

The spatial pattern of a natural European beech (*Fagus sylvatica* L.)–silver fir (*Abies alba* Mill.) forest: A patch-mosaic perspective

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Received 4 April 2007; received in revised form 16 July 2007; accepted 17 July 2007

Abstract

A grid of small sample plots was traced out in a West Carpathian (Central European) forest that has been minimally impacted by humans. Both regeneration and all live and dead trees were surveyed. Specifically investigated were the spatial variability of the stand basal area, the vertical stand structure, the occurrence of live and dead canopy trees, and regeneration. With the exception of the aggregated patterns of regeneration and under-canopy trees, the spatial patterns failed to correspond to the conception of coarse-grained patch mosaic. Its distinctness found expression in both the random distribution of live and dead canopy trees and the close-to-random spatial variability of the basal area. The predominance of plots showing diversified vertical structure called into question the homogeneity of patches even as small as canopy tree crowns. Nor was any relationship found between the occurrence of diversified vertical structures and the lower levels of the basal area. Rather, in the forest under study, the structural diversification of individual patches may depend more on resistance to the disturbance of large canopy trees than on competitive stress to which the sub-canopy and under-canopy trees are subjected.

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Keywords: *Fagus sylvatica*; *Abies alba*; Spatial analysis; Primeval forest; Development cycle; Forest structure; Gap dynamics; Shifting-mosaic steady state

1. Introduction

The dynamics of a forest patch are frequently idealised as a sequence of upgrade and downgrade series attributable to periods of relative predominance of biomass accumulation or biomass loss (Watt, 1947; Bormann and Likens, 1979; Shugart, 1984). This sequence is a product of three partly opposing processes: tree growth that leads to stand volume accumulation, tree die-off that results in volume drop, and regeneration that produces exchange of tree generations. Among these processes, the most deterministic appears to be tree growth, which is temporarily strongly auto-correlated owing to the tree architecture's slow rate of change and strong dependence on a range of relatively stable site variables (at least, in spans of few vegetation periods). Conversely, the most unpredictable is die-off, which may considerably change the appearance of a forest patch and greatly influence the trajectory of its further

development (Franklin et al., 2002; Splechtna et al., 2005; Nagel and Diaci, 2006).

Such tree die-off may result from several factors, both exogenous and endogenous. From the viewpoint of forest patch dynamics, it appears reasonable to distinguish two major sources of tree mortality: inter-tree competition and disturbances. The mortality caused by the former may be anticipated with some probability (Wyckoff and Clark, 2000; Bigler and Bugmann, 2003) and is implicitly incorporated into the stand development trajectory. However, disturbances are to a large degree unpredictable and, when they afflict large canopy trees, may lead to substantial changes in forest patch dynamics. Indeed, the disturbing phenomena are extremely complex in that many factors, both biological and physical, may make trees more susceptible to physical forces. The most common biological processes include competition, senescence, insect and disease attack, and simple growth, as well as climatic fluctuations that are unfavourable to growth (Bormann and Likens, 1979).

The spatial and temporal scale of disturbances is widely accepted as a major force driving the spatial patterns of forests

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(Runkle, 1982; Lorimer, 1989; Kubo et al., 1996; Pontauiller et al., 1997; Manrubia and Solé, 1997; Franklin et al., 2002). In this respect, the most relevant factors seem to be the magnitude, frequency, and intensity of disturbing events. In general, the smaller the scale and the higher the frequency of disturbances, the more diversified the horizontal and vertical forest structure (Shugart, 1984). Nevertheless, because forest fragments may be differently impacted by disturbance, a more or less recognisable mosaic of homogenous patches may appear (Wissel, 1992; Jaworski et al., 1994; Emborg et al., 2000; Jaworski and Paluch, 2001; Saniga and Schütz, 2001; Jaworski, 2004; Lin et al., 2004; Nagel et al., 2006).

The patches forming the mosaic are distinguishable on the basis of stand volume accumulation, age and size structure, canopy openness, occurrence of regeneration, and/or eventually, species composition (Leibundgut, 1979; Korpel', 1993; Podlaski, 2004). However, to date, little attention has been paid to a fundamental difference between 'patchiness' as a general feature of forest pattern resulting from the spatial and temporal correlation of ecological processes and 'accidental occurrence of less or more homogenous patches', which may be an effect of quite random natural phenomena.

The spatial relation between canopy openness and the occurrence of regeneration did induce researchers to frame the concept of gap dynamics (Watt, 1947; Shugart, 1984; Remmert, 1991), which assumes that the death of a canopy tree creates a gap of up to a few hundred square meters that becomes a localised site of regeneration and subsequent growth. As a rule, the cohort of trees filling the gap exhibits limited age and size variety, and a complex stand structure results from the asynchronous formation and filling of canopy openings rather than structural diversification of single patches. The basic spatial unit of the mosaic, characterised by a certain structural homogeneity, is an area corresponding to the crown width of large canopy trees. However, some authors have argued that structural similarity may be attributable to much larger areas, ranging from one to a few thousand square meters (Leibundgut, 1979; Korpel', 1993; Emborg et al., 2000). In this case, the patchiness results from some general spatial and temporal correlation of tree die-off processes, which then sets in motion regeneration and recruitment processes.

The objective of this study was to explore a near-virgin forest composed of climax shade-tolerant species in terms of the spatial distribution of live and dead canopy trees, the variability of the basal area, the vertical forest structure, and the occurrence of regeneration. Addressing this objective within a patch-mosaic framework raised the following questions: (1) Is there any spatial relationship between the number of live and the number of dead trees in neighbouring small patches of a size that corresponds to the horizontal projections of the canopy tree crowns? Are these small patches organised into units of a higher order to which a developmental stage attribute (*sensu* Leibundgut, 1979; Korpel', 1993) could be assigned or do they develop rather independently? (2) Is the heterogenous forest structure a result of the spatial coexistence of small homogenous patches or may some attributes of structural heterogeneity be assigned to these small patches themselves? (3)

What is the relationship between the basal area and the vertical forest structure in small spatial scales? Are the patches with maximal basal area characterised by a simple vertical forest structure that results from discontinuous regeneration and recruitment processes?

2. Study site

Except in the case of very poor soils, the lower montane belt of the Western Carpathians (between 600 and 1100 m a.s.l.) is covered by structured forests dominated by European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.), with some admixture of other species. On the basis of the Grime model, both these dominant species may be rated among C–S strategists (Brzeziecki and Kienast, 1994). Silver fir, a long-living arborescent species (in the Carpathians up to 400–450 years), is one of the most shade-tolerant trees, reaching up to 50 m in height. European beech is somewhat less shade tolerant, reaching up to 45 m in height and 200–250 years in age under typical Carpathian conditions (Jaworski, 1994). Additionally, thanks to wide crowns with a remarkable ability for lateral expansion, European beech is an extraordinary gap maker and gap filler (Schütz, 1998). However, because of easily decomposing wood and a labile root system requiring sufficient soil oxidation, it is somewhat more vulnerable to breakage and uprooting than is silver fir (Nagel and Diaci, 2006). Nevertheless, under typical conditions, the dynamics of the West Carpathian beech-fir forests are driven by small-scale disturbances; therefore, gaps that reach the forest floor and cover an area larger than a few hundred meters are infrequent.

This study was conducted in the Łabowiec reserve, located in the Sądecki Beskid of the Western Carpathians, one of a few protection areas established in 1905–1924 by Count A. Stadnicki, the forward-looking, highly educated forester, manager and owner of the Sądecki Beskid forests (Jaworski, 2002). As the reserve area has been enlarged several times (to over 53 ha), at present it consists of fragments that exhibit different degrees of human impact. Around the reserve, a Swiss irregular and regular shelterwood system with a long (30–60 years) regeneration period has been applied. This survey was conducted in the best preserved area (7.8 ha), which shows no signs of direct human activity (stumps and cut trees). Nevertheless, the development of this stand may have been influenced by such factors as air pollution or an excessive number of ungulates (to mention only the most important).

Located in the lower montane belt in the height zone 840–960 m a.s.l. on a north-eastern slope, the stand is well protected from the prevailing western and southern winds. The slope incline changes gradually from 5° at the foot to 30° at the upper part. Dominated by European beech (*F. sylvatica* L.) and silver fir (*A. alba* Mill.), the stand represents the most common in the lower montane belt of the Western Carpathians association of eutrophic beech forest *Dentario glandulosae-Fagetum*. The proportion of fir increases in the lower part of the reserve. Leached brown and acid brown soils (eutric and dystric cambisols, according to WRB (1998)) developed on flysch rocks prevail in the Łabowiec. The average annual temperature

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