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„Multiple environmental changes drive forest floor vegetation in a temperate mountain forest"

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Contents

Acknowledgements **2**
Introduction **3**
Methods **6**
Study Area 6
Sampling design 7
Data analysis 9
Results **13**
Changes in climate, deposition and soil chemistry 13
Changes in tree layer cover 13
Changes in ungulate browsing 14
Single species changes 14
Overall changes in the herb layer 15
Variation in plant species composition between plots over time 17
The factors that shape changes in composition 18
Discussion **20**
Overall herb layer changes and relations to environmental shifts 20
Relative contributions of drivers to herb layer changes 24
Conclusion **25**
References **26**

Appendix

Abstract 32
Zusammenfassung 33

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Introduction

Human activities have led to fundamental alterations of the environment causing unprecedented and accelerating losses of biodiversity world-wide (MEA 2005; Tittensor *et al.* 2014). Among the manifold pressures to biodiversity, climate change, land use change and excess N deposition have emerged as the most important for biodiversity losses (Foley *et al.* 2005; MEA 2005; Pereira, Navarro & Martins 2012). Yet their relative impact on biodiversity is difficult to disentangle and varies across spatial and temporal scales (Essl *et al.* 2015; Bernhardt-Römermann *et al.* 2015).

Differences in the ability of species to cope with environmental changes result in changes in interspecific interactions, their local abundances and eventually, in the loss of resident species, while others may immigrate (Hobbs *et al.* 2006; Parmesan 2006; Peñuelas *et al.* 2013). With progressing climate change, frequency and intensity of climatic extreme events (e.g. via drought or storms) and biotic disturbances (e.g. bark beetle outbreaks) are predicted to increase in forests (Weed, Ayres & Hicke 2013; Seidl *et al.* 2014), with decisive consequences for biodiversity (Thom & Seidl 2015). Land use changes, particularly the loss and fragmentation of forests have had strong negative impacts on global forest biodiversity (Pimm & Raven 2000; Vié, Hilton-Taylor & Stuart 2009; Newbold *et al.* 2015). In particular European temperate forests have been used intensively over many centuries causing fundamental changes in forest composition, structure and soils (Glatzel 1990; Perring *et al.* 2016) and the depletion of species richness of the herb layer (Flinn & Vellend 2005). Yet human land use (in form of silvicultural management) can have a positive effect on plant species richness of forest stands, but usually leads to a decline of typical understorey plant species (Battles *et al.* 2001; Müllerová, Hédl & Szabó 2015).

From the 19th century onwards, N deposition from fossil fuel combustion and agricultural fertilization is presumed to be responsible for a substantial decline of plant species richness (Gilliam 2006; Bobbink *et al.* 2010), alters community structures in temperate forests (Meunier *et al.* 2016) and is threatening biodiversity and ecosystem services of protected areas (Bleeker *et al.* 2011). Yet the extent of N deposition impacts strongly depends on site conditions as well as on the history and magnitude of deposition amounts (Dirnböck *et al.* 2014; Bernhardt-Römermann *et al.* 2015). In industrialized countries, air pollution did also cause large scale forest soil acidification in the second half of the last century but some recovery in soils (Cools & De Vos 2011; Akselsson *et al.* 2013) and forest vegetation (Reinecke, Klemm & Heinken 2014; Vanhellemont 2014) has been observed after drastic declines in S emissions from the 1980ies onwards (Vet *et al.* 2014). According to this study, also N deposition is starting to decline in many areas in Europe.

Forest understorey vegetation has a prominent role as a major component of forest biodiversity and for ecosystem function (Gilliam 2014). Yet, because of the complexity of forest ecosystems, it is particularly difficult to disentangle the impacts of multiple drivers on understorey properties. Microclimate, soil chemistry and irradiance are the main factors determining understorey species composition (Leuschner 1999; Leuschner & Lendzion 2009). These factors differ dramatically between forests and with forest stand age (Leuschner & Rode 1999) because tree composition and structure are largely controlling the microclimate at the forest floor (Geiger, Aron & Todhunter 2009; Norris, Hobson & Ibisch 2012) and because nutrient availability for plants is determined by leaf litter quantity and quality (Lovett *et al.* 2004; Verheyen *et al.* 2012). Since forest floor vegetation is so tightly related to characteristics of the overstorey (Whitney & Foster 1988), tree canopies and their characteristics have withhold or buffered climate change (Bertrand *et al.* 2011; De Frenne *et al.* 2013) and N deposition driven (Verheyen *et al.* 2012) changes in the forest understorey. This is why forest disturbance may have a triggering effect on future pathways of diversity (Thom *et al.* 2016).

Since long-term forest vegetation resurvey data is becoming increasingly available, it has allowed to assessing the relative effects of multiple drivers. Few studies found evidence that the forest floor vegetation has already responded to increased temperatures (Lenoir *et al.* 2008; Küchler *et al.* 2014; Savage & Vellend 2015). Several studies observed responses to increased soil N availability due to N deposition (Thimonier *et al.* 1994; Brunet, Diekmann & Falkengren-Grerup 1998; Diekmann *et al.* 1999; Bernhardt-Römermann *et al.* 2007; Keith *et al.* 2009; Reinecke *et al.* 2014; Naaf & Kolk 2016) and to acid rain (Thimonier *et al.* 1994; Diekmann *et al.* 1999; Hédl 2004) or recovery from acidification in recent years (Reinecke *et al.* 2014; Vanhellemont 2014). Further, local factors like forest management, disturbance regime and game density had severe impact and caused regional variation in the responses of the forest herb layer to deposition effects and global warming (Hédl 2004; Hopkins & Kirby 2007; Müllerová *et al.* 2015; Bernhardt-Römermann *et al.* 2015).

Notwithstanding the progress made in determining the relative contributions of the various drivers to changes in forest floor vegetation, the necessity to resort to the use of surrogate data (modelled climate and deposition, surrogate soil data, etc.) has often hampered a deeper insight. Here, we present a resurvey study from the Northern Limestone Alps in Austria that investigated the numerous reasons behind changes in the forest floor over a time span of 21 years. The data set is unique as to its collection of 143 permanent plots with on-site measured soil data, climate, air pollution, tree canopy changes, and browsing damage and allowed for a comprehensive multivariate analysis.

We conceptualized our understanding of the likely drivers of forest floor change (Fig. 1) and had the following specific questions: 1) Did the study area experience changes in climate, air pollu-

tion, soil conditions, browsing damage, disturbance and tree layer composition and structure over the last two decades with the potential to change the forest floor vegetation; 2) If so, what was the relative contribution of these drivers to changes in the forest floor species composition and structure. Our hypothesis was that all of the aforementioned drivers did simultaneously impact the forest floor vegetation with disturbance being the most important as to its strong control over the understorey light regime. Furthermore, we hypothesized that I) climate change favoured thermophilic and drought-tolerant species, that II) a decrease in S deposition led to an increase in basophilic and a decrease in acidophilic species and that III) accumulated N deposition caused a decrease in oligotrophic and an increase in eutrophic plant species. As to species diversity we hypothesized that IV) disturbance had the strongest effect causing an increase in species and a higher compositional variation among plots. We did not expect climate change effects on species diversity since immigration of thermophilic species should offset potential loss of cold-tolerant species, neither did we expect N deposition or the soil recovery from acidification to have a significant effect because the site is not strongly N limited and has a high puffer capacity for acid deposition.

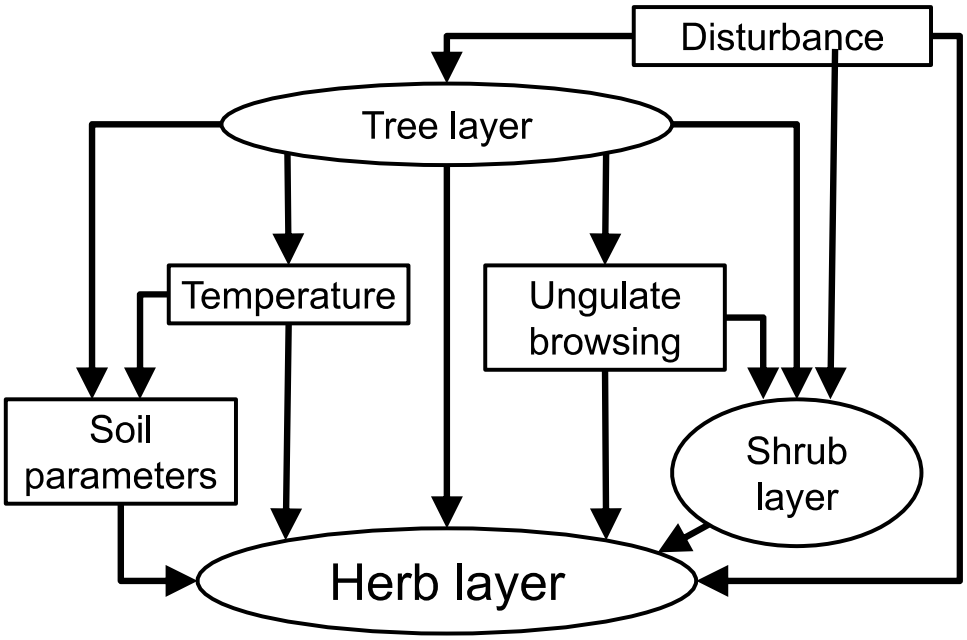

Fig. 1: Conceptual model that was used for the path analysis. Elliptic forms represent the different vegetation layers, boxes the environmental variables and arrows the hypothesized relationships among them: We assumed disturbance as the only factor controlling tree layer cover and also controlling shrub cover and directly affecting the herb layer via soil perturbations. The tree layer has a key role by influencing the microclimate and soil conditions, limiting the light availability for the understorey and thus the development of the herb and the shrub layer. Ungulate browsing may differ between open and dense forests and impacts the shrub and the herb layer. Although some relationships may have reciprocal influence, we decided to use only one-directional pathways to avoid a too complex model. Prior to the path analysis we conducted correlation tests between the predictor and the response variables (herb layer) and included only predictor variables that were significantly correlated with the response. During the path analysis insignificant pathways were removed if it improved the model.

Methods

STUDY AREA

The study site "LTER Zöbelboden" is located in the Austrian National Park Kalkalpen, Upper Austria (47°50'30" N, 14°26'30" E). It was established in 1992 by the Environment Agency Austria to be part of the effects monitoring within the UN Convention on Long-Range Transboundary Air Pollution (CLRTAP) and became part of the Austrian Long-term Ecosystem Research Network (LTER). To the southern and eastern edge of the area a plateau stretches at about 900 m a.s.l. which plunges into steep slopes to the north-west, forming the 90 ha catchment of Zöbelgraben with the lowest elevational point on 550 m a.s.l. The main bedrock is limestone, soils on the slopes are mainly lithic and rendzic leptosols , whereas on the plateau chromic cambisols and hygromorphic stagnosols dominate (Hülber *et al.* 2008). The main parts of the area are covered

by a near-natural temperate deciduous forest with European beech (*Fagus sylvatica* L.), maple (*Acer pseudoplatanus* L.), ash (*Fraxinus excelsior* L.), other deciduous tree species and the conifers Norway spruce (*Picea abies* Karst.), Larch (*Larix decidua* Mill.) and fir (*Abies alba* Mill.) forest, whereas on the plateau remnants of a spruce plantation of the early 20th century can be found. Since 1992 forest management has been restricted to the removal of bark beetle infested trees. Since 2004, the area has been hit by a series of stronger storms causing wind throw and subsequent bark beetle infestation of Norway spruce. The mean annual temperature (1980-2012) at Zöbelboden is 7.4 °C. The warmest month is July (15.3 °C) and the coldest month is January (-2.0 °C). Average annual precipitation is 1628 mm, inter-annual variation ranges from 1400 to 1800 mm (1990-2013), with the highest precipitation sums in July (198 mm) and lowest in February (101 mm). Snow cover usually maintains until March.

SAMPLING DESIGN

Vegetation records

Over the whole study area 165 quadratic 10x10 m permanent plots are distributed regularly, with 50 m distance (excluding some rock outcrops, clear-cut areas and young plantations of less than 20 years). The first vegetation survey took place in 1993 and resurveys were made in 2005, 2010 and 2014. All surveys were carried out in July and August to avoid phenological bias. All vascular plant species occurring at the plots were recorded and their cover was estimated in seven cover-abundance-classes according to Braun-Blanquet (1964). Woody species were assigned to five different vegetation strata depending on their height: herb layer (0-60 cm), shrub layer (60-300 cm), tree layer 3, tree layer 2 and tree layer 1.

To eliminate errors of misidentification of plant individuals, we pooled the closely related and taxonomically difficult species *Senecio ovatus* Willd. *and Senecio nemorensis* L.*, Dryopteris carthusiana* H.P.Fuchs and *Dryopteris dilatata* A.Gray to *Senecio nemorensis* agg. and *Dryopteris carthusiana agg.*, respectively. Bryophytes and lichens were disregarded due to an assumed high observer error. For the statistical analysis we transformed all cover abundance values to ordinal values (1–7).

Ungulate browsing

To measure the intensity of ungulate browsing we selected the six tallest individuals of each tree species within a height of 10 to 130 cm and recorded the seasonal gain in length of the main stem. Further we noted whether the main trunk showed damage by ungulate browsing in the year

of the record, the year before the record or both years and calculated the percentage of damaged individuals.

Tree layer cover

During the vegetation surveys additional parameters like total cover of tree layer 3, 2 and 1 and total shrub cover were estimated. We later calculated the total tree cover by summarizing the total cover of tree layer 3, 2 and 1.

Disturbance data

Areas affected by disturbances from windthrow or spruce bark beetle outbreaks between the first and the last survey year were identified based on aerial photographs and field survey records, using ArcGIS.

Soil data

We collected mixed soil samples at 64 plots between July and August 2014 to compare with the soil survey data of the years 1992 and 2004. These plots comprise every second permanent vegetation plot, hence being 100 m apart. For one mixed soil sample three individual soil cores with 4 cm diameter were taken from the upper mineral soil layer (0-10 cm) after litter removal. According to the sampling design of the 1992, the soil cores were taken in 4.5, 5.0 and 5.5 m distance to the permanent plots, with 2.5 m distance to the 1992 and 2004 sampling sites. In all surveys soil samples were dried at approximately 30°C, coarse aggregates crushed and dried again until constant weight. After a constant weight was reached samples were sieved through a 2 mm sieve. Soil suspensions were made by dissolving 5 g of each soil sample in 12.5 ml of 0.01 M $CaCl_2$ solution and pH was measured electrochemically with a pH electrode (Metrohm 654 pH meter in 1992 and 2004 and Argus X pH meter in 2014). For the determination of the C:N-ratio the soil samples were ground and further decarbonized using 3M HCl solution. The organic carbon content was measured after dry combustion using isotope-ratio mass spectroscopy (IRMS). This methods deviate from the analysis in 1992 where total content of organic C (TOC) was calculated by subtracting the total content of $CaCO_3$ from the total content of C (TC – TIC). Total content of C (TC) was analyzed by dry combustion (1300°) of the samples in O_2. Released CO_2 was detected coulometrically (Ströhlein Coulomat 702 and Si 111/6). Total content of $CaCO_3$ (TIC) was measured via addition of HCl and volumetrically determination of the released CO_2

(Scheibler). The total content of N was determined by a modified Kjeldahl method and did not deviate from the methods in 1992 and 2004. The organic N was converted to NH_{4+} by digestion with H_2SO_4 and a catalyst (Kjeldahlterm KT8 Gerhardt). The accumulated NH_{4+} was converted to NH_3 (distillation) and measured by potentiometric titration. To account for N oxygen compounds, salicylic acid was added prior to digestion.

Climate and deposition data

Since 1993 temperature and precipitation were measured directly at the plateau of the study site. Data of the nearby meteorological station Reichraming (approx. 5 km distance) and linear regression models (R^2=0.97, $p<0.001$ for temperature and R^2=0.7, $p<0.001$ for precipitation) were used to reconstruct the missing monthly mean temperature and precipitation sums values for the years prior to 1993. N and S deposition data were collected on two intensively measured plots in a spruce dominated forest on the plateau (IP I) and in a mixed deciduous forest on the slope (IP II).

Nitrate (NO_3^-) and ammonium (NH_4^+) as well as sulphate (SO_4^{2-}) in throughfall have been monitored since 1993. Throughfall at each site was measured with 15 regularly distributed bulk deposition samplers (Ø=20 cm). From 2006 onwards, 17 samplers were used at the IP I. Water samples were analyzed in weekly intervals up to 1999. From 1999 onwards, samples from two consecutive weeks were mixed (volume weighted) and analyzed biweekly. NO_3^- and SO_4^{2-} were determined by ion chromatography with conductivity detection (Dionex IC System 4000 I until 2002, thereafter with Dionex IC System Serie DX 500, soil water after 2002 was analyzed with Metrohm IC System 7xx-Serie). Concentration of NH_4^+ was analyzed with photometric analysis (Milton-Roy 1201 Spectrophotometer). Total inorganic N was derived from the sum of NO_3^- and NH_4^+ (for more detail see Jost *et al.* 2011).

DATA ANALYSIS

For all analyses R version 3.1.2 was used (R Core Team 2014).

Environmental variables

We used two sample t-tests for change detection in all normal distributed environmental variables and Wilcoxon signed rank test for non-normal distributions. Mean annual temperature (MAT) and mean annual precipitation sums (MAP) of the decades 1983–1992 and 2003–2012

were taken for comparison. Accumulated annual deposition rates were taken for the decades 1994–2003 and 2004–2013. Paired t-tests were also used to compare the soil C:N ratios and total tree cover of 1993 and 2014, the percentage of individuals damaged by ungulate browsing of 2005 and 2014. As for total tree cover we further made separate paired t-tests for disturbed and undisturbed plots. Since soil pH values were not normally distributed, we used Wilcoxon signed rank test to compare the data of the two survey years.

Herb Layer

We used univariate and multivariate statistical methods to compare species and community changes between the survey years 1993, 2005, 2010 and 2014. First, changes in single species abundances between the first and the last survey year were tested. Second, plot mean Ellenberg indicator values for light (L), temperature (T), soil moisture (F), soil pH (R) and nutrient availability (N) of the resurvey years were compared to the first survey year. Third, ordination was applied and dissimilarities in the three-dimensional community space between the first and the last record year were further analyzed with indicator values and a Structural Equation Model in order to infer cause-effect relationships.

Species abundance changes

We used paired t-tests to compare cover abundance values of single species with at least 20 occurrences on all plots of 1993 and 2014. For comparison only the plots were taken where the species occurred at least in one of the two years. If the species was absent in one of the years, null was taken as cover abundance value.

Community analyses

Following the discussion of (Diekmann 2003) mean Ellenberg indicator values of light (L), temperature (T), soil moisture (F), soil pH (R) and nutrient availability (N) were calculated for each plot and each survey year based on the Ellenberg indicator values of each single vascular plant species occurring. For both, single species data and Ellenberg indicator values, we used paired t-tests to compare the survey years.
We calculated the Sorensen index, its Nestedness-resultant fraction and the Simpson dissimilarity using betapart 1.3 (Baselga 2010). We used a t-test after 100 times of resampling 50 % of the sampling points to compare the indices of the resamples from 2014 and 1993.

We used Non-metric multidimensional scaling (nMDS) of the R package *vegan 2.2-1* with a dissimilarity matrix of Bray-Curtis distances to evaluate alterations in community composition over time (Oksanen *et al.* 2015). As dissimilarity matrix we took the herb layer data of the vegetation records of 143 plots of the survey years 1993, 2005, 2010 and 2014 (572 in total). nMDS is an ordination method which iteratively tries to find the best representation of a multidimensional dissimilarity matrix in a pre-defined low dimensional space. The less dissimilar the plots are in their species composition, the closer they are positioned in the nMDS space. The stress value indicates the quality of this representation: The lower the value, the better the data is represented in the nMDS space. We repeated the calculations for 200 times with random starting arrangements of plots to find the model with the least stress. We extracted the axis scores and conducted correlation tests of each of the axis scores and the mean Ellenberg indicator values using Pearson's moment correlation coefficient to find the environmental variables prescribed by the nMDS axis scores. We further subtracted the axis scores of 2014 with those of 1993 to get difference vectors (Δ axis scores). These vectors represent the magnitude and direction of change in species composition over time along prescribed environmental variables. We used Ellenberg indicator values to describe these variables. We applied MANOVA (Pillai-Bartlett test statistic) with the three Δ axis scores as response: First without a grouping variable to test whether there was a significant change in species composition in the 3-dimensional nMDS space and subsequently with disturbance as grouping variable in order to know whether there was an impact of disturbance on this change. We further used the Δ axis scores to calculate euclidean distance vectors for each point, representing the movement of each plot in the 3-dimensional space between the survey years 1993 and 2014. The length of these vectors resembles the magnitude of species composition change. We implemented these vectors as response variables in a structural equation model to test the influence of local environmental variables on these alterations. Following Grace *et al.* (2010) we conceived an initial model combining the on-site measured predictor variables and the response variable based on our theoretical knowledge (Figure 1). For all predictor variables, except disturbance, we calculated Δ values by subtracting the data from 2014 with those of 1993. Since our response variable consists only of positive values that represent the magnitude of change and not its direction, we transformed the negative Δ predictor values to positive ones to get undirected predictor variables. Disturbance was used as binary variable, with 1 = "disturbance occurred" and 0 = "no disturbance occurred" on the plot. We standardized all continues variables to make them comparable for the analysis (Schielzeth 2010). Considering the non-normal distribution of the data, we conducted correlation tests using Spearman's rank correlation. Predictor variables that were significantly correlated with the response variable were selected and implemented in the structural equation model (Table 1). Pathways were added or removed if they improved the model and were also biologically meaningful. For the path analysis

we used the *sem* function of the *lavaan* package (version *0.5-20*) with maximum-likelihood estimation with robust standard errors and Satorra-Bentler scaled test statistic (Rosseel 2012).

Table 1: Correlations between predictor variables and the herb layer composition change. Only predictors with significant ($P < 0.05$, bold) correlation and variables significantly correlated to them were implemented in the SEM model.

ΔHerb layer composition (Spearman's rank correlation coefficient)	r^2	*P*
|Δ Browsing|	0.03	0.768
|Δ Conifers|	0.16	0.056
|Δ shrub|	0.10	0.247
|Δ Tree layer cover|	0.39	**<0.001**
Disturbance	0.11	0.203
|Δ N|	0.06	0.473
|Δ F|	0.27	**0.001**
|Δ R|	0.26	**0.002**
|Δ T|	0.21	**0.012**

Results

CHANGES IN CLIMATE, DEPOSITION AND SOIL CHEMISTRY

Climate, deposition and soil chemistry were subject to significant shifts between the two time periods (Table 2). MAT increased and S deposition decreased significantly whereas MAP and N deposition did not exhibit any significant trends. Results of the soil analysis reveal a significant increase in soil pH whereas the decrease in the soil C:N ratio was not significant (*P = 0.10*).

Table 2: Trends of climate, deposition, and soil parameters at Zöbelboden. Significant p-values *(P < 0.05)* are given in bold.

Climate	n	1983-1992	SE	2003-2012	SE	Δ	*P*
MAP [mm]	10	1547.86	162.17	1668.54	269.72	120.68	0.244
MAT [°C]	10	6.91	0.51	7.86	0.52	0.95	**0.001**
Deposition	n	1994-2003	SE	2004-2013	SE	Δ	*P*
N-deposition IP1 [kg/ha/y]	10	18.79	3.81	17.00	2.89	-1.79	0.218
N-deposition IP2 [kg/ha/y]	10	12.51	1.97	11.41	1.81	-1.10	0.315
S-deposition IP1 [kg/ha/y]	10	8.27	3.12	4.49	1.09	-3.78	**<0.001**
S-deposition IP2 [kg/ha/y]	10	5.28	1.03	3.54	0.64	-1.75	**<0.001**
Soil parameters	n	1993	SE	2014	SE	Δ	*P*
pH (CaCl2)	49	6.17	0.79	6.25	1.00	0.08	**0.042**
C/N-ratio	49	14.89	3.14	13.92	3.37	-0.97	0.104

CHANGES IN TREE LAYER COVER

We did not detect a significant change in total tree cover across the study area (*P = 0.40*) and on undisturbed plots (P = 0.12) but a significant decrease (*P < 0.01*) on all disturbed plots.

CHANGES IN UNGULATE BROWSING

Percentage of juvenile tree species that were damaged by browsing increased significantly ($P < 0.001$) from 0.35 ±0.25 in 2005 to 0.55 ±0.26 in 2014.

SINGLE SPECIES CHANGES

Of the total of 275 species that were found in the surveys, 82 occurred in at least 20 plots. Thereof, 9 species increased significantly in cover, whereas 33 decreased significantly ($P < 0.05$) (Fig. 2).

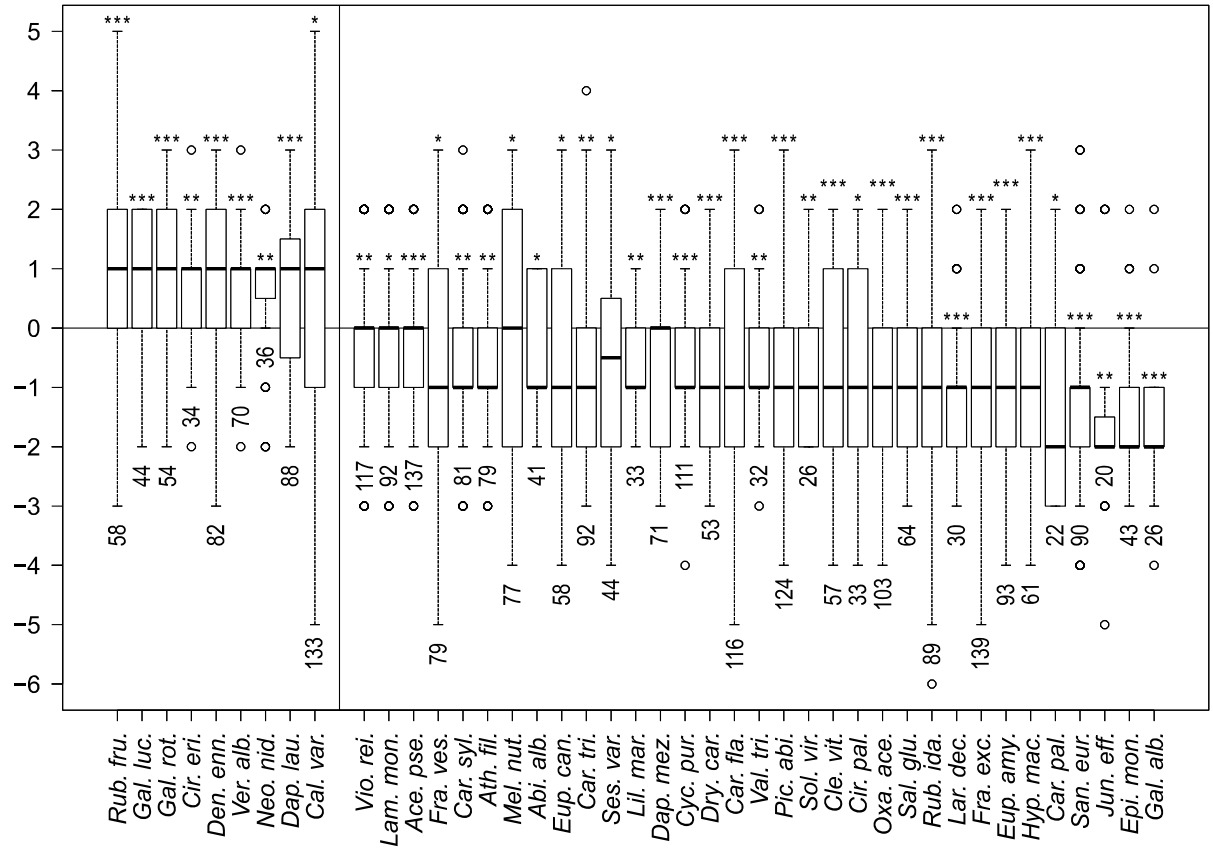

Fig.2: Significant cover abundance level changes of vascular plant species with at least 20 occurrences in the plots (n = 144). Asterisks symbolize the level of significance (* p<0.05, ** p<0.01, *** p<0.001). The solid vertical line separates the abundance increasing (left) from the abundance declining species (right). The total number of occurrences is stated below each boxplot.

OVERALL CHANGES IN THE HERB LAYER

Mean herb layer cover decreased from 63.3 ±30.9 % to 52.1 ±28.4 % (*P < 0.001*). The total number of vascular plant species occurring in the herb layer of the 143 plots dropped from 235 in 1993 to 207 in 2014. The Sorensen index increased significantly from 0.0023 to 0.0028 (*P < 0.001*). The Simpson dissimilarity of the all plots increased significantly from 0.9357 to 0.9373 (*P < 0.001*), whereas nestedness decreased from 0.021 to 0.017 (*P < 0.001*). All Ellenberg indicator values except for the N-value exhibited significant changes between the first and the last survey (Fig. 3). Temperature (T) and soil pH (R) values increased whereas light (L) and soil moisture (F) values decreased.

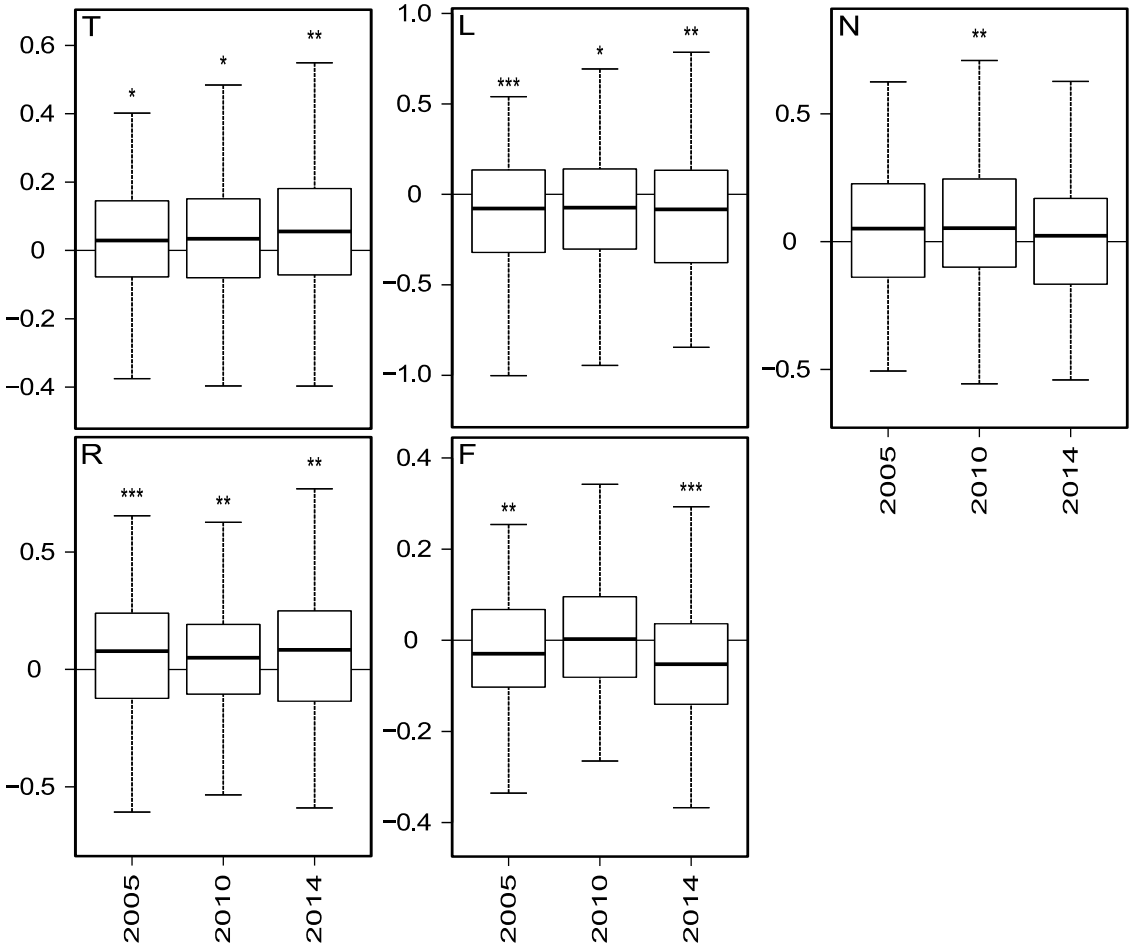

Fig.3. Boxplots of the deviation of unweighted mean Ellenberg community indicator values of 2005, 2010 and 2014 from the first survey 1993.The community indicator values represent means of the singular Ellenberg indicator values of each vascular plant species occurring per plot (n = 143). Asterisks symbolize the level of significance (* p<0.05, ** p<0.01, *** p<0.001).

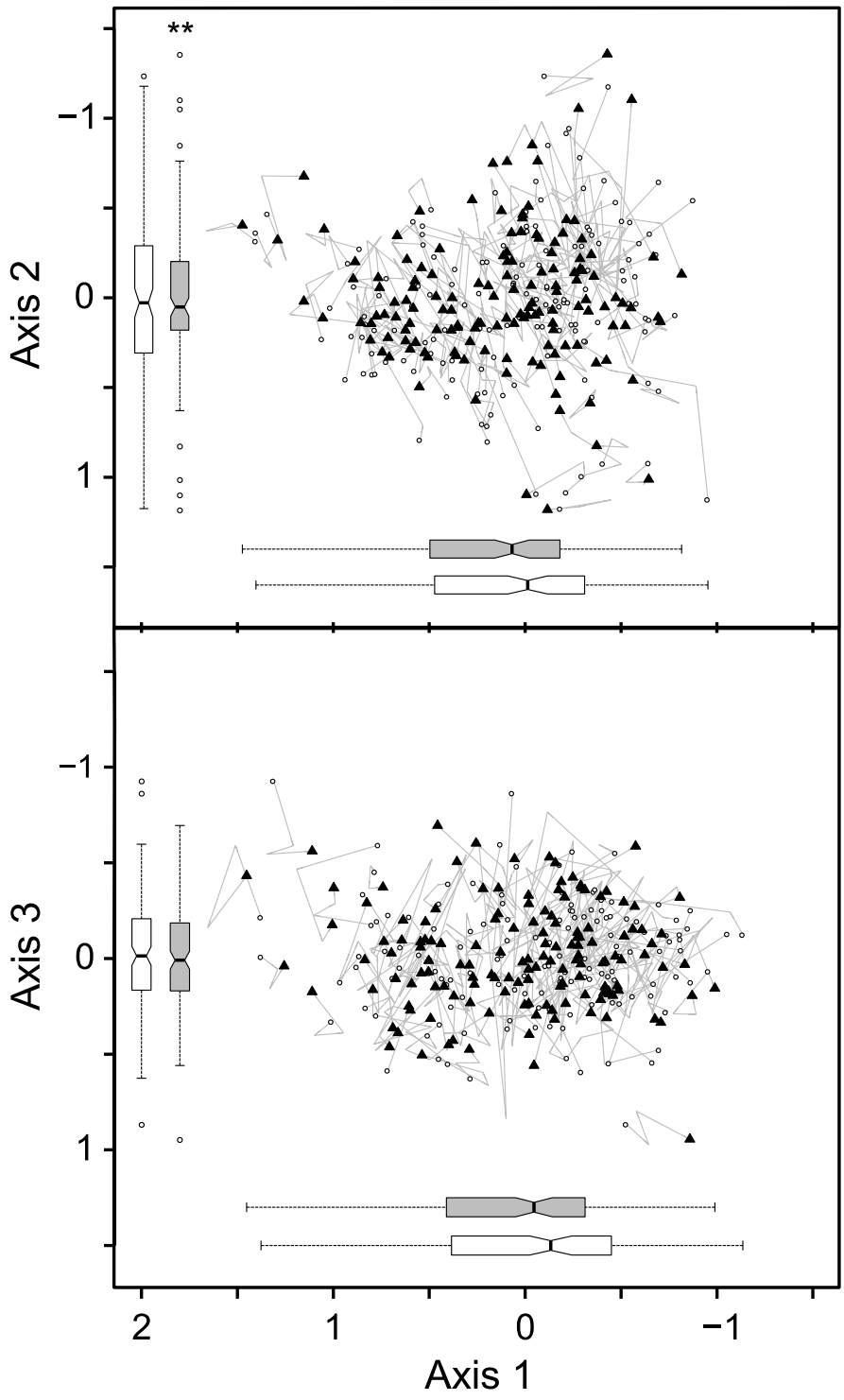

Fig.4. Results of the nMDS ordination plot (*stress = 15.8*) based on coverage data of vascular plant species in plots (n = 143) of the herb layer: White dots represent the records of 1993, black filled triangulars the 2014 records. The grey paths indicate the movement of plots between the surveys. The 2005 and 2010 records were taken as vertices for the paths. The boxplots depict the variance of the record years 1993 (white) and 2014 (grey). Asterisks symbolize whether there was a significant change in homogeneity of variance (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

VARIATION IN PLANT SPECIES COMPOSITION BETWEEN PLOTS OVER TIME

The three-dimensional nMDS ordination explains 79% of the variation of species composition between plots and has a stress value of 0.158 (Fig. 4). According to the widely accepted classification of Clarke (1993), nMDS ordinations with stress values <0.2 are considered to deliver an acceptable representation of the original distance matrix. nMDS-axis 1 is correlated significantly ($P < 0.05$) with all Ellenberg indicator values, nMDS-axis 2 with all but N and nMDS-axis 3 with R and L (Table 3). The variance in axis 2 scores decreased significantly ($P < 0.01$) from 1993 to 2014. Results of the MANOVA analysis reveal a substantial overall change in species composition (MANOVA without grouping variable: Pillai = 0.123, $F_{3, 140} = 6.55$, $P < 0.001$) and a significant impact of disturbance on the magnitude of this change (MANOVA with disturbance as grouping variable: Pillai = 0.136, $F_{3, 139} = 7.28$, $P < 0.001$).

Table 3. Correlations between the axes of the nMDS ordination and the calculated Mean Ellenberg indicator values. Significant p-values ($P < 0.05$) are given in bold.

Mean Ellenberg indicator value	Axis 1	Axis 2	Axis 3
Soil nitrogen (N)	**-0.80**	0.02	-0.04
Soil moisture (F)	**-0.74**	**-0.39**	**-0.06**
Light (L)	**0.73**	**-0.45**	**-0.18**
Soil pH (R)	**0.65**	**0.43**	**-0.26**
Temperature (T)	**-0.26**	**0.11**	-0.08

Table 4. Changes between 1993 and 2014 of the predictor variables that were implemented in the SEM (n = 143). Note that for the SEM only absolute Δ-values were used. Significant p-values are given in bold. As for disturbance only the number of plots that were affected by disturbance is given.

Explanatory variables	1993	SE	2014	SE	Δ	*P*
Δ tree layer cover (ΔTLC)	71.62	34.33	68.66	30.80	-2.96	0.402
Δ temperature (ΔT)	4.67	0.26	4.72	0.24	0.04	**0.005**
Δ soil moisture (ΔF)	5.25	0.26	5.20	0.25	-0.06	**<0.001**
Δ soil pH (ΔR)	6.71	0.52	6.78	0.49	0.07	**0.008**
Disturbance			49	*plots affected*		

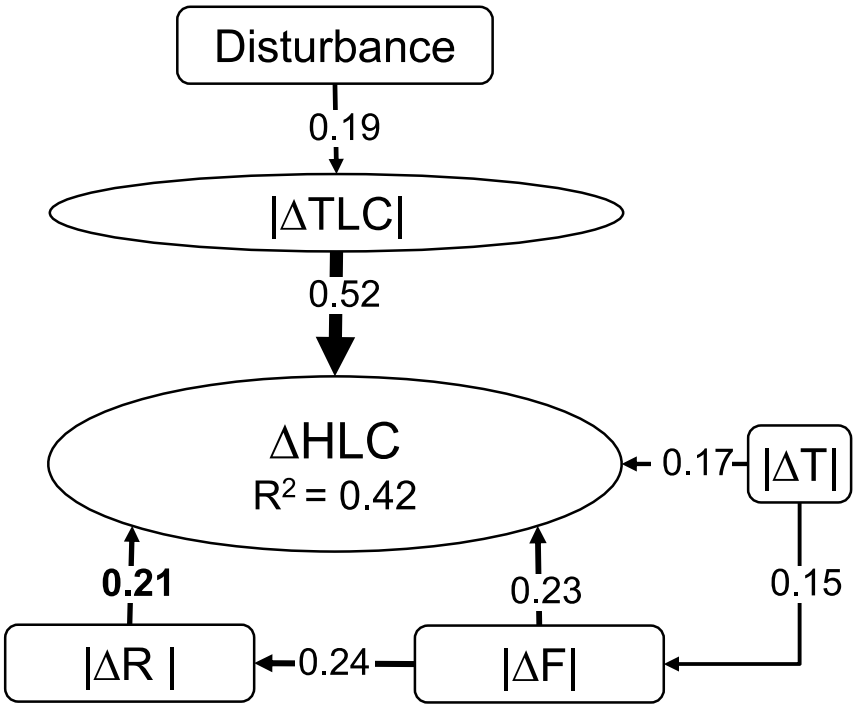

Fig.5. The final path model of the SEM analysis ($\chi^2 = 5.2$, *d.f. = 7, P = 0.64.*) depicts the influence of different predictor variables on herb layer composition change over time. Arrows represent relationships between variables and are labeled with standardized path coefficients. Thicker arrows symbolize stronger correlations. R^2 gives the proportion of variance explained by the exogenous variables. Full parameters of the pathway analysis are given in table 3.

THE FACTORS THAT SHAPE CHANGES IN COMPOSITION

The temporal trends of the exogenous variables implemented in the structural equation model are represented in Table 4. Whereas average tree layer cover remained stable at the study site, the Ellenberg indicator values T, F and R changed significantly: Temperature increased from 4.67 ±0.26 to 4.72 ±0.24 ($P < 0.01$) and soil reactivity from 6.71 ±0.52 to 6.78 ±0.49 ($P < 0.01$), whereas soil moisture decreased from 5.25 ±0.26 to 5.20 ±0.25 ($P < 0.001$). The final path model (Fig. 4) fitted the data well with $\chi^2 = 5.2$, d.f. = 7, $P = 0.64$. Note that p-values > 0.05 indicate that there is no significant deviation between data and the model. All pathways given in the model are significant ($P < 0.05$). Details of the influence of singular parameters are given in Table 5. Changes in tree layer cover (|ΔTLC|) had a major impact on the herb layer, followed by soil pH (|ΔR|), soil moisture (|ΔF|) and temperature (|ΔT|), explaining 43 % of the total variation of the herb layer composition changes (ΔHLC).

Table 5. Parameters of the SEM pathway analysis describing the relationships between endogenous (ΔHLC, |ΔTLC|) and exogenous variables (|ΔR|, |ΔF|, |ΔT|, disturbance): Estimate are unstandardized path coefficients, *z* is the test statistic (Estimate devided by standard deviation) and *P* (>|*z*|) the probability under the null hypothesis of no relationship between the variables. Std. Coeff. are coefficients standardized by standard deviation.

Pathway	Estimate	*z*	*P* (>|*z*|)	Std. Coeff.
Δ herb layer composition (ΔHLC)				
← |Δ tree layer cover| (|ΔTLC|)	0.51	6.04	< 0.001	0.52
← |Δ soil pH| (|ΔR|)	0.21	2.71	0.007	0.21
← |Δ soil moisture| (|ΔF|)	0.22	3.09	0.002	0.23
← |Δ temperature| (|ΔT|)	0.16	2.31	0.021	0.17
|Δ t*ree layer cover*| *(|ΔTLC|)*				
← disturbance	0.19	2.18	0.029	0.19
|Δ soil moisture| (|ΔF|)				
← |Δ temperature| (|ΔT|)	0.15	2.11	0.035	0.15
|Δ soil pH| (|ΔR|)				
← |Δ soil moisture| (|ΔF|)	0.24	2.57	0.010	0.24

Discussion

OVERALL HERB LAYER CHANGES AND RELATIONS TO ENVIRONMENTAL SHIFTS

Our analysis revealed that there was a directional change over time in forest floor species composition (which was more pronounced in disturbed than in undisturbed plots), a decrease in species richness and an increase in the dissimilarities between plots, that can be related to broad scale, environmental changes (climate change, air pollution) but also to local pressures (primarily tree canopy disturbance). These results are robust insofar as observer errors have been kept low (Hülber *et al.* 2008) and because environmental changes have been measured in-situ.

Among the directional changes, a recovery from soil acidification was the most apparent. We did not only observe an increase of the Ellenberg R value but also directly measured an increase in soil pH. Acid-tolerant species (e.g. *Juncus effusus* L., *Hypericum maculatum* Crantz) are found among the species that declined in cover whereas neutral or basiphilous species are found amongst the species that increased (e.g. *Galium lucidum* All., *Cirsium erisithales* Scop., *Calamagrostis varia* Host). This corroborates results from an earlier analysis in the study site (Hülber *et al.* 2008) and also reflects the results of more recent studies in temperate forest ecosystems, which were exposed to acid deposition (Reinecke *et al.* 2014; Vanhellemont 2014). Although the soils of the study area, having carbonate bedrock, are by no means sensitive to acid deposition, topsoils could have been affected and may be in recovery after sulphate deposition decreased considerably. Since part of the area was used as a pasture until around 1900, increasing base saturation during forest succession may play a role together with the fact that most forest soils in Austria were acidified because of overuse and related base cation depletion over centuries (Jandl *et al.* 2012).

Further, we found evidence that forest vegetation responded to an increase in temperatures with a relative increase in more thermophillic plants. Moreover, we observed a decrease of the Ellenberg F value suggesting that the study area became drier. Species adapted to wet soils diminished (*Cirsium palustre* L., *Juncus effusus*), whereas species restricted to drier and warmer conditions increased (e.g. *Galium lucidum*, *Daphne laureola* L.). Though mean annual precipitation sums did not change during the last three decades, increased temperatures, particularly in form of more frequent and extended heat waves (APCC 2014), cause higher evapotranspiration rates and hence drier conditions. Hartl-Meier *et al.* (2015) by using tree-ring isotopes, observed a significant reduction in tree growth during several drought events in the last decades. Their study underpins, that moisture limitation may play a role for changes of the forest understorey even in this rela-

tively humid mountain climate. Results of the path analysis show that thermophilization and drying are not mere artefacts from an increase in disturbance gaps, rendering sites more open to radiation and soil warming, but independent drivers of compositional changes in the herb layer. We also think that the shift from cooler and more humid to warmer and drier conditions triggered the decline in species richness in the study area. Species that could be found on the cool and moist end of the gradient might have disappeared whereas new species could probably not establish on warmer and drier sites due to dispersal limitations or a lack of drought-adapted species in the regional species pool. Yet overall, disturbances might have prevented even stronger species loss by the observed increase in the variation in site conditions among plots, which is typical in forests (Thom & Seidl 2015). As yet, evidences for temperature driven composition changes in temperate forests are scarce (Lenoir *et al.* 2010; Küchler *et al.* 2014; Savage & Vellend 2015). However, it is very likely that such changes first occur in areas where temperature increases are more pronounced compared to other regions such as in the European Alps (APCC 2014). It has also been reported that denser canopies may buffer the response of the herb layer to climate change (De Frenne *et al.* 2013). Although we could not detect a significant change ($P = 0.12$), the tree canopies in undisturbed plots of the study area tended to increase slightly. We calculated the total tree cover by summarizing the cover values of each tree layer implicating higher values in forests with more pronounced stratification. However, in late successional stages of forest stands lower layers are usually poorer developed due to the enhanced light limitation by a denser overstorey (Van & Franklin 2000). Hence, changes in total tree layer cover on undisturbed plots might not be visible in the data, but changes in light availability might have occurred. In plots affected by disturbance the tree layer cover decreased, its cooling effect and light limitation weakened enabling new species which are better adapted to warmer temperatures to colonize the forest floor (Overpeck, Rind & Goldberg 1990). How strong disturbance has coinfluenced the warming and drying signal in the forest floor vegetation is however not fully clear. In the relatively small disturbance gaps (<200m²) in the study area, no change in the soil temperature has been observed when compared to closed forests (Kobler *et al.* 2015). They also observed that soils in cleared gaps are wetter due to less transpiration from trees. For European beech forests, Leuschner & Lendzion (2009) showed that air humidity and soil moisture are the most important factors in limiting certain forest plant species to occur. Considering future climate predictions (APCC 2014) and the observed seasonal oscillation of precipitation zones (Giorgi & Coppola 2007), future drought events will very probably extend its range and become more frequent. Since gap size and structure strongly controls microclimatic changes (Ritter, Dalsgaard & Einhorn 2005) and frequency and strength of disturbances are predicted to increase in European forests (Seidl *et al.* 2014), these factors may become even more important for future compositional changes of forest ecosystems.

Annual N deposition rates in canopy throughfall was within the range of the proposed empirical critical load of 10-20 kg N ha^{-1} yr^{-1} (Bobbink *et al.* 2010) but exceeds this threshold when dry and occult deposition is taken into account (Mayer *et al.* 2013). In a prior analysis of forest floor vegetation changes in the study area, Hülber *et al.* (2008) have reported a homogenization in the species composition from acid, wet sites and base rich, dry sites towards more intermediate conditions. They related this trend to eutrophication in response to N deposition. However, disturbances disrupted this relationship since 2005 and climate change became more important as indicated in our analysis. As to N deposition effects it remains speculative if major forest floor changes already happened (Hülber *et al.* 2008), or if the site is not susceptible enough to this amount of N loads. High rates of N mineralization and shallow soils with high preferential flow rates causing major loss of N via leaching (Jost *et al.* 2011) render the study site relatively insensitive to N deposition. At least in the short to medium term, N deposition effects on forest plants seem to be weak in sites without major N limitation, even when N loads exceed the critical load (Dirnböck *et al.* 2014).

The decrease of the Ellenberg L value suggests that light availability on the forest floor decreased. This might also have caused the observed reduction of the herb layer cover. However, we did not detect an increase in overall canopy cover which might be due to the methodology (see discussion above). Nevertheless, Diekmann (2003) recommends the application of unweighted Ellenberg indicator values in species rich communities. Yet in forest ecosystems a weighted Ellenberg L value might better represent the light conditions of the forest floor (Diekmann 2003). However, in fact, the herb layer cover decreased significantly in contrast to the stable tree cover. The explanation of these diverging trends might deliver the disturbance regime: One third of the plots were affected by disturbances between 1993 and 2014, mainly by windthrow and the removal of bark beetle infested trees. As mentioned above, tree layer cover on the affected plots decreased and light availability for the herb layer increased, likely shaped by disturbance gap size (Canham *et al.* 1990). On the other hand, on the majority of the plots, which were not affected, canopies very likely became denser and thus light availability reduced driving the decrease of the herb layer cover. The latter was a general trend in many Central European forests because use for timber has declined during the last decades (Verheyen *et al.* 2012). Accordingly, we found a shift in the frequency of tree layer cover classes from dominance of plots with medium canopy closure to more evenly distributed frequencies of different tree cover classes (Fig. 6). We consider changes in irradiance the main control for herb layer cover in our site. Apart from irradiance, N deposition can also increase forest floor biomass (Gilliam *et al.* 2016). In fact, it has been shown that soil C:N ratios, usually lowered by N deposition, showed a negative relationship with forest floor herb and grass cover in the study site (Diwold, Dullinger & Dirnböck 2010). Nevertheless, this effect might have been too weak in our study

site since C:N ratios decreased only slightly. Drier conditions, as indicated by the Ellenberg F value, may have additionally contributed to the decrease of the herb layer cover. One additional factor controlling herb layer cover is the variability in the shrub cover. With more open tree canopies juvenile tree growth benefits and thereby shades the understorey plants. This is apparent in some parts of the area but in others ungulate browsing is strongly limiting tree regeneration.

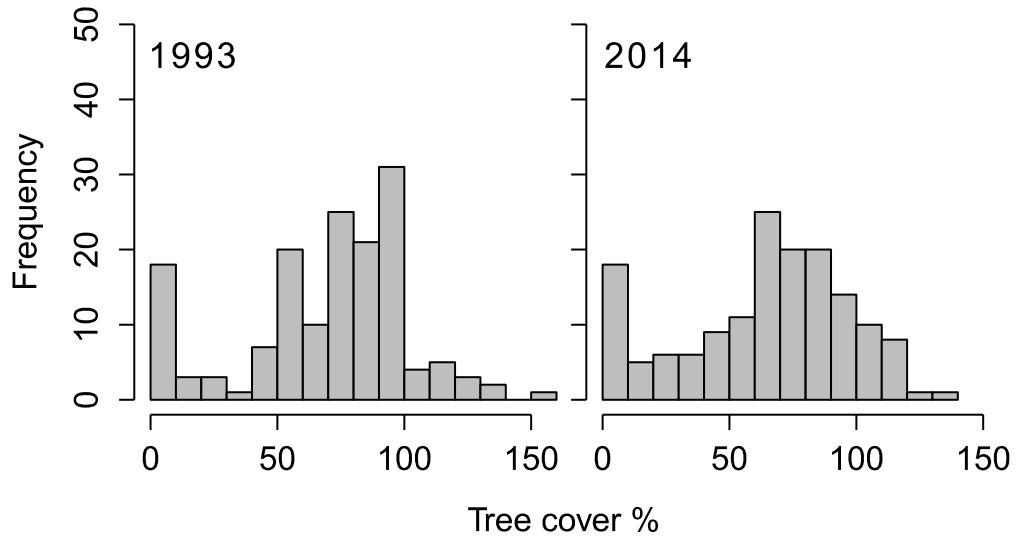

Fig.6. Frequency of estimated tree covers in 1993 and 2014, categorized to ten percent classes. The tree cover was calculated by summarizing the estimated cover values of each tree layer.

RELATIVE CONTRIBUTIONS OF DRIVERS TO HERB LAYER CHANGES

We conducted a path analysis to identify the relative contributions of environmental drivers to changes in the herb layer composition. Our hypothesis was that disturbance is the most important factor as it controls canopy closure and thus has severe indirect impact on light regime and microclimate on the forest floor. We measured the intensity of compositional change by calculating the 3-dimensional distance in the nMDS ordination for each plot between the surveys of 1993 and 2014. Hence, we could only implement absolute values of change of our predictor variables causing a reduction in correlation coefficients. However, the results of the path analysis give a good representation of the relative contribution of the most important drivers of compositional changes in the herb layer – though, in fact their relative importance might be even higher.

Our results confirm changes in tree cover as the major driver of forest floor vegetation changes and underpin the regulative effect of disturbances. The influence of disturbance is lower than expected, yet its relative importance is with certainty underrepresented since we did not have a measurement for the intensity (e.g. relative reduction in trees) and gap size of disturbance but only presence-absence data. The impact of disturbance on changes in forest floor plant communities may also greatly differ between sites within the study area because contrasting plant functional types occur on the relatively moist plateau soils and at dry slopes, i.e. plants investing in resource acquisition versus in resource conservation which thus are differently adapted to cope with forest disturbance (Seebacher *et al.* 2012). However, disturbance is the major force that causes the opening of forest canopies and is thus, together with tree cover the main driver that causes changes in the herb layer by altering light availability and microclimate on the forest floor. Since the intensity and gap size of disturbances is spatially very variable, disturbances enhance site variability by generating patches with different light and nutrient availability and may thus have promoted the increase of dissimilarity and the decrease of nestedness between plots. Soil pH, soil moisture and temperature had lower impact on the herb layer and reflect local variation in site conditions but also the influence of regional environmental shifts (like decreased S deposition and increased temperature) in the study site. Disturbances pave the way for immigration of new species that are better adapted to modified environmental conditions to establish in forest ecosystems as they temporarily remove the inhibiting effect of light limitation of the canopy on forest floor communities (Overpeck *et al.* 1990). The relative importance of soil moisture, soil pH and temperature in the path model is difficult to disentangle since the implemented mean Ellenberg indicator values may considerably correlate. We did not detect an influence of ungulate browsing on changes in herb layer composition, although browsing damage increased substantially. Yet the direction and intensity of browsing influence on plant communities is very

variable and may further vary between distinct understorey plant communities (Hobbs 1996). Hence, the signal might have been too weak for detection through our analysis. Moreover we did not find any significant correlation between the intensity of tree cover changes and changes of soil parameters and temperature, but relationships seem obvious since other studies already highlighted the influence of the tree layer on soil conditions and microclimate (Leuschner & Rode 1999; De Frenne *et al.* 2013). Furthermore, the relative contribution of singular drivers may vary across the spatial scale largely depending on local environmental factors e.g. site characteristics (Bernhardt-Römermann *et al.* 2015). Besides further drivers (e.g. former land use, herbivore pressure) and initial site conditions like soil nutrient status may also play an important role in how temperate forest communities respond to changing environmental conditions (Burton *et al.* 2011; Müllerová, Hédl & Szabó 2015; Naaf & Kolk 2016).

Conclusion

In our study, we identified effects of multiple environmental changes on forest floor vegetation albeit disturbances by windthrow and bark beetle outbreaks have been affecting the area. These disturbances are predicted to increase in future with intensifying climate change. Our study may therefore serve as showcase of the likely trajectories of forest vegetation changes in future. We showed that disturbance can shift the relative importance from drivers such as N deposition to climate related processes. Yet, further observation and modelling is necessary to quantify the relative importance of drivers of forest floor vegetation changes in a disturbance-prone future more precisely.

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Appendix

ABSTRACT

1. Human induced changes of the environment and their possible impacts on recent and future shifts of temperate forest understorey plant communities have been examined in many studies. While most of these studies were based on modelled or surrogated data making it difficult to disentangle cause-effect-relationships, we present a fully measured study taking into account a comprehensive set of potential environmental drivers.

2. In this study we used on-site measurements of climate, deposition, soil and forest disturbance and 21 years resurvey data collected from 143 permanent vegetation plots in the Northern Limestone Alps, Austria to detect relative contributions and interactions among these environmental drivers.

3. Our analysis reveals a strong directional shift of the forest understorey plant community. We found strong evidence for a recovery of the ground-layer vegetation from acidification as response to decreased sulfur (S) deposition. We did not observe a community response to atmospheric nitrogen (N) deposition but to altered climatic conditions (thermophilization and drying).

4. The path analysis reveals that disturbance-induced changes in the light regime are the main drivers of community shifts in the herb layer. Further, disturbances facilitate and accelerate the adaptation of forest understorey plant communities to changing environmental conditions and buffer regional species loss by enhancing local site heterogeneity. We could show that thermophilization and drying are independent drivers of understorey community changes and not mere side-effects of disturbance events.

5. Synthesis. We show that the last two decadal changes in climate and airborne deposition have driven changes in temperate forest herb-layer communities. We identified canopy disturbance by wind throw and bark beetle outbreaks as the major force that facilitated plant community adaptations and a shift in the relative importance from drivers such as deposition to climate related processes.

ZUSAMMENFASSUNG

Die vom Menschen verursachten Umweltveränderungen und deren Auswirkungen auf bisherige und zukünftige Veränderungen von Pflanzengesellschaften der Krautschicht temperierter Wälder lagen im Fokus vieler in den letzten Jahren erschienenen Studien. Da viele dieser Studien auf modellierten Daten basieren, ist es schwierig die tatsächlichen Ursachen dieser Vegetationsveränderungen festzustellen. In dieser Studie verwendeten wir direkt am Studienort, im Nationalpark Kalkalpen, erhobene Umweltdaten über Klima, Boden und Störungsereignisse bzw. Vegetationsdaten von 143 Permanentflächen, um den relativen Einfluss dieser Umweltfaktoren auf die Vegetationsveränderungen zwischen 1993 und 2014 festzustellen.

Die Ergebnisse unserer Analysen zeigen eine signifikante, gerichtete Veränderung der Krautschicht und lassen auf eine Erholung des Unterwuchses von den Auswirkungen des sauren Regens schließen. Wir konnten keine Veränderung der Krautschicht im Bezug zu Eutrophierung durch Stickstoffdepositionen feststellen aber eine Reaktion auf die veränderten Klimabedingungen (Thermophilisierung und Anpassung an erhöhte Trockenheit).

Mit den Ergebnissen der Strukturgleichungsmodell-Analyse konnten wir zeigen, dass die durch Störung induzierten Veränderungen der Lichtverhältnisse die treibenden Kräfte der Veränderungen der Pflanzengesellschaften in der Krautschicht sind. Weiters unterstützen und beschleunigen Störungen die Anpassung von Pflanzengesellschaften des Unterwuchses an veränderte Umweltbedingungen. Gleichzeitig verringern Störungen den Artenverlust der durch diese veränderten Umweltbedingungen entsteht dadurch, dass sie die lokale Standortsheterogenität erhöhen. Diese Studie zeigt dass Thermopilisierung und erhöhte Trockenheit unabhängigen Einfluss auf die Veränderung von Unterwuchs-Pflanzengesellschaften haben und nicht nur als Begleiterscheinung von Störungsereignissen zu werten sind.