

Selecting and testing indicators of forest history and sylvopastoral landscape dynamics

Inauguraldissertation
der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

Vorgelegt von
Jesse Machiel Kalwij
von den Niederlanden

Leiter der Arbeit:
PD Dr. Christoph Scheidegger
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Synthesis

Introduction

Natural or 'old-growth' forest stands typically originate through succession (Watt 1947), contain a significant proportion of old trees, dead wood, and have a high degree of patchiness and heterogeneity (Hendrickson 2003). In such forests, high species richness is achieved when all successional stages are simultaneously and continuously present (Halpern & Spies 1995). Grazing, either by cattle or by natural herbivores, has recently been suggested as an essential component for the persistence of open areas within a natural forest (Vera 2000). Pollen analysis, dating back as far as the Holocene, showed that large areas dominated by non-arboreal species must have existed on the European continent prior to human settlement. These pollen data and the disappearing of certain shade-intolerant species in absence of natural large herbivores, e.g. of sessile oak or hazel from forest reserves, were interpreted as not in accordance with Watt's gap phase model (Vera 2000). Vera therefore suggested a park-like landscape, such as a sylvopastoral landscape that is being kept open by large herbivores, as the closest modern analogy to the natural plant-herbivores interactions.

Sylvopastoral landscapes were historically widespread in Europe. Currently, due to a combination of agricultural intensification and abandonment of less productive areas, this landscape type has become increasingly rare (Kirby et al. 1995). The value of sylvopastoral landscapes for the ecological and cultural-historical heritage of Europe has long been recognized (Pillichody 1920). However, these landscapes only reside where the

agricultural value is supplemented with a recreational or cultural-historic value (Kirby et al. 1995). The spatial extent of wooded pastures in a sylvopastoral landscape results in a heterogeneous pattern of disturbance types and intensities with a variety of ecological niches in a relatively close distance to one another (Kirby et al. 1995). This pattern of disturbance is likely to affect the distribution of species; one can expect that dispersal-limited species are more frequently found in less disturbed areas. In a pasture-woodland landscape that is regularly disturbed by cattle grazing, forest management and occasionally by fire or windfall, dispersal-limited species are expected to have a clustered distribution that is associated with undisturbed areas.

The sylvopastoral landscape of the Parc Jurassien Vaudois is a hotspot of species that are threatened elsewhere in Switzerland, e.g. *Daphne cneorum* (Lauber & Wagner 2002), capercaillie *Tetrao urogallus* (Mollet et al. 2003) or *Lobaria pulmonaria* (Scheidegger et al. 2002). Recent pollen analysis suggests that this area may already have been in use for cattle grazing since the 13th century (Sjoegren 2005). Although species diversity in managed forests usually increases after abandonment (Halpern & Spies 1995, and literature cited therein), this may not be the case in a sylvopastoral landscape where the ratio of natural browsers and grazers differs from natural conditions due to anthropogenic disturbances (Van Wieren 1995). When cattle grazing pressure decreases while grazing intensity of natural herbivores is low, abandonment may result in the forest completely growing back randomly in a relatively short period of time. Such decline of open areas and subsequent loss of ecological niches may result in a temporary disappearance of shade-intolerant species such as sycamore maple. If a dispersal-limited

species, such as *L. pulmonaria*, is dependent on shade-intolerant species or is shade-intolerant itself, this may lead to a decline of an already vulnerable species.

This study aimed to reveal if and how land-use history affects present forest structure, species composition and species distribution of a sylvopastoral landscape. To achieve this, landscape dynamics of this landscape were investigated by analyzing the spatio-temporal patterns of tree regeneration for different land-use categories. Indicators of land-use history were identified to determine if present species richness was related to land-use and could be used to reconstruct the forest-stand history. We also tested the assumption that dispersal-limited species are associated with undisturbed forest-stands. These issues can be summarized in three main questions:

- (i) What are the spatial patterns of tree regeneration at a landscape scale?
- (ii) Can nested subsets of species be related to land-use history, and used as indicators?
- (iii) How well is the assumed dispersal-limited epiphytic lichen *Lobaria pulmonaria* associated with undisturbed forest stands?

Spatial patterns of forest structure and tree regeneration were analyzed in the first chapter. A practical challenge was in the quantification of scale-dependent patterns. In the second chapter, we investigated if grazing history or historical changes in tree cover and/or density affects current species composition or diversity, and if indicator taxa could be used to reconstruct land-use history. In the third chapter we compared the distribution

of *L. pulmonaria* with reconstructed stand-level disturbance events to test the validity of *L. pulmonaria* as an indicator of undisturbed forest stands.

Patterns of tree regeneration

We hypothesized that each land-use type has a different dominant process of tree regeneration, with a specific spatio-temporal component, leading to systematic differences in the spatial patterns of tree distribution. Spatial patterns of tree distribution were quantified in 36 plots (twelve each from currently grazed, abandoned, and ungrazed areas) from aerial photographs and LiDAR (Light Detection and Ranging) data. Small-scale patterns of tree regeneration were analyzed by calculating the nearest neighbor index (NNI) for the distances of small trees to large trees. Normalized lacunarity, as a cover-independent measure of tree-cover contagion (or 'gappiness'), was calculated for each land-use. We found that the spatial pattern of tree-cover contagion had remained constant for the grazed and the forested areas between 1933 and 1998. The tree-cover contagion of the abandoned area suggested that this area was already hardly used for cattle grazing in 1954, prior to its final abandonment in 1970. The NNI analysis revealed that small-scale tree regeneration was randomly distributed in abandoned areas. The spatial segregation of newly established trees in the grazed areas was in concurrence with the facilitation hypothesis. The patterns of tree regeneration were land-use specific and the high relative abundance of small trees in the abandoned area confirmed that abandonment of wooded pastures was succeeded by accelerated forest recovery.

Comparison of indicator categories

The presence of old-growth related species, a high plant species richness, or a high dead wood quantity is often used to reconstruct the land-use history or forest-stand age (e.g. Kuusinen & Siitonen 1998; or Wulf 2004). Correlations of three groups of indicators with forest-stand history were compared. A total of 86 plots were sampled for understory vascular plants and trees. A subset of 38 of these plots was sampled for epiphytic lichens from an *a priori* list of established indicator species. Plots were classified by grazing (in three categories: currently grazed, abandoned for grazing, or ungrazed), and tree-density change (in three categories: decrease, no change, or increase of canopy cover between 1933 and 1998). The relationship of species richness of vascular plants, lichens and trees with grazing, present forest cover, tree-height structure, and tree-density change between 1933 -1998 was analyzed and tested for the nestedness of species subsets; this is a primary requirement if species composition is to be used as an indicator of forest history rather than edaphic conditions. The rather constant tree species composition suggested that edaphic variation was low at the landscape scale. While vascular plant species richness was correlated with grazing history, forest cover and tree density, lichen richness could only be explained by tree-height structure. We interpreted these correlations by the stronger effects of light availability on vascular plants than on lichens. Lichens were not affected by grazing history. Although each indicator category had a strong nestedness of species subsets, the observed correlations were unsuitable for a reliable reconstruction of forest-stand history. In all probability, a mixture of responses of plant species to local environmental conditions may have hindered a straightforward interpretation of historical land-use. An investigation on a large spatial scale using a

single edaphic-independent, easily recognizable species such as the epiphytic lichen *Lobaria pulmonaria* might be a more straightforward and time efficient means to compare land-use history between areas.

Evaluation of an established indicator

The epiphytic lichen *Lobaria pulmonaria* is used as an indicator to identify European forests with a high ecological continuity (i.e., long-term undisturbed, old-growth forests) due to its assumed dispersal limitation and susceptibility to disturbance. An assumed limited dispersal ability has been suggested as a possible explanation of the clustered pattern of distribution of *L. pulmonaria* in the sylvopastoral 'Parc Jurassien Vaudois'. We tested the hypothesis that stand-level disturbances had a long-lasting negative impact on the occurrence of *L. pulmonaria*. Two 19th century stand-level disturbances were delineated using aerial photographs from 1933. We sampled 7769 potential host trees in a random sample of 251 plots of 1 ha, encompassing both disturbed and undisturbed areas. Presence of *L. pulmonaria*, tree species and diameter at breast height were recorded. Surprisingly, neither the historical stand-level disturbances nor grazing reduced the proportion of colonized trees as compared to undisturbed plots. Tree-level spatial analysis revealed a patchy distribution of colonized trees, which suggested that *L. pulmonaria* had colonized trees from nearby sources. Spatial analysis at the plot level showed that *L. pulmonaria* was spatially associated with the stand-level disturbances. 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 to prevent possible misinterpretation of ecological processes that the indicator aims to unravel.

Conclusions

Species diversity has long been used as a simplified characterization of the distribution of species (e.g. Simpson 1949) and has been correlated with forest-stand history (Boudreault et al. 2000; Honnay et al. 1999; Rolstad & Rolstad 1999; Rose 1976; Wulf 1997). However, our comparison of various indicators implied that the ecology behind local diversity is often complex even in a relatively homogenous forest. Our results suggest that current grazing and forest structure were more important to plant and lichen composition and abundance than forest-stand history. However, we were unable to find evidence that abandonment of a wooded pastures would lead to the disappearance of a dispersal-limited species or a decline in species richness. This interpretation also helps in explaining local high abundances of a dispersal-limited species. In spite of our result that presence and abundance of *L. pulmonaria* cannot be associated with undisturbed forest stands, the presence of this species continues to provide ecological information on the sylvopastoral landscape, but at a larger spatial scale. Presence of a dispersal-limited species does not necessarily indicate absence of disturbances, but implies that the frequency, intensity and spatial extent of these disturbances is low and small enough to permit the persistence of this particular species.

An important feature of this study was that empirical 'evidence' often turned out differently than expected. For example, our analysis of the canopy-cover dynamics indicated that an abandoned pasture may hardly have been in use as pasture prior to its

final abandonment. In addition, *Lobaria pulmonaria* was assumed to indicate absence of disturbance, but its distribution even suggested the opposite. Such unexpected developments emphasize the continuing need for detailed information on life-history traits such dispersal ability and empirical testing of established but unproven assumptions at the appropriate level of detail.

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Chapter 1

Title of the paper: Determining spatial patterns of tree regeneration in a pasture-woodland landscape using time-series of aerial photographs and LiDAR data.

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Abstract

A sylvopastoral landscape typically has a variety of closely situated areas with different land-uses, leading to different patterns of tree regeneration. We hypothesize that each key process governing regeneration, e.g. competition or facilitation, has its own spatial component, leading to systematic differences in the spatial patterns of tree regeneration and tree distribution between land-use types. We distinguished three land-use categories in a Swiss pasture-woodland landscape: *(i)* currently grazed wooded pastures, *(ii)* abandoned pastures, and *(iii)* long-term forests. Digital Boolean maps of tree cover were extracted from orthorectified aerial photographs of 1933, 1954, 1998, and of recent LiDAR (airborne laser scanning) data. For each category, we randomly selected 12 replicate plots and quantified the spatial distribution of tree-canopy cover for three time steps (1933, 1954 and 1998) using lacunarity as a cover-independent, multi-scale measure of spatial aggregation. Nearest neighbour index (NNI) was calculated to quantify small-scale tree regeneration patterns. In long-term forests, forest cover increased over time, while lacunarity remained unchanged, suggesting that logging intensity decreased, but that key processes did not. On abandoned pastures, average tree height was significantly lower than in grazed areas due to the high abundance of small trees. Canopy cover increased over time while lacunarity decreased, suggesting that the spatial pattern of tree regeneration was that of a long-term forest, which was confirmed by our NNI analysis. Lacunarity curves of 1933 - 1998 further suggested that the process of reforestation in the abandoned pasture already started before final abandonment. Our approach allowed a retrospective multi-scale quantification of tree-canopy contagion and showed that present patterns of tree-canopy cover distribution could be readily explained by landscape

history. We suggest that change in land-use leads to a gradual change in spatial processes-dominating forest dynamics.

Introduction

Dynamics of forested landscapes are often described as shifting mosaics (Lertzman and Fall 1998). Such mosaics may consist of patches with even-aged stands resulting, e.g., from a natural fire regime or from even-aged forestry (Schütz 2002). Gap dynamics represent another form of shifting-mosaic dynamics with smaller patches representing different successional stages triggered by the death of a large tree or a small group of trees, e.g. due to natural mortality or the harvesting of individual trees (Watt 1947). Land-use creates a similar mosaic of dominating processes, often with rather sharp boundaries, as management units are often delimited by ownership boundaries, and many management practices tend in agriculture and farming try to homogenize conditions within patches (Olsson et al. 2000). In addition, the land-use mosaic is likely to change over time, typically in a non-random way. Especially in the case of slow systems such as forests, we may often face transient dynamics rather than steady-state shifting-mosaic dynamics (Mladenoff et al. 1993).

In wooded pasture ecosystems, shifting mosaics are governed by complex plant-herbivore interactions and tree regeneration (Olff *et al.* 1999). Impeded by non-selective grazing of cattle, associational resistance with unpalatable plants has been shown to facilitate spruce regeneration (Smit et al. 2005). Competition for light has been suggested as an additional key process governing shifting-mosaic dynamics (Olff *et al.* 1999).

When pastures are abandoned, grazing pressure decreases and selective browsers, such as

roe deer or chamois, may replace cattle (Van Wieren 1995). Depending on local circumstances, effects of browsing pressure on the spatial pattern of tree regeneration may vary and the facilitative effect of unpalatable species could even be nullified when browsers are smaller or more selective than cattle (Crawley & Long 1995). If browsing density is low, trees may establish randomly, resulting in a closed forest and a loss of light-dependent species (Bartemucci et al. 2002). On the other hand, a sudden decrease of grazing intensity can also lead to temporal outcompeting of tree saplings by tall grasses or herbs (Rees et al. 2001). If tree saplings are outcompeted by light-demanding species, forest regeneration may only occur where light intensity is low, e.g. in the shadow range of an existing tree. This process is expected to lead to a shifting mosaic of solitary trees.

To determine if a change in land-use leads to a change in the spatial pattern of tree establishment, one would preferably use species-specific accurate data on the location, age and height of individual trees over a long period of time, and data on land-use and disturbance history of each management unit. Detailed, retrospective data on spatial and temporal patterns of tree establishment would help to interpret the spatial effects of key processes such as facilitation or secondary succession on tree regeneration. Each observed pattern represents a single observation of the process, so that replicates at the landscape scale are needed. The required extent and replication of local landscapes precludes a dendro-ecological approach.

Light detection and radar (LiDAR) data can be used to derive geometric properties of a single tree (Morsdorf et al. 2004) and are, especially on a landscape scale, one of the few time-efficient means to estimate location and height of individual trees (Popescu et al. 2003). Future time series of LiDAR data, therefore, will have high

potential for a detailed spatio-temporal analysis of forest gaps or vertical tree structure (Boutet and Weishampel 2003). Unfortunately, historical LiDAR data are scarce. Stereoscopic aerial photographs are often the only historical data sources available containing information on geographic relief and vegetation height (Fujita et al. 2003a, Fujita et al. 2003b). Manual classification or height estimation from aerial photographs, however, is time-consuming, subjective or imprecise (Naesset 2002). Although automated classification or height estimation from aerial photographs has often been subject to research (Itaya et al. 2004, Nuske and Nieschulze 2004), an accuracy at the individual tree level comparable to LiDAR-derived data is usually not achieved, in spite of ongoing software-improvements (Korpela 2004). However, automated extraction of forest-gap attributes, even from older black-and-white aerial photographs, has been successfully applied (Uuttera et al. 1998, Fujita et al. 2003a, Fujita et al. 2003b, Kennedy and Spies 2005).

Lacunarity analysis, a multi-scale method for describing patterns of spatial aggregation, provides a parsimonious analysis of the overall fraction of a map or transect covered by an attribute of interest, such as degree of contagion, degree of self-similarity, presence and scale of randomness, or existence of hierarchical structures (Plotnick et al. 1993, Plotnick et al. 1996). Lacunarity is commonly calculated over a range of window sizes and the plot of $\log(lacunarity)$ against the $\log(window\ size)$ is interpreted as a scaling function in which a higher value of lacunarity indicates a more heterogeneous landscape with the landscape element of interest being more clustered (Wu and Sui 2001). Lacunarity can be normalized to account for differences in the overall cover. The adjusted lacunarity index provides a cover-independent quantification of contagion (Wu

and Sui 2001), which can be used as an analytical approach to compare retrospectively derived patterns of tree establishment between different land-use types.

To determine if land-use types govern different spatial patterns of tree regeneration, the spatial variation in gap-arrangement needs to be compared. This study aimed to understand if and how spatial patterns of forest dynamics differ between land-use categories of a sylvopastoral landscape. We hypothesized that each land-use category has a different dominant process of tree regeneration, with a specific spatio-temporal component, leading to systematic differences in the spatial patterns of tree distribution. Therefore, we quantified the spatial scaling of gap contagion and tree regeneration of long-term forests and wooded pastures to compare between land-use categories. We evaluated these results with canopy-cover patterns in an abandoned pasture before and after abandonment to determine if and how patterns of tree regeneration in an abandoned pasture changed over time.

Materials & Methods

Study area

The management units of the study area encompass 1350 ha and are part of the Swiss Parc Jurassien Vaudois (PJV), located between 46°28'-34'N and 06°06'-16'E at an elevation of 1300-1450 m (Figure 1). The PJV is a sylvopastoral landscape characterized by forests and wooded pastures on carstic limestone bedrock (Vittoz 1998). Tree composition is dominated by Norway spruce (*Picea abies*), followed by scattered sycamore maple (*Acer pseudoplatanus*), beech (*Fagus sylvatica*), mountain ash (*Sorbus aucuparia*) and silver fir (*Abies alba*). Low-intensity forestry encompassed selective

logging of individual trees in quantities less than or as high as annual growth in order to maintain an uneven-aged forest (Schütz 2002). Around 1810 walls were built to separate continuous forests from wooded pastures (Rochat 1995). We defined these forest areas as 'long-term forests'. In the 1930s, a second period of wall-building started (Gillet and Gallandat 1996). During this period, wooded pastures with a considerable tree cover were closed to cattle grazing. We defined these as 'abandoned pastures'. Remaining pastures were defined as 'grazed'.

LiDAR data

Two sets of airborne LiDAR data, obtained in summer 2003 by Swisstopo (Swiss Federal Office of Topography), were used to construct a digital surface model (DSM) and a digital terrain model (DTM). The first raw LiDAR dataset consisted of the first returns; representing the maximum height with vegetation (irregularly spaced DSM-points; approx. 10,000 point / ha). The second, filtered dataset consisted of last returns, representing height of terrain without vegetation (DTM-points), *i.e.* where vegetation is sparse enough for pulses to reach the ground. GIS data analysis was done in ArcGIS 8.3 (Anonymous 2002). Both sets were interpolated by generating triangular irregular networks and subsequent conversion into grids of 0.5 m, an exact interpolation technique as recommended by Popescu (2002). The difference between the DSM and the DTM was used as an estimation of vegetation height. Vegetation exceeding 1.5 m is resistant to browsing and was considered as 'tree'. Horizontal canopy-cover data were derived by creating a Boolean map of 'tree' and 'no tree' and subsequent filtering: cells were considered as 'tree' if at least one neighboring cell was also 'tree', otherwise it was

recoded as 'no tree'. To obtain vertical tree-structure data, trees were identified by searching for a local height maximum in a 2.5 m radius and subsequently converting cells with a local height-maximum equal to vegetation height into point features containing spatial coordinates and tree height information.

Retrospective Boolean tree maps

Two Boolean tree maps were derived from black-and-white aerial photographs of 1933 (1:16,000), 1954 (1:19,000) and 1998 (1:18,000). The first two sets of images were acquired from Swisstopo and digitized at a resolution of 21 μm (cell size of approx 0.41m). Aerial photographs of 1998 (acquired from WSL) were digitized at a resolution of 21 μm using a flatbed scanner (cell size of approx 0.45 m). Aerial photographs were georeferenced, orthorectified and mosaiced in ERDAS IMAGINE 8.7 (Anonymous 2004), using panchromatic orthophotos of 1998 (SWISSIMAGE; acquired from Swisstopo) and the LiDAR-derived digital terrain model (DTM). Each mosaic of orthorectified aerial photographs was resampled to match the 0.5 m nominal ground resolution of the 1998 orthophotos. Classification of 'tree' and 'no tree' was done in four steps using ERDAS IMAGINE 8.7: *(i)* unsupervised classification into 10 classes; an iterative self-organizing data analysis technique that uses the minimum spectral distance to form clusters until 95% of assigned class-values remains unchanged on the next iterative step, *(ii)* regrouping of classes into the values 'tree' and 'no tree', *(iii)* a variance texture filter was applied to recode shade-related false classification from pastures (if the standard deviation in a 12.5 m radius exceeded the threshold value of 20, cells were recoded as 'tree'), and *(iv)* by defining cells as 'tree' if at least one neighboring cell was

also 'tree', otherwise it was recoded as 'no tree'. Since thresholding of a monochrome image involves selection of a certain intensity value, indistinct tree canopies are interpreted as grass layer causing the canopy-cover estimate to be biased (Korpela 2004). If aerial photographs and LiDAR data are obtained around the same time period, attributes derived from aerial photographs can be compared with LiDAR data to verify the accuracy of attributes extracted from aerial photographs. To assess the weight of the angle of incidence on the tree canopy length, the shadows of six farming houses were measured and tested between the years using a paired t-test.

Sample plot analysis

As forest structure is highly scale-dependent, we empirically determined the extent of local landscapes by the plot size at which the standard deviation of tree height no longer increased. This size was 1 ha for abandoned and forested areas, and 2 ha for grazed areas (results not shown). Therefore, circular non-overlapping plots of 2 ha were randomly positioned within each of the three land-use types of the study area (Figure 1), 12 for each land-use category. To obtain the same land-use history the 12 plots of the abandoned category were placed in the same single pasture. For each plot, average canopy cover P was determined from the LiDAR-based Boolean map. Tree height h and tree density d was determined from the LiDAR-derived tree point coverage. Canopy cover per time step was determined from the retrospective Boolean maps and from the Boolean map derived from LiDAR for reference purposes. The contagion of the Boolean tree maps was quantified by calculating the lacunarity index. A higher lacunarity index I reflects a more heterogeneous landscape with a higher degree of clustered 'tree' cells,

whereas lower lacunarity reflects a more homogenously distributed pattern of 'tree' cells. All lacunarity indices were calculated in ArcGIS 8.3 (Anonymous 2002) following the gliding box algorithm by Wu & Sui (2001). We used quadratic windows of width 1, 2, 4, 8, 16, 32, 64, 128 and 256 cells within circular plots with a radius of 160 cells. As this lacunarity analysis seems to miss some of the fine-scale patterning and does not directly relate to the spatial pattern of tree regeneration, we also performed a nearest neighbor (NN) analysis of young trees to old trees as a link to processes of tree regeneration (Ribbens et al. 1994). Distances of small trees (1.5 - 3.0m) to big trees ($> 6.0\text{m}$) $N_s N_{obs}$ and of big trees to big trees ($> 6.0\text{m}$) $N_b N_{obs}$ were calculated from the LiDAR-derived tree point coverage. The expected nearest neighbor distance NN_{exp} was also calculated from this coverage for each plot based on a random distribution of trees, irrespective of size, using a correction for the non-independence of nearest neighbor distances (Donnelly 1978). The nearest neighbor index NNI as the ratio between NN_{obs} and NN_{exp} is a measure of dispersion (in a random distribution $NNI = 1$, in a clumped distribution $NNI < 1$, and overdispersed $NNI > 1$) and was log-transformed to obtain a normal distribution of values.

Statistical analysis

The effect of land-use categories on tree-height distribution was compared for each land-use type with a Kolmogorov-Smirnov two-sample test. The normally distributed mean tree height h and tree density d were compared between the three land-use categories by two one-way analyses of variance (ANOVA). The LiDAR-derived and retrospective mean tree-cover data were arcsin square-root transformed and compared

between each land-use category to determine the change in canopy cover over time by four one-way ANOVAs. Pairwise comparisons were tested using Tamhane's T2, a conservative test allowing for unequal variances, where the commonly used Bonferroni comparisons were not applicable (Tamhane 1977).

To determine if a change in land-use resulted in a changed scaling function of contagion of 'tree' cells, lacunarity within and between each land-use type was compared over time. The normalized, cover-independent lacunarity index I_{adj} was determined by dividing $\log(Lacunarity)$ by $\log(1 / P)$ to correct for cover differences (Wu and Sui 2001). The lacunarity indices I_{adj} were averaged for each window size over all replicate windows from the same plot and plotted against the log-transformed window-size S .

A logistic regression of I_{adj} on S was fitted for each combination of plot i and year t , providing the two logistic regression parameters b_{0it} and b_{1it} . Each model was summarized by the location parameter $u_{it} = -b_{0it} / b_{1it}$. This parameter u_{it} estimates the window size at which I_{adj} equals 0.5. We tested the difference in mean u_{it} between land-use categories and years with a two-way repeated-measures ANOVA. In order to stabilize the variance, the ANOVA was performed on reciprocal values $u_{it}' = 1 / u_{it}$. Tamhane's T2, a conservative test allowing for unequal variances, was used where Bonferroni comparisons were not applicable (Tamhane 1977).

The significance of the departure from randomness of each nearest neighbor index NNI was tested with one-sample t-tests. To determine if land-use had a significant effect on the spatial distribution of small trees, the normally distributed NNI for small trees (1.5 - 3.0 m) and for large trees (> 6.0 m) were compared with a two-way ANOVA. To

correct for edge effects, the ANOVA was restricted to trees closer to a nearest neighbor than to the edge of their 2-ha plot ($n=8431$).

Results

Individual-based tree structure

Based on the histograms of the tree-size distribution, the vertical structure of the examined plots was strongly dependent on land-use type (Figure 2). The mean tree height of the long-term forest area was considerably and significantly higher (14.3 m) than the trees of the abandoned or the grazed areas, with significantly differing heights of 12.2 and 12.7 m, respectively (Table 1). This significant difference, however, was not reflected in a significant difference of tree density between forest and abandoned areas. The one-way ANOVA showed a significant effect of land-use category on tree density d (Table 1); $F = 24.12$; $df = 2, 33$; $p\text{-value} < 0.001$), with grazed areas being different from abandoned and forested areas. The three Kolmogorov-Smirnov tests showed that all tree-height distributions were significantly different from each other (all $p\text{-values} < 0.001$). These differences were due to the relatively higher abundance of small and middle-sized trees in the abandoned and grazed areas (Figure 2).

All NNI values were significantly overdispersed (one-sample t-tests; deviation from 1; all $p\text{-values} < 0.001$). The two-way ANOVA showed a significant interaction of land use category and tree size (Table 3). The comparison of the NNI showed that small trees of the grazed areas were significantly further away from big trees than other small trees within the abandoned areas (Figure 3). Not enough point data of small trees from the forest were available to perform a statistical analysis for each land-use category.

Multi-scale analysis of 'tree' contagion

The variation in 'tree' interpretation was independent of the angle of incidence (paired t-tests between 1933 and 1954, $t=1.94$, $df=5$, $P=0.109$; between 1954 and 1998, $t=2.22$, $df=5$, $P=0.077$; and between 1933 and 1998, $t=0.61$, $df=5$, $P=0.570$). The repeated measures ANOVA showed that the spatial scale of contagion of 'tree' cells was significantly different between the long-term forested areas and the grazed areas, but did not change over time for these two types (Figure 5 and Table 4). In contrast, the 'tree' contagion of the abandoned area was already significantly between a forested and a grazed area in 1933 and by 1998 had reached a canopy-cover pattern that was no longer significantly different from that of a long-term forested area. The mean lacunarity curves derived from the 1998 black-and-white aerial photographs coincided significantly with the lacunarity curves derived from the LiDAR data (Figure 4), except those of the abandoned area (Figure 5). The mean lacunarity curves of 1933, 1954 and 1998 for the grazed and forested areas showed no significant changes. In contrast, the mean lacunarity curve of the abandoned area in 1954 was between that of a grazed and a forested area. By 1998, this curve could no longer be distinguished from that of the long-term forested area. The spatial scale of 'tree' contagion of the abandoned pasture had adopted a canopy-cover pattern in 1998 that was no longer significantly different from a long-term forested area.

Discussion

Since the interpretation of tree cover was biased due to the unfeasibility to discriminate between an indistinct tree canopy and a heterogeneous grass layer, a direct comparison of tree canopy cover between the years seems unreliable. Therefore, the lacunarity index approach was more suitable to quantify and compare the automatic interpretation of aerial photographs for a spatio-temporal analysis of landscape dynamics. Variation in shadow length was unlikely to have affected this interpretation. We provided a cover-independent means for the comparison of patterns by summarizing and testing lacunarity-curves via u_{it} -values. However, for a comprehensive interpretation of a change in the pattern of tree regeneration, information on the vertical tree structure and a small-scale spatial structure is indispensable. Although a DSM can theoretically be extracted from stereoscopically overlapping pairs of aerial photographs, the image quality is often not sufficient for an individual-tree based DSM extraction (Baillard et al. 1998). The availability of LiDAR data presented us with the opportunity to combine retrospective black-and-white aerial photograph data with present-day data on individual trees.

The aggregated nearest neighbor index NNI of small trees in the abandoned areas was significantly lower than that of the grazed areas, suggesting that the associational resistance-driven pattern of shifting mosaics no longer applied. The nearest neighbor analysis therefore supported our hypothesis that removal of cattle allows trees to regenerate randomly in open areas. In addition, there was no evidence for aggregation, as would be expected from the alternative patch-growth hypothesis. The lacunarity indices of the 1933, 1954, 1998, and LiDAR-derived Boolean maps showed that no changes in the aggregation of forest-canopy cover had occurred in the grazed or forested areas. The

1954 lacunarity curve, however, suggested that grazing may have already been low prior to the final abandonment and that therefore the process of reforestation in this pasture had already started long before the final abandonment for grazing.

Density of wild animals, such as chamois (*Rupicapra rupicapra*), wild bores (*Sus scrofa*), and roe deer (*Capreolus capreolus*), has substantially increased over the last decades in the study area and has been reported to have a negative impact on the regeneration of palatable tree species, e.g. on *Abies alba* (Golay, Swiss Forestry Service, pers.comm.). However, this increased browsing intensity does not seem to be high enough to have had a negative impact on forest regeneration. Both tree density (Table 1) and tree cover (Table 2) in this abandoned pasture were as high as in the long-term forested areas. The abandoned pasture lacked the proportion of high trees that are characteristic of the long-term forest (Figure 2), which is induced by competition between trees for light (Koch et al. 2004). Our data showed that a relatively large proportion of small trees was present, which also suggests that tree saplings were not outcompeted by tall grasses or herbs. Large trees may provide the ecological niches that are essential for a forest with high species diversity. However, when abrupt abandonment is succeeded by a high proportion or cover of *Picea abies*, this could lead to a temporary outshading of light-dependant species (Diaci 2002) and sudden changes in land-use, such as abandonment after a long period of cattle grazing, could result in a temporal loss of diversity before the natural dynamics are recovered (Halpern and Spies 1995).

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Table 1. Mean height and density of trees per land-use type ($\pm$ standard error). Different letters indicate significant pairwise differences for tree height and tree density at the 5% level using Tamhane's T2 correction for multiple comparisons with unequal variance. N is the number of plots per disturbance category, while n is the number of trees per land-use category

Historical land-use	Tree height (m) h		Tree density (n / ha) d	
	n	h	N	d
Long-term forest	4397	14.3 ± 0.10^a	12	183.2 ± 9.60^a
Abandoned since 1970	4282	12.2 ± 0.09^b	12	178.4 ± 4.62^a
Grazed	2153	12.7 ± 0.13^c	12	89.7 ± 15.22^b

Table 2. Average tree cover per land-use type, derived from classification of aerial photographs and LiDAR data ($\pm$ standard error). Different letters indicate significant pairwise differences for sycamore maple 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 (arcsin of square root). N is the number of plots per disturbance category.

<i>Land use</i>	<i>Cover 1933</i>	<i>Cover 1954</i>	<i>Cover 1998</i>	<i>Cover LiDAR</i>	<i>N</i>
Long-term forest	0.54 ± 0.07^a	0.28 ± 0.03^a	0.33 ± 0.02^a	0.45 ± 0.02^a	12
Abandoned	0.43 ± 0.10^b	0.23 ± 0.02^a	0.31 ± 0.02^{ab}	0.45 ± 0.02^a	12
Grazed	0.31 ± 0.12^c	0.19 ± 0.03^a	0.20 ± 0.04^b	0.26 ± 0.05^b	12

Table 3. Results of two-way ANOVA of log-transformed nearest neighbour index *NNI* as dependent on the three land-use categories and tree size. Models were corrected for unequal sample sizes.

	<i>SS</i>	<i>df</i>	<i>F</i>	<i>p</i>
Model	211.80	5	189.64	0.000
Intercept	4021.55	1	18003.63	0.000
Tree size	167.38	1	749.340	0.000
Land use	2.55	2	5.701	0.003
Tree size * Land use	25.754	2	57.648	0.000
Error	1881.93	8425		
Total	15050.12	8431		

Table 4. Repeated-measures ANOVA of u , the average location parameters of the fitted logistic regression models of the lacunarity curves, for the three land-use types as derived from the subsequent retrospective and LiDAR-derived Boolean maps.

	df	SS	F
Between subjects			
Land-use	2	9.674	19.709 ***
Error	33	0.491	
Within subjects			
Year	3	6.577	39.025 ***
Land-use x Year	6	1.978	5.868 ***
Error	99	5.562	

*** $P < 0.001$

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Figure 1

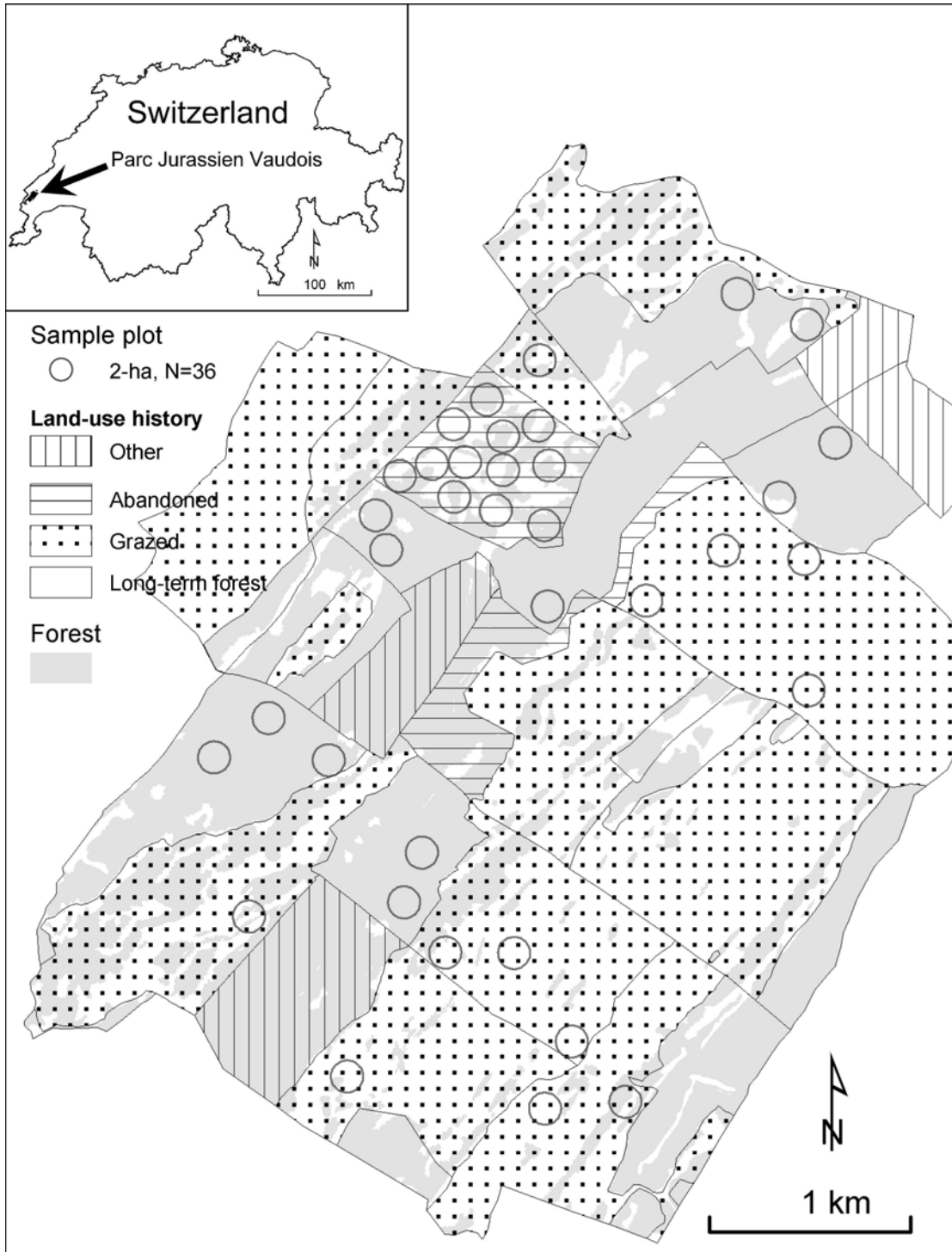


Figure 2

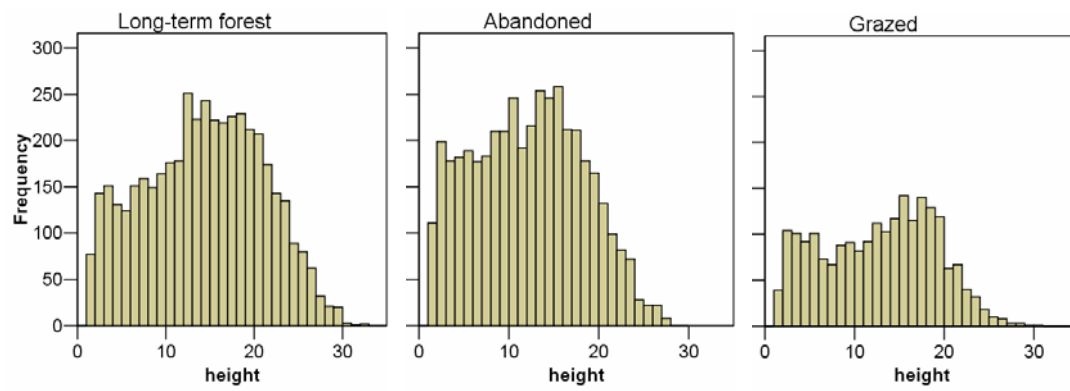


Figure 3

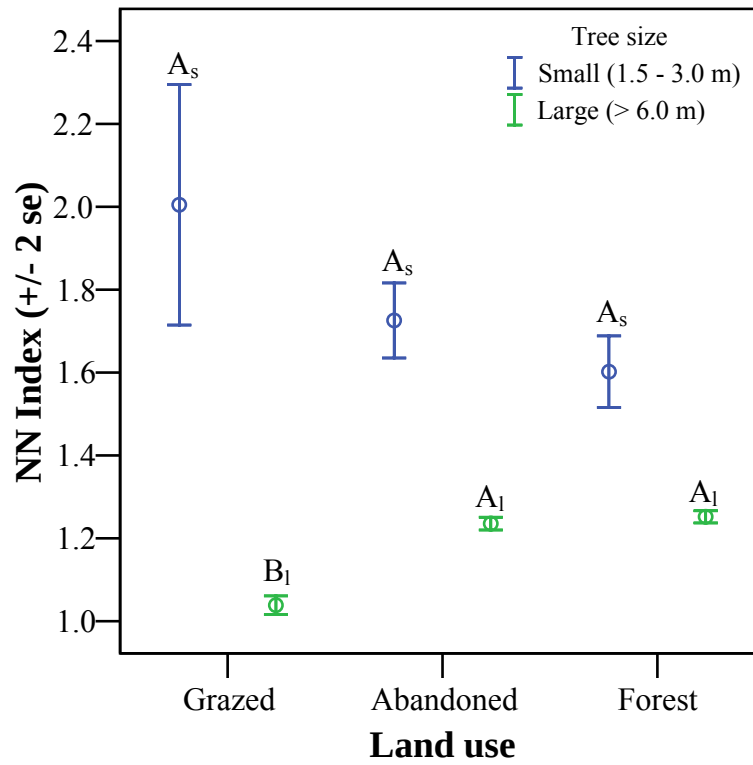


Figure 4

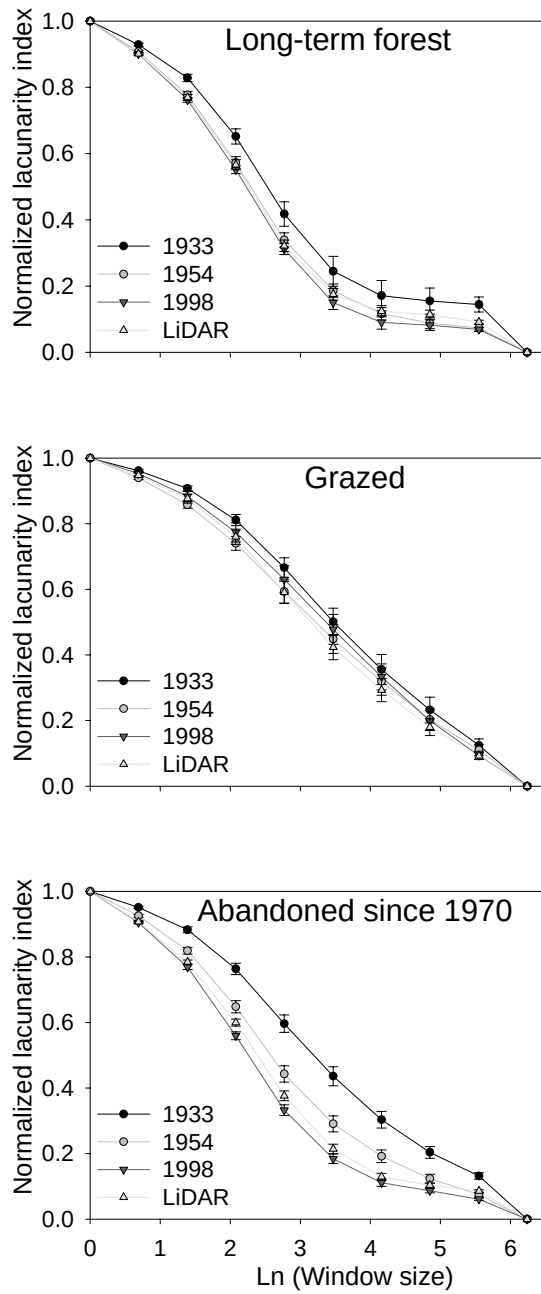
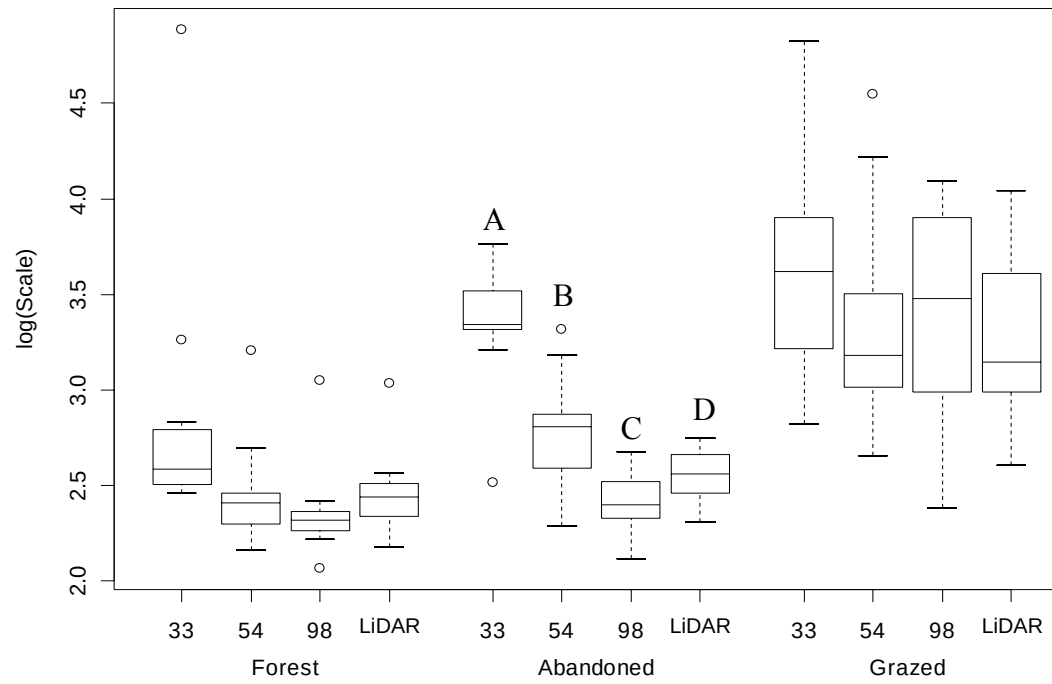


Figure 5



Chapter 2

Title of the paper: Indicators of land-use history: comparison of understory vascular plants with epiphytic lichen composition

For submission to: Biological Conservation *or* Biodiversity and Conservation

Authors: J. M. Kalwij¹, C. Smit², S. Werth¹, and C. Scheidegger

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Abstract

Forest-stand history is traditionally reconstructed with indicators such as understory plant-species composition, lichen diversity, tree structure, or dead wood quantity. This study compared correlations of two groups of indicators (vascular plants of the understory and epiphytic lichens) in the forest of a pasture-woodland landscape with forest stand history. A total of 86 sampling locations were selected and classified by two factors obtained from management records and aerial photographs: (i) grazing (three nominal categories: currently grazed, abandoned for grazing or ungrazed), and (ii) forest-stand history (three categories: decrease, no change, or increase of tree density and/or cover between 1933 and 1998). Plant species were sampled in 86 circular plots of 100 m². Tree species composition was recorded within a 1000 m² area around each plot-centre. Present forest cover and tree height structure was derived from LiDAR (light detection and ranging) data. Epiphytic lichen composition was recorded within a 1 ha circle around each plot in a subsample of 38 plots. Pearson's product-moment correlation was used to analyze the relationship between species richness of vascular plants and lichens with past and present land-use and forest-stand structure. Vascular plant-species richness was correlated with present tree cover, while lichen richness could only be predicted by tree-species richness. Composition and nestedness of plant species was explained by present grazing and light availability, rather than by former grazing. Lichen composition was only explained by forest-stand history, although this relationship was not convincing. Neither of the indicator categories allowed a reliable and detailed reconstruction of former land-use or forest-stand history.

Introduction

Old-growth forests typically originate through natural succession and are characterized by a significant proportion of old trees, dead wood, and have a high degree of patchiness and heterogeneity (Hendrickson 2003). In such forests, a high species richness is achieved when all successional stages are simultaneously and continuously present (Halpern and Spies 1995). Especially the existence of old-growth-related micro-habitats is negatively affected by a high intensity, frequency and spatial extent of disturbances. Highest species diversity or number of dispersal-limited species is therefore assumed to be correlated with the least disturbed forest stands. This correlation has been described as nestedness of species subsets, i.e. species composition at a disturbed site is a subset of the species present at an undisturbed site (Jonsson and Jonsell 1999), and is a primary requirement when indicator taxa are used to assess absence of disturbance.

Disturbances in a Swiss pasture-woodland landscape can comprise cattle grazing, forestry management, and even occasionally fire or wind-fall on forest stands (Kalwij et al. 2005b). As the spatial extent of these forest stands is traditionally small (Gallandat et al. 1995), this results in a heterogeneous pattern of disturbance types and intensities with a variety of ecological niches in relatively close distance to one another (Gillet and Gallandat 1996). As indicator taxa, such as epiphytic lichens (Rose 1976, Sverdrup-Thygeson and Lindenmayer 2003) or vascular plants of the understory (Honnay et al. 1999, Wulf 2004) have different environmental requirements and life-history traits, these taxa are likely to indicate disturbances differently. Both groups, however, are commonly used to assess absence or the degree of disturbances in forest stands.

Vascular plants of the understory are the most commonly used taxa to indicate forest-stand history (Honnay et al. 1998, Honnay et al. 1999, Jacquemyn et al. 2001b, Wulf 2004). A primary reason for choosing vascular plants is the relatively well-known species-specific life-history traits of plants. A complicating factor with plants, however, is the diversity in species richness and composition due to environmental variables such as edaphic variation or light conditions. Recent studies showed that the dispersal-limitation of plant species is a main explaining variable for local absence of species (Ehrlén and Eriksson 2000, Ozinga et al. 2005). If historical disturbances are intense enough and the spatial extent is beyond the dispersal capacity of a species, a persisting negative effect on the species composition can be expected. Provided that edaphic variation is known, remaining variation in species composition may be ascribed to land-use history (Wulf 2004).

Epiphytic lichens are, in contrast to understory plants, not directly affected by edaphic factors or grazing. Indirect negative effects of grazing may be observed when host trees are lacking as they were grazed, or when grazing has led to a fragmentation of the habitat (Johansson and Ehrlén 2003). Larger distances between habitats may result in a decline of especially dispersal-limited species (Sillett et al. 2000). Even if grazing intensity has declined and the host tree population is recovered to the original stand structure, a complete recovery of dispersal-limited species may show a significant delay (Dettki et al. 2000). This delay is the primary advantage of epiphytic lichens as indicators of old-growth forest above understory plants to detect historical disturbance events of forest stands that are no longer visible from tree size composition (Jonsson and Jonsell

1999). A disadvantage of many lichens, however, is the complicated and often unknown life-history or dispersal traits (Hilmo and Sastad 2001).

This study investigates how species richness and composition of vascular plants and epiphytic lichens depend on land-use history. We tested the hypotheses that (i) vascular plants of the understory can be used as indicators of former grazing, and that (ii) epiphytic lichens can be used as indicators of forest-stand history. To test these hypotheses we compared the correlations of species richness and composition of vascular plants and epiphytic lichens with past and present land-use. Past forest structure and land-use were reconstructed for a comparison of species richness and composition with the present situation.

Methods

Study area

The study area is situated in the Parc Jurassien Vaudois (PJV), Switzerland, between 46°28'-34'N and 06°06'-16'E. The PJV is a pasture-woodland landscape, characterized by *Picea abies* dominated forests and pastures. Since 1973, the PJV has a protected status that allows limited cattle grazing, forest management and recreational usages. The area is divided into parcels, each parcel owned by a different community and surrounded by stone walls. These walls were erected in the end of the 19th and first half of the 20th century to keep the cattle on the owners' parcel. Additional walls were build in the 1950s to keep cattle out of the forested areas and to restrict grazing to the more open areas (Vittoz 1998). Logging was employed throughout the area, which encompassed selective logging of individual trees, predominantly Norway spruce, in quantities less

than or as high as the annual growth in order to maintain an uneven-aged forest (Schütz 2002).

Data collecting

Vascular plants

Forest stands with a 30-50 year period of abandonment and adjacent forest stands were selected. Within these stands, 86 plots were selected from the aerial photographs and located in the field (Figure 6); where possible, pairs of plots were located on each side of a management unit border, minimizing the chance of finding differences in species composition due to dissimilar environmental conditions. Abundance of vascular plants in 86 vegetation relevés (circular plots of 100 m²) was recorded during the period July-August 2002, following the 9-level scale of Braun-Blanquet (Schaminée et al. 1995). Tree species composition was recorded within a 1000 m² area around each plot-centre for trees larger than 5 m and defined as overstory trees. Nomenclature followed Lauber & Wagner (2002).

Epiphytic lichens

In September 2002 lichen data were obtained for a subset of 38 plots sampled randomly from the 86 plots. Size of these plots was enlarged to 1 ha to enable a large enough tree-sample size. The *a priori* short-list of lichen species (Table 5) included both widespread, ubiquitous species and dispersal-limited species that had been previously proposed to indicate areas with undisturbed forest stands (Rose 1976, Nilsson et al. 1995). Where available, 6 *Picea abies* and 3 *Acer pseudoplatanus* with a minimum

diameter at breast height of 0.15 m were selected in fixed directions at random distance to centre, following Scheidegger et al. (2002). Presence of lichen species was determined within the reachable height (2.0 m) of these trees. Nomenclature followed that of Wirth (1995).

Environmental variables

Canopy cover history

The historical change in forest structure in an area of 1000 m² around the centre of each plot was assessed by a comparison of black-and-white aerial photographs of 1933 with panchromatic orthophotos of 1998 (SWISSIMAGE), all acquired from Swisstopo, the Swiss Federal Office of Topography. The photographs of 1933 were digitized, georeferenced, orthorectified, and mosaiced in IMAGINE OrthoBASE® 8.6 (Anonymous 2002), using a digital elevation model with a cell size of 25 m (DEM25, Swisstopo). For each plot the canopy changes during 1933 - 1998 were assessed visually: (i) decrease of canopy cover and/or tree density (N=4), (ii) no distinct changes (N=57), and (iii) increase of canopy cover and/or tree density (N=25).

Land-use history

Two management units were known to have been abandoned for cattle grazing since 1970 and 1954, respectively. The plots within these areas were defined as 'previously grazed plots' (see Figure 6). Present grazing within each plot, as additional environmental variable, was determined in the field: (i) presently grazed (N=22), (ii) previously grazed (N=11), and (iii) ungrazed (N=53).

Present tree cover, structure and density

LiDAR (Light Detection and Radar) data were used to assess tree density, canopy cover, mean tree height and standard deviation of tree height as a measure of heterogeneity of tree-height in a radius of 10 m around the centre of each plot. For details on the preparation and analysis of a digital vegetation model derived from LiDAR data, see Kalwij et al. (2005a; Submitted).

Data analysis

For the vascular plants, regional species richness was defined as the total number of plant species found in the 86 sites, and for lichens as the number species found in the subset of 38 sites. Local species richness was defined as the number of species per plot (Whittaker 1977) and species turnover (β -diversity) as the ratio between local and regional species richness (Harrison et al. 1992). Since species richness of plants and lichens were both normally distributed, Pearson's Product-Moment correlation coefficient was appropriate to determine the variation in understory plant and lichen species richness explained by the normally distributed overstory tree species richness and environmental variables (Legendre and Legendre 1998).

We used three different measures (beta-1, beta-2, and first axis of DCA) to assess gradient length and species turnover from species composition. The first two measures of species turnover were modifications of Whittaker's original beta ($S / \alpha - 1$), where S is defined as total number of species in the region, and α as average species richness. The original beta calculation was adapted to range between 0 (similarity) and 100

(dissimilarity) while taking total number of sites N into account (Harrison et al. 1992). Beta-1 is a quantification of the relationship between average and regional species richness: $\text{Beta-1} = (S / \alpha - 1) / (N - 1) * 100$. Beta-2 is a quantification of the relationship between maximum species richness and regional species richness: $\text{Beta-2} = (S / \alpha_{\max} - 1) / (N - 1) * 100$, where $\alpha_{\max}$ is the number of species at the most species-rich site (Harrison et al. 1992). A high species turnover is indicated by the difference between values of species richness and regional species richness. Binary presence data of species composition were used to calculate length of the first gradient axis of the detrended correspondence analysis for each dataset (Eilertsen et al. 1990). This gradient length was assessed in units of standard deviation of species turnover without downweighting of rare species (Okland 1999).

To compare species nestedness as a degree of order in species assemblages (Jonsson 2001), we used the matrix temperature (T-value) calculator (NESTCALC) of Atmar and Patterson (1995). A T-value of 0 indicates that a matrix is in complete nested order, while at a T-value of 100, no discernable order remains. Each dataset was transformed into a presence-absence matrix. To perform a Monte Carlo test of significance, T-value of each taxonomical group was compared to the T-value distribution of 1000 randomly generated matrices with a random species composition, but with similar number of species per site. T-values are presented in units of standard deviation from randomized matrices, instead of the actual T-value, to stress the relative degree of nestedness between the taxonomical groups (Atmar and Patterson 1995).

All environmental variables were related to patterns of species composition using canonical correspondence analysis (CCA) as a direct gradient analysis with CANOCO

(ter Braak and Smilauer 2002; no transformation or downweighting, unless stated otherwise) to partition variation explained by each variable and to construct a model of significant variables by using the forward selection option. A Monte Carlo randomization test with 1000 permutations was used to test the significance of each model including the next most important variable.

Results

Regional and local species richness

In total, 225 plant species were found in the 86 plots with an average species richness of 58.2 ± 1.1 (SE) for the understory plant species per site, and 3.3 ± 0.1 for the overstory tree species from the total of 5 species found. Of the *a priori* list of lichen species in the subset of 38 plots, the average species richness was 12.1 ± 0.4 per plot.

The understory plant species richness per site showed no correlation with the lichen species richness or with overstory tree species richness (Table 6). In contrast, a negative correlation with tree density and tree cover was found. Lichen species richness, on the other hand, was positively significantly correlated with the tree height heterogeneity *SD height*. The overstory tree species richness was negatively correlated with present grazing and positively correlated with the tree height variation. Neither mean tree height, nor local change in tree cover was significantly correlated to species richness of any of the distinguished species groups.

Species turnover

Since only 5 tree species were observed the smallest Beta-1, indicating a relatively high similarity among plots, was observed for the category of overstory tree species (Table 7). This category was, therefore, identified as the most uniform species group. The highest Beta-1 value was observed in the lichen category, which indicated that lichen plots were relatively dissimilar from each other. The same order from similarity to dissimilarity was found for the Beta-2 value, whereby the overstory tree species approached regional species richness best. Lichen species had the smallest spread along the first detrended correspondence analysis (DCA) axis (Table 7).

Species nestedness

The Monte Carlo tests of randomized species-by-site matrices showed that each species category had a high pattern of species nestedness (each category: 1000 permutations; $p < 0.001$). The degree of nestedness, however, differed between the categories; vascular plants of the understory showed highest relative nestedness with a T-value of 14.1 SD below average randomized T-value. Relative nestedness of lichen and overstory tree species was 11.2 SD and 9.9 SD below randomized T-values respectively.

Direct gradient analysis

Tree-structure related variables such as average tree-height, standard variation in tree-height, and tree density determined from LiDAR-data were the environmental variables that explained species richness best for vascular plants as well as for overstory

trees (Table 6). In contrast, none of these variables explained the variation in lichen species richness.

An ordination of the samples in two-dimensional space showed that understory plant-species composition could be explained by grazing history (Figure 7). The opposite was true, for the lichen or tree species composition, as no clear distinction was found that could be explained by land-use history. The canonical correspondence analysis revealed grazing as the second best predictor of species composition for the vascular plants of the understory, but this variable had no significant effect on lichen or tree species composition (Table 8).

Discussion

Out of the 554 species found by Vittoz (1998), we only found 225 vascular plant species in 86 plots. This is a reflection of our sampling design that included the forested areas of the study area only. Sites on shallow, bare, inundated, or otherwise aberrant soils were avoided. The average local species richness of 58.2 species per plot, however, is in accordance with Vittoz (1998). Since the species turnover of this taxonomical group suggests that edaphic variation between sites was relatively low, this gradient might be caused by past or present land-use.

Vascular understory plants, trees, and epiphytic lichens all showed a strong pattern of nestedness. Local species richness, however, could not be predicted by historical changes in forest-stand structure or present grazing. Only tree species richness was significantly explained by grazing, but even this correlation was weak. Present tree density, cover and height heterogeneity explained plant and lichen species richness, but

the strength of these correlations can only be considered as modest ($0.40 < r < 0.69$; Fowler et al. 1998). The correlation of plant species richness with tree cover and tree density could be explained by an increased local heterogeneity in light-availability of which both light-demanding and shade-tolerant species were able to profit (Halpern and Spies 1995).

The CCA ordination figures demonstrated the variation explained by each environmental variable (Figure 7). Samples of the vascular plants clustered by grazing history could be clearly distinguished. Sites in the two abandoned areas were relatively similar, which suggests that species characteristic for early successional stages of the forest vegetation were present, but that the whole range of forest species had not yet established. This observation was in agreement with Butaye et al. (2002), who found that 'old' forest-stands generally contain more slow dispersers than 'young' forest-stands and that distance of 'new' to 'old' forests is the main explaining variable. Since epiphytic lichens are more dependent on host tree availability than on edaphic conditions and grazing has an effect on tree species composition, we expected distinct clusters of lichens for past or present grazing. However, no clusters of lichen species could be related to grazing.

Grazing in a wooded pasture has a known negative effect on the establishment of tree saplings (Smit et al. 2005). The negative correlation between tree-species richness and grazing is explained by the absence of *Sorbus* species and *Abies alba* in the grazed areas. This latter is a highly palatable tree species that has been suggested as threatened in Switzerland due to increasing browsing intensity (Ott 1989), although comprehensive long-term studies on this subject do not yet exist (Senn and Suter 2003). Since our tree

dataset only contained two observations of *A. alba*, we were unable to perform a single species analysis.

Adding environmental data (e.g. dead wood biomass, tree-age structure) to our LiDAR derived forest-structure data may improve the interpretation of the observed nested subsets of species (Schaffers and Sýkora 2000). The data collection of such environmental data, however, is often time-consuming (Dupre et al. 2002) and to fully comprehend present species composition or richness more detailed knowledge on land-use history would be required. However, variation in species composition or richness is more likely to be caused by very local edaphic variation, present land-use, landscape connectivity (Jacquemyn et al. 2001a), or effects of local dispersal limitation (Ozinga et al. 2005). Therefore, neither vascular plants of the understory, nor epiphytic lichens could be considered as reliable indicators of former grazing or of history at a forest-stand scale.

In the present sampling design, the large amount of species and the combinations of historical and environmental variables hindered a reliable overall interpretation and explanation of species composition by land-use history. Although epiphytic lichen richness has been suggested as positively correlated to forest-stand age (Selva 1994, Kuusinen and Siitonen 1998, Boudreault et al. 2000), we were unable to find evidence that former grazing or a historic change in tree-canopy cover and/or density had such effect. An additional constraint of our design was the time spent for each sample plot (3-4 hours). Therefore, a single-species approach of an easy-recognizable epiphytic species might be a more accurate and time-efficient means to assess the spatial association with historical or present forest-stand disturbances. The epiphytic lichen *Lobaria pulmonaria* that is broadly assumed to be dispersal-limited seems to be a logical choice. However,

adoption of a single species as indicator should be preceded by thorough testing of the regional validity of the expected indication value (2005b).

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Table 5. *A priori* short-list of sampled lichen species.

Taxon	Host tree			
	<i>Picea</i>	<i>Abies</i>	<i>Acer</i>	<i>Fagus</i>
<i>Artonia leucopellea</i> ¹	x			
<i>Alectoria sarmentosa</i> ²	x	x		
<i>Bryoria capillaris</i> ²	x	x	x	x
<i>Bryoria implexa</i> ²	x	x	x	x
<i>Bryoria nadvornikiana</i> ²	x	x		
<i>Calicium abietinum</i> ²	x	x		
<i>Calicium viride</i> ²	x	x		
<i>Cetraria chlorophylla</i> ²	x			
<i>Chaenotheca chrysocephala</i> ²	x	x		
<i>Chaenotheca furfuracea</i> ³	x	x	x	x
<i>Cyphelium inquinans</i> ¹	x	x		
<i>Cyphelium karelicum</i> ¹	x	x		
<i>Evernia divaricata</i> ²	x	x		x
<i>Lecanactis abietina</i> ¹	x	x		
<i>Leptogium saturninum</i> ²			x	
<i>Lobaria pulmonaria</i> ¹			x	x
<i>Mycobilimbia sanguineoatra</i> ¹			x	
<i>Mycoblastus affinis</i> ¹		x		
<i>Mycoblastus sanguinarius</i> ¹	x	x		
<i>Nephroma bellum</i> ¹			x	
<i>Nephroma parile</i> ¹			x	
<i>Nephroma resupinatum</i> ¹			x	
<i>Parmelia submontana</i> ²			x	
<i>Parmelia sulcata</i> ³	x	x	x	x
<i>Parmeliella triptophylla</i> ¹	x	x	x	x
<i>Peltigera canina</i> ³			x	
<i>Peltigera leucophlebia</i> ²			x	
<i>Peltigera membranacea</i> ³			x	
<i>Ramalina farinacea</i> ³	x	x		
<i>Ramalina fraxinea</i> ³	x	x		
<i>Usnea cavernosa</i> ²	x	x		
<i>Usnea filipendula</i> ²	x	x	x	x
<i>Usnea prostrata</i> ²	x	x	x	x

¹ old-growth related (stand level)² autochthonous tree cover³ ubiquitous

Table 6. Pearson correlations between plant, lichen and tree species richness S and the environmental variables present grazing *Grazing*, forest-stand history *Loc.cov.dn*, (decrease, no change, or increase of tree density and/or cover between 1933 and 1998), and LiDAR-derived present tree cover *Tree cover*, tree density *Tree density*, tree height *Mean height* and variation in height *SD height*, all in a 10 m radius from each plot centre.

	N	S lichens	S trees	Grazing	Loc.cov.dn	Tree density	Tree cover	Mean height	SD Height
S plant species	86	-0.077	-0.009	0.196	0.183	-0.275 *	-0.243 *	-0.125	0.061
S lichen species	38		0.514 ***	0.087	0.070	0.000	0.122	0.249	0.357 *
S tree species	86			-0.309 ***	-0.114	0.024	0.025	0.189	0.341 **
Grazing	86				0.436 ***	-0.024	0.294 ***	0.101	-0.324 ***
Local cover change	86					-0.059	0.327 **	0.084	-0.094
Tree density	86						0.278 **	-0.360 ***	-0.225 *
Tree cover	86							0.428 ***	-0.237 *
Mean height	86								0.246 *

* Correlation is significant at the 0.05 level (2-tailed).
 ** Correlation is significant at the 0.01 level (2-tailed).
 *** Correlation is significant at the 0.001 level (2-tailed).

Table 7. Measure of species turnover for vascular understory plants, lichens and overstory tree species, and the difference of observed T-values from randomization as a measure of species nestedness in units of standard deviation. T-values are presented in units of standard deviation from randomized matrices to stress the relative degree of nestedness between the taxonomical groups

	<i>Plants</i>	<i>Lichens</i>	<i>Trees</i>
Beta-1	3.38	4.44	1.29
Beta-2	1.58	2.38	0.47
Length 1 st DCA gradient	2.087	1.865	2.510
T-values (SD)	-14.1	-11.2	-9.9

Table 8. A comparison of the models of the best environmental predictors of understory plant, lichen and overstory tree-species composition. Lambda-A λ gives the additional variance explained by each variable as it was included in the model. Variables were entered into the model with the forward selection procedure and rank lists the order of the variance that each variable explains (categorical variables: Present grazing *Pres_gra*, Past grazing *Aban_gra*, forest-stand history *Loc.can.cov.* (decrease, no change, or increase of tree density and/or cover between 1933 and 1998), LiDAR derived variables of present tree cover *Tree_cov*, tree density *Tree density*, tree height *Height_m* and variation in height *height_s*).

	Plants			Lichens			Trees		
	λ	<i>F</i>	<i>Rank</i>	λ	<i>F</i>	<i>Rank</i>	λ	<i>F</i>	<i>Rank</i>
Pres_gra	0.11	3.49	2 ***	0.07	2.04	7 *	0.05	1.69	4
Height_m	0.09	2.76	4 ***	0.06	1.73	3	0.05	1.71	3
Loc.can.cov.	0.06	2.08	1 ***	0.05	1.50	5	0.04	1.41	7
Tree density	0.06	2.09	6 ***	0.05	1.43	2	0.08	2.97	6 *
Aban_gra	0.05	1.63	3 **	0.06	1.88	6 *	0.05	1.79	1
height_s	0.03	1.03	5	0.04	1.22	4	0.03	1.10	2
Tree_cov	0.03	0.97	7	0.02	0.73	1	0.02	0.80	5

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

List of figures:

Figure 6. Overview of plot locations and land use within the study area, and position of the Parc Jurassien Vaudois in Switzerland.

Figure 7. Canonical correspondence analysis of the sample plots for the three groups.

Label symbols of plots indicate local grazing-history. Clusters are outlined according to local grazing-history.

Figure 6

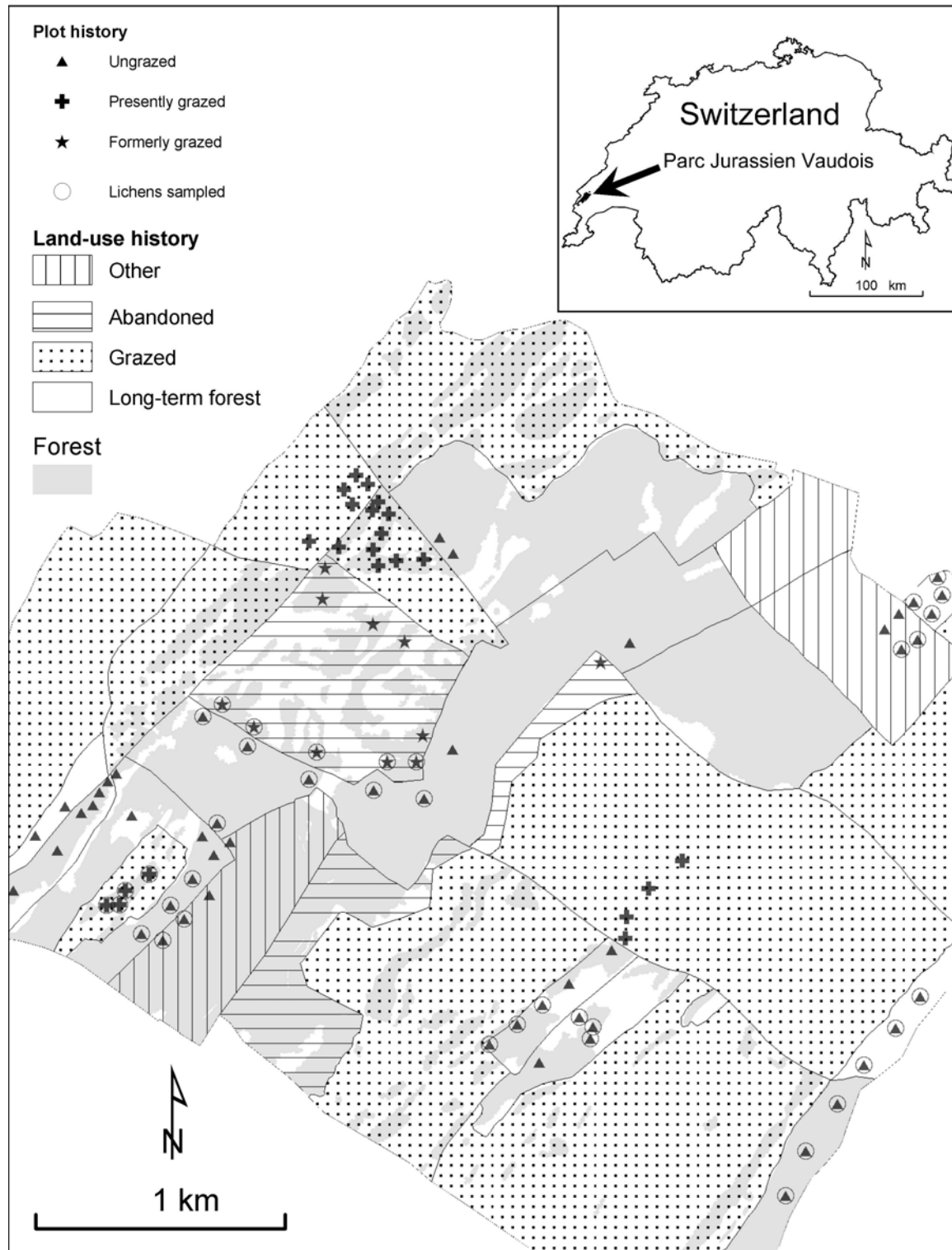
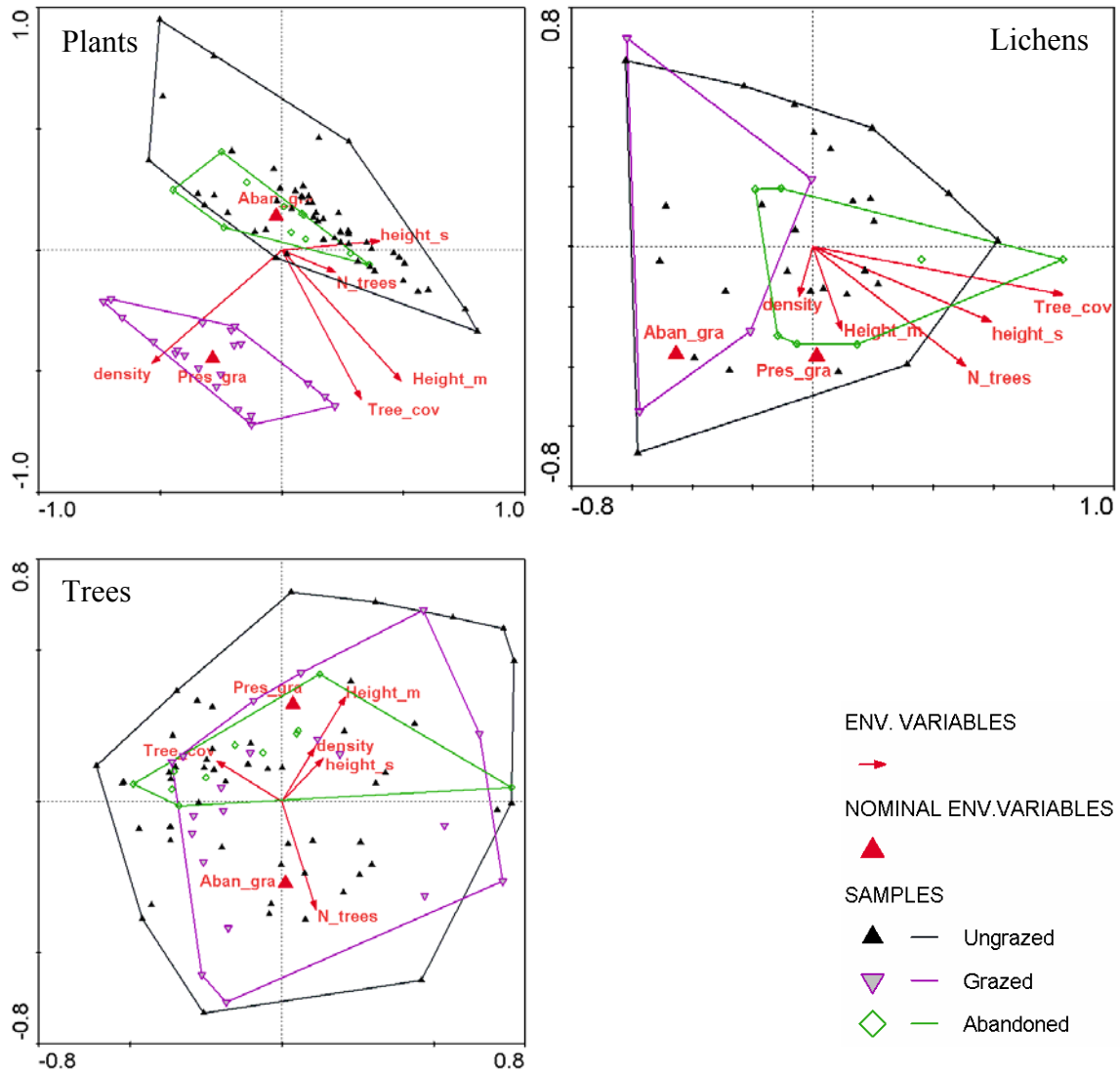


Figure 7



Chapter 3

Title of the paper: Effects of stand-level disturbance events on the spatial distribution of a lichen indicator of forest conservation value

Authors: J. M. Kalwij, H. H. Wagner, and C. Scheidegger

Running head: Evaluation of a conservation indicator

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Abstract:

The epiphytic lichen *Lobaria pulmonaria* is, due to its assumed dispersal limitation and susceptibility to disturbance, 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 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 to prevent possible misinterpretation of ecological processes that the indicator aims to unravel.

Key words: indicator; *Lobaria pulmonaria*; ecological continuity; epiphytic lichen; *Acer pseudoplatanus*; 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 which 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 population to the level prior to the disturbance than it would for the habitat. 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 (Kuusinen 1996; McCune et al. 2000; Rose 1976; Rose 1992),

forest connectivity (Esseen & 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 & Appelqvist 2001; Rolstad et al. 2002) criticizing the lack of operational definitions, 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 & 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.

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 (Gauslaa 1994; Kuusinen 1996; Lesica et al. 1991; Rose 1976; Selva 1994; 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 around 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 et al. 2001; Gauslaa & Solhaug 1996). However, a transplantation experiment by Hazell & 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 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 association 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 (Figure 8a). 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). Circular non-overlapping plots of 1 ha (N=251) were positioned randomly within the forest area of the

study area (Figure 8a). 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). *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 dataset consisted of first returns; representing maximum height with vegetation (approx. 10000 points / ha). The second, filtered dataset consisted of returns representing height of terrain without vegetation, i.e. where vegetation was sparse enough 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 (Anonymous 2002b). 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 1.5m 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 of 1933 were digitized, georeferenced and orthorectified in IMAGINE OrthoBASE® 8.6 (Anonymous 2002a), 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 ha-plot the canopy changes during 1933 - 1998 were assessed visually: (i) decrease of canopy cover and/or tree density (N=41), (ii) no distinct changes (N=147), and (iii) 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 (Figure 8): (i) intensive logging between 1850 and 1900 for charcoal production (Pichon, Swiss Forestry Service, pers.comm.), and (ii) intensive logging in 1870, followed by wind throw and, in the following year, a two-week fire (Rochat 1995). The perimeters of the areas 'Charcoal 1850-1900' (approx. 36 ha) and 'Logged & burnt 1871' (approx. 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 (Bolli et al., submitted). 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 & Renhorn 1998; Harper & 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 & Gallandat 1996), the perimeters of presently grazed areas were mapped. Plots that had more than 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 non-spatial analyses were performed in SPSS 12.0 (Anonymous 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 arcsin 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 (arcsin-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 (arcsin square-root transformed) per DBH class and plot was tested in separate two-way ANOVAs, 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 average 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_{obs}/D_{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 I , the more spatially aggregated is the observed arrangement of counts. For each plot, the following clustering indices were calculated: (i) I_A for the total number of sycamore maples per plot, (ii) I_L for the number of colonized sycamore maples, and (iii) 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 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 & 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 significance level of $\alpha=0.05$, where the observed v_i were permuted amongst 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 (8.6% colonized), compared to beech (0.4% colonized; Table 9). The three one-way ANOVAs showed a significant effect of disturbance category on host tree density f_A ($F = 7.42$; $df = 3, 247$; $p\text{-value} < 0.001$), on density of *L. pulmonaria* trees f_L ($F = 8.34$; $df = 3, 247$; $p\text{-value} < 0.001$), and on colonization proportion p_L ($F = 6.35$; $df = 3, 247$; $p\text{-value} < 0.001$). 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 10). 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 (Figure 9, left column).

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 10). Colonization proportion p_L increased considerably with increasing DBH (Figure 9, center column).

Spatial aggregation

At the tree level, a three-way ANOVA of the nearest neighbor distance NN 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 non significant (Table 10, bottom). Colonized trees were located much closer to their nearest colonized neighbor than uncolonized trees (Figure 9, right column).

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 11). 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* (Figure 8b). 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. 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 & O'Doherty 1999) of affected species. We can only interpret the present distribution of *L. pulmonaria*, and explain why this species is absent 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 had such high impact on the abundance of sycamore maple in grazed areas that potential host trees were observed in very low densities only. Conversely, our distribution data showed that stand-level disturbances led to high densities of sycamore maples (Table 9), irrespective of present tree cover (Table 10). Significantly 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 of the proportion of colonized trees p_L with DBH class suggest. A similar effect was described for *L. pulmonaria* on aspen (Kuusinen 1996) and for other epiphytic species (Hazell et al. 1998; Rolstad & Rolstad 1999). This could be explained by a combination of potential causes. Growth of *L. pulmonaria* is slow in Switzerland (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 & 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 (Figure 9), indicating a dynamic system with continuous dispersal and

colonization (Johansson & 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* (Figure 8) even suggested that the opposite may be true, although such a trend was not significant (Table 11). 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 especially the intermediate DBH classes (Figure 9), 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 (Figure 9), 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 (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 (Figure 9), suggesting that these trees were relatively 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 (Bolli, unpublished) revealed that at least one host tree on a hill in the centre 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 & 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 (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 (Figure 9), fell in line with the concept of ecological continuity (Norden & Appelqvist 2001), the tendency for positive spatial association of *L.*

pulmonaria with stand-level disturbance events (Figure 8 and Table 11) 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 (Figure 8). 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 for 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 late-successional stages or absence of disturbance 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 influences (Vittoz 1998). We did so to investigate potentially persisting effects of disturbance events at defined spatial and temporal scales following the critique of Rolstad et al. (2002) and Norden & 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 undefined forest stands from different regions (Boudreault et al. 2000; Rose 1976) or different countries (Gaio-Oliveira et al. 2004) were compared. However, our stand-level disturbance events (approx. 31 and 36 ha respectively) were large enough to conform with the minimum

forest stand size of 0.1-30 ha (Esseen & Renhorn 1998; Hazell & Gustafsson 1999; Norden & 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 (Hazell & Gustafsson 1999; Renhorn et al. 1997). 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 11). 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 10). 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 quantified the operational definitions on the concept of ecological continuity, as suggested by Rolstad et al. (2002) and Norden & 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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Table 9. Average tree f_A and lichen density f_L per disturbance category ($\pm$ standard error). Different letters indicate significant pairwise differences for sycamore maple 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; p_L : arcsin of square root). N is the number of plots per disturbance category.

	N	Trees (n/ha) f_A	<i>Lobaria</i> (n/ha) f_L	Colonized (%) p_L
Sycamore maple				
Undisturbed	164	18.7 $\pm$ 1.6a	3.1 $\pm$ 0.5a	8.6 $\pm$ 1.3 a
Grazed	42	4.7 $\pm$ 1.6b	0.4 $\pm$ 0.2b	2.8 $\pm$ 1.3 b
Charcoal	24	93.1 $\pm$ 5.9c	11.4 $\pm$ 4.2c	10.5 $\pm$ 3.0 c
Logged/burnt	21	26.7 $\pm$ 3.1d	5.0 $\pm$ 0.5c	19.0 $\pm$ 4.0 c
Total	251	24.1 $\pm$ 1.9	3.6 $\pm$ 0.6	8.6 $\pm$ 1.0
Beech				
Undisturbed	164	7.6 $\pm$ 0.9	0.1 $\pm$ 0.0	0.3 $\pm$ 0.1
Grazed	42	2.0 $\pm$ 0.6	0.0 $\pm$ 0.0	0.3 $\pm$ 0.3
Charcoal	24	7.7 $\pm$ 2.3	0.0 $\pm$ 0.0	0.7 $\pm$ 0.7
Logged/burnt	21	9.3 $\pm$ 1.4	0.1 $\pm$ 0.1	0.6 $\pm$ 0.5
Total	251	6.8 $\pm$ 0.7	0.1 $\pm$ 0.0	0.4 $\pm$ 0.1

Table 10. Results of two-way ANOVAs of f_A (top) and p_L (center) as dependent on disturbance category and DBH class, and of a three-way ANOVA of NN distance (bottom) as dependent on disturbance category, DBH class and presence of *Lobaria pulmonaria*. Models were corrected for unequal sample sizes.

	SS	df	F	<i>p</i>
Host tree density				
Model	753.7	22	34.26	0.000
Intercept	114.3	1	124.40	0.000
Present tree cover	0.4	1	0.48	0.490
Disturbance	271.4	3	98.44	0.000
DBH	197.0	5	42.88	0.000
Disturbance x DBH	144.6	13	11.13	0.000
Error	736.9	802		
Total	6056.0	825		
Colonized proportion				
Model	25.2	22	6.16	0.000
Intercept	0.6	1	3.27	0.071
Present tree cover	0.2	1	1.20	0.275
Disturbance	3.4	3	6.15	0.000
DBH	7.4	5	7.98	0.000
Disturbance x DBH	3.1	13	1.27	0.227
Error	90.9	489		
Total	204.8	512		
NN distance				
Model	426.7	35	8.38	0.000
Intercept	1671.8	1	1148.73	0.000
Disturbance	3.7	3	0.84	0.474
DBH	3.6	5	0.49	0.782
<i>Lobaria</i>	119.1	1	81.84	0.000
Disturbance x DBH	11.6	11	0.73	0.715
Disturbance x <i>Lobaria</i>	1.7	2	0.58	0.560
DBH x <i>Lobaria</i>	12.5	5	1.72	0.128
Disturbance x DBH x <i>Lobaria</i>	5.6	8	0.48	0.869
Total	26804.4	1911		

Table 11. Spatial analysis by distance indices (SADIE) of the occurrence of sycamore maple and *L. pulmonaria* in 251 circular 1-ha plots. The overall association between two variables is χ . Significant values ($p < 0.05$) are marked by an asterisk (*).

	Overall association χ					Index of aggregation I
	I_A	I_L	I_D	I_-	I_0	
Sycamore maple I_A	1					2.10*
<i>Lobaria</i> I_L	0.69*	1				1.79*
Disturbance I_D	0.46*	0.20	1			3.28*
Local decrease I_-	- 0.31*	- 0.44*	- 0.23*	1		1.51*
No local change I_0	- 0.24*	- 0.13	- 0.49*	- 0.12	1	1.99*
Local increase I_+	0.34*	0.28*	0.66*	- 0.42*	- 0.62*	2.17*

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Figure 8. Sample plots in the 'Parc Jurassien Vaudois', and interpolated distribution of *Lobaria pulmonaria* (Pixelmap 25 © 2004 Swisstopo (Kalwij DV236)).

Figure 9. Sycamore maple density f_A , colonization proportion p_L of *Lobaria pulmonaria*, and nearest colonized neighbor (NN) for colonized and uncolonized host trees, per DBH class. Each bar shows the sycamore maple density f_A (n/ha), the proportion of colonized host trees p_L (%), or compares the average distance to the nearest colonized neighbor for colonized and uncolonized host trees (m), for each DBH class and disturbance category ($\pm 2se$). The figure shows the untransformed values for ease of interpretation, whereas the significance tests as presented in Table 10 were based on the transformed values.

Figure 8.

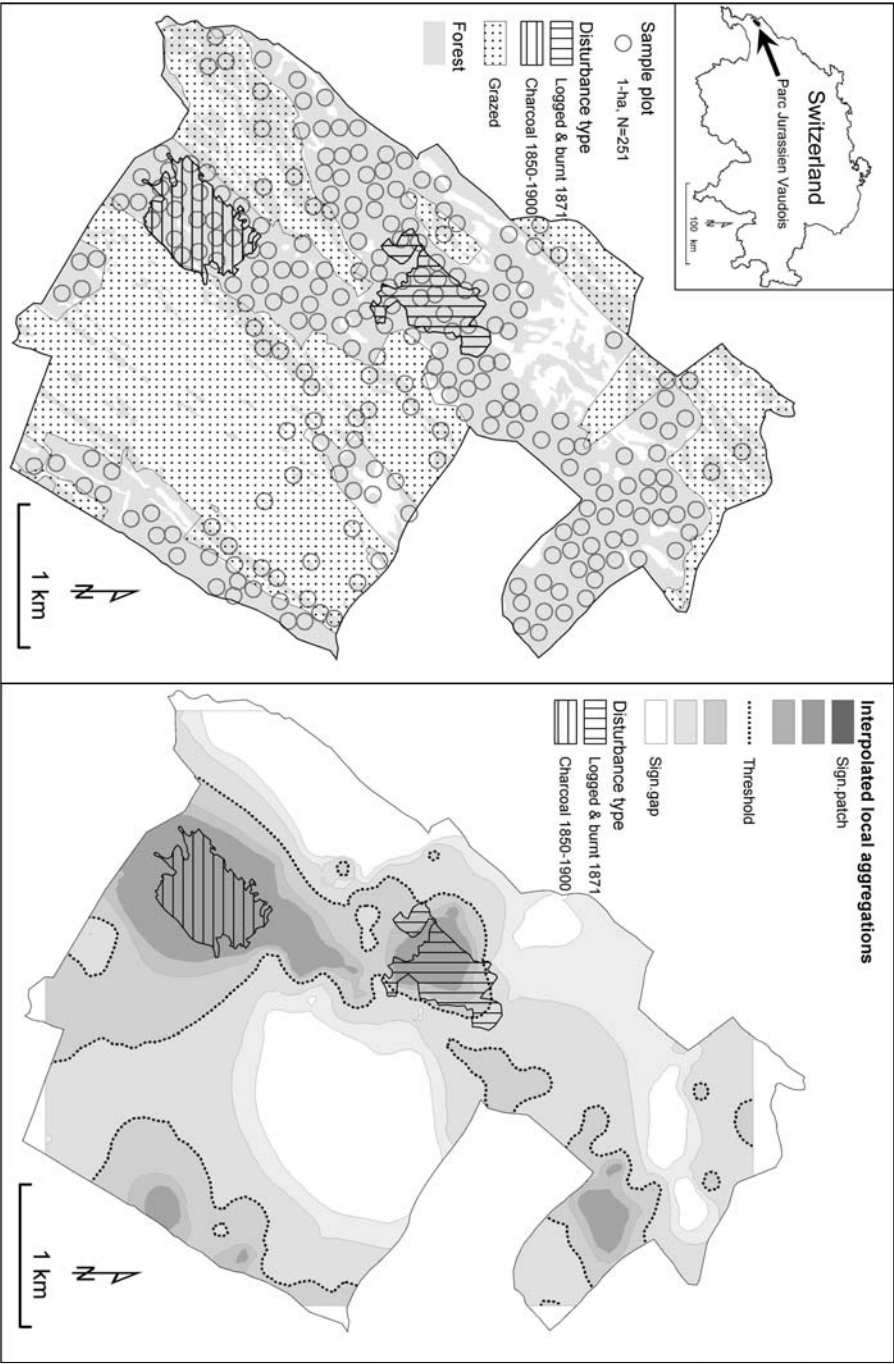
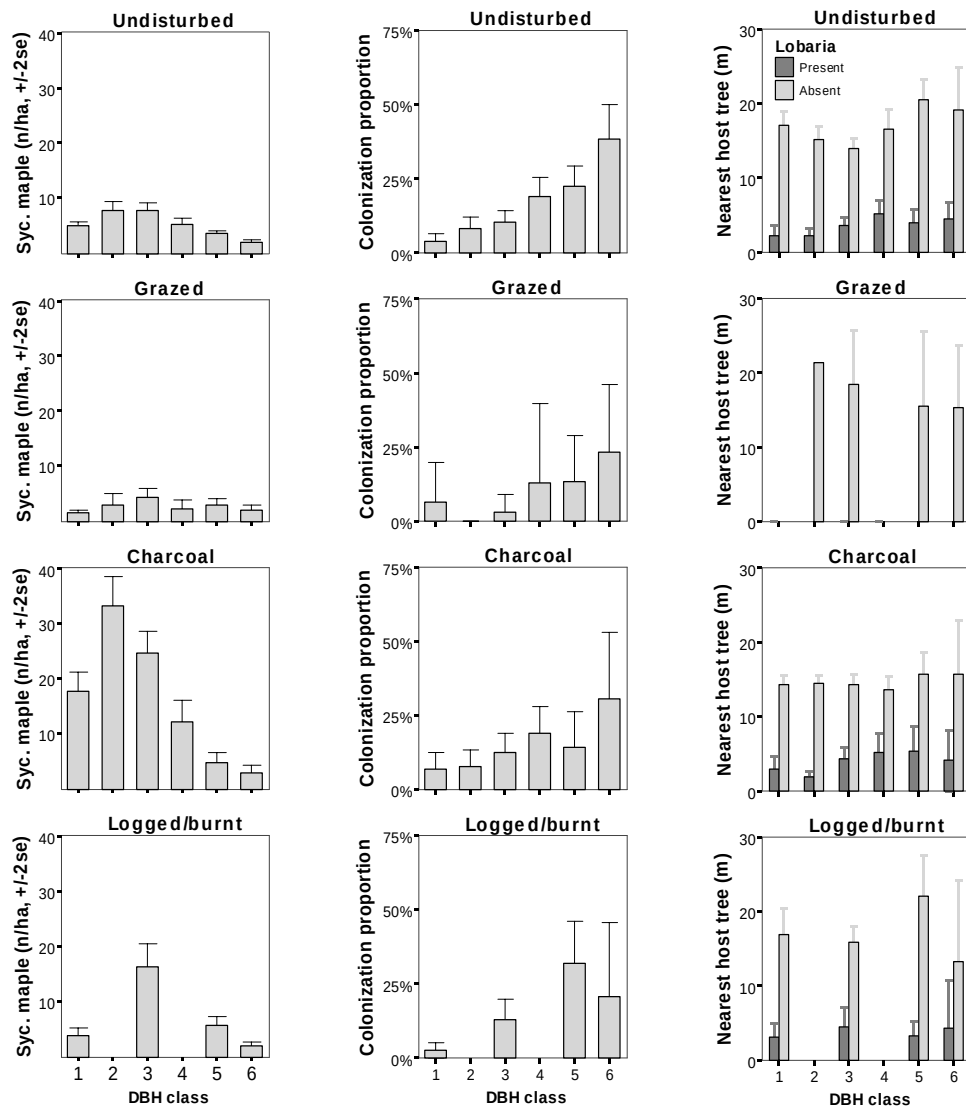


Figure 9.



Summary

The spatial extent of wooded pastures in a sylvopastoral landscape is traditionally small, resulting in a mosaic of disturbances and a variety of ecological niches in close distance to one another. Being regularly disturbed by cattle grazing, forest management and occasionally by fire or windfall, dispersal-limited species are assumed to have a clustered distribution that is associated with undisturbed areas of such a landscape. In the Swiss 'Parc Jurassien Vaudois', this assumption is apparently supported by high local abundances of the epiphytic lichen *Lobaria pulmonaria*, a suggested indicator of forests with a high 'ecological continuity' (i.e., long-term undisturbed, old-growth forests). The guiding hypothesis was that land-use types permit different forest dynamics across spatial and temporal scales, which affects tree dependant species such as epiphytic lichens, so that such taxa can be used to indicate the time since and intensity of disturbance. This hypothesis was examined by: (i) quantifying spatial patterns of tree distribution at a landscape scale, (ii) comparing correlations of different taxonomic groups with stand history, and (iii) testing *L. pulmonaria* as an indicator of absence of disturbance.

Spatial patterns of tree distribution and land-use history were quantified from aerial photographs (1933-2000) and field data to explain the spatial and temporal impact of land use on landscape structure, forest dynamics and *L. pulmonaria*. Spatio-temporal patterns of forest dynamics were quantified from aerial photographs and LiDAR.

Potential indicator taxa (understory vascular plants, trees and epiphytic lichens) were correlated with land use history: a combination of 1933 -1998 aerial photograph interpretation, forest structure derived from LiDAR, and historical records. Although

each indicator taxon had a strong pattern of species subset nestedness, no reliable correlations with forest-stand history were found.

Contrary to our expectation, a spatial analysis showed that, *L. pulmonaria* was positively associated with the stand-level disturbances. No evidence was found that abandonment of a wooded pasture would lead to the disappearance of dispersal-limited species or decline in species diversity. In addition we showed that application of an indicator species without a thorough verification of the association with the variable of interest could lead to misinterpretation of the ecological processes.

Appendix A: Internet protocol for single aerial photograph orthorectification

How to create orthophotos with Erdas Imagine Orthobase 8.5.1, using a single image (or more), a vertical and a horizontal reference file, in less than 20 minutes

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WSL, Switzerland

This document gives a routine for creating orthophotos and deals with some practical problems that can be encountered using ArcGIS and OrthoBASE. This protocol describes each step (and their potential pitfalls) regarding data preparation and orthorectification in detail. When both reference files are available and prepared properly, a single aerial photograph can be accurately orthorectified in less than 20 minutes.

Step 1	Preparing the horizontal and vertical reference files
Step 2	Estimating a camera calibration report
Step 3	Georeference the aerial photographs
Options	Orthorectification using external parameters of orientation

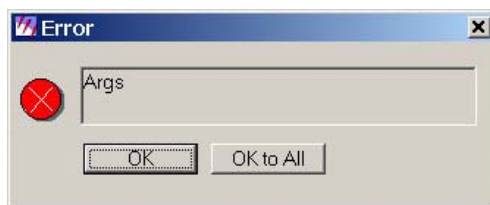
Note

This protocol has not been especially written for general application. Although thoroughly tested, the user must check for each step whether it is the appropriate one, giving the result desired, when applied to other datasets (with different properties). Any remarks or suggestion to improve this protocol are highly appreciated.

Preparing the horizontal and vertical reference files for Erdas Imagine Orthobase 8.5.1

Introduction

This document deals with some practical problems that were encountered when preparing the reference files for [georeferencing](#) some 1933 aerial photographs (AP). Although the import and export routines of ArcCatalogue and Erdas Imagine suggest a smooth compatibility between the two packages, this is not entirely the case. The problems and their solutions described are partially a result of incompatibility of (Swiss) projections between the Erdas Imagine and the ESRI ArcGIS software packages. The incompatibility is characterized by the error message ‘Args’ (meaning that some argumentation is wrong somewhere).



Material used:

1. SWISSIMAGE, colour Orthophoto mosaic of Switzerland (swisstopo DV023184)
2. Digital Elevation Model DHM25 (swisstopo DV455)

Software used:

1. ArcGIS 8.3
2. Erdas Imagine 8.5

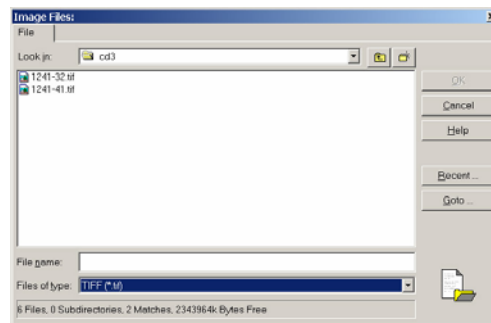
Erdas/ArcGIS file exchange

In order to reliably georeference APs, a horizontal reference (e.g. [orthophotos](#), [digitized topographical maps](#), or [vector data](#)) and a vertical reference ([DEM](#)) are recommended. These reference files are usually optimized for ArcGIS, and file format may be a problem when applied in the Erdas Imagine package. Some data sets are too large to be easily handled and some clipping in ArcMap may be required to prepare a manageable data set.

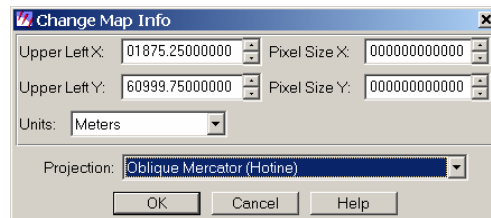
Horizontal reference: Orthophoto

The colour orthophoto mosaic of Switzerland can be bought from the [Swiss Federal Office of Topography](#) (swisstopo). The images are provided in uncompressed TIFF format (JPEG is also accepted and convenient for data storage, but the pyramid-files tend to become large which slows down the editing process). This format does not give any problems in Erdas, but some image information needs to be changed with the main Erdas task bar:

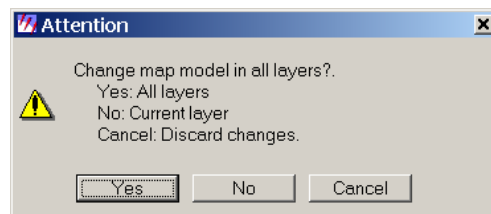
- Click **Tools, Image information**, a blank ImageInfo tablet pops up.
- Open the folder in which the TIFF files are located and select the file. Don't forget to change the file selection option to TIFF files and disable the 'Read only'-option, in case you have copied the files from a CD-ROM.



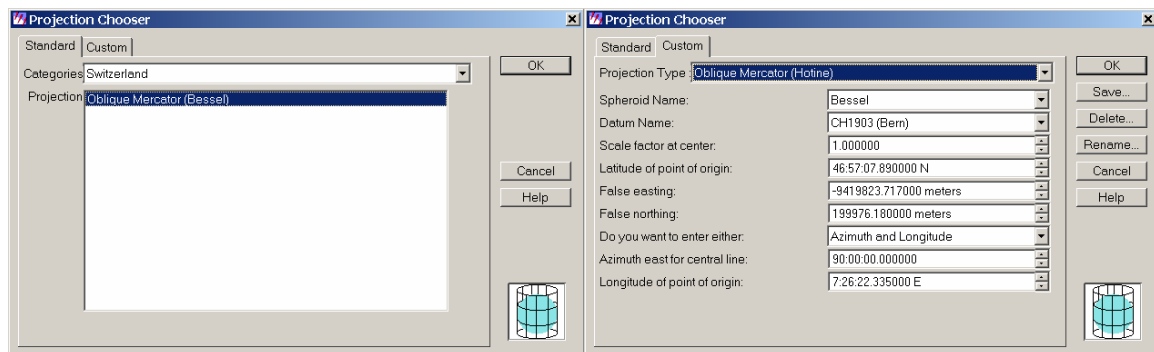
- click **Edit, Change map model**, and change the map **units** and **projection** to as shown below. The information Upper X, Y and pixel size is already provided by the TFW-file:



- click **OK**, to confirm the changes you made



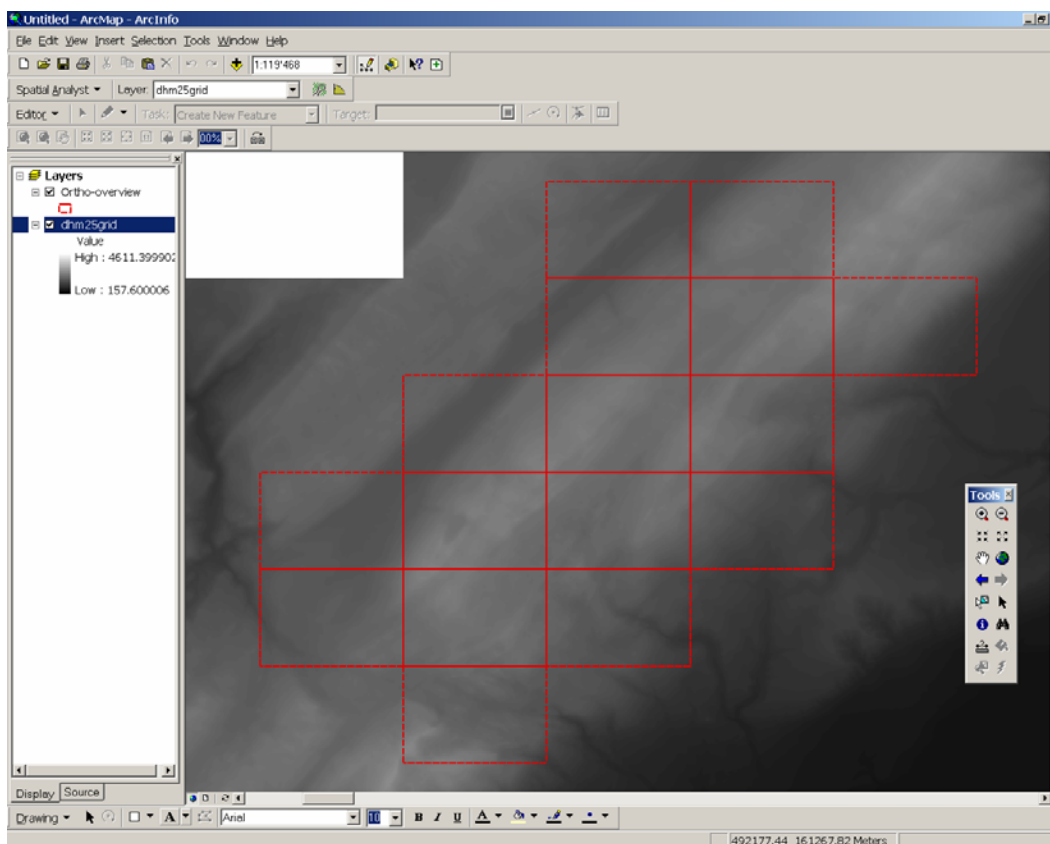
The adapted TIFF file should be ready now for horizontal reference usage.



Vertical reference: DEM

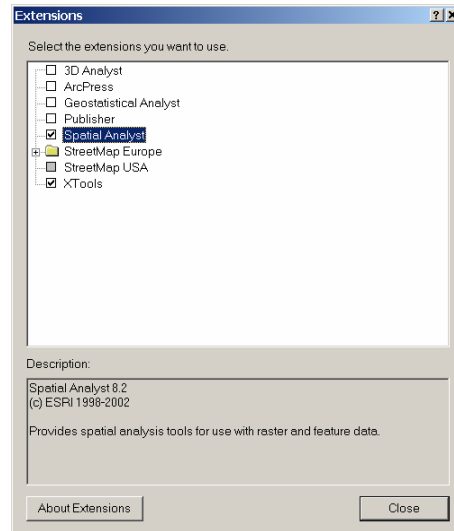
Of course, if a vertical reference file is unavailable, the height of each X,Y position can be estimated by using a topographical map, but this is time-consuming, susceptible of errors and relatively inaccurate.

The complete DEM of Switzerland can be bought from the [Swiss Federal Office of Topography](http://www.swisstopo.ch) (swisstopo). The DEM is a GRID-file called **dhm25grid**, with a cell size of 25x25 meter. The file is too large to handle, so it was clipped using a polygon layer. This layer is the area of interest (called *Ortho-overview* in the example below) and gives an overview of the location of the horizontal reference images that were used to orthorectify my aerial photographs. Note that the extend of the DEM to be clipped should ideally be widely defined.

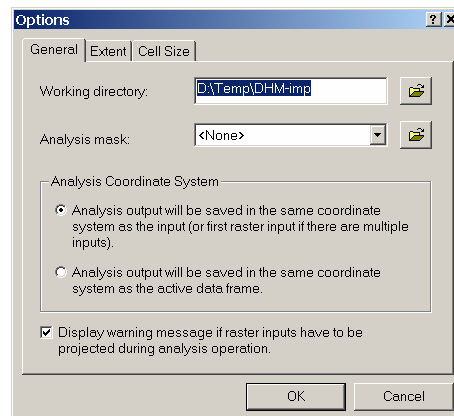


Make sure that the complete spatial analyst extension is enabled:

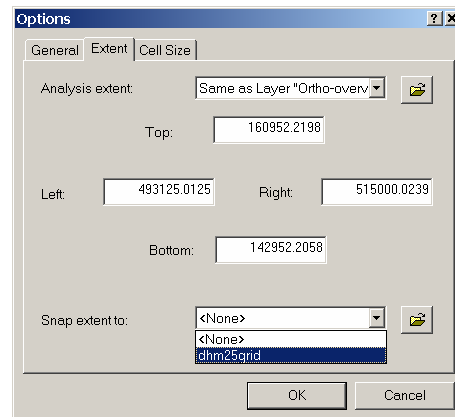
- click **Tools, Extensions, enable ‘Spatial analyst’ and Close**



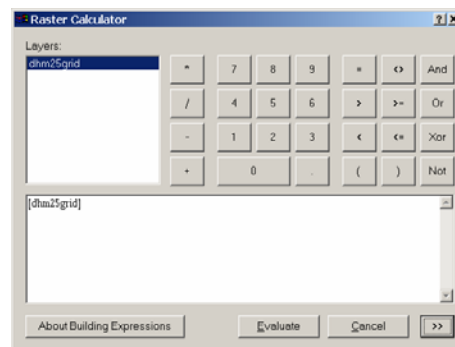
- limit the size of the DEM in **Spatial Analyst, Options**, and select a **working directory**



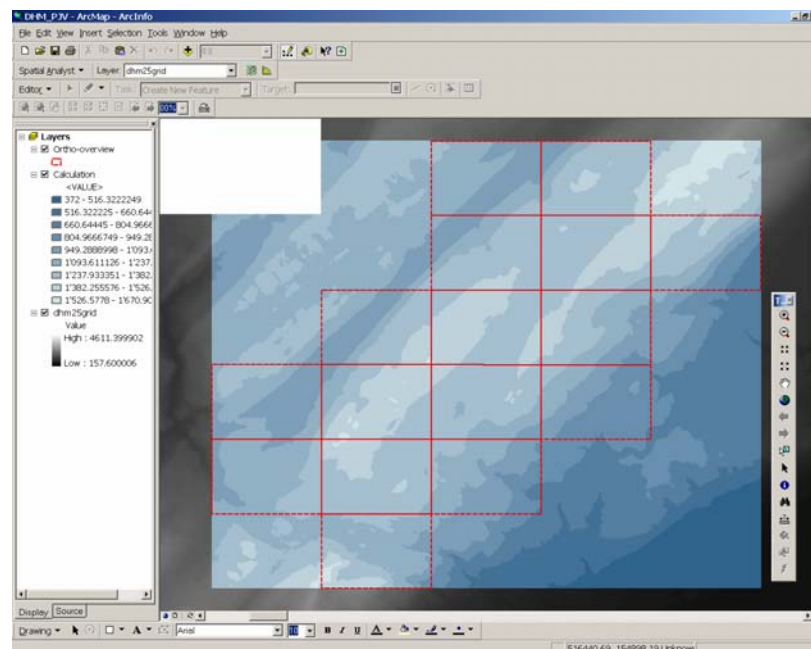
- click **Extent, same as layer “layer-name”, Snap extent to grid** (if this is not done, the grid cells may shift), the Analysis extent now changes to ‘As specified below’ and **OK**



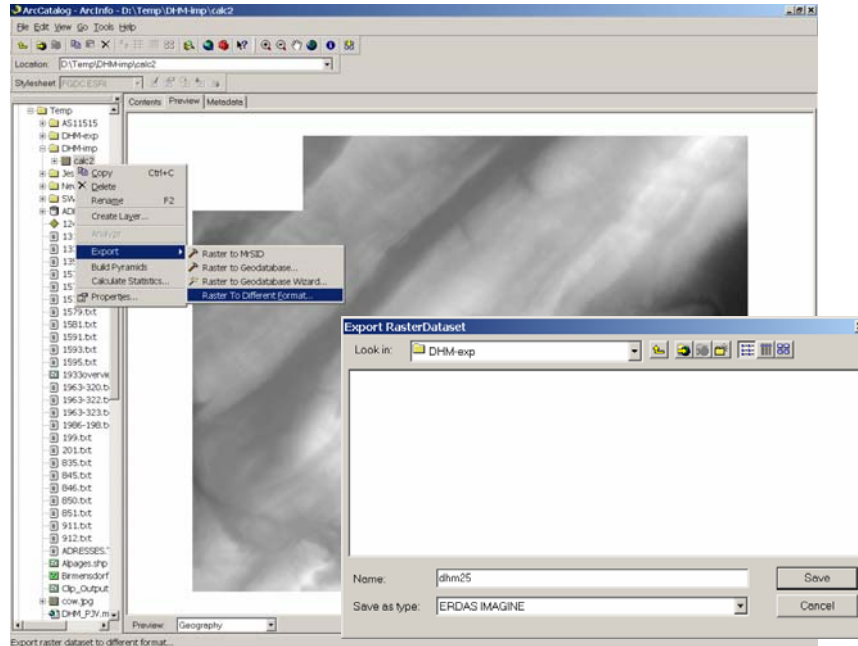
- click **Spatial Analyst, Raster calculator**, select the layer (DHM25 in this case) and **Evaluate**. Spatial analyst starts to calculate now, but doesn't change any values. What in fact happens, is that each cell is copied (evaluated) into a new layer.



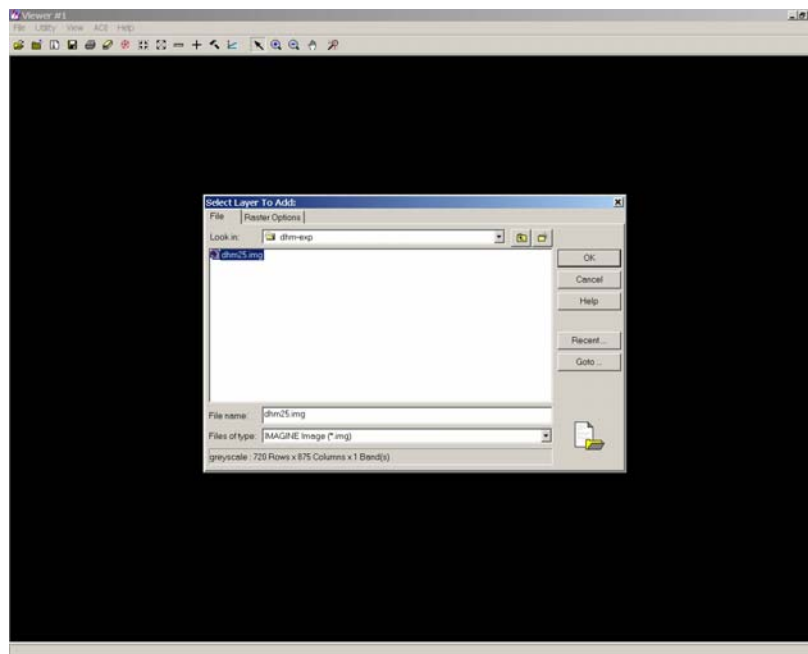
The result of the evaluation is added automatically in a new layer called 'Calculation'



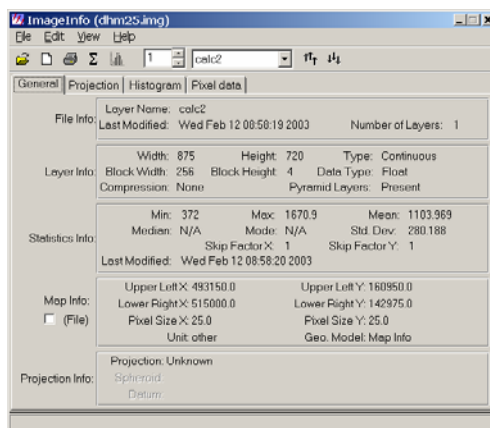
- open ArcCatalogue, select the layer that you have created in Spatial Analyst and confirm this by looking at the preview. Click the alternate (right) mouse button, **Export** and **Raster to different format**. Do not forget to change the file type to **ERDAS IMAGINE**. Save the new .img-file in a new directory to avoid confusion:



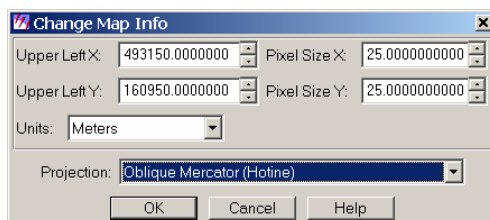
The file that has been created still needs to have a projection defined before it can be used as vertical reference. Open the viewer in Erdas Imagine and add the newly created image file.



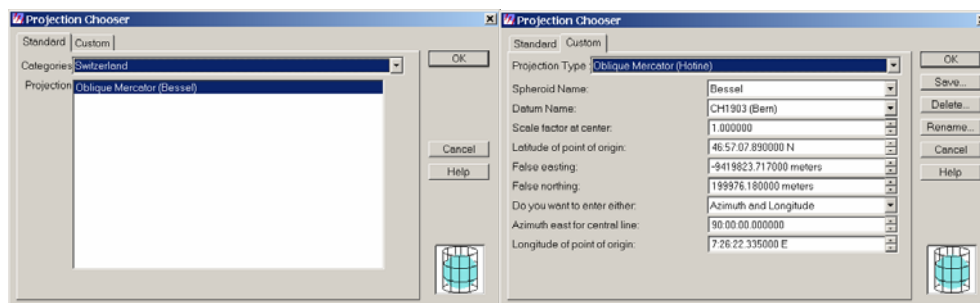
- in the viewer, open the layer information sheet by clicking **Utility, Layer info**



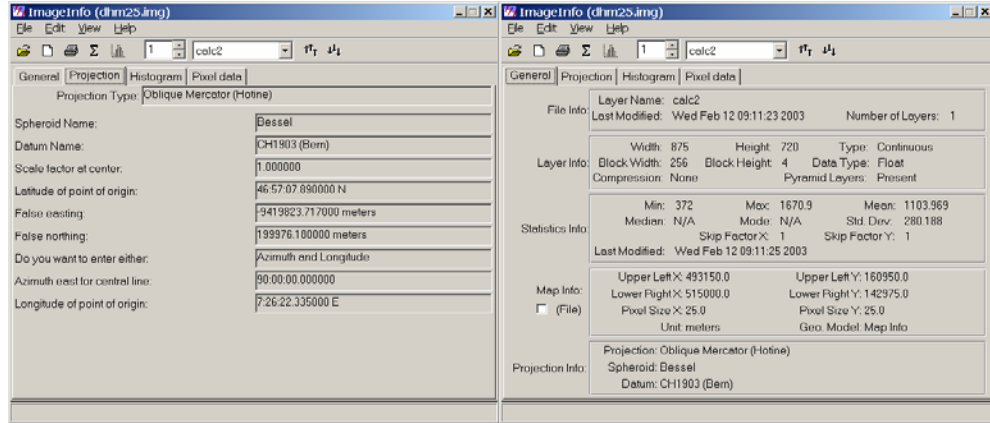
- define the units of the image by clicking **Edit, change map model**. Change units into meters and the projection into [Oblique Mercator \(Hotine\)](#). Click **OK**, then **Yes** to confirm your changes.



- after the model has been changed, the projection, spheroid and datum have to be defined by clicking **Edit, Add/Change projection** and choose projection **Oblique Mercator (Bessel)** for **Switzerland** in the standard tab sheet. You will notice that the information in the 'Custom' tab sheet has changed accordingly. Click OK to apply the changes



The Imageinfo for this example DEM is now as follows:



- confirm the height values by comparing the pixel data sheets for both the original DEM as well as for the newly created and adapted DHM25.img. The cell position of a measured XY-position (506250/158000) can be determined by using these formulas:

$$n_{column} = \frac{x_{measured} - x_{upper_left}}{x_{cell}}$$

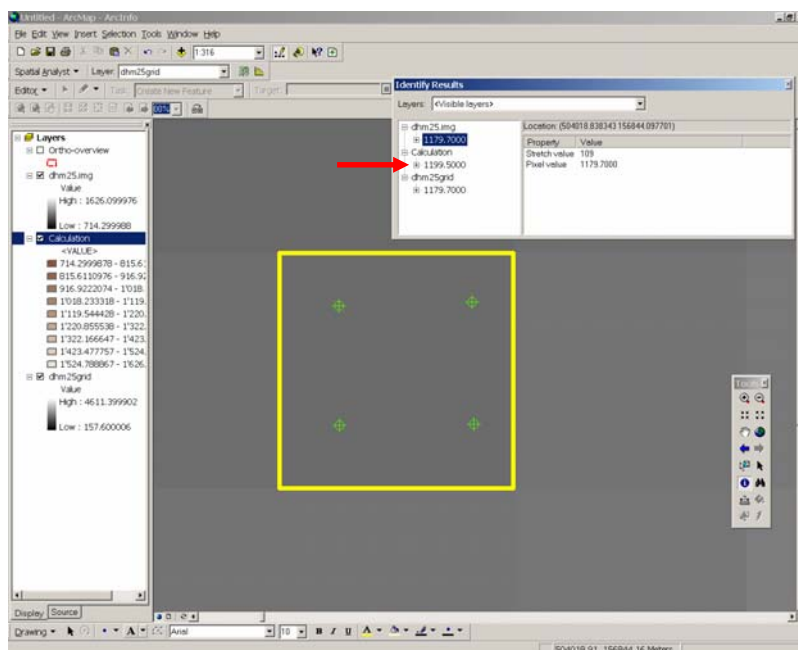
$$n_{row} = height - \frac{y_{measured} - y_{lower_right}}{y_{cell}} - 1$$

As you can see in the pixel data sheets for the original DEM (dhm25grid) and the DEM from the spatial analyst extension (dhm25.img), no change in values has occurred.

Row	522	523	524	525	526	527	528
114	1207.100	1209.700	1292.900	1295.600	1298.700	1301.600	1304.700
115	1289.600	1292.000	1294.700	1296.900	1299.400	1301.100	1303.600
116	1291.300	1294.000	1296.100	1297.700	1299.600	1300.800	1303.100
117	1293.700	1295.400	1296.300	1297.500	1299.500	1299.900	1302.100
118	1295.100	1295.800	1296.200	1298.000	1299.500	1301.100	1303.600
119	1295.900	1296.700	1297.500	1299.300	1301.000	1302.800	1304.700
120	1297.100	1298.000	1299.100	1301.400	1303.900	1305.100	1306.600
121	1298.700	1299.800	1302.200	1305.800	1307.100	1307.400	1308.600
122	1302.100	1303.300	1305.600	1309.000	1309.500	1309.700	1310.100
123	1307.700	1308.100	1309.900	1311.200	1311.400	1313.000	1313.100
124	1311.700	1311.500	1312.600	1313.700	1314.400	1315.300	1315.400
125	1314.000	1313.700	1314.000	1314.600	1314.800	1315.000	1315.100
126	1316.500	1315.800	1315.200	1315.500	1315.400	1314.300	1313.100
127	1319.000	1318.300	1316.500	1316.600	1316.300	1314.800	1313.100
128	1320.900	1320.700	1319.600	1319.800	1320.000	1319.800	1318.600
129	1323.500	1323.900	1321.200	1322.000	1322.600	1323.700	1323.100
130	1325.000	1325.000	1324.300	1324.900	1325.100	1326.200	1326.100

Row	1048	1049	1050	1051	1052	1053	1054
5756	1287.100	1289.700	1292.900	1295.600	1298.700	1301.600	1304.700
5757	1289.600	1292.000	1294.700	1296.900	1299.400	1301.100	1303.600
5758	1291.300	1294.000	1296.100	1297.700	1299.600	1300.800	1303.100
5759	1293.700	1295.400	1296.300	1297.500	1299.500	1299.900	1302.100
5760	1295.100	1295.800	1296.200	1298.000	1299.500	1301.100	1303.600
5761	1295.900	1296.700	1297.500	1299.300	1301.000	1302.800	1304.700
5762	1297.100	1298.000	1299.100	1301.400	1303.900	1305.100	1306.600
5763	1298.700	1299.800	1302.200	1305.800	1307.100	1307.400	1308.600
5764	1302.100	1303.300	1305.600	1309.000	1309.500	1309.700	1310.100
5765	1307.700	1308.100	1309.900	1311.200	1311.400	1313.000	1313.100
5766	1311.700	1311.500	1312.600	1313.700	1314.400	1315.300	1315.400
5767	1314.000	1313.700	1314.000	1314.600	1314.800	1315.000	1315.100
5768	1316.500	1315.800	1315.200	1315.500	1315.400	1314.300	1313.100
5769	1319.000	1318.300	1316.500	1316.600	1316.300	1314.800	1313.100
5770	1320.900	1320.700	1319.600	1319.800	1320.000	1319.800	1318.600
5771	1323.500	1323.900	1321.200	1322.000	1322.600	1323.700	1323.100
5772	1325.000	1325.000	1324.300	1324.900	1325.100	1326.200	1326.100

The projection can be checked by finding a single grid cell and check the values in all four corners as shown below. You should find that the values (heights) of the original DEM and the edited **dhm25.img** are exactly the same when added in ArcMap. The Calculation layer as shown below is an example of the shift that can occur when the option ‘snap to DHM25grid’ is not enabled in Spatial Analyst.



The dhm25.img file is now ready to be added as vertical reference file.

The protocol as described in the Erdas Imagine [user guide](#) can be followed or you can return to the [index page of the protocol](#).

Remarks

This protocol is not written for general application. When this protocol is applied to other datasets with different properties, the user must check for each step whether it is the appropriate one, giving the correct result. [Any remarks or suggestion to improve this protocol are appreciated](#). According to Pierre Terretaz, two new projections are proposed for Switzerland in Imagine 8.6: "Ch1903" and "Ch1903plus". These projections match CH1903_LV03 and CH1903+_LV95 in ArcGIS. The old "Oblique Mercator Bessel" is still proposed in 8.6, but the parameters are not up to date. MFB-GeoConsulting recommends using "Ch1903" in the future.

Acknowledgements

This protocol only exists thanks to the help of Pierre Terretaz (MFB-GeoConsulting), Patrick Thee (WSL), Christian Ginzler (WSL), and Jovita Pfammatter (swisstopo).

Dealing with digital aerial photographs

Introduction

Most aerial photographs are taken by metric cameras. A metric camera has marking points, called fiducial marks, recorded on the film. The distance between the fiducial marks are used by OrthoBASE to determine the distortion of the photos. The more accurate these fiducial distances and internal distortion of a camera are known, the more accurate OrthoBASE can determine the topographical distortion of the aerial photo. These exact values are normally measured by experts and [usually a calibration protocol exists and is available at the Swisstopo website](#), but sometimes the camera is unknown and the following procedure can be followed.

Unknown frame camera

No calibration report was available for the unknown camera that was used to take the APs in 1933. A procedure on how to estimate the fiducial mark distances is described by Niwa (http://support.erdas.com/focus3/files/Aerial_photo.pdf). Of course Niwa's procedure can be adapted, as long as the position of the fiducial marks and the orientation of the X-Y-axis are taken into account.

The APs were rotated (more or less north orientated) in Photoshop to facilitate finding appropriate ground control points (GCP). The scanning input resolution as given by [swisstopo](http://www.swisstopo.ch/en/image/LBdigi.htm) (<http://www.swisstopo.ch/en/image/LBdigi.htm>) was wrong for the 1933 APs and is actually less detailed: **21 micrometer** (= 1209.5 dpi), instead of 14 micrometer. The distance (number of pixels) between the fiducial marks was averaged over 6 photos and the original distances calculated, using the correct scanning resolution. The **reconstructed** calibration protocol and the orientation of the axes and fiducial marks are given as an example [here](#). The fiducial marks may be rather fuzzy. This results in rather high residual values (RMSE > 30 microns), but seems to be a good compromise, as the original camera is lost and will probable never be found and calibrated.

You can download the following example files:

- [excel file: how to estimate the position of the fiducial marks of 'Camera 17' without the calibration protocol](#)
- [PDF file: shows the estimated orientation of the fiducials of 'Camera 17'](#)
- [CAM file 'Camera 17': can be loaded into OrthoBASE](#)
- [excel file: how to estimate the position of the fiducial marks of '11.5 Ag 29' with the calibration protocol](#)
- [CAM file '11.5 Ag 29': can be loaded into OrthoBASE](#)

Protocol for Single or Multiple Frame Orthorectification of Digital Images

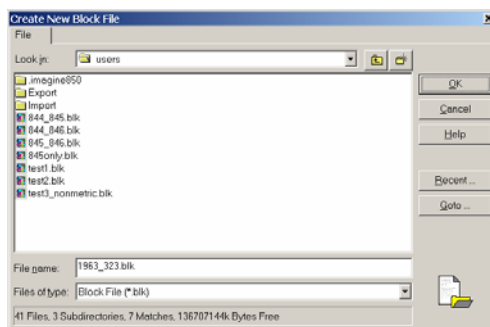
Introduction

Removing the internal distortion of aerial photographs is necessary when the user is interested in the correct location of the features the (s)he can see on aerial photographs. An extended explanation on the internal distortion of aerial photographs can be found [here](#). Before you start using **OrthoBASE**, the following material must be prepared as described [the previous step](#). Once these data sets are prepared, the user can orthorectify as many images as he/she wants.

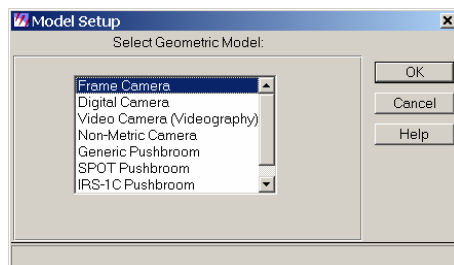
- Start Orthobase and create a new Orthobase project



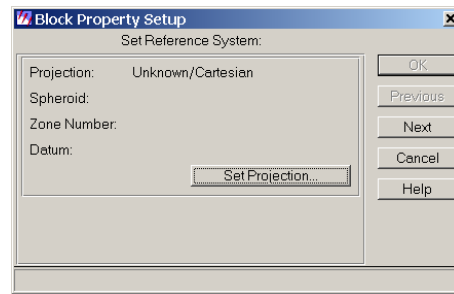
- give the project a new name, click OK. The extension .blk will be generated automatically. Click OK again to continue



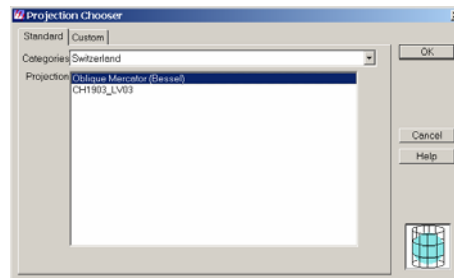
- select a frame camera:



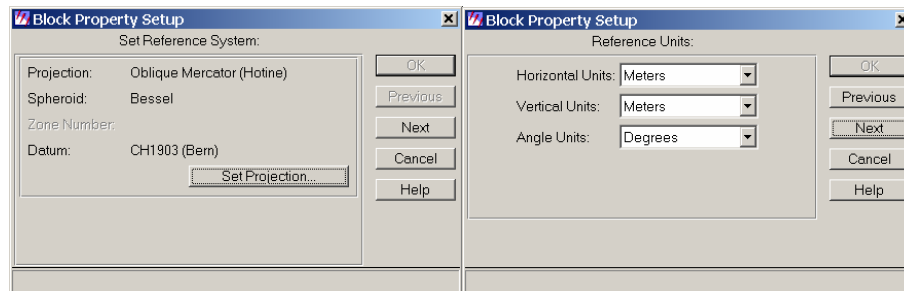
- set projection:



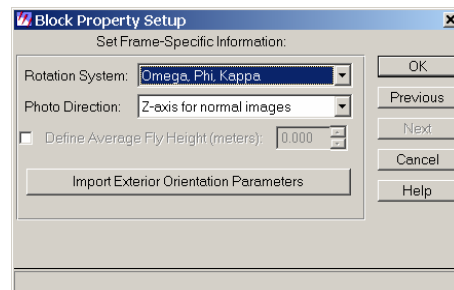
This must be the same as the projection you defined for the DEM and the horizontal reference file, in this case **Oblique Mercator (Bessel)**:



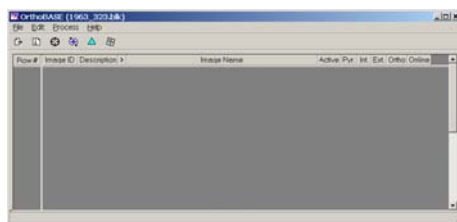
- the projection has changed now. Click next:



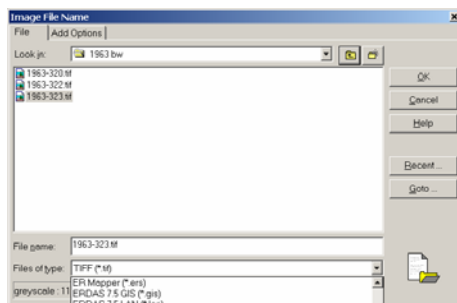
- confirm that these settings are the correct ones. You cannot change them afterwards. Click OK to confirm:



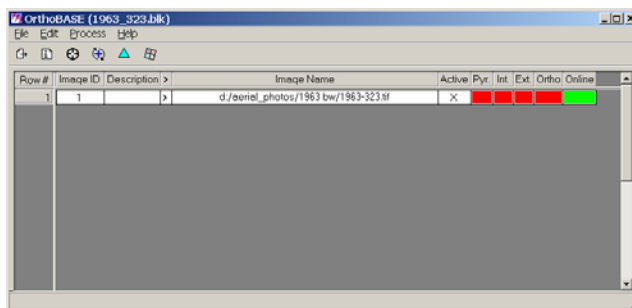
- the empty block file pops up:



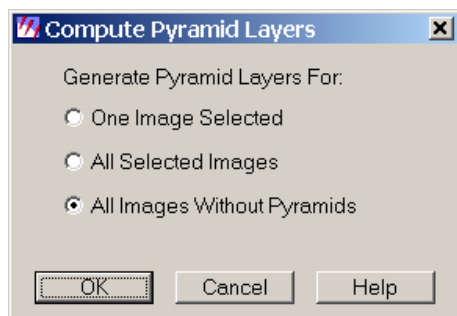
- click Edit, Add frame () to add the image-file you want to georeference. Do not forget to change the file selection option to *.TIFF and to uncheck the read-only function, in case you have copied the file from a CD-ROM:



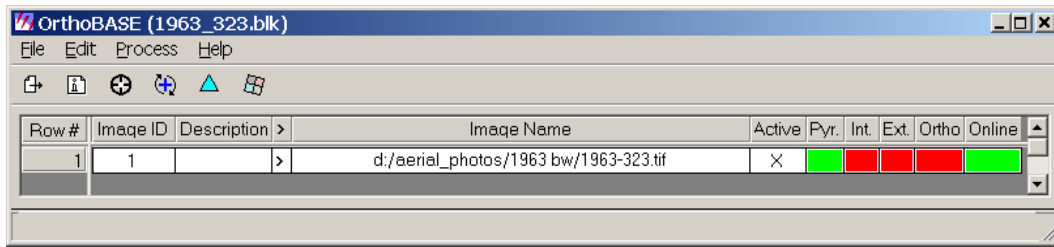
The image files are listed in the OrthoBASE dialogue now:



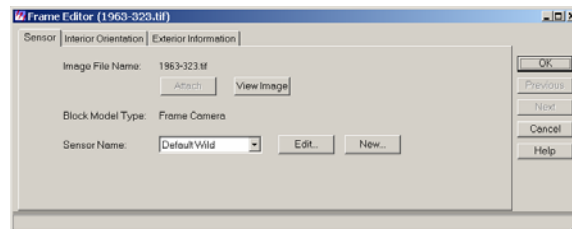
- click **Edit, Compute Pyramid layers**. Since this block file only contains one image, the choice you make here is unimportant, but by default should be the one as shown below, because this is the most time efficient option:



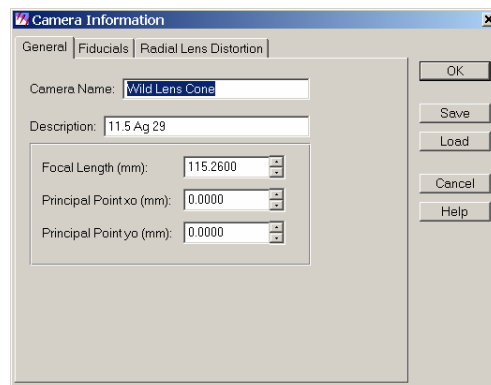
The red cell belonging to the column Pyr. Turns green now, indicating that Pyramide calculation has been successful:



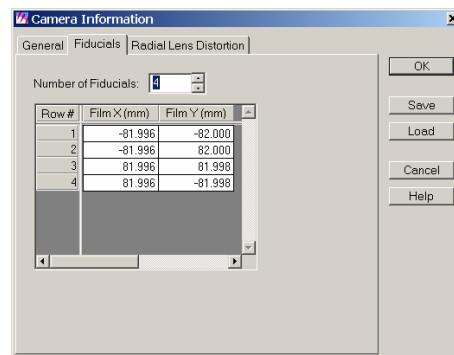
- click **Edit, Frame editor** or click the icon . The frame editor dialogue opens and the camera information can be changed:



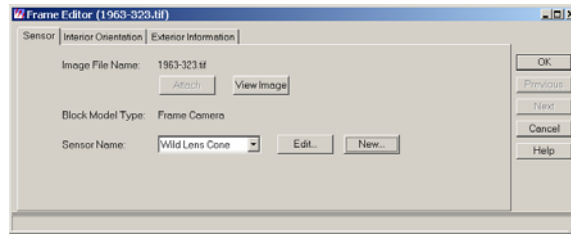
- Click **New** to add the appropriate camera. In this case the focal length was given by swisstopo on their [calibration protocol website](#):



- the fiducials were roughly calculated by using the values of the calibration report as is explained [here](#). If the same camera is used for georeferencing more than one image in other block-file, it could be useful to save the camera information in a [.CAM file](#).

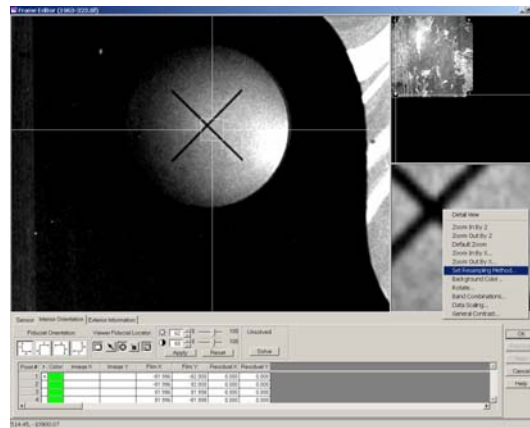


The frame editor information has changed now to the newly created camera:

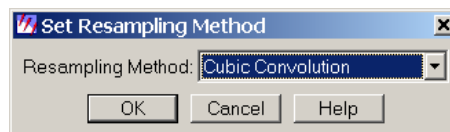


- click **Interior Orientation**: This is where you select the fiducial orientation (see fiducial orientation diagram below) and measure (locating) the fiducials on the image to be rectified.

- now open the **Fiducial Measurement Tool** by clicking the icon  (situated under the **View Fiducial Locator** heading) and select the proper XY-orientation, based on your camera calibration report. Once the image is displayed on top of the Frame Editor dialog you will have 3 views to work with:



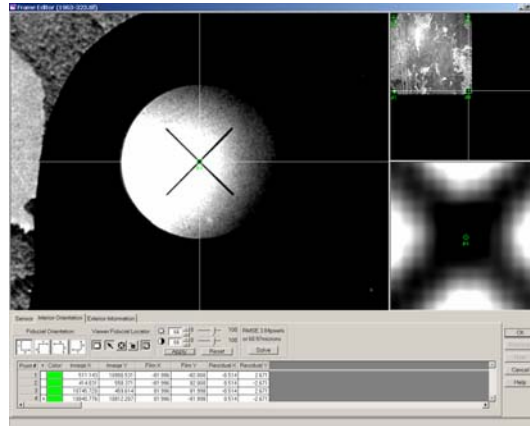
-Right click in the **Detail View** and select **Set Resample Method**, choose cubic convolution, this generally provides the clearest view of the detailed image.



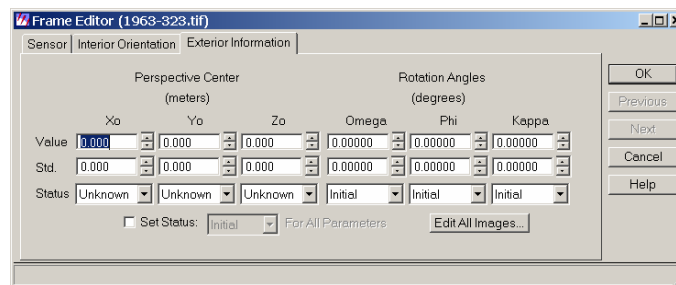
Adjust contrast/brightness if needed. You may have to make some adjustments especially if you are having difficulties seeing the fiducial marks. The image will adjust to the approximate location of the first fiducial. Adjust the size and location of the **Link Cursor** to fit over the fiducial. In the **Detail View** the fiducial should fill the viewer.

- Select **Place Image Fiducial** icon  (located under the **Viewer Fiducial Locator** heading). Move cursor over the fiducial center and left click. The Frame Editor cell array will automatically move to the approximate location of fiducial number 2. Adjust **Link Cursor** as before and place second measurement. To speed up the point placement, the **Place Image Fiducial** icon can be locked by

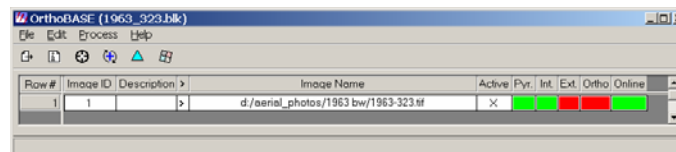
clicking on the Keep Current Tool . Add the rest of the fiducial measurements. [The placement order should match the fiducial diagram in camera calibration report.](#) If this is not the case then there are errors somewhere in the **Frame Editor**. When all measurements have been made, look at the Root Mean Square Error (**RMSE**) above the Solve button. Ideally, this value should be in the .1 to .3 pixel range. This is not the case in the example below, because a non-photogrammetrical scanner was used to scan the original image, and a RMSE of up to even 90 microns gives very acceptable results.



- set the Exterior information as shown below. These values will be calculated by OrthoBASE in a later stadium. Even if you have a rough idea of the positions, do NOT enter these. If any errors are made, the program may have difficulties dealing with these data, resulting in flipped or totally useless orthorectifications. However, if you know the exact values of the external parameter, you can follow the procedure as described in the protocol [Orthorectification of aerial photographs using parameters of orientation](#) (Graf).



- click OK to accept the entered values. The values can be changed in between or afterwards if necessary. The column **Int.** has turned green now:



The next step in the process is to locate ground control points (GCP) between your aerial photo-image and the reference image (with known projection coordinates).

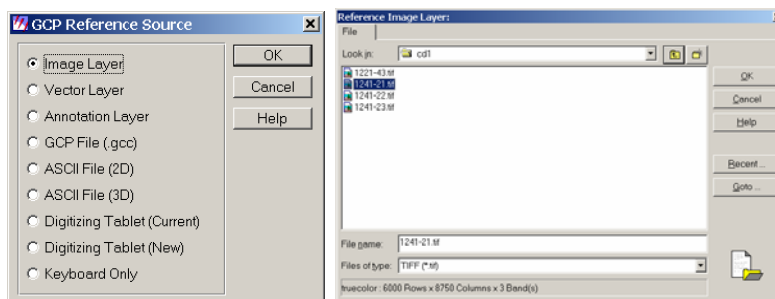
Select the **Point Measurement Tool** icon . The following dialogue pops up:

Before you start locating GCPs you should do the following:

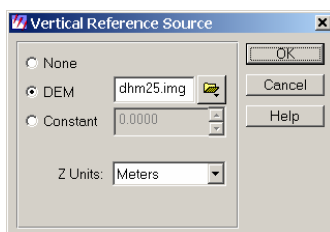
- Enable the Automatic (x,y) drive: 

- Enable the Automatic Z Value Updating 

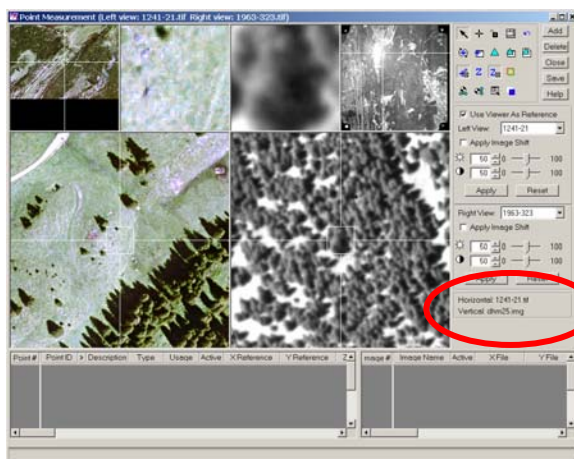
- click Horizontal Reference Source icon  and select the prepared reference file:



- click Vertical Reference Source icon  and select the prepared DEM file



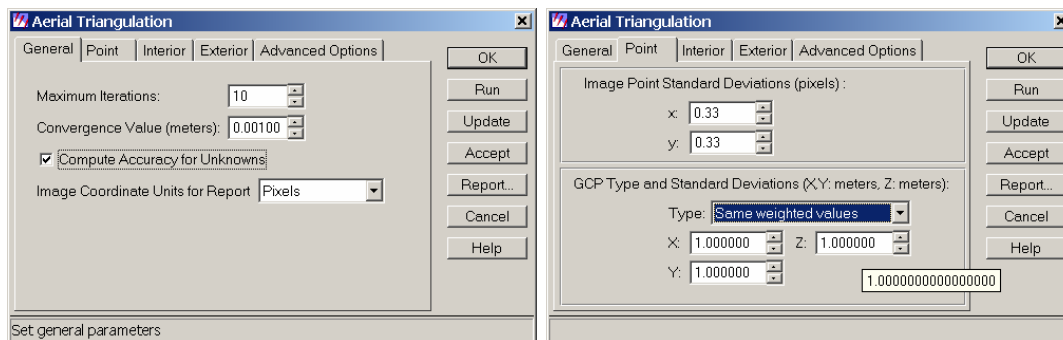
- enable the 'Use viewer as reference' option, and the dialogue will change to:



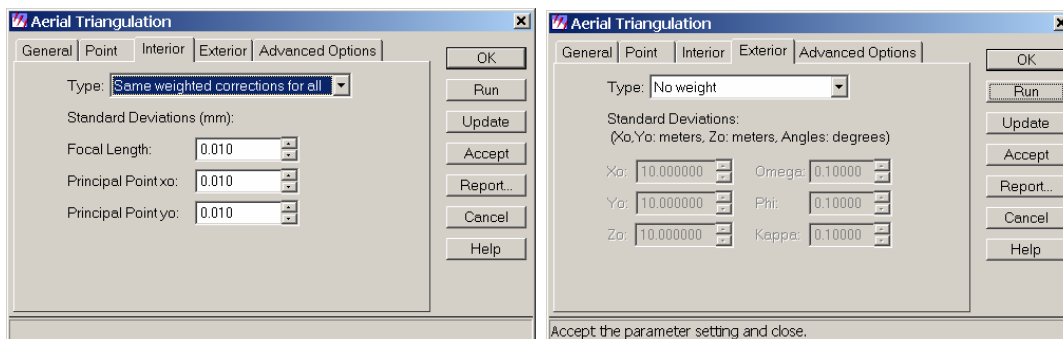
*Make sure that the reference files
are properly indicated here!*

Navigate using the icon  to where you want to place your GCP. Adjust magnification when needed. Create GCPs ([Type: Full Usage: Control](#)) on both images using the icon .

Important: Each time prior to placing a pair of GCP, click the 'Add' button. This opens up a new row in the coordinate screen at the bottom of the Point Measurement dialog. If you do not do this you will just move the location of the last entered GCP to the location of your new GCP, losing your previous GCP and your value time. Luckily there is an **Undo** option which resets your last action. Bear in mind that evenly distributed points increase the accuracy of the rectification. Use the 'show graphic' icon  to check the placement of your control points. The GCP will have x, y, and z coordinates on the Reference Coordinate dialog (lower left) and for each row there will be one corresponding row in the File Coordinate dialog (lower right).



Change to 'Same weighted corrections for all' because (all the) image(s) was/were taken with the same camera, of which the exact interior values are unknown. Leave the Exterior values as they are, because we did not use them. Run the 'triangulation':



A summary report pops up, click report to check the residual values of the GCPs and to locate outliers:

Triangulation Summary

Triangulation Iteration Convergence: Yes
 Total Image Unit-Weight RMSE: 0.8775

Control Point RMSE: Check Point RMSE:

Ground X: 1.4435 (5)	Ground X: 0.0000 (0)
Ground Y: 1.6553 (5)	Ground Y: 0.0000 (0)
Ground Z: 0.8357 (5)	Ground Z: 0.0000 (0)
Image X: 0.0851 (5)	Image X: 0.0000 (0)
Image Y: 0.0855 (5)	Image Y: 0.0000 (0)

Buttons: Close, Update, Accept, Report..., Help

If you have no outliers, this value should probably not exceed 1.5

If the residuals are too high, add more GCPs, and Run the Triangulation again. Once the residual values have decreased to an acceptable level, Accept the triangulation, Close the Summary dialogue. Close the Triangulation dialogue as well. Save and Close the point measurement dialogue as well. The block dialogue appears again, the **Ext.** column has turned green:

OrthoBASE (1963_323.blk)

Row #	Image ID	Description	Image Name	Active	Pyr.	Int.	Ext.	Ortho	Online
1	1		d:/aerial_photos/1963 bw/1963-323.tif	X					

Perform orthorectification by clicking the  icon. Re-name the file if you do not like the default name. Make sure that the DEM file is selected. The very limited number of GCP in this example resulted in errors up to 35 m. The more GCP are entered the better the result will be. Make sure that all the GCP have been set to Type *Full*, Usage *Control*, and are Active. If the Triangulation report shows an unacceptable residual for a GCP, one can disable the GCP by making it inactive, without actually deleting it. This saves time if the observer decides to keep the GCP anyway.

Point Measurement (Left view: 1241-21.tif, Right view: 1963-323.tif)

Buttons: Add, Delete, Close, Save, Help

☒ Use Viewer As Reference

Left View: 1241-21
 Apply Image Shift
 X: 50, Y: 50, Z: 100
 Apply, Reset

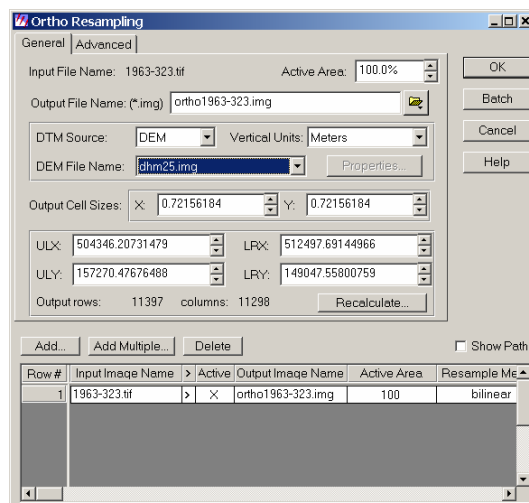
Right View: 1963-323
 Apply Image Shift
 X: 50, Y: 50, Z: 100
 Apply, Reset

Horizontal: 1241-21.tif
 Vertical: dhm25.mpg

Point #	Point ID	Description	Type	Usage	Active	X-Reference	Y-Reference	Z	Image #	Image Name	Active	X-File	Y-File
7			Full	Control	X	507585.003	150210.423		1	1963-323	X	7133.456	5820.87
8			Full	Control	X	510280.335	151629.094						
9			Full	Control	X	507908.280	151010.589						
10			Full	Control	X	5115.461	154630.332						
11			Full	Control	X	5115.461	154630.332						
12			Full	Control	X	5115.461	154630.332						

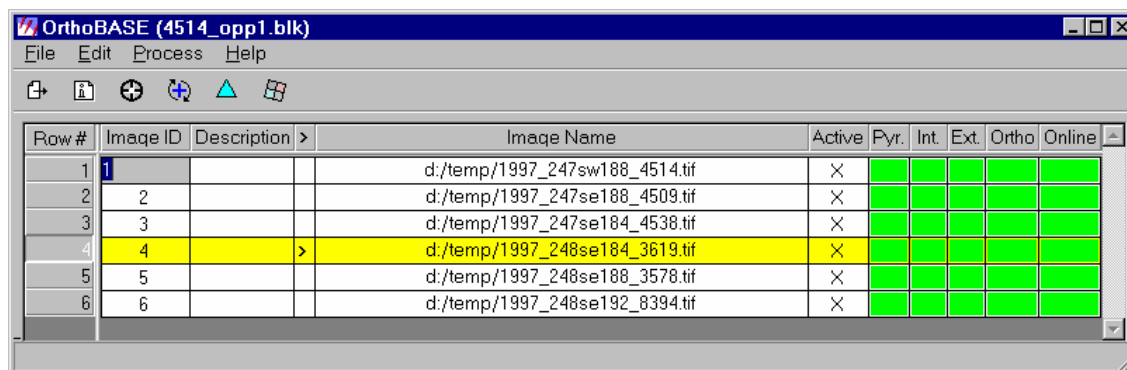
Example of an inactive GCP

Rerun the orthorectification, until the result is acceptable.



- Click Advanced and choose the Resample Method you wish to use. For further discussion on the advantages or disadvantages of the resampling methods see the ERDAS FIELD GUIDE, Chapter 8, *Resample Methods*. The ULX/Y, LRX/Y and Output Cell size are the same values as the input file by default. These can be changed if necessary.
- Check 'Ignore Zero in Stats' box. Click OK.

Once the orthorectification has been performed, all columns are green.



Note on error messages:

If the message “File flush failed” is encountered, it is probably better to delete all your work files (this includes the AUX- and RRD-files), and start from scratch.

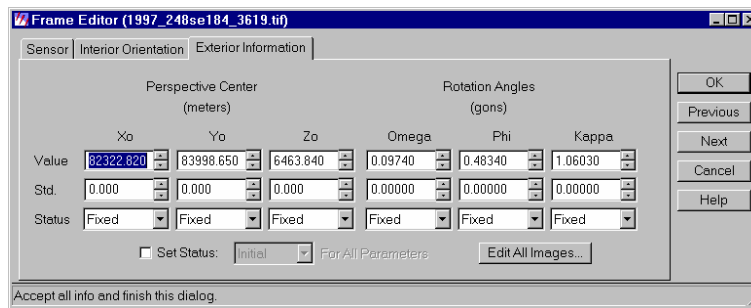
Orthorectification of aerial photographs using parameters of orientation.

[Roland Graf](#)

WSL, Switzerland

If you know the exact exterior information parameters, you do not need to locate ground control points and you can save yourself a huge amount of time.

- Enter the exact exterior information parameters (decimal places are important) and set their status to „fixed“.

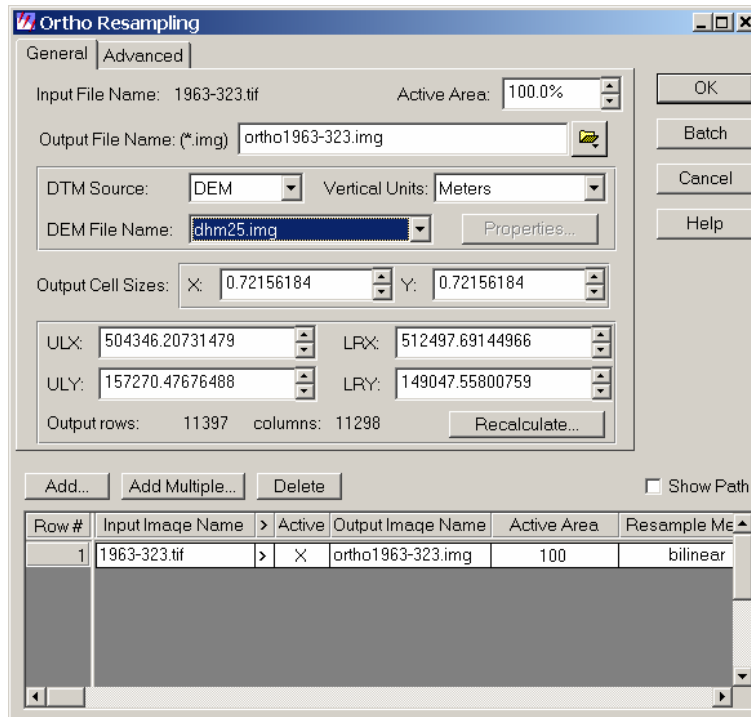


Important: Make sure, that the rotation angles are measured in the unit stated in the parentheses. In this case the measuring unit is in *gons*, which is often used in analytical photogrammetry. The units of rotation angles must be fixed when starting a new project (block file). It cannot be changed afterwards.

Click OK to accept the entered values. The external parameter values can be changed in between, or afterwards, if necessary. The columns *Int.* and *Ext.(!)* have turned green now:

Row#	Image ID	Description	Image Name	Active	Pyr.	Int.	Ext.	Ortho	Online
1			d:/temp/1997_247sw188_4514.tif	X					
2	2		d:/temp/1997_247se188_4509.tif	X					
3	3		d:/temp/1997_247se184_4538.tif	X					
4			d:/temp/1997_248se184_3619.tif	X					
5	5		d:/temp/1997_248se188_3578.tif	X					
6	6		d:/temp/1997_248se192_8394.tif	X					

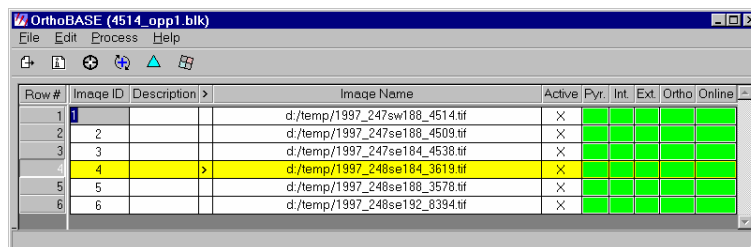
- Start orthorectification by clicking the icon . 
- Select your DEM source, and the output file name (and folder).
- Click Advanced and choose the Resample Method you wish to use.



For further discussion on the advantages or disadvantages of the resampling methods see the ERDAS FIELD GUIDE, Chapter 8, Resample Methods. The ULX/Y, LRX/Y and Output Cell size are the same values as the input file by default. These can be changed if necessary.

- Check 'Ignore Zero in Stats' box. Click OK.

Once the orthorectification has been performed, all columns are green.



Appendix B: Plot details of the vegetation relevés

Plot_ID	x	y	Cover history	Grazed	Lichen subset	Plot_ID	x	y	Cover history	Grazed	Lichen subset
jk001	506'425	155'603	No change	No	*	jk044	504'891	156'161	Increased	Yes	*
jk002	506'636	155'761	Increased	No	*	jk045	504'966	156'220	No change	Yes	*
jk003	506'536	155'684	No change	No	*	jk046	505'062	156'285	No change	Yes	*
jk004	506'742	155'846	No change	No		jk047	507'611	154'997	No change	No	*
jk005	506'913	155'982	No change	No		jk048	504'790	156'532	Increased	No	
jk006	506'968	156'027	No change	Yes		jk049	504'724	156'557	No change	No	
jk007	506'622	155'530	No change	No		jk050	504'606	156'440	No change	No	
jk008	506'828	155'626	Decreased	No	*	jk051	504'694	156'380	No change	No	
jk009	506'839	155'674	Decreased	No	*	jk052	504'518	156'221	No change	No	
jk010	506'784	155'713	No change	No	*	jk053	504'458	156'257	Increased	No	
jk011	507'196	156'340	No change	Yes		jk054	508'138	157'226	No change	No	*
jk012	506'972	156'115	No change	Yes		jk055	508'074	157'187	No change	No	*
jk013	507'061	156'228	No change	Yes		jk056	505'821	157'597	Increased	Yes	
jk014	506'869	157'135	No change	No		jk057	505'767	157'514	Increased	No	
jk015	506'986	157'213	No change	No		jk058	505'755	157'390	Increased	No	
jk016	505'961	156'623	No change	No	*	jk059	505'701	157'620	Increased	Yes	
jk017	506'162	156'587	Decreased	No	*	jk060	505'957	157'287	No change	No	
jk018	506'157	156'842	No change	No		jk061	506'085	157'219	No change	No	
jk019	506'275	156'786	Decreased	No		jk062	505'957	157'586	Increased	Yes	
jk020	506'132	156'735	No change	No	*	jk063	508'196	157'329	No change	No	*
jk021	506'014	156'736	No change	No	*	jk064	508'238	157'404	No change	No	*
jk022	505'277	156'917	No change	No	*	jk065	508'218	157'478	No change	No	*
jk023	505'355	156'965	No change	No	*	jk066	508'124	157'375	No change	No	*
jk024	505'480	156'876	No change	No	*	jk067	505'936	157'846	Increased	Yes	
jk025	505'456	156'799	No change	No	*	jk068	505'890	157'884	No change	Yes	
jk026	505'700	156'665	No change	No	*	jk069	505'841	157'827	No change	Yes	
jk027	505'733	156'775	No change	No	*	jk070	505'874	157'767	Increased	Yes	
jk028	504'929	156'688	Increased	No		jk071	505'978	157'778	Increased	Yes	
jk029	504'896	156'658	Increased	No		jk072	505'955	157'743	Increased	Yes	
jk030	504'862	156'615	No change	No		jk073	506'021	157'728	Increased	Yes	
jk031	504'836	156'562	No change	No		jk074	505'991	157'650	Increased	Yes	
jk032	504'992	156'521	Increased	No		jk075	506'224	157'635	No change	No	
jk033	505'275	156'439	No change	No		jk076	506'278	157'570	No change	No	
jk034	505'334	156'490	No change	No	*	jk077	506'160	157'546	Increased	Yes	
jk035	505'385	156'415	Increased	No		jk078	506'050	157'541	Increased	Yes	
jk036	505'321	156'362	No change	No		jk079	505'979	157'521	Increased	Yes	
jk037	505'236	156'268	No change	No	*	jk080	508'064	157'330	No change	No	
jk038	505'301	156'201	Increased	No		jk081	508'006	157'266	No change	No	
jk039	505'202	156'106	Increased	No	*	jk082	507'691	155'177	No change	No	*
jk040	505'148	156'161	No change	No	*	jk083	507'817	155'366	No change	No	*
jk041	505'115	156'020	No change	No	*	jk084	507'924	155'520	No change	No	*
jk042	505'031	156'046	No change	No	*	jk085	508'050	155'667	No change	No	*
jk043	504'941	156'162	Increased	Yes	*	jk086	508'149	155'794	No change	No	*

Appendix C: Plot details of *Lobaria* mapping

Name and position of 1-ha plots, and data on historical disturbance, local change in canopy cover and/or density.

plotid	x_plot	y_plot	Disturbance	Loc.changes	plotid	x_plot	y_plot	Disturbance	Loc.changes
Wer001	505'796	155'574	Undisturbed	No changes	Wer038	505'387	156'786	Undisturbed	No changes
Wer002	505'890	156'622	Undisturbed	No changes	Wer039	506'790	155'586	Undisturbed	Decreased
Wer003	506'638	155'734	Undisturbed	Increased	Wer040	506'077	156'386	Undisturbed	No changes
Wer004	507'401	155'052	Grazed	No changes	Wer041	505'924	156'155	Undisturbed	No changes
Wer005	505'374	156'472	Logged/burnt	Increased	Wer042	505'533	155'679	Logged/burnt	Increased
Wer006	506'454	155'357	Undisturbed	No changes	Wer043	507'246	154'353	Undisturbed	No changes
Wer007	504'647	156'210	Undisturbed	Increased	Wer044	505'369	155'836	Logged/burnt	No changes
Wer008	505'270	155'764	Undisturbed	No changes	Wer045	506'432	155'595	Undisturbed	No changes
Wer009	505'196	156'167	Logged/burnt	Increased	Wer046	505'034	155'916	Logged/burnt	No changes
Wer010	505'920	156'371	Undisturbed	No changes	Wer047	505'675	156'670	Undisturbed	No changes
Wer011	505'404	156'622	Undisturbed	No changes	Wer048	505'162	155'770	Logged/burnt	No changes
Wer012	506'205	155'988	Grazed	No changes	Wer049	506'043	155'946	Grazed	Decreased
Wer013	507'701	155'130	Undisturbed	No changes	Wer050	507'309	154'754	Grazed	No changes
Wer014	505'056	156'042	Logged/burnt	Increased	Wer051	506'026	156'484	Undisturbed	No changes
Wer015	504'942	155'981	Logged/burnt	No changes	Wer052	505'588	155'588	Undisturbed	No changes
Wer016	505'324	155'929	Logged/burnt	Increased	Wer053	505'902	156'519	Undisturbed	No changes
Wer017	506'301	155'309	Grazed	No changes	Wer054	504'832	156'218	Undisturbed	No changes
Wer018	506'066	155'292	Grazed	No changes	Wer055	504'618	156'065	Undisturbed	Increased
Wer019	505'525	156'741	Undisturbed	No changes	Wer056	507'478	154'886	Undisturbed	No changes
Wer020	507'253	154'578	Undisturbed	No changes	Wer057	505'634	155'803	Logged/burnt	Increased
Wer021	505'634	156'390	Logged/burnt	Increased	Wer058	506'726	155'880	Undisturbed	No changes
Wer022	504'999	156'673	Undisturbed	No changes	Wer059	507'287	155'290	Grazed	No changes
Wer023	506'864	154'963	Grazed	Decreased	Wer060	505'281	156'713	Undisturbed	No changes
Wer024	506'576	156'172	Grazed	No changes	Wer061	505'292	156'311	Logged/burnt	No changes
Wer025	506'227	155'691	Grazed	No changes	Wer062	505'144	157'022	Grazed	Increased
Wer026	505'985	155'698	Grazed	No changes	Wer063	504'924	156'308	Undisturbed	No changes
Wer027	505'854	155'753	Undisturbed	Decreased	Wer064	504'925	155'850	Undisturbed	No changes
Wer028	507'643	155'353	Grazed	No changes	Wer065	507'330	154'944	Grazed	Decreased
Wer029	507'056	155'578	Grazed	No changes	Wer066	507'547	155'267	Grazed	No changes
Wer030	507'682	155'450	Grazed	No changes	Wer067	506'370	156'196	Grazed	Decreased
Wer031	506'244	156'364	Undisturbed	Decreased	Wer068	505'634	156'577	Undisturbed	No changes
Wer032	507'424	154'778	Undisturbed	No changes	Wer069	505'257	155'626	Undisturbed	No changes
Wer033	505'496	155'855	Logged/burnt	No changes	Wer070	505'198	156'632	Undisturbed	Increased
Wer034	505'710	155'996	Undisturbed	Decreased	Wer071	505'443	156'057	Logged/burnt	Increased
Wer035	507'175	154'715	Grazed	Decreased	Wer072	504'761	155'972	Undisturbed	Increased
Wer036	505'419	156'156	Logged/burnt	Increased	Wer073	505'811	156'187	Undisturbed	Decreased
Wer037	505'391	156'367	Logged/burnt	Increased	Wer074	505'082	156'851	Undisturbed	No changes

plotid	x_plot	y_plot	Disturbance	Loc.changes	plotid	x_plot	y_plot	Disturbance	Loc.changes
Wer075	505'633	155'495	Undisturbed	No changes	Wer120	505'108	154'875	Charcoal	Increased
Wer076	506'816	155'721	Undisturbed	No changes	Wer121	506'697	157'643	Undisturbed	No changes
Wer077	507'042	154'596	Grazed	Decreased	Wer122	504'067	155'236	Undisturbed	No changes
Wer078	506'119	156'262	Undisturbed	Decreased	Wer123	505'025	154'748	Charcoal	Increased
Wer079	505'677	156'278	Logged/burnt	Increased	Wer124	504'801	154'803	Charcoal	No changes
Wer080	505'285	156'065	Logged/burnt	Increased	Wer125	506'655	153'897	Undisturbed	Decreased
Wer081	506'021	156'119	Undisturbed	No changes	Wer126	507'044	157'178	Undisturbed	No changes
Wer082	507'464	154'629	Undisturbed	No changes	Wer127	506'435	156'900	Undisturbed	No changes
Wer083	506'372	155'121	Grazed	No changes	Wer128	507'132	157'403	Undisturbed	No changes
Wer084	506'284	155'607	Grazed	No changes	Wer129	507'434	156'914	Undisturbed	No changes
Wer085	505'314	156'178	Logged/burnt	Increased	Wer130	506'628	157'098	Undisturbed	No changes
Wer086	505'962	155'243	Grazed	Increased	Wer131	506'364	156'717	Undisturbed	Decreased
Wer087	504'998	156'218	Grazed	Increased	Wer132	504'261	154'947	Grazed	Increased
Wer088	506'950	155'975	Undisturbed	No changes	Wer133	506'300	157'649	Undisturbed	Increased
Wer089	506'017	156'247	Undisturbed	Decreased	Wer134	506'756	153'704	Undisturbed	Decreased
Wer090	507'525	154'748	Undisturbed	No changes	Wer135	505'480	154'834	Undisturbed	No changes
Wer091	506'670	155'487	Undisturbed	No changes	Wer136	505'119	154'506	Charcoal	Increased
Wer092	507'432	155'616	Grazed	Decreased	Wer137	504'938	154'943	Charcoal	No changes
Wer093	505'626	156'071	Logged/burnt	Increased	Wer138	505'470	155'027	Undisturbed	No changes
Wer094	507'281	155'767	Undisturbed	No changes	Wer139	506'218	156'573	Undisturbed	No changes
Wer095	504'934	156'892	Grazed	Increased	Wer140	506'145	157'768	Undisturbed	Increased
Wer096	507'703	155'245	Undisturbed	No changes	Wer141	506'913	157'221	Undisturbed	No changes
Wer097	506'566	155'540	Undisturbed	No changes	Wer142	504'773	154'083	Undisturbed	No changes
Wer098	505'556	156'221	Logged/burnt	No changes	Wer143	504'429	155'624	Undisturbed	Decreased
Wer099	506'683	155'165	Grazed	No changes	Wer144	505'794	154'955	Grazed	No changes
Wer100	507'564	155'073	Undisturbed	No changes	Wer145	504'675	154'237	Charcoal	Increased
Wer101	504'569	155'382	Undisturbed	No changes	Wer146	507'635	156'919	Undisturbed	No changes
Wer102	507'496	157'025	Undisturbed	Decreased	Wer147	506'967	157'601	Undisturbed	Increased
Wer103	505'032	154'336	Charcoal	Increased	Wer148	507'459	156'735	Undisturbed	No changes
Wer104	504'792	155'586	Undisturbed	No changes	Wer149	506'805	157'341	Undisturbed	No changes
Wer105	507'644	157'059	Undisturbed	No changes	Wer150	505'364	155'343	Undisturbed	No changes
Wer106	505'248	155'088	Undisturbed	No changes	Wer151	504'599	154'104	Charcoal	No changes
Wer107	507'209	157'838	Undisturbed	Increased	Wer152	507'241	156'979	Undisturbed	No changes
Wer108	504'256	155'615	Undisturbed	Decreased	Wer153	506'248	156'811	Undisturbed	Decreased
Wer109	504'835	155'424	Grazed	No changes	Wer154	506'619	153'354	Undisturbed	No changes
Wer110	506'956	157'846	Undisturbed	No changes	Wer155	505'602	155'204	Undisturbed	Increased
Wer111	504'582	155'677	Undisturbed	No changes	Wer156	506'518	158'303	Grazed	Increased
Wer112	504'508	154'447	Charcoal	Increased	Wer157	504'603	155'500	Undisturbed	Decreased
Wer113	507'341	157'161	Undisturbed	Decreased	Wer158	507'574	156'762	Undisturbed	No changes
Wer114	504'553	154'295	Charcoal	Increased	Wer159	506'302	157'032	Undisturbed	No changes
Wer115	505'183	154'630	Charcoal	No changes	Wer160	506'659	158'088	Grazed	Increased
Wer116	506'947	154'173	Undisturbed	No changes	Wer161	503'775	154'953	Undisturbed	No changes
Wer117	504'707	154'510	Charcoal	Increased	Wer162	507'275	157'414	Undisturbed	Decreased
Wer118	505'420	155'140	Undisturbed	No changes	Wer163	504'555	155'794	Undisturbed	Decreased
Wer119	506'479	157'186	Undisturbed	No changes	Wer164	505'248	155'385	Undisturbed	No changes

plotid	x_plot	y_plot	Disturbance	Loc.changes	plotid	x_plot	y_plot	Disturbance	Loc.changes
Wer165	504'451	155'507	Undisturbed	Decreased	Wer209	506'814	153'836	Undisturbed	No changes
Wer166	505'653	154'890	Grazed	No changes	Wer210	505'350	154'746	Undisturbed	Increased
Wer167	505'239	154'932	Undisturbed	Decreased	Wer211	507'735	156'760	Undisturbed	No changes
Wer168	504'824	154'340	Charcoal	Increased	Wer212	504'685	154'361	Charcoal	Increased
Wer169	507'780	156'880	Undisturbed	No changes	Wer213	505'023	154'628	Charcoal	Increased
Wer170	503'790	154'694	Grazed	No changes	Wer214	507'118	157'516	Undisturbed	No changes
Wer171	504'902	154'610	Charcoal	Increased	Wer215	507'267	157'579	Undisturbed	No changes
Wer172	506'285	157'906	Undisturbed	No changes	Wer216	506'564	153'756	Undisturbed	No changes
Wer173	506'922	157'981	Undisturbed	Increased	Wer217	504'043	155'388	Undisturbed	No changes
Wer174	504'261	155'365	Undisturbed	Decreased	Wer218	504'685	155'884	Undisturbed	Decreased
Wer175	504'911	154'803	Charcoal	Increased	Wer219	506'334	156'544	Undisturbed	No changes
Wer176	506'018	157'779	Grazed	Increased	Wer220	505'610	155'335	Undisturbed	No changes
Wer177	507'413	157'272	Undisturbed	No changes	Wer221	505'111	154'989	Undisturbed	No changes
Wer178	507'291	157'285	Undisturbed	No changes	Wer222	505'242	155'210	Undisturbed	No changes
Wer179	504'826	155'733	Undisturbed	Decreased	Wer223	504'483	155'943	Undisturbed	Decreased
Wer180	504'804	155'307	Grazed	Decreased	Wer224	506'219	156'693	Undisturbed	Decreased
Wer181	503'919	155'194	Undisturbed	No changes	Wer225	506'970	157'348	Undisturbed	No changes
Wer182	506'986	154'030	Undisturbed	Decreased	Wer226	504'717	154'667	Charcoal	Increased
Wer183	504'254	155'489	Undisturbed	Decreased	Wer227	506'699	157'758	Undisturbed	No changes
Wer184	505'437	155'498	Undisturbed	No changes	Wer228	505'146	154'388	Charcoal	No changes
Wer185	504'774	153'958	Undisturbed	No changes	Wer229	504'433	154'248	Charcoal	Increased
Wer186	504'439	155'815	Undisturbed	Decreased	Wer230	504'786	154'229	Charcoal	Increased
Wer187	504'898	154'178	Charcoal	Increased	Wer231	504'719	155'429	Undisturbed	No changes
Wer188	504'895	154'494	Charcoal	Increased	Wer232	506'823	157'652	Undisturbed	No changes
Wer189	505'046	155'619	Undisturbed	Decreased	Wer233	504'000	154'940	Grazed	Decreased
Wer190	503'618	154'622	Undisturbed	No changes	Wer234	507'097	154'323	Undisturbed	No changes
Wer191	506'913	157'483	Undisturbed	No changes	Wer235	506'693	157'258	Undisturbed	No changes
Wer192	505'190	153'673	Undisturbed	Increased	Wer236	507'207	157'106	Undisturbed	No changes
Wer193	506'481	157'074	Undisturbed	No changes	Wer237	506'528	157'709	Undisturbed	Increased
Wer194	507'080	157'055	Undisturbed	No changes	Wer238	504'567	154'564	Charcoal	Increased
Wer195	505'411	153'549	Undisturbed	No changes	Wer239	504'454	155'396	Undisturbed	No changes
Wer196	506'098	156'682	Undisturbed	No changes	Wer240	505'490	155'281	Undisturbed	No changes
Wer197	504'902	155'560	Undisturbed	No changes	Wer241	504'597	155'171	Grazed	No changes
Wer198	507'543	157'211	Undisturbed	No changes	Wer242	505'354	154'933	Undisturbed	No changes
Wer199	506'372	157'788	Undisturbed	No changes	Wer243	506'597	153'510	Undisturbed	Decreased
Wer200	506'816	157'786	Undisturbed	No changes	Wer244	506'021	157'935	Grazed	Increased
Wer201	506'548	157'480	Undisturbed	Increased	Wer245	506'978	157'732	Undisturbed	No changes
Wer202	507'103	154'211	Undisturbed	Increased	Wer246	507'082	157'934	Undisturbed	No changes
Wer203	503'825	154'570	Grazed	No changes	Wer247	505'814	155'074	Grazed	No changes
Wer204	505'379	153'687	Undisturbed	Increased	Wer248	504'669	154'957	Grazed	No changes
Wer205	504'274	155'223	Undisturbed	Increased	Wer249	505'738	157'406	Undisturbed	Increased
Wer206	505'066	155'230	Undisturbed	Increased	Wer250	505'171	153'791	Undisturbed	Decreased
Wer207	506'756	157'504	Undisturbed	Increased	Wer251	504'700	155'738	Undisturbed	Decreased
Wer208	507'175	157'249	Undisturbed	No changes					

Appendix D: Posters

Poster 1. Kalwij, J.M., H. H. Wagner, O. Wildi & C. Scheidegger (13-01-2003) Can a pasture woodland be an "old forest"? Poster, IUFRO (International Union of Forest Research Organizations) Meeting, Leuven, Belgium.

Poster 2. Kalwij, J.M., S. Werth & C. Scheidegger (18-05-2003) Will *Lobaria* survive in this landscape? Poster, NCCR Exposition, Botanical Garden, Neuchâtel, Switzerland.

Poster 3. Kalwij, J.M., H. H. Wagner, O. Wildi & C. Scheidegger (06-02-2004) How vulnerable is the endangered lichen *L. pulmonaria* to disturbance? Poster, Biology '04, Fribourg (Switzerland), Switzerland.

Kalwij, J.M., H. H. Wagner, O. Wildi & C. Scheidegger (13-01-2003) Can a pasture woodland be an "old forest"? Poster, IUFRO (International Union of Forest Research Organizations) Meeting, Leuven, Belgium.

Abstract: Pasture woodland landscapes are regularly disturbed by cattle grazing and tree logging, as is the case in the Parc Jurassien Vaudois (CH). This is apparently contradicted by the observed high occurrence of *Lobaria pulmonaria* in the area. *L. pulmonaria* is a lichen assumed to be typical of forests with a high continuity (long-term undisturbed, old-growth forest). The impact of land-use on forest stands at different spatial and temporal scales is investigated to lay a foundation for a revision of the concept of Forest Continuity. The main questions addressed are: (1) on what spatial and temporal scale is Forest Continuity possible in a pasture woodland landscape; and (2) can patterns of change be predicted from land-use history? Changes in forest boundaries and tree density were derived from aerial photographs of 1933-2000. Historical maps (1896-1945) and aerial photographs were used to determine minimum forest patch age. Distances between patches were calculated to evaluate connectivity. Cattle pressure and logging intensity was reconstructed from management records. Patches within abandoned parcels showed a different pattern of change than patches within currently used parcels. We conclude that cattle grazing is a main factor determining landscape structure in a pasture woodland landscape. Different types of land-use will permit Forest Continuity at different spatial and temporal scales. This suggests that persistence of a species (such as *L. pulmonaria*) will largely depend on its dispersal abilities.



Can a pasture woodland be an “old forest”?

Kalwij, J.M., H.H.Wagner, O.Wildi, Ch.Scheidegger

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Introduction

Pasture woodland landscapes are regularly disturbed by cattle grazing and tree logging, as is the case in the Parc Jurassien Vaudois (CH). However, this is apparently contradicted by the observation of a large number of *Lobaria pulmonaria* in the area.



Lobaria pulmonaria, an indicator of Forest Continuity?

This epiphytic lichen is assumed to be typical of forests with a high degree of continuity (old-growth forest, undisturbed in the long-term). Here, the impact of land use on forest stands at different spatial and temporal scales has been investigated to lay a foundation for a revision of the interpretation of Forest Continuity.

Main question

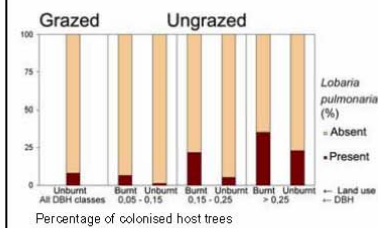
On what spatial and temporal scale does Forest Continuity function in a pasture woodland landscape?

Method

Recording of presence, location and DBH of host trees and determining occurrence of *L. pulmonaria* (100 randomly selected forest plots). Burning data and location were derived from forestry records and 1933 aerial photographs.

Results

The percentage of colonised trees was higher on plots in the ungrazed, burnt area. The greatest differences were found at the medium (χ^2 , $P < 0.00$) and largest ($P = 0.07$) DBH-classes.



Discussion

- Presently, a single burnt area has been sampled. Thus, independent replicates are still necessary to confirm these results.
- The impact of grazing seems to have a negative effect on the occurrence of host trees and, therefore, also on *L. pulmonaria*.
- At a local scale, heavy disturbance does not have a long term effect on a dispersal limited species such as *L. pulmonaria*.

Study area

Legend

Study area "Les Ambournex"

Location host-trees

- Colonised
- Uncolonised

Sample plots

To be visited in 2003

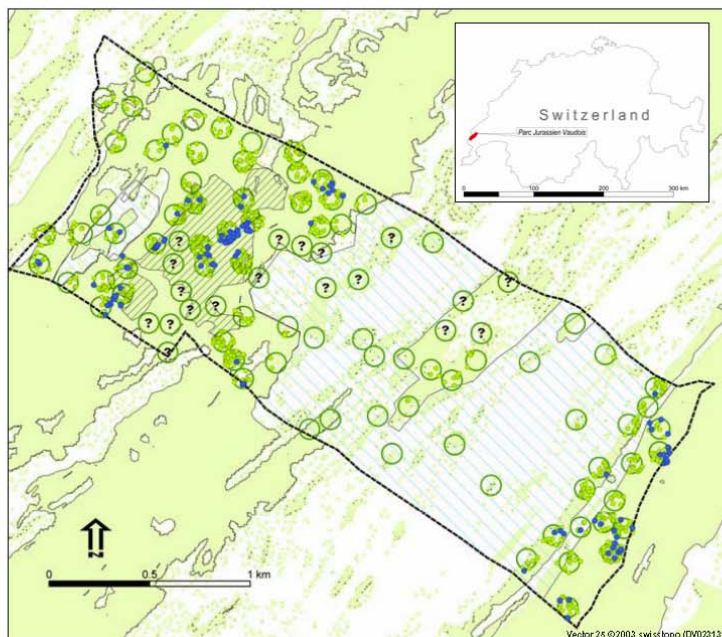
Area examined (1 ha)

Land use

- Grazed
- Logged & burnt in 1871

Land coverage (Swisstopo)

- Forest
- Isolated forest patch
- Pasture



Kalwij, J.M., S. Werth & C. Scheidegger (18-05-2003) Will *Lobaria* survive in this landscape? Poster, NCCR Exposition, Botanical Garden, Neuchâtel, Switzerland.

Abstract: The effect of landscape changes on the survival of a lichen species, *Lobaria pulmonaria*, that grows on trees are the topic of this study. *Lobaria* is rare and endangered in Switzerland, but common in the Parc Jurassien Vaudois, our study area. The species only rarely colonises new trees because its spores can only reach a short distance. The further away a particular tree is from the closest *Lobaria*, the more difficult it is for the lichen to colonise it. What complicates the situation, is that *Lobaria* only grows on old maples. Maples are often far away from each other in the study area which is dominated by spruce, and the young ones often eaten by cows. The more cows graze in an area, the less young maple trees can grow to old age. Old trees will eventually die, and with it *Lobaria*. For *Lobaria* to persist in the area, a suitable tree nearby must therefore be colonised before the old tree dies. This means that the more cow-grazing there is, the less *Lobaria* there will be. This is how landscape changes brought about by management decisions - e.g. where cows browse and where they don't - influence the survival of *Lobaria*.

Le lichen, l'érable et la vache

Le lichen pulmonaire (*Lobaria pulmonaria*) est une espèce de lichen menacée en Suisse, mais qu'on trouve assez fréquemment dans le Parc jurassien vaudois (PJV).

Ce lichen croît surtout sur l'érable. Il ne réussit que très rarement à coloniser de nouveaux arbres, probablement en raison de ses spores qui ne peuvent diffuser que sur de courtes distances. Dans le PJV, les érables sont éloignés les uns des autres, car le paysage typique des pâturages boisés est dominé par les forêts d'épicéas et de saules. Les vaches broutent souvent des plantules d'érables. Si l'activité de pâture est trop intense, elle provoque à long terme une diminution d'arbres hôtes adaptés pour accueillir le lichen pulmonaire. C'est pourquoi, il faut soigneusement planifier l'occupation du pâturage par le bétail.

Les lichens sont des éléments importants de la biodiversité des pâturages boisés. Le lichen pulmonaire est un représentant d'un groupe d'espèces de lichens rares et témoigne de la haute valeur en matière de protection de la nature que l'on accorde au peuplement forestier.

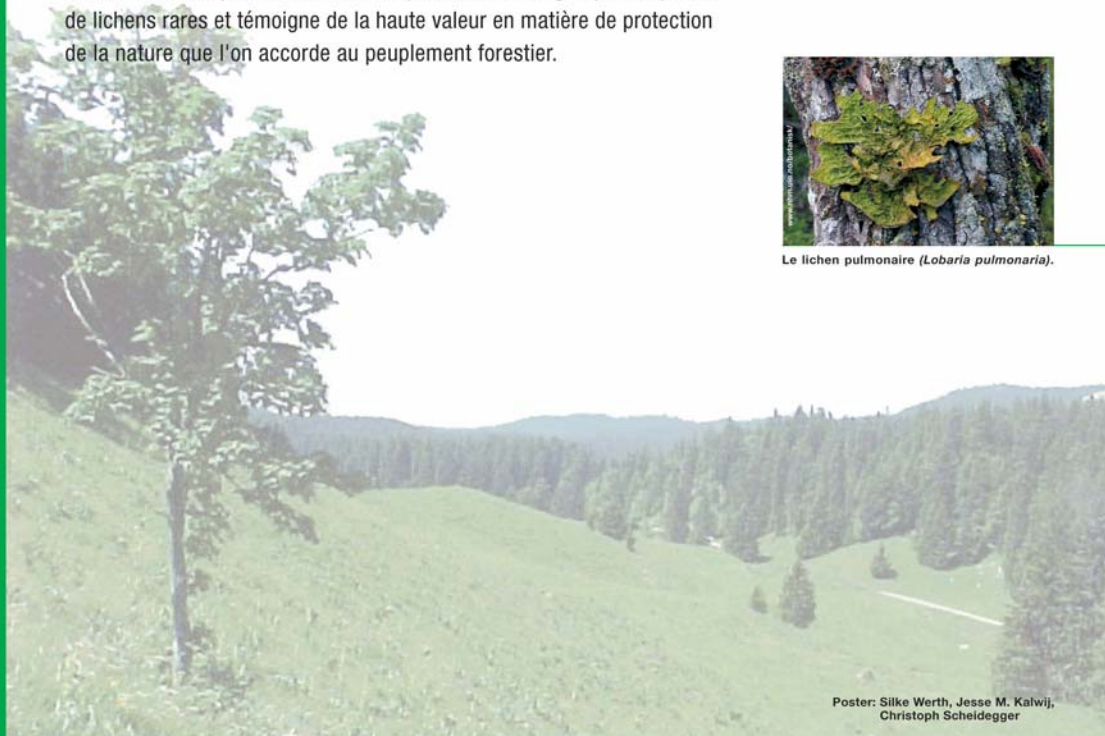


Vache broutant un jeune feuillu dans un pâturage boisé.
Photo: extrait de J.D. Gallandat et al (1995)

Érable sycomore dans un pâturage boisé dans la région du Marchairuz.



Le lichen pulmonaire (*Lobaria pulmonaria*).



Poster: Silke Werth, Jesse M. Kalwij, Christoph Scheidegger

Die Lungenflechte, der Ahorn und die Kuh

Grasende Kuh mit verbissenem jungem Laubbaum in einer Wytweide.
Foto: in J.D. Gallandat et al (1995)



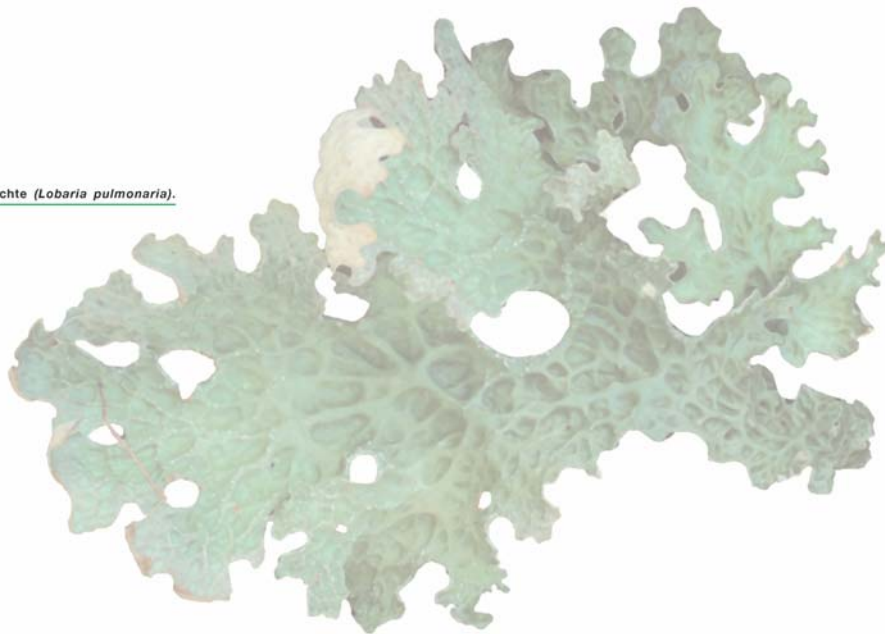
Bergahorn in einer Wytweide im Marchairuz-Gebiet.

Die Lungenflechte (*Lobaria pulmonaria*) ist eine Flechtenart, die in der Schweiz gefährdet ist, aber im Parc jurassien vaudois (PJV) recht häufig vorkommt. Die Lungenflechte wächst dort meist auf Ahorn, und es gelingt ihr nur selten, neue Bäume zu besiedeln - vermutlich weil ihre Sporen nur über kurze Distanzen verbreitet werden. Einzelne Ahorne sind im PJV weit voneinander entfernt, denn die typische Waldweidelandschaft ist von Fichtenmischwäldern und Weiden dominiert.

Weil grasende Kühe oft Ahornsämlinge fressen, kommt es bei hoher Beweidungsintensität langfristig zu einer Abnahme geeigneter Trägerbäume für die Lungenflechte. Daher muss die Beweidung im PJV sorgfältig geplant werden.

Flechten sind ein wichtiger Bestandteil der Biodiversität von Waldweiden. Die Lungenflechte ist eine Vertreterin einer Gruppe seltener Flechtenarten und weist auf einen hohen Naturschutzwert des Waldbestandes hin.

Die Lungenflechte (*Lobaria pulmonaria*).



Poster: Silke Werth, Jesse M. Kalwij,
Christoph Scheidegger

Kalwij, J.M., H. H. Wagner, O.Wildi & C. Scheidegger (06-02-2004) How vulnerable is the endangered lichen *L. pulmonaria* to disturbance? Poster, Biology '04, Fribourg (Switzerland), Switzerland.

Abstract: The endangered epiphytic lichen *Lobaria pulmonaria* is assumed to indicate undisturbed, old-growth forests. However, in the Parc Jurassien Vaudois (CH), this species occurs in large numbers, even though this sylvopastoral landscape is regularly disturbed by cattle grazing, tree logging, and occasionally by fire or windfall. The effect on the distribution of the lichen was tested for two types of disturbance: (1) episodic stand-replacing disturbance (intensive logging or fire, 100-150 years ago) and (2) a continuous, low intensity disturbance (grazing). Colonization by *L. pulmonaria*, host tree diameter at breast height (DBH) and current grazing status were recorded for each potential host tree within a random sample of 251 plots of 1 ha. Boundaries of two historic stand-replacing disturbances were reconstructed using aerial photographs from the year 1933. Surprisingly, a log-linear model showed that neither grazing nor the historical stand replacement resulted in the expected lower colonization rate of *L. pulmonaria*. However, there were a significantly higher number of host trees per plot within the perimeter of the historical stand-replacing disturbance. The observed correlation between DBH and colonization rate, did not indicate that *L. pulmonaria* is dispersal limited. The spatial distribution of the lichen suggests that *L. pulmonaria* is able to recolonize disturbed areas from nearby sources. Therefore, further research is needed to determine at which spatial and temporal scales disturbances affect the persistence of this model species.



How vulnerable is the endangered lichen *Lobaria pulmonaria* to disturbance?

Jesse M. Kalwij, H.H. Wagner, O. Wildi, C. Scheidegger

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Introduction

The lichen is assumed to indicate undisturbed, old-growth forests. In the study area, this species occurs in large numbers, even though this sylvopastoral landscape is regularly disturbed by cattle grazing, tree logging, and occasionally by fire or windfall.

Tested

The effect of two types of disturbance on the distribution of the lichen:

1. episodic, stand-replacing disturbances (intensive logging or fire, 100-150 years)
2. continuous, low intensity disturbance (grazing).

Hypothesis

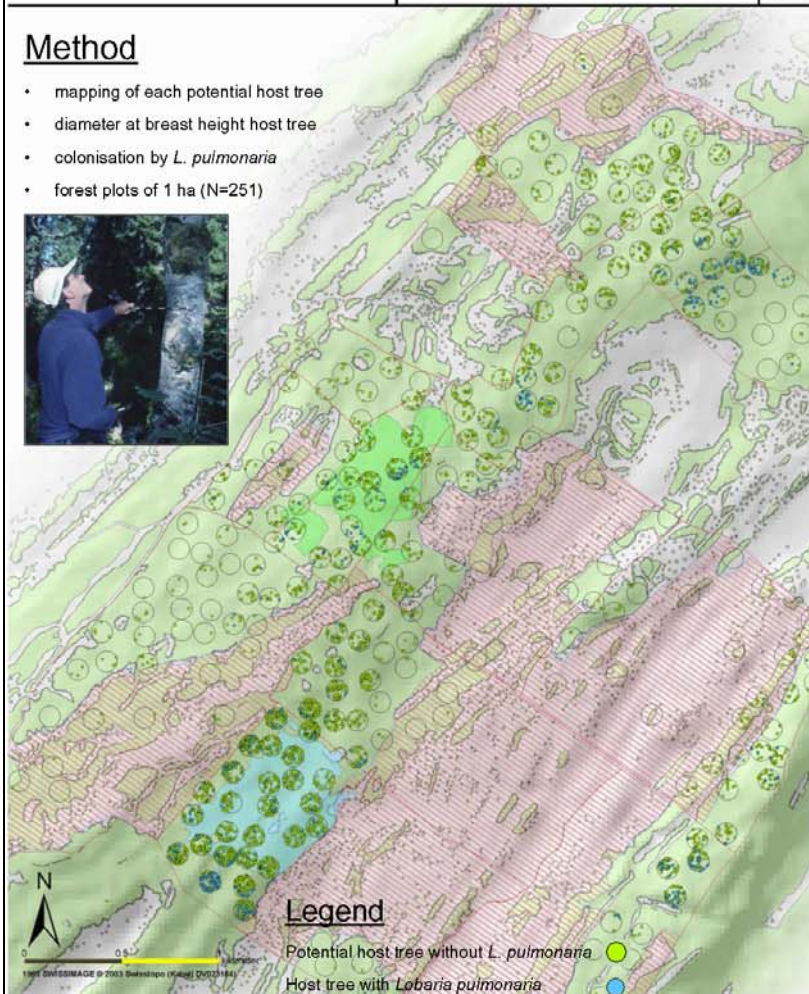
Disturbance level has a negative impact on the distribution of *L. pulmonaria*.



Lobaria pulmonaria, an indicator of 'old forest'?

Method

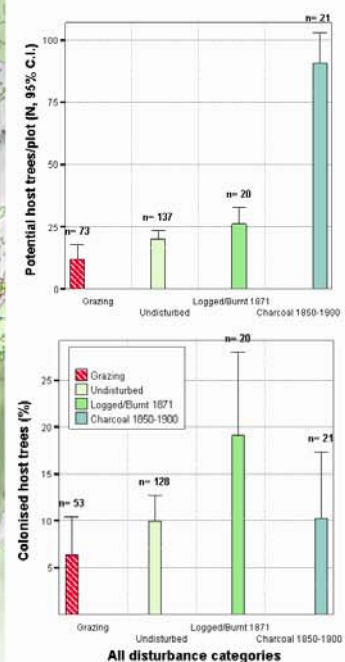
- mapping of each potential host tree
- diameter at breast height host tree
- colonisation by *L. pulmonaria*
- forest plots of 1 ha (N=251)



Study area



Results



Discussion

- Disturbance did not have the expected negative impact on the distribution of *Lobaria*, but showed a significantly higher number of potential host trees for the charcoal area.

- The spatial distribution of the lichen suggests that *L. pulmonaria* is able to recolonise disturbed areas from nearby sources.

- further research is needed to determine at which spatial and temporal scales disturbances affect the persistence of this model species.

Appendix E: Oral presentations

Presentation 1. Kalwij, J.M., H. H. Wagner, O.Wildi & C. Scheidegger (11-09-2003)

Long-term effects of disturbance on the occurrence of an endangered lichen in a pasture-woodland landscape. Oral presentation, 33rd GFOe (Ecological Society of Germany, Austria and Switzerland) Meeting, Halle (Saale), Germany.

Presentation 2. Kalwij, J.M., H. H. Wagner, O.Wildi & C. Scheidegger (31-10-2003) Is

the lichen *L. pulmonaria* really susceptible to disturbance? One of four winning abstracts of the abstract competition and oral presentation, ZOeK (Centre for Terrestrial Ecosystem Management and Protection) PhD-congress, Ascona TI (Switzerland).

Presentation 3. Kalwij, J.M., H. H. Wagner & O.Wildi (19-09-2004) Predicting stand

structure and dynamics in a sylvo-pastoral landscape using time-series of aerial photographs and LiDAR data. Oral presentation, 47th IAVS meeting (International Association for Vegetation Science Meeting), Kona (Hawaii), USA.

Presentation 4. Kalwij, J.M., H. H. Wagner & C. Scheidegger (31-03-2005) A multi-scale

quantification of stand-structure dynamics in a pasture-woodland landscape using time-series of aerial photographs and LiDAR data. NCCR Plant Survival International Conference, Leysin, VS, (Switzerland).

Kalwij, J.M., H. H. Wagner, O. Wildi & C. Scheidegger (11-09-2003) Long-term effects of disturbance on the occurrence of an endangered lichen in a pasture-woodland landscape. Oral presentation, 33rd GFOe (Ecological Society of Germany, Austria and Switzerland) Meeting, Halle (Saale), Germany.

Abstract: Pasture-woodland landscapes are regularly disturbed by cattle grazing and tree logging, as is the case in the Parc Jurassien Vaudois (CH). The endangered epiphytic lichen *Lobaria pulmonaria* is assumed to be typical of forests with a high degree of continuity (old-growth forest, long-term undisturbed). This assumption is apparently contradicted by the observation of a large number of this lichen in the area. The effect on the occurrence of *L. pulmonaria* was tested for two types of disturbance: fire (rare, direct disturbance of high severity) and grazing (frequent, indirect disturbance of low severity). Colonization by *L. pulmonaria*, DBH and current grazing were observed for each potential host tree within a hierarchical random sample of 100 forest plots. The perimeter of a historically documented forest fire in 1871 was reconstructed stereoscopically from 1933 aerial photographs. A log-linear model showed that the percentage of colonized trees was highest on plots in the ungrazed, burnt area. The greatest differences were found at medium (X^2 , $P < 0.001$) and largest ($P = 0.07$) DBH-classes. Grazing showed an indirect negative effect on the occurrence of *L. pulmonaria*. On a forest stand level, a high severity disturbance does not necessarily have a long term effect on *L. pulmonaria*. In contrary to the expectation, the indirect low severity disturbance (grazing) showed a more negative effect on *L. pulmonaria* than the high severity direct disturbance (fire). Further research is needed to determine the spatial and temporal scales at which disturbance affects the persistence of indicator species for ecological continuity.

Kalwij, J.M., H. H. Wagner, O.Wildi & C. Scheidegger (31-10-2003) Is the lichen *L. pulmonaria* really susceptible to disturbance? One of four winning abstracts of the abstract competition and oral presentation, ZOeK (Centre for Terrestrial Ecosystem Management and Protection) PhD-congress, Ascona TI (Switzerland).

Abstract: The endangered epiphytic lichen *Lobaria pulmonaria* is assumed to indicate undisturbed, old-growth forests. In the Parc Jurassien Vaudois (CH) however, the lichen occurs in large numbers, although this sylvopastoral landscape is regularly disturbed by cattle grazing and tree logging, and occasionally by fire or windfall. The effect on the distribution of the lichen was tested for two types of disturbance: episodic stand-replacing disturbance (intensive logging or fire, 100-150 years ago) and a continuous, low intensity disturbance (grazing). Colonization by *L. pulmonaria*, host tree diameter at breast height (DBH) and current grazing status were recorded for each potential host tree within a random sample of 251 plots of 1 ha. Boundaries of two historic stand-replacing disturbances were reconstructed using aerial photographs from the year 1933. Surprisingly, a log-linear model showed that neither grazing nor the historical stand replacement resulted in the expected lower colonization rate of *L. pulmonaria*. However, there was a significantly higher number of host trees per plot within the perimeter of the historical stand-replacing disturbance. The observed correlation between DBH and colonization rate, indicates that *L. pulmonaria* is dispersal limited. Nevertheless, the spatial distribution of the lichen suggests that *L. pulmonaria* is able to recolonize disturbed areas from nearby sources. Therefore, further research is needed to determine at which spatial and temporal scales disturbances affect the persistence of this model species.

Kalwij, J.M., H. H. Wagner & O. Wildi (19-09-2004) Predicting stand structure and dynamics in a sylvo-pastoral landscape using time-series of aerial photographs and LiDAR data. Oral presentation, 47th IAVS meeting (International Association for Vegetation Science Meeting), Kona (Hawaii), USA.

Abstract: Sylvo-pastoral landscapes consist of a mosaic of land-use types, induced by the interaction among a variety of factors, e.g. site conditions, disturbance and land-use. Together, these factors lead to forest heterogeneity at multiple spatial and temporal scales. This study aimed to predict patterns of forest dynamics from land-use types (grazed, abandoned pasture, closed-canopy forest) using modern techniques. Therefore, we quantified spatial patterns of gap dynamics and tree regeneration in a Swiss pasture-woodland and compared these to land-use types over time. Digital canopy surface models (DSM) were extracted from aerial photographs (1954, 1980, 1998) using a high-resolution digital terrain (elevation) model as a reference. LiDAR (airborne laser scanning) DSM and data of a long-term permanent plot were used for verification purposes. Indices of spatial distribution patterns, e.g. forest-gap geometry, connectivity and density, were calculated for each land-use type. Results show that in grazed areas, trees were over dispersed within homogeneous stands. Tree density remained constant at larger spatial extents, but individuals became more aggregated. On abandoned pastures, tree cover increased, but not tree density. Neither tree density nor gap dynamics of closed forests showed significant changes over the time period studied. This approach allowed reliable quantification of forest dynamics at the landscape level. Differences between land-use specific patterns of tree distribution within the considered landscape can be explained by the predominance of plant-herbivore interactions, replacement mechanisms, forest growth and edaphic factors.

Kalwij, J.M., H. H. Wagner & C. Scheidegger (31-03-2005) A multi-scale quantification of stand-structure dynamics in a pasture-woodland landscape using time-series of aerial photographs and LiDAR data. NCCR Plant Survival International Conference, Leysin, VS, (Switzerland).

Abstract: Processes governing tree regeneration are assumed to differ between currently grazed wooded pastures, abandoned pastures, and long-term forests. We hypothesize that each dominant process has its own spatial component, leading to systematic differences in the spatial patterns and spatio-temporal dynamics of tree-patches between the three land-use types. For each type, we randomly selected three replicate plots and quantified the spatial distribution of tree-patches for three time steps using lacunarity, a cover-independent multi-scale measure of spatial aggregations of tree-patches and gaps. Plot size was determined by the spatial extent at which the standard deviation of vegetation height stabilized with increasing plot size. A digital elevation model (DEM) and present vegetation height were interpolated from LiDAR (airborne laser scanning) data for the purpose of orthorectification, verification of Boolean classification and comparison of present vegetation height. Digital Boolean maps (tree-patch or gap) with a resolution of 0.5 m were extracted from orthorectified aerial photographs of 1954, 1980, and 1998. Within each plot, lacunarity as a function of window size was calculated for each time step. In long-term forests lacunarity decreased over time within homogenous stands, suggesting that past logging intensity was higher than present. Tree-patch cover remained constant at larger spatial extents, but patches became more aggregated. On abandoned pastures, average vegetation height was similar to that of a closed forest and tree cover had increased over time, but not patch density. Neither tree-patch cover nor lacunarity of the selected pastures showed changes over time, suggesting that present land-use was sustainable for the examined time period. Our approach allowed a multi-scale quantification up to the landscape level of changes in tree-patches and gaps over several time steps and showed that present patterns of tree-patch distribution could be readily explained by landscape history.

Appendix F: Contributions as co-author

Bolli, J., J. M. Kalwij, H. H. Wagner, P. Cherubini, C. Scheidegger, and A. Rigling. 2005

Feb 24. The use of tree-ring analysis for reconstructing perimeter and intensity of
a historic disturbance in the Jura Mountains, Switzerland. *Landscape Ecology*
Submitted

Sýkora, K. V., J. M. Kalwij, and P. J. Keizer. 2002. Phytosociological and floristic

evaluation of a 15-year ecological management of roadside verges in the
Netherlands. *Preslia* 74:421-436.

Werth, S., H. H. Wagner, R. Holderegger, J. M. Kalwij, and C. Scheidegger. 2005a.

Spatially explicit population genetics of *Lobaria pulmonaria*. *Molecular Ecology*
:In preparation

Werth, S., H. H. Wagner, J. M. Kalwij, and C. Scheidegger. 2005b. Modeling the

persistence and genetic structure of an epiphytic lichen in a dynamic landscape.
Landscape Ecology :In preparation

Acknowledgements

Writing a thesis is often a lonely process, especially if this is in a foreign country, away from friends, family and partner. However, I consider myself privileged to have had the help, support and friendship of so many people during this period. Although the formal thesis layout of the University of Berne does not leave space for the *Koreferenten*, there should be no doubt that Helene Wagner has been the best daily supervisor that I could have wished for. Thanks to her immense enthusiasm, patience and confidence in my abilities she managed to guide me to the point where I am now. Helene, you were always willing to discuss my proposals and to revise my papers over and over again. I admire your willingness and persistence to focus on all the details of my work. Christoph Scheidegger was the man who brought me to Switzerland and made this thesis possible. Christoph, I am grateful to you for introducing me to the world of *Lobaria pulmonaria* and your ever-inspiring motivation to observe the ecosystem beyond my own project. Due to your initial skepticism about my preliminary field results, I was forced to analyze my results even more thoroughly and it was great to see your enthusiasm grow during the elaboration of my project. Otto Wildi and Brigitta Ammann, thank you for the inspiring discussions we had, support and the constructive comments that you were always prepared to talk about, in spite of your many other obligations.

One of the main reasons for me to study biology was the pleasure of doing field work, being exposed to the elements and to discuss the ecosystem *in vivo*. I therefore greatly enjoyed the many discussions and fieldtrips with the other participants of our NCCR project: Daniel Beguin, Jacqueline Bolli, Alexia Dufour, Francois Gillet, Florence Mazier, Marie-Agnes Moravie, Per Sjoegren, and Chris Smit. Many people have assisted

me during my long weeks in the *Parc Jurassien Vaudois* and only because of their help I was able to collect the large dataset that I have so much profited from: Sanne Knol, Annette van Zonneveld, Silke Werth, and even my mother, Valentine, contributed. In the second field season, field work was made much more comfortable when Daniel Cherix offered us to use the *Chalet à Roch Dessous* of the University of Lausanne, right in the middle of the study area. I will never forget the stunning surrounding of this area and its serenity at nighttime (except when the dormice quarreled).

The Swiss Federal Research Institute for Forest, Snow and Landscape (WSL) is probably one of the best places possible to be a PhD student. Its infrastructure and the presence of so many professionals offered an excellent environment to successfully complete a PhD thesis. My gratitude goes to too many people to list by name: the people from my section Genetic Ecology, the library, the logistic department, the library, the informatics, the remote sensing section, and the list continues. However, my special appreciation goes to Silke Werth, with whom I have shared an office, tent, field house and many long hours of discussion for more than three years. Silke, I admire your patience with my morning moods and will dearly miss you as my office partner.

Life in Zurich would not have been the same without the support of many new friends and my flat mates (Tim Diekötter, Monika Gisler, and Kris Novak). However, Annette, my most important friend and life-partner, stayed in the Netherlands. Annette, I cannot express my admiration for your patience and your efforts to come to Zurich every month for three years in a row. Whether it was while talking to you on the phone, during my field work or at the lake in Zurich, it was always great to have your support and I am confident that our future will be prosperous, wherever that will be in this world.

Curriculum vitae of Jesse Machiel Kalwij

QUALIFICATIONS

2002 – present	PhD in biology at the University of Berne, Switzerland. Selecting and testing indicators of forest history and landscape dynamics.
1995 – 2000	Master of Science degree in biology at the Wageningen Agricultural University, The Netherlands (WAU), specialisation in vegetation science and experimental plant ecology .
1994 – 1996	Propaedeutic degree in biology at the WAU
1988 - 1994	Pre-University Education Certificate at the Jerusalem Catholic Comprehensive School, Venray, The Netherlands

GRANTS & AWARDS

Centre for Invasion Biology, University of Stellenbosch (2005) award for a two-year postdoctoral fellowship at the University of Stellenbosch, South Africa.

NCCR Plant Survival Competitive Travel Grant (2004) to attend the 47th IAVS conference in Kona, Hawai'i, USA.

Winner abstract competition (2003) at the PhD conference of the Centre for Terrestrial Ecology, Switzerland.

LANGUAGES

Dutch (mother tongue)

English (fluently), German (fluently), Afrikaans (good), French (basic)

PERSONAL PARTICULARS

Nationality:	Dutch/Nederlandse
Date of birth:	23rd of November 1976
Place of birth:	Venray, The Netherlands
Marital state:	Single
Driving license:	Passenger cars

EXTRA-CURRICULAR INTERESTS

- Plant taxonomy, alpine ecology, wildlife
- Outdoor activities (trekking, walking, swimming, cycling, fishing and horseback riding)

Curriculum vitae of Jesse Machiel Kalwij

WORK EXPERIENCE

-
- | | |
|-------------------------|---|
| January 2002 - present | PhD candidate. Under the supervision of Professor Dr. Brigitta Ammann of the University of Berne, PD Dr. Christoph Scheidegger, PD Dr. Otto Wildi, and Dr. Helene Wagner of the WSL, I am presently finishing my thesis that deals with selecting and testing of indicator species of land-use history in a pasture-woodland landscape in Switzerland. |
| May– November 2001 | Vegetation scientist for a vegetation survey. Employed by the Wageningen University, I repeated an inventory of relevés in the verges of roads and published the results. This fieldwork has been conducted along freeways in the Netherlands. |
| March 2000 – April 2001 | Botanist for Tau Consultants (Pty) Ltd. For more than a year, I worked as a botanist and GIS researcher for a small consultancy bureau in the Okavango Delta and Chobe National Park, Botswana. My main task was reporting on a plant-ecological survey done in Chobe NP. Other tasks included tracking down and observing lions, conducting roadstrip counts for herbivore monitoring and presenting our company's work for groups of tourists. |
| February– November 1999 | Master of Science thesis in experimental plant ecology at WAU. During this period a colleague and I worked on a thesis concerning the influence of <i>Acacia tortilis</i> on soil fertility. This plant ecological research included the statistical analysis and reporting of data, and enclosed a period of three months working in Tanzania under basic circumstances. The elaboration of the research was conducted under the supervision of Professor Hans de Kroon and Dr. Fulco Ludwig. |
| June– December 1998 | Master of Science thesis in vegetation science at the WAU. In this period a colleague and I worked on a thesis about the development of the vegetation in a nature development project in the Netherlands, which also involved gaining practical experience with Geographical Information Systems (GIS). This study was performed under the supervision of Professor Karlè Šýkora. |
| January – May 1998 | Practical period at the University of Pretoria (UP), Republic of South Africa. Under the supervision of Professor George Bredenkamp of the Department of Botany of the UP and Professor Karlè Šýkora, I gained experience in scientific field work in the discipline of vegetation science. During this time an interest in sustainable management of game and field was awakened. I gained field experience in the Kruger NP (South Africa), Borakalalo NP (South Africa), Chobe NP (Botswana), and various private game ranches and smaller parks. |

Notes and comments

