Significant decrease in epiphytic lichen diversity in a remote area in the European Alps, Austria

Wolfgang Mayer[a], Veronika Pfefferkorn-Dellali[b], Roman Türk[a], Stefan Dullinger[c,d], Michael Mirtl[e], Thomas Dirnböck[e,*]

[a] *University of Salzburg, Hellbrunnerstraße 34, 5020 Salzburg, Austria*
[b] *Kleingmainer Gasse 5c, 5020 Salzburg, Austria*
[c] *VINCA, Gießergasse 6/7, 1090 Wien, Austria*
[d] *University of Vienna, Department of Conservation Biology, Vegetation and Landscape Ecology, Rennweg 14, A-1030 Vienna, Austria*
[e] *Environment Agency Austria, Department for Ecosystem Research and Monitoring, Spittelauer Lände 5, 1090 Vienna, Austria*

Abstract

We present long-term (1993–2010) monitoring results of lichens from a remote site in Austria. Whereas gaseous pollution is negligible in this area, levels of long-range air pollution of S and N via rain and fog are high. Lichen cover on tree trunks have decreased significantly. Accordingly, we found that the population of all species had declined. The analyses demonstrated significant changes in lichen community composition. The lichen flora suffered a significant decrease in diversity. Our hypothesis is that the breakdown of epiphytic lichens is mainly due to eutrophication through long-term N deposition, and more particularly to ammonia in precipitation and in fog. Since many areas in the European Alps receive high wet deposition loads, a decrease in the abundance and diversity of epiphytic lichens is most probably a widespread phenomenon.

Zusammenfassung

Die Studie beschreibt Langzeittrends (1993–2010) von epiphytischen Flechten in einem Luftschadstoff-Hintergrundgebiet in Österreich. Die nassen Immissionen von Schwefel und Stickstoff sind ausgeprägt, die gasförmige Belastung ist eher gering. Die Deckung von Flechten ging stark zurück. Multivariate Analysen zeigen, dass sich auch die Artenzusammensetzung signifikant veränderte. Auch die Flechtenartenvielfalt nahm drastischen ab. Die Langzeitwirkung von Eutrophierung aufgrund von nassen Stickstoffeinträgen, besonders Ammonium, wird als Ursache für die Veränderungen erkannt. Hohe Konzentrationen von Ammonium und Nitrat im häufig auftretenden Nebel dürften eine große Rolle spielen. Da ähnliche Immissionssituationen in vielen Hintergrundgebieten der Alpen auftreten, kann man annehmen, dass der hier beispielhaft gezeigte Flechtenartenverlust ein großflächiges Phänomen ist.

*Corresponding author. Tel.: +43 1 31304 3442; fax: +43 1 31304 3533.
E-mail address: thomas.dirnboeck@umweltbundesamt.at (T. Dirnböck).

Introduction

International efforts have successfully reduced sulphur (S) emissions and lowered the deteriorating effects of acid precipitation on terrestrial and aquatic ecosystems (Bouwman, van Vuuren, Derwent, & Posch 2002). On the other hand, human nitrogen (N) emissions resulting from agriculture, fossil fuel emissions and biomass burning now lead to acidification and eutrophication in most forest ecosystems in humid temperate regions (Galloway et al. 2004). Forests in Europe receive inorganic N deposition ranging from less than $5\,kg\,N\,ha^{-1}\,year^{-1}$ up to $60\,kg\,N\,ha^{-1}\,year^{-1}$ (Butterbach-Bahl & Gundersen 2011). There is an urgent need to monitor the effects of these air pollutants as well as the success or failure of environmental policies aiming at reducing S and N emissions. As indicators of air pollution effects, lichens have been thoroughly studied and are widely used (Conti & Cecchetti 2001). They are thus gaining importance as indicators of air pollution effects on biodiversity (Asta et al. 2002; Svoboda 2007).

The recovery of lichens from the effects of formerly high concentrations of SO_2 is well documented (Hauck 2010; Nimis & Purvis 2002). Their recovery has not only been driven by a reduction of acidifying S in the atmosphere, but also by an increase in N emissions. Elevated NH_3 concentrations in the air have additionally lowered tree bark acidity, thereby improving the substrate for acid-sensitive lichen species (Cape, Eerden, Sheppard, Leith, & Sutton 2009; van Herk 2001). On the other hand, N in the form of wet deposition also causes eutrophication. As a result, the net effect of airborne N on epiphytic lichens depends on the proportion of N compounds found at a particular site (Sparrius 2007; van Dobben & ter Braak 1998). In areas where local emission sources are negligible, N is predominantly deposited as NO_3^- and NH_4^+ in rainfall, snow and fog from long-range transport, while NH_3 is transported only over limited distances (Bleeker et al. 2009). A study focusing on Northern European sites which are located far away from emissions sources. van Herk, Mathijssen-Spiekman, & de Zwart (2003) found that wet NH_4^+ (and to a lesser extent wet NO_3^-) deposition determines the occurrence of acidophytic lichen species. The study concluded that subsequent bark acidification and eutrophication was one of the most severe threats to natural lichen communities in remote areas of Europe. Similar results were found in Slovenia (Jeran et al. 2007), the Czech Republic (Anděl 2001), Switzerland (Ruoss 1999) and Austria (Türk 1985).

Here the authors present an analysis of long-term monitoring data from an area in the Austrian Northern Alps. Whereas S deposition showed a downward trend over more than a decade, N deposition has remained more or less stable – but above the critical load for eutrophication. We asked the following questions: (i) Did the cover of lichens on tree barks decrease during the 18 years of observation? (ii) Was there a decline in lichen species diversity? (iii) Was there a change in the species composition of epiphytic lichen communities? (iv) Were there any changes indicating that N and/or S pollution were acting as a driving force?

Materials and methods

Study site

The study site Zöbelboden has a size of 90 ha and is situated in the northern part of the "Kalkalpen" (Limestone Alps) national park in Austria (N 47°50′30″, E 14°26′30″), at an altitude of 550 m up to 956 m a.s.l. (Dirnböck & Mirtl 2009). Long-term air pollution measurements of S and N are shown in Appendix A: Figs. 1 and 2.

Lichen monitoring

Epiphytic lichens were first recorded in 1993 and then in 1999, 2005 and 2010 (Table 1). Epiphytic lichen plots were marked. Strict random sampling was not appropriate for this study given the uneven distribution of tree species within the study area and the topography. Therefore, host trees were selected by a stratified sampling approach so that the same number of trees of each species was recorded in the different areas of the catchment (plateau, upper and lower part of the slope, west, north and east slope). Only trees which survived the entire observation period were evaluated (Table 1).

Different monitoring methods were applied. Two of these were selected to cover the longest time series available and to analyze data of the highest quality and comparability: (1) from 1993 onwards lichen species cover was recorded on one half of the stem circumference (on the side where lichen cover was highest in 1993). These so-called Hofmann plots range from 0.1 m to 1.5 m above ground up to 1.1 m to 3.9 m above ground. Cover was estimated visually by applying an ordinal scale of 1–8 (1–2 individual, cover up to 1%, 1–5%, 5–12.5%, 12.5–25%, 25–50%, and 50–75%). In addition, total lichen cover was estimated. (2) From 1999 onwards lichens were recorded according to the German lichen mapping guideline (VDI-Richtlinie 3799 1995) in addition to (1). At a stem height between 1.2 m and 1.7 m, a 50 cm × 20 cm mesh with 10 grid cells was fixed. The presence of all lichen species per cell was recorded. Single species frequency was calculated as the number of cells occupied and the total frequency of lichens as the number of cells occupied by any of the occurring lichen species. The nomenclature of lichens follows (Türk & Hafellner 2010).

Statistical methods

Changes of epiphytic lichens over time were evaluated using a single species and a species composition approach. Changes in total lichen cover on the Hofmann plots (1993 until 2010) and in the total frequency of lichens on the VDI

Table 1. Tree species studied and number of trees surviving the entire monitoring period with two observation methods (Hofmann 1993 and VDI guideline 3799, 1995). B: broadleaf trees; C: conifers.

	Hofmann 1993–2010	VDI 1999–2010
Ash tree (B, *Fraxinus excelsior* L.)	3	4
European beech (B, *Fagus sylvatica* L.)	7	8
Sycamore (B, *Acer pseudoplatanus* L.)	7	10
European larch (C, *Larix decidua* Mill.)	18	21
Norway spruce (C, *Picea abies* (L.) Karst.)	3	4
Total	38	47

plots (1999 until 2010) were tested with a paired Wilcoxon test, and a *t*-test, respectively. Lichen diversity indicators were calculated for the Hofmann plots and changes were evaluated with a paired Wilcoxon test. We used R 2.6.2 (R Development Core Team 2008) for all statistical analyses.

Time trends for single species

To quantify changes in cover estimates and in the frequency of a species across all permanent plots, we used Marginal Models for square contingency tables (Thompson 2004), a statistical framework that accounts for cover classes rather than continuous cover values and the fact that consecutive observations of a species at the same plot are not independent of each other. The model was fitted with the *R* function MPH.fit for Multinomial-Poisson Homogeneous Models (Lang 2002) using the G^2-statistic (Agresti 2002). The coefficient β is a quantitative measure of the general trend in species cover or changes in frequency between years.

Temporal trends in lichen communities

Changes in species composition over time were evaluated using non-metric Multidimensional Scaling (nMDS) and a consecutive test to determine whether plots significantly changed their position in the ordination space with Multivariate Analysis of Variance (MANOVA). For details we refer to (Hülber et al. 2008). The dissimilarity matrix used in the nMDS ordination was constructed using Bray–Curtis distances. The plot data from all the years of observation were included in that matrix. A three-dimensional nMDS space was chosen. We used the metaMDS function of the vegan library (Oksanen 2005). For each plot, differences in the scores of the 3-dimensional nMDS axes of two years were used as response variables in a MANOVA test without a group variable. A significant deviation of the intercept from zero indicates an overall shift in species composition between years (Pillai-Bartlett test statistic). Before applying MANOVA, the normal distributions of the scores from each year on each axis were tested with a Shapiro–Wilk-Test. We found only 4 out of 42 cases where these values were not normally distributed.

In order to infer causes of species composition changes we used weighted mean Ellenberg indicator values (Wirth 2010) from the monitoring plots. Indifferent species and species with missing Ellenberg values were omitted from the analysis. The significance of the time trend for weighted mean Ellenberg values was tested with a Wilcoxon rank sum test. Additionally, we tested the correlation between the rate of change in species composition and that in Ellenberg indicator values. Differences in the above nMDS scores between 2010 and 1993 and differences in the Ellenberg *N*, *R* and *L* values for the same time span were tested for significant correlations using Kendall's Tau.

Temporal changes in diversity

Cumulative species numbers of both VDI and Hofmann plots were only considered from 1999 onwards because in 1993 the VDI method was not applied. Plot-based diversity measures (species number and Shannon index) were calculated from the VDI data (1999–2010) because this method is less prone to observer error. We considered either all species or macrolichens alone as well as Ellenberg indicator groups. Differences between years were tested by means of a paired Wilcoxon test.

Results

A total of 141 epiphytic and epixylous lichen species have been found since the year 1993 (Appendix A: Table 1). The total cover of epiphytic lichens on tree trunks decreased significantly (Fig. 1). Lichen cover on tree trunks was 80% on average in 1993 but only 30% in the year 2010 ($p < 0.001$, paired Wilcoxon test; Fig. 1A). Whereas lichen cover on coniferous tree trunks had declined ($p < 0.001$, paired Wilcoxon test for 1993–2010; Fig. 1B), the decrease was less homogeneous on broadleaf trees: lichen cover increased slightly until 2005 and there was a strong decrease thereafter. The decline from 1993 to 2010 is still significant ($p = 0.004$, paired Wilcoxon test; Fig. 1C). Based on the VDI plot data, the results show a significant decrease in total frequency between 1999 and 2010 ($p = 0.001$, paired *t*-test)
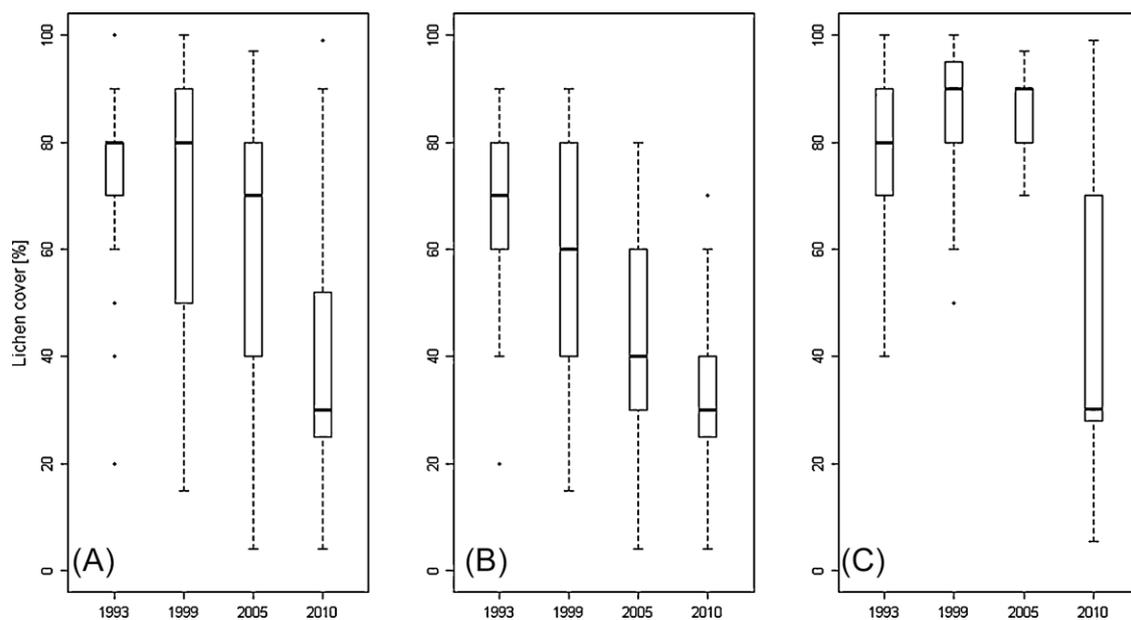
Fig. 1. Total cover (%) of epiphytic lichens in the Hofmann plots between 1993 and 2010. (A) All plots, (B) coniferous trees, (C) broadleaf trees. Boxplots show the median (bold line), 50% percentile (box), 75% percentile (whisker), and outliers (points).

with little difference between conifers and broadleaf tree species.

Single species

The cover of most lichen species declined towards the end of the monitoring period – although these trends were evaluated (with MPH models) as statistically significant for the whole monitoring period only in the case of *Hypogymnia physodes* and *Melanelixia fulinosa.* ssp. *glabratula* (Table 2). In addition, the results showed a significant decrease in *Lepraria* sp. ($p = 0.016$) between 2005 and 2010 in the VDI plots.

Lichen communities

All nMDS ordinations had a stress value lower than 20% (Table 3) indicating that the three axes summarize the differences in species composition among plots reasonably well (Oksanen 2005). The results showed that the lichen community composition had changed over time, both on conifer and on broadleaf trees (Fig. 2). Plots were found to have shifted predominantly along the second ordination axis so that the differences in the scores of the second axis represent an indicator of the rate of change through time. MANOVA results underpin these temporal trends, suggesting a directional change in species composition for the majority of the plots, i.e. that the same species, or at least ecologically

Table 2. Results of Marginal Models for cover changes in single lichen species recorded from the Hofmann plots (1993–2010, $n = 38$) and VDI plots (1999–2010, $n = 47$). Beta is the Marginal Model coefficient indicating increasing (positive) and decreasing (negative) trends; p-Beta is the probability of Beta = 0, indicating the significance of a trend. Significant trends with a $p < 0.05$ are given in bold. All species for which Marginal Models could be fitted are listed.

	Hofmann plots (1993–2010)		VDI plots (1999–2010)	
	Beta	p-Beta	Beta	p-Beta
Cladonia coniocraea	–	–	0.31	0.694
Cladonia digitata	0.48	0.466	0.04	0.927
Hypogymnia physodes	**−2.53**	**0.001**	−4.14	0.220
Lecanora argentata	−0.93	0.404	–	–
Lepraria sp.	0.69	0.374	−0.16	0.702
Loxospora elatina	−0.51	0.529	0.26	0.779
Melanelixia fulinosa. ssp. *glabratula*	0.49	0.606	**−1.45**	**0.018**
Parmelia saxatilis	−0.49	0.508	–	–
Parmeliopsis ambigua	−1.00	0.392	0.01	0.955
Pertusaria albescens	−0.72	0.324	–	–
Phlyctis argena	−0.76	0.266	−0.41	0.289

Table 3. Significance of time trends in epiphytic lichen communities for the Hofmann plots ($n = 38$) and the VDI plots ($n = 47$) between consecutive observation years and for the entire period. Trends were tested by applying a Multivariate Analysis of Variance (MANOVA) for the shift of the plots' axis scores (three dimensional ordination nMDS) between years. Significant changes ($p < 0.05$) are given in bold letters.

		p-values	
Monitoring plots	Observation period	Conifers	Broadleaf trees
Hofmann	1993–1999	**0.001**	**0.003**
Conifers: stress 15.7	1999–2005	0.117	0.1
Broadleaf: stress 17.2	2005–2010	**0.039**	**0.001**
	1993–2010	**<0.001**	**<0.001**
VDI	1999–2005	0.069	**0.047**
Conifers: stress 12.6	2005–2010	**0.045**	0.754
Broadleaf: stress 14.5	1999–2010	**0.027**	**0.035**

similar species, consistently decreased or increased at each consecutive time step (Table 3). The changes throughout the entire time period are highly significant, independent of the applied monitoring method. However, the different methods applied indicate that the main shifts in species composition occurred at different time intervals: in the Hofmann plots major changes occurred between 1993 and 1999 and between 2005 and 2010; on the VDI plots species composition was most strongly altered between 2005 and 2010 or between 1999 and 2005 on coniferous and broadleaf trees, respectively (Table 3).

The change in the Ellenberg *N*, *R*, and *L* values was significant only with regard to the *N* value on broadleaf trees and the *L* value on conifer trees (Table 4). The correlation analysis revealed no relationship with the rate of change in species composition (for differences on the 2nd nMDS axis see above) in the Ellenberg *N*, *R* or *L* values (Table 4).

Lichen diversity

Across both the VDI and the Hofmann plots, 88 lichen species (41 macrolichens and 47 crustose lichens) were found in 1999. Until 2010, the total number of species decreased to 72 (29 macrolichens and 43 crustose lichens) (see Appendix A: Table 1). The loss in the overall species diversity was reflected by a concomitant loss of 1.5 lichen species per plot between 1999 and 2010 in the VDI plots ($p < 0.001$, paired Wilcoxon test). Macrolichens decreased by 1 species ($p < 0.001$, paired Wilcoxon test). Also the Shannon index decreased significantly ($p = 0.002$, paired Wilcoxon test). In general, the decline in epiphytic lichen diversity was higher on broadleaf trees than on conifers. On broadleaf trees, the loss of oligotrophic species (Ellenberg *N* value < 4) and of acidophytic species (Ellenberg *R* value < 4) was always higher than the loss of nitrophytic species (Ellenberg *N* value > 6) and basiophytes (Ellenberg *R* value > 5). Whereas
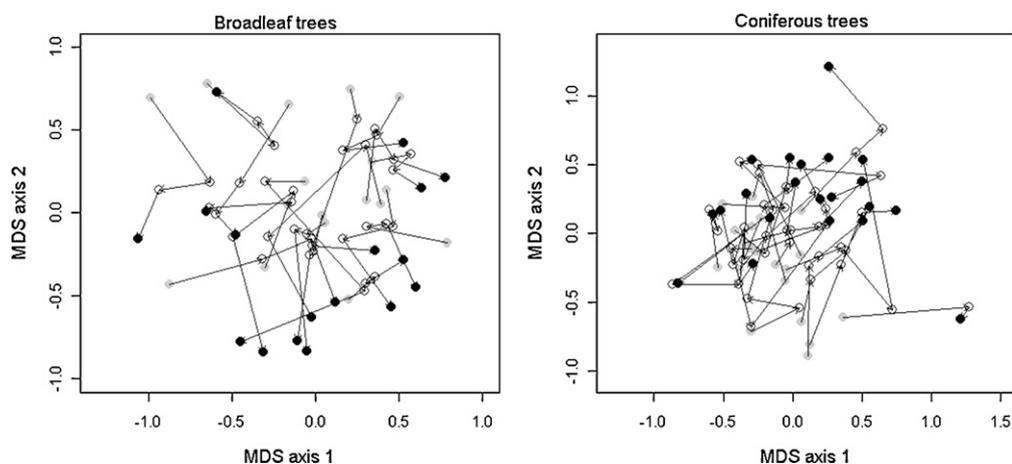
Fig. 2. Temporal changes in lichen species composition of Hofmann plots on coniferous and broadleaf trees in four study years illustrated with MDS scores (multidimensional scaling). Scores for individual trees are linked with arrows. Study years are indicated by different symbols: 1993: grey; 1999 and 2005: open circle; 2010: black.

Table 4. Differences in weighted mean Ellenberg N, R and L values between 1993 and 2010 (Hofmann plots; tested with a paired Wilcoxon rank sum test). Correlation of the rate of change in species composition (second axis of the nMDS analyses) and weighted mean Ellenberg N, R and L values (Kendall's T correlation coefficient). B: broadleaf host trees, C: conifer host trees.

Tree species	Ellenberg indicator	Differences 1993–2010		Correlation with nMDS scores	
		Median of the difference	p-value	Kendall's T coefficient	p-value
B	N	**0.25**	0.045	0.03	0.903
B	R	0	0.963	0.01	0.968
B	L	0.01	0.747	0.07	0.715
C	N	−0.01	0.070	0.14	0.386
C	R	0.01	0.733	0.23	0.158
C	L	**−0.48**	<0.001	−0.11	0.492
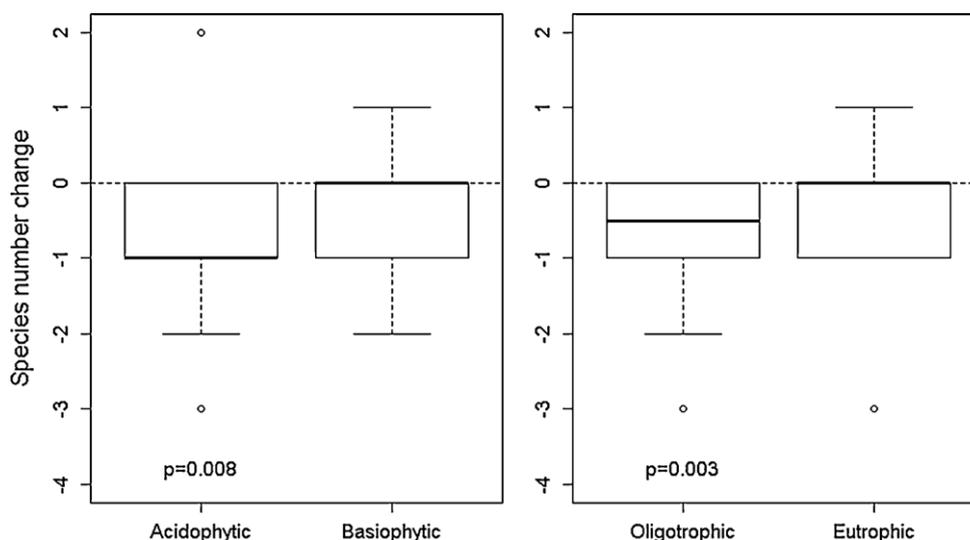
Fig. 3. Changes in lichen species numbers between 1999 and 2010 (VDI plots) for four indicator groups on broadleaf trees. Acidophytic species: ellenberg R value < 3; basiophytic species: R value > 5; oligotrophic species: N value < 3; eutrophic species: N value > 6. P-values below boxplots indicate changes significantly different from zero.

oligotrophic and acidophytic lichens significantly decreased on average by 0.5 species and 1 species per plot, neither the nitrophytic nor the basiophytic species experienced a significant change (Fig. 3). No difference between the various indicator groups was found on coniferous host trees.

Discussion

Long-term monitoring of permanent plots is a widely applied method for the detection of air pollution effects, although it is prone to be affected by methodological changes and observation errors (Scott & Hallam 2003). After starting monitoring we added a sampling method that has become a common standard in Europe (Asta et al. 2002). However, the old sampling method was pursued simultaneously. Therefore we were able to combine the analysis of a longer time series (with an – assumingly – higher observer error) and the analysis of a shorter data series, collected with a method less prone to observer error. The resulting trends were not completely identical but allowed a concise generic interpretation.

Moreover, we found no differences between the diversity changes in the whole set of lichens and those observed in macrolichens, which are relatively easy to identify.

Disentangling the effects of lowered acid deposition, concurrent eutrophication through high N loads and other factors is a challenging task (Hultengren, Gralén, & Pleijel 2004; Nimis & Purvis 2002; Sparrius 2007; van Dobben & ter Braak 1998). S deposition has decreased continuously at LTER Zöbelboden, as it has in many other parts of Europe (Bouwman et al. 2002). Since N loads have remained more or less stable from 1993 onwards with some interannual variations, the acid deposition has decreased (see Appendix A: Fig. 1). Hence, a recovery of the lichen flora from acidification has been expected. Indeed, the monitoring data suggest that such a recovery has taken place, as the number of acidophytes appears to have experienced a more pronounced decrease than the number of basiophyte species. The signal is relatively weak, however, and limited to broadleaf tree bark.

Since lichens were released from acidification, eutrophication remains a major cause of the observed breakdown of epiphytic lichens in the study area. Between 1999 and

2010, macrolichen diversity dropped by 29%. Deposition trends do not show concurrent changes. A significant increase (4–$7\,\mu g\,m^{-3}$) was observed only for NO_2 air concentrations between 2000 and 2010 (see Appendix A: Fig. 2), but no significant effects can be expected at these concentrations (Sparrius 2007). Our hypothesis is that chronic nitrogen deposition has led to the loss of species. It has been shown that cumulative loads of N deposition (rather than high levels in single years) were responsible for biodiversity effects in experimental N addition studies (de Schrijver et al. 2011).

The number of nitrophytic species did not increase, although a decrease in the number of oligotrophic species was observed. Species may not react in the same way because of differential lag times in extinction and colonization processes, i.e. N-sensitive species may have already vanished while nitrophytic species have as yet not managed to colonize the monitoring plots (van Herk et al. 2003). One such nitrophobous species is the foliose lichen *H. physodes* (Barkman 1958; Franzen-Reuter 2004). *Hypogymnia* propagates via soredia, which are highly vulnerable in their juvenile phase when the species has to compete against established crustose and foliose lichens. Species that are more sensitive than *H. physodes*, such as those from the genera *Usnea* and *Bryoria*, were already rare in 1993 and had vanished from the plots completely after 1999 (see Appendix A: Table 1). Not recorded on the plots but apparent on tree trunks within the study area is the increasing abundance of green algae, an observation which was also found to coincide with the eutrophication effects of nitrogen deposition (Barkman 1958; van Herk et al. 2003).

In contrast to wet deposition, gaseous pollution is too low to affect epiphytic lichens. Concentrations of SO_2, NO_2 (see Appendix A: Fig. 1) and NH_3 (not measured but very unlikely to be above $1\,\mu g\,m^{-3}$; see (Löflund et al. 2002)) produce their effects only at higher concentrations (Cape et al. 2009; Sparrius 2007). van Herk et al. (2003) found that NH_4^+ is the major air pollution compound affecting epiphytic lichens in areas far from emission sources. Most likely, this is also the case at LTER Zöbelboden where about half of the inorganic N deposited occurs in the form of NH_4^+ (see Appendix A: Fig. 1). Furthermore, fog occurs frequently together with high concentrations of NH_4^+–N (see Appendix A: Fig. 2). By contrast, NH_4^+–N and NO_3^-–N concentrations in precipitation are an order of magnitude lower (unpublished data). Hence, our hypothesis is that N loads in fog were playing an important part in the observed lichen damage.

Whereas the total lichen cover on conifers steadily decreased, the decline on broadleaf trees was rather abrupt after 2005 (as discussed above). On the other hand, the decrease in lichen diversity was much more pronounced on broadleaf trees. We suppose that these differences were caused by stemflow and by the different buffer capacities of coniferous and broadleaf tree bark (Türk & Wirth 1975; van Herk 2001). Stemflow typically occurs in broadleaf trees with their funnel-shaped canopy and smooth bark but is negligible in conifers (Levia & Frost 2003). Stemflow can

have a direct impact through its acidifying and eutrophying pollutant inputs by 'downwash' (Hauck & Runge 2002) and it can also cause physical damage, particularly during storm events and where epiphytic lichens are in poor condition already (Franzen-Reuter & Frahm 2007). The decline in lichen cover between 2005 and 2010 might be associated with such downwash events after a period of pollutant stress on those lichen communities.

Apart from air pollution, tree canopy changes have the potential to strongly affect lichens. The Ellenberg indicator value for light preferences (*L*) indicated a trend towards shadier conditions although there were no significant changes in the radiation at the forest floor, as measured from hemispherical photographs, in the areas where the host trees are located. Still, closures of the tree canopy may have occurred at some plots not detected by measurements. However, this may have masked part of the eutrophication effect because species with high Ellenberg *L* values also tend to have high *N* values (Diekmann 2003).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2013.05.006.

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