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Original article

Uncertainty in the detection of disturbance spatial patterns in temperate forests

P. Šamonil[a,*], J. Timková[b], I. Vašíčková[a,c]

[a] Department of Forest Ecology, The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Lidická 25/27, 60200 Brno, Czech Republic
[b] Department of Probability and Mathematical Statistics, Faculty of Mathematics and Physics, Charles University in Prague, Ke Karlovu 3, 12116 Praha 2, Czech Republic
[c] Department of Forest Botany, Dendrology and Geobiocenology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemedelska 1, 61300 Brno, Czech Republic

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ABSTRACT

The use of individual-based models in the study of the spatial patterns of disturbances has opened new horizons in forest ecosystem research. However, no studies so far have addressed (i) the uncertainty in geostatistical modelling of the spatial relationships in dendrochronological data, (ii) the number of increment cores necessary to study disturbance spatial patterns, and (iii) the choice of an appropriate geostatistical model in relation to disturbance regime. In addressing these issues, we hope to contribute to advances in research methodology as well as to improve interpretations and generalizations from case studies.

We used data from the beech-dominated Žofínský Prales forest reserve (Czech Republic), where we cored 3020 trees on 74 ha. Block bootstrap and geostatistics were applied to the data, which covered five decades with highly different disturbance histories. This allowed us to assess the general behavior of various mathematical models. Uncertainty in the spatial patterns and stability of the models was measured as the length of the 95% confidence interval (CI) of model parameters.

According to Akaike Information Criterion (AIC), the spherical model fitted best at the range of ca. 20 m, while the exponential model was best at the range of ca. 60 m. However, the best fitting models were not always the most stable. The stability of models grew significantly with sample size. At <500 cores the spherical model was the most stable, while the Gaussian model was very unstable at <300 cores. The pure nugget model produced the most precise nugget estimate. The choice of model should thus be based on the expected spatial relations of the forest ecosystem under study. Sill was the most stable parameter, with an error of ±6–20% for ≥1110 core series. By contrast, practical range was the most sensitive, with an error of at least ±59%. The estimation of the spatial pattern of severe disturbances was more precise than that of fine-scale disturbances.

The results suggest that with a sample size of 1000–1400 cores and a properly chosen model, one reaches a certain precision in estimation that does not increase significantly with growing sample size. It appears that in temperate old-growth forests controlled by fine-scale disturbances, it is necessary to have at least 500 cores to estimate sill, nugget and relative nugget, while to estimate practical range at least 1000 cores are needed. When choosing the best model, the stability of the model should be considered together with the value of AIC. Our results indicate the general limits of disturbance spatial pattern studies using dendrochronological and geostatistical methods, which can be only partially overcome by sample size or sampling design.

1. Introduction

Knowledge of disturbance history is essential for an understanding of the dynamics of forest ecosystems and the ecological relationships among ecosystem components. Tree layer disturbances influence microclimatic conditions (Beatty and Stone,

* Corresponding author. Fax: +420 541 246 001.
E-mail address: pavel.samonil@vukoz.cz (P. Šamonil).

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1986), the structure and species diversity of various groups of organisms (Nachtergale et al., 2002; Gravel et al., 2010), as well as pedocomplexity (Šamonil et al., 2008, 2011, 2014; Ibañez and Bockheim, 2013). Disturbances connect the biotic and abiotic components of ecosystems, and numerous feedback mechanisms exist between both of them. Through eco-evolutionary dynamics including ecosystem engineering and niche construction (Corenblit et al., 2011), tree species communities and relevant landforms mutually form each other. The precise way this occurs is among the most important and complex gaps in the science of ecosystems research, for which disturbance history and regime are of key importance.

Dendrochronology represents a traditional tool in the study of forest disturbance history. Coordinates of individual trees have been increasingly used in dendrochronological research over the past few decades in order to record the fine scale of disturbances (e.g., Payette et al., 1990; Parish and Antos, 2004; Fraver and White, 2005; Stoffel et al., 2006) and to calculate spatial data characteristics (e.g., Frelich and Graumlich, 1994; Parshall, 1995; Shimatani and Kubota, 2011; Šamonil et al., 2013). However, further research progress in the assessment of disturbance spatial patterns is partly limited by the current lack of knowledge about the spatial autocorrelation in dendrochronological data as well as the unknown robustness of achieved results.

Using an extensive data set including 1021–1368 tree cores originating from beech-dominated old-growth forest in the Czech Republic (in total 74 ha, Šamonil et al., 2013), we attempted to: (i) elucidate the uncertainty in geostatistical modelling of spatial relationships in dendrochronological data in relation to the sample size and selected mathematical model, (ii) recommend a procedure for calculating disturbance spatial patterns including the sample size selection in comparable forest types. We hope this evaluation of the behavior of dendrochronological data in space as well as our assessment of uncertainty in the resulting picture of disturbance history has methodological as well as ecological importance. Our results should allow researchers of future studies to choose appropriate methods (design of data collection, selection of appropriate model to fit data) and will support the proper interpretation and generalization of the results.

2. Material and methods

2.1. Site characteristics

Data were collected in the Žofínský Prales forest reserve in the Czech Republic (hereafter Žofín, Šamonil et al., 2013). The reserve is situated along an altitudinal gradient of 735–830 m a.s.l. Bedrock is almost homogenous and consists of granite. Annual average rainfall is 917 mm; annual average temperature is 4.3 °C. *Fagus sylvatica* dominates in the forest (62% of the living tree volume), followed by *Picea abies* (34%). Other tree species (*Abies alba*, *Acer pseudoplatanus*, *Acer platanoides*, *Sorbus aucuparia*, *Ulmus glabra*) compose 4% of the living tree volume. Fine-scale disturbances represent the main driving factor of forest dynamics, but severe disturbances in the forest over the past two centuries have been identified as well (Šamonil et al., 2013).

2.2. Data collection

In 2008 we set up a regular network of 354 points with 44.25 m spacing, which covered 74 ha of the reserve. The nodes of this grid were located geodetically with an accuracy of ca. 0.05 m and were used as the basis for subsequent tree censuses and geomorphological and dendrochronological surveys. In 2008 we measured the locations of all trees within the locality with diameter at breast height (DBH) ≥10 cm.

Six tree cores (nine in the case of a gap occurrence) were taken from non-suppressed trees closest to each of the 354 nodes, one from each tree. From the total of 18,899 standing and 2862 lying trunks recorded in 2008, we cored 3020 individuals at a height of 1.3 m in 2008–2011. We considered the number of rings at this 1.3 m height to be the recruitment age, and former growth was not further studied in detail (see details in Šamonil et al., 2013).

2.3. Data analysis

2.3.1. Basic laboratory analysis

The cores were dried and polished using fine sandpaper. We measured the widths of the growth rings using the past 4 program (SCIEM, 2007), and we rejected cores without sub-bark growth rings, damaged cores and cores that were missing more than 30 mm of the pith. A total number of 1986 cores were accepted for the subsequent evaluation of disturbance history. We used a pith locator (Applequist, 1958) to evaluate the number of tree rings to the pith and we crossdated individual core series using the past 4 program and COFECHA (Holmes, 1983).

2.3.2. Evaluation of disturbance history

In a previous study (Šamonil et al., 2013), we studied disturbance history for an irregular network of precisely located trees based on (i) the initial growth of trees–if it occurred under the canopy or in a gap, and (ii) the subsequent growth of trees—if release was detected in radial growth. These two variables provide different information. While initial growth indicates rather the existence of a gap in a particular decade (recent as well as very old gaps were included), release indicates the year of a disturbance event (there is an uncertainty of few years, Rozas, 2001). To avoid unreliability in the detection of disturbance events by the initial growth of trees, we included only release events in our evaluation of the uncertainty in disturbances.

We calculated the release threshold according to Black and Abrams (2003). The boundary line is defined as the maximum percent of growth change (GC) that is physiologically possible at a given level of prior growth (PG). PG is the mean annual increment of the 10 years preceding any annual ring, and GC is the change of mean annual increment between two 10-year intervals, enabling us to eliminate false releases produced by short-term climatic extremes (Nowacki and Abrams, 1997). Local GC maxima were compared with the (species-specific) boundary line values (BL) in Šamonil et al. (2013). Growth changes ≥20% of BL were considered as releases. We rejected pulses that were <20% of BL as inconclusive.

2.3.3. Uncertainty in the spatial pattern of disturbances

Next, we attempted to determine how the quality of the estimate of data spatial autocorrelation changes with sample size. In particular, we examined the characteristics of variograms, i.e., practical range, nugget, relative nugget and sill. We preferred practical range to range because this variable can also be calculated for steadily growing models, such as exponential and Gaussian models (e.g., Webster and Oliver, 2007). Range generally represents the distance (if any) at which detected disturbance events are no longer autocorrelated (Fig. 1). This can be interpreted as the diameter of a typical gap formed by the disturbance studied. The practical range equals to the distance when the semivariogram γ (Eq. (1)) reaches 95% of the sill. The sill represents the level of variance of random data that is not spatially autocorrelated. The partial sill is obtained by subtracting the nugget from the sill and it represents the variability explained by the model. The nugget effect generally represents micro-scale variation at the beginning of a model, connected for example with the effect of microsite, tree species or with measurement error. The relative nugget effect is defined