the coexistence of the both highly shade tolerant fir and beech or whether other factors, such as e.g. site heterogeneity or differences in intra- and inter-specific competition, may be more important.

Whereas extensive research on forest dynamics has been carried out in silver fir-beech old-growth forest remnants in Central and South-Eastern Europe (Splechtna et al., 2005; Paluch, 2007; Kral et al., 2010; Diaci et al., 2011; Nagel et al., 2014), there is a lack of studies at the eastern limit of the natural beech-silver fir vegetation zone (27°E, Romania and Bulgaria; Lombardi et al., 2012). In the framework of a national inventory of virgin forests in Romania, a project carried out by the Royal Dutch Society of Nature Conservation (KNNV) and the Forest Research Institute of Romania, Veen et al. (2010) classified a total area of 218,494 ha as virgin forests, with beech and silver fir being the most abundant tree species (over 70%). The South Carpathians still harbour viable populations of large carnivores, such as bears (*Ursus arctos*), wolves (*Canis lupus*) and lynxes (*Lynx lynx*). This makes these forests particularly interesting as reference areas for natural forest dynamics, as the trophic cascade and the interactions between predators, herbivores and plants, which influence ecosystem structure and dynamics (Ripple et al., 2014), are still complete.

Forest structure and spatial diversity result from past dynamics and present complex interactions of many processes (Chen et al., 2004). In the last decades, research on old-growth forests mainly focused on disturbances, which have been recognized as important drivers of forest dynamics. Silver fir-beech forests are described as relatively stable forest ecosystems with a mainly small-scale disturbance regime, dominated by single-tree mortality and small-scale gap dynamics (Motta et al., 2011), although disturbances of moderate severity may occur from time to time (Splechtna et al., 2005; Nagel et al., 2014). Several studies carried out in Eastern and South-Eastern Europe also suggest an influence of indirect anthropogenic disturbances, in particular air pollution and human-induced increase in ungulate populations, on the structural dynamics of mixed mountain forests, leading to a synchronous silver fir decline in old-growth forest remnants in Czechia, Slovakia, Slovenia, Croatia and Bosnia-Herzegovina (Šamonil and Vrška, 2007; Diaci et al., 2010; Ficko et al., 2011; Nagel et al., 2015).

Old-growth forest structures have commonly been described by diameter distributions (e.g. Goff and West, 1975), which are also used as forest management tool to control and specifically shape forest structure in uneven-aged single-tree selection forests (Schütz, 2001). While diameter distributions are a suitable means to analyse the demographic structure of forests and the tree species within, point pattern analyses can be used to study the spatial (horizontal) distribution of (e.g. differently sized) trees and interactions between the different species (Pommerening, 2002; Rozas et al., 2009). Processes, such as disturbances, age- or competition-induced mortality, seed dispersal, tree recruitment and species-specific interactions leave distinct imprints on the horizontal and vertical structure of natural forest ecosystems, which should be detectable through spatial pattern analysis (Franklin et al., 2002; Getzin et al., 2006; Wiegand et al., 2007). Strong inter- and intraspecific competition, e.g., tends to even distances between trees resulting in regular patterns, whereas facilitation and seed dispersal mechanisms as well as habitat heterogeneity may lead to clumped patterns (Stoyan and Penttinen, 2000; Wiegand and Moloney, 2004). Random patterns suggest no direct strong influence of any process in shaping spatial interactions (Szwagrzyk and Czerwczak, 1993). Relationships between spatial patterns and biological processes can help to explain the causal mechanisms that facilitate species coexistence (Goreaud and Pélissier, 2003; Wiegand et al., 2007). Since different processes acting separately or simultaneously can create the same pattern, and changes in the intensity of a process can generate different patterns, the fine-scale spatial distributions of trees remain in particular in complex mixed-species forests poorly understood (Condit et al., 2000).

Up to now, spatial point pattern analysis has been scarcely used for assessing forest structure and explaining different ecological processes in silver fir – European beech old-growth forests (Lingua et al., 2011; Garbarino et al., 2012; Janik et al., 2014). In the absence of long-term monitoring data, it can, however, be a very valuable tool to recognize processes that may explain species coexistence and possible spatio-temporal changes in species composition and/or dominance. Patterns of mortality and of living trees in different size strata (e.g. canopy layers) hold information on disturbances and tree species recruitment, and the analysis of spatial relations between trees of the same or other species belonging to the same or another size strata can help to detect mechanisms of inter- and intraspecific competition or facilitation at different stages of development. We assessed the structural patterns of a primeval silver fir-beech forest in the Southern Carpathians (Romania) to obtain deeper insight in the interactions and mechanisms of coexistence of two shade-tolerant species with similar ecological requirements (Ellenberg and Strutt, 2009) and to study the role of beech for forest structure. In particular, we tested the following hypotheses:

- (1) Beech and silver fir have a high ability to coexist and show similar population structures. Due to low ungulate densities, silver fir has an adequate share in regeneration and tree recruits.
- (2) The spatial patterns of the two species differ due to small but significant differences in regeneration ecology, growth rates and shade tolerance during later life stages. As beech saplings are more competitive than fir at higher light levels (i.e. in larger gaps), we expect small beech trees to be clustered at larger scales than fir which might be rather recruited in randomly distributed single-tree gaps.
- (3) The share of beech in species composition influences forest structure, particularly the vertical layering of the forest.

2. Materials and methods

2.1. Study area

The study area is located in the virgin forest Sinca (centred at 45°40'0"N and 25°10'14"E) in the Southern Carpathians, Romania (Fig. 1). In 2003, this forest was classified as virgin forest (Veen et al., 2010), but it is still not protected by law. In 2011, the WWF (World Wide Fund for Nature) Romania, together with the local private forest district (the forest administrator) and the local council of Sinca (the forest owner), prepared the necessary documentation and started the procedure to declare this valuable forest with a surface of 323.7 ha as a nature reserve. Approximately 300 ha will be the core area of the reserve, having a strong virgin character without any signs of human impact.

The present study was carried out on an area of 240 ha, belonging to the *Pulmonario rubrae*-Fagetum Soo (1964) (Tauber, 1987), with variable proportions of beech and silver fir. The climate is temperate continental with a mean annual precipitation of 1000 mm and a mean annual temperature of 4.5 °C. The bedrock consists of crystalline schist and the main soils are cambisols with ample water and nutrient supply. The terrain is characterized by steep slopes between 30–40° and elevations ranging from 850 to 1350 m a.s.l.

The ungulate density reported in the hunting area to which our study site belongs includes 150 roe deer and 50 red deer, i.e. approximately 1.5 animals per 1 km² (hunting association, personal communication). This seems to be low compared to densities of 13 red deer per 1 km² reported from the Dinaric Mountains (Nagel et al., 2015). We thus expect browsing damages to be low as well.

2.2. Field measurements

The 240 ha study area was divided into systematic grid cells of 100 × 100 m. Twenty-one of these cells were randomly selected and a sample plot of 35 × 35 m (1225 m²) was established in the centre of each cell. Within each sample plot, all standing trees with a diameter at breast height (dbh) ≥ 6 cm were stem-mapped using the Field Map Data Collector (IFER, 2013). Their coordinates, dbh, and total height were measured, and the species and vitality attributes (live/dead) recorded. The lying dead wood (thick-end diameter ≥ 15 cm and length ≥ 3 m) was recorded with the species, the diameter at both ends and the total length. For both standing and

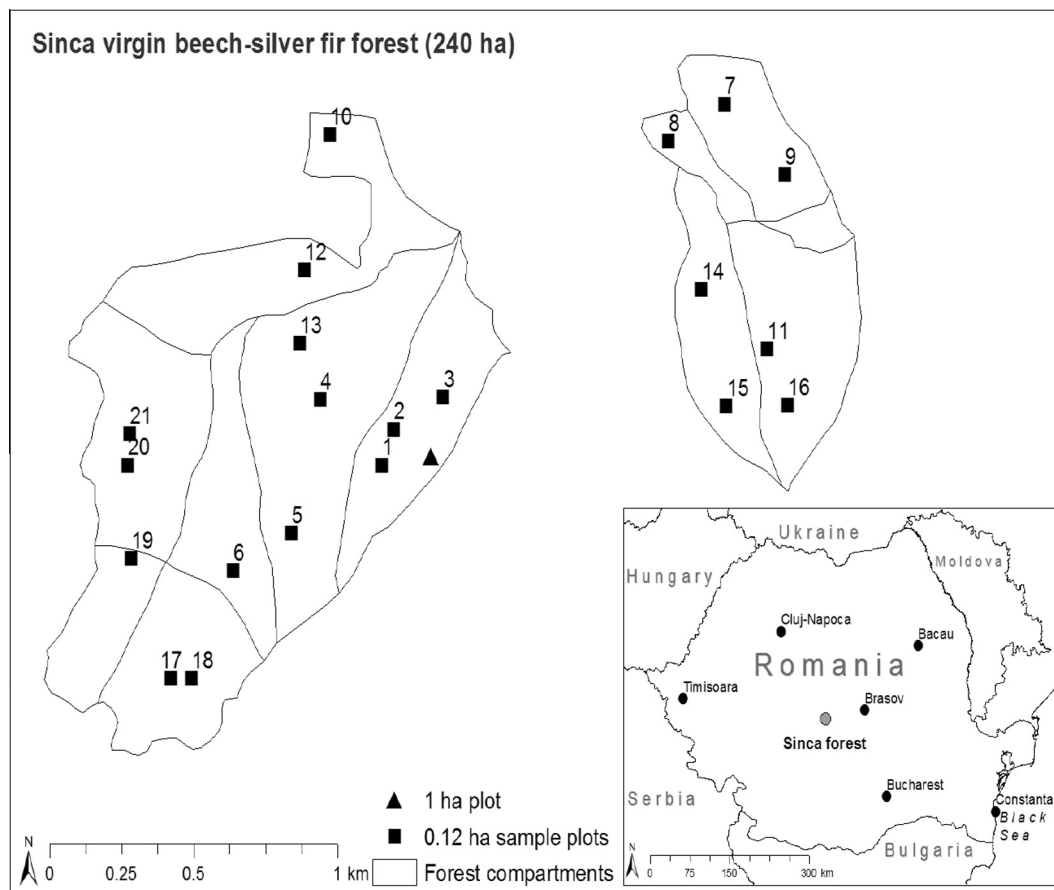


Fig. 1. The location of the Sinca virgin forest in Romania (bottom right) and its core area with the research plot network. The number represents the label of the sampling plots.

lying dead wood, the decay classes were assessed according to Keller (2011) as fresh, hard, rotten, mouldering or mull wood.

Trees belonging to the natural regeneration (all individuals ≥ 10 cm in height and < 6 cm in dbh) were sampled on four regeneration sub-plots, the centres of which were located 12.37 m from each corner on both diagonals of the 35×35 m plot. Each subplot consisted of three concentric regeneration circles (RC): a 5 m^2 circle (RC1) for seedlings between 10 and 39.9 cm in height, a 10 m^2 circle (RC2) for saplings 40 to 129.9 cm in height, and a 20 m^2 circle (RC3) for saplings with a minimum height of 130 cm and a maximum dbh of 5.9 cm. Saplings and seedlings lower than 130 cm height were assessed for ungulate browsing to the leading shoot.

A 1-ha permanent plot established in 2003 was re-measured (species, dbh, height, live/dead, coordinates) in June 2013 in order to provide information on stand dynamics over 10 years. The threshold for the assessment of the trees on this plot was a minimum height of 1.5 m.

2.3. Data analysis

The volume of living trees and standing dead wood was determined applying a double-logarithmic regression: $\log(\text{volume}) = a_0 + a_1 \times \log(\text{dbh}) + a_2 \times \log(\text{height}) + a_3 \times \log(\text{dbh})^2 + a_4 \times \log(\text{height})^2$, where a_0, a_1, a_2, a_3, a_4 are species-specific regression coefficients (Giurgiu and Draghiciu, 2004). The volume of lying dead wood was estimated using the formula for the volume of a truncated cone, considering only the portion lying within the plot boundaries.

The trees were classified into three canopy layers: overstorey trees taller than 2/3 of the top height, midstorey trees with height between 1/3 and 2/3 of the top height, and understorey trees shorter than 1/3 of the top height. The top height was defined as the average height of the 20% largest trees in the stand (Kramer and Akça, 1995) and was calculated for each plot separately. The data of the 21 plots were pooled to model the dbh-height curves as well as the diameter distributions for each species. The dbh-height relationships of beech and fir were fitted best with the equation of Prodan (1951). To describe the relationship between dbh and crown diameter we used the crown projection data recorded in 2003 on the one hectare plot. Two crown diameters (in N–S and W–E orientation) were measured. We tested the shape of diameter distributions according to the method described by Janowiak et al. (2008) and Alessandrini et al. (2011). All statistical analyses were performed using Statistica 12 (StatSoft, Inc., 2013).

Tree-to-tree and species interactions were investigated with point pattern analysis. We used the pair-correlation function $g(r)$, a function which is derived from Ripley's function $K(r)$ (Ripley, 1976) and widely applied in the current ecological research (Getzin et al., 2006; Martinez et al., 2010; Janik et al., 2014). The pair-correlation function is a distance-dependent correlation function, which, based on point-to-point distances, describes the clumping and regularity of the point (e.g. tree) distribution (univariate pair-correlation function $g11(r)$) or the attraction (positive association) and repulsion (negative association) (bivariate pair-correlation function $g12(r)$) between individuals of two populations (e.g. beech and fir) at a given distance r . It is defined as the expected density of points with a specific characteristic (e.g. "beech", called pattern 1) within a ring with width Δr at a given radius r from an arbitrary set of points with the same characteristic (univariate pair-correlation function $g11(r)$) or different characteristic (e.g. "fir", pattern 2) respectively (bivariate pair-correlation function $g12(r)$), divided by the effective density of the points of interest within a ring with width Δr at the distance r from points with the same (respectively different) characteristic (Stoyan and Stoyan, 1994; Wiegand and Moloney, 2004). By replacing the circles used in Ripley's K function with rings, the pair-correlation

function can isolate specific distance classes of interest for various ecological processes (Wiegand and Moloney, 2004) and allows direct interpretation due to its character as probability density function similarly to a neighbourhood density function (Stoyan and Penttinen, 2000; Wiegand and Moloney, 2004).

We used the univariate pair-correlation function $g11(r)$ with complete spatial randomness (CSR) (homogeneous Poisson process – no variation in tree density over an area) as null model to analyse and compare the horizontal distribution patterns (random, aggregated or regular) of tree populations of different species (beech and silver fir) and in various canopy layers (over-, mid-, and understorey), and to determine the spatial scales (distance ranges) at which possible deviations from a random distribution occurred.

To investigate whether the tree mortality is a random process (the random mortality hypothesis) we applied the univariate pair-correlation function $g11(r)$ with the random labelling null model, which is the appropriate null hypothesis for a posterior event such as the death of trees (Goreaud and Pélissier, 2003; Wiegand and Moloney, 2004). The simulated patterns of dead trees is generated from the dataset (the joined pattern of dead and live trees) by keeping the point locations fixed and permutating the marks (e.g. dead label) randomly. Due to the low number of dead trees in some of the plots, we performed the spatial pattern analysis only in 18 plots, considering all dead trees within each plot, irrespective of the species. The same null model, but with the bivariate pair-correlation function $g12(r)$ was used to analyse the spatial relationship between dead canopy trees belonging to the over- or midstorey and living trees of each species in the understorey (also trees < 6 cm dbh). We decided to use only the data of the 1-ha permanent plot for this more detailed investigation, as hardly any of the small plots had a sufficient number of dead trees in the upper height strata, while 25 dead trees in the 1-ha plot belonged to the overstorey and midstorey strata.

We used the bivariate pair-correlation function $g12(r)$ applying the toroidal shift null model (spatial independence of the distribution patterns of two populations) (Wiegand and Moloney, 2004) to assess the spatial associations between beech and fir (possible indication to inter-specific competition), and between tree populations in different canopy layers of the same species (intra-specific competition) or the other species (inter-specific competition).

For these analyses, 95% simulation envelopes were calculated from the 2.5th-lowest and 2.5th-highest value of the 99 Monte Carlo simulations of the null model. We used also a goodness-of-fit test (GoF, Diggle, 2003) to verify the occurrence of the type I error (Loosmore and Ford, 2006). A distribution is classified as clumped, random or regular in the univariate analysis, when the value is located above, within or below the 95% confidence intervals, respectively. Similarly for bivariate analyses, two populations are significantly positively correlated (attraction), spatially independent or significantly negatively correlated (repulsion), when the value is located above, within or below the 95% confidence intervals, respectively.

The analyses were performed for r varying from 1 to 15 m (with 1 m lag distance), not exceeding half the length of the 35×35 m plots, to limit the influence of the margin effects. Similarly, the analyses using the data of the 1-ha permanent plot were performed for distances up to 45 m (less than half the length of the 100 m plot side).

All univariate and bivariate point pattern analyses were performed using the grid-based software Programita (Wiegand and Moloney, 2004). Results of the 21 plots were pooled in one average graphic function, using the 'combine replicates tool' included in the Programita software (Wiegand and Moloney, 2004), to get information about the average spatial pattern of this forest. For this reason, the spatial analyses were conducted considering the 21 plots as pseudo-replications.

3. Results

3.1. Structural characteristics

The average density of living trees ≥ 6 cm dbh was $555.8 \pm 31.8 \text{ ha}^{-1}$ (mean \pm SE), the basal area $57.6 \pm 1.8 \text{ m}^2 \text{ ha}^{-1}$ and the growing stock $917.9 \pm 39.6 \text{ m}^3 \text{ ha}^{-1}$ (Table 1). The beech-silver fir forest was dominated by beech accounting for 63.6% of the growing stock, 58.3% of the basal area and 53.7% of the stem number. The proportion of beech in basal area (PBBA) varied from 24.8% to 95.2% (coefficient of variation: 33.2%). Other species, namely *Acer pseudoplatanus* and *Carpinus betulus*, were found with very few individuals in only one of the plots.

36% of all trees belonged to the overstorey and understorey respectively, and 27% to the midstorey. The share of trees in the different canopy layers varied with species: while a higher percentage of beech belonged to the overstorey (42%) than to the understorey (31%), the opposite was found for silver fir with 29% of trees belonging to the overstorey and 45% to the understorey. The representation in the midstorey was the same for both species. Overstorey trees accounted for more than 91% of the growing stock. The number of large trees (dbh > 80 cm) per hectare was 15 ± 2.5 (mean \pm standard error) for beech and 12 ± 3.1 for silver fir. The largest beech had a dbh of 113 cm and the largest silver fir a dbh of 123.5 cm; the tallest tree measured was a silver fir with 51.6 m, the tallest beech had a height of 45 m. The number of such tall trees, however, was rather rare. The average top height (mean height of the 20% largest trees per plot) was 35.4 ± 0.87 m (mean \pm standard error).

Beech is taller than fir in the small diameter classes (< 45 cm dbh), whereas it is the opposite in the intermediate and large diameter classes (Fig. 2a). The difference in crown diameter between the two species increased with dbh (e.g. the crown diameter of a beech with 80 cm dbh is 13 m compared to 8 m of a silver fir with the same dbh) (Fig. 2b).

The pooled (21 plots, total area 2.57 ha) cumulative (beech and silver fir together) dbh distributions and the species-specific dbh distributions showed a rotated sigmoidal form (Fig. 3). We found in beech dominated plots with $> 75\%$ PBBA (4 plots with a total area of 0.49 ha), a significantly higher density of fir than of beech in the dbh classes ≤ 18 cm, whereas in silver fir dominated plots with PBBA $< 40\%$ (4 plots with a total area of 0.49 ha) the density of beech was higher in the low diameter classes (Fig. 3).

The dead-to-live wood ratio was on average 15%. The deadwood volume on the 21 plots ($134.9 \pm 18.8 \text{ m}^3 \text{ ha}^{-1}$) consisted of two-thirds silver fir (Table 2). Lying deadwood made up 69% of the total deadwood volume. The average density of snags was $59.1 \text{ trees ha}^{-1}$, with more than twice dead silver fir

(40.8 trees ha^{-1}) than beech (18.3 trees ha^{-1}). The proportion of 'fresh' and 'hard' deadwood together was 17% of the total deadwood volume, whereas the highest amount of dead wood was in the most advanced decay stages such as 'mouldering' (27%) and 'mull wood' (31%).

The amount of deadwood was negatively correlated with PBBA (Fig. 4a). There was no significant relation, however, between the volume of living trees in different canopy layers and PBBA nor between the stand basal area and PBBA (Fig. 4b and c).

The regeneration (4476.2 ± 1073.3 saplings per ha) consisted of 87% beech. The proportion of silver fir was lower in the height class 10–39.9 cm (10%) than in the saplings ≥ 40 cm (17%) (Table 3). The density of beech regeneration over all height classes and for each height class decreased significantly with increasing terrain slope compared to silver fir that was not sensitive to slope steepness. Altitude was not correlated with the regeneration density of both species. A similar pattern was also found for aspect, except in the height class 10–39.9 cm for beech where the regeneration density was significantly higher on north-facing sites (2417 saplings per ha) compared to south- and east-facing sites (approx. 250 saplings per ha). Browsing damage to the leading shoot recorded on < 130 cm high saplings was rare but two times higher for silver fir (3.6%) than for beech (1.6%). The density of beech regeneration ≥ 40 cm height decreased significantly with increasing canopy closure (% of canopy opening visually estimated above each regeneration subplot, data not shown), whereas the regeneration density of silver fir was not correlated with canopy closure.

3.2. Development on the one-hectare monitoring plot

The basal area on the 1-ha plot was with $53.3 \text{ m}^2 \text{ ha}^{-1}$ slightly lower, and the mean dbh (33.1 cm) and mean height (20.9 m) were slightly higher than on average of the forest (data of 2013). The dominant species was beech, with a basal area of $37.7 \text{ m}^2 \text{ ha}^{-1}$ (71%), a mean dbh of 48.6 cm and a mean height of 28.9 m, while the mean dbh of silver fir was 22.9 cm and the mean height 15.7 m (all values calculated only for trees with a dbh ≥ 6 cm, to be directly comparable with the average data of the 21 sample plots). Beech dominated the large diameter classes, while silver fir showed higher tree densities in dbh classes up to approx. 40 cm (Fig. 5).

The forest structure remained quite stable between the two inventories. The overall changes were less than 1% in the total number of trees and less than 5% in basal area. The 10-year mortality rate from 2003 to 2013 was 7.2% (or 5.4% of basal area). It was higher in silver fir (9.3%) than in beech (4.2%), but only with regard to the number of trees. Mortality in percentage of basal area was similar for both species (5.7% and 5.2%, respectively). The

Table 1
Characteristics of the Sinca virgin beech-silver fir forest within the survey area of 240 ha, differentiated by canopy layers (overstorey, midstorey and understorey) (mean \pm standard error). 21 sample plots with each covering 1225 m^2 .

		Stem density (N ha^{-1})	Basal area ($\text{m}^2 \text{ ha}^{-1}$)	Growing stock ($\text{m}^3 \text{ ha}^{-1}$)	Dbh (cm)	Tree height (m)
Overstorey	Beech	126.7 ± 18.6	30.5 ± 2.7	558.9 ± 55.7	56.8 ± 2.1	32.6 ± 0.8
	Silver fir	73.1 ± 11.2	19.8 ± 2.8	299.8 ± 46.0	57.7 ± 3.1	33.9 ± 1.1
	Total	200.9 ± 22.4	50.5 ± 1.7	861.1 ± 38.7	57.3 ± 2.2	33.3 ± 4.1
Midstorey	Beech	78.9 ± 15.1	2.3 ± 0.4	21.8 ± 4.5	19.1 ± 1.1	16.7 ± 0.6
	Silver fir	67.2 ± 12.0	2.8 ± 0.4	25.7 ± 4.2	23.2 ± 1.2	16.9 ± 0.6
	Total	147.3 ± 17.2	5.3 ± 0.4	48.4 ± 4.2	21.5 ± 1.1	17.0 ± 0.5
Understorey	Beech	92.9 ± 19.5	0.8 ± 0.2	3.1 ± 0.7	8.7 ± 0.3	8.7 ± 0.2
	Silver fir	114.3 ± 18.0	1.1 ± 0.2	5.2 ± 0.9	10.9 ± 0.5	7.7 ± 0.3
	Total	207.6 ± 18.9	1.9 ± 0.2	8.4 ± 0.9	10.0 ± 0.3	8.2 ± 0.2
All height strata	Beech	298.5 ± 28.2	33.6 ± 2.6	583.8 ± 55.27	32.0 ± 2.3	21.2 ± 1.1
	Silver fir	254.6 ± 23.6	23.7 ± 2.8	330.8 ± 46.8	29.5 ± 3.1	18.6 ± 1.6
	Total	555.8 ± 31.8	57.6 ± 1.8	917.9 ± 39.6	28.6 ± 0.9	19.0 ± 0.5

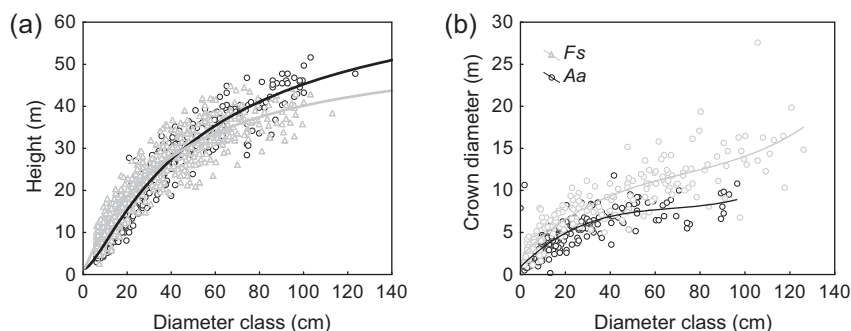


Fig. 2. (a) Dbh-height relationship of European beech (*Fs*) and silver fir (*Aa*), fitted with the equation of [Prodan \(1951\)](#) ($N_{Fs} = 760$; $R^2 = 0.92$, $N_{Aa} = 654$; $R^2 = 0.95$). (b) Dbh-crown diameter relationship of beech and fir ($N_{Fs} = 214$; $R^2 = 0.87$, $N_{Aa} = 328$; $R^2 = 0.80$; polynomial equation of order 3).

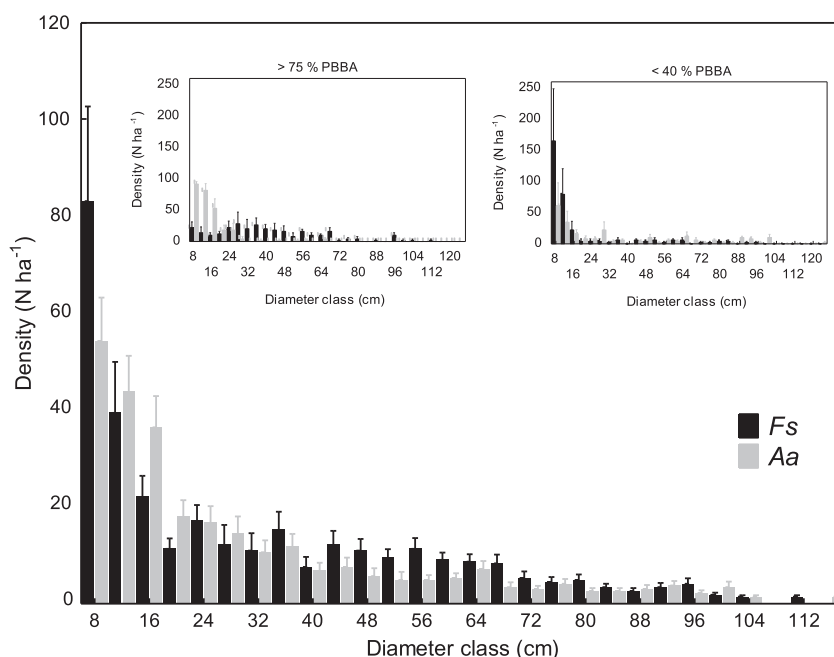


Fig. 3. Species-specific diameter distribution of all 21 plots (2.57 ha) (central graph), of the beech dominated plots (0.49 ha) (top left graph, PBBA > 75%, 4 plots) and of the silver fir dominated plots (0.49 ha) (top right graph, PBBA < 40%, 4 plots). Error bars show the standard error. 4 cm diameter classes. *Fs* = *Fagus sylvatica* and *Aa* = *Abies alba*.

species-specific dbh distributions of 2003 and 2013 ([Fig. 5](#)), however, revealed different development tendencies for the two species: (i) a slight increase of beech trees in the smallest dbh class and a decrease in large beech trees (around 95–115 cm dbh); (ii) a decrease in small silver fir up to 20 cm dbh.

3.3. Spatial patterns

The spatial distributions of the living silver fir and beech trees (≥ 6 cm dbh) were mainly random, with significant clustering at distances of 3 and 8 m for fir and 7 to 8 m for beech. This clustering was due to the understorey trees, which were clumped between 1 and 8 m for beech and 2 and 8 m for silver fir ($p < 0.01$) ([Fig. 6](#)). The overstorey beech trees were regularly distributed ($p < 0.01$) at short distances (0–3 m; [Fig. 6](#)) and randomly at distances > 3 m, whereas silver fir overstorey trees were randomly distributed at all distances. Trees in the middle layer showed a random spatial distribution over all distances.

A negative spatial relation was found between overstorey beech and overstorey silver fir from 1 to 3.5 m ($p < 0.01$; [Fig. 6](#)), while no interaction was found between understorey beech trees and understorey fir trees. The understorey beech trees were negatively

associated with overstorey beech trees up to 2.5 m ($p < 0.01$) ([Fig. 7](#)) but not with overstorey silver fir. No negative interaction was found between overstorey beech and understorey fir, and between overstorey fir and understorey beech or fir.

Dead trees were randomly distributed (data not shown). On the one-hectare monitoring plot, however, dead trees belonging to the over- and midstorey strata were negatively associated ($p < 0.01$) to living understorey beech trees at short to medium distances (1–8 m). This was especially the case for beech < 6 cm dbh, while it was less pronounced for understorey beech ≥ 6 cm dbh. Nevertheless, the negative spatial relation between dead trees and living understorey beech ≥ 6 cm dbh was still visible at short (1–3 m) and at medium distances (5–10 m, [Appendix A1](#)). In contrast, living understorey silver fir trees with a dbh ≥ 6 were randomly distributed around the dead over- and midstorey trees. However, a significant ($p < 0.05$) negative spatial relationship was found up to 6 m between the dead over- and midstorey trees and living fir < 6 cm dbh.

The trees which reached the threshold of 1.5 m height between 2003 and 2013 (recruits) were significantly clumped at short distances (0–4 m, $p < 0.01$; [Appendix A2](#)), whereas the trees which died between the two inventories were clustered at distances from

Table 2

Deadwood volume (total, lying and standing dead wood) and number of snags per species (mean \pm standard error, minimum–maximum).

		Beech	Silver fir	Total
Volume ($\text{m}^3 \text{ha}^{-1}$)	Total deadwood	44.1 \pm 8.7	90.8 \pm 15.7	134.9 \pm 18.8
		0.2–110.0	0–250.8	1.7–292.2
	Lying deadwood	31.9 \pm 7.0	61.7 \pm 12.2	93.6 \pm 14.5
		0–98.4	0–161.2	1.0–209.3
Snag density (N ha^{-1})	Standing trees	18.3 \pm 3.1	40.8 \pm 5.9	59.1 \pm 7.9
		0–57.1	0–89.9	0–146.9
Deadwood volume by decay classes ($\text{m}^3 \text{ha}^{-1}$)	Fresh deadwood	0.3 \pm 0.2	0.6 \pm 0.3	0.9 \pm 0.5
	Hard deadwood	8.1 \pm 3.4	13.9 \pm 4.7	21.9 \pm 5.7
	Rotten deadwood	12.0 \pm 4.1	22.2 \pm 6.6	34.2 \pm 8.7
	Mouldering deadwood	13.7 \pm 5.4	23.1 \pm 5.5	36.8 \pm 7.0
	Mull wood	10.0 \pm 3.8	31.1 \pm 8.8	41.7 \pm 9.1
	Not specified	–	–	0.5 \pm 0.4

8 to 11.5 m. No significant spatial relationship was found between the recruits (2003–2013) and the over- and midstorey trees, which were already dead in 2003.

4. Discussion

4.1. Structural characteristics of the Sinca forest

The findings of our study suggest a high stability and resilience of the Sinca primeval fir–beech forest on the one hand but a possible change in species composition on the other hand. The rotated sigmoid (RS) form of the overall diameter distribution (21 plots, total area 2.57 ha, fir and beech together) as well as of the cumulative diameter distribution on the 1-ha plot underline the old-growth character and structure enhancing resilience of the studied forest (Goff and West, 1975; Westphal et al., 2006; Alessandrini et al., 2011). According to Diaci et al. (2011), the RS shape is typical for forests composed of shade tolerant beech and silver fir, which are mainly subject to low to moderate severity disturbances (Splechtna et al., 2005; Paluch, 2007; Šamonil et al.,

2009) and for which a U-shaped mortality model (Goff and West, 1975) can be anticipated. The fact that not only the cumulative but also the species-specific dbh distributions of beech and fir were of RS shape, may indicate that both species show a more or less balanced demographic structure within the studied area of the Sinca old-growth forest. This suggests an overall structural stability, possibly leading to only small temporal fluctuations of stand parameters.

While beech dominated in the living tree population and particularly in the overstorey (64%), silver fir contributed two-thirds to the total deadwood amount. This share was more or less stable across decay classes (varying between 63% and 75%) and only slightly higher in standing than in lying deadwood. Possible differences in decay rates of beech and fir may have influenced the deadwood ratio between the two species. Analyses of beech and silver fir stumps in the central Apennines (Italy) suggested that both species have similar decay rates (Lombardi et al., 2013), but these are influenced by many factors such as the agent of tree mortality and the size and position (in particular soil contact) of the snag or log. Beech trees, which die naturally, are often affected by tinder fungus (*Fomes fomentarius*) prior to death (Müller-Using and Bartsch, 2009), which may accelerate decomposition of beech compared to fir and thus lead to an underrepresentation in the deadwood share. Nevertheless, the high percentage of fir in the deadwood volume may indicate a higher mortality of fir than of beech within the last decades, which is supported by the observed negative correlation of deadwood volume with the percentage of beech in stand basal area. While this corresponds to the observed silver fir decline in several old-growth forests in Central and South-Eastern Europe (Šamonil and Vrška, 2007; Diaci et al., 2010 and 2011; Ficko et al., 2011), the 55% share of silver fir in the understorey suggests fluctuations in the species composition of the Sinca forest rather than a long-term succession towards an even stronger dominance of beech. This is supported by the observation that silver fir dominated the lowest dbh classes in beech dominated plots and vice versa. Korpel' (1995) described the phenomenon of species alternation to be characteristic for silver fir–beech old-growth forests. The tendency of beech and silver fir to replace each other was reported also from old-growth forests in the Dinaric mountains (Klopčič and Bončina, 2011). In a study on gap regeneration and replacement patterns in an old-growth fir–beech forest in Bosnia–Herzegovina, a higher probability for reciprocal than of self-replacement was found at the pole tree stage for both species, although self-replacement was also quite frequent (Nagel et al., 2010). The local dominance of one or the other species, however, could also be a result of former disturbances creating varying light conditions. Beech grows faster than fir particularly at higher light levels (Stancioiu and O'Hara, 2006).

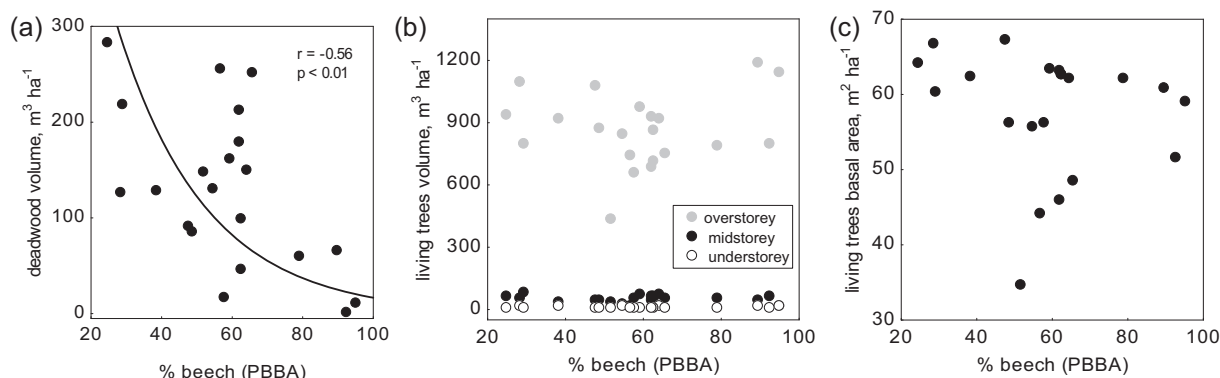


Fig. 4. Relations between deadwood volume (a), living trees volume (b) and living trees basal area (c) and the proportion of beech on basal area (PBBA) on each of the 21 sample plots.

Table 3

Natural regeneration per species and regeneration circle (RC1 – 5 m² for seedlings with height of 10–39.9 cm; RC2 – 10 m² for saplings 40–129.9 cm in height; RC3 – 20 m² for saplings with height >130 cm and dbh <6 cm) (N ha⁻¹ mean ± standard error). Minimum and maximum values (indicated in brackets) correspond to the average of the four regeneration sub-plots per plot.

	RC1 (N ha ⁻¹)	RC2 (N ha ⁻¹)	RC3 (N ha ⁻¹)	Total (N ha ⁻¹)
Beech regeneration	2233.3 ± 651.3 (0–10500)	761.9 ± 292.5 (0–5000)	821.4 ± 330.9 (0–7000)	3916.7 ± 1076.7 (0–17375)
Silver fir regeneration	238.1 ± 88.8 (0–1000)	154.7 ± 70.0 (0–1000)	166.7 ± 51.9 (0–750)	559.0 ± 139.2 (0–2250)
Total regeneration	2471.4 ± 652.1 (0–10500)	916.6 ± 300.9 (0–5000)	988.1 ± 340.8 (0–7125)	4476.2 ± 1073.3 (0–17500)

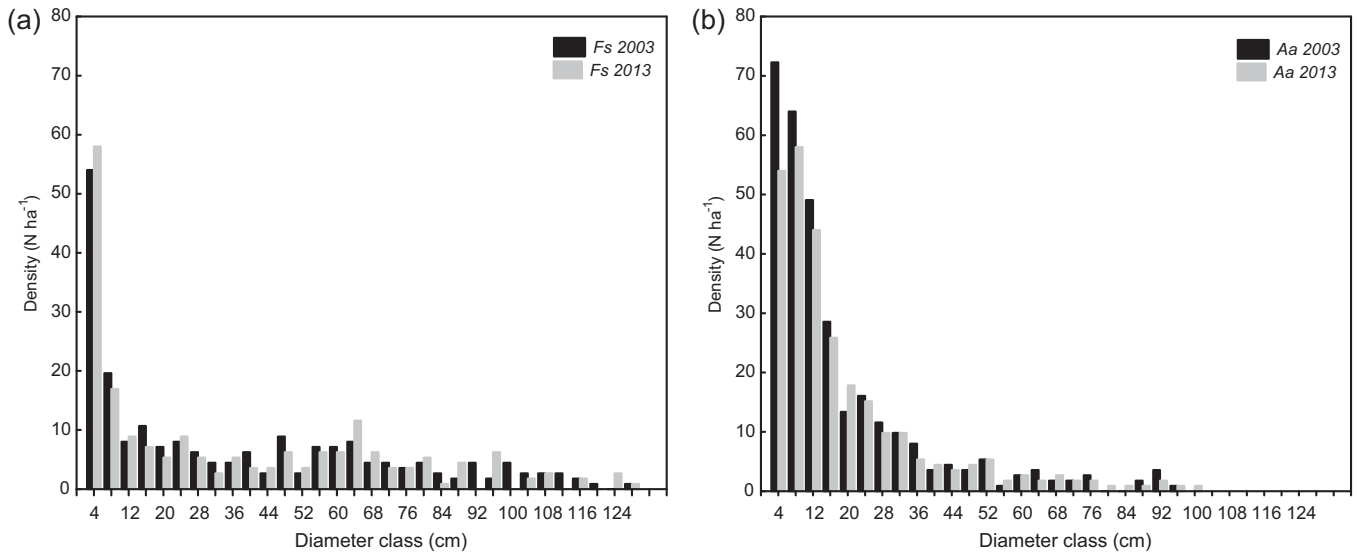


Fig. 5. Dynamics of diameter distribution per species over the last 10 years (2003–2013) on the 1 ha plot. 4 cm dbh classes. (a) *Fs* = *Fagus sylvatica* and (b) *Aa* = *Abies alba*.

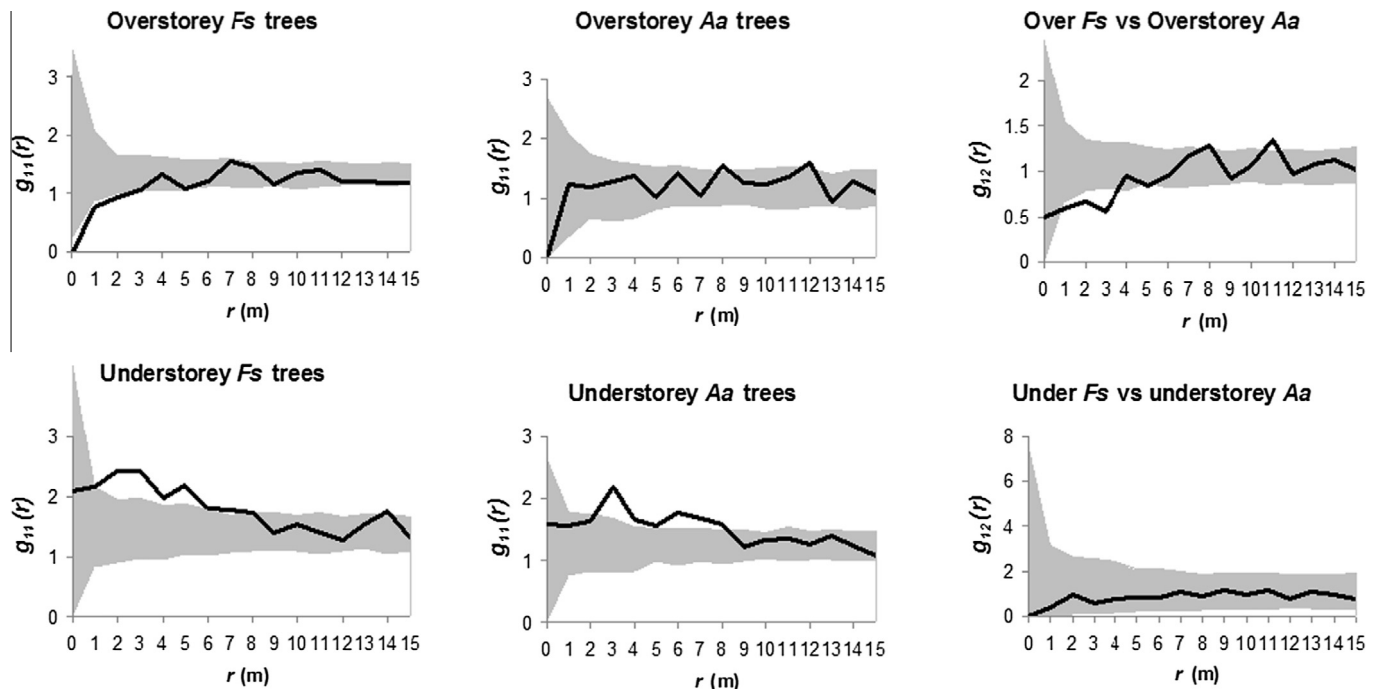


Fig. 6. The spatial patterns of trees belonging to different height layers per species using the univariate pair-correlation function (g_{11}) and the spatial relationship between species in overstorey and understorey using the bivariate pair-correlation function (g_{12}). 21 plots. *Fs* = *Fagus sylvatica* and *Aa* = *Abies alba*.

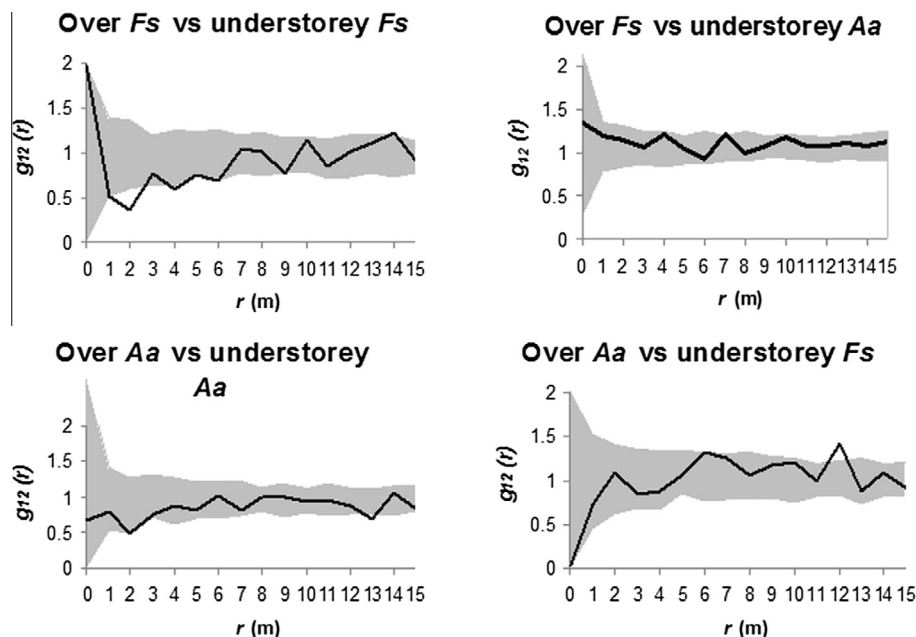


Fig. 7. Spatial relationship between beech and fir trees belonging to different height layers. Bivariate pair-correlation function (g_{12}). 21 plots. *Fs* = *Fagus sylvatica* and *Aa* = *Abies alba*.

Former disturbances of intermediate to high severity may thus have led to a dominance of beech in the upper canopy, while only small-scale, single-tree disturbances over a long period of time may have favoured the recruitment of silver fir, which has the ability to react faster than beech to small-scale disturbances after long periods of suppression (Motta et al., 2011). Analyses of the photosynthetic response of beech and fir to gap size and position in a managed fir-beech forest in Slovenia showed that silver fir has a competitive advantage over beech in small gaps with predominant diffuse light environment and low direct light levels (Čater et al., 2014).

The natural regeneration in the Sinca forest was again dominated by beech (87%) (Table 3). Although fir is much more susceptible to ungulate browsing than beech (Motta, 1996; Senn and Suter, 2003) and studies in other old-growth silver fir-beech forests demonstrated a strong impact on the composition, dynamics and recruitment of tree regeneration over large time periods (Klopčič et al., 2010; Diaci et al., 2011; Nagel et al., 2015), the low density of silver fir regeneration found in our study cannot be attributed to this factor. Compared to mean browsing rates of 21–31% in Slovenian fir-beech forests (Ficko et al., 2011), the average browsing rate found in our study was very low (3.6% for fir and 1.6% for beech). In contrast to areas with high ungulate browsing, where a strong decrease in the share of silver fir with increasing seedling height was observed (Klopčič et al., 2010; Diaci et al., 2011) so that fir was found almost exclusively in the smallest height classes (Nagel et al., 2015), the proportion of silver fir in the Sinca forest increased from 10% in 10–39.9 cm tall saplings to 17% in saplings ≥ 40 cm in height and < 6 cm dbh (Table 3). This indicates a higher shade tolerance of fir than beech during later life stages, which has also been suggested by Nagel et al. (2010, 2014) based on species-by-species replacement patterns in gaps across different tree life stages as well as on tree-ring patterns and life history traits of fir, beech and maple in an old-growth forest in Bosnia-Herzegovina. Whether this possibly higher shade tolerance will give fir a competitive advantage over beech and allow it to gain further ground during its development cycle, will depend on the future disturbance regime. The decrease of beech regeneration

density with increasing terrain slope and the higher density of the 10–39.9 cm tall beech regeneration on north-facing than on south- and east-facing slopes indicate, that site heterogeneity might play a certain role in the regeneration success of beech and fir, although this was not confirmed by the results of the point pattern analysis.

The low average proportion of ‘fresh’ and ‘hard’ deadwood (17% of the total deadwood volume) in the study area and the low mortality rate on the 1-ha plot from 2003 to 2013, which did not surpass a 10-year baseline mortality of 5–10% (Frelich and Lorimer, 1991; Woods, 2004), suggest that intermediate or severe disturbances did not happen in the Sinca forest for at least one decade. The mean dead wood volume recorded in our study ($134.9 \pm 18.8 \text{ m}^3 \text{ ha}^{-1}$, Table 2) is in the lower range of values reported for other European old-growth beech-conifer (silver fir and spruce) forests in particular in the West Carpathians and the Dinaric Alps, which vary strongly between 91 and $420 \text{ m}^3 \text{ ha}^{-1}$ (Saniga and Schütz, 2001; Nagel et al., 2006; Paluch, 2007; Holeksa et al., 2009; Kral et al., 2010; Motta et al., 2011; Kucbel et al., 2012). Also the mean deadwood to live wood ratio was rather low (15%) compared to the average of $36 \pm 21\%$ from 16 long-established (> 50 years ago) montane mixed beech forest reserves (including several primeval fir-(spruce)-beech forests) published by Christensen et al. (2005).

In general, the average forest characteristics of the Sinca forest (stem density, basal area and volume of living trees, deadwood volume), lie in the range of other mixed beech-silver fir old-growth forests located in Central and South-Eastern Europe. The mean basal area and growing stock found were lower than those reported from primeval forests in the Dinaric Alps (Motta et al., 2015; Keren et al., 2014), but higher than of old-growth forests in the West Carpathians (Korpel, 1995; Paluch, 2007; Holeksa et al., 2009). Differences may be due to site conditions, the disturbance regime, the dominant development stage (Korpel, 1995) and the size of the study area (Hobi et al., 2015), methodical differences such as the minimum threshold for assessment or, in the case of the growing stock, the volume tariffs applied, and to possible direct or indirect anthropogenic influence in the past (Vrška et al., 2009). Also an influence of the species composition cannot be ruled out.

The Sinca forest is dominated by beech (58.3% of the total basal area and 63% of the overstorey trees), while in most of the forests with very high basal area and growing stock the percentage of conifers was much higher.

Other than expected, the PBBA, however, did not show any significant influence on the overall basal area within the Sinca forest, and also the vertical structure, expressed in the volume of living trees in different canopy layers, was not influenced by the PBBA (Fig. 4). Many mixed beech-silver fir old-growth forests in Eastern and Southeastern Europe retained a relatively stable growing stock over time (Korpel, 1995; Diaci et al., 2011), while the share of the species present changed. In a recent study about intra- vs. interspecific competition in managed mixed beech-silver fir stands, Río et al. (2014) found that neither fir nor beech basal area growth were significantly influenced by the dominance of the reciprocal species.

4.2. Spatial patterns

The horizontal distribution of trees belonging to different canopy layers support the theory that the Sinca virgin forest was shaped by mainly single-tree disturbances, which are thought to be the principal natural pathway of canopy recruitment in old-growth forests of shade-tolerant species such as beech and fir (Korpel, 1995). We did not find any evidence of recent intermediate severity disturbances, although these cannot be ruled out based on our sampling design. The predominantly random pattern of the dead trees as well as of the living trees in the upper and middle canopy storey, and the clustered distribution of living understorey trees at distances of 1–8 m indicate a disturbance regime dominated by randomly distributed small-scale events, such as the death of individual trees or groups of few trees due to pathogens, insects, herbivores, or windthrow, or from unknown genetic differences. This is in line with results of Szwagrzyk and Czerwczak (1993) who analysed the spatial patterns of trees in virgin forests of the Western Carpathians.

While the overstorey fir trees were randomly distributed over all distances, the overstorey beech trees showed a regular distribution at distances up to 3 m (Fig. 6). This suggests an intense intraspecific competition between canopy beech trees growing close to each other, also known as density-dependent mortality (e.g. Busing, 1991). Kenkel (1988) showed that surviving trees had a post-mortality pattern, which was more regular than expected under random natural-thinning: the density-dependent self-thinning caused by depletion of resources leads to a shift from random to regular pattern (Getzin et al., 2006). The random distribution of silver fir overstorey trees over all distances may be explained by their smaller crown radii compared to beech and the different crown shape, which allow them to grow closer together.

The significantly clumped occurrence of understorey trees found at short and medium distances (1–8 m; Fig. 6) agrees with the gap dynamics paradigm (Runkle, 1982), suggesting that young trees are recruited in gaps created by the death of canopy trees. The maximum distance for which clustering of understorey trees was observed corresponds with the most frequent gap sizes (up to 200 m²) found in beech dominated forests (Kuchel et al., 2010; Hobi et al., 2015), although larger gap sizes of one to several thousand m² were also recorded in fir-beech old-growth forests (Splechna et al., 2005; Nagel and Diaci, 2006; Firm et al., 2009). Other than expected, the scales at which clustering occurred did not differ between beech and silver fir. Other factors than gap size might also play a role in the spatial distribution of the understorey trees. Paluch (2005) suggested that the aggregated distribution of silver fir understorey found in the Western Carpathian mountains is more likely linked to edaphic heterogeneity than to light

availability, and also Getzin et al. (2006, 2008) explained the aggregation of understorey trees with habitat heterogeneity. Moreover, the limited seed dispersal (Grubb, 1977; Harms et al., 2001) caused by gravity, predation and dispersal by animals or by vertical stand structure (i.e. in closed stands dispersal of fir seeds by wind is reduced), could determine the spatial distribution of seedlings. Seed rain patterns, however, are only partly responsible for recruitment dynamics (Sagnard et al., 2007). The fact that no spatial interaction (neither negative nor positive correlation) was found between understorey beech and understorey silver fir trees suggests that even if seed dispersal may have been predominantly within the crown projection area of the parental trees (Petritan et al., 2014), other factors influencing the survival of the seedlings (e.g. small-scale disturbance and competition) finally led to a random intermingling of the two species at a stage ≥ 6 cm dbh.

We found a negative interaction between overstorey beech and understorey beech trees at short distances but not between overstorey fir and understorey beech (Fig. 7). This might indicate a greater intraspecific than interspecific competition, which is thought to be one of the possible conditions for stable coexistence (Silvertown, 2004). The spatial segregation between juvenile and mature beech can be due to the dependence of the juvenile trees on light availability (Rozas, 2003). Under a denser canopy layer dominated by beech, even shade tolerant beech seedlings showed higher mortality rate due to lower light levels and temperatures than in small to medium sized gaps (Szwagrzyk et al., 2001). Understorey fir trees did not show any segregation with overstorey trees of either beech or fir. This is in line with earlier studies by Stancioiu and O'Hara (2006) and Schütz (2001) who found a higher capacity of silver fir to tolerate lower light levels and to optimally use the canopy space through vertical arrangement.

We did not find any aggregation of understorey trees (neither for trees ≥ 1.5 m in height and < 6 cm dbh nor for trees ≥ 6 cm dbh but smaller than 1/3 of top height) around dead canopy trees (overstorey and midstorey) within the 1-ha plot (Appendix A1), although the death of trees enhances light availability. On the contrary, a significant segregation of dead canopy trees with small understorey trees (beech and fir ≥ 1.5 m height and < 6 cm dbh) up to a distance of 5–10 m was observed (Appendix A1). This might be explained by the growth vigour of beech, which is dominating the canopy in the 1-ha plot: Small canopy gaps might be filled within few years either by lateral crown expansion (Splechna et al., 2005; Collet et al., 2011) or by accelerated height growth of formerly suppressed trees (Poulson and Platt, 1996; Firm et al., 2009). Findings of Nagel et al. (2010) in an old-growth fir-beech forest in the Dinaric Mountains indicated that the gap-filling process is mainly controlled by advance regeneration rather than by post-treefall establishment of seedlings. Thus, mainly larger trees may profit most from the death of a canopy tree and hinder the survival or growth of small saplings.

Overall, the spatial patterns found only slightly differ between beech and fir and support a random spatial intermingling of the two species at least at later life stages. This suggests that the coexistence of beech and fir is determined by other factors than small-scale site heterogeneity.

5. Conclusions

The findings of this first study on the structure and dynamics of a primeval fir-beech forest at the eastern limit of the natural silver fir-beech vegetation zone indicate structural stability of the forest at least under the present disturbance regime (i.e. of the last few decades), although gradual changes in species composition are possible. In contrast to our hypothesis, the regeneration density of silver fir was much lower than of beech, although ungulate

browsing was negligible. The overrepresentation of silver fir in the understorey ≥ 6 cm dbh and the observed species alternation in plots, where the canopy layer was strongly dominated by either fir or beech (i.e. beech had much higher densities in the low dbh classes in plots dominated by fir and vice versa) let us conclude that this will lead to temporal fluctuations rather than to a long-term shift in species composition.

The spatial distribution patterns of the living and dead trees suggest a disturbance regime dominated by randomly distributed small-scale events. We did not find any evidence of recent intermediate or large-scale disturbances, but, based on our sampling design, we cannot fully exclude that such events may have left traces outside the studied plots. Although the general spatial patterns of beech and fir were similar, they revealed some species-specific differences, namely (i) a regular distribution pattern of overstorey beech trees at distances up to 3 m compared to a random distribution of overstorey silver fir over all distances, and (ii) a negative interaction between understorey and overstorey beech trees at small distances, while no significant relation between understorey fir and overstorey beech or fir was observed. Both findings indicate a higher intraspecific competition of beech than of fir on the one hand, and a higher shade tolerance of fir at least in later stages of development on the other hand. We suggest that these may be the most determining factors for the coexistence of the two species. Long-term studies and retrospective analyses of tree growth patterns are needed, however, to verify this hypothesis and to gain a deeper insight into the complex mechanisms of species coexistence.

Unlike our expectations, the PBBA did not influence the general characteristics of the living trees nor its vertical layering shown in the distribution of volume to different canopy layers. Our findings suggest that forest managers have the liberty to vary the share of beech in species composition of fir–beech forests without influencing the overall forest structure or productivity too much.

Acknowledgments

This work was supported by a Swiss Research Fellowship (Sciex-NMSch, Project 12.091 – MODIST). We are grateful to Lucian Toiu and Nicu Tudose for their help collecting the field data. We appreciate the permission and logistic support given by Sorin Urdea, manager of the “Padurile Sincii” Forest District, to conduct the study in the Reserve. We are grateful for constructive comments and suggestions of the two anonymous reviewers, which were really helpful to improve the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.07.015>.

References

- Alessandrini, A., Biondi, F., Di Filippo, A., Ziaco, E., Piovesan, G., 2011. Tree size distribution at increasing spatial scales converges to the rotated sigmoid curve in two old-growth beech stands of the Italian Apennines. *For. Ecol. Manage.* 262, 1950–1962.
- Busing, R.T., 1991. A spatial model of forest dynamics. *Vegetatio* 92, 167–179.
- Cater, M., Diaci, J., Rozenbergar, D., 2014. Gap size and position influence variable response of *Fagus sylvatica* L. and *Abies alba* Mill. *For. Ecol. Manage.* 325, 128–135.
- Chen, J., Song, B., Moeur, M., Rudnicki, M., Bible, K., Shaw, D.C., Braun, D.M., Franklin, J.F., 2004. Spatial relationships of production and species distribution in an old-growth Pseudotsuga–Tsuga forest. *For. Sci.* 50, 364–375.
- Christensen, M., Hahn, K., Mountford, E.P., Odor, P., Standovar, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., Vrska, T., 2005. Dead wood in European beech (*Fagus sylvatica*) forest reserves. *For. Ecol. Manage.* 210, 267–282.
- Collet, C., Fournier, M., Ningre, F., Hounzandji, A.P.-I., Constant, T., 2011. Growth and posture control strategies in *Fagus sylvatica* and *Acer pseudoplatanus* saplings in response to canopy disturbance. *Ann. Bot.* 107, 1345–1353.
- Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Itoh, A., LaFrankie, J.V., Lee, H.S., Losos, E., Manokaran, N., Sukumar, R., Yamakura, T., 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288, 1414–1418.
- Diaci, J., Rozenbergar, D., Boncina, A., 2010. Stand dynamics of Dinaric old-growth forest in Slovenia: are indirect human influences relevant? *Plant Biosyst.* 144, 194–201.
- 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.
- Diggle, P.J., 2003. *Statistical Analysis of Spatial Point Patterns*, second ed. Edward Arnold, London.
- Dittmar, O., 1990. Untersuchungen im Buchen-Plenterwald Keula. Ein Vergleich zwischen dem Buchen-Plenterwald Keula und dem gleichaltrigen Buchenhochwald anhand langfristiger Versuchsflächen. *Forst und Holz* 45, 419–423.
- Dittmar, O., 1992. Vorteile und Nachteile der langfristigen einzelstammweisen Nutzung in den Buchen-wäldern Nordwest-Thüringens. *Schweiz. Z. Forstwes.* 143, 431–441.
- Ellenberg, H., Strutt, G.K., 2009. *Vegetation Ecology of Central Europe*. Cambridge University Press, Cambridge, UK.
- Ficko, A., Poljanec, A., Boncina, A., 2011. Do changes in spatial distribution, structure and abundance of silver fir (*Abies alba* Mill.) indicate its decline? *For. Ecol. Manage.* 261, 844–854.
- Firm, D., Nagel, T.A., Diaci, J., 2009. Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. *For. Ecol. Manage.* 257, 1893–1901.
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A., Thornburgh, D., Berg, D.R., Lindenmayer, D., Harmon, M., Keeton, W., Shaw, D.C., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* 155, 309–423.
- Frelich, L., Lorimer, C., 1991. Natural disturbance regimes in Hemlock hardwood forests of the upper Great-Lakes region. *Ecol. Monogr.* 61, 145–164.
- Garbarino, M., Mondino, E.B., Lingua, E., Nagel, T.A., Dukic, V., Govedar, Z., Motta, R., 2012. Gap disturbances and regeneration patterns in a Bosnian old-growth forest: a multispectral remote sensing and ground-based approach. *Ann. For. Sci.* 69, 617–625.
- Getzin, S., Dean, C., He, F., Trofymow, J., Wiegand, K., Wiegand, T., 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography* 29, 671–682.
- Getzin, S., Wiegand, T., Wiegand, K., He, F., 2008. Heterogeneity influences spatial patterns and demographics in forest stands. *J. Ecol.* 96, 807–820.
- Giurgiu, V., Draghiciu, D., 2004. *Modele matematico-auxologice si tabele de productie pentru, arborete*. ed. Ceres, Bucuresti (in Romanian).
- Goff, F.G., West, D., 1975. Canopy-understorey interaction effects on forest population structure. *For. Sci.* 21, 98–108.
- Goreau, F., Pélissier, R., 2003. Avoiding misinterpretation of biotic interactions with the intertype-function: population independence vs. random labelling hypothesis. *J. Veg. Sci.* 14, 681–692.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52, 107–145.
- 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. *J. Ecol.* 89, 947–959.
- Hobi, M.L., Commarmot, B., Bugmann, H., 2015. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *J. Veg. Sci.* 26, 323–336.
- Holeksa, J., Saniga, M., Szwarzgryk, J., Czerniak, M., Staszynska, K., Kapusta, P., 2009. A giant tree stand in the West Carpathians – an exception or a relic of formerly widespread mountain European forests? *For. Ecol. Manage.* 257, 1577–1585.
- IFER, 2013. Field-map – tool designed for computer aided field data collection (WWW Document). <<http://fieldmap.cz/>> (accessed 07.11.13).
- Janik, D., Adam, D., Hort, L., Kral, K., Samonil, P., Unar, P., Vrska, T., 2014. Tree spatial patterns of *Abies alba* and *Fagus sylvatica* in the Western Carpathians over 30 years. *Eur. J. For. Res.* 133, 1015–1028.
- Janowiak, M.K., Nagel, L.M., Webster, C.R., 2008. Spatial scale and stand structure in northern hardwood forests: implications for quantifying diameter distributions. *For. Sci.* 54, 497–506.
- Keller, M. (Ed.), 2011. *Swiss National Forest Inventory. Manual of the Field Survey 2004–2007*. Swiss Federal Research Institute WSL, Birmensdorf, CH.
- Kenkel, N.C., 1988. Pattern of self-thinning in jack-pine – testing the random mortality hypothesis. *Ecology* 69, 1017–1024.
- 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.
- 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? *Eur. J. For. Res.* 129, 277–288.
- Klopčic, M., Boncina, A., 2011. Stand dynamics of silver fir (*Abies alba* Mill.)–European beech (*Fagus sylvatica* L.) forests during the past century: a decline of silver fir? *Forestry* 84, 259–271.

- Korpel', Š., 1995. Die Urwälder der Westkarpaten. Gustav Fischer, Stuttgart, Jena, New York (in German).
- Kral, K., Janík, D., Vrška, T., Adam, D., Hort, L., Unar, P., Samonil, P., 2010. Local variability of stand structural features in beech dominated natural forests of Central Europe: implications for sampling. *For. Ecol. Manage.* 260, 2196–2203.
- Kramer, H., Akça, A., 1995. Leitfaden zur Waldmeßlehre. Sauerländer's Verlag, Frankfurt/a. M (in German).
- Kucbel, S., Jaloviar, P., Saniga, M., Vencurik, J., Klimaš, V., 2010. Canopy gaps in an old-growth fir–beech forest remnant of Western Carpathians. *Eur. J. For. Res.* 129, 249–259.
- Kucbel, S., Saniga, M., Jaloviar, P., Vencurik, J., 2012. Stand structure and temporal variability in old-growth beech-dominated forests of the northwestern Carpathians: a 40-years perspective. *For. Ecol. Manage.* 264, 125–133.
- Leibundgut, H., 1982. Europäische Urwälder der Bergstufe. Haupt, Bern, p. 308.
- Lingua, E., Garbarino, M., Mondino, E.B., Motta, R., 2011. Natural disturbance dynamics in an old-growth forest: from tree to landscape. *Proc. Environ. Sci.* 7, 365–370.
- Lombardi, F., Klopčič, M., Di Martino, P., Tognetti, R., Chirici, G., Boncina, A., Marchetti, M., 2012. Comparison of forest stand structure and management of silver fir–European beech forests in the Central Apennines, Italy and in the Dinaric Mountains, Slovenia. *Plant Biosyst.* 146, 114–123.
- Lombardi, F., Cherubini, P., Tognetti, R., Cocozza, C., Lasserre, B., Marchetti, M., 2013. Investigating biochemical processes to assess deadwood decay of beech and silver fir in Mediterranean mountain forests. *Ann. For. Sci.* 70, 101–111.
- Loosmore, N.B., Ford, E.D., 2006. Statistical inference using the G or K point pattern spatial statistics. *Ecology* 87, 1925–1931.
- Martinez, I., Wiegand, T., Gonzalez-Taboada, F., Obeso, J.R., 2010. Spatial associations among tree species in a temperate forest community in North-western Spain. *For. Ecol. Manage.* 260, 456–465.
- Motta, R., 1996. Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the Western Italian Alps. *For. Ecol. Manage.* 88, 93–98.
- Motta, R., Berretti, R., Dukić, V., Garbarino, M., Govedar, Z., Lingua, E., Maunaga, Z., Meloni, F., 2011. Toward a definition of the range of variability of central European mixed Fagus–Abies–Picea forests: the nearly steady-state forest of Lom (Bosnia and Herzegovina). *Can. J. For. Res.* 41, 1871–1884.
- Motta, R., Garbarino, M., Berretti, R., Meloni, F., Vacchiano, G., 2015. Development of old-growth characteristics in uneven-aged forests of the Italian Alps. *Eur. J. For. Res.* 134, 19–31.
- Müller-Using, S.I., Bartsch, N., 2009. Decay dynamic of coarse and fine woody debris of a beech (*Fagus sylvatica* L.) forest in Central Germany. *Eur. J. For. Res.* 128, 287–296.
- Nagel, T.A., Diaci, J., 2006. Intermediate wind disturbance in an old-growth beech–fir forest in southeastern Slovenia. *Can. J. For. Res.* 36, 629–638.
- Nagel, T.A., Svoboda, M., Diaci, J., 2006. Regeneration patterns after intermediate wind disturbance in an old-growth Fagus–Abies forest in southeastern Slovenia. *For. Ecol. Manage.* 226, 268–278.
- 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 Ecol.* 208, 307–318.
- Nagel, T.A., Svoboda, M., Kobal, M., 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecol. Appl.* 24, 663–679.
- Nagel, T.A., Diaci, J., Jerina, K., Kobal, M., Rozenberger, D., 2015. Simultaneous influence of canopy decline and deer herbivory on 1 regeneration in a conifer–broadleaf forest. *Can. J. For. Res.* 45, 266–275.
- Niinemets, U., Valladeres, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* 66, 1–43.
- Paluch, J.G., 2005. The influence of the spatial pattern of trees on forest floor vegetation and silver fir (*Abies alba* Mill.) regeneration in uneven-aged forests. *For. Ecol. Manage.* 205, 283–298.
- Paluch, J.G., 2007. The spatial pattern of a natural European beech (*Fagus sylvatica* L.)–silver fir (*Abies alba* Mill.) forest: a patch-mosaic perspective. *For. Ecol. Manage.* 253, 161–170.
- Petritan, I.C., Marzano, R., Petritan, A.M., Lingua, E., 2014. Overstory succession in a mixed *Quercus petraea*–*Fagus sylvatica* old growth forest revealed through the spatial pattern of competition and mortality. *For. Ecol. Manage.* 326, 9–17.
- Pommerening, A., 2002. Approaches to quantifying forest structures. *Forestry* 75, 305–324.
- Poulson, T.L., Platt, W.J., 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. *Ecology* 77, 1234–1253.
- Prodan, M., 1951. Messung der Waldbestände, vol. 26. J.D. Sauerländer's Verlag, Frankfurt/M.
- Río, M., Condés, S., Pretzsch, H., 2014. Analyzing size-symmetric vs. size-asymmetric and intra- vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. *For. Ecol. Manage.* 325, 90–98.
- Ripley, B.D., 1976. The second-order analysis of stationary point processes. *J. Appl. Prob.* 13, 255–266.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. *Science* 343. <http://dx.doi.org/10.1126/science.1241484>.
- Rozas, V., 2003. Regeneration patterns, dendroecology, and forest-use history in an old-growth beech–oak lowland forest in Northern Spain. *For. Ecol. Manage.* 182, 175–194.
- Rozas, V., Zas, R., Solla, A., 2009. Spatial structure of deciduous forest stands with contrasting human influence in northwest Spain. *Eur. J. For. Res.* 128, 273–285.
- Rozenberger, D., Mikac, S., Anic, I., Diaci, J., 2007. Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech fir forest reserves in South East Europe. *Forestry* 80, 431–443.
- Runkle, J.R., 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63, 1533–1546.
- Sagnard, F., Pichot, C., Dreyfus, P., Jordano, P., Fady, B., 2007. Modelling seed dispersal to predict seedling recruitment: recolonization dynamics in a plantation forest. *Ecol. Model.* 2003, 464–474.
- Šamonil, P., Vrška, T., 2007. Trends and cyclical changes in natural fir–beech forests at the north–western edge of the Carpathians. *Folia Geobot.* 42, 337–361.
- Šamonil, P., Antolík, L., Svoboda, M., Adam, D., 2009. Dynamics of windthrow events in a natural fir–beech forest in the Carpathian mountains. *For. Ecol. Manage.* 257, 1148–1156.
- Saniga, M., Schütz, J.P., 2001. Dynamics of changes in dead wood share in selected beech virgin forests in Slovakia within their development cycle. *J. For. Sci.* 47, 557–565.
- Schütz, J.P., 2001. Der Plenterwald und Weitere Formen Strukturierter und Gemischter Wälder, Berlin Parey.
- Senn, J., Suter, W., 2003. Ungulate browsing on silver fir (*Abies alba*) in the Swiss Alps: beliefs in search of supporting data. *For. Ecol. Manage.* 181, 151–164.
- Silvertown, J., 2004. Plant coexistence and the niche. *Trends Ecol. Evol.* 19, 605–611.
- Splechna, B.E., Gratzner, G., Black, B.A., 2005. Disturbance history of a European old-growth mixed-species forest – a spatial dendro-ecological analysis. *J. Veg. Sci.* 16, 511–522.
- Stancioiu, P.T., O'Hara, K.L., 2006. Leaf area and growth efficiency of regeneration in mixed species, multiaged forests of the Romanian Carpathians. *For. Ecol. Manage.* 222, 55–66.
- StatSoft, Inc., 2013. STATISTICA (Data Analysis Software System), version 12. <<http://www.statsoft.com>>.
- Stoyan, D., Penttinen, A., 2000. Recent applications of point process methods in forestry statistics. *Stat. Sci.* 15, 61–78.
- Stoyan, D., Stoyan, H., 1994. Fractals, Random Shapes, and Point Fields: Methods of Geometrical Statistics. Wiley, Chichester.
- Szwagrzyk, J., Czerwczak, M., 1993. Spatial patterns of trees in natural forests of East-Central Europe. *J. Veg. Sci.* 4, 469–476.
- Szwagrzyk, J., Szewczyk, J., Bodziarczyk, J., 2001. Dynamics of seedling banks in beech forest: result of 10-year study on germination, growth and survival. *For. Ecol. Manage.* 141, 237–250.
- Tauber, F., 1987. Contributii la sintaxonomia fagetelor carpato-dacice (Symphyto-Fagenalia subordo novum). *Contrib. Bot.* 27, 179–191.
- Trotsiuk, V., Hobi, M.L., Commarmot, B., 2012. Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). *For. Ecol. Manage.* 265, 181–190.
- Veen, P., Fanta, J., Raev, I., Biris, I.A., de Smidt, J., Maes, B., 2010. Virgin forests in Romania and Bulgaria: results of two national inventory projects and their implications for protection. *Biodivers. Conserv.* 19, 1805–1819.
- Višnjić, Č., Solaković, S., Mekić, F., Balić, B., Vojniković, S., Dautbašić, M., Gurda, S., Ioras, F., Ratnasingam, J., Abrudan, I.V., 2013. Comparison of structure, regeneration and dead wood in virgin forest remnant and managed forest on Grmeč Mountain in Western Bosnia. *Plant Biosyst.* 147, 913–922.
- 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? *For. Ecol. Manage.* 258, 347–356.
- Westphal, C., Tremer, N., Oheimb, G.v., Hansen, J., Gadow, K.v., Hardtle, W., 2006. Is the reverse J-shaped diameter distribution universally applicable in European virgin beech forests? *For. Ecol. Manage.* 223, 75–83.
- Wiegand, T., Moloney, K.A., 2004. Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104, 209–229.
- Wiegand, T., Gunatilleke, S., Gunatilleke, N., 2007. Species associations in a heterogeneous Sri Lankan dipterocarp forest. *Am. Nat.* 170, E77–E95.
- Wirth, C., Gleixner, G., Heimann, M., 2009. Old-growth forests: function, fate and value. *Ecological Studies* 207. Springer, New York, Berlin, Heidelberg.
- Woods, K.D., 2004. Intermediate disturbance in a late-successional hemlock northern hardwood forest. *J. Ecol.* 92, 464–476.