

Growth dynamics after historic disturbance in a montane forest and its implications for an endangered epiphytic lichen

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Abstract

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Endangered forest species are often negatively affected by disturbances, which may have long-lasting effects on the distribution, abundance and genetic diversity of such species. To understand the effects of historic disturbances, detailed knowledge of the conditions for survival and recolonisation is needed, and this requires precise information on the perimeter and severity of historic disturbance events. We reconstructed a major historic disturbance (intensive logging followed by windthrow and fire in 1871) in the Swiss Jura mountains to analyse its effect on the disturbance-sensitive epiphytic lichen *Lobaria pulmonaria*. Tree-ring analysis of old and young Norway spruce trees (*Picea abies* L.), sampled systematically on a 100 m grid, revealed that (1) the disturbance was of intermediate severity, (2) a large, well-defined area of disturbance was created, and (3) an undisturbed zone remained in the centre of the disturbed area. A comparison with lichen genetic data from a previous survey revealed that genetic diversity was particularly high in the remnant zone. These results suggest that the lichen survived there, and that it re-colonised the disturbed area both from the edge and from the remnant undisturbed zone. This illustrates that a detailed reconstruction of historic disturbances, as achieved with dendroecology, is very important for understanding the recolonisation process and thus, the conditions for the long-term persistence of disturbance-sensitive species in a dynamic landscape.

Key words: Dendroecology, fire, *Lobaria pulmonaria*, logging, tree-ring analysis.

Introduction

The effects of disturbances on rare or endangered species play an important role for the conservation of present species diversity. Especially sessile organisms with limited dispersal abilities may be sensitive to disturbance such as fire and the resulting patch dynamics. This applies to many epiphytic lichens with a long generation time and inefficient mechanisms of dispersal (Rose 1976, 1992). However, to clarify how disturbance-sensitive these organisms are, we need to relate spatial patterns of occurrence and genetic diversity of such species to past disturbances.

The opportunity to study such a relationship is given in the Swiss Jura mountains, where a large and genetically diverse population of the foliose lichen *Lobaria pulmonaria* occurs (Zoller et al. 1999), despite regular disturbance such as grazing and tree-logging, or rare events of windthrow or fire (Kalwij et al. 2005). *Lobaria pulmonaria* is widespread (Yoshimura 1998), yet regionally threatened (Wirth et al. 1996; Scheidegger et al. 2002) and often used as a flagship species in conservation activities of primeval forests (Kondratyuk et al. 1998), where it is an indicator of ecological continuity (Rose 1992). Even though the lichen has been suggested to be dispersal-limited (Scheidegger 1995; Walser et al. 2001; Walser 2004; Öckinger et al. 2005), Werth et al. (2006b) and Kalwij et al. (2005) found a high proportion of colonised trees in the presumably disturbed area. However, a survey on the genetic diversity of the lichen in this area (Werth et al. 2006b) revealed distinct spatial patterns of genotype diversity (Fig. 1). Survey plots within the presumably disturbed area had low genotype diversity and shared few genotypes, with two exceptions: (1) two genetically diverse survey plots right in the centre of the disturbed area, sharing two genotypes, and (2) two diverse survey plots close to the western border of the disturbed area, sharing no genotypes. These distinct genotype patterns suggest an effect of past spatial disturbance patterns, such as the presence of remnant undisturbed patches within the disturbance perimeter.

From the perspective of an epiphytic lichen, single trees are patches which are dynamic in that they emerge, grow and fall (Snäll et al. 2005). The occurrence of *L. pulmonaria* is, therefore, likely to have been affected by the disturbance in two ways: First, by increased mortality of host trees and thereby, a reduction of available habitat patches. Second, by a decrease in host tree density, which results in an increase in the distance between habitat patches. However, the distance to occupied host trees, e.g. in undisturbed areas, is likely to be crucial for successful recolonisation of a disturbed area by *L. pulmonaria*. Therefore, to understand the spatial pattern of genotype diversity of the patch-tracking lichen *L. pulmonaria* found at present, a more spatially-explicit reconstruction of the historic disturbance is essential.

Historical records can provide important information on the time and character of the disturbance. Indeed, historical records document intensive logging followed by windthrow and fire in this area in the years 1870 and 1871 (Rochat 1995), and forest management plans report of a severe past disturbance (Plan d'aménagements 'Le Lieu' from 1900, municipal archive of Le Séchey, Switzerland). However, these historical records do not provide any information on the exact perimeter of the disturbance nor the location of surviving trees. Aerial photographs would be more appropriate to investigate the spatial extent of the disturbance, however they might often not be available for a disturbance that happened more than a hundred years ago. The earliest aerial photographs of the study region were taken in 1933. Though they proved useful for a first delineation of the disturbance perimeter (Kalwij et al. 2005), sixty years of

regeneration after the disturbance might cause some uncertainty in the determination of the perimeter and the location of trees that have survived. A spatially-explicit age reconstruction of the trees in the study area is needed to determine the perimeter of the disturbance and locate trees that have survived, which can only be achieved using dendroecology. Dendroecology is a powerful approach to investigate historic forest disturbances (Henry and Swan 1974; Lorimer 1985; Banks 1991; Cherubini et al. 1996; Cherubini et al. 2002; Rubino and McCarthy 2004). Tree rings are a unique source of long-term data providing precise, local information about growth conditions with an annual resolution (Schweingruber 1989).

In this dendroecological study we first analyse the age distribution of trees to determine the spatial extent of the historic disturbance and to identify any remnant undisturbed areas. We assume that the disturbed area is characterized by the absence of trees older than 1871 (disturbance event) and enhanced tree regeneration after 1871. We then examine tree growth dynamics after the disturbance to assess its severity, assuming that improved light conditions are reflected by increased stem growth. Finally, we reanalyse data from Werth et al. (2006b) to discuss the implications of the reconstructed disturbance patterns for the interpretation of the present spatial genetic diversity patterns of *L. pulmonaria*, and to see whether patterns of disturbance can explain the observed differences in genetic diversity among the lichen survey plots within the disturbed area.

Methods

Study area

The study area is located in the 'Parc Jurassien Vaudois', Canton Vaud, Switzerland (46°33'N; 6°12'E) at 1300–1400 m a.s.l. The region is characterised by a relatively humid and cold climate; the annual precipitation is 1630 mm (Marchairuz, 1447 m a.s.l. (46°15'N; 6°15'E) and the mean January and July temperatures are –5.3°C and 11.4°C (Trois Chalets, 1321 m a.s.l. (46°32'N; 6°13'E). The bedrock consists of limestone-marl alterations (Falconnier 1950) and the region is characterised by processes of karst formation. The dominating soil type is rendzina (FAO 1988), which is generally well drained. The 'Parc Jurassien Vaudois' is a traditionally managed sylvo-pastoral landscape. Forests and wooded pastures are dominated by Norway spruce (*Picea abies* L.) mixed with less abundant sycamore maple (*Acer pseudoplatanus* L.), beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Miller). The research area encompasses one forest management unit of 37 ha, which is enclosed by a human-made stonewall of one meter in height, and surrounded by forest and wooded pasture. According to historical records, the major combined disturbance occurred in the years 1870 and 1871 (Rochat 1995). After intensive logging inside the forest management unit in the year 1870, windthrow in the same year and a fire in the following year diminished the stand. The fire, ignited by lightning, kept burning for three weeks and incinerated the humus layer of the forest floor (Rochat 1995). Forest management records (Plan d'aménagements 'Le Lieu' from 1900, 1923, 1949, 1965, municipal archive of Le Séchey, Switzerland) document that, beside the unique intensive logging event, the forest was normally managed by applying the classical 'Plenterwald' system (forest management system for uneven-aged stands; Schütz 2002) since 1864. This method, which is based on vertical structuring by maintaining equal portions of trees of different diameter and height

classes and on yield individualisation, is rare nowadays in Switzerland (Schütz 2002), but is still applied in the 'Parc Jurassien Vaudois'.

Sampling

The sampling design was based on an initial estimate of the disturbance perimeter from stereoscopic interpretation of aerial photographs taken in the year 1933 (Kalwij et al. 2005). A total of 84 sampling points, 33 inside and 51 outside the estimated disturbance perimeter, were defined on a regular 100 m grid. The preferred host tree of *Lobaria pulmonaria* in the study area is sycamore maple (Kalwij et al. 2005). Nevertheless, our sampling focused mainly on Norway spruce because it is the dominant tree species in the area, and thus provides more information on stand history and the disturbance pattern.

Reconstructing the stand history requires determining the age and analysing the growth patterns of the even-aged cohort that followed the disturbance. This is most likely achieved by sampling old trees. An approach to identify old trees and possible survivors of a stand-replacing disturbance is to focus on large-diameter trees (Kipfmüller and Baker 1998). Although, the largest-diameter trees are not necessarily the oldest trees in a stand (Cherubini et al. 1998), it is the best feasible approach. We therefore cored the Norway spruce with the largest stem diameter at breast height (DBH) within a radius of 30 m of each sampling point in May 2004 to assess age and growth patterns. Using an increment borer, an increment core was extracted approximately 50 cm above root collar and as close to the centre (pith) of the tree as possible. DBH was measured and sample coordinates were recorded using a handheld GPS (Garmin 12XL) with external antenna.

For the interpretation of growth patterns, we additionally sampled 91 Norway spruce saplings (1–3 m height) grown under different light conditions. These saplings were later used as a reference to infer the light conditions under which the old sample trees grew up after the disturbance, based on comparisons of ring width during youth growth. Our sample included 84 saplings selected from within a radius of 30 m from each sampling point as well as seven saplings grown in full light in pastures just outside the study area. Stem discs or increment cores were extracted approximately 50 cm above root collar. Stem diameter at the extraction point and tree height were measured and the GPS coordinates recorded. The 91 young trees (hereafter referred to as 'reference saplings') were grouped into three categories: (1) shade condition: the tree was situated in the centre of a thicket under dense, closed canopy ($n=10$); (2) half-shade condition: the tree was situated under open canopy ($n=11$); (3) full light condition: solitary tree that was situated on a pasture ($n=7$); trees growing under light conditions between shade and half-shade ($n=63$) were excluded from further analysis.

To estimate the age of the oldest host trees of *L. pulmonaria* in or near the study area, we also took increment cores of six sycamore maples with the largest DBH within a distance of 500 m from the initially estimated disturbance perimeter (according to a survey conducted by Kalwij et al. 2005). Three trees inside and three trees outside the initially estimated perimeter based on aerial photographs were sampled in the same manner as the mature Norway spruce described above.

Dendroecological analysis

All increment cores and stem discs were sanded using a belt sander in order to prepare the cores for measuring. Tree rings were counted and tree-ring width was measured under a binocular microscope using a measuring table (Lintab) and the software program TSAP (Rinntech, Heidelberg, Germany). In order to obtain exact dating, all ring-width curves were cross-dated using TSAP and the software Cofecha, Version 6.06P (Holmes 1986): the resulting year-to-year agreement between the interval trend of each cross-dated ring-width curve and the mean ring-width curve of all samples (Gleichläufigkeit; Eckstein and Bauch 1969) was above 70 % for 60.7 % of the samples and between 50 % and 70 % for 39.3 % of the samples. If the pith of the tree was not intersected by the increment borer, a pith locator (concentric circles matched to the curvature of the inner rings) was used to estimate the number of missing rings to the pith (Bräker 1981). Extracting cores exactly at the germination point of the sample trees was not possible since the germination point is located close to the root collar and thus difficult to reach using an increment borer. To avoid underestimation of tree age, the following formula was used to estimate the missing number of years since germination: $r=A/B$ where $A=0.5$ m is the estimated distance to the germination point and $B=0.068$ m/y is the average height growth per year of the sampled saplings under half-shade conditions. The sampled sycamore maples were excluded from this procedure since their growth patterns might differ from those of Norway spruce. Growth trends of the sampled sycamore maples were not analysed.

Spatial pattern of genetic diversity in Lobaria pulmonaria

Based on an initial survey of potential and colonised host trees of *L. pulmonaria* within 251 randomly selected plots of 1 ha (Kalwij et al. 2005), Werth et al. (2006b) collected and genotyped lichen samples from 41 plots. In each plot, a minimum of 20 thalli were sampled. In 36 plots, fewer than 20 trees were colonised by *L. pulmonaria*, and an equal number of samples was collected from all trees. If 20 or more host trees were present, 1 sample was collected per tree. The samples' genotypes were determined using six microsatellite markers (details in Werth et al. 2006b). Based on the revised disturbance perimeter derived from this dendroecological study, we re-analysed the data from 32 plots lying in our study area, excluding 9 plots affected by a different historic disturbance.

Genotype diversity D (i.e., the probability of sampling two different multilocus genotypes) was assessed at two levels, within trees (tree-level diversity D_t) and among trees from the same plot (deme-level diversity D_d). The unbiased estimator of D_t contained a correction for sampling with replacement:

$$D_t(i) = \frac{N_i}{N_i-1} \left(1 - \sum_g p_{gi}^2 \right),$$

where p_{gi} is the relative frequency of genotype g among the N_i thalli sampled from tree i . For D_d , only pairs of thalli from different trees were compared, thus precluding sampling with replacement. Thalli were weighted inversely proportional to N_i , so that D_d estimates the probability of sampling two different genotypes when taking one thallus from each tree:

$$D_d(k) = 1 - \sum_{i \neq j}^k \frac{1}{N_i N_j} \sum_g p_{gi} p_{gj},$$

where trees i and j are sampled from plot k .

We subsequently compared genotype diversity between plots grouped according to the disturbance pattern we reconstructed. Four plots with a single colonised tree and 103 trees with a single sampled thallus were excluded from plot- or tree-level analysis, respectively.

Results

Age distribution

Thirty-three Norway spruce established after 1871, the year when the fire disturbance occurred. The spatial distribution of these trees revealed a somewhat larger and slightly differently shaped area of disturbance compared to the initially estimated disturbance perimeter (Fig. 2). Under the exclusion of two sample trees growing on pastures and being located over 150 m away from the next tree that germinated after 1871, a contiguous area of approximately 25 ha was occupied with sample trees ($n = 31$) that germinated after the disturbance. In the middle of the disturbed area, there was an island of remnants, i.e. trees germinated before 1871 ($n = 2$, plus one sycamore maple), who survived the disturbance.

The age structure of all sample trees showed a period of increased recruitment after 1870 lasting for approximately three decades (1872–1903) (Fig. 3). This relatively short period of enhanced regeneration occurred only in the disturbed area (Fig. 2). Recruitment dates outside the disturbed area varied more, ranging from 1580 to 1950, with most trees dated between 1680 and 1860 (Fig. 3).

Growth patterns

Mean ring-width growth of trees regenerating after the disturbance within the disturbed area ranged from 1 to 3 mm per year, and slightly decreased over time (Fig. 4 A). In contrast, trees outside the disturbed area had annual growth rates of only 0.5–1.5 mm in tree-ring width per year, without temporal trend (Fig. 4 C). Tree-ring growth of the two remnant Norway spruce trees in the disturbed area also increased after the disturbance: mean ring width was 0.65 mm thirty years before the disturbance and 1.32 mm thirty years after the disturbance (Fig. 4 B). Tree-ring growth slowly decreased since the disturbance event until present (Fig. 4 B).

Mean youth growth (tree-ring growth at 50 cm height during the first 30 years after germination) of trees that germinated in the disturbed area (2–3 mm ring width per year) clearly exceeded the average of all sampled trees established between 1771 and 1871 outside the disturbed area (Fig. 5: cambial age > 6 years) and was similar to that of the reference saplings growing under full light conditions (Fig. 5: cambial age 6–18 years). The reference saplings under full light conditions (pasture) even grew more slowly in the beginning, when they were exposed to grazing pressure or competition with herbs. On the other hand, the reference saplings under full light conditions still

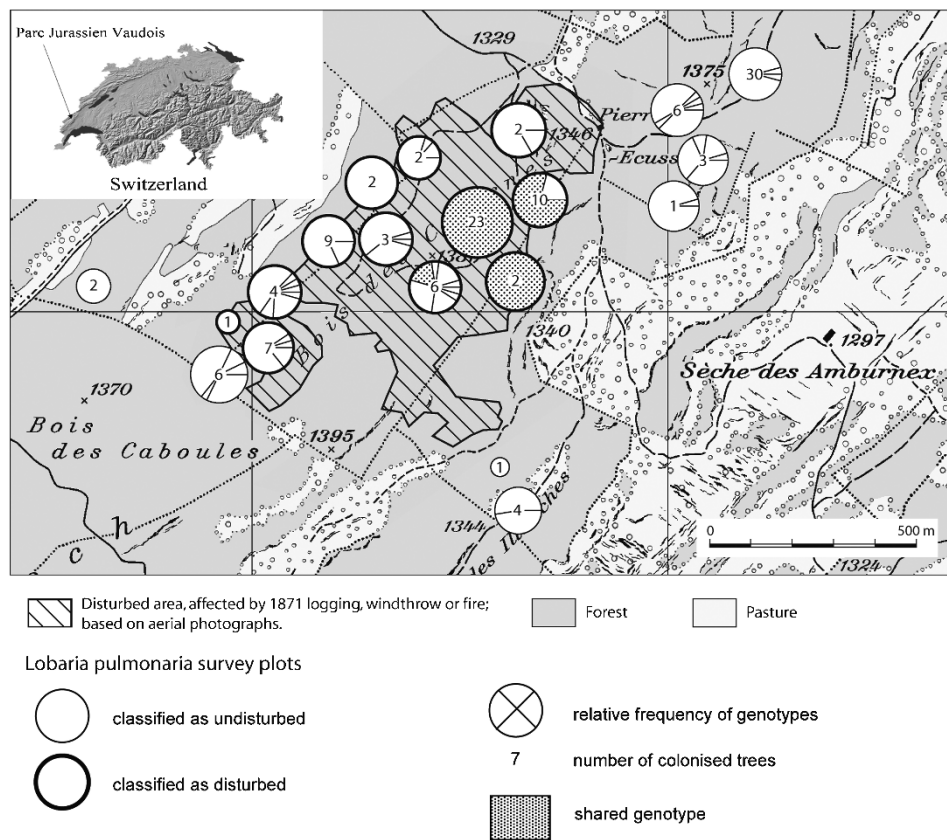


Fig. 1. Study area and genotype distribution of the lichen *Lobaria pulmonaria* in 1-ha plots from Werth et al. (2006b) in and around the estimated disturbed area based on aerial photographs. Base map reproduced by permission of Swisstopo (JA082265).

showed high growth rates after the 18th growth year until present, whereas the growth rates of trees in the disturbed area continuously decreased.

Spatial pattern of genetic diversity in Lobaria pulmonaria

Based on six microsatellite markers, the 704 sampled lichen thalli belonged to 128 multilocus genotypes. Only 17 genotypes were found in more than one plot, and 20 of 32 plots did not share any genotypes. The two genetically diverse plots in the centre of the disturbed area that shared two genotypes (Fig. 1) were found to be located on the remnant island. Three disturbed plots to the East of the island had large lichen populations that consisted exclusively or mostly of a single genotype shared with one of the two island plots (Fig. 1).

Based on the new perimeter estimate, a total of 10 plots were located in the disturbed area, two on the remnant island, and twenty plots in undisturbed areas. The genotype diversity of the two island plots was comparable to that of undisturbed plots,

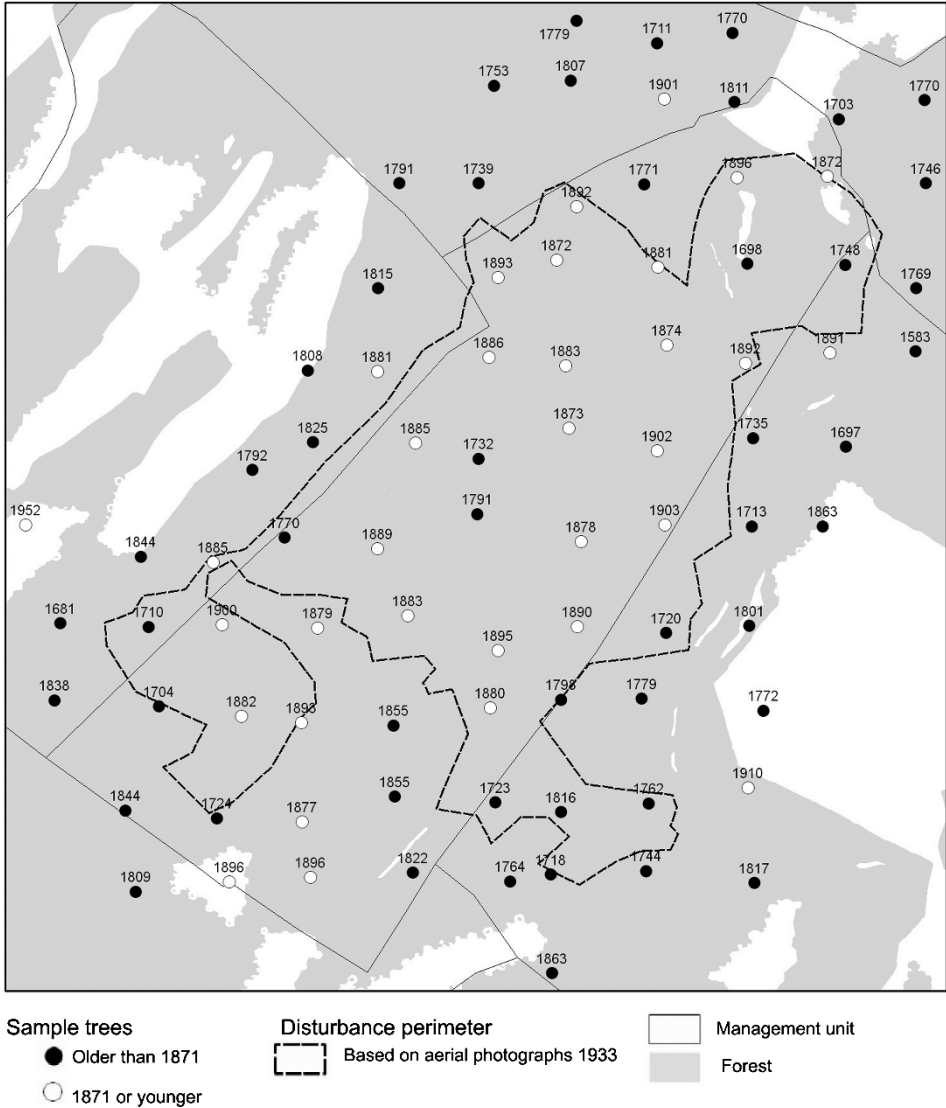


Fig. 2. Study area showing the location of the sampled Norway spruce and the estimated germination years. The initial disturbance perimeter based on aerial photographs and the management unit borders as well as pastures are marked.

both at the tree and the deme level (Fig. 1). The disturbance category had a significant effect on tree-level genotype diversity D_t (Kruskal-Wallis test, $p = 0.026$). Pairwise comparison using Mann-Whitney U tests with Bonferroni correction showed that D_t was significantly higher in the area of the remnant island (island plots) than in the

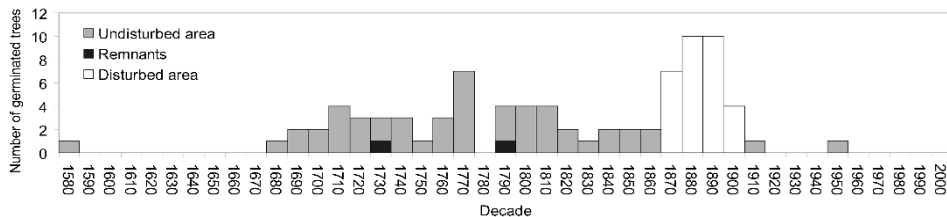


Fig. 3. Age structure of the sampled Norway spruce in the disturbed area (white bars), in the remnant zone (black bars), and in the undisturbed surrounding area (grey bars). Each bar shows the number of estimated germinations per decade.

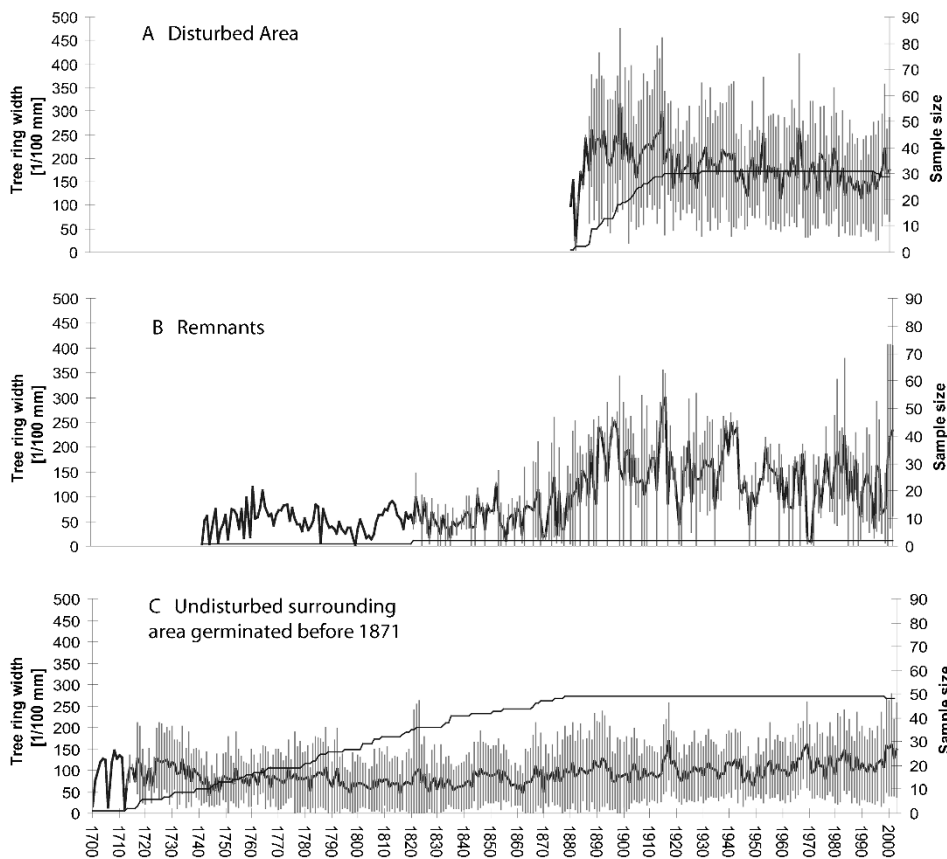


Fig. 4. Average tree – ring width per calendar year of the sampled Norway spruce. (A) disturbed area, (B) remnant zone, and (C) undisturbed surrounding area (only trees that germinated before 1871). Bold black line: Tree-ring width; grey lines: Standard deviation; thin black line: Sample size.

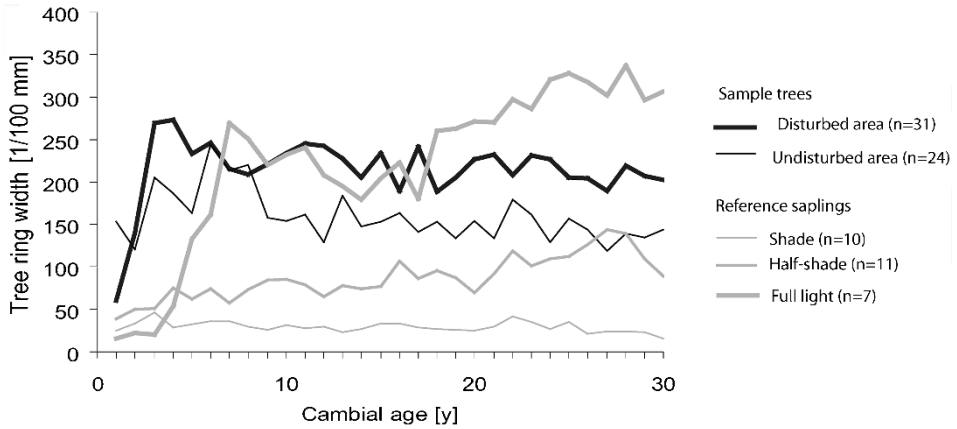


Fig. 5. Youth growth of the sampled trees. Average tree-ring width per growth year (cambial age) in the disturbed area (trees germinated after 1871) and in the undisturbed surrounding area (only trees that germinated between 1770 and 1871). Additionally, youth growth of the reference saplings is shown (grey lines) for saplings grown in full shade, half shade and full light.

disturbed area ($p = 0.005$) but not significantly different from the undisturbed area ($p = 0.261$). Effects at deme level were not tested due to the small sample size.

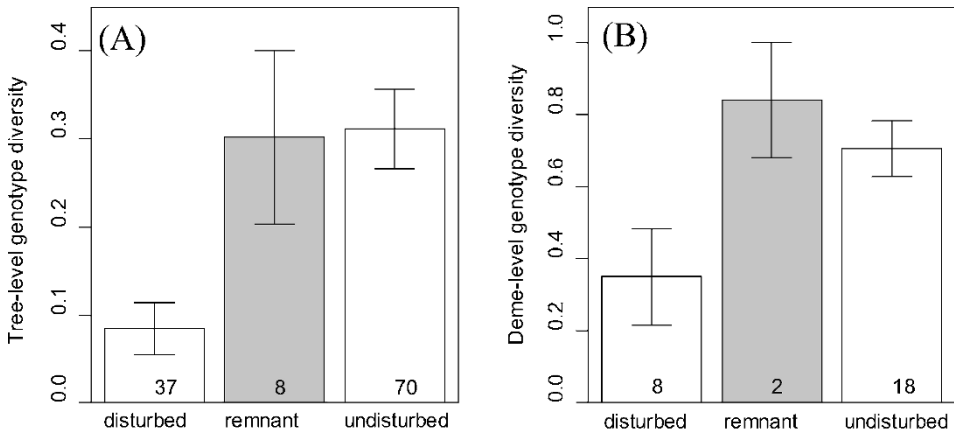


Fig. 6. Mean tree-level (left: D_t) and deme-level (right: D_d) genotype diversity within the area of the remnant zone (grey) compared to disturbed and undisturbed plots. Numbers denote the respective number of trees (left) or plots (right), error bars indicate standard errors.

Discussion

Disturbance perimeter

The analysis of the spatial age distribution revealed a large area where the stand established after the disturbance. Although, the reconstructed age structure is static, i.e. only living trees can be sampled and mortality is unknown, the sampled trees clearly showed a uniform age structure with a period of increased recruitment in the first few decades following the disturbance in this area. A dominance of post-disturbance regeneration is widely used as indicator of disturbed areas, and a dramatic increase in regeneration following a disturbance indicates a rather severe, stand-replacing disturbance (Harcombe 1986; Taylor 1993; Linder et al. 1997; Bergeron et al. 2002; Fulé et al. 2003; Lindbladh et al. 2003).

There are some clear deviations between the perimeter estimation based on old aerial photographs (Kalwij et al. 2005) and the perimeter determined through our dendroecological approach. The revised area of disturbance is composed of one large area and a small area, based on three sample trees, north of the large area. Since all three trees in this small area originated in a short period after 1871, and since fires can spread long distances through spotting, i.e. wind transport of burning twigs and leaves (Turner and Romme 1994), this area might have burnt as well. This assumption is also supported by the fact that the youth growth patterns of these trees did not differ from the patterns observed in the trees from the large disturbed area, indicating a similar disturbance history.

The disturbed area, which we reconstruct today, originated from the combination of three disturbance events: Intensive logging, windthrow and fire. A causal relationship between these events must be assumed. Creating openings in a stand, as was done by the intensive logging, considerably increases the risk of windthrow (Schütz 1990). Debris left behind from logging and windthrow provided a substantial fuel load for ignition and spread of the fire the following year. This makes it difficult to separate the three disturbance events in the reconstruction of the disturbed area and suggests that most of the disturbed area was burnt. The disturbance was of anthropogenic origin and therefore, the disturbed area was mainly contained within the forest management unit where the logging was conducted.

Disturbance severity

Disturbance severity refers to the impact of a disturbance on the ecosystem irrespectively of the physical force (i.e. intensity) of the disturbance (Ryan 2002), e.g., the survival and recolonisation patterns of any organisms in the disturbed area. A remnant zone containing two sampled Norway spruce and one sycamore maple that survived the fire was found in the middle of the disturbed area. Some features of the remnant zone, for instance a change in fuel properties, might have posed a physical constraint to the fire spread. Low fuel availability and high moisture conditions are likely to constrain fire spread if the fire intensity is not extreme (Turner and Romme 1994).

Tree-ring growth analysis can provide actual estimates of the disturbance severity (Lorimer 1985). All trees that recruited in the disturbed area showed high youth growth rates similar to solitary trees on pastures. A rapid youth growth rate is characteristic for trees that recruit under open canopy following a disturbance event (Fritts 1976; Rigling

et al. 2004), thus indicating stand-replacing disturbances (Henry and Swan 1974; Lorimer 1985; Niklasson et al. 2002). Increased growth might also be related to nutrient release in the form of ash (Lageard et al. 2000). But since these positive influences of fire on soil properties are short-term effects with a duration of often less than 10 years (Driscoll et al. 1999; Neary et al. 1999; Arocena and Opio 2003; Rigling et al. 2004), and since precipitation rates and drainage of the soil in the study area are assumed to be rather high, nutrient release cannot account for the increased growth rates prevailing for many decades. A growth release trend of over 100% was detected in the two remnant Norway spruce comparing tree-ring growth three decades before and after the disturbance. Such an increase in growth typically occurs when a tree is exposed to a much higher light intensity after the removal of competitors in the field layer or of small trees competing for below-ground resources (Lorimer 1985; Lageard et al. 2000; Rigling et al. 2004). The observed growth releases and the high youth growth rates provide strong evidence that the combined disturbance (intensive logging, windthrow and fire) left a large open area.

Fire intensity depends on the fuel conditions preceding ignition (Neary et al. 1999). Logging and windthrow in the year before the fire may have provided an optimal fuel load and fuel connectivity for a rather intensive fire. Larger stems with economical value might have been removed from the area, but the remaining dead branches and foliage provided fine fuel on the forest floor, which usually results in high fire intensities (Agee et al. 2000). Additionally, intensive logging could have increased windspeed in the understory as a result of a sparser canopy and thereby increased fire spread (Finney 2001). And finally, a period of dry weather conditions in 1871 (only 54% of the average yearly precipitation sum (1866 -1874), meteorological station La Brévine (46°59'N, 06°36'E); MeteoSwiss) may have resulted in the low moisture content of the fuel necessary for combustion in an area where forest fires are generally rare.

We reconstructed the area of disturbance based on one sample tree per sampling point in a 100 m grid. This sampling design provided us with points in space where the disturbance could be reconstructed. However, there is some uncertainty concerning the area between our sample points where we cannot exactly know if the area was disturbed or not, and increasing the number of sample trees would have decreased the uncertainty. Nevertheless, the combination of the age analysis with the growth analysis allows conclusions on the severity of the disturbance. The high youth growth comparable to saplings growing in open light conditions of our sample trees and the marking growth release of the remnant trees suggest that the area was open around the sampled trees. Based on these results concerning age distribution and growth patterns, the considerations of fuel conditions discussed above, and the description of the area after the combined disturbance in the forest management plans, we conclude that the fire was of intermediate severity: The fire was not extreme in all areas, since it left a remnant zone amidst the burnt area. On the other hand, the fire was stand-replacing and created an open area of approximately 25 ha.

*Survival and recolonisation of *Lobaria pulmonaria**

The survival of the lichen *L. pulmonaria* in the disturbed area depended on the survival of appropriate host trees, i.e. sycamore trees. Five out of the six sampled sycamore maples turned out to have regenerated after the disturbance, while the only sycamore maple that regenerated before the disturbance was found in the remnant zone. Since only the six sycamore maples with the largest DBH were sampled and since

the survival of a tree in a fire is positively correlated with its stem diameter and bark thickness (Ryan 2002), it must be assumed that the number of sycamore maples inside the disturbed area dramatically decreased after the fire. Additionally, lichens must be considered as light flashy fuels which are quickly consumed by fire (Ryan 2002). Therefore, it must be assumed that *L. pulmonaria* populations inside the disturbed area were at least heavily depleted after the event, if not totally eradicated. However, in the remnant zone which was spared by the fire, *L. pulmonaria* may have survived the heat since desiccated lichen thalli show a heat tolerance up to 75°C (Nash 1996). Thus, the lichen may have recolonised the burnt area from source trees in the remnant zone. This hypothesis was supported by the significantly higher genotype diversity of the lichen in plots from the remnant zone compared to disturbed plots, many of which contained large numbers of thalli from only 1–2 genotypes. The re-analysis of the genetic data from Werth et al. (2006b) showed that in the two lichen sampling plots within the remnant zone, both tree- and deme-level genetic diversity were comparable to those observed in undisturbed plots. The high level of clonality in the remaining disturbed plots suggests few independent colonisation events and subsequent spread of clonal propagules within the disturbed area (Werth et al. 2006b).

It is likely that three plots to the East of the remnant zone, i.e., in the main wind direction, were colonised from there, as they contained mainly or exclusively a single genotype that was also observed in one of the island plots. The possible source plot in the remnant zone was located at a distance of 180–320 m from the three disturbed plots. This dispersal distance is in accordance with a finding by Werth et al. (2006a) who found considerable levels of propagule influx in snow samples at a distance of at least 200 m from any possible source. Although we cannot rule out colonisation from an unknown closer source to the East or South of the three disturbed plots, the very low frequency of shared genotypes observed among undisturbed plots from the study area renders this possibility unlikely.

The identified remnant zone thus contributes substantially to the interpretation of the lichen genetic data. These findings support the conclusion by Werth et al. (2006a) that *L. pulmonaria* might not be as dispersal-limited as previously anticipated. Results from simulation modelling also indicated that in addition to local dispersal, an extensive amount of long-distance dispersal is needed to explain the spatial genetic structure of *L. pulmonaria* in our study area (Wagner et al. 2006). Based on the revised disturbance perimeter accounting for the remnant zone, almost the entire disturbed area was within 200 m of the disturbance boundary. Thus, given that dispersal across distances of 200 m or more is possible, the disturbed perimeter of our study area may well have been recolonised through dispersal out of neighbouring areas, including the remnant zone. To conclude, as long as large populations of *L. pulmonaria* are found nearby, and suitable sites for establishment are present (Werth et al. 2006a), the colonisation potential of the species is sufficient to enable recolonisation of disturbed sites of moderate size, such as e.g. clearings allowed under the Swiss forestry legislation. More research is needed to study the effect of large disturbances, such as clear cuts and fires of large size in North American forest ecosystems, on the recolonisation and persistence of *L. pulmonaria* and other epiphytic lichen species.

Conclusions

The aim of this study was to provide spatially explicit information on the perimeter and severity of the combined disturbance in order to interpret the genetic diversity of the epiphytic lichen *Lobaria pulmonaria* in the disturbed area, and thereby increase knowledge on the disturbance-sensitivity and recolonisation potential of this indicator lichen. The dendroecological study confirmed that the combined disturbance created an open area, refined the border of the disturbed area and revealed that a remnant zone in the centre of the disturbed area remained undisturbed. The comparison with lichen genetic data suggests that *Lobaria pulmonaria* may have survived in the remnant zone, whereas the disturbed area most likely had to be recolonised. This illustrates that (1) a spatially explicit reconstruction of historic disturbances is important for understanding the recolonisation process of disturbance-sensitive species and thus the conditions for species persistence in a dynamic landscape, and (2) that the analysis of tree age distribution and growth patterns is a low-cost method that allows the spatially explicit reconstruction of the perimeter and severity of disturbances in forested landscapes.

Zusammenfassung

Historische Störungsereignisse im Wald können das Vorkommen störungs-sensitiver Arten stark beeinflussen. Um die Auswirkungen einer Störung auf Vorkommen und die genetische Diversität einer solchen Art untersuchen zu können, benötigen wir eine detaillierte Kenntnis über die damaligen Überlebens- und Wiederbesiedlungsbedingungen. Dies erfordert jedoch eine räumlich-explicite Rekonstruktion des Störungsperimeters sowie des Schweregrades der Störung. In der hier vorliegenden Arbeit rekonstruierten wir eine historische Störung (intensiver Holzschlag gefolgt von Windwurf und Feuer im Jahre 1871) im Schweizer Jura mit dem Ziel, die heutige Verteilung und genetische Diversität der störungs-sensitiven, epiphytischen Flechte *Lobaria pulmonaria* in diesem Gebiet erklären zu können.

Anhand einer Jahrringanalyse von 84 alten und 91 jungen systematisch-gesammelten Rottannen (*Picea abies* L.) auf einem 100 m-Raster, wurde (i) der Störungsperimeter und (ii) der Schweregrad bestimmt. Die Alters- und Wachstumsanalyse ergab, dass (1) es sich um eine mittelschwere Störung handelte, die jedoch einen Grossteil des damaligen Bestandes vernichtete, (2) dass die Störungsfläche räumlich rekonstruierbar ist und (3) dass eine Zone im Zentrum der Störungsfläche von der Störung verschont wurde.

Die Identifikation dieser störungsfreien Insel erlaubte eine exaktere Interpretation der genetischen Flechtendaten. So erklärt sie die höhere genetische Diversität der Flechtenplots, die innerhalb dieser Insel gefunden wurden, damit, dass die Flechte hier inmitten der Störung überleben konnte. Die Studie illustriert, dass eine räumlich-explicite Rekonstruktion historischer Störungen, wie sie durch dendroökologische Analysen erreicht werden kann, für das Verständnis von Wiederbesiedlungsprozessen und Artvorkommen in heutigen Landschaften von grosser Bedeutung sein kann.

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