EFFECTS OF STAND-LEVEL DISTURBANCES ON THE SPATIAL DISTRIBUTION OF A LICHEN INDICATOR

J. M. KALWIJ,¹ H. H. WAGNER, AND C. SCHEIDEGGER

Swiss Federal Research Institute WSL, Zuercherstrasse 111, CH-8903 Birmensdorf, Switzerland

Abstract. Due to its assumed dispersal limitation and susceptibility to disturbance, the epiphytic lichen *Lobaria pulmonaria* is used as an indicator of undisturbed forest stands. The hypothesis was tested that stand-level disturbances have a long-lasting negative impact on the occurrence of *L. pulmonaria*. Two 19th century stand-level disturbances were reconstructed using aerial photographs from 1933. For 7769 potential host trees within a random sample of 251 plots of 1 ha, the presence of *L. pulmonaria*, tree species, and diameter at breast height were recorded. An analysis of variance showed that neither historical stand-level disturbances nor current grazing reduced the proportion of colonized trees. Spatial analysis at the tree level revealed a patchy distribution of colonized trees, suggesting *L. pulmonaria* colonization from nearby sources. Spatial analysis at plot level even showed a positive spatial association of *L. pulmonaria* with historic disturbances. We conclude that the presence of *L. pulmonaria* may provide information about conservation value of a landscape, but not necessarily at a forest stand scale. Although indicator species, such as *L. pulmonaria*, may be an efficient means to assess the conservation value of a forest, spatially and temporally explicit knowledge of the species' life history characteristics is indispensable in order to prevent possible misinterpretation of ecological processes that the indicator aims to unravel.

Key words: *Acer pseudoplatanus*; ecological continuity; epiphytic lichen; indicator; *Lobaria pulmonaria*; old growth; spatial analysis; SADIE.

INTRODUCTION

A high conservation value of forests is generally achieved, and can persist over long time spans, when all successional stages are simultaneously and continuously present (Lindenmayer et al. 2000). In such forests, stands typically originate through natural succession, with a significant proportion of old trees, old-growth microhabitats, and a high degree of patchiness and heterogeneity (Hendrickson 2003). Old-growth forest species have common, yet very specific life history traits such as the ability to establish and persist in old-growth associated microhabitats only (Rolstad et al. 2002). Consequently, the presence of such old-growth related species could distinguish undisturbed ecosystems from more recently established habitats that have endured a break in the continuity of the ecosystem. Long-term undisturbed habitats are thereby defined as habitats with a high ecological continuity (Gauslaa 1994, Kuusinen 1996, Sillett et al. 2000).

The current perception of ecological continuity suggests that the persisting effect of a disturbance event can be verified by the lack of indicator species (Rose 1976). If an indicator species is dispersal limited, it would take longer for the species to restore the pop-

ulation to the level prior to the disturbance than it would for the habitat to recover. Here, however, scale is important even for poor colonizers, as the distance between disturbed and undisturbed areas determines the usefulness of the indicator species (Peterken 1974). Therefore it is necessary to know how long and to what extent disturbance events affect the distribution of a dispersal-limited indicator species.

Many lichenological studies have correlated indicators of ecological continuity with forest stand age (Rose 1976, 1992, Kuusinen 1996, McCune et al. 2000), forest connectivity (Esseen and Renhorn 1998), or stand-level disturbance events (Boudreault et al. 2000). However, the concept of ecological continuity has been criticized as incomplete, with recent studies (e.g., Norden and Appelqvist 2001, Rolstad et al. 2002) criticizing the lack of operational definition (e.g., on dispersal ability, or on the temporal and spatial scaling of processes involved). The impact of historical disturbance events on the abundance of indicator species of ecological continuity is often anecdotal and can sometimes be related to other variables, such as environmental or geographic gradients (Norden and Appelqvist 2001, Rolstad et al. 2002). Therefore, the dependence on old-growth microhabitats and the dispersal ability of indicator species as well as fragmentation and the stand history of forests need to be clearly defined when assessing the ecological continuity of a forest stand.

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¹ Present address: Stellenbosch University, Department of Entomology, Private Bag X1, Matieland 7602 South Africa. E-mail: kalwij@sun.ac.za

The epiphytic lichen *Lobaria pulmonaria* (L.) Hoffm. is, due to its assumed limited dispersal ability (Walser 2004), one of the most commonly used species to indicate ecological continuity (Rose 1976, Lesica et al. 1991, Gauslaa 1994, Selva 1994, Kuusinen 1996, Sillett et al. 2000). Like many other lichens, *L. pulmonaria* can reproduce asexually in the form of relatively large vegetative soredia (diaspore of algal cells enveloped by the fungal symbiont) or isidioid soredia (elongated outgrowths from the soralia that break off for dispersal) and sexually by means of ascospores, which are formed in a later stage of thallus development (Denison 2003). Under Central European conditions *L. pulmonaria* thalli need to be about 20 years of age before a reasonable amount of soredia starts being produced (Scheidegger et al. 1997). These vegetative soredia are not likely to disperse as far as ascospores (Levin et al. 2003) owing to their larger size. Since we know that soredia production is poor in younger stands (Hilmo 2002) and that successful establishment of vegetative propagules is positively correlated with host tree diameter at breast height (Riiali et al. 2001), it seems plausible that a stand-level disturbance event would have a persisting effect on *L. pulmonaria*.

Another argument supporting the indicator value of *L. pulmonaria* is its sensitivity to changes in the habitat; a sudden exposure of the thallus to high light intensity (e.g., following logging of a forest stand) has been shown to cause permanent light damage (Gauslaa and Solhaug 1996, Gauslaa et al. 2001). However, a transplantation experiment by Hazell and Gustafsson (1999) showed that the lichen can survive on trees retained after logging of a forest stand, and that the location of the thallus on the host tree stem is a more important factor determining survival of the lichen than being sheltered by surrounding trees. Surviving thalli could increase the recolonization rate, which would lower the indicative value for absence of disturbance. Since dispersal limitation as well as sensitivity of *L. pulmonaria* to disturbance is disputed, testing the validity of *L. pulmonaria* as an indicator of stand-level disturbance events may clarify if and how this species can be an indicator of ecological continuity.

This study investigates how the spatial distribution of the epiphytic lichen *L. pulmonaria* is related to different disturbances within a landscape, where a remarkably high but patchy abundance was noted (Stofer et al. 2004). Since tracking of recolonization in disturbance experiments would take too long, a retrospective approach was adopted to test the validity of *L. pulmonaria* as an indicator of disturbance events at a stand level. Disturbances in the study area comprise present cattle grazing and two historic stand-level disturbances. We hypothesize that these disturbance events lead to a low density of host trees colonized by *L. pulmonaria*, while absence of such events results in high densities of colonized host trees. To test this hypothesis we quantified and compared the spatial as-

sociation of *L. pulmonaria* and its potential host trees with reconstructed stand-level disturbance events within and among 1-ha observation units. We also discuss the validity of *L. pulmonaria* to assess forest conservation value and as an indicator of ecological continuity at different spatial scales.

MATERIALS AND METHODS

Study site

The study area is part of the Parc Jurassien Vaudois (PJV) in Switzerland, located between 46°28'–34' N and 06°06'–16' E at an elevation of 1300–1450 m (Fig. 1a). The PJV is a sylvopastoral landscape, characterized by forests dominated by Norway spruce (*Picea abies* (L.) Karst.) and pastures on carstic limestone bedrock (Vittoz 1998). The area has relatively few, unevenly distributed host trees (sycamore maple, *Acer pseudoplatanus* L., and beech, *Fagus sylvatica* L.) of *L. pulmonaria*. The field data were collected in the northern part of the PJV in 2003. This area comprised 1316 ha, 41% of which was grazed at that time. Low-impact logging was employed throughout the area, which encompassed selective logging of trees of all size classes in quantities less than or as high as the annual growth in order to maintain an uneven-aged forest (Schütz 2002).

Field data

The perimeters of the forest patches were retrieved from an existing Boolean forest map (1:25 000; Swisstopo, Swiss Federal Office of Topography, Wabern, Switzerland). Circular non-overlapping plots of 1 ha ($N = 251$) were positioned randomly within the forest area of the study area (Fig. 1a). Within each plot, the location of each sycamore maple and beech with a diameter at breast height (dbh) of at least 10 cm was mapped using a handheld GPS device (Garmin12XL with external antenna; Garmin, Romsey, Hampshire, UK). *Lobaria pulmonaria* can occur in the canopy or on the stem of a host tree, but was never observed exclusively in a canopy in this survey. Therefore sampling concentrated on host tree stems. Presence or absence of *L. pulmonaria* and the dbh (classes: 1 = 10–12.5 cm, 2 = 12.5–17.5 cm, 3 = 17.5–22.5 cm, 4 = 22.5–27.5 cm, 5 = 27.5–32.5 cm, or 6 = >32.5 cm) were recorded for each mapped tree ($N = 7769$).

Present tree cover

LiDAR (Light Detection and Radar) data were used to assess tree canopy cover. Two sets of airborne LiDAR data, obtained in summer 2003 by Swisstopo, were used to construct a digital surface model and a digital terrain model. The first data set consisted of first returns; representing maximum height with vegetation (~10 000 points/ha). The second, filtered data set consisted of returns representing height of terrain without vegetation (i.e., where vegetation was sparse enough

FIG. 1. Stand-level disturbances within the study area and (a) location of sample plots, forest, and grazed areas (Swisstopo Pixelmap 25, 2004), and (b) interpolated distribution of the lichen indicator *Lobaria pulmonaria*. Dark shaded areas represent patches of local aggregation, while lighter shaded areas represent gaps.

for pulses to reach the ground). Both sets were interpolated by generating triangular irregular networks and subsequent conversion into grids of 0.5 m using ArcGIS 8.3 (ESRI 2002). Height difference between the two digital models was used as an estimation of vegetation height. Canopy cover data was calculated from the percentage of vegetation exceeding 1.5 m and included as covariable in the data analysis.

Local forest structure changes

Change in local forest structure at a 1-ha scale was assessed by a comparison of black-and-white aerial photographs of 1933 with panchromatic orthophotos of 1998 (SWISSIMAGE), all acquired from Swisstopo. The photographs from 1933 were digitized, georeferenced, and orthorectified in IMAGINE OrthoBASE 8.6 (Leica-Geosystems GIS and Mapping, Atlanta, Georgia, USA), using a digital elevation model with a cell size of 25 m (DEM25, Swisstopo), and resampled to match the 0.5 m nominal ground resolution of the 1998 orthophotos. For each 1-ha plot the canopy changes during the period from 1933 to 1998 were assessed visually: (a) decrease of canopy cover and/or tree density ($N = 41$), (b) no distinct changes ($N = 147$), and (c) increase of canopy cover and/or tree density ($N = 63$).

Stand-level disturbance events

Two stand-level disturbances were known for stands within the study area (Fig. 1): (a) intensive logging between 1850 and 1900 for charcoal production (B. Pichon, Swiss Forestry Service, *personal communication*), and (b) intensive logging in 1870, followed by wind throw and, in the following year, a two-week fir (Rochat 1995). The perimeters of the areas “Charcoal 1850–1900” (~36 ha) and “Logged & burnt 1871” (~31 ha) were delineated from stereoscopic analysis of the orthophotos of 1933. The reconstructed perimeter and intensity of the 1871 stand-level disturbance was validated and refined in a dendroecological study (J. Bolli, J. M. Kalwij, H. H. Wagner, P. Cherubini, C. Scheidegger, and A. Rigling, *unpublished manuscript*). Youth growth patterns of sampled Norway spruces indicated an open area after 1871, confirming the interpretation of the 1933 aerial photographs.

Edge effects of large-scale stand-level disturbances have been shown to affect local microclimatic conditions and lichen composition (Esseen and Renhorn 1998, Harper and Macdonald 2002). Therefore, plots falling even partially within the perimeters of the stand-level disturbances were considered part of the disturbed area ($N = 24$ for “Charcoal 1850–1900,” and $N = 21$

for “Logged & burnt 1871”). Since stand structure and abundance of sycamore maple and beech in this landscape are likely to be affected by grazing (Gillet and Gallandat 1996), the perimeters of presently grazed areas were mapped. Plots that had >50% of their surface in a grazed area were considered “Grazed” ($N = 42$). Since forest management aimed to minimize the impact of logging and was of the same low intensity throughout the area, remaining plots were labeled “Undisturbed” ($N = 164$).

Data analysis

All nonspatial analyses were performed in SPSS Version 12.0 (SPSS 2003). Due to the small number of colonized beech trees, beech was excluded from the statistical analyses. Mean number of sycamore maples per hectare plot, f_A , number of colonized sycamore maples per hectare plot, f_L , and proportion of colonized sycamore maples, p_L , for the different disturbance categories “Undisturbed,” “Grazed,” “Charcoal 1850–1900,” and “Logged & burnt 1871” were compared by one-way analyses of variance (ANOVA). The ANOVA was based on square-root transformed values for f_A and f_L , and on arcsine of the square-root for p_L (Underwood 1997). Due to unequal variances, significance of the pairwise differences between the disturbance categories was assessed using Tamhane’s T2 instead of Bonferroni adjustments (Tamhane 1977), as implemented in SPSS.

A linear regression model was calculated to test the effect of host tree density, f_A (square-root transformed), on colonization proportion, p_L (arcsine square-root transformed), for each of the disturbance categories. One reason *L. pulmonaria* may not have colonized all plots could be due to dispersal limitation. Therefore, plots without *L. pulmonaria* were excluded from this analysis.

The effect of dbh class and disturbance category on host tree density, f_A (square-root transformed), and on colonization proportion, p_L (arcsine square-root transformed), per dbh class and plot was tested in separate two-way ANOVA, excluding plots without *L. pulmonaria* for the analysis of p_L . The normally distributed variable “Present tree cover” was used as covariable.

The spatial aggregation of colonized trees was quantified by determining the distance to nearest colonized neighbor (NN) for each colonized or uncolonized sycamore maple. A three-way ANOVA was used to test for the difference in the mean NN distance (square-root transformed) between colonized and uncolonized trees accounting for interactions with dbh class, disturbance category, and present tree cover. To avoid edge effects, ANOVA was restricted to sycamore maples closer to a colonized tree than to the edge of their 1-ha plot, and clusters of stems with shared base were excluded ($N = 1911$).

To characterize the spatial association of the tree and lichen species among plots, spatial analysis by distance

indices (SADIE) was used to calculate cluster indices and tested for statistical significance (Perry et al. 1999). For both species, the index of aggregation, I , was defined as $D_{\text{obs}}/D_{\text{exp}}$, where D_{obs} is the minimum distance that individuals are required to move to neighboring plots to obtain a regular distribution, and where D_{exp} is the same quantification under randomized plot distribution. The larger is I , the more spatially aggregated is the observed arrangement of counts. For each plot, the following clustering indices were calculated: (a) I_A for the total number of sycamore maples per plot, (b) I_L for the number of colonized sycamore maples, and (c) I_D as a Boolean value for both historical stand-level disturbances. The categorical variable “Local forest structure change” was converted into three Boolean dummy variables to obtain I_- , I_0 and I_+ for “Local decrease,” “No change,” and “Local increase,” respectively.

For each plot i an index of clustering v_i was calculated, which measures the degree to which each plot contributes to a cluster of nearby plots of high values (patch) or to a cluster of nearby plots of low values (gap). Local values of v_i below -1.5 were interpreted as gaps, while values exceeding 1.5 were interpreted as patches (Perry et al. 1999).

The overall associations, χ , and local spatial associations, χ_i , for the individual plots i of the pairwise combinations of cluster indices I were calculated by the SADIE software to determine the local coincidence of variables (Perry and Dixon 2002); coincidence of clusters would result in a large value of local association, χ_i . Sample size adjustment for small-scale spatial autocorrelation in both sets of clustering indices in the SADIE software followed the method of Dutilleul (1993). This is a correction of the degrees of freedom, making similar distributional assumptions as a t test without affecting the degree of association. The statistical significance of overall association, χ , was tested by means of a two-tailed permutation test with a significant level of $P = 0.05$, where the observed v_i were permuted among the sample units (Perry et al. 1999).

Since local clustering indices, v_i , and association values, χ_i , are continuous, contour maps were constructed for visual interpretation of the spatial arrangement of patches. A regularized radial basis function was used as an exact deterministic interpolation technique to derive maps of local associations, v_i , in ArcGIS 8.3 (Johnston et al. 2001).

RESULTS

Effect of stand-level disturbance

Based on the 7769 examined trees, *L. pulmonaria* showed a strong preference for sycamore maple (0.086 colonized), compared to beech (0.004 colonized; Table 1). The three one-way ANOVA showed a significant effect of disturbance category on host tree density, f_A ($F = 7.42_{3, 2475}$, $P < 0.001$), on density of *L. pulmonaria*

TABLE 1. Tree density (f_A) and lichen density (f_L) per disturbance category (p_L).

		Trees (no./ha) f_A		<i>Lobaria</i> (no./ha) f_L		Colonized, p_L	
	N	Mean	SE	Mean	SE	Mean	SE
Sycamore maple							
Undisturbed	164	18.7 ^a	1.6	3.1 ^a	0.5	0.086 ^a	0.013
Grazed	42	4.7 ^b	1.6	0.4 ^b	0.2	0.028 ^b	0.013
Charcoal	24	93.1 ^c	5.9	11.4 ^c	4.2	0.105 ^c	0.030
Logged & burnt	21	26.7 ^d	3.1	5.0 ^c	0.5	0.190 ^c	0.040
Total	251	24.1	1.9	3.6	0.6	0.086	0.010
Beech							
Undisturbed	164	7.6	0.9	0.1	0.0	0.003	0.001
Grazed	42	2.0	0.6	0.0	0.0	0.003	0.003
Charcoal	24	7.7	2.3	0.0	0.0	0.007	0.007
Logged & burnt	21	9.3	1.4	0.1	0.1	0.006	0.005
Total	251	6.8	0.7	0.1	0.0	0.004	0.001

Notes: Different letters indicate significant pairwise differences for sycamore maple (*Acer pseudoplatanus*) at the 5% level using Tamhane's T2 correction for multiple comparisons with unequal variances. The table lists untransformed frequencies for ease of interpretation, whereas the significance tests were based on an ANOVA of transformed values (f_A and f_L , square-root transformed; p_L , arcsine square-root transformed). N is the number of plots per disturbance category; the beech species is *Fagus sylvatica*.

trees, f_L ($F = 8.34_{3,247}$, $P < 0.001$), and on colonization proportion, p_L ($F = 6.35_{3,247}$, $P < 0.001$). The pairwise comparisons showed significant differences in sycamore maple density, f_A , between all disturbance categories. In contrast, the differences in density of *L. pulmonaria* trees, f_L , and in colonization proportion, p_L , between the two stand-level disturbances were not significant.

No significant correlation was found between sycamore maple density, f_A , and colonization proportion, p_L , for any of the disturbance categories (undisturbed: $N = 61$, $R^2 = 0.004$, $P = 0.642$; grazed: $N = 6$, $R^2 = 0.098$, $P = 0.493$; charcoal: $N = 23$, $R^2 = 0.15$, $P = 0.061$; logged & burnt: $N = 16$, $R^2 = 0.114$, $P = 0.185$).

Effect of host tree population structure

A two-way ANOVA of f_A revealed a significant interaction between disturbance category and dbh class, but no effect of present tree cover (Table 2). A higher sycamore maple density, f_A , was found in both "Charcoal 1850–1900" as well as in "Logged & burnt 1871," for the middle (12.5–22.5 cm) dbh classes (Fig. 2, upper graphs).

A similar ANOVA of p_L showed strong effects of disturbance and dbh class, but no effect of present tree cover or significant interaction (Table 2). Colonization proportion, p_L , increased considerably with increasing dbh (Fig. 2, center graphs).

Spatial aggregation

At the tree level, a three-way ANOVA of the nearest neighbor (NN) distance showed a highly significant difference in NN between colonized and uncolonized sycamore maples. This difference did not depend on disturbance category nor on dbh class, as all interaction terms were not significant (Table 2, lower section). Colonized trees were located much closer to their nearest

colonized neighbor than uncolonized trees (Fig. 2, lower graphs).

At the plot level, a significant spatial aggregation was found for sycamore maples, I_A , as well as for colonized host trees, I_L (Table 3). The number of sycamore maples per plot, I_A , showed significant association with local increase in tree density, I_+ , and with stand-level disturbances, I_D . *Lobaria pulmonaria*, I_L , on the other hand was, apart from an obvious association with sycamore maple, significantly associated with local increase, I_+ . Although not significant *L. pulmonaria*, I_L , had the tendency to be associated with disturbance, I_D . This near-significant association could be ascribed to the fact that local increase, I_+ , and disturbance, I_D , are not independent variables. The map of the interpolated local aggregation values, X_L , showed four distinct clusters of *L. pulmonaria* (Fig. 1b). Two of these clusters largely overlapped with the area of the reconstructed stand-level disturbances.

DISCUSSION

Within the context of testing indicator species of undisturbed forest stands, we investigated how the spatial distribution of *L. pulmonaria* was affected by grazing and two historic stand-level disturbances. We assumed that the effect of selective logging of individual trees was limited to the tree level, therefore of minor importance at the stand-level scale and did not adversely affect local clusters of *L. pulmonaria*. Such effects, however, may differ between lichen species and study area (Hedenas and Ericson 2003). Disturbance effects not only depend on the disturbance intensity, spatial extent, and time elapsed since the event, but also on the dispersal ability (Nilsson et al. 2001) and generation time (Caro and O'Doherty 1999) of affected species. We can only interpret the present distribution of *L. pulmonaria*, and explain why this species is absent

TABLE 2. Results of a two-way ANOVA of f_A and p_L as dependent on disturbance category and dbh class, and of a three-way ANOVA of nearest neighbor (NN) distance as dependent on disturbance category, dbh class, and presence of *Lobaria pulmonaria*.

Variable	SS	df	F	P
Host tree density, f_A				
Model	753.7	22	34.26	<0.0001
Intercept	114.3	1	124.40	<0.0001
Present tree cover	0.4	1	0.48	0.490
Disturbance	271.4	3	98.44	<0.0001
dbh	197.0	5	42.88	<0.0001
Disturbance $\times$ dbh	144.6	13	11.13	<0.0001
Error	736.9	802		
Total	6056.0	825		
Colonized proportion, p_L				
Model	25.2	22	6.16	<0.0001
Intercept	0.6	1	3.27	0.071
Present tree cover	0.2	1	1.20	0.275
Disturbance	3.4	3	6.15	<0.0001
dbh	7.4	5	7.98	<0.0001
Disturbance $\times$ dbh	3.1	13	1.27	0.227
Error	90.9	489		
Total	204.8	512		
Nearest neighbor (NN) distance				
Model	426.7	35	8.38	<0.0001
Intercept	1671.8	1	1148.73	<0.0001
Disturbance	3.7	3	0.84	0.474
dbh	3.6	5	0.49	0.782
<i>Lobaria</i>	119.1	1	81.84	<0.0001
Disturbance $\times$ dbh	11.6	11	0.73	0.715
Disturbance $\times$ <i>Lobaria</i>	1.7	2	0.58	0.560
<i>Lobaria</i> $\times$ dbh	12.5	5	1.72	0.128
Disturbance $\times$ dbh $\times$ <i>Lobaria</i>	5.6	8	0.48	0.869
Error	2728.9	1875		
Total	26 804.4	1911		

Note: Models were corrected for unequal sample sizes.

in seemingly suitable habitats, when we know its dispersal abilities. A complicating factor that determines the distribution of *L. pulmonaria* is its dependence on appropriate host trees, which may at times be scarce themselves. Therefore, we must discuss the distribution of host trees before interpreting effect of disturbances on *L. pulmonaria*. The spatial association between *L. pulmonaria* and stand-level disturbances was used to test the hypothesis that an absence or lower density of indicator species demonstrates disturbance of a forest stand.

Presence of potential host trees

Sycamore maple in this study area was described as a species profiting from temporally enhanced light conditions, such as gap dynamics related to succession in natural forests (Vittoz 1998). Cattle substantially reduced the abundance of sycamore maple in grazed areas. Conversely, our distribution data showed that stand-level disturbances led to high densities of sycamore maples (Table 1), irrespective of present tree cover (Table 2). Significant higher density of sycamore maple, f_A , and number of colonized sycamore maple, f_L , in the historically disturbed plots suggest that colonization proportion, p_L , might be correlated with host tree density, which would imply rapid colonization

following host tree expansion. However, no significant correlation was found between sycamore maple density, f_A , and colonization proportion, p_L , for any of the disturbance categories. Instead, the chance for colonization of sycamore maple seemed to increase in time, as the strong increase in the proportion of colonized trees, p_L , with dbh class suggests. A similar effect was described for *L. pulmonaria* on aspen (Kuusinen 1996) and for other epiphytic species (Hazell et al. 1998, Rolstad and Rolstad 1999). This could be explained by a combination of potential causes. Growth of *L. pulmonaria* can be slow in some habitats (Scheidegger 1995). Individual thalli may persist for decades (Gu et al. 2001), which would mean that once a lichen is established, a population may persist as long as the host tree continues to exist. As thick trees are usually older and provide more trunk surface than thin trees, the cumulative probability of colonization is higher (Riiali et al. 2001). Furthermore, the bark of large, old trees is usually rougher, providing favorable environmental conditions regarding humidity (Barkman 1958) and pH value (Gustafsson and Eriksson 1995). However, our results suggest that the high number of colonized trees in the historically disturbed areas is due to a high number of trees from the thinner dbh classes (Fig. 2), indicating a dynamic system with continuous dispersal

FIG. 2. Sycamore maple density (f_A), colonization proportion (p_L) of *Lobaria pulmonaria*, and distance to the nearest colonized neighbor (NN) for colonized (light gray bars) and uncolonized (dark gray bars) host trees, per dbh class and disturbance category. Values are expressed as mean + 2 SE. For ease of interpretation, untransformed values are shown, whereas the significance tests presented in Table 2 were based on the transformed values.

and colonization (Johansson and Ehrlén 2003). Our results therefore suggest that *L. pulmonaria* may have profited either from a temporal increase in host tree availability independent of host tree population structure or from increased light conditions during absence of a closed canopy.

Persistence of disturbance effects on *L. pulmonaria*

Disturbance was hypothesized to result in a lower abundance of *L. pulmonaria*. However, contrary to our expectation, the distribution of *L. pulmonaria* did not show a negative association with the two stand-level disturbances. The interpolated distribution map of *L. pulmonaria* (b) even suggested that the opposite may be true, although such a trend was not significant (Table 3). Apparently 100–150 years are long enough for both the ecosystem functioning as well as the indicator species to recover to the assumed state prior to the disturbance. Yet, with a high proportion of trees from the

intermediate dbh classes especially (Fig. 2), the stand structure of sycamore maple is far from equal to undisturbed areas. Since we also showed that colonized trees are more clustered towards their nearest colonized neighbor than uncolonized trees (Fig. 2), two possible scenarios of recolonization may explain the patchy distribution of *L. pulmonaria*.

Possibly *L. pulmonaria* disappeared completely following the disturbances, as would be expected from its sensitivity to permanent light damage (Gauslaa et al. 2001) or other sudden changes in microhabitat (Barkman 1958). Recolonization may have occurred by occasional long-distance dispersing diaspores, as *Lobaria pulmonaria* thalli of identical multilocus genotypes found over distances of 140 m (Walser 2004) and up to 2 km (S. Werth, unpublished data) in our study area suggest. This possibility is supported by the occurrence of isolated colonized trees with small dbh in the grazed areas (Fig. 2), suggesting that these trees were rela-

TABLE 3. Spatial analysis by distance indices (SADIE) of the occurrence of sycamore maple and *Lobaria pulmonaria* in 251 circular 1-ha plots.

Variable	Overall association, $\chi^{\dagger}$					Index of aggregation (I)
	I_A	I_L	I_D	I_-	I_0	
Sycamore maple, I_A	1.00					2.10*
<i>Lobaria</i> , I_L	0.69*	1.00				1.79*
Disturbance, I_D	0.46*	0.20	1.00			3.28*
Local decrease, I_-	-0.31*	-0.44*	-0.23*	1.00		1.51*
No local change, I_0	-0.24*	-0.13	-0.49*	-0.12	1.00	1.99*
Local increase, I_+	0.34*	0.28*	0.66*	-0.42*	-0.62*	2.17*

* $P < 0.05$. $\dagger$ A two-tailed permutation test was used to ascertain the statistical significance of overall association (χ) and aggregation (I).

tively recently colonized and not part of a persisting lichen population.

In the alternative scenario, not all thalli were eradicated by the disturbance. Tree ring data (J. Bolli, J. M. Kalwij, H. H. Wagner, P. Cherubini, C. Scheidegger, and A. Rigling, *unpublished manuscript*) revealed that at least one host tree on a hill in the center of “Logged & burnt 1871” was not eradicated in 1871. No data were collected in “Charcoal 1850–1900,” but we assume that some remnants survived this stand-level disturbance too. We observed that especially sycamore maples in the largest dbh class often had a high abundance of *L. pulmonaria*, reaching as high as the crown level. Hazell and Gustafsson (1999) showed that direction of exposure had a strong impact on survival of *L. pulmonaria* thalli on trees retained from harvesting. This supports the alternative hypothesis that residual and colonized sycamore maples could have continued to host thalli on suitable parts of the tree. In either scenario, early colonized or remnant colonized trees could have served as a source from which nearby potential host trees were colonized. The degree to which each scenario contributes to the present distribution could be determined by estimating the historic gene flow (Sork et al. 1999) and will be addressed in a forthcoming paper (S. Werth, *unpublished data*).

*Is L. pulmonaria an indicator
of ecological continuity?*

Although the patchy distribution of colonized trees, suggesting that *L. pulmonaria* was dispersal limited (Fig. 2), fell in line with the concept of ecological continuity (Norden and Appelqvist 2001), the tendency for positive spatial association of *L. pulmonaria* with stand-level disturbance events (Fig. 1b, Table 3) did not. Our results showed that the distribution of *L. pulmonaria* was clustered and that the two largest of the four lichen patches occurred in and around areas where stand-replacing disturbances occurred (Fig. 1). This suggests that disturbances may not have been severe enough or at a spatial scale large enough to cause a persisting break in the lichen population, contradicting the theory that *L. pulmonaria* is indicative of forest

stands with an ecological continuity, sensu Rose (1976). If a high abundance of suitable substrate is more characteristic for an earlier successional stage after a stand-level disturbance event, as our results suggest, it is difficult to find an ecological justification as to how this species can indicate absence of stand-replacing disturbances within the investigated area.

We identified forest stands with a known disturbance history within a landscape that could develop into the same vegetation type under absence of anthropogenic influence (Vittoz 1998). We did so to investigate potentially persisting effects of disturbance events at different spatial and temporal scales following the critique of Rolstad et al. (2002) and Norden and Appelqvist (2001). Our sampling design was to minimize any climatic or regional gradient. We therefore only needed to take the spatial dependence of our observations into account. The spatial extent of the two stand-level disturbances may not seem as large as in previous studies, where lichen populations of undifferentiated forest stands from different regions (Rose 1976, Boudreault et al. 2000) or different countries (Gaio-Oliveira et al. 2004) were compared. However, our stand-level disturbance events (~31 and 36 ha, respectively) were large enough to conform with the minimum forest stand size of 0.1–30 ha (Esseen and Renhorn 1998, Hazell and Gustafsson 1999, Norden and Appelqvist 2001, Rolstad et al. 2002).

Although *L. pulmonaria* has been shown to suffer from permanent light damage under high light intensity (Gauslaa et al. 2001), the lichen is also light dependent; it has been shown to profit from semi-open environments and is disfavored in dark and more dense forests (Renhorn et al. 1997, Hazell and Gustafsson 1999). Our spatial analysis showed that *L. pulmonaria*, I_L , was more associated with local increase of canopy cover and/or tree density, I_- , than with the stand-level disturbance events, I_D , but that the opposite was true for sycamore maple, I_A (Table 3). Although the explanatory variables local increase, I_- , and stand-level disturbance events, I_D , were not independent in this analysis, this indicates fewer sycamore maples in areas with local

increase in tree density and/or tree cover than in areas with a stand-level disturbance.

Lobaria pulmonaria will be less susceptible to a decrease of air humidity (e.g., following the opening of the canopy) when precipitation is high. Our study area has a high mean annual precipitation relative to the rest of Switzerland (Spreafico 1992). Precipitation is unlikely to be limiting and present canopy cover had no significant effect on host tree density or colonization proportion (Table 2). Our results therefore suggest that *L. pulmonaria* may have profited from an increased availability of potential host trees, but could also have profited from improved light conditions prior to the closing up of the canopy layer.

Conclusions for ecological continuity

This paper quantifies the operational definition on the concept of ecological continuity, as suggested by Rolstad et al. (2002) and Norden and Appelqvist (2001). Since *L. pulmonaria* was not negatively correlated with disturbance at the forest stand level, frequency and abundance of this lichen cannot be considered as an indicator for continuity for this study area. Either processes of recolonization were so fast that colonization occurred even when trees were relatively young, or the tested indicator species was not susceptible enough to become locally and persistently extinct. This study does not dispute the value of *L. pulmonaria* as an indicator to assess forest conservation value at a landscape level; we did not compare landscapes. However, we did show that, at least in our study area, *L. pulmonaria* is less dispersal limited than would be required for an indicator of ecological continuity at a forest-stand level. Frequency and abundance of this species are therefore not the appropriate measures to indicate continuity at the spatial and temporal scales considered. Our results even suggest that disturbances could be beneficial for *L. pulmonaria* when early successional stages result in more potential host trees and create a beneficial habitat (such as improved light conditions), provided that a viable population is within range and that spatial extent of the disturbance is not much larger than dispersal ability of the organism. This study argues that, although indicator species may be an efficient means to assess conservation value of a forest, spatially and temporally explicit knowledge of the species' life history characteristics is indispensable to prevent a possible misinterpretation of the ecological processes that the indicator aims to unravel.

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ERRATUM

In the recent paper by J. M. Kalwij, H. H. Wagner, and C. Scheidegger (2005), "Effects of stand-level disturbances on the spatial distribution of a lichen indicator," *Ecological Applications* **15**(6):2015–2024, the key to the shading of the histogram bars in the bottom panel of Fig. 2 is given incorrectly in the legend. The legend should have indicated that the dark gray bars represent colonized host trees, and the light gray bars represent uncolonized host trees.