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Tree spatial patterns and stand attributes in temperate forests: The importance of plot size, sampling design, and null model

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ABSTRACT

Detection of tree spatial patterns and structural attributes in a forest stand can provide critical information on occurring dynamics, and steer management decisions. However, since tree spatial distribution depends on factors that operate at different scales, including environmental heterogeneity and tree-to-tree interactions, both the extent to which measurements are taken and the choice of null model for spatial analysis (including site heterogeneity or not), can considerably influence investigation outcomes and related inferences.

In this study, we aim to evaluate the effect of plot size, sampling design (single or combined plots), and null model for spatial analysis, on point pattern analysis and stand attribute assessment in temperate forests. Analyses were performed on 4-ha plots in two old-growth and two previously managed stands in central Europe. For each site, we calculated tree density, mean diameter, mean height and basal area, and performed point pattern analysis (pair-correlation function) under complete spatial randomness (CSR) and heterogeneous Poisson (HP) null models. We then assessed stand attributes and spatial patterns on subplots, and calculated their deviation from the 4-ha reference plot.

As expected, accuracy of stand attribute assessment improved by increasing subplot size. However, while accuracy of small (0.25-ha) plots was quite high for basal area, it was rather low for tree density, especially in the old-growth stands. Outcomes of point pattern analysis in 0.25-ha plots were variable, generally presenting low agreement with the reference. Larger plots assured more consistent results, but deviations from the reference were still rather high when CSR null model was used. In all the sites, subplot agreement improved using HP model.

Our investigation indicates that 0.25-ha plots are mostly reliable for assessing stand attributes in previously managed forests. However, tree distribution can be very variable both in these and in old-growth stands, therefore spatial patterns cannot be reliably detected with one small plot. Combining several small plots, and using null models accounting for site heterogeneity, are efficient strategies to detect small-scale spatial patterns, but plot larger than 1-ha should still be used to assess large-scale patterns in high-diversity forest stands.

1. Introduction

In the natural environment, trees are not uniformly distributed, but form a complex mosaic with patches of different age, size, species, which reflect past endogenous and exogenous processes, and influence future ones (Watt, 1947; Dale, 1999; Stoyan and Penttinen, 2000). Spatial patterns in forests cover a wide range, which require adequate observation scales (Dungan et al., 2002). Mapping forest canopy on a global or regional scale (e.g. Simard et al., 2011) certainly cannot be performed with the same resolution as studies on microsite influence on seedling establishment (e.g. Germino et al., 2002). For studies on ecological processes such as tree recruitment, competition and mortality, the perspective of individual stems is often the most appropriate (Song et al., 1997), and recording the position of each individual ensures the minimum grain size and maximum possible resolution (Zenner and Peck, 2009). The spatial extent generally corresponds to the forest stand, which can be defined as a more or less homogeneous patch of the forest (West, 2004). However, operating at single tree level with the aim of fully capturing ecological processes within a stand, would require huge field sampling efforts. This leads to restricting investigation to a subsample, i.e. a relatively large plot representative of the stand, or many smaller plots scattered over the area. The spatial scale issue in forest science is therefore closely related to the sampling strategy, in particular to the size and number of plots.

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Table 1
Elevation, descriptive features and stand attributes of Giumalau (GIU), Slatioara (SLA), Millifret (MIL) and Latemar (LAT) (mean value in the 4-ha plots) sites.

	Elevation (m a.s.l.)	Category	Age Structure	Species Composition	Density ($n\ ha^{-1}$)	Dbh (cm)	Height (m)	Basal area ($m^2\ ha^{-1}$)
GIU	1150	old-growth	Uneven	Pure	559	22.9^b (20.8)	15.2^c (12.4)	42
SLA	1450	old-growth	Uneven	Mixed	1240	15.7^c (17.9)	11.1^d (9.6)	55.1
MIL	1400	prev.manag.	Even	Pure	846	26.3^a (9.1)	24.0^a (4.4)	51.5
LAT	1900	prev.manag.	Uneven	Mixed	453	29.6^a (15.4)	16.9^b (7.6)	39.7

For diameter (Dbh) and tree height (Height), standard deviation is reported in brackets, and different letters (superscript) indicate significant difference between the areas according to one-way ANOVA test with Tukey's pairwise comparisons.

How to achieve precise and accurate estimates of forest attributes and structure, by efficiently reducing time and cost of field work, is a subject of debate in forest science (Bormann, 1953; Kenkel et al., 1989; Gray, 2003; Lynch, 2016). Previous studies have shown that some forest attributes, such as number of large trees (Zenner and Peck, 2009), deadwood elements (Lombardi et al., 2015), and abundance of rare species (Corona et al., 2011), require more and larger plots compared to commonly investigated attributes such as stand basal area (Du et al., 2015). Other studies have investigated the effect of observation scales on the spatial autocorrelation among stand characteristics (Král et al., 2014) and on tree size distribution (Alessandrini et al., 2011). However, to our knowledge, no study has specifically assessed the effect of plot size on point pattern analysis (PPA). This approach has received increasing attention in forest ecology, being used to investigate regeneration (Kuuluvainen and Rouvinen, 2000; Janík et al., 2016), mortality (Castagneri et al., 2010; Aakala et al., 2012), intra and interspecific competition (Doležal et al., 2006; Petritan et al., 2014) and facilitation (Lingua et al., 2008; Muhamed et al., 2015) processes, spatiotemporal changes in the relationships between species and size classes (Janík et al., 2014), and the influence of natural disturbances (Nagel et al., 2006) and management (Wolf, 2005) on forest structure. Just considering temperate forests (in subtropical and tropical forests sampling plots are generally larger, Getzin et al., 2014), the spatial extent of such investigations varies considerably, ranging from 0.25 ha in pioneer studies (Kenkel, 1988) to 25 ha (Johnson et al., 2014). Small plots cannot be expected to properly represent large forest patches related to medium to large-scale disturbances (Nagel et al., 2006), but plots < 1 ha have been widely used to investigate tree spatial patterns in different environments (Svoboda et al., 2010; Aakala et al., 2012; Marzano et al., 2012; Petritan et al., 2014), as most inter-tree interactions are expected to occur within 10 m scales (Stoyan and Penttinen, 2000; Getzin et al., 2008). Nonetheless, small plots have intrinsic limitations, such as fewer trees compared to larger plots, and proportionally greater edge effect (Wiegand and Moloney, 2014). Combining information from several plots, considered as pseudo-replications, has been proposed (Illian et al., 2008; Wiegand and Moloney, 2014) and used (De Luis et al., 2008; Raventós et al., 2010; Petritan et al., 2014; Piermattei et al., 2016) to reinforce and stabilize results from small plots, in order to obtain a more robust view of spatial patterns in the forest stand.

Beside plot size and arrangement, PPA can be deeply influenced by the null model used (Dale, 1999). The simplest one, and still widely used in ecological studies (Baddeley et al., 2014; Velázquez et al., 2016), is the complete spatial randomness (CSR). It considers that any point of the pattern has an equal probability of occurring at any location within the study plot, i.e., that the observed events are consistent with a homogeneous Poisson process (Wiegand and Moloney, 2014). In a forest stand, CSR implies that site (soil, topography, etc.) is homogeneous, a condition that hardly occurs in practice (Velázquez et al., 2016). An alternative null model, widely applied to study plant spatial distribution and relationships in a natural environment (such as trees in forest stands; Svoboda et al., 2010; Piermattei et al., 2016), where environmental heterogeneity (e.g. different topography or soil conditions) can affect spatial distribution (Getzin et al., 2008; Baddeley et al., 2014), is the heterogeneous Poisson (HP) null model. This differs from CSR in that the intensity λ (x, y) of the process depends on location (x, y), but the occurrence of any point remains independent of that of any other (Wiegand and Moloney, 2004). The selection of the null model is a critical step in PPA, influencing analysis outcomes and therefore interpretation of the observed patterns. Nonetheless, specific studies evaluating the influence of the null model on PPA assessed from different plot sizes, to our knowledge, are still lacking.

In this study, we evaluated how plot size, sampling design (single or combined plots), and null model for spatial analysis, affect the assessment of tree spatial patterns and stand attributes in temperate forests. Analyses were conducted on four mountain forests in central Europe, including pure and mixed, even- and uneven-aged, old-growth and previously managed stands. We aimed at testing the following hypotheses: (1) increasing plot size improves the accuracy of stand attribute and spatial pattern assessment; (2) combined information on stand attributes obtained from four 0.25-ha plots is similar to that of 1-ha plots, but less accurate on spatial patterns; (3) PPA accuracy of small plots can be improved adopting a null-model accounting for spatial heterogeneity.

2. Materials and methods

2.1. Study sites

Our analysis was conducted on four temperate mountain forests in central Europe (Table 1).

Giumalau (GIU), in the Romanian Carpathians, within the Codrul Secular Giumalau Forest Reserve (47°26′N; 25°28′E). The reserve, established in 1941, comprises 309.5 ha of pure *Picea abies* L. (Karst.) (Norway spruce) forest, including old-growth stands where the survey was conducted (Lamedica et al., 2011).

Slatioara (SLA), in the Romanian Carpathians, on a mid-mountain slope within the Codrul Secular Slatioara Forest Reserve (47°27′N; 25°37′E). The study was performed in an old-growth mixed forest stand mainly composed of Norway spruce, *Abies alba* Mill. (silver fir) and *Fagus sylvatica* L. (European beech).

Millifret (MIL), on the Cansiglio plateau, northern Italy, within the Pian di Landro – Baldassare Nature Reserve (46°03′N; 12°20′E). This 130-ha forest, protected since 1971, comprises pure even-aged European beech stands, previously managed by the shelterwood system.

Latemar (LAT), in the western Dolomites, eastern Italian Alps (43°22′N; 11°33′E). Mixed *Larix decidua* Mill. (European larch), *Pinus cembra* L. (Swiss stone pine) and Norway spruce subalpine forest was affected by extensive cutting and livestock grazing in the past centuries, but human activities have gradually decreased since the Second World War.

2.2. Field data collection and stand attributes

In each site, we established one 4-ha (200 × 200 m) permanent plot. All living trees with diameter at breast height (dbh) ≥ 0.5 cm were identified and labelled, and stem base coordinates (x, y), dbh, and