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Spatial variability of general stand characteristics in central European beech-dominated natural stands – Effects of scale



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ABSTRACT

Unlike many studies on the stand structure of European beech-dominated natural forests we explicitly examined the spatial variability of six general stand characteristics: density, basal area and volume of living trees, volume of deadwood, total volume and the proportion of deadwood in the total volume. We asked whether and how these stand characteristics are spatially organized and autocorrelated, and how their spatial autocorrelation varies among particular characteristics, study sites and observation scales.

The study was conducted at three forest stands dominated by Fagus sylvatica L. and co-dominated by Picea abies (L.) Karsten and Abies alba Mill., which represent the few sizable remnants of beech-dominated natural forests in central Europe. Vector stem position maps of the three sites were examined by the computer-simulated placement of differently sized square sample plots (10×10 ; 20×20 ; 30×30 ; 50×50 and 70×70 m). The six general stand characteristics were calculated for every simulated sample plot. Experimental semivariograms were calculated for all sampling plot (grain) sizes, model semivariograms were only fitted for 20×20 m plots.

The spatial variability of stand characteristics significantly changes with the scale of observation. At the finest grain the spatial autocorrelation is mostly quite low and usually very nearly approximate the nugget model. However, autocorrelation increases with increasing sampling plot size. A peak in the first lag of the semivariograms was observed only at the finest grains, documenting the competition of large trees, whereas a recurring pattern of patches with similar stand characteristics was identified at larger observation scales. Nested structures formed by the high nugget and relatively less distinct but still apparent sill/range and fluctuation signal were detected in most of the model semivariograms, indicating different sources of variability operating at multiple scales. Moreover, significant differences among particular stand variables were demonstrated. The relative nugget varied from 61% (stand density) to 96% (stand volume) at the 20×20 m sampling plots; the autocorrelation ranges varied from more than 320 m to 64 m, respectively.

The irregular periodic patchiness found (usually 400–1100 m² in size) may serve as a model for close-to-nature forestry, which emulates the spatial structures of natural forests. The level of positive spatial autocorrelation acknowledged for stand density should be reflected in an effective sampling design. For better estimates of the variance in this variable, sampling in a regular grid or stratified sampling is suggested.

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1. Introduction

Numerous recently-published papers have studied the stand structure and dynamics of European beech-dominated natural forests using various approaches, including evaluations of stand diameter distribution (Motta et al., 2011), analysis of canopy gaps (Rugani et al., 2013), field (Boncina, 2000) or GIS-based (Král et al.,

2010b) mapping of patches of forest developmental phases, dendrochronological studies of disturbance regime (Splechtna et al., 2005) or assessments of tree spatial patterns (Szwagrzyk and Czerwczak, 1993). Most investigations of this type have also been carried out at some of the sites studied in this paper, in particular the Žofín forest (Janík et al., 2013; Kenderes et al., 2009; Král et al., 2010b; Šamonil et al., 2013; Šebková et al., 2012). Nevertheless, none of these studies tried to evaluate whether the variously observed stand structure patterns are reflected in the spatial variability of general stand characteristics such as stand density, basal

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area (BA) and stand volume (further also referred to as stand variables). Yet, this information is undoubtedly highly interesting from the ecological viewpoint, as it indicates whether the accumulating and decaying above-ground woody biomass (hence also carbon sequestration) is distributed randomly or in a spatially organized pattern (and if yes, then how and to what extent). This knowledge may also have important implications for sampling design for unbiased estimates of aboveground woody biomass and other stand variables either in forest inventories or ecologically-oriented research. The effect of high local stand variability has already been demonstrated in a preceding study in the same study sites (Král et al., 2010a). This present paper extends the issue using the viewpoint of spatial statistics, which may help uncover underlying processes responsible for different variability at different scales.

Studies on spatial variability of forest stands are known from tropical (Bellehumeur et al., 1997), boreal (Gilbert and Lowell, 1997) and temperate forests of South (Fajardo and Gonzalez, 2009) and North America (Chen et al., 2004). To our knowledge, however, no study has been conducted that explicitly examines the spatial variability of general stand characteristics in a European temperate forest. In addition, no other study has dealt with the issue of spatial autocorrelation of the coarse woody debris (CWD) volume and its relation to total volume, although it is an important structural component of forest ecosystems that has been recognized as one of the strongest indicators of forest biodiversity (Pesonen et al., 2009).

Studies addressing spatial variability and the autocorrelation of different variables in forests typically use stem maps as input data and geostatistics (variography) as a statistical method. Among these analyses we may distinguish two basic approaches: (i) the semivariograms are calculated directly from discrete point data (stem maps) for variables related to size, growth or age of tree individuals (Biondi et al., 1994; Fajardo et al., 2007; Fajardo and McIntire, 2007; Fajardo and Gonzalez, 2009); and (ii) the semivariograms are calculated from differently sized areal samples for variables related to the forest stand – e.g. stand density, BA, or volume per hectare (Bellehumeur and Legendre, 1997; Chen et al., 2004; Gilbert and Lowell, 1997). In the first approach (i) the extent of analyses is usually small (10–100 m) and detected ranges are very short (5–30 m) due to high stochastic variation among individuals. The latter approach (ii) is usually able to identify phenomena operating at larger scales – the observed ranges are longer (40–130 m) and the extent of analyses used is correspondingly larger (150-300 m). The latter approach is also better suited to our intentions; the above mentioned studies, however, usually estimated and modelled the semivariance from zero distances. Consequently, the effect of the closest, mutually-overlapping sample plots largely determined the overall shape of the semivariogram and thus the estimated autocorrelation of the variable (e.g. Chen et al., 2004). In our study we also use overlapping samples (sliding boxes); but, in interpretation we focus on the spatial autocorrelation of at-least adjacent and further-distant samples. As these are naturally much less autocorrelated, they require separate and more careful evaluation.

However, the observation of a forest through areal sample plots is indeed a tricky issue. In practice, when the sampling unit size is too small and includes only one or two tree stems, the adjacent sample units are empty. This results in a weak spatial autocorrelation structure because sampling is almost at a stochastic spacing level. On the contrary, when the sampling unit size is too large, spatial autocorrelation is not significant, because the sampling unit may be larger than the spatial range of the pattern (Fortin and Dale, 2005). In fact, the scale of observation literally determines what is to be observed (Wu et al., 2000; Wu, 2004), and a failure to detect significant spatial patterns does not necessarily mean that none exist, and revised sampling may be able to detect them (Fortin

and Dale, 2005). This implies that for a comprehensive description of forest spatial patterns a truly multiscale analysis is needed. Two general approaches to multiscale analyses may be distinguished (Wu et al., 2000): (i) the direct multiscale approach that uses inherently multiple-scale methods, and (ii) the indirect multiscale approach that uses single-scale methods repeatedly at different scales – the scale multiplicity is here realized by data resampling. In this study we use variography, and although it is partially a multiscale approach, the discrete input data (stem maps) were resampled at different sample unit sizes since the size of the sample plots may significantly influence the pattern observed in the forest (Bellehumeur and Legendre, 1997; Bellehumeur et al., 1997).

No less important than the sample unit size (resolution grain) is the extent of a particular study. As stated by Levin (1992), the scales of observation are always limited; most ecological studies are carried out on scales of meters or tens of meters, while larger scope observations (maintaining the necessary detail) are rare. Limitations in study extent inevitably limit our perception of the observed system. Simply, if the study extent is smaller than the area of the phenomena, no pattern is likely to be detected (Dungan et al., 2002); larger study extents can reveal spatial patterns that remain hidden in spatially limited studies. A wide extent of study is thus another benefit of our research carried-out at three study sites of beech-dominated natural forest in the Czech Republic, one of which has an area of more than 70 ha.

In natural forests the stand structure is formed by complex interactions among many factors and processes operating at various spatial and temporal scales, including species' traits, fine-scale environmental variation, seed dispersal and success of regeneration, competition among tree individuals, tree senescence and neighbourhood interactions, gap dynamics, and stochastic processes such as windthrows and outbreaks of insects and diseases (Biging and Dobbertin, 1992; Chen et al., 2004; Dale, 1999; Pedersen and Howard, 2004). We presume that the resulting spatial heterogeneity of the stand structure of beech-dominated natural forests is reflected in the spatial variability of general stand characteristics. This general presumption is further elaborated in the following specific hypotheses and related questions. We adopted the approach proposed by Fajardo et al. (2008) and McIntire and Fajardo (2009) and a priori link the ecologically meaningful hypotheses with the expected semivariance pattern (Fig. 1) and then look for their support in the data.

Hypothesis 1 (*From random variation to spatial autocorrelation*). We hypothesize that if the size of the sample plots are close to the natural spacing of pre-mature and mature tree individuals, the random tree spatial pattern usually found in natural temperate forests (Janík et al., 2013; Pommerening, 2002) results in the random spatial variation of stand variables calculated through these fine-scale samples (Fig. 1a – the nugget model).

By enlarging the grain size of sampling we move from unpredictable individual cases of trees presence/absence to a description of spatial organization at larger scales that is generally more likely to exist in any ecological system (Levin, 1992). In our case we expect that processes that may lead to 'clustering' (e.g. habitat differentiation, past disturbances) start to play a more important role at these larger scales. Therefore we further hypothesize that the spatial autocorrelation of the stand variables increases with enlarging sample unit size, which in semivariograms will be demonstrated by decreasing relative nugget and sill and growing range with increasing sample unit size (Fig. 1a).

Hypothesis 2 (*Patchiness*). Quantitative analysis of the stem-map of the Žofín forest by an artificial neural network has identified various patches of specific stand structure (Král et al., 2010b),

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