



Individual-based approach to the detection of disturbance history through spatial scales in a natural beech-dominated forest

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Keywords

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Nomenclature

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Abstract

Question: We connected tree-census and dendrochronological research data (74.2 ha) in order to answer the following questions: How do we apply an individual-based approach, which allows us to abandon the traditional patch model, in the research of disturbance history through spatial scales? What is the disturbance history of the natural forest? How do we understand the influence of the Kyrill storm, which affected the reserve on 18 January 2007? How does the disturbance history in dendrochronological records correspond to real disturbances?

Location: Žofínský Prales (48 °40' N, 14 °42' E, 735–830 m a.s.l., granite, Czech Republic)

Methods: Repeated tree-censuses (>20 000 trees) were carried out in 1975, 1997 and 2008. These surveys served as the basis of dendrochronological research, during which 3 020 trees were sampled. A boundary line (BL) approach and geostatistical techniques were used to detect disturbance intensity and its spatial pattern.

Results: The mean disturbance rate was 11.0% canopy loss per decade (maximum 33.7%) in the core zone. Bordering forests were directly affected by humans after 1800. A maximum of nine disturbance events were recorded per tree, but there were also 3% of non-suppressed trees without records of disturbance events. The Kyrill storm represented a singular event in the forest history from the point of view of its exceptional spatial pattern (ranges up to 320.0 m), but not from the perspective of disturbance intensity. The relationship between disturbance intensity (y) and the range of spatial autocorrelation (x) can be explained by the equation $y = 10.6863 + 0.0783 \cdot x$ ($R^2 = 0.546$, $P = 0.009$). The spatial variability of releases $\geq 50\%$ of BL corresponds to real disturbance events, while the insertion of weak releases led to the overestimation of range. The frequency of releases was affected by a decrease in air pollution at the beginning of the 1990s.

Conclusions: Effects of small-scale disturbances predominate in forest dynamics. Disturbance intensity was often not directly in accordance with the range of spatial autocorrelation. The ecological role of disturbance is therefore biased if disturbance intensity is used as the sole criterion. The results suggest the importance of historical and geographical contingency in ecosystem development.

Introduction

Knowledge of the disturbance history of natural forests is necessary for an understanding of their dynamics and tree

species interactions. In addition to direct impacts on the spatial structure of the forest, disturbances also influence the species diversity of different taxonomic groups of organisms, soil formation and soil variability (Nachtergale

et al. 2002; Šamonil et al. 2008a, 2010a; Gravel et al. 2010). Disturbances determine future ecosystem development, which can be convergent (as the traditional steady-state concept usually supposes) or divergent (as revealed by studies using nonlinear dynamical systems theory; Phillips 2004). Several issues concerning the character of natural ecosystem development remain insufficiently explored.

Research on Central European forest reserves revealed the dominant role of small-scale disturbances in forest dynamics (e.g. Průša 1985). However, results are always closely connected to the specific spatial level of particular studies. In densely populated Central Europe only fragments of natural broadleaved forests have been preserved. Primeval forests, in some cases in the form of reserves, were often transformed by humans into managed forests after extensive disturbances, and their spontaneous development was hence interrupted (e.g. Šebková et al. 2012). Remaining fragments thus may not be representative examples of vegetation dynamics at the landscape scale. Scientific studies so far lacked a wider landscape context as well as a longer time horizon in Central Europe. Extrapolating results from small sites to the landscape level can lead to a considerable distortion of reality (see Šamonil et al. 2008b; Manzoni & Porporato 2009). The role of intensive disturbances in the dynamics of broadleaved forests as well as the interaction between individual disturbance factors operating at different spatial levels is still poorly known. Understanding the interaction of fine-scale processes with coarser-scale disturbances is a critical issue in the current study of forest dynamics (Gratzer et al. 2004). Historical meteorological studies (Dobrovolný & Brázdil 2003) describe the significant occurrence of extreme climatic events in the Central Europe in the past, and palaeoecological studies (van der Knaap et al. 2004) prove the relevance of extreme events for the co-existence of trees. Research on disturbance history across spatial scales, including intense infrequent events, can lead to a deeper understanding of the interdependence of multi-layered factors of temperate forest dynamics. On a more theoretical level, it can lead to a deeper understanding of the relationship between historical contingency and ecological rules during ecosystem development (Ricklefs et al. 1999; Phillips 2004).

The technical application of dendrochronological methods – a traditional tool for the evaluation of disturbance history – is usually accompanied by a number of arbitrary decisions that may affect the resulting picture of forest history significantly (Rubino & McCarthy 2004). Besides the question of detection of release in tree radial growth (Black et al. 2009; Stan & Daniels 2010), an important issue is the interpretation of the detected release in relation to space; i.e. what area is represented by the dendrochronological data and how to process the data with regard to space.

Previous studies usually failed to interconnect different spatial scales of research. Disturbance history was described separately for individual spatial levels, or dendrochronological data from a fine scale were interconnected with the other data types (e.g. aerial photographs) describing the broad landscape context (Piovesan et al. 2005; Splechtna & Gratzer 2005). The latter approach is justifiable but it requires resolving issues connected to the compatibility of different kinds of data as well as to spatial scale connectivity.

While detailed research of disturbance history in small areas uses point dendrochronological records from a specific individuals (1-ha area; Splechtna et al. 2005), this is not the case at the stand or landscape level (Frelich & Lorimer 1991a; Fraver et al. 2009; Panayotov et al. 2011). Records from tree individuals at this level are usually degraded by a conversion to average data for the entire study plot. The number of cored individuals on a research plot simply becomes a measure of the determination certainty of disturbance events. This, in fact, leads to a significant retreat from a progressive, spatially-explicit, individual-based approach (e.g. Pacala et al. 1996; Grimm 1999) to a traditional patch approach (e.g. Levin & Paine 1974; Panayotov et al. 2011; review in Gratzer et al. 2004). Furthermore, new subjective decisions are involved: what percentage of individuals on the plot must contain the release to be attributed to the entire plot, how large study plots should be etc.? These studies do not deal with interactions between individuals, but focus on the dynamics of discrete and (theoretically) internally homogeneous patches. Linking dendrochronological data to a given study plot rather than to tree-individuals (and their point locations) allows neither resolving disturbance history at the finest spatial scale between tree individuals, nor the study of disturbance through various spatial scales. An individual-based approach shifts the focus of forest dynamics modelling from the dynamics of discrete patches to the interactions among individual organisms, thus encapsulating the theory of “neighbourhood” dynamics (Gratzer et al. 2004; Janik et al. 2011). This approach is applicable to the study of interactions between disturbance histories of point data represented by the locations of cored trees in the dendrochronological record.

To create continuity across spatial scales without degrading the dendrochronological record, detailed information about the position of all sampled trees is required. We used unique repeated tree-census surveys (stem position mapping) from Žofínský Prales (Czech Republic). These surveys were undertaken in a 74.2 ha area in 1975, 1997 and 2008. The locality is among the largest and oldest long-term research plots in the temperate zone where a complete tree census (stem mapping) of all living and dead trees of DBH ≥ 10 cm has been carried out (>20 000

individuals). The locality belongs to the International Long-Term Ecological Research network (CZ-LTER, www.lter.cz) and currently is included into the Smithsonian Institution Global Earth Observatory (SIGEO, www.sigeo.si.edu) as the first plot in continental Europe. Tree census record served as the basis for our dendrochronological study. Detailed historical forest records including old forest maps suggest that the core zone of the forest has never been logged. It has been strictly protected since 1838 (deadwood was removed until 1882). The forest reserve has the longest history of continuous protection in the Czech Republic and, according to our knowledge, is the fourth oldest, continuously protected reserve in Europe (Welzholz & Johann 2007). Repeated tree-census records enable us to describe the detailed disturbance history of a unique remnant of natural beech-dominated forests, which, moreover, was strongly disturbed by the windstorm Kyrill on 18 January 2007. This study asks the following questions: (1) How do we apply an individual-based approach in the research of disturbance history across various spatial scales? (2) What is the disturbance history in the core zone of the reserve, and is it possible to find an event similar to the Kyrill storm in the past? (3) How did the bordering forests develop? (4) How does disturbance history as revealed by dendrochronological data correspond to real disturbances found through repeated tree-censuses?

Methods

Site characteristics

Natural conditions

Our research took place in the Novohradské Hory mountains, in the Žofínský Prales National Nature Reserve (hereafter Žofín, Fig. 1).

The reserve is situated along an altitudinal gradient of 735–830 m a.s.l.; gentle NW slopes predominate. Bedrock is almost homogenous and consists of finely to medium-grained porphyritic and biotite granite. Annual average rainfall is 917 mm. The wettest month is June with an average rainfall of 135 mm. Annual average temperature is 4.3 °C. Žofín is drained by several smaller streams to the Tisový stream, which flows around part of the reserve (Fig. 1), continuing towards the river Černá. Plant communities can be classified in the following associations: *Galio odorati-Fagetum* (most frequent), *Mercuriali perennis-Fagetum*, *Calamagrostio villosae-Fagetum*, and *Luzulo-Fagetum*. Spring-area plant communities can be classified as the alliance *Caricion remotae* (division to associations *Cardamino-Chrysosplenium alternifolii* and *Caricetum remotae* is usually not possible), or as the association *Equiseto-Piceetum* (Braun-Blanquet 1921; Boublík et al. 2009).

Thin trees were most frequent, and their frequency decreased smoothly with increasing diameter class (Fig. 2). *Fagus sylvatica* predominated in all diameter classes, followed by *Picea abies*. *Abies alba* represented 1% of standing volume and the remaining tree species together also represented 1% of standing volume (*Ulmus glabra*, *Acer pseudoplatanus*, *Acer platanoides*, *Sorbus aucuparia*). *Fagus sylvatica* represents 70.3% of all living trees (152 tree-individuals with DBH ≥ 10 cm ha⁻¹), 57.1% of the basal area (19.7 m² ha⁻¹) and 61.4% of living tree-volume (343.6 m³ ha⁻¹, see also Král et al. 2010a,b).

Natural disturbance factors and forest spatial patterns

A fine-scale mosaic of forest patches in different phases of the “forest cycle” (Korpel 1995; Šamonil & Vrška 2007; Král et al. 2010a) predominates in the current tree-layer structure (Král et al. 2010b). Pit-mounds (microtopographical shapes caused by a single uprooted tree, with or already without the uprooted trunk) currently cover 11.6% of the total area, with 7.7% consisting of mound areas and 4.0% of pit areas (Šamonil et al. 2011).

The predominantly fine-scale mosaic of forest patches contrast sharply with the few hectares of blowdowns produced by the Kyrill storm on 18 January 2007 (Fig. 2). The uneven distribution of pit-mounds in time suggests (Šebková et al. 2012) that this strong event is unlikely to be unique in the history of Žofín. Chadt (1908), Kruml (1960), Dobrovolný & Brázdil (2003) and Brázdil et al. (2004) documented historical evidence of strong winds, but also biotic disturbance factors (*Ips typographus* L.) in the region. Data from these studies are presented in Fig. 3.

Historical human impact

According to historical forest records, the core zone of the reserve (50.0 ha) has never been logged. However, historical documents also show that the stands bordering the current reserve in the vicinity of streams as well as a thin belt within the core zone were probably affected directly by humans in the past (Fig. 1; Pícha 2010). Nevertheless, according to D’Amato & Orwig (2008), the significant part of bordering stands can be classified as old-growth, with occasional individuals older than 244 yr. These data correspond with the first glasswork construction in the vicinity of Žofín, which could potentially affect forest development by woody biomass removal (Pícha 2010). Since past human activities appear to have been significant in the border areas, some calculations were made separately for the core

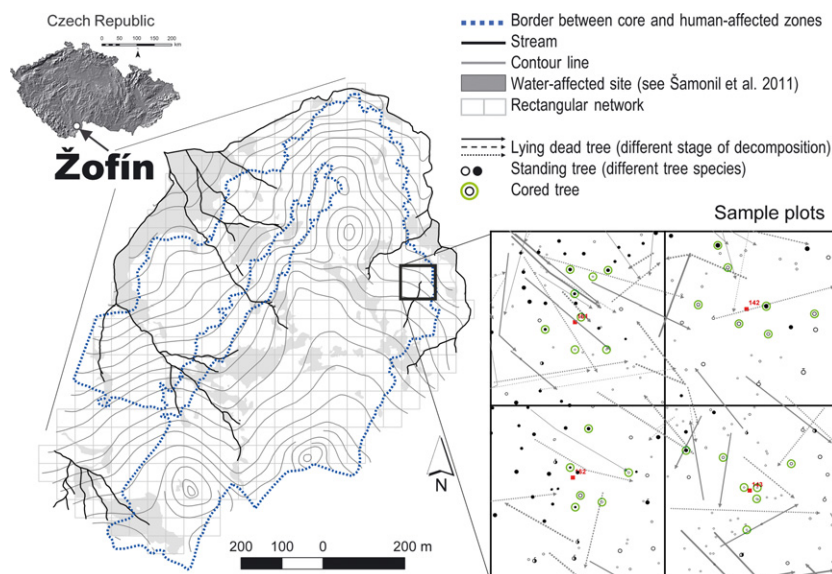


Fig. 1. The study area: Žofínský Prales National Nature Reserve (hereafter Žofín) in the Novohradské Hory mountains, Czech Republic. 74.2 ha were overlain with a regular network of 353 sample plots. We cored 6–(9) trees surrounding the centres of plots.

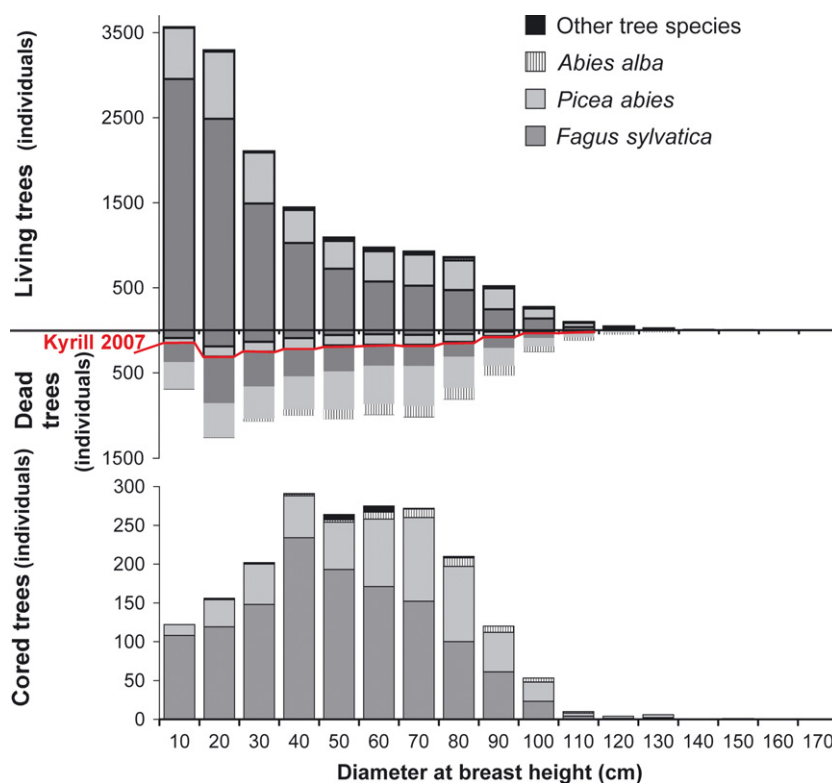


Fig. 2. Diameter distribution of Žofín (74.2 ha) and the diameter distribution of sampled trees (1986 cores, only those cores accepted for disturbance history evaluation are represented). Trees disturbed during the Kyrill storm are presented separately within all dead trees.

zone of the reserve (50.0 ha, hereafter the “core zone”) and the border areas, plus the inner belt of the reserve (24.2 ha, hereafter the “human-affected zone”). The

whole area (74.2 ha) has been monitored from the perspective of tree layer development since 1975 (see Section Forest structure).

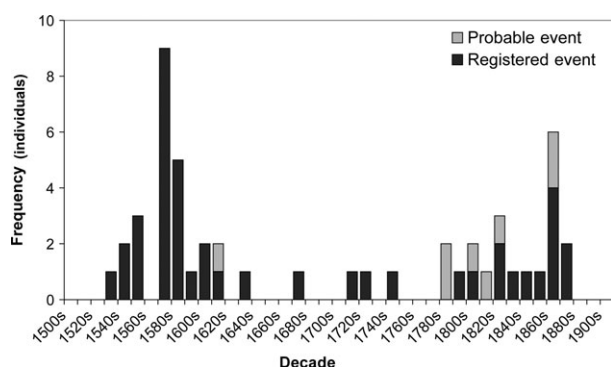


Fig. 3. Decadal historical occurrence of strong winds within 50 km surrounding Zofín in the Czech Republic derived from Chadt (1908) and Brázdil et al. (2004).

Data collection

Forest structure

The locations of all trees with diameter at breast height (DBH) ≥ 10 cm, and selected tree properties (tree species, DBH, health condition – dead standing or lying tree, broken tree, stump etc.) were recorded repeatedly within an area of 74.2 ha in 1975, 1997 and 2008. A stem-position map resulted from each census (Průša 1985; Král et al. 2010a,b). Since the locality was affected intensively by Kyrill, we also evaluated the influence of this storm on the basis of the visual appearance of disturbed trees (presence of leaves, branchlets etc.).

In 2008, we set up a regular network of points with 44.25 m spacing as the basis for the tree census, which covered 74.2 ha of the reserve. The centres of square plots were located geodetically with an accuracy of ca 0.05 m, and were used as the basis for the following tree censuses, dendrochronological, natural regeneration, soil as well as pit-mound surveys.

Disturbance history

Dendrochronological cores were extracted at breast height on each of the 354 square plots, one from each cored tree. Six cores per plot (nine in the case of gap occurrence on a plot with a higher number of young trees) were taken from non-suppressed trees closest to the plot centre. Besides living trees, we also cored dead trees broken or uprooted during the Kyrill storm. If trees occurred at the same distance from the centre, we preferred rarer tree-species. The stem-position map from 1997 was used in the field, and it enabled us to eliminate recent disturbances from sampling; we cored only trees released before 1997. Visually accepted cores were evaluated subsequently in a dendrochronological laboratory. Samples excluded were replaced by a

sample from a neighbouring tree on the plot. Three cycles of the sampling and partial laboratory processing were carried out. From the total of 18 899 standing and 2 862 lying trunks recorded in 2008 we tried to core 3 020 individuals in 2008–2011.

The number of rings at the height of 1.3 m was considered as the recruitment age. Former growth was not studied in detail. The year individuals reached the height of 1.3 m was calculated on the basis of random sampling of 43 individuals of *F. sylvatica*, and 26 individuals of *P. abies*. In these cases the trunk base was also cored. On average, *F. sylvatica* reached 1.3 m at the age of 8.16 yr (median = 7.0, max = 38, SD = 7.60 yr), and *P. abies* at the age 10.81 yr (median = 10.5, max = 24, SD = 7.09 yr). In order to follow all methodological steps of disturbance history assessment (e.g. Lorimer & Frelich 1989; Frelich 2002; Splechtna et al. 2005), we extracted cores to calculate gap origin threshold, measured crown areas and studied the social status of trees. A detailed description of these datasets is given in Section Disturbance event detection.

Data analysis

Basic laboratory analyses

The cores were processed at the laboratory of the Department of Forest Ecology, VUKOZ (<www.pralesy.cz>) using standard dendrochronological techniques (e.g. Schweingruber et al. 1990). The cores were dried and smoothed with fine sandpaper. The widths of the growth rings were measured using the PAST 4 program (SCIEM 2007), with 0.01 mm accuracy. Cores without sub-bark growth rings, damaged cores and cores that were missing more than 30 mm of the pith were rejected. A total number of 1986 cores were accepted for disturbance history evaluation (Fig. 2). A pith locator (Applequist 1958) served to estimate the number of rings to the pith. Cross-dating of cores was carried out according to the marker-year method of Yamaguchi (1991) and was validated statistically using the PAST 4 program and by COFECHA (Holmes 1983). However, series intercorrelation (range 0.151–0.359) and average mean sensitivity (range 0.231–0.323) were relatively poor. The high growth plasticity revealed corresponds well with other natural beech-dominated forests in Central Europe (Splechtna et al. 2005; Nagel et al. 2006; Firm et al. 2009; Šamonil et al. 2009).

We calculated the mean annual growth of the main tree species for the human-affected and core zones separately using strict criteria of core series intercorrelation (THP ≥ 4.7 and GL ≥ 63). We used 2 232 suitable cores without applying the criterion of distance to the pith for procedure. Only 85 individuals of *F. sylvatica* (total 1 203 cores), 120 *P. abies* (total 275), and 7 *A. alba* (total 7) complied with the requirements in the core zone. In the

human-affected zone, 179 *P. abies* (total 496 cores) and 23 *A. alba* (total 49) complied with the requirements. At the other site, no individuals of *F. sylvatica* met the criteria, which we therefore had to reduce to $\text{THP} \geq 4.0$ and $\text{GL} \geq 60$. This resulted in 15 cores complied with the requirements (total 202 cores).

Disturbance event detection

Disturbance history was evaluated on an irregular network of points, represented by precisely located cored trees. We separately studied (1) the initial growth of trees – if it occurred under canopy or in gap; and (2) disturbance events during subsequent growth – on the basis of release detection in the radial growth of trees.

Evaluation of initial growth

The threshold of gap origin was calculated according to Lorimer et al. (1988) and Lorimer & Frelich (1989). Mean early growth rate was evaluated on five rings, 3 cm from the pith (in 57 juvenile suppressed *F. sylvatica*, 44 suppressed *P. abies*, 64 juvenile *F. sylvatica* in gaps, 47 juvenile *P. abies* in gaps, 108 mature *F. sylvatica* and 245 mature *P. abies*). The threshold of gap origin was 1.45 mm for *F. sylvatica* and 1.58 mm for *P. abies*. According to the alternative method of Splechtna et al. (2005), the threshold of gap origin was similar for *F. sylvatica*; 1.54 mm (not applied below). Because of the absence of appropriate tree individuals at the site, the threshold of gap origin could not be calculated for other tree species. The remaining broad-leaved trees were evaluated according to *F. sylvatica*, and *A. alba* according to *P. abies*.

Release detection

We detected the release threshold according to Black & Abrams (2003); prior growth (PG) and growth change (GC) were calculated for each tree ring of all tree ring series (Nowacki & Abrams 1997). PG represents the absolute mean annual increment of the 10 yr preceding any annual ring, and GC represents the change of mean annual increment (in percent) between two 10-yr intervals enabling us to eliminate false releases produced by short-term climatic extremes. GC was calculated according to Nowacki & Abrams (1997). This method was also recommended by Rubino & McCarthy (2004). Local GC maxima were compared with the boundary line values (BL; see below) in order to establish which GC maxima represented the release. In this study, the boundary line for *F. sylvatica* and *P. abies* was constructed according to Black & Abrams (2003), by dividing the set of all 217 061 increments of *F. sylvatica* and 108 215 increments of *P. abies* into

intervals of 0.5 mm. In respect of high values of GC, intervals up to 1 mm PG were divided, according to Splechtna et al. (2005), into shorter intervals of 0.25 mm. The 10 (5 in case of 0.25 mm wide intervals) highest values were then fitted to an exponential function in the Statistica 7.0 program (<www.statsoft.cz>). The boundary line can be expressed in the case of *F. sylvatica* by the function $\text{PGC} = 291.059 + 3446.79 \cdot \exp(-4.47647 \cdot \text{PG}) - 70.474 \cdot \text{PG}$ ($R^2 = 0.969$), and in the case of *P. abies* by $\text{PGC} = 245.897 + 1374.69 \cdot \exp(-3.02039 \cdot \text{PG}) - 42.856 \cdot \text{PG}$ ($R^2 = 0.977$). Neither *A. alba* nor *A. pseudoplatanus* reached the recommended number of increments (Black et al. 2009), with 13 776 and 3 050 increments, respectively. On this account, *A. alba* was evaluated on the basis of the regional boundary line of Splechtna et al. (2005) and the possibility of the application of this source was verified by Šamonil et al. (2009) in the Czech Republic (the Carpathians). Marginally represented broadleaved tree species were evaluated according to *F. sylvatica*. Individual growth accelerations were compared with the BL. Growth changes at the level $\geq 100\%$ of BL were considered as major releases, GCs in the range 50–99% of BL as moderate releases, and GCs in the range 20–49% of BL as weak releases. We rejected pulses that were <20% of BL as inconclusive.

To prevent overestimating the proportion of canopy area disturbance by comprising lateral releases, the calculation of disturbance history was limited only to trees which did not reach the tree canopy. The threshold diameter beyond which the probability was under 5% that a tree could have been overtopped just before the initiation of the growth increase was calculated according to Lorimer & Frelich (1989) (see also D'Amato & Orwig 2008). An analysis of 1 546 randomly sampled beeches and 747 spruces indicated that <5% of the *F. sylvatica* trees with $\text{DBH} = 75$ cm and *P. abies* = 60 cm were overtopped. Release events were not tallied for individuals with diameters greater than this threshold (without thickness of bark), at the time of a disturbance event. Mean bark thickness was 9.38 mm for *F. sylvatica* of $\text{DBH} = 75$ cm ($N = 20$, $\text{SD} = 2.18$ mm) and 7.23 mm for *P. abies* of $\text{DBH} = 60$ cm ($N = 20$, $\text{SD} = 1.35$ mm). Diameters were estimated for every year a tree was in the records, using cumulative radial increment.

Calculation of disturbed tree canopy

Decadal disturbance history was evaluated separately for the human-affected and core zones. As a measure of disturbance intensity, we used the proportion of disturbed tree canopy (sample depth). For that purpose, we modelled the current relation between the area of exposed crown and DBH. Data were fitted by linear, power and

polynomial models of the 2nd order. The best model was selected according to the coefficient of determination. Model $y = 0.6019x^{1.13}$ ($R^2 = 0.772$, $N = 411$) best fitted the relation between DBH (x) and area of crown (y) in case of *F. sylvatica* (the model was also adopted for other broadleaved tree species). In the case of *P. abies* $y = 0.4743x^{1.0204}$ ($R^2 = 0.789$, $N = 225$; adopted also for *A. alba*). Chronologies were truncated when the sample depth dropped below 30 trees.

The gaps after the Kyrill storm were classified by unsupervised maximum likelihood classification from orthorectified Colour Infra Red (CIR) aerial photographs from 2008.

Spatial pattern of disturbance history

The accurate location of all trees allowed us to use geostatistical techniques to study the development of variability of disturbance events through spatial scales. This analysis was only carried out within the core zone. Techniques of dendrochronological research do not allow the evaluation of disturbance events younger than 10 yr (see Nowacki & Abrams 1997). To elimination that effect, tree-census data from the period 1997–2008 were used. On the basis of tree-census data, we were able to identify exactly which trees were uprooted, broken or affected by biotic factors (e.g. *I. typographus*) in 2007–2008 (considered to be the effect of the Kyrill storm), 1998–2006 and 1975–1997. Since disturbances underwent simultaneous dendrochronological evaluation before 1997, we were able to compare both datasets in the period 1975–1997. Disturbance history before 1975 was evaluated using dendrochronological data only (at least 500 trees per decade had to be present).

For all tree species, indicator variograms were used to assess the spatial autocorrelation of weak, moderate and major releases in dendrochronological data using the range of these variograms as an indicator of maximum autocorrelation distance (Isaaks & Srivastava 1989; Wackernagel 2003). At the same time variograms were calculated for three thresholds of DBH in the case of tree-census data. The calculation was performed on trees where the probability was: (1) >95% that a tree was not overtopped (Lorimer & Frelich 1989); broadleaved tree species with DBH ≥ 75 cm and coniferous tree species with DBH ≥ 60 cm were included; (2) >50% that a tree was not overtopped; broadleaved tree species with DBH ≥ 37 cm and coniferous tree species with DBH ≥ 41 cm were included; and; (3) >25% that a tree was not overtopped; broadleaved tree species with DBH ≥ 24 cm and coniferous tree species with DBH ≥ 22 cm were included. An experimental variogram summarizes the semivariance statistic $\gamma(h)$ for the range of distance intervals h :

$$\gamma(h) = \frac{1}{2N_h} \sum_{i=1}^{N_h} [Y(x_{i+h}) - Y(x_i)]^2 \quad (1)$$

where $Y(x_i)$ and $Y(x_{i+h})$ represent values at locations separated by distance h , and N_h is the number of observation pairs included in the distance interval (lag). Semivariance values were calculated according to equation (1) in R software, package gstat (R Development Core Team 2006). We selected lags sized 5 m up to 20 m distance, 10 m lags up to 100 m, and 25 m lags up to 425 m distance. The distance value representative for each lag is equal to the mean separation distance of all observations pairs included in the interval.

Selected regression models were fitted to sample experimental variograms using R package gstat (R Development Core Team 2006). Spherical, exponential, power, Gaussian and nested models were fitted using the weighted non-linear least-squares method and the best fitting model of each experimental variogram was selected according to the characteristics of the model (sum of squares, coefficient of determination).

Results

Curves of mean radial growth of trees differed significantly between the core and human-affected zones (Fig. 4), and the latter showed significant growth acceleration of *F. sylvatica* and *P. abies* after 1800. The simultaneous fast decrease of sample depth indicated that mainly juvenile trees were evaluated during this period, and advanced regeneration responded to cutting with high probability. Despite the fact that intensive growth impulse was not found in the core zone, curves of *A. alba* and *P. abies* mean growth indicated higher values after 1800. A noticeable slump of *A. alba* radial growth appeared between the 1960s and 1980s, although subsequent recovery was observed. The drop was less obvious in *F. sylvatica* and featureless in the case of *P. abies*.

The Kyrill storm was a singular event in forest development from the point of view of its spatial pattern, but not from the point of view of disturbance intensity (Figs. 5–7). In general, the spatial pattern of the disturbances was not always proportional to the intensity of the disturbance, measured by canopy area disturbance (see below). The tree-census revealed that the Kyrill storm did not affect forest structure randomly (Fig. 2). The tallest *A. alba* and *P. abies*, belonging to higher diameter classes, as well as spruce-dominated stands on water-affected sites were disturbed more intensively. The proportion of disturbed *F. sylvatica* was significantly lower compared with the proportion of tree species in the forest structure. The interpretation of orthorectified CIR aerial photographs from 2008

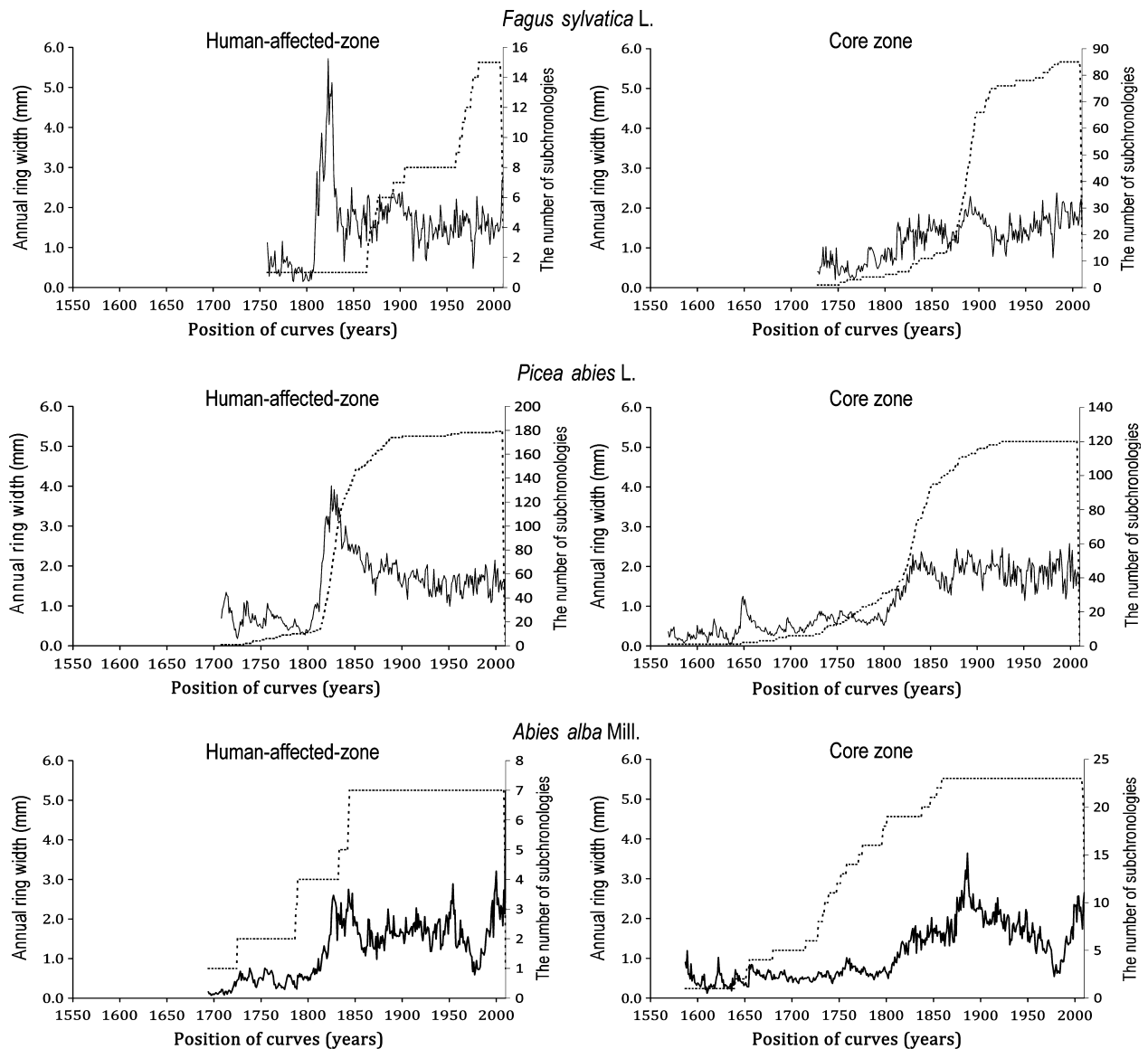


Fig. 4. Mean annual growth of the main tree species in the human-affected and core zones. In total, 2232 suitable tree cores were used for mean annual growth calculation (only 429 cores of different tree species satisfied the requirements for intercorrelation in the core or human-affected zones).

showed the proportion of gaps after the Kyrill storm as ca. 9% of the total territory of the core zone.

In the dendrochronological data, the mean disturbance rate was 11.0% canopy loss per decade (median 9.2%, maximum 33.7%) in the core zone. In the human-affected zone, the mean disturbance rate was 7.4% (median 6.3%; maximum 18.9%; Fig. 5). Peaks of intensive canopy disturbances corresponded to peaks of tree regeneration, with an approximately one-decade delay. Within the 350 yr of dendrochronological records, the tree canopy was disturbed most intensively in the period 1880–1889, followed by the decade 1980–1989. Besides a higher frequency of tree regeneration, juvenile trees more often grew in gaps

after disturbances (Fig. 5). Whereas the proportion of tree individuals with gap origin exceeded 80% in the 1880s and 1980s, it rarely reached 50% during the remaining periods. The differences were more considerable in the human-affected zone where the proportion of individuals with gap origin repeatedly exceeded 90%. However, we can suppose that these trees frequently germinated under the canopy (saplings are frequently older than the time since the disturbance event). Human-affected stands were disturbed most intensively in the period 1800–1820. While peaks of canopy area disturbance were obvious in both zones in the period 1980–1989, other peaks did not mutually correspond.

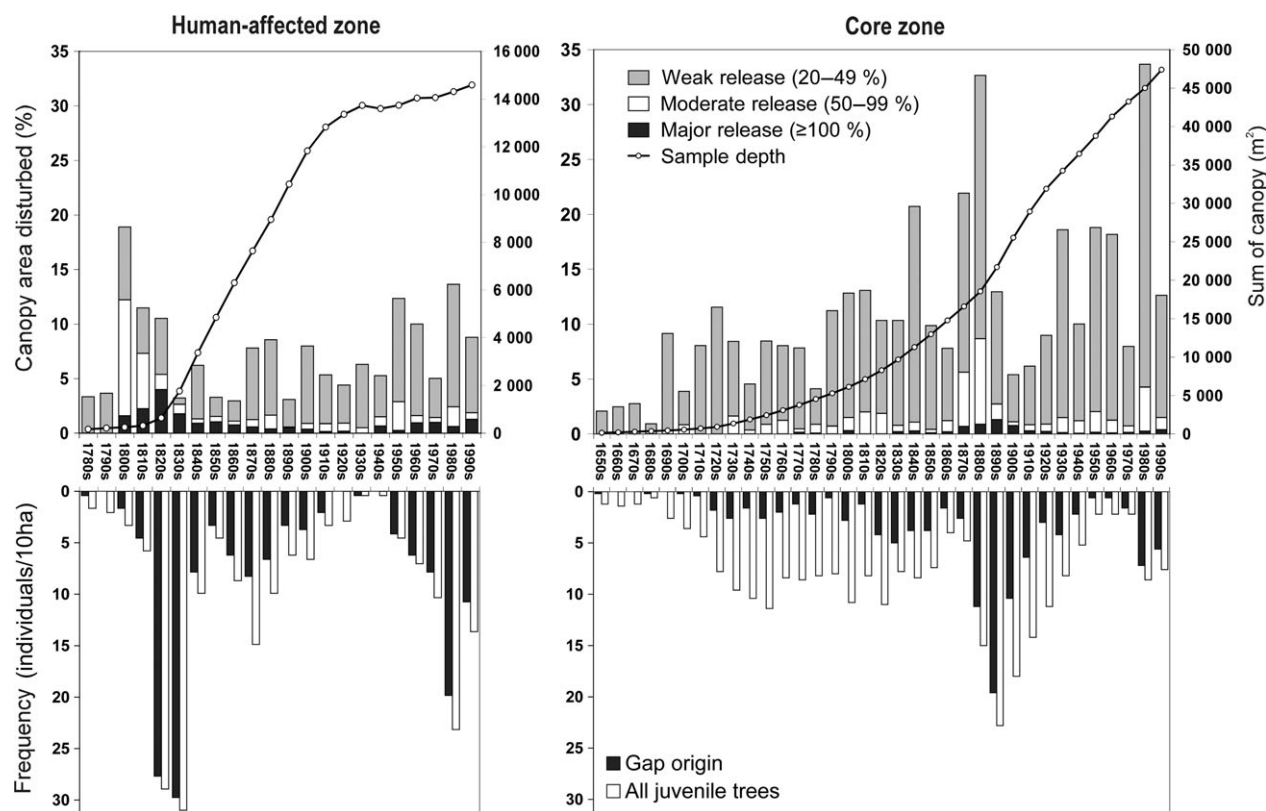


Fig. 5. Summary disturbance history of Žofín in the human-affected and core zones based on dendrochronological data. Columns represent canopy area disturbed, or number of juvenile trees; sum of canopy represents the relevant area of exposed crowns (for details, see Section Calculation of disturbed tree canopy).

The range of spatial autocorrelation of dead trees (broken or uprooted) was at least 141.8 m during the Kyrill storm, and increased commensurately with the social dominance of trees up to 320.0 m (Table 1; Fig. 6). The spatial variability of these dead trees was the best fitted by an exponential model, which was the most appropriate also for the majority of other tree-census data (Table 1). Although forests seemed to be noticeably disturbed in the

period 1980–1989, the range of spatial autocorrelation of dead trees did not exceed 18 m in the period 1975–1997 (Fig. 5; Table 1).

At the same time, the variability development of releases $\geq 50\%$ of BL corresponded relatively to real disturbance events, established on the basis of the tree-censuses in this period (Table 2; Figs. 7–8). The insertion of weak release into the spatial variability calculation usually

Table 1. Characteristics of best-fitting models of tree-census data variability in periods of survey. The period 2007–2008 is considered to be the effect of the Kyrill storm (see Section Forest structure). The social status of disturbed trees was evaluated using the regression model between DBH and social status (in total 2293 trees were evaluated from the point of view of social status).

Period	Threshold of calculation	Model	Nugget	Sill	Range (m)	R ²	Relative nugget (l)
2007–2008	>25% non-suppressed trees	Exponential	0.08	0.16	141.8	0.97	0.53
	>50% non-suppressed trees	Exponential	0.10	0.15	177.1	0.97	0.65
	>95% non-suppressed trees	Exponential	0.10	0.16	320.0	0.98	0.60
1998–2006	>25% non-suppressed trees	Exponential	0.08	0.10	22.5	0.91	0.74
	>50% non-suppressed trees	Spherical	0.10	0.12	20.7	0.92	0.82
	>95% non-suppressed trees	Exponential	0.05	0.16	15.4	0.96	0.34
1975–1997	>25% non-suppressed trees	Exponential+Power	0.10	0.12	16.1	0.98	0.85
	>50% non-suppressed trees	Exponential	0.12	0.14	18.0	0.90	0.83
	>95% non-suppressed trees	Exponential	0.12	0.17	10.2	0.91	0.66

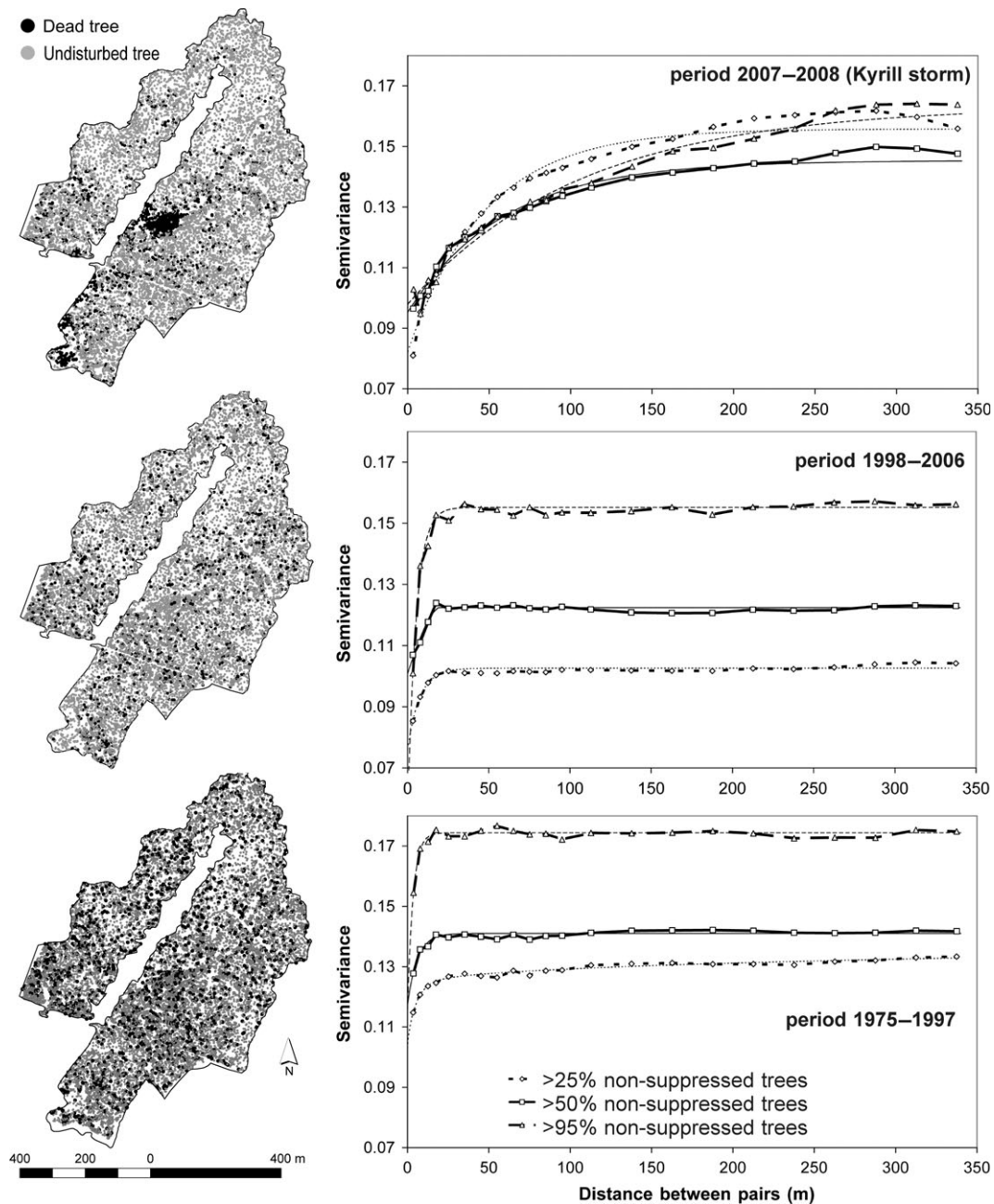


Fig. 6. The development of dead tree variability in the core zone during the periods 2007–2008 (Kyrill storm), 1998–2006 and 1975–1997 on the basis of the repeated tree-censuses in the whole area (74.2 ha). We analysed diameter classes of trees separately, with >25% of non-suppressed trees, >50% of non-suppressed trees, and >95% of non-suppressed trees (for details, see Section Spatial pattern of disturbance history). The courses of best-fitting models are also presented (see Table 1).

led to the overestimation of range and an increase in relative nugget (see Isaaks & Srivastava 1989). Moderate and major releases were also nearer to neighbouring truly disturbed trees in comparison to weak releases, where false or lateral releases could be more probable (Fig. 9). Dendrochronological data were the best fitted by different

types of models. The majority of models exposed the threshold of spatial autocorrelation as between 0 (pure nugget) and 30 m, rarely exceeding 60 m. Although values of ranges exceeded 200 m in some cases, these models proved high values of relative nugget. In general, the relation between disturbance intensity (y) and range of spatial

Table 2. Characteristics of best-fitting models of dendrochronological data variability. We evaluated spatial variability of disturbance events (represented by releases in the radial growth of trees) by indicator variograms. Calculations were truncated when the sample depth dropped below 500 trees; BL – boundary line.

Period	Threshold of growth change	Model	Nugget	Sill	Range (m)	R ²	Relative nugget (l)
1975–1997	≥ 20 % BL	Exponential	0.186	0.250	35.7	0.95	0.74
	≥ 50 % BL	Spherical	0.039	0.071	25.7	0.93	0.55
1990–1999	≥ 20 % BL	Spherical	0.067	0.126	22.3	0.93	0.53
1980–1989	≥ 20 % BL	Exponential	0.168	0.225	22.0	0.94	0.75
	≥ 50 % BL	Spherical	0.031	0.051	21.3	0.88	0.62
1970–1979	≥ 20 % BL	Exponential	0.055	0.080	14.6	0.83	0.69
1960–1969	≥ 20 % BL	Exponential	0.068	0.156	19.5	0.92	0.43
1950–1959	≥ 20 % BL	Spherical	0.138	0.166	60.7	0.83	0.83
1940–1949	≥ 20 % BL	Gaussian	0.086	0.098	31.7	0.74	0.87
1930–1939	≥ 20 % BL	Exponential	0.016	0.141	17.4	0.98	0.12
1920–1929	≥ 20 % BL	Spherical	0.088	0.094	222.8	0.66	0.93
1910–1919	≥ 20 % BL	Gaussian	0.025	0.067	6.4	0.95	0.37
1900–1909	≥ 20 % BL	Pure nugget	0.054	0.054	–	–	1.00
1890–1899	≥ 20 % BL	Pure nugget	0.114	0.114	–	–	1.00
	≥ 50 % BL	Gaussian	0.018	0.027	6.5	0.58	0.69
1880–1889	≥ 20 % BL	Exponential	0.170	0.217	57.5	0.96	0.78
	≥ 50 % BL	Exponential	0.049	0.085	26.0	0.92	0.57
1870–1879	≥ 20 % BL	Exponential	0.153	0.184	69.0	0.88	0.83
	≥ 50 % BL	Spherical	0.006	0.060	15.6	0.95	0.10
1860–1869	≥ 20 % BL	Pure nugget	0.091	0.091	–	–	1.00
1850–1859	≥ 20 % BL	Gaussian	0.001	0.084	7.0	0.69	0.01
1840–1849	≥ 20 % BL	Gaussian	0.076	0.145	17.0	0.89	0.52
1830–1839	≥ 20 % BL	Pure nugget	0.097	0.097	–	–	1.00
1820–1829	≥ 20 % BL	Linear	0.097	–	–	0.53	–
1810–1819	≥ 20 % BL	Gauss. + Gauss.	0.000	0.120	9.6 and 184.7	0.94	0.00
1800–1809	≥ 20 % BL	Exponential	0.069	0.107	29.1	0.85	0.65
1790–1799	≥ 20 % BL	Pure nugget	0.083	0.083	–	–	1.00
1780–1789	≥ 20 % BL	Exp. + Gauss.	0.000	0.055	11.8 and 223.0	0.85	0.00
1770–1779	≥ 20 % BL	Spherical	0.051	0.069	44.8	0.49	0.75
1760–1769	≥ 20 % BL	Pure nugget	0.067	0.067	–	–	1.00

autocorrelation (x) can be explained by the equation $y = 10.6863 + 0.0783 \cdot x$ ($R^2 = 0.546$, $P = 0.009$, spatial correlation index was used as a weight, Fig. 10). However, it is difficult to predict the spatial characteristics of a disturbance event based on disturbance intensity.

Weak releases predominated in the disturbance history of Žofín; they occupied 84.6% of all releases in the core zone and 77.6% in the human-affected zone. The proportion of moderate and major releases increased in periods of more intense disturbances. This was more obvious in the human-affected zone, where the sum of moderate and major releases reached 51–81% in the period 1800–1839. While the total proportion of major disturbances was 8.3% in the human-affected zone, it was only 2.1% in the core zone. The structure of releases associated with tree individuals was strongly dependent on DBH (consequently also on the age and social status of trees; Fig. 11). *F. sylvatica* as well as *P. abies* had, on average, 2.8 disturbance events/tree (releases plus gap origin) in the core zone and 2.0 events/tree in the human-affected zone. From this point of

view, human activities caused a simplification of forest dynamics. *A. alba* had, on average, 3.5 events/tree in both zones. However, there were also 3% of trees without release or gap origin in the core zone, and 6% of such trees in the historically managed zone. On the other hand, at most nine disturbance events were recorded in one tree. The proportion of juvenile individuals with gap origin was species specific. In the core zone, 54.8% *P. abies* and 41.3% of *F. sylvatica* individuals indicated gap origin, while only 8.9% of *A. alba* individuals did so. The proportion of trees with gap origin was more obvious in the human-affected zone, where 86.5% of *P. abies* and 61.6% of *F. sylvatica* indicated gap origin.

Discussion

Methodological approach

Repeated tree-censuses on an area of 74.2 ha give us a unique dataset for dendrochronological research. With detailed knowledge of the tree layer in 1997, we were

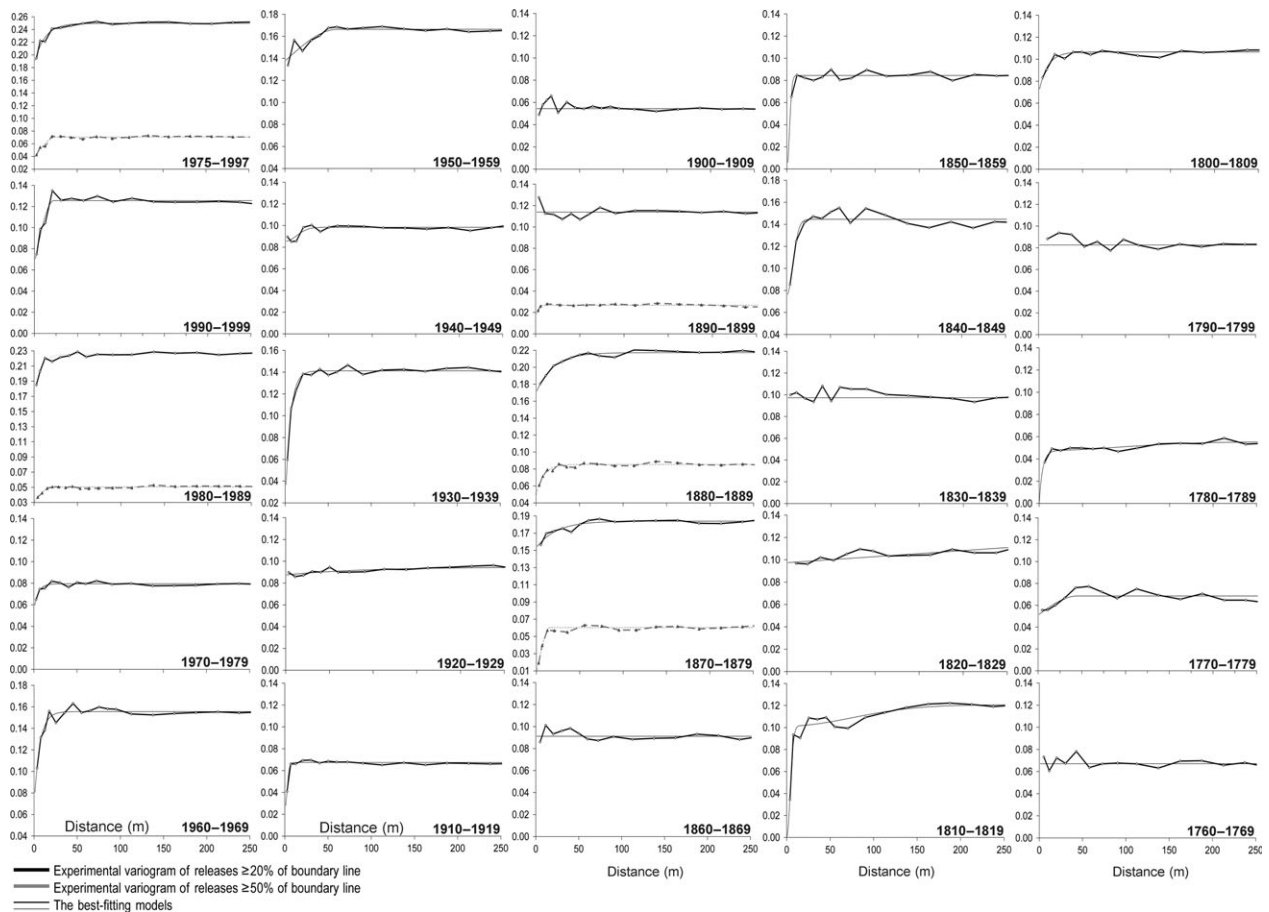


Fig. 7. Development of spatial variability of disturbances in the core zone based on dendrochronological data in the period 1760–1999. The process of variogram construction is described in Section Spatial pattern of disturbance history. The characteristics of best-fitting models are included in Table 2.

able to clearly distinguish recent, dendrochronologically undetectable disturbance events. These events were usually vaguely eliminated during sampling by researchers up to now (e.g. Fraver et al. 2009). Since recent disturbances were precisely separated in Žofín, we could say that 3% of trees did not reach release in their whole life even though they were non-suppressed in 1997. This group caused the undervaluation of canopy area disturbance as well as noise during the calculation of spatial relations. Even trees close to each other sometimes exhibited different releases, which was proved in the high nugget of variograms and low values of the spatial correlation index ($1 - \text{relative nugget}$). Furthermore, the predominance of weak releases within the dendrochronological records and a mean gap size of only 88–99 m² in the period 1971–2004 (Kenderes et al. 2009) suggested especially fine-scale disturbances. This implies that the application of dendrochronological techniques has its own limits. Future research should test for responses of trees to known disturbance events empirically (see Stan

& Daniels 2010), and define dendrochronologically detectable threshold events; that is, a “nugget of disturbance history”. To this end, Šamonil et al. (2009) empirically derived the threshold response of *F. sylvatica* to disturbance on 12.13% of BL, using a repeated tree-census in the Western Carpathians. A shift in the weak release threshold, from 20% of BL to this border, would increase the number of releases to about 57% in Žofín.

The limitation of noise that resulted from different responses of neighbouring trees to disturbance was resolved by Shimatani & Kubota (2011). They used 386 tree cores on 2.25 ha (Japanese). The authors evaluated a variable which we can call “disturbance relationship” of trees on the basis of their spatial pattern using cluster analysis. This led, in our opinion, to an unsuitable retreat from spatially-explicit, individual-based models to traditional patch models (Pacala et al. 1996; Grimm 1999; Gratzner et al. 2004), and possibly also to partial tautology, because the distance between individuals was not an independent variable during the subsequent study of disturbance spatial

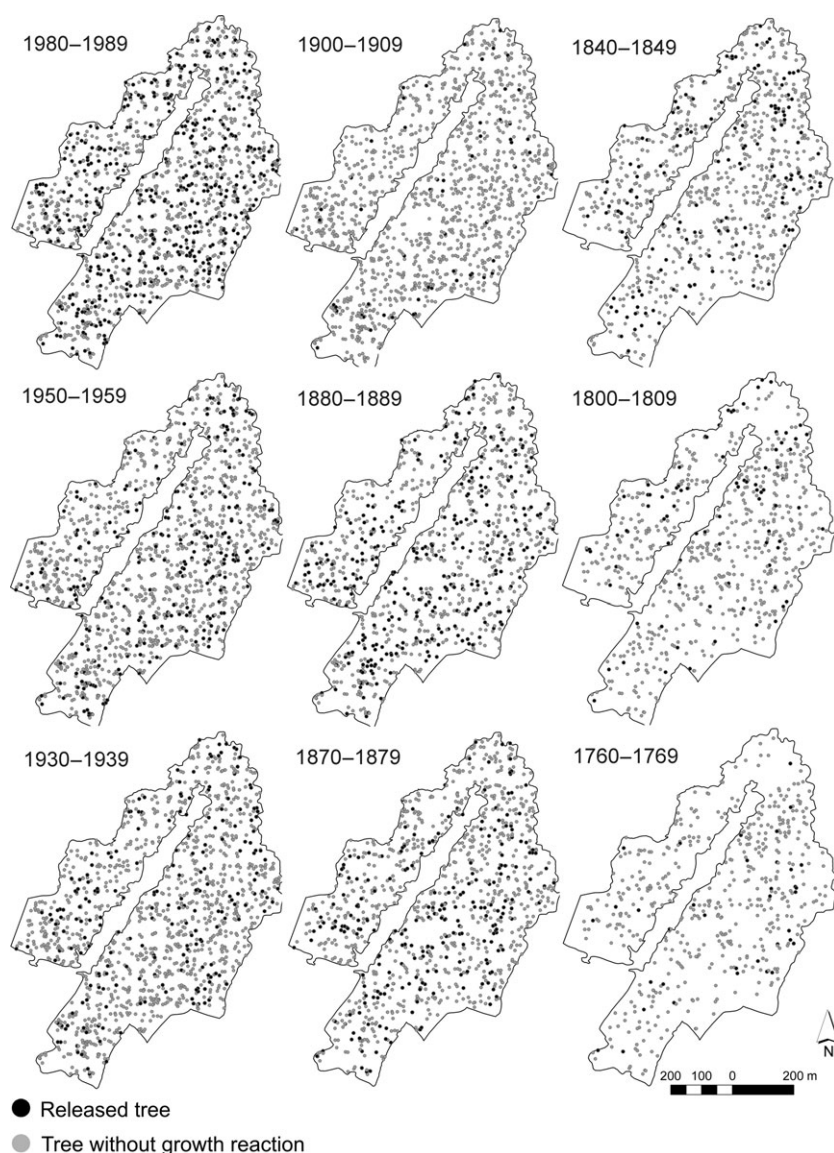


Fig. 8. Selected maps of disturbance spatial pattern in the core zone. Trees with release $\geq 20\%$ of the boundary line are considered to be disturbed; the characteristics of models are included in Table 2 (for details, see Section Spatial pattern of disturbance history).

pattern. We rather opted for the continuous concept of space with a high amount of data, and we accepted the limits of dendrochronological techniques. However, these limits should be solved in the future in connection with searching for the empirical response of trees to disturbances. Zielonka et al. (2010) also applied point data of tree individuals rather than area data for the evaluation of the disturbance history of a 100 ha plot. Nevertheless, authors were rather motivated by low amount of data (only 97 cores) rather than analysing disturbance history through spatial scales, and they used traditional techniques of data processing. Moreover, tree positions were determined by GPS, and the inaccuracy of this method limits

the evaluation of disturbance synchronicity for the most important distance of 5–10 m. We avoided this uncertainty by the construction of a rectangular network with a geodetic 0.05 m accuracy, and tree individuals were measured with ca. 0.5 m accuracy.

A spatially-explicit, individual-based approach allows for the study of disturbance history through spatial scales as well as for the evaluation of spatial relations between individuals and tree populations against the background of disturbance events. This approach is also applicable at sites of tens of hectares in size. A traditional, separate plots approach is not always appropriate for such sites because of the required number of cored trees per plot or the

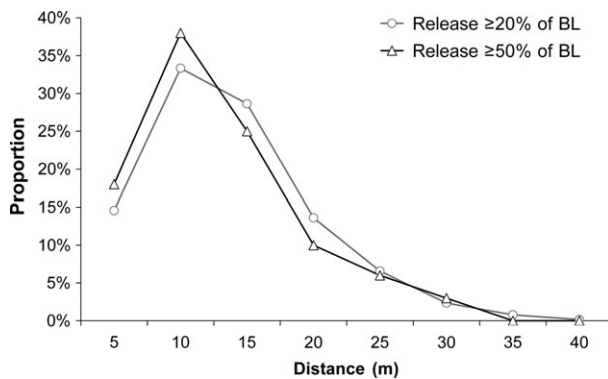


Fig. 9. The distribution of minimal distances between cored trees responding to disturbances (release $\geq 20\%$ and $\geq 50\%$ of boundary line), and nearest neighbouring trees that died in the period 1975–1997 in the core zone.

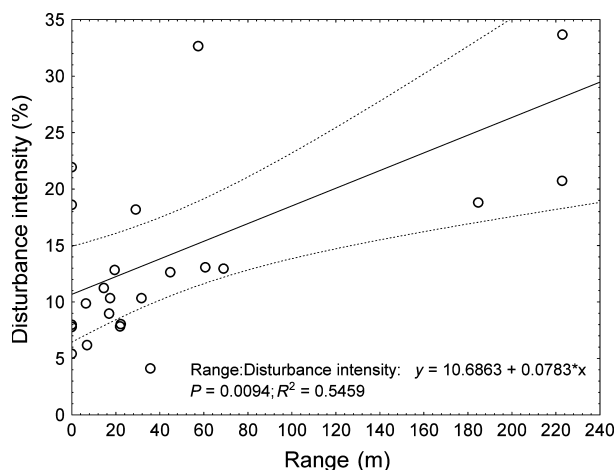


Fig. 10. Relation between disturbance intensity and range of spatial autocorrelation in dendrochronological data. Decadal information from Fig. 5, 7 and Table 2 were used.

number of plots (e.g. Frelich & Lorimer 1991a; Fraver et al. 2009; Panayotov et al. 2011). At the same time, we avoided some subjective steps essential to the application of traditional methods. For example, if we consider dendrochronological records as point data in space, we do not need to determine the threshold of disturbance intensity per plot (measured by the number of trees that responded to a disturbance event). The application of directional- and cross-variograms, as well as analyses of spatial point patterns (Illian et al. 2008), potentially allow a more detailed evaluation of disturbance phenomena (wind direction, relation to geomorphology, etc.). Moreover, the ecological role of disturbances seems to be biased during the modelling of tree-species coexistence if disturbance intensity and returning interval are used as the sole criteria (see Gravel et al. 2010). Fajardo & Gonz  les (2009) used a similar

geostatistical approach to their study of replacement patterns and species coexistence on a 1 ha plot in an *Araucaria-Nothofagus* forest in Chile.

Disturbance history of beech-dominated forests

The development of mean radial growth was modelled by local factors and a comparison with the trends of temperature in Central Europe (e.g. Dobrovoln  y et al. 2010) did not demonstrate straightforward connections. Exceptional growth increments, the peak of disturbed canopy area and plentiful tree regeneration were apparently caused by intensive selective cutting in the human-affected zone after 1800. Some older trees have survived into the present. The reasons for tree felling could be: (1) the acquisition of wood for the newly constructed glassworks; (2) making the stream area accessible for floating; and (3) forest protection against *I. typographus*, which culminated in the region at this time (Chadt 1908). Because curves of *A. alba* and *P. abies* mean growth indicated higher values after 1800 also in the core zone, we cannot exclude limited direct human impact in this area either.

The obvious slump in the radial growth of *A. alba* between the 1960s and 1980s was probably caused by air pollution, which culminated in Central Europe at this time. Elling et al. (2009) claimed that a mean annual atmospheric concentration level of $10 \mu\text{g SO}_2 \text{ m}^{-3}$ was critical for *A. alba*'s health. Despite the fact that our study site is quite far from emission sources (see Šebesta et al. 2011), on the basis of a large-scale European dataset of modelled SO_2 atmospheric concentrations in the 1980s (<www.emep.int>), we suppose that a critical concentration could have been reached at the site in the 1980s. Other tree species seemed to be less sensitive to air pollution. Pollution could be an important factor of the observed gradual increase of *F. sylvatica* to the detriment of *A. alba*, and partially also to *P. abies* during the past few decades (Pru  sa 1985). It could also play a role in the intensive canopy area disturbance in the 1980s. We think that an accelerated dying of *A. alba* stands and the overestimation of releases because of the positive response of trees to a decrease of air pollution in the 1990s were the main factors of high disturbance intensity in the 1980s. Growth changes could be compared with a regional master chronology to eliminate this effect in the future (e.g. Thompson et al. 2007). Effect of air pollution can be the reason for discrepancies between exceptional canopy area disturbance and its low level of spatial autocorrelation in the period 1980–1989. We think that the synergic effects of storms (historically documented in 1870 and 1875), snow breakage (1881) and *I. typographus* (1870–1874; see Chadt 1908; Kruml 1960; Br  zdil et al. 2009) also contributed to high disturbance in the period 1870–1889.

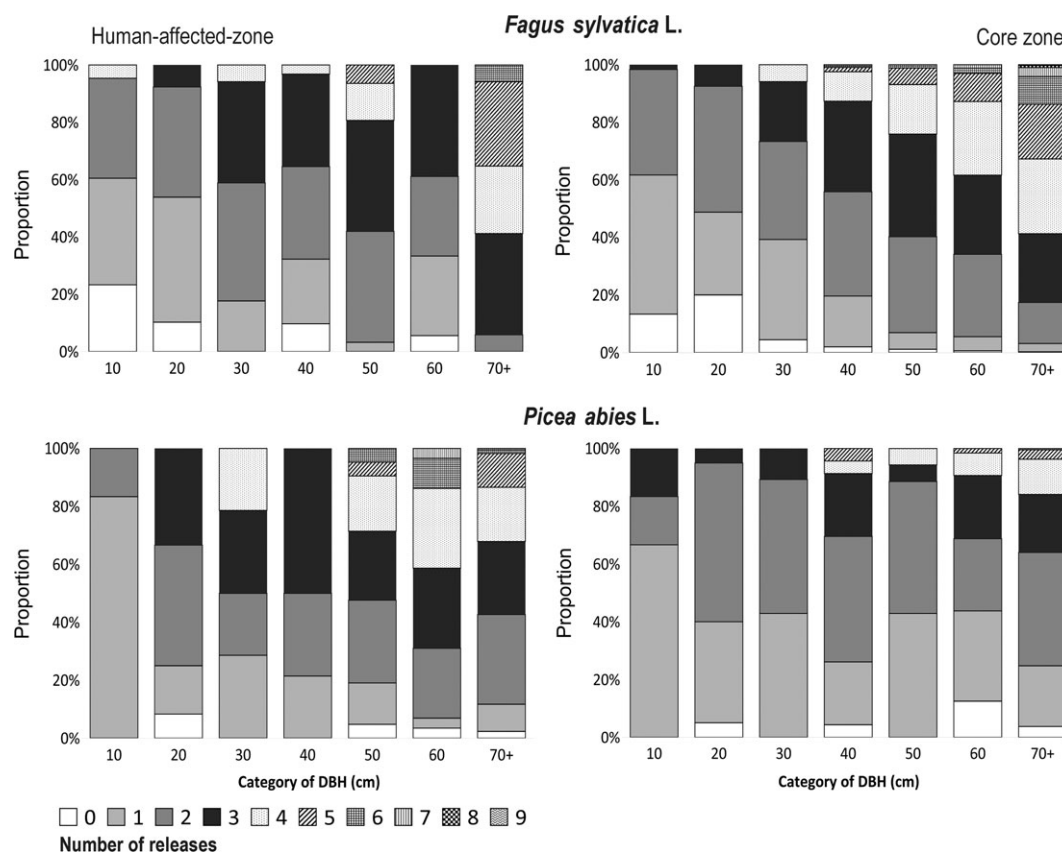


Fig. 11. Representation of trees with different numbers of disturbance events (gap origin + releases) according to the tree species and diameter class at the time of sampling (for details, see Section Disturbance event detection).

The Kyrill storm affected not only forest structure but also tree species diversity. On the one hand, extraordinarily large gaps opened new “niches” for rare tree species at early succession stages (*Salix caprea*, *S. aucuparia*, *A. pseudoplatanus*). On the other hand, the storm disturbed the highest *A. alba* and *P. abies* individuals, which allowed a higher dominance of *F. sylvatica* to the detriment of these secondary tree species (see Montoya et al. 2010). While we found the range of spatial autocorrelation up to 320.0 m after the Kyrill storm, the majority of other events had a range up to 40 m, rarely up to 60 m. We observed that disturbances of similar intensity can have very different spatial patterns and therefore a different role in forest ecology. In a dendrochronological study from the same forest type (but different geological bedrock), Splechna et al. (2005) did not find significant departures from the complete spatial randomness null model at a fine spatial scale. The predominant range of disturbances between 10 and 40 m corresponded roughly to the range of weathering-soil-horizon thickness (= B-horizon, = Cambic or Spodic horizon; see Šamonil et al. 2011), but was significantly shorter compared to ranges of other soil properties (thickness of upper horizons, carbon content, soil reac-

tion). We suppose that the renewal of organic and A-horizons after uprooting events is more rapid than in the mineral B-horizons where restoration lasts for many years after the levelling of typical pit-mound micro-morphological forms (Šamonil et al. 2010b). Disturbances can therefore be more important factors of B-horizon development, and other soil properties can be primarily modelled by different factors (geomorphology etc.).

Although we found significant canopy area disturbance in the 1980s, Kendereš et al. (2009) found a stable total gap area of 9–11%, with low canopy dynamics occurring annually in 0.1% of Žofín during the period 1971–2004. Small gaps, weak responses to disturbance, high numbers of releases through the whole life of the tree and short values of ranges suggest that the steady-state stage of forest development could play an important role in forest dynamics (Král et al. 2010a). Forest stands within this stage are characterized by a rich vertical structure, where dead canopy trees are immediately replaced by another tree. The formation of gaps is not essential during this stage. The existence of a steady-state stage of forest development was proved by Král et al. (2010a) in Žofín. Stands also agreed with the definition of steady-state

stands (or balanced all-aged stands), according to Frelich & Lorimer (1991b). On the other hand, some trees probably grew up in a gap and were not suppressed during their whole life; only 4% of trees had gap origin in the core zone. In general, this indicates high variability in the process of regeneration, as there are unusually small pulsating gaps on the one hand, and wider non-closed gaps (including edaphic gaps) for longer periods on the other hand (Šamonil et al. 2011). The results suggest that historical and geographical contingencies influence ecosystem development via sequence, timing and initial conditions of disturbance events, and could be more important factors than global laws. Phillips (2004) considers these local factors as irreducibly significant, which led researchers to shift away from searching for general rules to the incorporation of such local factors.

Splechna & Gratzner (2005) found a relatively low disturbance rate in *Picea-Abies-Fagus* natural forests in Austria, where the proportion of the total area in gaps (gap fraction) was 3.3–13.8% in the period 1962–1996, and mean gap size was 229–243 m². The results of Szwagrzyk & Szwagrzyk (2001) and Firm et al. (2009) suggest higher disturbance rates in old-growth *Fagus-Abies-Picea* stands in Poland and Slovenia. However, the volume of their data is low compared to the spatial variability of forest structure (Král et al. 2010a,b), which limits possible generalizations. Our results generally correspond to studies from northern hardwoods in the USA, or temperate forests in Asia. Fraver et al. (2009) detected a decadal mean canopy area disturbance of 9.6% in different forest types in Maine, and according to Frelich & Lorimer (1991a) up to 15% of the forest area was converted to gaps in a single decade in *Acer saccharum* and *Tsuga canadensis* stands in Upper Michigan.

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