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# Changes in biodiversity and species composition of temperate beech forests in Switzerland over 26 years

## Veränderungen der Biodiversität und Artenzusammensetzung gemäßigter Buchenwälder in der Schweiz während 26 Jahren

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### Abstract

Ongoing climate warming affects vegetation in multiple ways, although it is difficult to distinguish its influence from other drivers of vegetation change. We studied how forest vegetation in the Albiskette (canton of Zurich, Switzerland), mainly dominated by European beech (*Fagus sylvatica*), changed from 1993 to 2019, while the mean temperature rose by 1.5 °C. To investigate how species richness and vegetation composition had changed during these 26 years, we resampled 46 permanently marked nested-plot series (30 $m^2$, 200 $m^2$ and 500 $m^2$). Using paired *t*-tests, we analysed changes in biodiversity metrics and mean ecological indicator values and related the quantified changes to potential explanatory variables via linear regressions. Using the *z*-values from the power law species-area relationships, we analysed potential changes in beta diversity. Both species richness and herb layer cover significantly decreased from 1993 to 2019 across the three grain sizes. The *z*-values for the transition from 200 $m^2$ to 500 $m^2$ were significantly higher in 2019. The mean light value in the 500-$m^2$ plots in 2019 was also significantly lower than in 1993. Species richness, Shannon diversity and Shannon evenness decreased with increasing tree layer cover. With increasing herb layer cover, species richness increased in the 30-$m^2$ plots and the relative species loss decreased in the 30-$m^2$ and 200-$m^2$ plots. The relationship between species loss and increased canopy cover confirmed that light availability acts as an important driver for species richness. Whether the loss in both herb cover and species is also related to recent summer drought events such as 2018 can only be clarified through further resurveys. Decreases in *z*-values indicate lower beta diversity and more homogenous vegetation in 2019. The decrease in species richness was more pronounced in the 500-$m^2$ plots than in the smaller plots. In some cases, explanatory variables had an effect on the change in species diversity only in the 30-$m^2$ and 200-$m^2$ plots, but not in the 500-$m^2$ plots, indicating that other drivers prevail. The change in species diversity and the influencing factors were clearly scale dependent. Further investigation is required to determine

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whether our findings are merely region-specific or also valid in other biogeographical regions. To ensure that further species loss does not go unnoticed, we recommend the continuation of coordinated resurvey studies and monitoring.

**Keywords:** beech forest, biodiversity, canopy closure, climate change, drought, ecological indicator value, permanent plot, resurvey, Switzerland, vegetation change

**Erweiterte deutsche Zusammenfassung am Ende des Artikels**

## 1. Introduction

Vegetation changes, i.e. shifts in species composition and species richness, can be caused by natural succession, gap dynamics or anthropogenic global change (DAVIS et al. 2005). Global change drivers, such as land use change (POSCHLOD et al. 2005), atmospheric air pollution (BOBBINK et al. 2010), climate change (LENOIR et al. 2008, LACHAT et al. 2010, RIGLING et al. 2013) and the spread of exotic species (e.g. CONEDERA et al. 2018) clearly differ from natural succession or gap dynamics, which are both strongly driven by light availability and direct regrowth of neighbouring species. (e.g. ZOONEVELD 1995, ROMME et al. 2011, KRAMER et al. 2014). Since changes in vegetation may vary with respect to the scale of investigation (from plot to local or global) and habitat characteristics (VELLEND et al. 2017), findings about the relative importance of different drivers of vegetation change often remain inconclusive. One way to detect changes in vegetation are vegetation resurveys. In such resurveys, historical vegetation plots are re-visited, and the new data are compared to the historical data (JANTSCH et al. 2013, KAPFER et al. 2016, DIERSCHKE & BECKER 2020). Changes in species presence/absence and abundance may indicate changes in environmental conditions. In particular, ecological indicator values (ELLENBERG et al. 1991, LANDOLT et al. 2010) correspond fairly well with growth-relevant factors measured in the field (e.g. DIEKMANN 2003).

In temperate forests, plant species richness varies due to differing climatic conditions, disturbance regimes (including management and light availability), and nutrient availability (WOHLGEMUTH et al. 2008, ZELLWEGER et al. 2016). With progressing climate change and nitrogen deposition, changes in community composition and distribution as well as species upshift are observed in temperate forest vegetation (LENOIR et al. 2008, SCHERRER et al. 2017). Another source of change in temperate forests is the spread of exotic (tree) species, which is facilitated by global warming (WALTHER 1997, 2000, WAGNER et al. 2017) and can be amplified by gap-creating extreme events such as storms, wildfires and droughts followed by biotic disturbances (e.g. bark beetle outbreaks) (ENGESSER et al. 2008, MARINGER et al. 2012). Additionally, land use change in forests may strongly impact forest biodiversity, with both negative and positive effects on the species richness of different species groups (DUPOUEY et al. 2002, BEUDERT et al. 2015, NEWBOLD et al. 2015, GOSSNER et al. 2019, SEIDL et al. 2019). In temperate forests, the abandonment of coppicing leads to a decrease of species richness (MÜLLEROVÁ et al. 2015), and the vegetation of unmanaged forests has been found to be less species rich than the vegetation of managed forests (PAILLET et al. 2010). In a meta-analysis BOBBINK et al. (2010) concluded that with increasing nitrogen deposition the species richness of the herb layer decreases in temperate forests. However, according to the study of VET et al. (2014), nitrogen deposition has recently declined in many areas in Europe. Nevertheless, the nitrogen level is still far higher than it was in the 1950s.

To which extent forests in the Central Plateau of Switzerland are influenced by the above-mentioned factors remains unclear. The present study investigates changes in species diversity and species composition of forest habitats of the Albis-Uetliberg mountain chain close to Zurich. In 2019, we resampled 46 permanent nested plots of 30, 200 and 500 m² that were originally recorded as part of the systematic vegetation sampling network of the National Forest Inventory (NFI) in 2003 (WOHLGEMUTH et al. 2008). Because biodiversity depends on the analysed grain size (GILADI et al. 2011, REITALU et al. 2012), potential vegetation change and its drivers may vary with scale, too. We therefore addressed the following research questions: (1) How did species diversity and composition change between 1993 and 2019 across the three plot sizes? (2) How did the averaged indicator values of the plant species change? (3) Which drivers (climate change, forest management and/or nitrogen deposition) correspond with changes in the vegetation?

## 2. Methods

### 2.1 Study area

The study area is located on the Swiss Central Plateau, west of Lake Zurich in the canton of Zurich. Extending from Waldegg to Sihlbrugg, the Albiskette covers an area of 80 km$^2$, its elevation ranging from 490 to 860 m a.s.l. (Fig. 1). The top of the Albiskette is largely forested (WEP 2010). According to cantonal vegetation mapping (AMT FÜR LANDSCHAFT UND NATUR DES KANTONS ZÜRICH 1997), 80% of the forests belong to the sub-alliance *Eu-Fagion*, 15% to the alliance of *Alno-Fraxinion* (10% *Carici remotae-Fraxinetum*), one to the alliance of *Molinio-Pinion* and one to the alliance of *Alnion glutinosae* (ELLENBERG & KLÖTZLI 1972; Supplement E2). A total of 46 vegetation plots located in the 1-km grid of the first National Forest Inventory (LFI; EAFV 1988) were examined. In 1993, WOHLGEMUTH & KULL (1995) surveyed these plots as a pilot study for the Swiss Federal Institute for Forests, Snow and Landscape Research (WSL).

Five plots are located in the Sihlwald Nature Forest Reserve, which is situated in the Albiskette. In this area, forest management was abandoned in 2000. In the other 41 plots, moderate-intensity forest management or timber harvesting is carried out.

### 2.2 Vegetation sampling in 1993

The vegetation plots consist of 30 m$^2$, 200 m$^2$ and 500 m$^2$ concentric circles marked with a metal tube in the centre. Plot centres were in addition referenced using distance and aspect measurements from usually three marked trees or other orientation points. The 46 plots were surveyed during May and September 1993. Vascular plant species were recorded in all three plot sizes using the 7-step cover-abundance scale of BRAUN-BLANQUET (1964), merging the categories r and + (i.e. + as the lowest unit). Herb, shrub and tree layers were each surveyed and estimated independently. Original field data of plot vegetation are documented in Supplement E1, stand structure and site variables of each plot in Supplement E3. Stand structure such as estimated coverage (percent) and height (m) of all layers (moss, herb, shrub, tree) and site variables were assessed in all plot sizes.

### 2.3 Vegetation sampling in 2019

The resurvey of the 46 vegetation plots was carried out from May to September 2019, with survey dates corresponding closely to the original recording dates. We localised the plot centres with documented orientation points, differential GPS (Trimble Geo 7x) and a metal detector (Schonstedt GA-92XTi). In 17 cases we found the original metal pipe or wooden stakes used for marking in 1993, resulting in no localisation error. In 19 cases we found the plot centre using the measurements from the

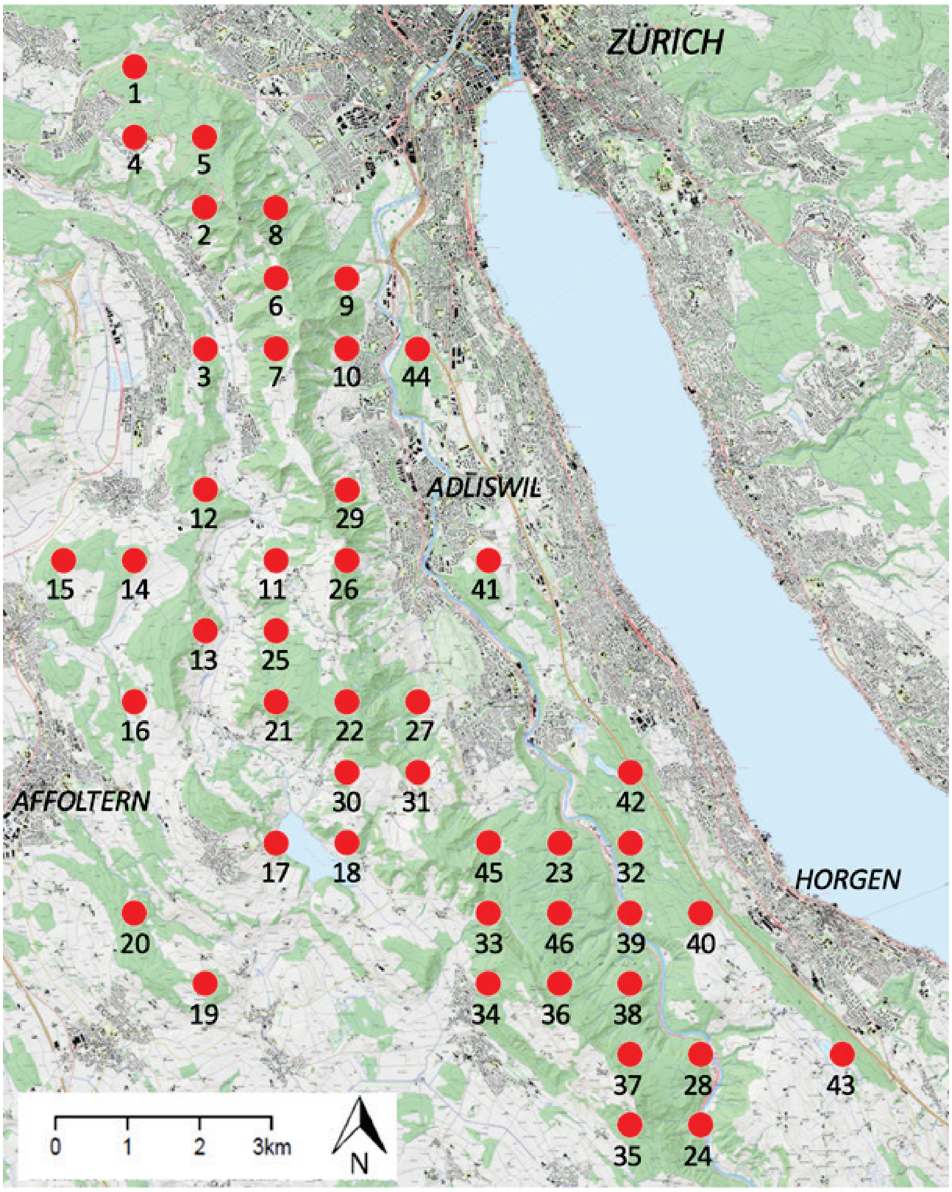


**Fig. 1.** Geographic location of the resurvey plots. Green areas are covered by forests. Background map: swissTLM 2019 (SWISSTOPO 2019).

**Abb. 1.** Die Lage der Untersuchungsflächen. Die grünen Bereiche bilden die Waldflächen ab. Hintergrundkarte: swissTLM 2019 (SWISSTOPO 2019).

marked orientation points, possibly leading to small displacements of the plots. In 10 cases we georeferenced the plot centre with differential GPS, which indicated a possible error of 2.5 m. The method of the vegetation survey was based on the survey of the 1993 data. Woody plants taller than 70 cm were assigned to the shrub layer, and plants taller than 3 m were considered as the tree layer.

## 2.4 Data analysis

### 2.4.1 Data processing

We standardised the nomenclature of the 1993 and current vegetation data according to JUILLERAT et al (2017). We performed the statistical analyses with the software R, version 3.6.1 (R CORE TEAM 2019), and calculated mean indicator values with Vegedaz (Ver. 2019, KÜCHLER 2019). Due to the (nearly) exact relocation, the original and revisited vegetation plots could be compared as pairs (KAPFER et al. 2016). For the analyses, we transformed the 7-step cover-abundance scale of BRAUN-BLANQUET (1964) into percentage values using the geometric mean of the lower- and upper-class limits. Covers of species occurring in more than one layer were summed up.

For each analysis, we examined the normal distribution and variance homogeneity of the residuals using visual inspection of model diagnostics and boxplots. Since the residuals were approximately normally distributed, and their variance approximately homogeneous, we applied parametric methods throughout.

### 2.4.2 Structure and site variables

We compared the layer covers (herb, shrub, tree layer) from 1993 with the covers of the current survey using paired *t*-tests. Using Fisher's Exact test, we tested whether the occurrence of disturbances (presence or absence) depended on the year of the survey.

### 2.4.3 Biodiversity indices

We used the following indices as biodiversity measures:

- Species richness (*S*): the number of species in a plot;
- Shannon diversity (*H*): the species richness combined with the relative abundance of each species (HILL 1973);
- Shannon evenness (*E*): the uniformity of abundance of the different species (SMITH & WILSON 1996).

We tested the differences between the indices for 1993 and 2019, using paired *t*-tests in each case. In addition to these indices, the relative species loss (disappearance) and relative species increase (appearance) (HALLET et al. 2019) were calculated.

### 2.4.4 Species-area relationships

To study the increase of species richness with area, we calculated *z*-values for each of the three grain-size transitions. The *z*-values are derived from the power-law species-area relationship $S = cA^z$, where $S$ is species richness, $A$ area, $c$ and $z$ modelled parameters. The power-law is an appropriate model for species-area relationships in continuous vegetation (DENGLER et al. 2020), and *z*-values are standardised measures of multiplicative beta diversity (POLYAKOVA et al. 2016; see also JURASINSKI et al. 2009). We tested the differences between the 1993 and 2019 *z*-values with paired *t*-tests.

### 2.4.5 Species turnover

Species turnover refers to the change in the composition of a biotic community of a defined habitat due to the addition and loss of species (TUOMISTO 2010). We identified species with a significant change in frequency using the sign test (CLOPPER & PEARSON 1934). In order to compare differences in cover (transformed cover), we used a paired *t*-test for each species. In addition, we counted the species that disappeared over all plots and those that newly appeared.

### 2.4.6 Indicator values

We calculated mean ecological indicator values per plot for temperature, light, moisture, soil reaction and nutrients based on LANDOLT et al (2010). For these calculations, we only used the herb layer data and weighted species by cover. We tested the differences between 1993 and 2019 by paired *t*-tests.

### 2.4.7 Explanatory variables

We tested to which explanatory variables (Supplement E4) a change in biodiversity was related. In order to quantify the change in species diversity, we used the difference (2019 value – 1993 value) between the indices. Changes in light availability, changes in tree and shrub cover and changes in indicator values were used as explanatory variables. Further, the linear regression between the elevation of the plots (m a.s.l.) and the change in species diversity was used to measure whether there is a shift in species diversity to higher elevation. To determine whether the difference in the survey dates had an influence on the change in the biodiversity indices, we calculated a regression between the date differences and the differences in the biodiversity indices. Regarding the influence of disturbance, i.e. small-scale disruption of the soil surface or canopy openings, we divided the plots into three groups: disturbance sources disappeared, disturbance remained and new disturbance agents appeared. We tested the influence of the groups on change in indices using ANOVA.

## 3. Results

### 3.1 Change in structural and location variables

We found a highly significant reduction in the herb layer coverage from 1993 to 2019 in all plot sizes by 20% (Fig. 2). In contrast, the cover values of both the shrub and tree layer did not change significantly. The number of plots with disturbances was lower in 2019 than in 1993, but mean disturbance frequency did not differ significantly between the years.

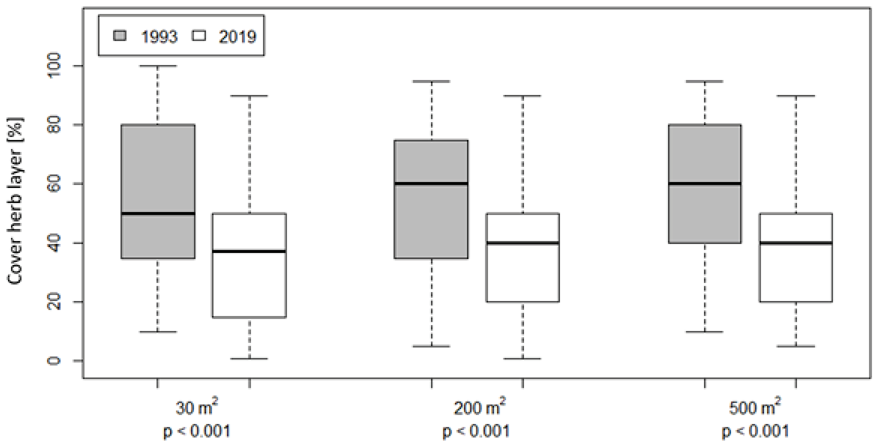


**Fig. 2.** Herb layer cover in percent for the three plot sizes in 1993 and 2019. The significances derived with paired *t*-tests are given below the plot size. The boxes represent the 0.25 and 0.75 quartiles, the median is the line in the box, the whiskers are in the 1.5 interquartile range.

**Abb. 2.** Deckung der Krautschicht in Prozent für die drei Aufnahmeflächengrößen in den Jahren 1993 und 2019. Die mittels gepaarten *t*-Tests ermittelten Signifikanzen der Unterschiede sind jeweils unter den Flächengrößen angegeben. Die Boxen repräsentieren die 0,25- und 0,75-Quartile, der Median ist die Linie in der Box, die Whiskers befinden sich im 1,5-Interquartilbereich.

### 3.2 Change in biodiversity

All plot sizes showed significantly lower species richness in 2019 compared to 1993. With an average of 4.5 fewer species in the 200-$m^2$ plot and 9 fewer species in the 500-$m^2$ plot, the decrease was highly significant ($p < 0.001$). In the 30-$m^2$ plot we found an average decrease of 2.5 species ($p = 0.025$) (Table 1 and Fig. 3). There were no significant differences in Shannon diversity and Shannon evenness between the years (Table 1). The complete plot data of both surveying periods are provided in Supplement E1.

### 3.3 Species turnover

In 2019, we could not find 70 species that had been recorded in 1993, but we found 23 that were not present in the older survey. In the 30-$m^2$ plots, the frequency of *Galium odoratum* and *Carex flacca* decreased significantly. In the 200-$m^2$ plots, six species became significantly rarer over time, while only *Ilex aquifolium* became more common (emerging in 13 plots vs. disappearing in 1 plot; +26%). In the 500-$m^2$ plots, 16 species significantly decreased in frequency (Table 2).

We found increases and decreases in the degrees of cover particularly for woody species (Table 3). While *Fraxinus excelsior* showed the strongest decline in cover, with losses in all three plot sizes and in all layers (from 30 $m^2$ to 500 $m^2$, for tree layer: 6.7–9.4%, shrub layer: 3.6–5.1%; herb layer: 2.9–5.1%), *Ilex aquifolium* was the only species that increased in cover (0.6–0.7%).

### 3.4 Change in the species-area relationship

The mean $z$-value from 200 $m^2$ to 500 $m^2$ was significantly lower in 2019 than in 1993. All other comparisons showed no significant differences (Table 4).

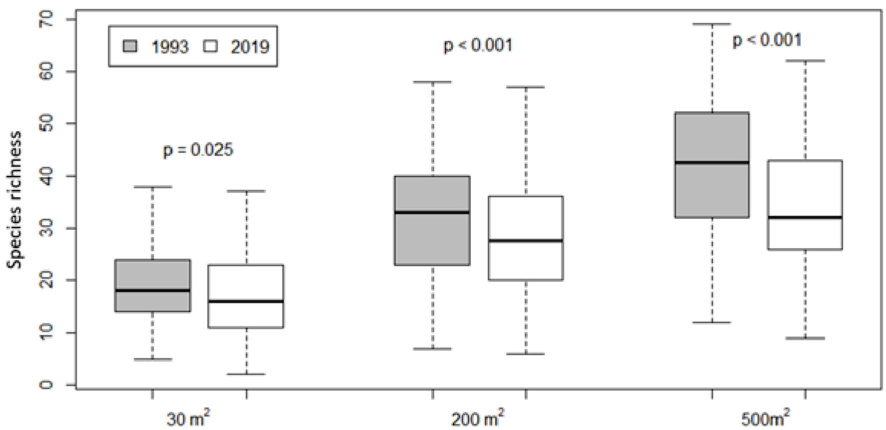


**Fig. 3.** Species richness in 1993 and 2019 across the three plot sizes. The differences were tested with paired $t$-tests. The boxes represent the 0.25 and 0.75 quartiles, the line in the box is the median and the whiskers are in the 1.5 interquartile range.

**Abb. 3.** Artenzahlen der jeweiligen Aufnahmeflächengrößen in den Jahren 1993 und 2019. Die Unterschiede wurden mit gepaarten $t$-Tests geprüft. Die Boxen repräsentieren die 0,25- und 0,75-Quartile, die Linie in der Box ist der Median und die Whiskers befinden sich im 1,5-Interquartilbereich.

**Table 1.** Values of the biodiversity indices ($S$ = Species richness; $H$ = Shannon diversity; $E$ = Shannon evenness) and the structural variables (cover degree in % of HL = herb layer; SL = shrub layer; TL = tree layer), the number of plots with disturbances and the elevation range of the plots. The $p$-values were derived from paired $t$-tests.

**Tabelle 1.** Werte der Biodiversitätsindizes ($S$ = Artenzahl; $H$ = Shannon-Index; $E$ = Shannon-Evenness) und der Strukturvariablen (Deckungsgrad in % der HL = Krautschicht; SL = Strauchschicht; TL = Baumschicht), die Anzahl von Aufnahmeflächen mit Störungen sowie die Höhenlage. Die $p$-Werte basieren auf gepaarten $t$-Tests.

| | 30 m² | | | | 200 m² | | | | 500 m² | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Min | Max | Mean | $p$-Value | Min | Max | Mean | $p$-Value | Min | Max | Mean | $p$-Value |
| S 1993 | 5 | 38 | 19.0 | **0.025** | 7 | 58 | 32.5 | **< 0.001** | 12 | 69 | 42.8 | **< 0.001** |
| S 2019 | 2 | 37 | 16.5 | | 6 | 57 | 28.0 | | 9 | 62 | 33.8 | |
| H 1993 | 0.30 | 2.58 | 1.50 | 0.966 | 0.57 | 2.61 | 1.98 | 0.580 | 0.64 | 2.84 | 2.20 | 0.180 |
| H 2019 | 0.05 | 2.65 | 1.49 | | 0.32 | 3.08 | 1.94 | | 0.54 | 3.28 | 2.11 | |
| E 1993 | 0.16 | 0.72 | 0.52 | 0.418 | 0.24 | 0.72 | 0.57 | 0.576 | 0.26 | 0.74 | 0.59 | 0.485 |
| E 2019 | 0.08 | 0.78 | 0.54 | | 0.13 | 0.88 | 0.59 | | 0.19 | 0.91 | 0.60 | |
| HL [%]1993 | 10 | 100 | 54 | **< 0.001** | 5 | 95 | 56 | **< 0.001** | 10 | 95 | 58 | **< 0.001** |
| HL [%] 2019 | 1 | 90 | 34 | | 1 | 90 | 36 | | 5 | 90 | 38 | |
| SL [%]1993 | 0 | 80 | 18 | 0.319 | 1 | 60 | 23 | 0.360 | 1 | 70 | 25 | 0.481 |
| SL [%] 2019 | 0 | 80 | 15 | | 1 | 70 | 20 | | 1 | 70 | 22 | |
| TL [%]1993 | 5 | 100 | 73 | 0.673 | 5 | 95 | 72 | 0.972 | 5 | 95 | 72 | 0.966 |
| TL [%] 2019 | 0 | 95 | 71 | | 35 | 95 | 72 | | 35 | 95 | 71 | |
| Disturbance 1993 | Number: 17 | | | | Number: 24 | | | | Number: 28 | | | |
| Disturbance 2019 | Number: 13 | | | | Number: 21 | | | | Number: 25 | | | |
| Altitude | 490–860 m a.s.l. | | | | | | | | | | | |

**Table 2.** Species that have become significantly rarer (-) or more frequent (+), tested with the sign test ($\alpha = 0.05$). Number of plots in which the species increased and decreased, respectively.

**Tabelle 2.** Arten, die signifikant seltener (-) oder häufiger (+) geworden sind, getestet mit dem Vorzeichentest ($\alpha = 0{,}05$). Anzahl Plots, in welchen die Art neu hinzugekommen ist bzw. in denen sie verschwunden ist.

| Species | Increase | Decrease | *p*-value | Change |
|---|---|---|---|---|
| Plots 30 m² | | | | |
| *Galium odoratum* | 2 | 12 | 0.013 | - |
| *Carex flacca* | 0 | 7 | 0.017 | - |
| Plots 200 m² | | | | |
| *Ilex aquifolium* | 13 | 1 | 0.002 | + |
| *Galium odoratum* | 0 | 10 | 0.002 | - |
| *Sorbus aria* | 0 | 8 | 0.008 | - |
| *Fragaria vesca* | 0 | 6 | 0.031 | - |
| *Phyteuma spicatum* | 3 | 12 | 0.035 | - |
| *Brachypodium sylvaticum* | 3 | 12 | 0.035 | - |
| *Primula elatior* | 1 | 8 | 0.039 | - |
| Plots 500 m² | | | | |
| *Sorbus aria* | 0 | 12 | < 0.001 | - |
| *Cornus sanguinea* | 0 | 9 | 0.004 | - |
| *Brachypodium sylvaticum* | 0 | 9 | 0.004 | - |
| *Anemone nemorosa* | 3 | 15 | 0.008 | - |
| *Fragaria vesca* | 1 | 10 | 0.012 | - |
| *Epilobium montanum* | 0 | 7 | 0.016 | - |
| *Sambucus nigra* | 0 | 7 | 0.016 | - |
| *Phyteuma spicatum* | 3 | 13 | 0.021 | - |
| *Taraxacum officinale* | 1 | 9 | 0.021 | - |
| *Dryopteris dilatata* | 2 | 11 | 0.022 | - |
| *Luzula pilosa* | 0 | 6 | 0.031 | - |
| *Pinus sylvestris* | 0 | 6 | 0.031 | - |
| *Galium odoratum* | 0 | 6 | 0.031 | - |
| *Impatiens parviflora* | 2 | 10 | 0.039 | - |
| *Poa trivialis* | 1 | 8 | 0.039 | - |
| *Deschampsia cespitosa* | 1 | 8 | 0.039 | - |

### 3.5 Changes of indicator values

The mean light values were significantly lower in the 500-m² plots in 2019 compared to 1993 (Supplement E5 and Fig. 4). There was no significant change in the 30-m² and 200-m² plots. Regarding moisture, temperature, soil reaction and nutrient values, there were no significant changes for any plot size (Fig. 4).

### 3.6 Explanatory variables

The cover of the tree layer (canopy) correlated negatively with species richness, Shannon diversity and Shannon evenness, and positively with relative species loss (Fig. 5, Table 5, Supplement E6).

With increasing herb layer cover, the species richness increased in the 30-m² plot (Fig. 6) and the relative species loss decreased (Supplement E7). We found a negative effect of an increased tree and shrub layer cover (summed) on Shannon diversity in the 200-m² plot and 30-m² plots as well as on Shannon evenness of the 200-m² plots. (Supplement E8).

**Table 3.** Species with significant changes in the coverage ratio in the different strata with their coverage difference (cover 2019 - cover 1993) and the respective pointer values. The *p*-values were derived from paired *t*-tests. The list is sorted by the p-values in ascending order.

**Tabelle 3.** Arten mit signifikanter Änderung im Deckungsgrad in den verschiedenen Schichten mit deren Deckungsdifferenz (Deckung 2019 – Deckung 1993). Die *p*-Werte stammen aus gepaarten *t*-Tests. Die Liste ist aufsteigend nach den p-Werten sortiert.

| Layer | Species | *p*-value | Difference cover [%] |
|---|---|---|---|
| 30 $m^2$ | | | |
| tree | *Fraxinus excelsior* | 0.011 | -6.7 |
| herb | *Fraxinus excelsior* | 0.019 | -2.1 |
| herb | *Mercurialis perennis* | 0.024 | -4.8 |
| herb | *Galium odoratum* | 0.026 | -0.9 |
| herb | *Fagus sylvatica* | 0.036 | -3.3 |
| herb | *Acer pseudoplatanus* | 0.037 | -2.2 |
| shrub | *Fraxinus excelsior* | 0.039 | -2.9 |
| 200 $m^2$ | | | |
| tree | *Fraxinus excelsior* | < 0.001 | -7.4 |
| herb | *Fraxinus excelsior* | 0.002 | -3.6 |
| herb | *Mercurialis perennis* | 0.003 | -7.5 |
| tree | *Picea abies* | 0.004 | -5.5 |
| herb | *Acer pseudoplatanus* | 0.009 | -3.7 |
| shrub | *Acer pseudoplatanus* | 0.011 | -4.0 |
| shrub | *Fraxinus excelsior* | 0.012 | -3.4 |
| herb | *Galium odoratum* | 0.015 | -1.1 |
| herb | *Fagus sylvatica* | 0.026 | -3.1 |
| shrub | *Ilex aquifolium* | 0.031 | 0.6 |
| 500 $m^2$ | | | |
| tree | *Fraxinus excelsior* | < 0.001 | -9.4 |
| herb | *Fraxinus excelsior* | < 0.001 | -5.1 |
| shrub | *Hedera helix* | < 0.001 | -2.2 |
| herb | *Mercurialis perennis* | 0.001 | -6.9 |
| tree | *Picea abies* | 0.002 | -6.7 |
| shrub | *Fraxinus excelsior* | 0.004 | -5.1 |
| herb | *Galium odoratum* | 0.007 | -1.3 |
| shrub | *Ilex aquifolium* | 0.008 | 0.7 |
| shrub | *Acer pseudoplatanus* | 0.008 | -4.2 |
| herb | *Lamium galeobdolon* | 0.013 | -1.3 |
| tree | *Acer pseudoplatanus* | 0.023 | -4.2 |
| shrub | *Tamus communis* | 0.024 | -0.1 |
| herb | *Rubus fruticosus* aggr. | 0.024 | -7.2 |
| tree | *Abies alba* | 0.026 | -2.1 |
| shrub | *Sorbus aria* | 0.040 | -0.3 |
| herb | *Allium ursinum* | 0.040 | -3.7 |

**Table 4.** Mean *z*-values for the area enlargement. The *p*-values were derived from paired *t*-tests.

**Tabelle 4.** Mittlere *z*-Werte zu den Flächenvergrößerungen. Die *p*-Werte stammen aus gepaarten *t*-Tests hergeleitet.

| | *z*-value 1993 | *z*-value 2019 | *p*-value |
|---|---|---|---|
| Area enlargement 30 $m^2$ – 200 $m^2$ | 0.295 | 0.295 | 0.998 |
| Area enlargement 30 $m^2$ – 500 $m^2$ | 0.302 | 0.275 | 0.228 |
| Area enlargement 200 $m^2$ – 500 $m^2$ | 0.315 | 0.235 | 0.010 |

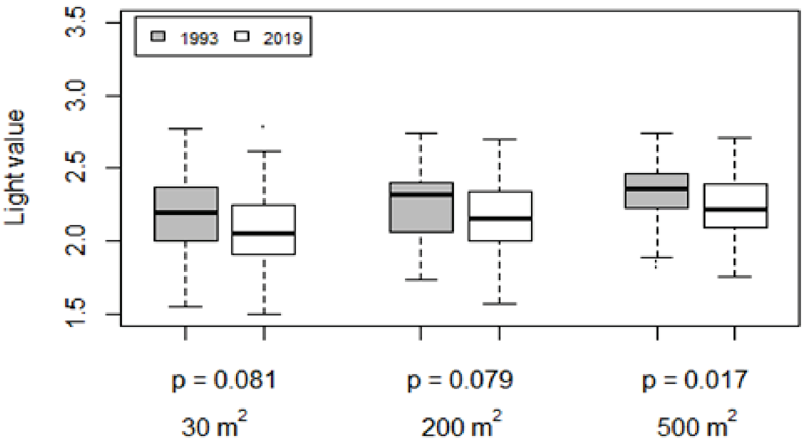


**Fig. 4.** Changes in mean light values between 1993 and 2019 across the three plot sizes. Indicator values according to LANDOLT et al. (2010). The *p*-values were derived from paired *t*-tests. The boxes represent the 0.25 and 0.75 quartiles, the line in the box is the median and the whiskers are in the 1.5 interquartile range and the outliers are represented as dots.

**Abb. 4.** Veränderungen der mittleren Lichtzahlen zwischen 1993 und 2019, abhängig von der Plotgrösse. Zeigerwerte gemäss Landolt et al. (2010). Die *p*-Werte basieren auf gepaarten *t*-Tests. Die Boxen repräsentieren die 0,25- und 0,75-Quartile, die Linie in der Box ist der Median und die Whiskers befinden sich im 1,5-Interquartilbereich und die Ausreisser sind als Punkte Dargestellt.

We found a significant relationship between the species richness recorded in 1993 and the change in species richness. For all plot sizes, the higher the species richness was in 1993, the larger the species loss in 2019. In addition, the relative species increase decreased with the original species richness in the 30-m² plots (Table 5, Supplement E10).

The regressions between species loss and the 2019 indicator values showed that the higher the current light value is, the smaller the species loss was (Supplement E9). For all other indicator values (1993 indicator values, 2019 indicator values, and the difference between the new and old indicator values), we found no significant regression with the biodiversity indices. Also, there was no relationship between the change in biodiversity indices and the time of recording, elevation above sea level, change in disturbance or shrub cover (Table 5).

## 4. Discussion

### 4.1 Change in species diversity and composition

While herb layer cover significantly decreased from 1993 to 2019, no significant changes occurred in the other structural and site variables (tree layer cover, shrub layer cover, disturbance frequency). HELM et al. (2017) also found a loss of cover in the herb layer in their mountain forest survey, and studies by BRUNET & TYLER (2000) and ARCHAUX & WOLTERS (2006) showed that the productivity of the herb layer in forests can be reduced due to drought. In our case, the pronounced summer drought of 2018 (METEOSCHWEIZ 2019) needs to be considered (SCHULDT et al. 2020). The loss of cover in the herb layer may have been

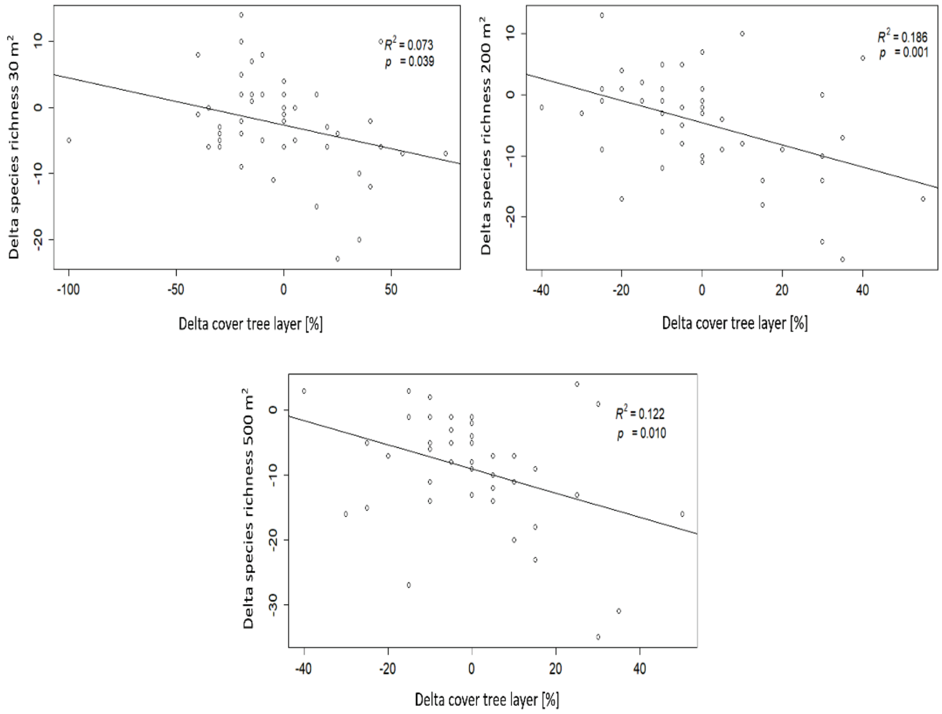


**Fig. 5.** Linear relationships between the change in tree cover [%] (2019 value – 1993 value) and the changes in species richness (2019 value – 1993 value).

**Abb. 5.** Lineare Beziehungen zwischen der Änderung der Deckung durch die Baumschicht [%] (Wert 2019 – Wert 1993) und den Änderungen des Artenzahl (Wert 2019 – Wert 1993).

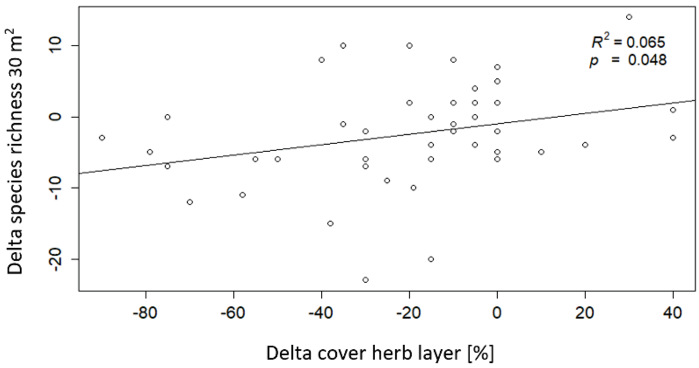


**Fig. 6.** Linear regressions between herb layer cover [%] and species richness (2019 value – 1993 value).

**Abb. 6.** Lineare Regressionen zwischen der Krautschichtdeckung [%] und der Artenzahl (Wert 2019 – Wert 1993).

**Table 5.** *p*-values of the regressions between the changes in biodiversity indices (species richness, Shannon diversity, Shannon evenness, species loss rate, species increase rate) and the change in layer cover values, as well as the difference in survey dates. The "Disturbance" column lists the *p*-values of the differences in the indices for new or disappearing sources of disturbance. The column "m a.s.l." lists the *p*-values of the relationships between elevation and the biodiversity indices.

**Tabelle 5.** *p*-Werte der Regressionen zwischen den Veränderungen der Biodiversitätsindizes (Artenzahl, Shannon-Index, Shannon-Evenness, Artenverlust-Rate, Artenzunahme-Rate) und der Veränderung der Schichtdeckungen sowie der Differenz der Erhebungszeitpunkte. In der Spalte "Disturbance" sind die *p*-Werte der Unterschiede der Indizes bei neu hinzukommenden der verschwindenden Störungsquellen aufgelistet. In der Spalte "m a.s.l." sind die *p*-Werte der Beziehung zwischen der Höhenlage und den Biodiversitätsindizes aufgelistet.

| | Δ HL | Δ SL | Δ TL | Δ STL | S 1993 | Disturbance | m a.s.l. | Δ date |
|---|---|---|---|---|---|---|---|---|
| Δ S 30 $m^2$ | **0.048** | 0.548 | **0.039** | 0.162 | **< 0.001** | 0.169 | 0.751 | 0.351 |
| Δ S 200 $m^2$ | 0.057 | 0.258 | **0.002** | 0.205 | **0.029** | 0.562 | 0.590 | 0.489 |
| Δ S 500 $m^2$ | 0.360 | 0.096 | **0.010** | 0.937 | **0.001** | 0.572 | 0.291 | 0.977 |
| Δ H 30 $m^2$ | 0.062 | 0.584 | **0.013** | 0.072 | 0.575 | 0.261 | 0.559 | 0.144 |
| Δ H 200 $m^2$ | 0.111 | 0.811 | **< 0.001** | **0.008** | 0.398 | 0.850 | 0.626 | 0.090 |
| Δ H 500 $m^2$ | 0.136 | 0.695 | 0.066 | 0.104 | 0.302 | 0.788 | 0.983 | 0.113 |
| Δ E 30 $m^2$ | 0.156 | 0.876 | 0.067 | 0.075 | 0.070 | 0.581 | 0.755 | 0.091 |
| Δ E 200 $m^2$ | 0.339 | 0.310 | **0.012** | **0.005** | 0.366 | 0.734 | 0.405 | 0.073 |
| Δ E 500 $m^2$ | 0.251 | 0.229 | 0.380 | 0.075 | 0.992 | 0.772 | 0.819 | 0.083 |
| Species loss 30 $m^2$ | **0.016** | 0.160 | **0.046** | 0.457 | 0.397 | 0.165 | 0.599 | 0.432 |
| Species loss 200 $m^2$ | **0.025** | 0.326 | **0.008** | 0.292 | 0.760 | 0.722 | 0.863 | 0.332 |
| Species loss 300 $m^2$ | 0.152 | 0.136 | **0.024** | 0.969 | 0.915 | 0.405 | 0.608 | 0.549 |
| Species increase 30 $m^2$ | 0.106 | 0.502 | 0.259 | 0.602 | **0.019** | 0.098 | 0.181 | 0.785 |
| Species increase 200 $m^2$ | 0.392 | 0.356 | 0.137 | 0.743 | 0.071 | 0.389 | 0.053 | 0.595 |
| Species increase 500 $m^2$ | 0.351 | 0.252 | 0.181 | 0.845 | 0.108 | 0.382 | 0.118 | 0.945 |

caused by heat stress during summer 2018 or by recurring drought spells in recent years (e.g. LACOPETTI et al 2021). Another possible cause for the decreased herb layer cover mentioned in several studies is reduced light availability due to denser canopies as a consequence of natural succession (DORMANN et al. 2020, DEPAUW et al. 2020). Coinciding with this interpretation, we found a decrease in mean light indicator values; however, the unchanged estimates of canopy covers between the two survey years do not support this explanation.

### 4.1.1 Species richness

Compared to the 1993 data, we found significantly lower species richness in 2019, irrespective of plot size, while Shannon diversity and Shannon evenness remained unchanged. The latter is probably because no individual species became dominant, and the cover of the herb layer decreased considerably. European forest resurvey studies have often found a decrease in species richness, which has been attributed to denser canopies (WALTHER 1997, BARTHA 2008, LELLI et al. 2020). In our study, we found a decrease in species richness as well, but we did not find an overall increase in the tree layer cover. However, we did find that species richness decreased especially in plots where canopies became denser. The decrease in light values also indicates canopy closure. Other studies found changes in species composition, but no change in species richness: in montane forests, SCHERRER et al. (2017)

found an upward shift in species composition, while RECZYŃSKA & ŚWIERKOSZ (2017) in thermophilous oak forests observed a shift from communities of moderately oligotrophic and mesic character to nutrient richer but drier communities. A resurvey study of forests in the Czech Republic showed strong species losses in the herb layer since the mid-20th century (MÜLLEROVÁ et al. 2015). A meta-study of European temperate forests showed no general change in species diversity, but large variation between the results of individual studies (BERNHARDT-RÖMERMANN et al. 2015). Such inconclusive patterns can be related to differences in spatial grain, spatial extent (international, regional, local) and analysed time periods.

### 4.1.2 Species area-relationship

According to our results of species-area relationships, beta diversity at the grain size of 500-m² has decreased since 1993, meaning that the vegetation composition has become more homogenous. This could possibly be explained by the exclusion of light-demanding species, as reflected in the lower light values in the 500-m² plots. Such light-demanding species were rare but present in 1993, thus contributing to higher beta diversity. There are several theories that attempt to explain the species-area relationship (SHEN et al. 2009). We presume that species richness in forests of the study region decreased during the last 30 years as a result of ongoing canopy closure or increasing tree density (CIOLDI et al. 2020). The Central Plateau in Switzerland has generally shown decreasing canopy closure over the past decade (CIOLDI et al. 2020), but 20% of our plots are located within the Sihlwald reserve, a forest area that has remained unmanaged since 2000 (HAELER et al. 2021).

### 4.1.3 Species turnover

The plant species showing a decrease in mean cover were predominantly typical forest floor species (*Galium odoratum*, *Phyteuma spicatum*, *Fragaria vesca*, *Brachypodium sylvaticum*, *Primula elatior*, *Anemona nemorosa*, *Epilobium montanum*, *Dryopteris dilatata*, *Luzula pilosa*), tree or shrub species from rather warm and light sites (*Sorbus aria*, *Cornus sanguinea*, *Sambucus nigra*, *Pinus sylvestris*) and competitive generalists (*Taraxacum officinale* aggr., *Poa trivialis*, *Deschampsia cespitosa*). The cover of the forest-floor herbs may have decreased due to drought (ARCHAUX & WOLTERS 2006), while the cover of thermophile shrubs probably decreased due to increased shading. In particular, Fraxinus excelsior lost cover in the canopy as well as in regrowth (seedlings and saplings), with percentages ranging between 5% and 9% at the scale of 500-m$^2$ circles. This decline of ash is widespread in Europe, mainly triggered by the disease called ash dieback (PAUTASSO et al. 2013).

Only *Ilex aquifolium* became significantly more common and increased in cover. The increase of laurophyllous species in Switzerland has been observed both south and north of the Alps over the past decades, which may be due to climate change and milder winters (WALTHER 1997). Less intensive use of forests may also contribute to the increasing occurrence of laurophyllous species (WOHLGEMUTH et al. 2020). While laurophyllisation often occurs through the spread of laurophyllous neophytes (WALTHER 2000), in our study area we did not find an increase of neophytes. This is probably because disturbed sites, where these species could establish, did not occur more frequently in 2019. Furthermore, as it was the case in 1993, the study sites in 2019 were not close to settlements from where neophytes typically spread into nearby forests (e.g. CONEDEREA et al. 2018).

### 4.2 Change in indicator values

Like in our study, WALTHER (1997), KÜCHLER et al. (2015) and BECKER et al. (2016) found decreasing light values in forest resurveys. An obvious reason for this process is the advancing forest stand development, or the overgrowth of the crowns due to less frequent forest openings. In several resurvey studies, climate change could be detected by changes in indicator values (e.g. FELDE et al. 2012, HELM et al. 2017). In contrast to the present study, where no change in temperature or moisture values was found, these studies investigated mountain habitats. The change in species composition (and therefore indicator values) is more pronounced in cold-adapted and open habitats (GOTTFRIED et al. 2012).

### 4.3 Drivers of vegetation change

Increasing canopy closure, and thus decreasing light availability, seems to have had a negative influence on species diversity. Such negative effects of closing canopies were previously demonstrated by WALTHER (1997) and BERNHARDT-RÖMERMANN et al. (2015). Continuous shading causes the local disappearance of light-demanding species (VALVERDE & SILVERTOWN 1997). This coincides with our finding that species loss occurred primarily in plots where the mean light value of 2019 indicated low light availability. This relationship reinforces the finding that species diversity in temperate forests is dependent on light availability. While the reduction of species richness can be related to harsher growth conditions if shadow increases, decreasing cover in the herb layer can be caused by transient effects such as extreme drought spells during the growing season. Such an extreme event took place in the summer of 2018, one year before the resurvey (METEOSCHWEIZ 2019, SCHULDT et al. 2020, LACOPETTI et al 2021). We assume that the summer drought in 2018 caused the death of many individual plants in the herb layer, ultimately leading to a reduction of the herb cover between 1993 and 2019. As there is a positive relationship between biomass and species diversity (AXMANOVÁ 2012), the desiccation process due to the extraordinary summer drought may have affected rare plant species disproportionately.

We did not find any effects of disturbance on the biodiversity indices. By contrast, SCHMIDT (2005) showed that the species richness of vascular plants is higher in managed forests than in completely unmanaged forests. The study by PAILLET et al. (2010) showed that bryophyte, lichen, fungi, xylobiont beetle and ground beetle species diversity is higher in unmanaged forests, but vascular plant species diversity benefits from management. The positive effect on vascular plant species diversity can be explained by the intermediate-disturbance hypothesis (CONNELL 1978, WOHLGEMUTH et al. 2002). It is likely that an influence of disturbance could be found if more precise data on management and intensity of disturbance sources were available.

The commonly observed shift in species diversity to higher elevations due to climate warming (e.g. KÜCHLER et al. 2015, SCHERRER 2017, RUMPF et al. 2017) could not be shown in the present study. This is possibly due to the rather small elevation difference (from 490 to 860 m a.s.l.), resulting in small climatic differences.

## 5. Conclusions

Between 1993 and 2019, the 46 surveyed forest stands experienced a significant decrease in species richness and a general reduction in herb layer cover. In contrast, Shannon diversity and Shannon evenness remained the same. The *z*-values of the species area relationship were lower in the 2019 surveys than in 1993. Some typical forest plants decreased in mean cover, with the reduction of *Fraxinus excelsior* in both frequency and abundance being most pronounced. Out of all species, only *Ilex aquifolium* became more frequent in the stands. The change in mean indicator values for light suggests that the stands were on average darker in 2019 than in 1993 (significant change in 500-m² plots). The other mean indicator values did not differ between the two surveys, indicating no corresponding environmental changes. Stand structure (i.e. tree layer cover or canopy closure) was found to be a possible driver for the observed changes in species richness.

Plant species in the herb layer of forests provide important information on site characteristics and disturbance dynamics (DAVIS et al. 2005). The observed reduction in species richness and herb layer cover in beech forests between 1993 and 2019 can be at least partly attributed to shading effects due to canopy closure. Whether the species loss is also related to recent drought events that may transiently lead to a reduction in the herb layer cover, and thus to species loss, can only be clarified through further resurveys. We presume that increasing summer drought spells may cause a permanent decline in the plant species diversity of temperate forests.

## Erweiterte deutsche Zusammenfassung

**Einleitung** – Im letzten Jahrhundert wurden anthropogen verursachte Umwelteinflüsse, wie veränderte Landnutzungen (POSCHLOD et al. 2005), atmosphärische Luftverschmutzung (BOBBINK et al. 2010) und die Klimaveränderung (LENOIR et al. 2008, LACHAT et al. 2010, RIGLING et al. 2013) zu den Hauptverursachern für die Veränderung der Artenzusammensetzung und Artenvielfalt. Insbesondere die fortschreitende Klimaerwärmung wirkt sich auf vielfältige Weise auf die Vegetation aus, obwohl es schwierig ist, ihren Einfluss von anderen Treibern der Vegetationsveränderung zu unterscheiden. Wir untersuchten, wie sich die Waldvegetation der Albiskette (Kanton Zürich, Schweiz), die hauptsächlich von Rotbuchen (*Fagus sylvatica*) dominiert wird, zwischen 1993 und 2019 veränderte.

**Methoden** – Um festzustellen, wie sich die Artenvielfalt und die Vegetationszusammensetzung während dieser 26 Jahre veränderten, haben wir 46 dauerhaft markierte Nested-Plot-Serien (30 m², 200 m² und 500 m²) wiedererhoben. Mit gepaarten *t*-Tests analysierten wir die Veränderungen der Biodiversitätsindices (Artenzahl, Shannon-Index und Shannon-Ebenheit), die Veränderungen sowohl der prozentualen Schichtdeckungen als auch der mittleren Zeigerwerte der Pflanzenarten. Mit linearen Regressionen setzten wir die quantifizierten Veränderungen in Beziehung zu möglichen erklärenden Variablen. Unter Verwendung der *Z*-Werte aus der Art-Areal-Beziehungen erfolgte eine Analyse der Veränderung der Beta-Diversität. Mithilfe des Vorzeichentests identifizierten wir Arten mit einer signifikanten Änderung der Frequenz. Um Unterschiede in der Deckung einzelner Arten festzustellen, verwendeten wir für jede Art einen gepaarten *t*-Test. Zusätzlich zählten wir die Arten, die über alle Plots hinweg verschwanden und diejenigen, die neu auftraten.

**Ergebnisse** – Sowohl die Artenzahl als auch die Krautschichtdeckung nahmen von 1993 bis 2019 in allen drei Plotgrößen signifikant ab. Die Auswertung der Art-Areal-Beziehung zeigte, dass die *Z*-Werte des 2019-Datensatzes für die Flächenvergrösserung von 200 bis 500 $m^2$ signifikant tiefer waren als im 1993-Datensatz. Die mittleren Lichtzahlen waren in den 500 $m^2$-Plots 2019 signifikant niedriger als 1993. In den anderen Plotgrößen lag keine signifikante Veränderung vor. Hinsichtlich der Feuchte-, Temperatur-, Reaktions- und Nährstoffzahlen resultierten in allen Plotgrößen keine deutlichen Veränderungen. Die seltener gewordenen Arten sind in den meisten Fällen typische Waldarten *(Galium odoratum, Anemone nemorosa, Brachypodium sylvaticum, Luzula pilosa und Epilobium montanum)* oder konkurrenzstarke Generalisten *(Taraxacum officinale* aggr. und *Poa trivialis*). Abgenommen hat die mässig schattentolerante Baumart *Sorbus aria*, die bevorzugt in Wäldern warmer Lagen und auf felsigen Standorten wächst. An Deckung verloren hat insbesondere *Fraxinus excelsior.* Dafür ist *Ilex* *aquifolium* häufiger geworden und hat im Deckungsgrad zugenommen. Die Beziehungen der erklärenden Variablen zu den Biodiversitätsindizes zeigten, dass die Artenzahl, Shannon-Diversität und Shannon-Ebenheit mit zunehmender Baumschichtdeckung abnahmen. Des Weiteren fanden wir, dass der Verlust der Artenvielfalt mit der Abnahme der Krautschichtdeckung korrespondierte. Bei den Parametern Aufnahmezeitpunkt, Höhe über Meer, Veränderung der Störung und der Deckung durch die Strauchschicht konnte keine Beziehung zur Veränderung der Biodiversitätsindizes festgestellt werden.

**Diskussion** – Die Beziehung zwischen Artenverlust und der erhöhten Deckung durch die Baumschicht bestätigte, dass die Lichtverfügbarkeit ein wichtiger Faktor für die Artenvielfalt der Vegetation ist. Der Verlust der Krautschichtdeckung, welche sich ebenfalls negativ auf die Artenvielfalt auswirkte, könnte mit der Austrocknung der Vegetation in vergangenen Hitzesommern zusammenhängen. HELM et al. (2017) fanden in ihrer Bergwaldstudie ebenfalls einen Deckungsverlust in der Krautschicht, und Studien von BRUNET & TYLER (2000) sowie ARCHAUX & WOLTERS (2006) zeigten, dass die Produktivität der Krautschicht in Wäldern durch Trockenheit reduziert werden kann. Der Deckungsverlust in der Krautschicht könnte mit dem Hitzestress im Sommer 2018 oder durch wiederkehrende Dürreperioden in den letzten Jahren zusammenhängen (z. B. LACOPETTI et al. 2021). Eine weitere mögliche Ursache für die verringerte Krautschichtdeckung, welche in mehreren Studien genannt wird, ist die verringerte Lichtverfügbarkeit aufgrund dichterer Baumkronen als Folge der natürlichen Sukzession (DORMANN et al. 2020, DEPAUW et al. 2020). Die abnehmenden *Z*-Werte könnten möglicherweise durch den Wegfall von lichtbedürftigen Arten erklärt werden, was sich in den niedrigeren Lichtwerten in den 500 $m^2$-Plots zeigt. Solche lichtbedürftigen Arten waren 1993 zwar selten, aber vorhanden und trugen somit zu einer höheren Beta-Diversität bei.

Insbesondere die Deckung der thermophilen Sträucher nahm wahrscheinlich aufgrund der zunehmenden Beschattung ab. Dass *Fraxinus excelsior* sowohl im Kronendach als auch im Aufwuchs (Sämlinge und Schösslinge) an Deckung verlor, entspricht dem weit verbreiteten Rückgang der Art in Europa infolge der Krankheit "Eschentriebsterben" (PAUTASSO et al. 2013). Nur *Ilex aquifolium* wurde signifikant häufiger und nahm in der Deckung zu. Die Zunahme von laurophyllen Arten in der Schweiz wurde in den letzten Jahrzehnten sowohl südlich als auch nördlich der Alpen beobachtet, was auf den Klimawandel und milder werdende Winter zurückgeführt wird (WALTHER 1997).

Die abnehmenden Lichtwerte korrespondieren gut mit den Ergebnissen anderer Wiedererhebungsstudien in Wäldern (WALTHER 1997, KÜCHLER et al. 2015 & BECKER et al. 2016). Ein möglicher Grund für diesen Prozess ist die fortschreitende Waldbestandsentwicklung bzw. das Dichterwerden und Zuwachsen der Kronen. Der zunehmende Kronenschluss und die damit abnehmende Lichtverfügbarkeit limitiert die lichtbedürftigen Pflanzenarten. Kontinuierliche Beschattung verursacht das lokale Verschwinden lichtbedürftiger Arten (VALVERDE & SILVERTOWN 1997). Die negativen Auswirkungen auf die Artenvielfalt wurden auch in einer Metastudie über die Entwicklung von europäischen Wäldern nachgewiesen (BERNHARDT-RÖMERMANN et al. 2015). Dies deckt sich mit unserer Feststellung, dass der Artenverlust vor allem in Plots auftrat, in welchen der mittlere Lichtwert von 2019 auf eine geringe Lichtverfügbarkeit hinwies. Während die Abnahme der Artenvielfalt bei zunehmender Beschattung mit Lichtmangel zu erklären ist, kann die abnehmende Deckung in der Krautschicht durch Dürreperioden und damit durch Wassermangel während der Vegetationsperiode verursacht werden. Wir gehen davon aus, dass die Sommertrockenheit im Jahr 2018 das Absterben vieler Einzelpflanzen in der Krautschicht verursachte, was zu einer Reduktion der Krautschicht zwischen 1993 und 2019 führte.

Weitere Untersuchungen sind erforderlich, um festzustellen, ob unsere Ergebnisse lediglich regionalspezifisch sind oder auch für andere biogeografische Regionen gelten. Um sicherzustellen, dass ein weiterer Artenverlust nicht unbemerkt bleibt, empfehlen wir die Fortführung von koordinierten Wiedererhebungen und ein Monitoring.

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## Author contributions

T.W. did the original sampling and conceived the idea of the resurvey, which was repeated by E.S. as a Master thesis under the supervision of the three co-authors. E.S. analysed the data and led the writing, while all others gave substantial input during manuscript revision.

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## Supplements

**Additional supporting information may be found in the online version of this article.**

**Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.**

**Supplement E1.** Vegetation data of 1993 and 2019.

**Anhang E1.** Vegetationsdaten von 1993 und 2019.

**Supplement E2.** Forest communities in the 46 plots, listed by alliances and associations.

**Anhang E2.** Waldgesellschaften in den 46 Plots, nach Verbänden und Assoziationen aufgelistet.

**Supplement E3.** Site characteristics and the method of survey according to the initial survey form.

**Anhang E3.** Standorteigenschaften und deren Erhebungsart gemäß Formular der Ersterhebung.

**Supplement E4.** Derivation of the variables, indices and used R-function of the tested variables. One-factorial analysis of variance = aov; linear regression = lm.

**Anhang E4.** Herleitung und benutzte R-Funktion der getesteten Variablen. Einfaktorielle Varianzanalyse = aov; lineare Regression= lm.

**Supplement E5.** Mean indicator values of species in the herb layer according to LANDOLT et al. (2010) for 2019 and 1993, as well as the *p*-values of the differences based on paired *t*-tests.

**Anhang E5.** Mittlere Zeigerwerte der Krautschicht gemäß LANDOLT et al. (2010) der Jahre 2019 und 1993 sowie die *p*-Werte der Unterschiede basierend auf gepaarten *t*-Tests.

**Supplement E6.** Linear relationships between the change in tree cover [%] (2019 value – 1993 value) and the changes in biodiversity indices (2019 value – 1993 value) and the change in species richness per plot.

**Anhang E6.** Lineare Beziehungen zwischen der Veränderung der Deckung der Baumschicht [%](Wert 2019 – Wert 1993) und den Veränderungen der Biodiversitätsindizes (Wert 2019 – Wert 1993) sowie der relative Artenverlust in den Plots.

**Supplement E7.** Linear regressions between the change in herb layer cover [%] and the relative species loss in the plots.

**Anhang E7.** Lineare Beziehungen zwischen der Veränderung der Deckung der Krautschicht [%] und des relativen Artenverlusts in den Plots.

**Supplement E8.** Linear regressions between the change in tree and shrub cover (summed) [%] and the changes in biodiversity indices (2019 value – 1993 value).

**Anhang E8.** Lineare Beziehungen zwischen der Veränderung der Deckung der Baum- und Strauchschicht (summiert) [%] und den jeweiligen Veränderungen der Biodiversitätsindizes (Wert 2019 – Wert 1993).

**Supplement E9.** Linear regressions between the species richness in 1993 and the change in the species richness (2019 value – 1993 value) and the relative species increase in the plots.

**Anhang E9.** Lineare Beziehungen zwischen der Artenzahl 1993 und der Veränderung der Artenzahl (Wert 2019 – Wert 1993) sowie die relative Artenzunahme in den Plots.

**Supplement E10.** Relationship between species loss rate and light value in 2019 in the three different plot sizes.

**Anhang E10.** Beziehung zwischen der Artenverlust-Rate und der Lichtzahl im Jahr 2019 in den drei verschiedenen Aufnahmeflächengrößen.

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**Supplement E1.** Vegetation data of 1993 and 2019

**Anhang E1.** Vegetationsdaten von 1993 und 2019

| Layer | Plot number | 1 | 1 | 1 | 2 | 2 | 2 | 3 | 3 | 3 | 4 | 4 | 4 | 5 | 5 | 5 | 6 | 6 | 6 | 7 | 7 | 7 | 8 | 8 | 8 | 9 | 9 | 9 | 10 | 10 | 10 | 11 | 11 | 11 | 12 | 12 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Year | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 |
| | Area [m²] | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 |
| | Coordinates x | 678000 | 678000 | 678000 | 679000 | 679000 | 679000 | 679000 | 679000 | 679000 | 678000 | 678000 | 678000 | 679000 | 679000 | 679000 | 680000 | 680000 | 680000 | 680000 | 680000 | 680000 | 680000 | 680000 | 680000 | 681000 | 681000 | 681000 | 681000 | 681000 | 681000 | 680000 | 680000 | 680000 | 679000 | 679000 | 679000 |
| | Coordinates y | 247000 | 247000 | 247000 | 245000 | 245000 | 245000 | 243000 | 243000 | 243000 | 246000 | 246000 | 246000 | 246000 | 246000 | 246000 | 244000 | 244000 | 244000 | 243000 | 243000 | 243000 | 245000 | 245000 | 245000 | 244000 | 244000 | 244000 | 243000 | 243000 | 243000 | 240000 | 240000 | 240000 | 241000 | 241000 | 241000 |
| | Altitude [m.a.s.l.] | 610 | 610 | 610 | 680 | 680 | 680 | 590 | 590 | 590 | 680 | 680 | 680 | 705 | 705 | 705 | 785 | 785 | 785 | 650 | 650 | 650 | 625 | 625 | 625 | 520 | 520 | 520 | 525 | 525 | 525 | 710 | 710 | 710 | 630 | 630 | 630 |
| | Exposition | NNE | NNE | NNE | NNW | NNW | NNW | E | E | E | S | S | S | NW | NW | NW | SW | SW | SW | W | W | W | ENE | ENE | ENE | NE | NE | NE | ENE | ENE | ENE | N | N | N | N | N | N |
| | Inclination [°] | 8 | 8 | 8 | 40 | 40 | 40 | 36 | 36 | 36 | 14 | 14 | 14 | 10 | 10 | 10 | 16 | 16 | 16 | 16 | 16 | 16 | 18 | 18 | 18 | 14 | 14 | 14 | 22 | 22 | 22 | 30 | 30 | 30 | 12 | 12 | 12 |
| | Tree layer cover [%] | 70 | 35 | 55 | 90 | 40 | 40 | 95 | 95 | 95 | 85 | 80 | 80 | 70 | 85 | 85 | 90 | 50 | 45 | 90 | 75 | 75 | 90 | 90 | 90 | 45 | 45 | 50 | 25 | 95 | 90 | 90 | 65 | 60 | 35 | 60 | 60 |
| | Shrub layer cover [%] | 20 | 35 | 40 | 5 | 50 | 50 | 30 | 2 | 1 | 1 | 10 | 5 | 15 | 10 | 25 | 40 | 10 | 10 | 40 | 5 | 5 | 40 | 10 | 5 | 1 | 15 | 15 | 5 | 50 | 50 | 1 | 30 | 30 | 15 | 30 | 30 |
| | Herb layer cover [%] | 60 | 60 | 60 | 50 | 80 | 80 | 10 | 40 | 40 | 40 | 95 | 95 | 50 | 40 | 40 | 10 | 60 | 60 | 70 | 90 | 90 | 50 | 30 | 30 | 20 | 90 | 80 | 45 | 5 | 30 | 50 | 50 | 50 | 90 | 60 | 60 |
| H | Abies alba | . | 0.3 | 0.3 | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | 0.3 | 0.3 | . | . | 0.3 | . | . | 0.3 | . | . | 0.3 | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 |
| T | Abies alba | . | . | . | . | . | . | . | . | . | . | 11 | 11 | . | . | . | . | . | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 |
| S | Abies alba | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 11 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 |
| H | Acer campestre | . | . | . | . | . | . | . | . | 0.3 | . | . | . | . | . | . | 0.3 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| T | Acer campestre | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| S | Acer campestre | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2.2 | 2.2 | 2.2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Acer platanoides | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . |
| T | Acer platanoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| S | Acer platanoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Acer pseudoplatanus | 2.2 | 2.2 | 2.2 | 35 | 35 | 35 | 2.2 | 2.2 | 2.2 | 11 | 11 | 11 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 2.2 | 11 | 11 | 11 | 11 | 35 | 35 | 0.3 | 0.3 | 0.3 |
| T | Acer pseudoplatanus | 35 | 11 | 11 | . | 11 | 11 | . | 0.3 | 11 | 2.2 | 11 | 11 | . | 35 | 35 | 87 | 87 | 87 | 35 | 35 | 35 | . | 11 | 11 | . | 2.2 | 2.2 | 11 | 11 | 11 | . | . | 2.2 | . | 11 | 11 |
| S | Acer pseudoplatanus | 11 | 2.2 | 2.2 | . | . | 0.3 | . | . | . | . | 35 | 35 | 2.2 | 11 | 2.2 | 11 | 11 | 11 | . | 2.2 | 11 | . | 2.2 | 2.2 | . | 0.3 | 2.2 | . | 0.3 | 0.3 | . | . | . | 11 | 2.2 | 2.2 |

| Layer | Plot number | 13 | 13 | 13 | 14 | 14 | 14 | 15 | 15 | 15 | 16 | 16 | 16 | 17 | 17 | 17 | 18 | 18 | 18 | 19 | 19 | 19 | 20 | 20 | 20 | 21 | 21 | 21 | 22 | 22 | 22 | 23 | 23 | 23 | 24 | 24 | 24 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Year | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 |
| | Area [m²] | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 |
| | Coordinates x | 679000 | 679000 | 679000 | 678000 | 678000 | 678000 | 677000 | 677000 | 677000 | 678000 | 678000 | 678000 | 680000 | 680000 | 680000 | 681000 | 681000 | 681000 | 679000 | 679000 | 679000 | 678000 | 678000 | 678000 | 680000 | 680000 | 680000 | 681000 | 681000 | 681000 | 684000 | 684000 | 684000 | 686000 | 686000 | 686000 |
| | Coordinates y | 239000 | 239000 | 239000 | 240000 | 240000 | 240000 | 240000 | 240000 | 240000 | 238000 | 238000 | 238000 | 236000 | 236000 | 236000 | 236000 | 236000 | 236000 | 234000 | 234000 | 234000 | 235000 | 235000 | 235000 | 238000 | 238000 | 238000 | 238000 | 238000 | 238000 | 236000 | 236000 | 236000 | 232000 | 232000 | 232000 |
| | Altitude [m.a.s.l.] | 700 | 700 | 700 | 640 | 640 | 640 | 625 | 625 | 625 | 650 | 650 | 650 | 660 | 660 | 660 | 680 | 680 | 680 | 665 | 665 | 665 | 580 | 580 | 580 | 825 | 825 | 825 | 860 | 860 | 860 | 565 | 565 | 565 | 525 | 525 | 525 |
| | Exposition | SE | SE | SE | NNW | NNW | NNW | N | N | N | W | W | W | E | E | E | SSE | SSE | SSE | NNW | NNW | NNW | W | W | W | WNW | WNW | WNW | ENE | ENE | ENE | SE | SE | SE | ESE | ESE | ESE |
| | Inclination [°] | 42 | 42 | 42 | 3 | 3 | 3 | 5 | 5 | 5 | 14 | 14 | 14 | 24 | 24 | 24 | 8 | 8 | 8 | 5 | 5 | 5 | 16 | 16 | 16 | 10 | 10 | 10 | 32 | 32 | 32 | 14 | 14 | 14 | 6 | 6 | 6 |
| | Tree layer cover [%] | 85 | 95 | 95 | 85 | 70 | 80 | 15 | 80 | 85 | 90 | 90 | 90 | 100 | 85 | 75 | 60 | 80 | 80 | 75 | 80 | 75 | 35 | 70 | 70 | 60 | 80 | 70 | 5 | 5 | 5 | 80 | 80 | 80 | 80 | 90 | 90 |
| | Shrub layer cover [%] | 1 | 10 | 10 | 0 | 60 | 60 | 30 | 5 | 2 | 0 | 5 | 5 | 5 | 50 | 50 | 15 | 50 | 50 | 5 | 30 | 30 | 35 | 20 | 20 | 50 | 5 | 3 | 5 | 15 | 25 | 1 | 30 | 30 | 10 | 5 | 5 |
| | Herb layer cover [%] | 30 | 35 | 75 | 95 | 70 | 70 | 80 | 75 | 75 | 25 | 50 | 50 | 35 | 65 | 65 | 100 | 10 | 10 | 80 | 30 | 30 | 80 | 95 | 85 | 70 | 75 | 75 | 80 | 90 | 90 | 95 | 85 | 80 | 90 | 70 | 70 |
| H | Abies alba | . | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | . | . | . | . | 0.3 | 0.3 | . | . | . | . | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | . | 0.3 | 0.3 | . | 0.3 | 0.3 |
| T | Abies alba | . | . | . | . | 0.3 | 11 | 11 | 11 | 11 | . | . | . | . | 2.2 | 11 | . | . | . | . | . | 2.2 | . | 11 | 35 | . | . | 11 | 2.2 | 2.2 | 2.2 | . | . | . | 2.2 | 2.2 | 2.2 |
| S | Abies alba | . | . | . | . | . | . | . | . | . | . | . | . | . | 2.2 | 0.3 | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . |
| H | Acer campestre | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | . | . | . | . | . | . | . | . | . |
| T | Acer campestre | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2.2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2.2 | 2.2 |
| S | Acer campestre | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Acer platanoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 2.2 | 2.2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| T | Acer platanoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 35 | 35 | 35 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| S | Acer platanoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Acer pseudoplatanus | 2.2 | 2.2 | 2.2 | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | . | . | . | . | 2.2 | 2.2 | 11 | 11 | 11 | 11 | 11 | 11 | . | . | 0.3 | . | 0.3 | 0.3 |
| T | Acer pseudoplatanus | 35 | 35 | 35 | . | . | . | . | . | . | . | . | . | . | 0.3 | 11 | . | 11 | 11 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 11 | 11 |
| S | Acer pseudoplatanus | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | . | 2.2 | 2.2 | . | . | . | 11 | 11 | 11 | 35 | 60 | 60 | 0.3 | 11 | 11 | . | . | . | . | 0.3 | 0.3 |

| Layer | Plot number | 25 | 25 | 25 | 26 | 26 | 26 | 27 | 27 | 27 | 28 | 28 | 28 | 29 | 29 | 29 | 30 | 30 | 30 | 31 | 31 | 31 | 32 | 32 | 32 | 33 | 33 | 33 | 34 | 34 | 34 | 35 | 35 | 35 | 36 | 36 | 36 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Year | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 |
| | Area [m²] | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 |
| | Coordinates x | 680000 | 680000 | 680000 | 681000 | 681000 | 681000 | 682000 | 682000 | 682000 | 686000 | 686000 | 686000 | 681000 | 681000 | 681000 | 683000 | 683000 | 683000 | 684000 | 684000 | 684000 | 681000 | 681000 | 681000 | 682000 | 682000 | 682000 | 685000 | 685000 | 685000 | 683000 | 683000 | 683000 | 683000 | 683000 | 683000 |
| | Coordinates y | 239000 | 239000 | 239000 | 240000 | 240000 | 240000 | 238000 | 238000 | 238000 | 233000 | 233000 | 233000 | 241000 | 241000 | 241000 | 236000 | 236000 | 236000 | 235000 | 235000 | 235000 | 237000 | 237000 | 237000 | 237000 | 237000 | 237000 | 236000 | 236000 | 236000 | 235000 | 235000 | 235000 | 234000 | 234000 | 234000 |
| | Altitude [m.a.s.l.] | 700 | 700 | 700 | 740 | 740 | 740 | 620 | 620 | 620 | 540 | 540 | 540 | 615 | 615 | 615 | 755 | 755 | 755 | 745 | 745 | 745 | 570 | 570 | 570 | 790 | 790 | 790 | 730 | 730 | 730 | 780 | 780 | 780 | 795 | 795 | 795 |
| | Exposition | W | W | W | SE | SE | SE | ENE | ENE | ENE | NE | NE | NE | ENE | ENE | ENE | E | E | E | E | E | E | WNW | WNW | WNW | N | N | N | – | – | – | SW | SW | SW | SSW | SSW | SSW |
| | Inclination [°] | 24 | 24 | 24 | 42 | 42 | 42 | 16 | 16 | 16 | 24 | 24 | 24 | 19 | 19 | 19 | 22 | 22 | 22 | 24 | 24 | 24 | 22 | 22 | 22 | 18 | 18 | 18 | | | | 28 | 28 | 28 | 36 | 36 | 36 |
| | Tree layer cover [%] | 70 | 40 | 45 | 75 | 65 | 65 | 100 | 95 | 95 | 95 | 95 | 85 | 80 | 15 | 20 | 100 | 95 | 90 | 60 | 90 | 80 | 90 | 80 | 80 | 100 | 60 | 70 | 20 | 90 | 75 | 95 | 60 | 60 | 95 | 80 | 80 |
| | Shrub layer cover [%] | 0 | 10 | 15 | 70 | 20 | 30 | 5 | 5 | 5 | 0 | 20 | 30 | 0 | 20 | 20 | 5 | 10 | 15 | 5 | 10 | 10 | 1 | 15 | 30 | 20 | 50 | 60 | 80 | 60 | 60 | 10 | 5 | 5 | 2 | 5 | 5 |
| | Herb layer cover [%] | 65 | 30 | 30 | 95 | 30 | 30 | 60 | 40 | 50 | 10 | 50 | 50 | 60 | 80 | 80 | 50 | 60 | 60 | 20 | 40 | 40 | 60 | 70 | 80 | 80 | 60 | 75 | 50 | 55 | 55 | 20 | 20 | 20 | 50 | 95 | 95 |
| H | Abies alba | 0.3 | 0.3 | 2.2 | . | . | . | . | . | . | . | . | 0.3 | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . |
| T | Abies alba | . | 0.3 | 11 | . | . | . | . | . | . | . | 2.2 | 11 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | . | . | . | . | . | . | . | 2.2 | 2.2 |
| S | Abies alba | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Acer campestre | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . |
| T | Acer campestre | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| S | Acer campestre | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Acer platanoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . |
| T | Acer platanoides | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| S | Acer platanoides | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Acer pseudoplatanus | 11 | 35 | 35 | 2.2 | 2.2 | 2.2 | 11 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | 11 | 11 | 35 | 11 | 11 | 11 | 2.2 | 11 | 11 | 0.3 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 35 | 35 | 35 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 |
| T | Acer pseudoplatanus | . | 0.3 | 11 | . | 11 | 35 | 11 | 35 | 11 | . | . | . | 0.3 | 11 | 11 | . | 0.3 | 11 | . | 2.2 | 11 | . | . | . | 35 | 35 | 11 | . | . | 2.2 | . | . | 11 | . | . | 11 |
| S | Acer pseudoplatanus | . | . | . | . | . | . | . | 2.2 | 2.2 | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | 2.2 | 2.2 | 2.2 | 0.3 | 2.2 | 2.2 | 0.3 | 11 | 11 | . | . | . | . | . | . |

| Layer | Plot number | 37 | 37 | 37 | 38 | 38 | 38 | 39 | 39 | 39 | 40 | 40 | 40 | 41 | 41 | 41 | 42 | 42 | 42 | 43 | 43 | 43 | 44 | 44 | 44 | 45 | 45 | 45 | 46 | 46 | 46 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Year | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 | 1993 |
| | Area [m²] | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 |
| | Coordinates x | 685000 | 685000 | 685000 | 684000 | 684000 | 684000 | 685000 | 685000 | 685000 | 685000 | 685000 | 685000 | 685000 | 685000 | 685000 | 686000 | 686000 | 686000 | 683000 | 683000 | 683000 | 685000 | 685000 | 685000 | 688000 | 688000 | 688000 | 682000 | 682000 | 682000 |
| | Coordinates y | 232000 | 232000 | 232000 | 234000 | 234000 | 234000 | 233000 | 233000 | 233000 | 234000 | 234000 | 234000 | 235000 | 235000 | 235000 | 235000 | 235000 | 235000 | 240000 | 240000 | 240000 | 237000 | 237000 | 237000 | 233000 | 233000 | 233000 | 243000 | 243000 | 243000 |
| | Altitude [m.a.s.l.] | 725 | 725 | 725 | 615 | 615 | 615 | 490 | 490 | 490 | 620 | 620 | 620 | 540 | 540 | 540 | 580 | 580 | 580 | 655 | 655 | 655 | 495 | 495 | 495 | 700 | 700 | 700 | 660 | 660 | 660 |
| | Exposition | SSW | SSW | SSW | NE | NE | NE | NE | NE | NE | NE | NE | NE | W | W | W | – | – | – | N | N | N | – | – | – | SSW | SSW | SSW | NE | NE | NE |
| | Inclination [°] | 32 | 32 | 32 | 8 | 8 | 8 | 24 | 24 | 24 | 7 | 7 | 7 | 9 | 9 | 9 | 0 | 0 | 0 | 14 | 14 | 14 | | | | 12 | 12 | 12 | 5 | 5 | 5 |
| | Tree layer cover [%] | 95 | 80 | 80 | 100 | 45 | 45 | 35 | 95 | 85 | 100 | 80 | 70 | 100 | 30 | 55 | 100 | 60 | 75 | 60 | 70 | 60 | 50 | 95 | 95 | 90 | 80 | 80 | 5 | 80 | 80 |
| | Shrub layer cover [%] | 5 | 5 | 5 | 30 | 60 | 70 | 50 | 60 | 60 | 60 | 30 | 25 | 10 | 60 | 50 | 5 | 40 | 40 | 40 | 25 | 30 | 40 | 1 | 5 | 20 | 5 | 5 | 20 | 20 | 20 |
| | Herb layer cover [%] | 20 | 30 | 40 | 40 | 60 | 60 | 50 | 10 | 10 | 20 | 50 | 50 | 60 | 50 | 50 | 60 | 70 | 70 | 40 | 90 | 90 | 40 | 30 | 30 | 30 | 80 | 80 | 95 | 35 | 35 |
| H | Abies alba | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | . | 0.3 | 0.3 | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 |
| T | Abies alba | . | . | 0.3 | . | . | . | . | . | . | . | . | . | . | 11 | 11 | . | . | . | . | . | . | . | . | . | . | . | 2.2 | . | . | . |
| S | Abies alba | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Acer campestre | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . |
| T | Acer campestre | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| S | Acer campestre | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Acer platanoides | . | 0.3 | 0.3 | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | 0.3 | . | . | . | . | 0.3 | 0.3 | . | . | 0.3 | . | . | . |
| T | Acer platanoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| S | Acer platanoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Acer pseudoplatanus | 0.3 | 2.2 | 2.2 | . | . | . | 0.3 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | 11 | 11 | 11 | 0.3 | 0.3 | 0.3 | . | 0.3 | 0.3 | 11 | 11 | 11 | 2.2 | 2.2 | 11 | 0.3 | 0.3 | 0.3 |
| T | Acer pseudoplatanus | . | 11 | 11 | . | . | . | . | . | 11 | . | . | . | . | . | 2.2 | . | 2.2 | 11 | 60 | 35 | 35 | . | . | . | 35 | 35 | 35 | . | . | . |
| S | Acer pseudoplatanus | . | . | . | . | . | . | . | 2.2 | 2.2 | . | 0.3 | 0.3 | 2.2 | 35 | 35 | 35 | 11 | 11 | . | 0.3 | 0.3 | 11 | 11 | 11 | 2.2 | 2.2 | 11 | . | 0.3 | 0.3 |

| Layer | Plot number | 1 | 1 | 1 | 2 | 2 | 2 | 3 | 3 | 3 | 4 | 4 | 4 | 5 | 5 | 5 | 6 | 6 | 6 | 7 | 7 | 7 | 8 | 8 | 8 | 9 | 9 | 9 | 10 | 10 | 10 | 11 | 11 | 11 | 12 | 12 | 12 | 13 | 13 | 13 | 14 | 14 | 14 | 15 | 15 | 15 | 16 | 16 | 16 | 17 | 17 | 17 | 18 | 18 | 18 | 19 | 19 | 19 | 20 | 20 | 20 | 21 | 21 | 21 | 22 | 22 | 22 | 23 | 23 | 23 | 24 | 24 | 24 | 25 | 25 | 25 | 26 | 26 | 26 | 27 | 27 | 27 | 28 | 28 | 28 | 29 | 29 | 29 | 30 | 30 | 30 | 31 | 31 | 31 | 32 | 32 | 32 | 33 | 33 | 33 | 34 | 34 | 34 | 35 | 35 | 35 | 36 | 36 | 36 | 37 | 37 | 37 | 38 | 38 | 38 | 39 | 39 | 39 | 40 | 40 | 40 | 41 | 41 | 41 | 42 | 42 | 42 | 43 | 43 | 43 | 44 | 44 | 44 | 45 | 45 | 45 | 46 | 46 | 46 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Year | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 | 2019 |
| | Area [m²] | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 | 30 | 200 | 500 |
| | Coordinates x | 678000 | 678000 | 678000 | 679000 | 679000 | 679000 | 679000 | 679000 | 679000 | 678000 | 678000 | 678000 | 679000 | 679000 | 679000 | 680000 | 680000 | 680000 | 680000 | 680000 | 680000 | 680000 | 680000 | 680000 | 681000 | 681000 | 681000 | 681000 | 681000 | 681000 | 680000 | 680000 | 680000 | 679000 | 679000 | 679000 | 679000 | 679000 | 679000 | 678000 | 678000 | 678000 | 677000 | 677000 | 677000 | 678000 | 678000 | 678000 | 680000 | 680000 | 680000 | 681000 | 681000 | 681000 | 679000 | 679000 | 679000 | 678000 | 678000 | 678000 | 680000 | 680000 | 680000 | 681000 | 681000 | 681000 | 684000 | 684000 | 684000 | 686000 | 686000 | 686000 | 680000 | 680000 | 680000 | 681000 | 681000 | 681000 | 682000 | 682000 | 682000 | 686000 | 686000 | 686000 | 681000 | 681000 | 681000 | 683000 | 683000 | 683000 | 684000 | 684000 | 684000 | 681000 | 681000 | 681000 | 682000 | 682000 | 682000 | 685000 | 685000 | 685000 | 683000 | 683000 | 683000 | 683000 | 683000 | 683000 | 685000 | 685000 | 685000 | 684000 | 684000 | 684000 | 685000 | 685000 | 685000 | 685000 | 685000 | 685000 | 685000 | 685000 | 685000 | 686000 | 686000 | 686000 | 683000 | 683000 | 683000 | 685000 | 685000 | 685000 | 688000 | 688000 | 688000 | 682000 | 682000 | 682000 |
| | Coordinates y | 247000 | 247000 | 247000 | 245000 | 245000 | 245000 | 243000 | 243000 | 243000 | 246000 | 246000 | 246000 | 246000 | 246000 | 246000 | 244000 | 244000 | 244000 | 243000 | 243000 | 243000 | 245000 | 245000 | 245000 | 244000 | 244000 | 244000 | 243000 | 243000 | 243000 | 240000 | 240000 | 240000 | 241000 | 241000 | 241000 | 239000 | 239000 | 239000 | 240000 | 240000 | 240000 | 240000 | 240000 | 240000 | 238000 | 238000 | 238000 | 236000 | 236000 | 236000 | 236000 | 236000 | 236000 | 234000 | 234000 | 234000 | 235000 | 235000 | 235000 | 238000 | 238000 | 238000 | 238000 | 238000 | 238000 | 236000 | 236000 | 236000 | 232000 | 232000 | 232000 | 239000 | 239000 | 239000 | 240000 | 240000 | 240000 | 238000 | 238000 | 238000 | 233000 | 233000 | 233000 | 241000 | 241000 | 241000 | 236000 | 236000 | 236000 | 235000 | 235000 | 235000 | 237000 | 237000 | 237000 | 237000 | 237000 | 237000 | 236000 | 236000 | 236000 | 235000 | 235000 | 235000 | 234000 | 234000 | 234000 | 232000 | 232000 | 232000 | 234000 | 234000 | 234000 | 233000 | 233000 | 233000 | 234000 | 234000 | 234000 | 235000 | 235000 | 235000 | 235000 | 235000 | 235000 | 240000 | 240000 | 240000 | 237000 | 237000 | 237000 | 233000 | 233000 | 233000 | 243000 | 243000 | 243000 |
| | Altitude [m.a.s.l.] | 610 | 610 | 610 | 680 | 680 | 680 | 590 | 590 | 590 | 680 | 680 | 680 | 705 | 705 | 705 | 785 | 785 | 785 | 650 | 650 | 650 | 625 | 625 | 625 | 520 | 520 | 520 | 525 | 525 | 525 | 710 | 710 | 710 | 630 | 630 | 630 | 700 | 700 | 700 | 640 | 640 | 640 | 625 | 625 | 625 | 650 | 650 | 650 | 660 | 660 | 660 | 680 | 680 | 680 | 665 | 665 | 665 | 580 | 580 | 580 | 825 | 825 | 825 | 860 | 860 | 860 | 565 | 565 | 565 | 525 | 525 | 525 | 700 | 700 | 700 | 740 | 740 | 740 | 620 | 620 | 620 | 540 | 540 | 540 | 615 | 615 | 615 | 755 | 755 | 755 | 745 | 745 | 745 | 570 | 570 | 570 | 790 | 790 | 790 | 730 | 730 | 730 | 780 | 780 | 780 | 795 | 795 | 795 | 725 | 725 | 725 | 615 | 615 | 615 | 490 | 490 | 490 | 620 | 620 | 620 | 540 | 540 | 540 | 580 | 580 | 580 | 655 | 655 | 655 | 495 | 495 | 495 | 700 | 700 | 700 | 660 | 660 | 660 |
| | Exposition | NNE | NNE | NNE | NNW | NNW | NNW | E | E | E | S | S | S | NW | NW | NW | SW | SW | SW | W | W | W | ENE | ENE | ENE | NE | NE | NE | ENE | ENE | ENE | N | N | N | N | N | N | SE | SE | SE | NNW | NNW | NNW | N | N | N | W | W | W | E | E | E | SSE | SSE | SSE | NNW | NNW | NNW | W | W | W | WNW | WNW | WNW | ENE | ENE | ENE | SE | SE | SE | ESE | ESE | ESE | W | W | W | SE | SE | SE | ENE | ENE | ENE | NE | NE | NE | ENE | ENE | ENE | E | E | E | E | E | E | WNW | WNW | WNW | N | N | N | – | – | – | SW | SW | SW | SSW | SSW | SSW | SSW | SSW | SSW | NE | NE | NE | NE | NE | NE | NE | NE | NE | W | W | W | – | – | – | N | N | N | – | – | – | SSW | SSW | SSW | NE | NE | NE |
| | Inclination [°] | 8 | 8 | 8 | 40 | 40 | 40 | 36 | 36 | 36 | 14 | 14 | 14 | 10 | 10 | 10 | 16 | 16 | 16 | 16 | 16 | 16 | 18 | 18 | 18 | 14 | 14 | 14 | 22 | 22 | 22 | 30 | 30 | 30 | 12 | 12 | 12 | 42 | 42 | 42 | 3 | 3 | 3 | 5 | 5 | 5 | 14 | 14 | 14 | 24 | 24 | 24 | 8 | 8 | 8 | 5 | 5 | 5 | 16 | 16 | 16 | 10 | 10 | 10 | 32 | 32 | 32 | 14 | 14 | 14 | 6 | 6 | 6 | 24 | 24 | 24 | 42 | 42 | 42 | 16 | 16 | 16 | 24 | 24 | 24 | 19 | 19 | 19 | 22 | 22 | 22 | 24 | 24 | 24 | 22 | 22 | 22 | 18 | 18 | 18 | | | | 28 | 28 | 28 | 36 | 36 | 36 | 32 | 32 | 32 | 8 | 8 | 8 | 24 | 24 | 24 | 7 | 7 | 7 | 9 | 9 | 9 | 0 | 0 | 0 | 14 | 14 | 14 | | | | 12 | 12 | 12 | 5 | 5 | 5 |
| | Tree layer cover [%] | 70 | 60 | 70 | 80 | 60 | 60 | 80 | 70 | 75 | 70 | 80 | 80 | 50 | 50 | 50 | 60 | 50 | 50 | 80 | 70 | 70 | 60 | 60 | 60 | 80 | 80 | 70 | 50 | 70 | 70 | 90 | 80 | 80 | 75 | 60 | 60 | 50 | 50 | 80 | 50 | 80 | 90 | 70 | 70 | 70 | 90 | 90 | 90 | 80 | 70 | 70 | 80 | 80 | 70 | 80 | 80 | 80 | 80 | 80 | 70 | 80 | 70 | 70 | 30 | 35 | 35 | 40 | 70 | 70 | 70 | 70 | 75 | 70 | 80 | 80 | 80 | 80 | 80 | 95 | 90 | 85 | 80 | 80 | 80 | 80 | 65 | 50 | 70 | 70 | 70 | 70 | 70 | 70 | 60 | 60 | 70 | 95 | 70 | 60 | 95 | 90 | 90 | 75 | 60 | 70 | 80 | 80 | 80 | 50 | 50 | 50 | 80 | 80 | 80 | 70 | 70 | 70 | 0 | 70 | 70 | 75 | 80 | 80 | 95 | 90 | 70 | 50 | 80 | 80 | 80 | 70 | 70 | 80 | 80 | 70 | 95 | 95 | 95 |
| | Shrub layer cover [%] | 5 | 5 | 5 | 5 | 20 | 20 | 20 | 50 | 50 | 80 | 40 | 40 | 20 | 30 | 30 | 1 | 1 | 1 | 10 | 20 | 20 | 1 | 1 | 1 | 0 | 5 | 30 | 5 | 15 | 15 | 5 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 40 | 10 | 5 | 5 | 10 | 10 | 15 | 20 | 40 | 40 | 20 | 70 | 70 | 20 | 20 | 10 | 5 | 5 | 5 | 10 | 10 | 10 | 20 | 50 | 50 | 15 | 10 | 10 | 10 | 15 | 15 | 0 | 5 | 5 | 30 | 35 | 35 | 40 | 20 | 20 | 0 | 10 | 15 | 20 | 25 | 30 | 5 | 10 | 25 | 20 | 30 | 30 | 5 | 5 | 7 | 20 | 20 | 20 | 2 | 20 | 40 | 50 | 40 | 40 | 5 | 10 | 10 | 0 | 10 | 10 | 50 | 60 | 70 | 5 | 5 | 5 | 20 | 30 | 10 | 40 | 20 | 20 | 5 | 20 | 20 | 15 | 20 | 55 | 10 | 40 | 30 | 10 | 20 | 20 | 10 | 20 | 10 | 0 | 2 | 2 |
| | Herb layer cover [%] | 40 | 40 | 40 | 50 | 50 | 50 | 10 | 10 | 40 | 30 | 30 | 30 | 80 | 45 | 45 | 50 | 50 | 40 | 50 | 40 | 40 | 45 | 40 | 40 | 1 | 5 | 15 | 30 | 20 | 20 | 40 | 50 | 50 | 20 | 20 | 40 | 30 | 30 | 30 | 20 | 10 | 5 | 50 | 40 | 40 | 20 | 20 | 20 | 35 | 35 | 35 | 10 | 10 | 10 | 90 | 90 | 90 | 65 | 65 | 65 | 40 | 40 | 40 | 50 | 40 | 40 | 60 | 70 | 60 | 50 | 40 | 40 | 10 | 15 | 15 | 80 | 80 | 80 | 2 | 15 | 15 | 50 | 50 | 50 | 50 | 60 | 60 | 40 | 70 | 70 | 1 | 1 | 5 | 40 | 60 | 60 | 15 | 30 | 50 | 20 | 20 | 20 | 40 | 30 | 50 | 15 | 10 | 10 | 45 | 50 | 50 | 20 | 20 | 20 | 10 | 40 | 20 | 60 | 80 | 80 | 2 | 5 | 5 | 5 | 5 | 25 | 20 | 30 | 30 | 20 | 40 | 50 | 50 | 50 | 60 | 5 | 5 | 5 |
| H | Abies alba | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | . | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | 2.2 | 11 | 0.3 | 0.3 | 0.3 | . | 0.3 | 0.3 | . | . | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | 0.3 | 0.3 | 0.3 | 0.3 | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | 2.2 | 0.3 | . | . | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 |
| T | Abies alba | . | . | . | . | . | . | . | . | . | . | 11 | 11 | . | . | . | . | . | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | . | . | . | . | 0.3 | 2.2 | . | . | . | . | . | . | . | 2.2 | 2.2 | . | . | . | . | . | 2.2 | . | . | . | . | 0.3 | 2.2 | . | . | . | . | . | . | . | 2.2 | 2.2 | . | 2.2 | 11 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | . | . | 2.2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2.2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | . | . | . | . | . | . | . | . | 2.2 | . | . | . |
| S | Abies alba | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2.2 | 2.2 | 2.2 | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | 2.2 | 2.2 | . | . | . | . | . | . | . | . | . | . | . | . | . | 11 | 11 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Acer campestre | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| T | Acer campestre | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2.2 | 11 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2.2 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2.2 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| S | Acer campestre | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 11 | 2.2 | 0.3 | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | 2.2 | 2.2 | 0.3 | . | . | . | . | . | . |
| H | Acer platanoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | 0.3 | 0.3 | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . |
| T | Acer platanoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2.2 | 2.2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| S | Acer platanoides | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . |
| H | Acer pseudoplatanus | . | . | . | 35 | 35 | 35 | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 11 | 11 | 2.2 | 2.2 | 2.2 | 0.3 | 11 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | 2.2 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 2.2 | 2.2 | 0.3 | 0.3 | 2.2 | 0.3 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | . | . | . | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 2.2 | 11 | 11 | 11 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 0.3 | 2.2 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 2.2 | 11 | 11 | 11 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 0.3 | 0.3 | 0.3 | 0.3 | 2.2 | 0.3 | 2.2 | . | 0.3 | 0.3 | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | . | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 2.2 | 2.2 | 2.2 | . | . | 0.3 | 0.3 | 0.3 | 0.3 |
| T | Acer pseudoplatanus | 60 | 35 | 35 | . | 11 | 11 | . | . | . | 2.2 | 11 | 2.2 | 11 | 35 | 11 | 60 | 60 | 60 | 11 | 2.2 | 2.2 | 0.3 | 2.2 | 2.2 | . | . | . | 35 | 35 | 35 | . | . | 2.2 | . | 2.2 | 2.2 | . | . | 11 | . | . | . | . | . | . | . | . | . | . | . | . | 11 | 11 | 11 | . | . | . | 35 | 35 | 11 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 11 | 11 | 2.2 | 11 | 11 | . | 11 | 11 | . | 11 | 11 | . | 0.3 | 11 | 0.3 | 2.2 | 2.2 | . | . | 2.2 | 11 | 11 | 11 | . | 0.3 | 2.2 | . | . | . | . | 2.2 | 2.2 | . | . | . | . | . | . | . | 2.2 | 2.2 | . | . | . | 2.2 | 2.2 | 11 | . | . | 11 | 0.3 | 0.3 | 0.3 | 2.2 | 11 | 11 | 35 | 35 | 35 | . | . | . |
| S | Acer pseudoplatanus | . | . | . | . | . | . | . | . | . | 2.2 | 2.2 | 2.2 | . | 11 | 2.2 | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | 2.2 | 2.2 | . | . | . | . | . | . | . | . | . | 2.2 | 0.3 | 0.3 | 2.2 | 2.2 | 2.2 | 2.2 | 2.2 | 0.3 | . | . | . | 0.3 | 0.3 | 0.3 | 11 | 11 | 11 | . | 2.2 | 2.2 | 0.3 | 0.3 | 2.2 | . | . | . | . | . | . | 2.2 | 0.3 | 0.3 | . | 2.2 | 2.2 | 11 | 2.2 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | 2.2 | . | . | . | 2.2 | 2.2 | 11 | . | . | 0.3 | . | . | 2.2 | . | . | . | . | . | . | 11 | 2.2 | 2.2 | 2.2 | 2.2 | 2.2 | . | . | . | . | 2.2 | 0.3 | . | 0.3 | 0.3 | . | . | . | 0.3 | 0.3 | 0.3 | . | 0.3 | 0.3 |
| H | Aconitum lycoctonum subsp. vulparia | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Actaea spicata | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | 0.3 | . | . | 0.3 | . | . | . | . | . | . | . | . | . | 0.3 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| H | Aegopodium podagraria | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2.2 | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | 11 | 0.3 | 0.3 | . | . | . | 2.2 | 0.3 | 0.3 | . | . | . | . | . | . | . | . | . | 11 | 11 | 2.2 | . | . | . | . | . | . | . | . | . |

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**Supplement E2.** Forest communities in the 46 plots, listed by alliances and associations.

**Anhang E2.** Waldgesellschaften in den 46 Plots, nach Verbänden und Assoziationen aufgelistet.

| **Verband**<br>Assoziation | Anzahl | Prozent |
|---|---|---|
| ***Eu-Fagion*** | **37** | **80%** |
| *Galio odorati-Fagetum typicum* | 14 | 30% |
| *Cardamino-Fagetum typicum* | 9 | 20% |
| *Milio-Fagetum* | 4 | 9% |
| *Pulmonario-Fagetum typicum* | 4 | 9% |
| *Pulmonario-Fagetum melittetosum* | 3 | 7% |
| *Aro-Fagetum* | 2 | 4% |
| *Galio odorati-Fagetum luzuletosum* | 1 | 2% |
| ***Alno-Fraxinion*** | **7** | **15%** |
| *Carici remotae-Fraxinetum* | 4 | 9% |
| *Aceri-Fraxinetum* | 2 | 4% |
| *Pruno-Fraxinetum* | 1 | 2% |
| ***Alnetalia glutinosae*** | **1** | **2%** |
| *Carici elongatae-Alnetum glutinosae* | 1 | 2% |
| ***Molinio-Pinion*** | **1** | **2%** |
| *Cephalanthero-Pinetum silvaticae* | 1 | 2% |

**Supplement E3.** Site characteristics and the method of survey according to the initial survey form.

**Anhang E3.** Standorteigenschaften und deren Erhebungsart gemäß Formular der Ersterhebung.

| Site characteristics | Survey method |
|---|---|
| Layer cover | Estimate in percent in all plot sizes |
| Location | Categories: plain, slope, crest , canyon, gorge, staging |
| Forest type | Categories: high forest, coppice-with-standards, coppice, wood pasture, plantation or edge of the forest |
| Dynamics | Categories: clearing, storm areas, fire, flooding |
| Forest development stage | Categories: young stands, initial phase, optimal phase, terminal phase, decomposition phase, rejuvenation phase, regeneration phase, planter phase |
| Structure | Categories: single-layer, multi-layer, staged, grouped structure |
| Coniferous proportion | Percent cover of conifers |
| Canopy cover | Categories: compact, normal, light, jagged, inexistent |
| Nature protection | Number of tree species, lying dead wood, dry wood, strong trees, special forest communities |
| Disturbances | Categories: none, road, path, board, fill up, artificial ditch, aisle, slope, tread damage, recreation facility |
| Small structures | Categories: none, rocks, boulders, tree stumps, rhizomes, branches, hollows, ditches, crests, brooks, ponds, spring, screes, stand borders, mosaic structure |
| Homogeneity | Scale from 1 - 5 (1= inhomogeneous; 5= homogeneous) and reason for inhomogeneity: soil, humans, silviculture, small relief, light, others |

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**Supplement E4.** Derivation of the variables, indices and used R-function of the tested variables. One-factorial analysis of variance = aov; linear regression = lm.

**Anhang E4.** Herleitung und benutzte R-Funktion der getesteten Variablen. Einfaktorielle Varianzanalyse = aov; lineare Regression= lm.

| Explanatory variables | Derivation of the variable | Function in R |
|---|---|---|
| Change in tree layer cover = Δ BS | Estimate [%] 2019 – estimate [%] 1993 | lm |
| Change in shrub layer cover = Δ SS | Estimate [%] 2019 – estimate [%] 1993 | lm |
| Change in herb layer cover = Δ KS | Estimate [%] 2019 – estimate [%] 1993 | lm |
| Indices 1993 = S 1993 | Species richness, Shannon index, Shannon evenness 1993 | lm |
| Change in disturbance = disturbance | Formation of three groups:<br>Disturbance (yes/no) present in both years<br>Disturbance only present in 1993<br>Disturbance only present in 2019 | aov |
| Indicator values 1993, indicator values 2019, change of indicator values | Moisture, light, temperature, reaction and nutrient value according to Landolt et al. (2010) | lm |
| Elevation = m a. s. l. | Elevation of the plots in m a.s.l. | lm |
| Difference of the survey date = Δ Date | Date of the survey 2019 – date of the survey 1993 | lm |

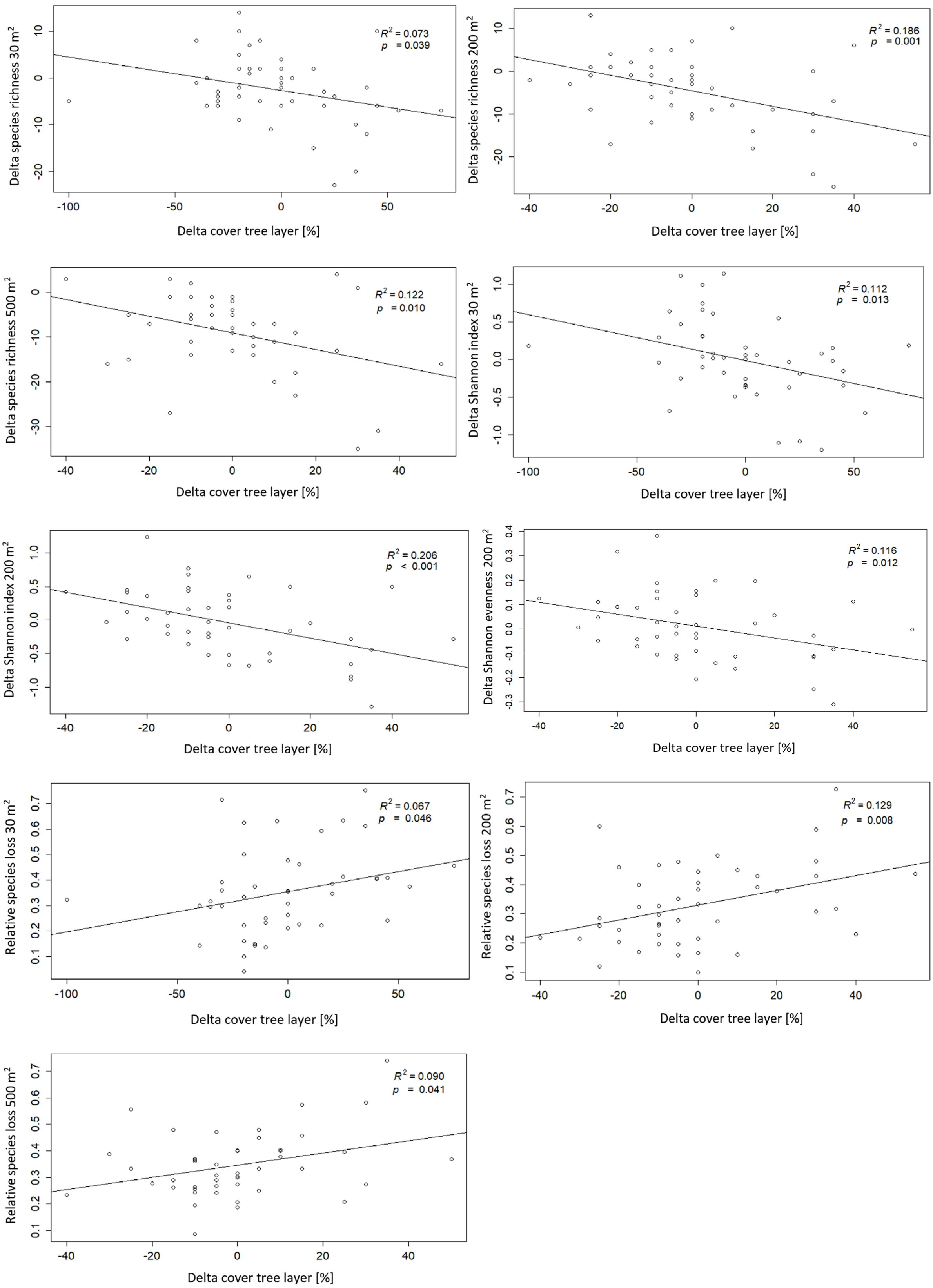
**Supplement E5.** Mean indicator values of species in the herb layer according to LANDOLT et al. (2010) for 2019 and 1993, as well as the *p*-values of the differences based on paired *t*-tests.

**Anhang E5.** Mittlere Zeigerwerte der Krautschicht gemäß LANDOLT et al. (2010) der Jahre 2019 und 1993 sowie die *p*-Werte der Unterschiede basierend auf gepaarten *t*-Tests.

| | 30 $m^2$ | | | 200 $m^2$ | | | 500 $m^2$ | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1993 | 2019 | *p*-value | 1993 | 2019 | *p*- value | 1993 | 2019 | *p*- value |
| Moisture value | 3.12 | 3.09 | 0.601 | 3.13 | 3.10 | 0.345 | 3.14 | 3.12 | 0.633 |
| Light value | 2.19 | 2.08 | 0.081 | 2.27 | 2.17 | 0.079 | **2.34** | **2.22** | **0.017** |
| Temperature value | 3.31 | 3.28 | 0.449 | 3.30 | 3.31 | 0.854 | 3.31 | 3.33 | 0.544 |
| Reaction value | 3.18 | 3.13 | 0.223 | 3.17 | 3.14 | 0.440 | 3.17 | 3.15 | 0.620 |
| Nutrient value | 3.09 | 3.09 | 0.898 | 3.09 | 3.10 | 0.9078 | 3.12 | 3.11 | 0.932 |

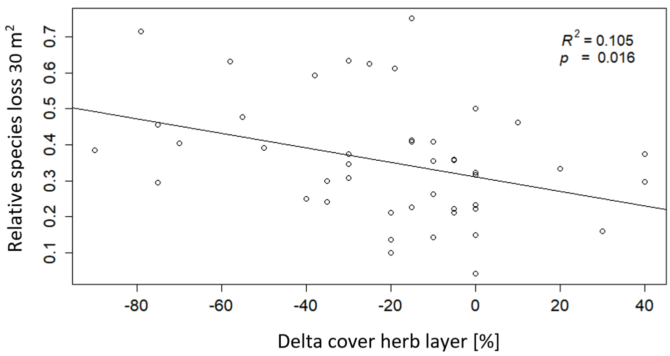
**Supplement E6.** Linear relationships between the change in tree cover [%] (2019 value - 1993 value) and the changes in biodiversity indices (2019 value - 1993 value) and the change in species richness per plot.

**Anhang E6.** Lineare Beziehungen zwischen der Veränderung der Deckung der Baumschicht [%] (Wert 2019 – Wert 1993) und den Veränderungen der Biodiversitätsindizes (Wert 2019 – Wert 1993) sowie der relative Artenverlust in den Plots.



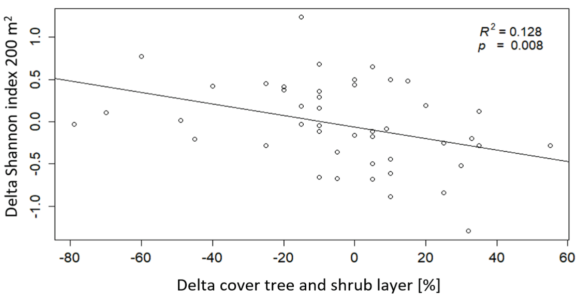
**Supplement E7.** Linear regressions between the change in herb layer cover [%] and the relative species loss in the plots.

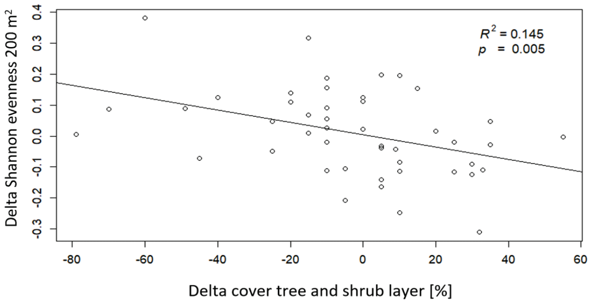
**Anhang E7.** Lineare Beziehungen zwischen der Veränderung der Deckung der Krautschicht [%] und des relativen Artenverlusts in den Plots.




**Supplement E8.** Linear regressions between the change in tree and shrub cover (summed) [%] and the changes in biodiversity indices (2019 value - 1993 value).

**Anhang E8.** Lineare Beziehungen zwischen der Veränderung der Deckung der Baum- und Strauchschicht (summiert) [%] und den jeweiligen Veränderungen der Biodiversitätsindizes (Wert 2019 – Wert 1993).



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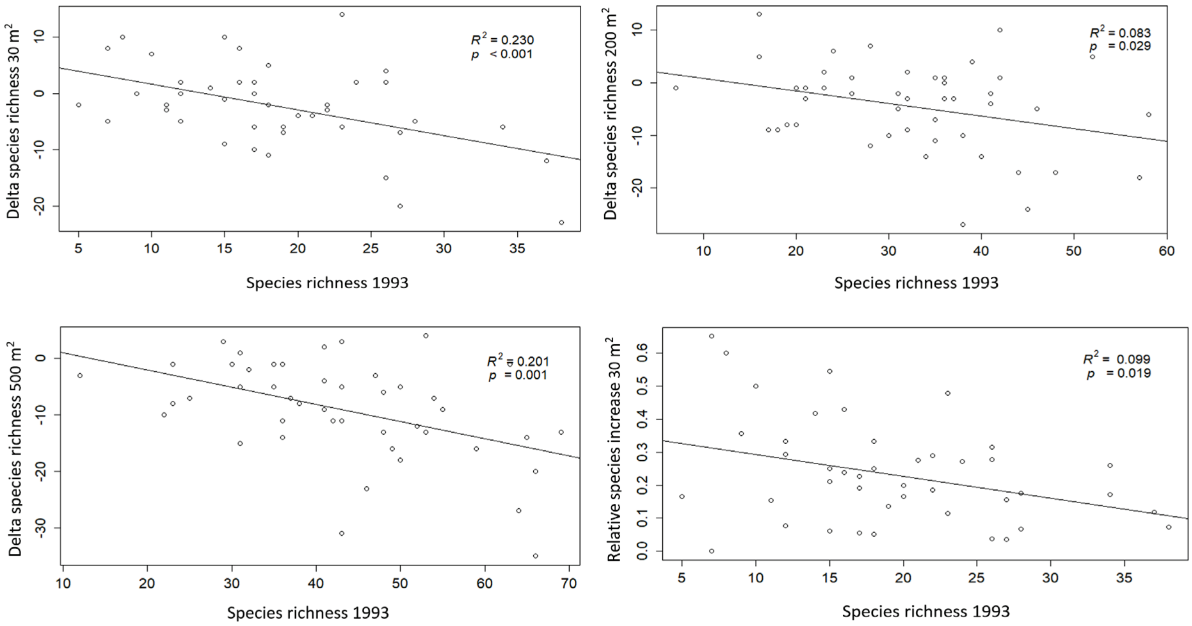
**Supplement E9.** Linear regressions between the species richness in 1993 and the change in the species richness (2019 - 1993) and the relative species increase in the plots.

**Anhang E9.** L Lineare Beziehungen zwischen der Artenzahl 1993 und der Veränderung der Artenzahl (2019 – 1993) sowie die relative Artenzunahme in den Plots.




**Supplement E10.** Relationship between species loss rate (new species divided by species richness present at both survey times) and light value in 2019 in the three different plot sizes.

**Anhang E10.** Beziehung zwischen der Artenverlust-Rate (Anzahl neu hinzugekommener Arten / Anzahl vorhandener Arten zu beiden Erhebungszeitpunkten) und der Lichtzahl im Jahr 2019 in den drei verschiedenen Aufnahmeflächengrößen.