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(Article begins on next page)

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Toward a definition of the range of variability of central European mixed *Fagus-Abies-Picea* forests: the nearly steady-state forest of Lom (Bosnia and Herzegovina)

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**Abstract**

Knowledge on the range of variability of montane European forests is hampered by limited data on natural disturbance regime and by the small size of old-growth remnants. We studied the mixed *Fagus-Abies-Picea* Forest reserve of Lom (55.8 ha) in Bosnia and Herzegovina at three different scales: a grid of 40 sampling points to describe the structural characteristics and their range of variability, 3 transects to analyse gap size and gap fraction and a 1.1 ha permanent plot to reconstruct age structure and disturbance history. The forest is characterized by high volume of living trees (763 $m^3ha^{-1}$ in the 55.8 ha core area and 1160 $m^3ha^{-1}$ in the permanent plot) and of coarse woody debris (327 $m^3ha^{-1}$ and 383 $m^3ha^{-1}$ respectively). The percentages of forest area in canopy and expanded gaps are 19% and 41%, respectively. The median canopy gap size is 76.9 $m^2$, and ranges from 11.1 $m^2$ to 708.0 $m^2$. There are big (up to 120 cm dbh) and very old trees (441, 432 and 416 years for silver fir, Norway spruce and beech respectively). During the last three centuries the disturbance patterns have been characterized by single-tree or small group mortality. In central Europe this forest is at the end of a gradient from forests characterized by intermediate disturbances to those where very small-scale processes predominate.

# 1 Introduction

Scientific understanding of the nature of disturbance events and successional or recovery processes in natural ecosystems has increased dramatically during the last decades (Frelich 2002; Pickett and White 1985). In old-growth research a major paradigm shift has occurred from the view that equilibrium processes predominated in ecological systems (the Clementsian view) to one that systems, especially forests, are largely structured by disturbances (Pickett and White 1985). At the same time, while past management was concentrated on extracting products from the forest, there has been a shift in focus to what is being retained, with legacies of the disturbances considered to be critical for maintaining biodiversity (Kohm and Franklin 1997). In regions where there are large and well preserved old-growth that can be used as a reference (Spies and Duncan 2009), more recent approaches utilize information on the natural disturbance regime as a guideline for sustainable management (Bergeron and Harvey 1997; Long 2009).

Worldwide analyses of old-growth forest ecosystems have shown that the temporal and spatial interplay between individual tree mortality and larger disturbances at varying scales, from small gaps to landscapes, creates a multitude of developmental pathways ranging from single-cohort stands after severe disturbances to nearly steady-state forests (Antos and Parish 2002; Parish and Antos 2006). Description of the complete forest development cycle is particularly difficult in the regions where natural processes have been almost completely obscured by anthropogenic land-use as in central Europe. In this region, wind, snow and insects are considered the main disturbance agents (Schelhaas et al. 2003). Anthropogenic effects have been of long duration and interacted with natural factors so that some natural disturbance effects have been obscured by human activities and they now cannot be completely distinguished (Garbarino et al. 2009).

The montane belt of central Europe,is largely dominated by beech (*Fagus sylvatica* L.) that is often associated with silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) Karst.) (Horvat et al. 1974; Mayer and Ott 1991). This forest type has played an important role in European silviculture not only because of its wide range and economical value but also because mixed old-growth forests of central Europe have been used as a model for single tree selection silviculture (Pretzsch et al. 2008; Schütz 1990; Brang 2005).

The interest of European foresters in old-growth forest started in the 19th century (Göppert 1868; Wessely 1853). At the end of the 19th century, when the silviculture was culturally dominated by simplified, monospecific and monolayered models, the development of a close-to-nature approach was mainly based on the development, or the restoration, of mixed multi-layered forests (Biolley 1920; Gayer 1898; Gurnaud 1886). In the second half of the 19th century the stand structure of small remnants of the central and southern European *Fagus-Abies-Picea* old-growth was analysed and used as a model to develop a single tree selection silviculture (Korpel 1995; Leibundgut 1982; Susmel 1980). These studies focused on the late seral stage (Korpel 1995) and were still influenced by the equilibrium theory of communities (Standovár and Kenderes 2003). They largely neglected the role of the disturbances, which were viewed as extraordinary events interfering with "normal" forest structure and development (Puettmann et al. 2009; Seidl et al. 2011).

Among central European countries, Bosnia and Herzegovina is relatively rich in primeval and old-growth forests that have captured the attention of European foresters for many decades (Fröhlich 1930; Hofmann 1985; Leibundgut 1960; Susmel 1956).

Specific objectives of the study were to (1) describe structural characteristics and development of the Forest reserve of Lom, (2) highlight spatio-temporal patterns of the disturbance regime and 3) compare Lom with other Central European old growth in order to describe the natural range of variability structure and disturbance regime of Central European *Fagus-Abies-Picea* forests and 4) discuss management implications.

2. Material and methods

2.1. Study area

This study was conducted in the Lom forest reserve (centered at 44.482 N and 16.427 E) in the Dinaric Alps, in the Klekovača mountain range in Bosnia and Herzegovina (Fig. 1). The annual average precipitation is around 1600 mm, with maximum in December and minimum in July. Mean annual temperature is around 7.8°C (Drinic 730 m a.s.l., 7 km from the reserve). The bedrock is limestone with a characteristic carsic geo-

morphology (cliffs, gentle slopes, sinkholes and small flat areas). The elevation ranges from 1250 to 1522 m a.s.l. The vegetation type is *Piceo-Abieti-Fagetum illyricum* (Maunaga 2001). The reserve has a total surface of 297.8 ha and a core area of 55.8 ha. The reserve was established in 1956 and represents a well preserved old-growth mixed montane forest (Drinić 1956; Pintarić 1999). Browsing of terminal shoots, fraying and bark stripping by red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) are rare. The Klecovaca mountain range hosts big predators like wolf (*Canis lupus* L.), brown bear (*Ursus arctos* L.) and European linx (*Linx linx* L.).

2.2. Sampling procedures

We measured living trees for diameter at breast height (dbh, 130 cm height) ≥ 7.5 cm and the coarse woody debris (CWD) grouped into snags (standing dead trees, dbh ≥ 7.5 cm and height ≥ 1.3 m), downed logs (fallen stems or branches ≥ 7.5 cm diameter and length > 1 m), and stumps (short, vertical remains from cutting or windthrow, top diameter ≥ 7.5 cm and height < 1.30 m). The separation of snags from logs was established at a 45° leaning angle. We sampled at three different scales: a) a regular grid of temporary sampling points across the whole core area, b) three 40 m wide parallel belt transects and c) a 1.1 ha long-term permanent plot.

a) Core area

We superimposed a regular 120 m grid to the 1:10000 raster map of the core area resulting in 40 sampling points (Fig. 1). At each sampling point, four types of measurements were applied (Castagneri et al. 2010): (a1) in a 615.5 m$^2$ circular plot (radius = 14 m) we recorded species dbh (to the nearest 0.01 m) and height (to the nearest 0.5 m) for all living trees; (a2) in a 113.1 m$^2$ round plot (radius = 6 m) species and height of each understory and gap tree (h > 10 cm and dbh < 7.5 cm) were recorded; (a3) on a 50 m line intersect oriented northward from the centre of the sampling point, we measured, as described above, each log crossing the line (Van Vagner 1968); and (a4) in a 50 x 4 m rectangular plot centered on the previous line we measured stumps (diameter at the ground and at the top) and snags (dbh). For each element of CWD species

(when possible) and decay class (Nagel and Svoboda 2008) were recorded (class 1 fresh, class 5 very old).

Volume for living trees and snags were calculated according to local volume tables. Volume for logs, stumps and broken snags was calculated according to methods described in Motta et al. (Motta et al. 2006).

Principal component analysis (PCA) was used to explore the correlation structure of four categories of variables: structure of living trees, coarse woody debris, regeneration, and environmental (topographical and anthropogenic) variables. Data for living trees, dead trees, and regeneration were collected in the field. Anthropogenic variables (e.g. proximities to roads or to core area borders) were calculated in a GIS environment using Euclidean distances (Roath and Krueger 1982). Topographic variables were derived from a 30 m resolution digital elevation model (ASTER Global Digital Elevation Model) (Slater et al. 2009).

PCA multivariate analyses were performed using the PC-ORD 5 statistical package (McCune and Mefford 2006). The statistical significance of all ordination analyses were tested by the Monte Carlo permutation method based on 10000 runs with randomized data.

b) Gaps

Three parallel belt transects (Nakashizuka 1989) 40 m wide (length ranging between 60 and 100 m) were randomly established, with a minimum distance of 300 m apart, within the core area of the Lom Forest Reserve (Bottero et al. Submitted) (Fig. 1). Both canopy gaps (gap fraction) and expanded gaps were measured (Runkle 1982). The canopy gap was measured as the hole in the canopy defined by the tree crowns bordering the gap, and the expanded gap was the area delineated by the trunks of these adjacent trees. Gaps were defined as openings in the forest canopy larger than 10 m$^2$ caused by the mortality of one or more trees with a diameter at 1.30 m height (DBH) > 25 cm. Therefore, canopy openings were only considered gaps if at least a remnant of a gapmaker was present. Dead trees less than 25 cm DBH were not considered large enough to create a canopy gap. When gap fillers reached a height of 20 m, the gap was considered closed. We measured radii (distance and direction) from the centroid of the gap to each vertical crown projection and the corresponding bole of the trees bordering the gap to calculate gap (gap and expanded gap respectively) size (Runkle 1985).

c) Permanent plot

Based on the results of the PCA and after extensive reconnaissance we selected a typical late seral stand rich in live and dead biomass, far from the road system and located on a gentle slope, in order to reduce the topography influence. In the stand we established a 1.1 ha permanent plot (Fig. 1) where we mapped and labeled each living tree and each piece of CWD (same definitions used for the network).

For the living trees (dbh> 7.5 cm) we recorded species, x-y coordinates, dbh, total height, height to the lowest live branch in two opposite directions and crown projections on the ground in four directions. In order to describe the vertical structure of tree crowns, we applied the TSTRAT algorithm (Latham et al. 1998). The algorithm determines a vertical height cut-off point and assigns trees to strata (dominant, intermediate or suppressed for other strata) depending on the relative position of shorter trees to the height cut-off points.

For each CWD piece we recorded species (when possible), dbh (snags), length (logs) height (snags and stumps), diameter at each end (logs and stumps) and the decay class (Nagel and Svoboda 2008). We noted if logs were from uprooted or snapped trees (Worrall et al. 2005). Volume for living trees and for CWD was calculated in the same way as previously described for the network of sampling points.

2.3 Dendroecological research

To determine tree age and growth patterns in the permanent plot one core was collected at 50 cm above ground from all living trees. In the laboratory, all cores were fixed to wooden supports and prepared with a razor until an optimal surface resolution was obtained. Tree ring widths were measured to the nearest 0.01 mm, using the LINTAB device and TSAP-Win software package (Rinntech, Heidelberg, Germany).

For cores that included the pith, age was recorded as the number of rings between the pith and the cambium. For cores that fell short of the pith, pith location was estimated graphically. Once pith location had been estimated, missing radius was estimated starting from the innermost ring. Rings taken from the innermost part of the core were then counted until a segment equal in length to the estimated missing radius; this

number was added to the number of rings in the core to obtain the estimated tree age at the coring height (Motta and Nola 2001). This method assumes that the estimated missing rings form concentric circles. Individuals with a rotten core, and those for which it was impossible to estimate pith location and the number of missing rings, were not considered for age structure but evaluated for growth releases.

To identify past disturbance events we analyzed growth releases in the cores. Releases from suppression were identified using a running mean radial-averaging method (Fraver and White 2005; Rubino and McCarthy 2004). We applied a conservative approach where only abrupt (>100% growth increment) and sustained (>15 years) release were selected (Lorimer and Frelich 1989). The software JOLTS (version 6.01P by R.L. Holmes, University of Arizona, USA) was used for this purpose (Berg et al. 2006; Brose and Waldrop 2006). A chronology of all the releases recorded in the permanent plot was constructed and release data were summarized as the percentage of trees in a given decade showing a growth release (Motta et al. 1999).

Accurate ring counts and crossdating are challenging in late seral developmental stages where most of the trees have potentially spent a relevant part of their life in the shaded understory. In suppressed trees, especially in the beech, ring anomalies and missing rings are frequent and the assignment of precise calendar dates is not possible. For this reason the rate of successful crossdating was very low (less than 50%). In order to take into account this uncertainty and others bias introduced by the procedure utilized for age estimation the age structure was constructed for 10-yr classes (Payette et al. 1990). The disturbance chronology has the same limitations but in this case we can hypothesize that the rate of potential errors due to ring anomalies or missing rings is lower because after the end of the suppression and the canopy accession (where we can detect a release) the assignment of the correct calendar year to each tree ring is much more reliable.

3) Results

3.1) Core area

All the temporary sampling plots were mixed-species and had a multilayered structure. The average density of live canopy trees was 489 ha$^{-1}$ (Table 1). Beech comprised 60.5%, silver fir 24.9%, Norway spruce 14.1% and other species 0.6% of live stems. The average volume was 763 m$^3$ha$^{-1}$ and the average basal area was 47

$m^2ha^{-1}$. Beech comprised 48.0%, silver fir 27.9%, Norway spruce 23.4% and other species 0.7% of live volume. The average density of regeneration was 4837 individuals $ha^{-1}$. Beech comprised 43.9%, silver fir 37.0%, Norway spruce 16.2% and other species 2.9% of regeneration individuals. While most of the silver fir and Norway spruce saplings showed clear apical dominance, most of the beech saplings grew plagiotropic, or flat. The diameter distribution exhibited a rotated sigmoidal form (Fig. 2), characteristics of old-growth stands (Goff and West 1975; Goodburn and Lorimer 1999).

The CWD average volume was 327 $m^3ha^{-1}$ (Table 2). CWD represents 42.9% of volume of living trees. Within the total volume of CWD, the volume of logs (72.2%) was much greater than the volume of snags (24.9 %) and stumps (2.9%). Regarding the CWD profile, all the decay classes were represented but decay class 4 was the modal value followed by classes 5, 3, 2 and class 1, which represent the recent dead trees and which had less volume than the others (Table 3). The absence of bark and the decay rate made field identification of the species problematic for most of the samples.

Inside the core area, the absence of external or environmental factors shaping forest structure was highlighted by the PCA. The multivariate ordination analysis revealed weak relationships between forest structure and environmental variables, highlighting a relative absence of structural gradients within the core area (Table 4). In fact, the correlation coefficients between environmental variables and principal components were very low, ranging from -0.009 to 0.346. The first 3 axes were significant and accounted for a cumulative 64.1 % of the total variation.

3.2) Gaps

56 gaps were sampled on the three parallel belt transects. The mean canopy gap fraction was 19.3%, while the percentage of forest area in expanded gaps amounted to 41.4%. The median canopy gap size was 76.9 $m^2$, but gap size was variable, ranging from 11.1 $m^2$ to 708.0 $m^2$. A similar pattern was observed for the expanded gap size, which had a median of 192.9 $m^2$, and range of 41.7 $m^2$ to 1085.2 $m^2$ (Fig. 3; Table 5).

Most gaps were less than 100 $m^2$ (62.5%), whereas only 3.6% of gaps were larger than 500 $m^2$. Although canopy gaps smaller than 100 $m^2$ were the most frequent, they occupied only 26.5% of the total canopy gap

area, while canopy gaps larger than 500 m$^2$ occupied 22.5% of the total canopy area.

## 3.3) Permanent plot

### a) Stand characteristics

The living tree density was 617 ha$^{-1}$ (Table 6). Beech comprised 61.1%, silver fir 26.7% and Norway spruce 12.1% of living individuals.  The volume was 1159.9 m$^3$ha$^{-1}$ and the basal area was 69.3 m$^2$ha$^{-1}$. Beech comprised 17.7%, silver fir 45.5% and Norway spruce 37.7% of living volume. The diameter distribution exhibited the same rotated sigmoidal form observed in the whole core area (Fig. 4).  The two diameter distributions (core area and permanent plot) were not significantly different (Kolmogorov-Smirnov two samples goodness-of-fit test; $\alpha = 0.05$). The tallest tree was a 46 m Norway spruce. The cut off points of the vertical layers were 29.4 m for the dominant, 22.3 m for the intermediate. Silver fir (49.5%) and Norway spruce (44.7%) were the two most represented species in the dominant layer (Fig. 5). On the other hand beech was the most represented species in both the intermediate (59.8%) and suppressed layers (74.0%).

The volume of CWD was 383 m$^3$ha$^{-1}$. CWD represented 33.3% of the volume of living trees. Among the CWD, the volume of snags (51.4%) was greater than the volume of logs (45.7 %) and stumps (2.9%). 37.4% of standing dead trees were snags with broken tops. For the intact standing dead trees, the average dbh was 21.7 cm (range 7.5-117 cm), while for the broken snags the average dbh was 61,0 cm (range 10-106 cm). The average size at the large end of the log was 32.9 cm (range 7.5-120 cm). Among the logs, 15.7% had a large end diameter > 50 cm.

Regarding the CWD profile, all the decay classes were represented but the decay class 4 was the modal value, followed by classes 3, 5, 2 and class 1 (Table 3).

### b) Dendroecology

The oldest trees of each species were 441, 432 and 416 years for spruce, silver fir and beech respectively. Ages were underestimated because years to reach the coring height were not included; in addition wedging

or absent rings near the pith are frequent as a consequence of suppression. For this reason we were not able to estimate the age of 115 trees (19% of the total).

Tree establishment has occurred irregularly throughout the last four centuries, both in terms of total number of trees established and in term of species incidence (Fig. 6). Dominance of beech (the most successful species in term of regeneration) in the more recent decades was expected. On the other hand it was not clear why the relative abundance of Norway spruce was high in some decades between 230 and 360 years, or why the age distribution of silver fir was irregular. A pulse in establishment of the three species was observed between 200 and 250 years ago. The small number of trees younger than 70 years was due to the fact that trees < 7.5 cm dbh were not cored.

As expected there was little relationship between both diameter and height with age. In the dominant layer the age range was 440-120 years and the modal age class was 300 years (Fig. 7) while in the intermediate and suppressed layers the range of ages was 430-90 (modal class 250 years) and 370-40 years (modal class 80 years) respectively.

We identified 557 releases (65.5% beech, 25.0% silver fir and 9.5% Norway spruce) in the decades where the sample depth was greater than 50 trees (1690-1990). Growth releases occurred throughout the history of the stand (Fig. 8). The incidence of releases in each decade was relatively low, with the highest incidence in the decades centered on 1940 (14.7% of trees showing releases); there were only two other decades with an incidence of abrupt growth release > 10%: 1690 (11.2%) and 1930 (10.1%). No relationships were found between decade of tree establishment (e.g. between 200 and 250 years ago) and incidence of releases (neither establishment in the same decade nor establishment in the following 2-5 decades). Examination of the stand map showed that releases were scattered not only in time but also in space throughout the plot in each decade, indicating no spatio-temporal trends.

4) Discussion

4.1) A relatively uniform and stable old-growth forest.

The structure (vertical structure, CWD profile, size and the age of the trees) and the small-scale gap dynamic of the whole Lom core area are consistent with an old-growth stage. A few signs of anthropogenic activities (stumps probably from single-tree illegal logging) were found near the borders (north-east and north-west) between the core area and the buffer zone and along the main trail crossing the whole reserve but their impact could be considered irrelevant both at the stand and at the core area scale.

The core area of the Lom forest reserve was structurally uniform as evidenced by the relatively small range and SD of each analyzed parameter (Tabs. 1, 2 & 4). The only parameter with high variability, as expected, was the density of regeneration. In addition, the forest structure was relatively stable in time as evidenced by the comparison of the structure described in this research with those previously described by Maunaga (2001) in the whole Lom reserve (including the buffer area) and by Drinic (1956) in 4 large representative sampling plots.

4.2) Disturbance history and species coexistence

The gap size (Table 5) and the combination of age structure (establishment) and abrupt growth releases (disturbances) provided no evidence of stand-replacing or intermediate disturbances for at least the last three centuries (Figs. 6 & 8). The absence of large gaps was confirmed by a further remote sensing analysis conducted on a larger area (Garbarino et al. Submitted). There was no evidence of decades with high incidence of disturbances and associated regeneration pulses. Size (diameter) and age were only weakly related, as it is frequently observed for shade tolerant species, given that trees can spend long periods, even decades or centuries, in the shaded understory layers (Fig. 7). The disturbance regime in the last three centuries has been dominated by small gaps created by uprooted, snapped and standing dead trees (Bottero et al. Submitted). These events allowed the establishment of new regeneration cohorts and, mainly, allowed previously intermediate or suppressed trees to reach the canopy layer.

All three dominant species are able to regenerate and persist in the stand in the absence of intermediate and/or major disturbances. The three species showed a similar age range and longevity (Fig. 6), therefore, our data do not support the hypothesis of a different length of life cycle for beech and the two conifers (Korpel 1995; Podlaski 2008). Beech is the dominant species both in the gaps and in the suppressed layers beneath the main canopy. Actually, beech has faster growth than silver fir and Norway spruce over a range of light conditions, particularly at higher light levels (Stancioiu and O'Hara 2006). Even though regeneration depends on the frequency of mast years, beech (Piovesan and Adams 2001) is generally the most successful species in establishing after a small or an intermediate-scale disturbance event. The relative rarity of beech in the intermediate and dominant layers could be explained by the different ability of the suppressed trees to react to small-scale disturbances. When beech is suppressed for a long period, it loses the ability to produce an upright excurrent stem and becomes plagiotropic, or flat-topped (Rozenbergar et al. 2007). For this reason, it is much more difficult for suppressed individuals of beech to respond, compared to suppressed silver fir and Norway spruce, making beech under-represented in the intermediate and dominant layers (Schütz 1992, 2001).

The reason for the irregular silver fir and Norway spruce age distribution is probably due to the fact that these two species have more restrictive establishment and early growth requirements. Since Norway spruce is able to survive long periods of suppression and it is also able to react promptly to a canopy opening, the observed irregular age structure was probably the result of some past events, not highlighted by the release chronology, or of some life-history peculiarity relating to regeneration requirements and rate of mortality. In order to clarify the spatio-temporal dynamics and the species relationships in this forest type, other studies in montane central European mixed old-growth forests are required. Furthermore, the present age structure is a record of both establishment and subsequent survival up to the moment of sampling, and a lack of trees of some species dating from a given period may be due to a lack of establishment and/or high mortality rates of trees regenerating at that time (Johnson et al. 1994).

The small scale mortality processes observed at Lom limited the establishment of less shade tolerant species like sycamore maple (*Acer pseudoplatanus* L.) that had an incidence of 0.3% among the trees and 3.2% among the regeneration. In the upper part of the reserve, in the buffer zone outside the core area, sycamore

was more abundant, possibly due to the fact that forests in the upper montane belt stands are naturally more open (the vegetation type is referred as *Aceri-Fagetum subalpinum*). Alternatively it could be a legacy of past anthropogenic disturbances (logging and grazing) or, even the consequence of some past natural disturbance promoting the co-existence between beech and maple as observed in North America (Poulson and Platt 1996).

Finally, even if the density of wild ungulates is relatively low compared with densities observed in other old-growth in the same region (Diaci et al. 2010; Klopcic et al. 2010), it is possible that browsing has influenced mortality and early growth of the more palatable species (e.g. silver fir and sycamore maple).

4.3) Lom compared with other central European old-growth forests

The occurrence of ultilayered structure, advanced age reached by the oldest trees of the three predominant species, high volumes of CWD and living trees among the highest measured in Central European old-growth (Holeksa et al. 2009), place this stand among the most remarkable old-growth stands of this forest type (Table 7).

Recent studies in central European mixed montane old-growth forests (Dobrowolska and Veblen 2008; Firm et al. 2009; Kenderes et al. 2009; Kucbel et al. 2010; Nagel and Diaci 2006; Nagel and Svoboda 2008; Nagel et al. 2006; Splechtna et al. 2005; Szwagrzyk and Szewczyk 2001) have delineated a forest disturbance regime ranging from intermediate to very small-scale disturbances. The main disturbance is the wind associated with autogenic mortality. There is no evidence of large-scale stand replacing disturbances originated by wind and insect outbreaks as observed in central European montane forests dominated by Norway spruce (Jonášová and Prach 2004; Svoboda et al. 2010; Zielonka et al. 2010). At the same time there is no evidence of fire as a disturbance agent as has been observed and hypothesized in the central-southern European subalpine larch (*Larix decidua* Mill.), cembran pine (*Pinus cembra* L.) forests (Blarquez and Carcaillet 2010; Carcaillet et al. 2009) and, more generally, in the European boreal forests (Niklasson and Granström 2000; Shorohova et al. 2009).

The observed dynamic places the Lom core area at the far end of a gradient from forests controlled by

intermediate disturbances to those where very small-scale processes predominate. The abundance of advance regeneration coupled with the absence of intermediate disturbances has maintained, in space and in time, a canopy dominated by shade tolerant species. This phase, dominated by very small-scale mortality, partially autogenic and partially originated by wind, can last several centuries, maintaining a near equilibrium condition.

4.4) Disturbance regime and management implications

The Lom reserve is a typical example of the forest stands used as a model by European foresters in the second half of the 20th century to develop the single tree selection silviculture (Korpel 1995; Leibundgut 1982; Susmel 1980) which was largely promoted in Europe and, in a few regions, intensively adopted (Diaci 2006). This approach was often described as "naturalistic" or "close-to-nature" but did not take into account the pivotal role of the disturbances (and the range of variability of natural disturbance regime) in natural ecosystems. Lom is one of the largest remnants of the central European primeval forests but has a relatively small size and so we cannot capture the full range of the spatio-temporal variability that may emerge at larger scale (Fraver et al. 2009). Despite the 300 year record we cannot exclude the possibility that larger intermediate or stand replacing disturbances did occur in the past and could play a role in the long-term forest dynamic. Such disturbances could modify species composition and local structure before returning to a regime of gap dyanmics (Romme et al. 1998; Sprugel 1991).

In central Europe most of remaining old-growth is found in small isolated stands that escaped harvest because of inaccessibility or other reasons (Peterken 1996) and have experienced varied environmental and human impacts (Motta and Edouard 2005; Motta and Lingua 2005). Therefore it is necessary to collect a large number of case studies in order to avoid a "blind men and the elephant" bias. In the last decade, accumulation of evidence has shown that disturbances are key processes in forest ecosystem dynamics but, it is also apparent, that for some forest types, near equilibrium can persist in some stands for relatively long periods (Parish and Antos 2004, 2006) with both intermediate and small-scale disturbances part of the disturbance regime.

European stakeholders and foresters are increasingly aware of the important role of disturbances in ecosystem dynamics and are developing silvicultural systems designed to reproduce or restore a degree of old-growth character in actively managed forests (Bauhus et al. 2009; Keeton 2006). In the application of this "new" close-to-nature silviculture, attention must shift from products extracted from the forest to what is being left (CWD, big and old trees) (Kohm and Franklin 1997). The objective is to increase the old-growth and late successional habitats currently under-represented in the landscape (Motta et al. 2010) and to regenerate managed forests mimicking natural processes. In order to enhance both ecosystem services and the sustainable forest management in central Europe it is also necessary to apply a robust ecosystem management approach (Christensen et al. 1996) where disturbances, especially natural disturbance regimes, should be considered in the management of natural resources in order to maintain resilience and biological diversity of the system (Kuuluvainen 2002).

Accumulation of evidence from old-growth forest is playing an important role for building an adequate knowledge base in central Europe on forest management practices to foster complexity, but challenges remain regarding their social acceptance and practical implementation (Long 2009).

References

Antos, J.A., and Parish, R. 2002. Structure and dynamics of a nearly steady-state subalpine forest in south-central British Columbia, Canada. Oecologia **130**: 126-135.

Bauhus, J., Puettmann, K., and Messier, C. 2009. Silviculture for old-growth attributes. For. Ecol. Manage. **258**(4): 525-537.

Berg, E.E., Henry, J.D., Fastie, C.L., Volder, A.D.d., and Matsuoka, S.M. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. For. Ecol. Manage. **227**(3): 219-232.

Bergeron, Y., and Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. **92**: 235-242.

Biolley, H.E. 1920. L'amenagement des forêts par la méthode expérimentale et spécialement la méthode du contrôle. Attinger Ed, Paris.

Blarquez, O., and Carcaillet, C. 2010. Fire, Fuel Composition and Resilience Threshold in Subalpine Ecosystem. PLoS ONE **5**(8): e12480.

Bottero, A., Garbarino, M., Dukić, V., Govedar, Z., Lingua, E., Nagel, T.A., and Motta, R. Submitted. Gap-phase dynamics in the old growth forest of Lom (Bosnia-Herzegovina).

Brang, P. 2005. Virgin forests as a knowledge source for central European silviculture: reality or myth? Forest Snow and Landscape Research **79**(1/2): 19–32.

Brose, P.H., and Waldrop, T.A. 2006. Fire and the origin of Table Mountain pine - pitch pine communities in the southern Appalachian Mountains, USA. Can. J. For. Res. **36**(3): 710-718.

Carcaillet, C., Ali, A.A., Blarquez, O., Genries, A., Mourier, B., and Bremond, L. 2009. Spatial variability of fire history in subalpine forests: from natural to cultural regimes. Ecoscience **16**(1): 1-12.

Castagneri, D., Garbarino, M., Berretti, R., and Motta, R. 2010. Site and stand effects on coarse woody debris in montane mixed forests of Eastern Italian Alps. For. Ecol. Manage. **260**(9): 1592-1598.

Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., Antonio, C.d., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J., Peterson, C.H., Turner, M.G., and Woodmansee, R.G. 1996. The report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. Ecol. Appl. **6**(3): 665-691.

Diaci, J. 2006. Nature-based silviculture in Slovenia: origins, development and future trends. *In* Studia Forestalia Slovenica Nr.126. Biotechnical Faculty, University of Ljubljana, Ljubljana. pp. 119-131.

Diaci, J., Rozenbergar, D., and Boncina, A. 2010. Stand dynamics of Dinaric old-growth forest in Slovenia: Are indirect human influences relevant? Plant Biosyst. **144**(1): 194-201.

Dobrowolska, D., and Veblen, T.T. 2008. Treefall-gap structure and regeneration in mixed *Abies alba* stands in central Poland. For. Ecol. Manage. **255**(8/9): 3469-3476.

Drinić, P. 1956. Taksacioni elementi sastojina jele, smrče i bukve prašumskog tipa u Bosni. Radovi Poljoprivredno – Šumarskog fakulteta Univerziteta u Sarajevu **god. I, br. 1**: 107-160.

Firm, D., Nagel, T.A., and Diaci, J. 2009. Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. For. Ecol. Manage. **257**(9): 1893-1901.

Fraver, S., and White, A.S. 2005. Identifying growth releases in dendrochronological studies of forest disturbance. Can. J. For. Res. **35**(7): 1648-1656.

Fraver, S., White, A.S., and Seymour, R.S. 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. J. Ecol. (Oxford) **97**: 289-298.

Frelich, L.E. 2002. Forest dynamics and disturbance regimes. Cambridge University Press, Cambridge.

Fröhlich, J. 1930. Der südosteuropäische Urwald und seine Überführung in Wirtschaftswald. Cent.Bl. Gesamt. Forstwes. **56**(1-17): 49-65.

Garbarino, M., Weisberg, P.J., and Motta, R. 2009. Interacting effects of physical environment and anthropogenic disturbances on the structure of European larch (*Larix decidua* Mill.) forests. For. Ecol. Manage. **257**(8): 1794-1802.

Gayer, K. 1898. Der Waldbau.Vierte, verbesserte Auflage. Berlin P. Parey, Berlin.

Goff, F.G., and West, D. 1975. Canopy-understory interaction effects on forest population structure. For. Sci. **21**: 98-108.

Goodburn, J.M., and Lorimer, C.G. 1999. Population structure in old-growth and managed northern hardwoods: an examination of the balanced diameter distribution concept. For. Ecol. Manage. **118**(1-3): 11-29.

Göppert, H.R. 1868. Skizzen zur Kenntnis der Urwälder Schlesiens und Böhmens. Blochman & Sons, Dresden.

Gurnaud, A. 1886. La sylviculture française et la méthode du contrôle. Jacquin, Besançon.

Hofmann, A. 1985. La foresta vergine. Ital. For. Mont. **40**(6): 317-336.

Holeksa, J., Saniga, M., Szwagrzyk, J., Czerniak, M., Staszynska, K., and Kapusta, P. 2009. A giant tree stand in the West Carpathians-An exception or a relic of formerly widespread mountain European forests? For. Ecol. Manage. **257**(7): 1577-1585.

Horvat, I., Glavač, V., and Ellenberg, H. 1974. Vegetation Südosteuropas. Urban & Fischer, Stuttgart.

Johnson, E.A., Miyanishi, K., and Kleb, H. 1994. The hazards of interpretation of static age structures as shown by stand reconstruction in *Pinus contorta - Picea engelmannii* forest. J. Ecol. **82**: 923-931.

Jonášová, M., and Prach, K. 2004. Central-European mountain spruce (*Picea abies* (L.) Karst.) forests: regeneration of tree species after a bark beetle outbreak. Ecol. Eng. **23**(1): 15-27.

Keeton, W.S. 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. For. Ecol. Manage. **235**(1/3): 129-142.

Kenderes, K., Kral, K., Vrska, T., and Standovár, T. 2009. Natural gap dynamics in a Central European mixed beech-spruce-fir old-growth forest. Ecoscience **16**(1): 39-47.

Klopcic, M., Jerina, K., and Boncina, A. 2010. Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: are red deer an important factor? Eur. J. For. Res. **129**(3): 277-288.

Kohm, K.A., and Franklin, J.F. 1997. Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington D.C.

Korpel, S. 1995. Die Urwälder der Westkarpaten. Fischer, Jena.

Kucbel, S., Jaloviar, P., Saniga, M., Vencurik, J., and Klimaš, V. 2010. Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. Eur. J. For. Res. **129**(3): 249-259.

Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fenn. **36**(1): 97-125.

Latham, P.A., Zuuring, H.R., and Coble, D.W. 1998. A method for quantifying vertical forest structure. For. Ecol. Manage. **104**(1/3): 157-170.

Leibundgut, H. 1960. Risultati delle ricerche in foreste vergini europee. Ann. Acc. Ital. Sci. For. **9**: 277-287.

Leibundgut, H. 1982. Europäische Urwälder der Bergstufe. Paul Haupt, Bern.

Long, J.N. 2009. Emulating natural disturbance regimes as a basis for forest management: A North American view. For. Ecol. Manage. **257**: 1868-1873.

Lorimer, C.G., and Frelich, L.E. 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can. J. For. Res. **19**: 651-663.

Maunaga, Z. 2001. Management plan for forests with special purpose in the strict natural reservations "Janj" and "Lom". Bosnia and Herzegovina Forestry project. Republic of Srpska., Banja Luka.

Mayer, H., and Ott, E. 1991. Gebirgswaldbau. Schutzwaldpflege. Gustav Fischer, Stuttgart.

McCune, B., and Mefford, M.J. 2006. PC-ORD. Multivariate Analysis of Ecological Data. Version 5. MjM Software, Gleneden Beach, Oregon, U.S.A.

Motta, R., Berretti, R., Castagneri, D., Lingua, E., Nola, P., and Vacchiano, G. 2010. Stand and coarse woody debris dynamics in subalpine Norway spruce forests withdrawn from regular management. Ann. For. Sci. **67**(8): 803p801_803p808.

Motta, R., Berretti, R., Lingua, E., and Piussi, P. 2006. Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. For. Ecol. Manage. **235**(1-3): 155-163.

Motta, R., and Edouard, J.L. 2005. Stand structure and dynamics in a mixed and multilayered forest in the Upper Susa Valley (Piedmont, Italy). Can. J. For. Res. **35**(1): 21-36.

Motta, R., and Lingua, E. 2005. Human impact on size, age, and spatial structure in a mixed European larch and Swiss stone pine forest in the Western Italian Alps. Can. J. For. Res. **35**(8): 1809-1820.

Motta, R., and Nola, P. 2001. Growth trends and dynamics in subalpine forest stands in the Varaita valley (Piedmont, Italy) and their relationships with human activities and global change. J. Veg. Sci. **12**(2): 219-230.

Motta, R., Nola, P., and Piussi, P. 1999. Structure and stand development in three subalpine Norway spruce (*Picea abies* (L.) Karst.) stands in Paneveggio (Trento, Italy). Global Ecol. Biogeogr. **8**(6): 455-473.

Nagel, T.A., and Diaci, J. 2006. Intermediate wind disturbance in an old-growth beech-fir forest in southeastern Slovenia. Can. J. For. Res. **36**: 629-638.

Nagel, T.A., and Svoboda, M. 2008. Gap disturbance regime in an old-growth *Fagus-Abies* forest in the Dinaric Mountains, Bosnia-Herzegovina. Can. J. For. Res. **38**(11): 2728-2737.

Nagel, T.A., Svoboda, M., and Diaci, J. 2006. Regeneration patterns after intermediate wind disturbance in an old-growth *Fagus-Abies* forest in southeastern Slovenia. For. Ecol. Manage. **226**(1/3): 268-278.

Nakashizuka, T. 1989. Role of Uprooting in Composition and Dynamics of an Old-growth Forest in Japan. Ecology **70**(5): 1273-1278.

Niklasson, M., and Granström, A. 2000. Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. Ecology **81**: 1484-1499.

Parish, R., and Antos, J.A. 2004. Structure and dynamics of an ancient montane forest in coastal British Columbia. Oecologia **141**: 562-576.

Parish, R., and Antos, J.A. 2006. Slow growth, long-lived trees, and minimal disturbance characterize the dynamics of an ancient montane forest in coastal British Columbia. Can. J. For. Res. **36**: 2826-2838.

Payette, S., Filion, L., and Delwaide, A. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré Ecological Reserve, Québec. Can. J. For. Res. **20**: 1228-1241.

Peterken, G.F. 1996. Natural woodland. Ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge.

Pickett, S.T.A., and White, P.S. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Pintaric, K. 1999. Forestry and forest reserves in Bosnia and Herzegovina. *In* Virgin forests and forest reserves in Central and East European countries. History, present status and future development. Proceedings of the invited lecturers' reports presented at the COST E4 Management Committee and Working Groups meeting in Ljubljana, Slovenia, 25-28 April, 1998. *Edited by* J. Diaci. pp. 1-15.

Piovesan, G., and Adams, J.M. 2001. Masting behaviour in beech: linking reproduction and climatic variation. Can. J. Bot. **79**(9): 1039-1047.

Podlaski, R. 2008. Dynamics in Central European near-natural *Abies-Fagus* forests: does the mosaic-cycle approach provide an appropriate model? J. Veg. Sci. **19**(2): 173-182.

Poulson, T.L., and Platt, W.J. 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. Ecology **77**(4): 1234-1253.

Pretzsch, H., Grote, R., Reineking, B., Rötzer, T., and Seifert, S. 2008. Models for Forest Ecosystem Management: A European Perspective. Ann. Bot. **101**(8): 1065-1087.

Puettmann, K.J., Coates, K.D., and Messier, C. 2009. A Critique of Silviculture. Managing for Complexity. . Island Press, Washington DC.

Roath, L.R., and Krueger, W.C. 1982. Cattle grazing and behavior on a forested range. J. Range Manage. **35**: 332-338.

Romme, W.H., Everham, E.H., Frelich, L.E., Moritz, M.A., and Sparks, R.E. 1998. Are Large, Infrequent Disturbances Qualitatively Different from Small, Frequent Disturbances? Ecosystems **1**(6): 524-534.

Rozenbergar, D., Mikac, S., Anic, I., and Diaci, J. 2007. Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech fir forest reserves in South East Europe. Forestry **80**(4): 431-443.

Rubino, D.L., and McCarthy, B.C. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. Dendrochronologia **21**(3): 97-115.

Runkle, J. 1985. Comparison of methods for determining fraction of land area in treefall gaps. For. Sci. **31**(1): 15-19.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forest of eastern North-America. Ecology **63**: 1533-1546.

Schelhaas, M.J., Nabuurs, G.J., and Schuck, A. 2003. Natural disturbances in the European forests in the 19th and 20th century. Glob. Change Biol. **9**: 1620-1633.

Schütz, J.P. 1990. Sylviculture 1. Principes d'éducation des forêts. Presses Polytechniques et Universitaires Romandes, Lausanne.

Schütz, J.P. 1992. Die waldbaulichen Formen und die Grenzen der Plenterung mit Laubbaumarten. Schweiz. Z. Forstw. **143**: 442-460.

Schütz, J.P. 2001. Opportunities and strategies of transforming regular forests to irregular forests. For. Ecol. Manage. **151**(1-3): 87-94.

Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganičová, K., Netherer, S., Arpaci, A., Bontemps, J.-D., Bugmann, H., González-Olabarria, J.R., Lasch, P., Meredieu, C., Moreira, F., Schelhaas, M.-J., and Mohren, F. 2011. Modelling natural disturbances in forest ecosystems: a review. Ecol. Model. **222**(4): 903-924.

Shorohova, E., Kuuluvainen, T., Kangur, A., and Jõgiste, K. 2009. Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. Ann. For. Sci. **66**(2): 1-20.

Slater, J.A., Heady, B., Kroenung, G., Curtis, W., Haase, J., Hoegemann, D., Shockley, C., and Tracy, K. 2009. Evaluation of the New ASTER Global Digital Elevation Model. National Geospatial-Intelligence Agency - USA.

Spies, T.A., and Duncan, S.L. (eds). 2009. Old growth in a new world: a Pacific Northwest Icon Reexamined. Island Press, Washington DC.

Splechtna, B.E., Gratzer, G., and Black, B.A. 2005. Disturbance history of a European old-growth mixed-species forest - a spatial dendro-ecological analysis. J. Veg. Sci. **16**(5): 511-522.

Sprugel, D.G. 1991. Disturbance, equilibrium, and environmental variability: What is "Natural' vegetation in a changing environment? Biol. Conserv. **58**(1): 1-18.

Stancioiu, P.T., and O'Hara, K.L. 2006. Regeneration growth in different light environments of mixed species, multiaged, mountainous forests of Romania. Eur. J. For. Res. **125**(2): 151-162.

Standovár, T., and Kenderes, K. 2003. A review on natural stand dynamics in beechwoods of East Central Europe. Appl. Ecol. Env. Res. **1**(1/2): 19-46.

Susmel, L. 1956. Caratteri comparati delle abetine primarie delle Alpi dinariche e delle abetine secondarie delle Alpi orientali italiane. Ann. Acc. Ital. Sci. For. **5**: 115-146.

Susmel, L. 1980. Normalizzazione delle foreste alpine. Liviana Editrice, Padova.

Svoboda, M., Fraver, S., Janda, P., Bace, R., and Zenállìková, J. 2010. Natural development and regeneration of a Central European montane spruce forest. For. Ecol. Manage. **260**(5): 707-714.

Szwagrzyk, J., and Szewczyk, J. 2001. Tree mortality and effects of release from competition in an old-growth *Fagus-Abies-Picea* stand. J. Veg. Sci. **12**(5): 621-626.

Van Vagner, C.E. 1968. The line intersect method in forest fuel sampling. For. Sci. **14**: 20-26.

Visnjic, Č., Vojnikovic, S., Ioras, F., Dautbasic, M., Abrudan, I.V., Gurean, D.M., Lojo, A., Trestic, T., Ballian, D., and Bajric, M. 2009. Virgin Status Assessment of Plješevica Forest in Bosnia - Herzegovina. Notulae Botanicae Horti Agrobotanici Cluj-Napoca **37**(2): 22-27.

Wessely, J. 1853. Die österreichischen Alpländer und ihre Forste. Braunmüller, Wien.

Worrall, J.J., Lee, T.D., and Harrington, T.C. 2005. Forest dynamics and agents that initiate and expand canopy gaps in *Picea-Abies* forests of Crawford Notch, New Hampshire, USA. J. Ecol. (Oxford) **93**(1): 178-190.

Zielonka, T., Holeksa, J., Fleischer, P., and Kapusta, P. 2010. A tree-ring reconstruction of wind disturbances in a forest of the Slovakian Tatra Mountains, Western Carpathians. J. Veg. Sci. **21**(1): 31-42.

Table 1

|  | Density | Basal area | Volume | Regeneration |
|---|---|---|---|---|
|  | [n ha$^{-1}$] | [m$^2$ ha$^{-1}$] | [m$^3$ ha$^{-1}$] | [n ha$^{-1}$] |
| Silver fir | 122 | 22.2 | 366.1 | 1790 |
| Norway spruce | 69 | 10.4 | 178.3 | 782 |
| Beech | 296 | 14.3 | 213.0 | 2123 |
| Other species | 3 | 0.3 | 5.7 | 142 |
| Total | 489 | 47.1 | 763.1 | 4837 |

| | | | | |
|---|---|---|---|---|
| Range | 190-859 | 22.9-71.6 | 352.8-1232.9 | 559-18159 |
| St. dev. | 120 | 11.0 | 198.0 | 4031 |

Table 2

| | Snag [m$^3$ ha$^{-1}$] | Log [m$^3$ ha$^{-1}$] | Stump [m$^3$ ha$^{-1}$] | Total [m$^3$ ha$^{-1}$] |
|---|---|---|---|---|
| Volume | 81.4 | 236.4 | 9.5 | 327.3 |
| Range | 0-298.8 | 49.3-487.2 | 0-33.4 | 88.1-578.2 |
| St. dev. | 80.9 | 109.2 | 7.5 | 128.2 |

Table 3

| Decay class | Core area $[m^3ha^{-1}]$ | Permanent plot $[m^3ha^{-1}]$ |
|:---:|:---:|:---:|
| 1 | 6.4 | 7.6 |
| 2 | 41.6 | 45.1 |
| 3 | 77.7 | 91.9 |
| 4 | 105.9 | 187.6 |
| 5 | 95.8 | 51.1 |
| Total | 327.3 | 383.3 |

Table 4

| Axis | PC1 | PC2 | PC3 |
|---|---|---|---|
| % of variance | 26.85 | 19.73 | 17.55 |
| p | 0.0001 | 0.0005 | 0.0001 |
| **Environmental and anthropogenic variables** | | | |
| Aspect | -0.009 | 0.217 | -0.101 |
| Elevation | -0.156 | -0.286 | -0.135 |
| Slope | -0.046 | 0.096 | -0.077 |
| Road proximity | -0.099 | -0.273 | 0.345 |
| Core proximity | 0.067 | -0.021 | -0.248 |
| **Forest structure variables** | | | |
| Basal area | 0.462 | 0.703 | 0.021 |
| Fir trees | -0.452 | 0.714 | -0.353 |
| Spruce trees | 0.815 | -0.17 | 0.396 |
| Beech trees | -0.47 | -0.788 | -0.037 |
| CWD | -0.192 | -0.455 | 0.078 |
| Stumps | 0.026 | -0.116 | -0.292 |

| | | | |
|---|---|---|---|
| Regeneration density | -0.134 | 0.14 | 0.674 |
| Fir regeneration | 0.867 | -0.162 | -0.022 |
| Spruce regeneration | -0.016 | -0.086 | -0.812 |
| Beech regeneration | -0.758 | 0.212 | 0.515 |

Table 5

| Gap characteristics | Canopy gaps | Expanded gaps |
|---|---|---|
| Mean gap fraction (%) | 19.0 | 41.0 |
| Range | 11.2 - 21.5 | 29.0 - 44.6 |
| Median gap size (m$^2$) | 76.9 | 192.9 |
| Range | 11.1 - 708.0 | 41.7 - 1085.2 |

Table 6

| | Density [n ha$^{-1}$] | Basal area [m$^2$ ha$^{-1}$] | Volume [m$^3$ha$^{-1}$] |
|---|---|---|---|
| Silver fir | 165 | 31.4 | 522.8 |
| Norway spruce | 75 | 23.6 | 430.5 |
| Beech | 377 | 14.3 | 204.6 |
| Total | 617 | 69.3 | 1157.9 |

Table 1. Structural characteristics (density, basal area, volume of living trees and density of the regeneration) in the core area.

Table 2. Volume of snags, logs and stumps in core area.

Table 3. CWD decay in the core area and in the permanent plot.

Table 4 – Pearson correlation coefficients with the first 3 ordination axes for environmental, anthropogenic, and forest structure variables. All the variables referred to a particular species (fir, spruce, and beech) are a proportion of the total density of living trees or regeneration (seedlings and saplings).

Table 5. Summary of canopy and expanded gap characteristics.

Table 6. Structural characteristics (density, basal area and volume) of the 1.1 ha permanent plot.

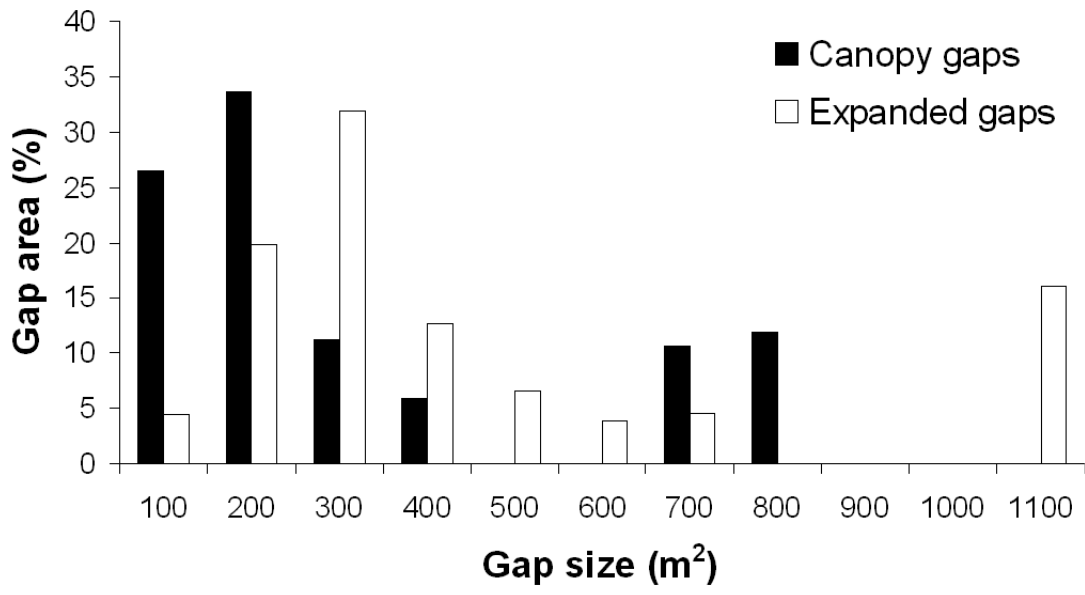Table 7. Stand characteristics for some mixed central European *Fagus-Abies-Picea* old-growth forest.
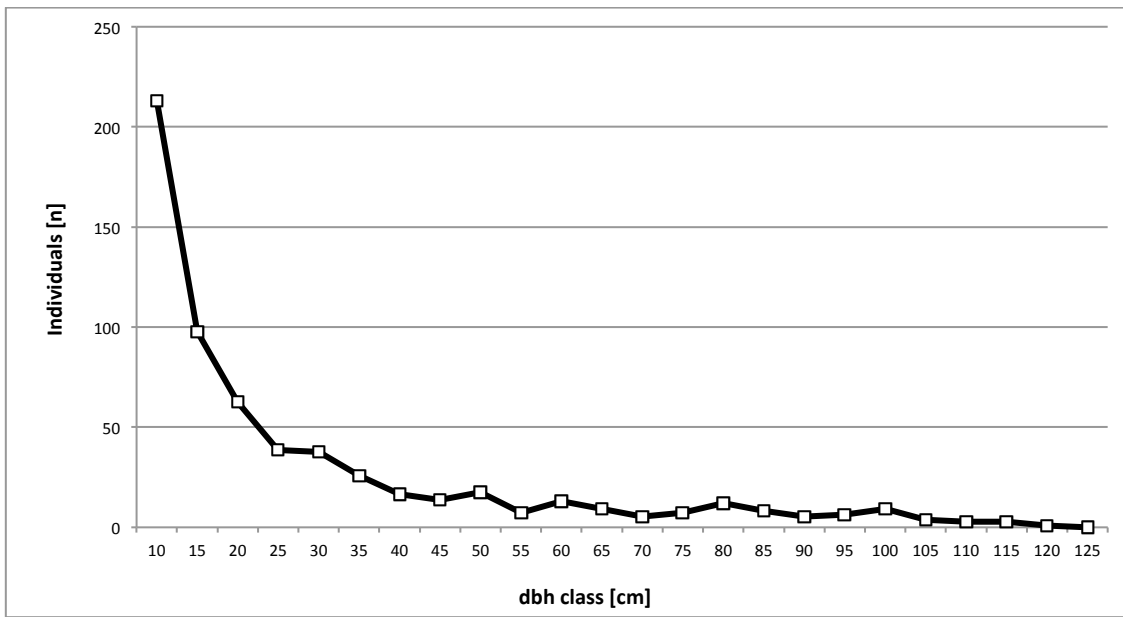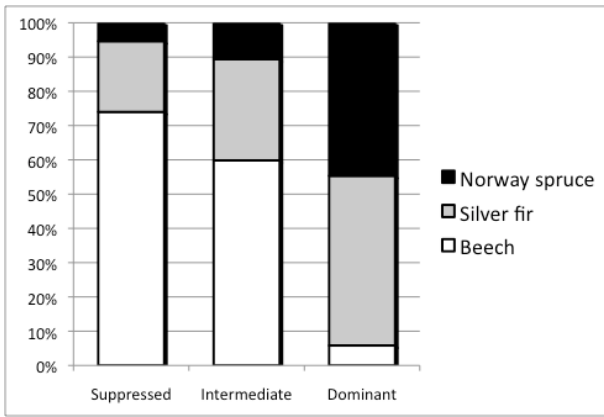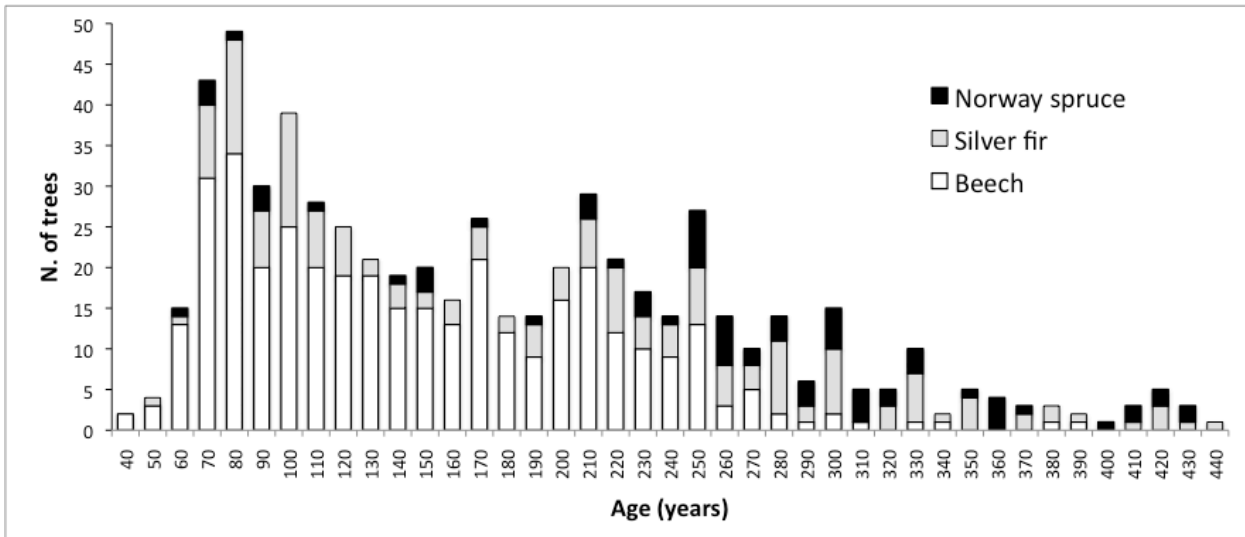
Fig 1
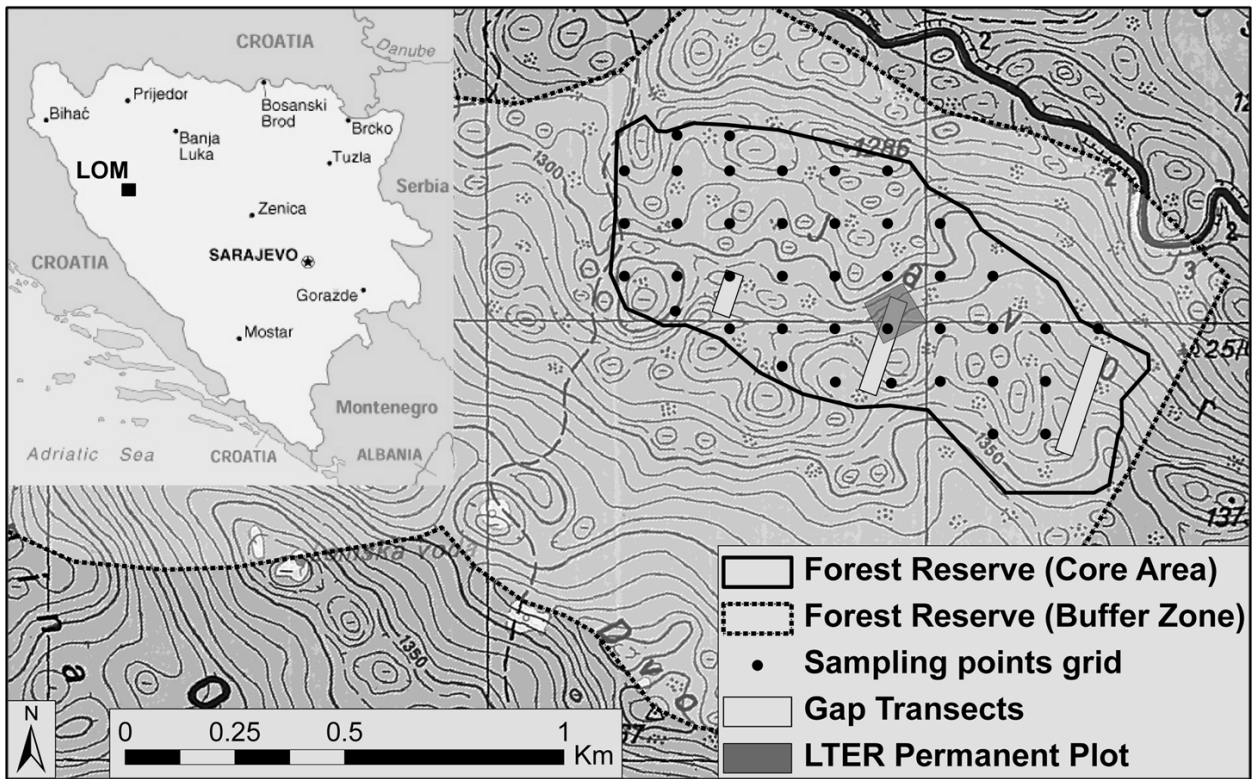
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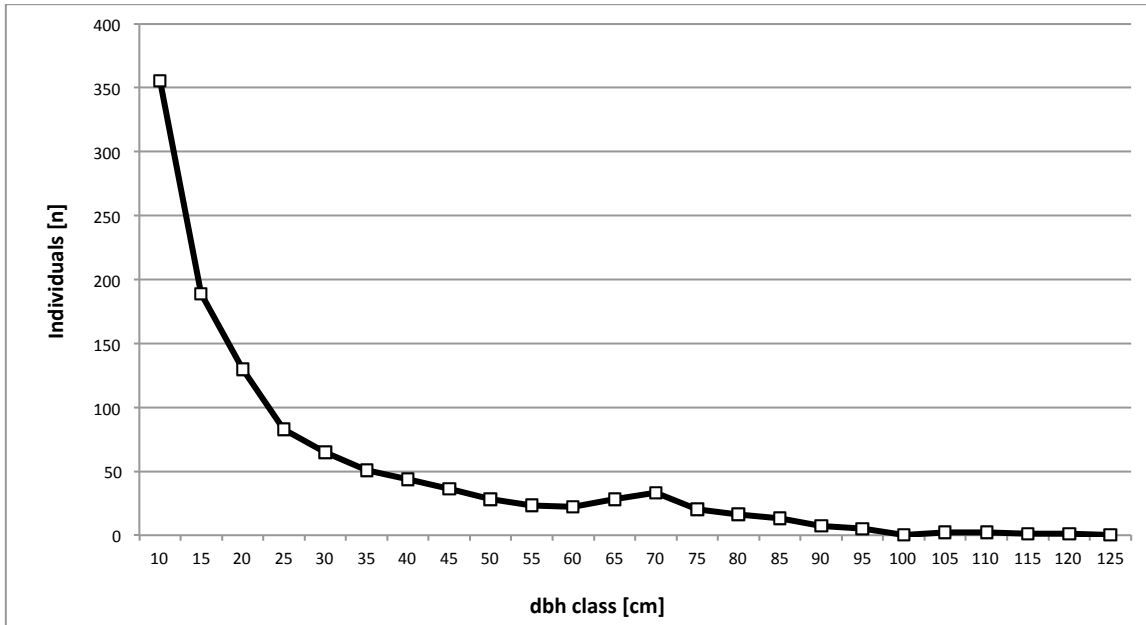


Fig. 3

Fig 4
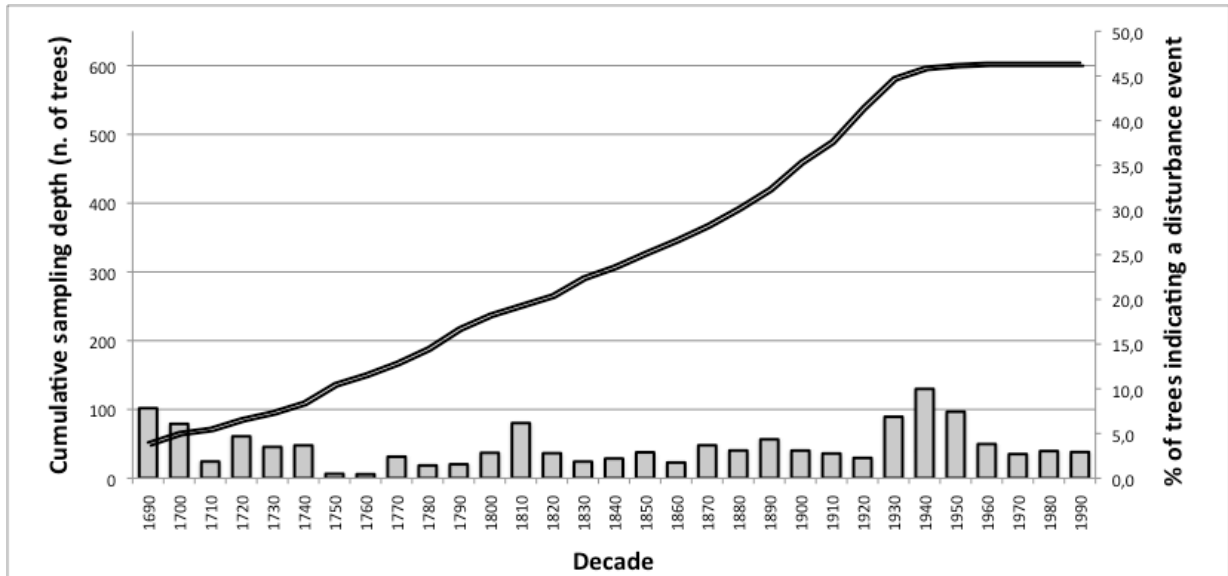
Fig 5



Fig 6

Fig 7

Fig 8

Fig. 1. Map of the Lom forest reserve (core area and buffer zone) showing location of the 40 plots, the gap transects and the 1.1 ha Long Term Ecology Research permanent plot.

Fig. 2. Size distribution of living trees in the core area (network of 40 sampling points)

Fig. 3. Proportion of total gap area in gap size classes of canopy and expanded gaps.

Fig. 4. Size distribution of living trees in the 1.1 ha permanent plot.

Fig. 5. Tree species composition in three layers of the vertical structure in the permanent plot.

Fig. 6. Age structure of living trees in the 1.1 ha permanent plot.

Fig. 7. Age structure in the three layers of the vertical structure showing the wide age range within each layer and the age overlap between the three layers

Fig. 8. Disturbance chronology (percent of trees showing abrupt growth release >100% lasting more than 15 years) including sample depth (total number of trees ) for each decade. The disturbances are presented for a sample depth > 50 individuals.