

Spatial Statistics 2011 – Mapping Global Change

Natural disturbance dynamics in an old-growth forest: from tree to landscape

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Abstract

Forest structure is the result of past disturbances, regeneration establishment, competition, and mortality dynamics. Natural disturbances can create single dead tree to larger canopy gaps creating both small and large scale patterns and processes. The analysis of forest spatial pattern can provide information on these dynamics shaping forest ecosystems. Knowledge about primeval forest dynamics is relevant for their conservation and is an important reference for delineating sustainable forest management.

The main aim of this research was to assess forest structure and understand spatial patterns and related disturbance processes in a mixed silver fir-Norway spruce-beech old-growth forest. The study site is the forest reserve of Lom, an old-growth forest located in Bosnia and Herzegovina. We analysed forest structure at different scales and with different approaches : a) landscape, b) forest, and c) single tree.

A Kompsat-2 satellite image was used for forest canopy gaps delineation (a). The classification was based on an artificial neural network and allowed the identification of 297 canopy gaps (50-1776 m²). The size and spatial pattern of the gaps were found to be different between core area and buffer zone.

Forest structure (b) in the core area was analysed applying a 120 m grid sampling design (40 plots). From this preliminary analysis we identified a stand with typical old-growth characteristics in the central part of the core area and a 1 ha intensive sampling plot was established (c). Inside the plot all trees were mapped, measured, and a core extracted to assess tree age. Spatial structure was investigated by means of Point Pattern Analysis and LISA (Local Indices of Spatial Autocorrelation). The three scales and approaches produced consistent results. The landscape approach confirmed the hypothesis that small-scale processes predominate at Lom especially within the core area of the reserve. At the forest stand level the presence of small scale disturbance/mortality processes was confirmed.

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Selection and peer-review under responsibility of Spatial Statistics 2011

Keywords: old-growth forest; natural disturbances; Gaps; spatial pattern; forest structure

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1. Introduction

Forest structure is the result of past disturbances, regeneration establishment, competition, and mortality dynamics [1]. Natural disturbances can create single dead tree to larger canopy gaps creating both small and large scale patterns and processes. The analysis of forest spatial pattern can provide information on these dynamics shaping forest ecosystems [1,2]. Knowledge about primeval forest dynamics is relevant for their conservation and is an important reference for delineating sustainable forest management.

The montane belt of most of the southern European mountain ranging from the Alps to the Balkan peninsula are largely dominated by beech (*Fagus sylvatica* L.) often associated with silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst.). This forest type plays an important role in the European silviculture not only for its wide range or its economical value but also because the mixed old-growth forests of central Europe have been used as a reference for important silvicultural models. Remnants of primeval mixed fir-spruce-beech forests are still present in the Balkan peninsula, the conservation of which is guaranteed by forest reserves [3]. An example of these protected area is the Lom forest reserve [4,5].

The main aim of this research was a) to assess spatial patterns of canopy gaps in the overall forest reserve, b) to describe forest structure of the core area of the reserve, and c) to analyse tree spatial pattern in an old growth stand inside the core area.

2. Methods

2.1. Study area

The study was conducted in the Lom Forest Reserve located within the Klecovača mountainous region (north western Bosnia-Herzegovina). The Reserve (298 ha) was established in 1956 in order to protect the old-growth remnant, delineating a strict reserve area (56 ha) with no discernable anthropogenic influence and a surrounding buffer zone (242 ha) where some anthropogenic disturbance took place in the past [4].

The forest is a mixed fir – spruce- beech forest with the presence of maple (*Acer pseudoplatanus* L.) in the upper part. Silver fir is the dominant species, followed by Norway spruce, and beech that occupy mainly suppressed layers [5].

2.2. Field sampling

We investigated the spatial pattern of canopy gaps on the overall forest reserve and the forest structure inside the core area. For the canopy gaps analysis we produced maps using a remote sensing approach and the map accuracy was assessed through ground control points collected in a field campaign (2010).

Inside the core area we applied a 120 m grid sampling design, recording dendrometric parameters for both living tree and deadwood in 40 plots (Fig.1). A standardized sampling protocol already applied in other forest reserves [6,7] was used. Starting from this preliminary analysis we individuated in the central part of the core area a stand with typical old-growth characteristics (multilayered vertical structure, large and old-trees, with high level of both living and dead biomass) in order to establish a 1.1 ha intensive sampling plot (see [5] for survey details). Inside the plot all trees, snags, stumps, and logs were mapped, measured, and an increment core was extracted from each trees in order to assess the age.

2.3. Data analysis

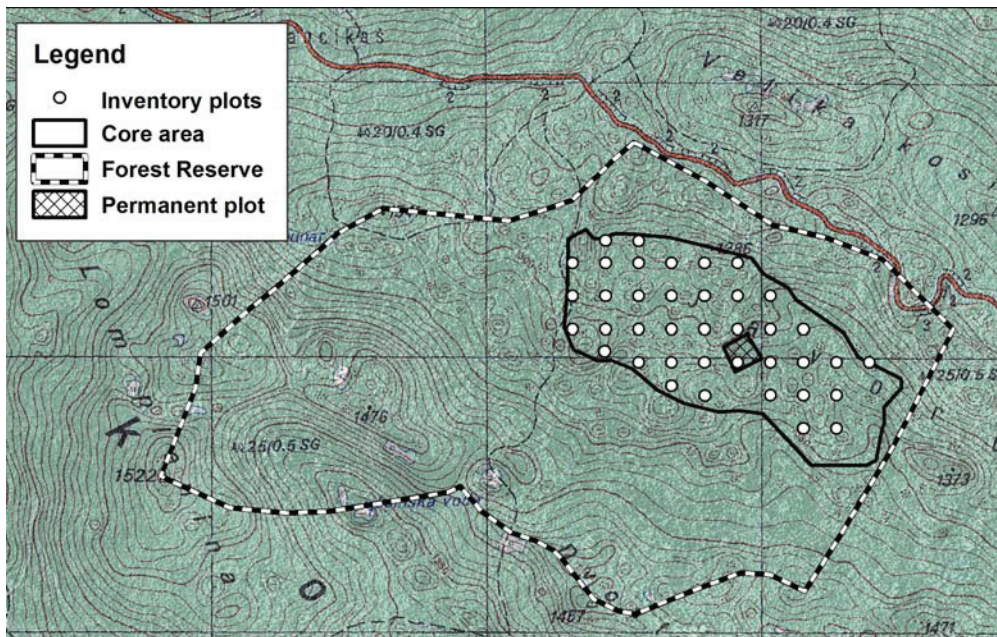


Fig. 1. Study area with the localization of inventory and permanent plots.

The forest canopy gap map was derived from a high resolution Kompsat-2 image acquired in June 2009 [8]. In order to analyze the spatial pattern of gaps we computed *Ripley's K(d)* and *O-ring* statistics (the latter in order to avoid misinterpretation of *K*-function analysis due to the cumulative effects [9]) by means of Programita software [10]. We applied the square root transformation $L(d)$ that makes the $K(d)$ function linear, stabilizes its variance and has an expected value of approximately zero under the Poisson assumption [1]. We treated the gaps as object of finite size avoiding the centroid extraction and subsequent point approximation that could lead to misleading results if the size of objects varies significantly [10,11]. For the null model we applied a random rotation and positioning within the boundaries of the area of interest [11]. We carried out the analysis for the core area and the buffer zone separately, in order to understand and compare natural and human influenced gaps pattern respectively.

The same indices were computed for trees in the permanent plot, both for the overall tree population and stratified by species, age classes, and vertical strata position. The vertical strata definition was assessed following Latham et al. [12]. Different null hypotheses were chosen accordingly to the processes involved in the spatial pattern delineation, in order to avoid misinterpretation of the results [13]. Complete spatial randomness (CSR) was adopted as null model for the univariate analyses. For the living vs. dead stems analysis, we chose the null hypothesis of random mortality applying the random labeling method [14], since the mortality agents can only work within the limits set by the distribution of living trees prior to the disturbance events themselves [15]. For the old vs. young trees analysis the “antecedent conditions” hypothesis was applied. For all the others set of analysis we chose the independence hypothesis. In order to investigate if spatial structure was related to tree age (i.e. establishment period), we computed Moran

I(d) and local indices of spatial autocorrelation (LISA) such as Local $G_i^*(d)$ statistics (including Max G_i^* , and Max G_i^* distance)[16].

3. Results

Inside the forest reserve we detected 650 gaps, 548 in the buffer zone and 102 in the core area. The density was 2.3 and 1.7 gap ha^{-1} respectively. The maximum gap size was larger in the buffer zone (1776 m^2) than in the core area (320 m^2). The spatial pattern of gaps inside the overall forest reserve revealed a clumped distribution, but differences were found between core area and buffer zone (fig. 2). In the buffer zone a clumped distribution was found while in the core area the gap distribution was not significantly different from CSR. The *Ripley's K* results were consistent with the *O-ring* analysis.

The average tree density inside the core area was 489 tree ha^{-1} (60% beech, 25% silver fir, 14% Norway spruce), and mean basal area was 47.1 $m^2 ha^{-1}$ (47% silver fir, 30% beech, 22% Norway spruce). The living tree volume was quite high, accounting for 763.1 $m^3 ha^{-1}$ (range 353-1233 $m^3 ha^{-1}$), while the deadwood was 327.3 $m^3 ha^{-1}$.

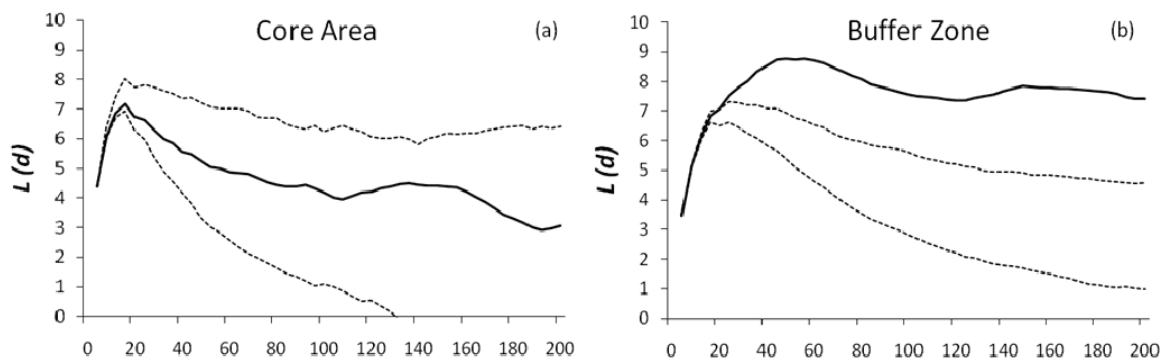


Fig. 2. (a) *Ripley's K(d)* for canopy gaps inside the core area and (b) in the buffer zone. Dashed lines are the confidence envelopes (99%). The square root transformation, $L(d)$, was applied.

The permanent plot is very rich both in living (1157.9 $m^3 ha^{-1}$) and dead biomass (383.3 $m^3 ha^{-1}$). Silver fir (45%) and Norway spruce (37%) accomplished the majority of tree volume while beech predominates in number of individuals (63%). The oldest trees were respectively 441 years old for silver fir, 432 for Norway spruce, and 393 for beech. We identified three different layers of trees: dominant (height > 29.4 m); intermediate (29.4 m < h > 22.3 m), and suppressed (h > 22.3 m). Beech was the dominant species (73 %), in the suppressed layer and while the conifers were the most represented (50% silver fir, 44% Norway spruce) in the dominant one. The spatial arrangement of standing dead trees and stumps did not differ from the random mortality hypothesis. Young trees were found to be clumped for all the species (Fig. 3). Aggregation decreased along with tree ageing and from suppressed to dominant layer. Cross regeneration was found to be the rule between the two coniferous species, while beech tend to establish far from old trees. Heterogeneous patterns were found between species x age classes analysis revealing different establishment strategies and mortality processes among the three species. The only significant ($p < 0.05$) global *Moran's I* correlogram was the beech was one, revealing a spatial age structure with a patch size of 25 m.

Age (years)	Overall			Fs			Aa			Pa		
<150	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green
150-300	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green
> 300	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green
Distance	Short	Medium	Long	Short	Medium	Long	Short	Medium	Long	Short	Medium	Long

Strata	Overall			Fs			Aa			Pa		
Dominant	Red	Green	Green	Green	Green	Green	Red	Green	Green	Green	Green	Green
Intermediated	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green
Suppressed	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green
Distance	Short	Medium	Long	Short	Medium	Long	Short	Medium	Long	Short	Medium	Long

Fig. 3. Spatial arrangement of trees inside the permanent plot. Green block means aggregation, Red block means repulsion. The distance values are aggregated in short (1-15 m), medium (15-30 m), long (30-50 m) distance classes.

Attraction was found between fir and spruce both considering young trees (< 150 years) and adult trees (age between 150 and 300 years), while repulsion was found between beech and the two conifers in the same classes. Young firs tend to be associate to old spruce trees (>300 years), and same pattern was found between young spruces and old firs. The analyses conducted for the conifer species revealed repulsion between old and young trees.

The LISA analyses revealed weak autocorrelation for tree age at small scale (single tree or small number of trees).

4. Discussion

The Lom reserve represents a well preserved Balkan old-growth forest with high value of volume both of living trees and deadwood.

The random distribution of natural canopy gaps inside the core area is consistent with other studies dealing with temperate forests in Europe [11] and North America [17]. The spatial distribution of canopy openings is a parameters to be considered in forest management in order to mimick natural disturbances.

The aggregation among trees was the dominant pattern influencing the current forest structure, especially for small and young trees. The tendency toward a random or more regular distribution as tree ageing or increasing their size has been observed in different forests [9,18].

The Lom old growth forest is currently shaped by single tree/small scale disturbances and mortality processes. The absence of major and intermediate disturbances was probably consistent in the last 3 centuries. The establishment for the three species seems to be continuous and the subsequent recruitment in the upper layers more relate to canopy gaps, especially for beech. A local dynamic of species alternation is evident between silver fir and Norway spruce, while beech tends to constitute a matrix occupying the gaps between conifers.

The three scales and approaches produced consistent results. The landscape approach confirmed the hypothesis that random small-scale processes predominate at Lom especially within the core area of the reserve. At stand level the predominance of small scale processes was confirmed by the spatial structure analyses that evidenced the single tree nature of these processes.

Acknowledgement

The research was partially supported by Planet Action Project "Bosnian old-growth forests" (<http://www.planet-action.org/>).

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