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Long-term changes of epiphytic lichen species composition over landscape gradients: an 18 year time series

Jiří LIŠKA and Tomáš HERBEN

Abstract: The study aimed to determine how the response of the epiphytic lichen vegetation to sulphur air pollution is affected by interaction with other factors (distance from pollution sources, habitat, altitude, initial eutrophication of the tree bark). It was based on a series of four successive recordings taken over a period of 18 years with increasing pollution levels and on the same set of 139 solitary trees. Relationships between habitat variables and lichen community composition are assessed using canonical correspondence analysis. The data set comprised 69 lichen species. Ordination of initial species composition on trees revealed two major gradients: eutrophication and acidity.

The species composition significantly changed with time, with a general decrease of the total number of lichen species per tree. In general, species sensitive to air pollution decreased, while tolerant species increased in number. Change over time differed depending on the position of the tree within the landscape (relative to one major source of pollution, the town of Tábor, whereas the distance to the other source, Sezimovo Ústí, was not significant) and on the initial species composition found on the tree. Trees under the effect of eutrophication changed their species composition less, indicating that the effect of eutrophication (mainly increased bark pH) may ameliorate the effects of air pollution; a local effect of eutrophication also seems to play an important role. Distance to pollution sources had only a small impact on the rate of change and perhaps other local conditions (sheltered or humid position, altitude) play a role in this interaction. There was a decrease of the overall heterogeneity of the data set over time. This means that the gradients in species composition attributable to these variables became less important over time. Therefore, one of the effects of air pollution is also a general homogenization of the lichen vegetation of the solitary trees.

Key words: air pollution, bioindication, canonical correspondence analysis, lichen vegetation, multivariate analysis, permanent recordings

Introduction

The relationship between air quality and abundance of epiphytic lichens is a well-known phenomenon and has been widely used to assess air quality and to monitor air quality over time (Nimis, Scheidegger & Wolseley 2002). Typically, an indirect estimate of air quality is based on a single set of recordings of species data made at one point in time. This approach has inherent weaknesses: it assumes that the lichen community composition (i) responds to pollution levels, (ii) this response is fast enough for the system to have approached equilibrium, and (iii) lichen habitats are standardized enough so that there is no interaction between habitat parameters and the impact of pollution (for the further discussion of these assumptions see Hawksworth 2002). This does not necessarily matter when air quality estimates using lichens are not the goal, but the persistent difficulty with such data is that they do not provide us with an estimate of the rate of change, which is important when a fast-changing system such as a lichen flora is to be examined. The whole reasoning would be unsound if the lichen response is much slower than the change in the environment.

J. Liška and T. Herben: Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic. E-mail: liska@ibot.cas.cz
T. Herben: Department of Botany, Faculty of Science, Charles University, Benátská 2, CZ-128 01 Praha 2, Czech Republic.

Most of the repeated studies conducted up until now have assessed the change in flora as a result of some change in the pollution level [e.g., closure of a factory as an emission source in Sweden (Skye & Hallberg 1969); decreasing pollution level in London (Rose & Hawksworth 1981) or decreasing impact caused by dilution of emissions (Showman 1981)]. This enables the second assumption above to be tested; in particular, response rates can be compared across species.

The third assumption (no interaction between habitat and the pollution level) may be overcome by a careful standardization of the trees studied (including phorophytes of one species only) or by standardization of habitats, i.e. minimization of ecological factors other than air pollution (shade, humidity, tree species, pollution sheltering, dust eutrophication, etc.). This approach largely solves the practical problem, but it has two pitfalls: (i) a high level of standardization is rather difficult to attain in the field and requires omitting a large portion of potentially interesting habitats and thus losing much information, and (ii) pollution-habitat interaction itself may be of interest. An obvious example of the latter might be the substratum-dependent response of some species (e.g. *Evernia prunastri*, *Parmelia sulcata*, *Usnea hirta*—see Herben & Liška 1988), but this is by no means the only case of the pollution-habitat interaction. In particular, a common ecological factor influencing the natural habitats of lichens is eutrophication of tree bark (particularly by dust). This factor is one of the most important of those known to interact with response of lichens to air pollution [(sulphur dioxide, acid rain), see van Herk (2001) and van Dobben & ter Braak (1998, 1999)]. Since this factor is continuous, its effect cannot be fully eliminated by standardization of investigated lichen habitats.

The study aims to assess the strength of the interactions between temporal change of the epiphytic lichen communities and other environmental factors such as distance from pollution sources, habitat and altitude. It is based on a series of four sequential recordings made on the same set of trees during an 18 year period. The trees were standardized for some factors (shade, tree age) while allowing variation in selected habitat factors (particularly eutrophication). The effects of these habitat variables on lichen community composition were assessed using canonical correspondence analyses.

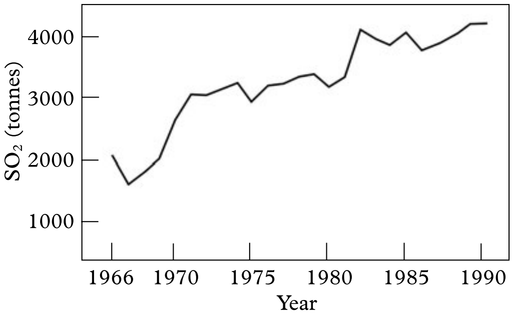

FIG. 1. Temporal change of emissions from the main pollution source in Sezimovo Ústí.

Methods

Study area

The area investigated is within a 10–20 km radius around the town of Tábor, South Bohemia (latitude 49°25′N, longitude 14°40′E). The average elevation is 400–500 m and forests comprise approximately one-third of the area. The mean annual temperature is 7°C, mean monthly temperatures varies from −2·9°C in January to 17·1°C in July, and the annual rainfall is 500–700 mm. Westerly winds are predominant, but south-easterly winds are frequent in autumn and winter. The region has a moderate level of pollution compared with other areas of the Czech Republic, but the pollution levels were increasing from the 1960s until the early 1990s. The principal pollution sources are high emissions of SO_2 from two thermal powerplants using brown coal. The first one in Sezimovo Ústí started in 1966 and average annual sulphur emissions from a 100 m high chimney increased from *c.* 2000 tons (1966) to over 4000 tons in 1989 (Fig. 1). The second pollution source located in Tábor started in 1969 and average annual sulphur emissions from a 74 m high chimney increased from *c.* 1000 tonnes in 1969 to over 2000 tonnes in 1990. The ratio between maximum (winter) and minimum (summer) emissions were 4:1 for both sources. Both power plants are located in the centre of the study area and are relatively close to each other (*c.* 5 km apart). In winter, domestic sources burning brown coal also contribute to pollution considerably. Average monthly SO_2 concentrations in the town centre were 40–100 µg m^{-3}. According to previous investigations (Liška 1975, 1984), the study area has a relatively rich epiphytic lichen flora on isolated trees with an abundance of some sensitive species (e.g. *Usnea hirta*, *Lecanora varia*). Other more sensitive species occur at a lower frequency (e.g. *Ramalina* spp., *Physconia distorta*). Nevertheless, some very sensitive species reported from this region in the 19th century have completely disappeared, for example *Lobaria pulmonaria* and *Sticta* spp. (Bernard 1887).

Data collection

Lichen vegetation was investigated on isolated trees with diameters >20 cm. To obtain a representative number of phorophytes several different tree species were included. The most frequent phorophytes were *Tilia* spp., *Fraxinus excelsior*, *Acer platanoides* and *Quercus* spp. Conifers and *Betula pendula* were excluded because of the high acidity of their bark (Barkman 1958). Most of the trees selected were solitary and to ensure representation of the whole pollution gradient, some trees near buildings or busy roads were included in the study. Lichen communities on tree bases influenced by very local effects such as dog fouling and local sources of dust were not included in the survey.

A total of 212 trees was selected and sampled in the 1973–75 period but in the repeated recordings (1978–79, 1985–86 and 1991–92) some trees had been felled, so that a set of 139 trees was used in the final data analysis. Acid air pollution began to decrease during the 1990s because of industrial changes following change in the political regime and the lichen monitoring programme was terminated in 1992.

On each sampling occasion, the trunk and the base of each tree were examined up to a height of 2 m and the species listed. A total of 69 lichen species were recorded. The abundance and vitality of each species was estimated according to a three-point combined scale, where damaged thalli are given the lowest score (1 – scarce damaged thalli or 1–2 healthy thalli; 2 – abundant damaged thalli or scarce healthy thalli; 3 – frequent healthy thalli; cf. Pišút & Lisická-Jelínková 1974). Nomenclature follows Vězda & Liška (1999).

Data analysis

A change in the numbers of species was examined using repeated measures ANOVA (with the tree as subject), recording time as a fixed factor at the within-subject level and altitude, distance from the town of Tábor and distance from the pollution source in the town of Sezimovo Ústí as covariates at the subject level. Linear responses were assumed due to the relatively short distances involved; adding quadratic terms did not result in a significant increase in fit.

Overall change in species composition was expressed using the Sørensen's dissimilarity index,

$$\frac{b+c}{2a+b+c},$$

where a is the number of species common to both samples, and b and c are numbers of species unique to the first and second sample, respectively. The same index was used to express heterogeneity of the total set of trees in each recording time; its value was calculated as the average of all possible comparisons between trees within the recording time. Linear components of the temporal trend of individual species were calculated using contrast coefficients (relying on the fact that recordings were approximately equidistant) as $-3x_1 - x_2 + x_3 + 3x_4$, where x_1, x_2, x_3 and x_4 are the frequencies of that species at the first, second, third and fourth recording times, respectively.

Data were also analysed using multivariate techniques. Correspondence analyses (assuming unimodal species response to environmental factors) were used as the estimated gradient length exceeded four "half-changes" (Lepš & Šmilauer 2003). All analyses were run on a reduced data set from which species with frequency scores never exceeding 1 (i.e. occurring on a single tree) were omitted. The species data from the first recording were initially analysed using detrended correspondence analysis (Jongman *et al.* 1987). The analysis was run using both qualitative and quantitative data on species, but because this preliminary analysis showed little difference between the two types of data, only results of the analysis of quantitative data are presented. This analysis produced an ordination of initial states of the trees.

The relationship between the lichen community structure and environmental variables was assessed using canonical correspondence analyses. These enable the identification of independent (environmental) variables that predict gradients in species composition, under the assumption that species responses to environmental gradients are unimodal (Palmer 1993; Lepš & Šmilauer 2003). For these analyses, species lists from the trees were used as untransformed values of the abundance/vitality scale. The following independent variables were used in the calculations: recording date, altitude, distance from Tábor, distance from Sezimovo Ústí and first and second ordination axes score of the tree from the initial DCA. Further, tree identity (recoded using 138 dummy variables) was used to perform repeated measurement analyses at the tree level.

Several analyses were run with different combinations of environmental variables and covariables (Table 1). In the analyses testing interaction between the time change and the environmental variables (altitude, distances from the pollution sources, ordination axes scores), interaction terms were created to account for non-additive response to time change.

The significance of relationships between species composition and environmental variables were tested using Monte Carlo randomization tests. For testing of time proper, recordings (split plots) were completely randomized within each tree (whole plot). For the tests of interactions between time and other predictors, trees (whole plots) were completely randomized relative to these predictors; recording within tree (split plots) were left unchanged. Five hundred Monte Carlo randomizations were performed. All calculations were performed using CANOCO ver. 4.5 (ter Braak & Šmilauer 1998).

TABLE 1. *The principal lichens recorded in the lichen surveys and the number of trees on which each species was recorded on each sampling occasion. Species recorded on <10 trees have been omitted*

	Recording time			
Species	1973–5	1978–9	1985–6	1991–2
Amandinea punctata	82	80	78	81
Bryoria fuscescens	10	4	5	4
Candelaria concolor	34	31	37	40
Candelariella xanthostigma	46	45	44	41
Evernia prunastri	48	45	42	40
Hypogymnia physodes	94	99	96	106
Hypocenomyce scalaris	23	27	55	68
Lecanora carpinea	43	43	38	37
L. conizaeoides	24	45	72	99
L. chlarotera	44	43	32	27
L. pulicaris	12	9	10	13
L. varia	19	19	23	25
Lecanora sp.	21	18	8	11
Lepraria sp.	9	12	9	5
Parmelia exasperatula	43	36	16	25
P. sulcata	86	77	58	70
Phaeophyscia orbicularis	24	25	25	23
Phlyctis argena	8	14	21	27
Physcia adscendens	38	34	34	35
P. dubia	35	36	32	39
P. stellaris	22	13	3	4
Physconia enteroxantha	7	8	7	10
P. grisea	12	9	12	12
Pseudevernia furfuracea	25	24	16	18
Scoliciosporum chlorococcum	35	42	64	80
Strangospora moriformis	15	11	6	9
Usnea hirta	33	23	20	22
Xanthoria candelaria	32	27	20	32
X. parietina	43	36	22	22

To screen off potential intercorrelation between predictor variables, stepwise selection of variables was used to identify the best predictors of species composition. In such analyses, a variable was entered into the analysis if the extra fit due to this variable was significant at $P<0{\cdot}05$. Again, Monte Carlo permutation tests (with 500 permutations) were used to test the significance of the fit. At any given step, the variable giving the highest significance was entered.

Results

A total of 69 epiphytic lichen species were recorded (Table 1), although not all of them were found in all recording periods. The most common species were *Hypogymnia physodes*, *Amandina punctata* and *Lecanora conizaeoides*. The numbers of species were much lower on trees closer to Tábor; the difference was significant using ANOVA (Table 2). Altitude was a much weaker correlate and distance from the second town was not a significant factor. The number of species per tree changed during the observation period, decreasing at the beginning of the observation period and then increasing again (Fig. 2). Timing of this change differed depending on the distance from Tábor; while the trees close to the town began to gain species already in the third recording, the decrease of species numbers on more distant trees continued until the third recording and evidence of any increase was delayed until the fourth recording.

Ordination of initial species composition of lichen communities on trees revealed two

TABLE 2. *Repeated measures ANOVA of species richness on individual trees. Symbol × indicates interaction*

	d.f.	*F* ratio	*P*
Altitude	1135	1·98	0·162
Distance to Tábor	1135	12·04	0·001
Distance to Sezimovo Ústí	1135	0·00	0·993
Recording time	3405	7·26	<0·001
Altitude × Time	3405	3·00	0·031
Distance to Tábor × Time	3405	2·20	0·088
Distance to Sezimovo Ústí × Time	3405	0·19	0·903

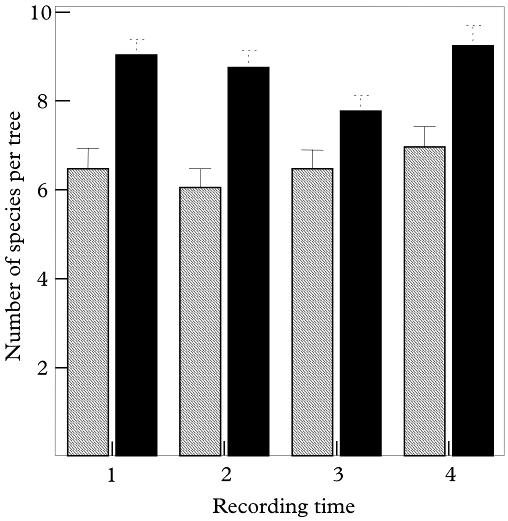

FIG. 2. Numbers of species per tree at the four recording times. Hatched bars: distance from Tábor <5 km, black bars: distance from Tábor >5 km. Recording times: 1: 1973–5, 2: 1978–9, 3: 1985–6, 4: 1991–2. Error bars indicate standard error of the mean (n=139).

major gradients: eutrophication and acidity (Fig. 3). The first axis explains 13·2% and the second axis 6·6% of the total variation in species composition. The first gradient primarily separates trees with eutrophicated bark with positive scores from those with non-eutrophicated (rather acidic) bark with low scores. The former are typically occupied by “nitrophilous” species e.g. *Amandinea punctata*, *Phaeophyscia* spp., *Physcia* spp., *Xanthoria* spp., whereas the latter are typically occupied by “nitrophobous” species e.g. *Hypogymnia physodes*, *Pseudevernia furfuracea*. Tolerant acidophytic species such as *Lecanora conizaeoides*, *Hypocenomyce scalaris* are typically associated with trees of the latter group.

Species composition changed strongly over the recording period with the strongest change occurring from recording time 2 to recording time 3 (Fig. 4, Table 3). The change was correlated with the distance from Tábor; while it was not dependent on this distance during the first interval (the trend was negative but not insignificant), it became positively correlated with distance during the later periods (Table 4).

Both canonical correspondence analysis and analysis of species trends using contrast coefficients revealed response of individual lichen species to this time gradient (Fig. 5). Distribution of species scores in response to time was very uneven, with a few species showing a marked increase over time, while the majority showed a decrease. The shift from stable to decreasing species was more gradual than between stable and increasing species. There was a marked difference between tolerant acidophytic species (*Lecanora conizaeoides*, *Scoliciosporum chlorococcum*, *Hypocenomyce scalaris*, *Phlyctis argena*), which increased over the observation period, and all other recorded species. Other tolerant acidophytic lichens (*Hypogymnia physodes*, *Pseudevernia furfuracea*) are closer to the central (more stable) cluster. Sensitive species (either acidophytic species such as e.g. *Usnea hirta*, *Evernia prunastri*, or subneutrophytic species as e.g. *Physcia stellaris*) are in the negative part of the central cluster.

Multivariate analysis of the species composition also confirmed that species dynamics were rather different depending on the position of the tree within the landscape. Although their effect in terms of proportion of variation explained was not high, each of the variables examined (distance from each source of pollution and altitude) was significant when tested independently of the other variables (Table 5). Distance from Tábor having the strongest effect of geographical variables (see Table 6). Initial species composition as expressed by the

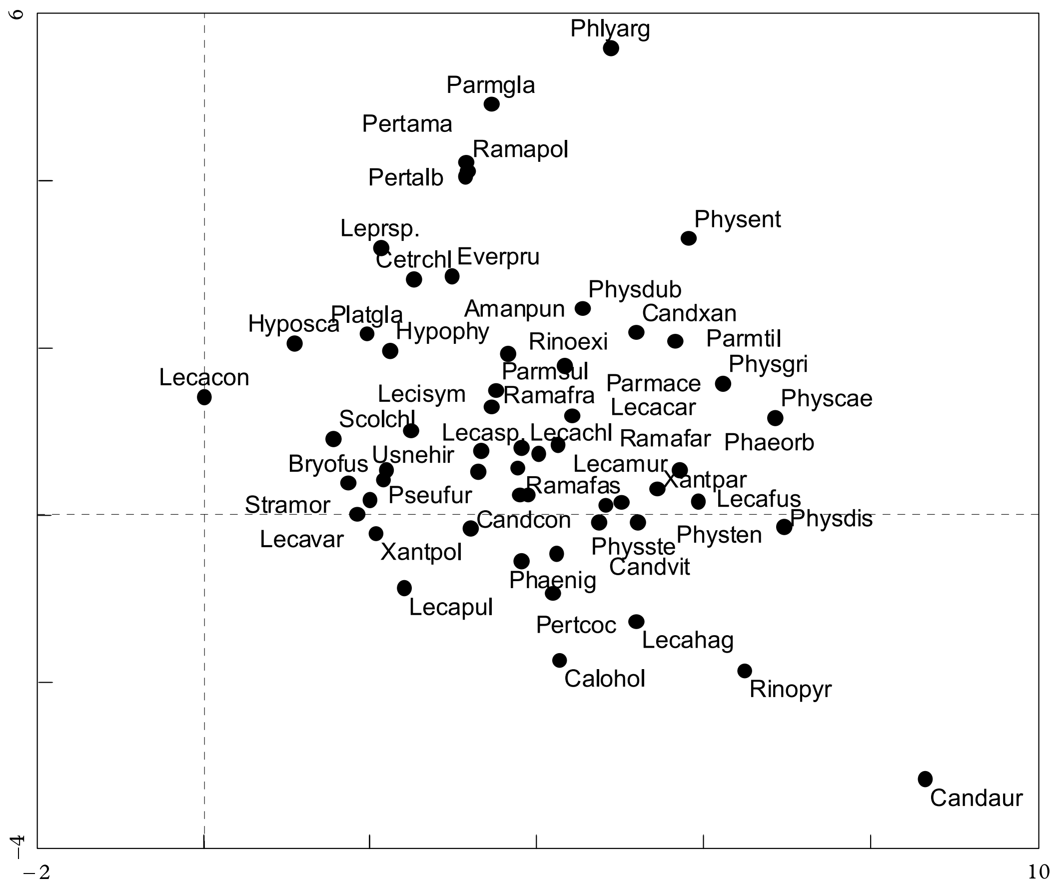

FIG. 3. Species ordination using detrended correspondence analysis of the species recorded in the first survey. The first axis explains 13·2% and the second axis 6·6% of the total variation in community composition. Species abbreviations: Amanpun *Amandinea punctata*, Bryofus *Bryoria fuscescens*, Calohol *Caloplaca holocarpa*, Candau *Candelariella aurella*, Candco *Candelaria concolor*, Candref *Candelariella reflexa*, Candvit *Candelariella vitellina*, Candxan *Candelariella xanthostigma*, Cetrchl *Cetraria chlorophylla*, Everpru *Evernia prunastri*, Hypophy *Hypogymnia physodes*, Hyposca *Hypocenomyce scalaris*, Hypotub *Hypogymnia tubulosa*, Lecacar *Lecanora carpinea*, Lecachl *Lecanora chlarotera*, Lecacon *Lecanora conizaeoides*, Lecaexp *Lecanora expallens*, Lecahag *Lecanora hagenii*, Lecamur *Lecanora muralis*, Lecania *Lecania* sp., Lecapul *Lecanora pulicaris*, Lecasp *Lecanora* sp., Lecasym *Lecanora symmicta*, Lecavar *Lecanora varia*, Leciel *Lecidella elaeochroma*, Lecisp *Lecidea* sp., Leprsp *Lepraria* sp., Parmace *Parmelia acetabulum*, Parmamb *Parmeliopsis ambigua*, Parmcf *Parmelia cf. exasperata*, Parmexa *Parmelia exasperatula*, Parmful *Parmelia fuliginosa*, Parmsax *Parmelia saxatilis*, Parmsuba *Parmelia subargentifera*, Parmsubr *Parmelia subrudecta*, Parmsul *Parmelia sulcata*, Parmtil *Parmelia tiliacea*, Pertalb *Pertusaria albescens* Pertama *Pertusaria amara*, Pertcoc *Pertusaria coccodes*, Pertsp *Pertusaria* sp., Phaenig *Phaeophyscia nigricans*, Phaeorb *Phaeophyscia orbicularis*, Phlyarg *Phlyctis argena*, Physads *Physcia adscendens*, Physaip *Physcia aipolia*, Physcae *Physcia caesia*, Physdis *Physconia distorta*, Physdub *Physcia dubia*, Physent *Physconia enteroxantha*, Physgri *Physconia grisea*, Physste *Physcia stellaris*, Physten *Physcia tenella*, Platgla *Platismatia glauca*, Pseufur *Pseudevernia furfuracea*, Ramafar *Ramalina farinacea*, Ramafas *Ramalina fastigiata*, Ramafra *Ramalina fraxinea*, Ramapol *Ramalina pollinaria*, Rinoexi *Rinodina exigua*, Rinopyr *Rinodina pyrina*, Scolchl *Scoliciosporum chlorococcum*, Stramor *Strangospora moriformis*, Usnehir *Usnea hirta*, Xantcan *Xanthoria candelaria*, Xantfal *Xanthoria fallax*, Xantpar *Xanthoria parietina*, Xantpol *Xanthoria polycarpa*.

ordination score on the DCA axes of the 1974 species composition had the strongest overall effect.

Testing interaction between initial species composition and time identified a group of species that increased on eutrophicated trees

TABLE 3. *Heterogeneities of the whole data set at individual recording times measured by the average value of the Sørensen index*

Recording time	Sørensen index
1973–5	0·666
1978–9	0·662
1985–6	0·638
1991–2	0·593

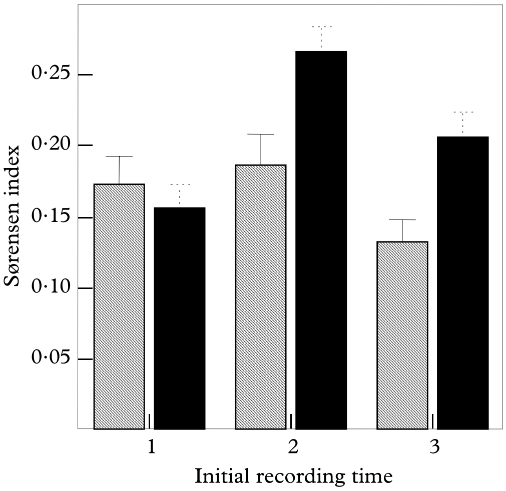

FIG. 4. Change in species composition (expressed as Sørensen index) over the three recording intervals; 1=1973/5–1978/9; 2=1978/9–1985/6, 3=1985/6–1991/2. Hatched bars: distance from Tábor <5 km, black bars: distance from Tábor >5 km. Error bars indicate standard error of the mean (*n*=139).

(i.e. those with a high score on the first ordination axis in 1974) and/or decreased on non-eutrophicated trees (Fig. 6), for example *Pseudevernia furfuracea* and *Usnea hirta*. In contrast, a second group, including *Parmelia exasperatula, Physcia stellaris* and *Xanthoria parietina*, decreased on eutrophicated trees and/or increased on non-eutrophicated trees. In a similar fashion, species differ with respect to whether they increased on trees close or far away from the town of Tábor (Fig. 7).

Discussion

At the gross level, the data show a decrease in total number of lichen species per tree. This is a typical trend for short term as well as long term change in the study area and it clearly documents that the pollution effect was the strongest stress factor in the area over the observation period. However, the effect is not linear and starts to reverse towards the end of the observation period. The timing of this reversal depends on the proximity to the pollution source; the trees lying closer to the source commenced recovery earlier (although they continued to support much lower overall numbers).

The distance from Tábor had a strong effect on the species turnover and overall changes in species composition. While the thermal power station in Tábor is a less important pollution source than the one in Sezimovo Ústí, the overall effect of distance to Tábor is higher, probably because of its larger population, which accounts for much higher output from local heating mainly in winter. Moreover, the chimney at the Sezimovo Ústí power station is higher which leads to a less pronounced effect over short distances; this may play a role since both sources are rather close to each other (5 km). The rate of change was also dependent on distance; while change was similar on all trees during the first period (1975–1979), in subsequent periods the change on more distant (i.e. less polluted) trees became much larger (Fig. 5).

As might be expected, there was a marked differentiation of species in their ability to resist increasing pollution. In very general terms, species sensitive to air pollution show a decrease, while tolerant species show an increase. The CCA scores for the very rare species have to be interpreted with caution, because rarer species are likely to get higher and less reliable values in contrast to more common species (Lepš and Šmilauer 2003). Species with extreme CCA scores (both positive or negative) are often uncommon on solitary trees and therefore they have low frequency in the data set; for some species, an uncertainty in identification (*Lecanora*

TABLE 4. *Pearson correlation coefficients for species composition change (expressed by the Sørensen index) with altitude and distances from the two pollution sources*

Interval (recording times† compared)	Altitude	Distance to Tábor	Distance to Sezimovo Ústí
1–2	− 0·031	− 0·055	− 0·084
2–3	0·164	0·222**	0·187
3–4	0·106	0·269**	0·011
1–3	0·137	0·188**	0·125
2–4	0·140	0·245**	0·116
1–4	0·178*	0·232**	0·129

* *P*<0·05; ** *P*<0·01.

†Recording times: 1: 1973–5, 2: 1978–9, 3: 1985–6, 4: 1991–2.

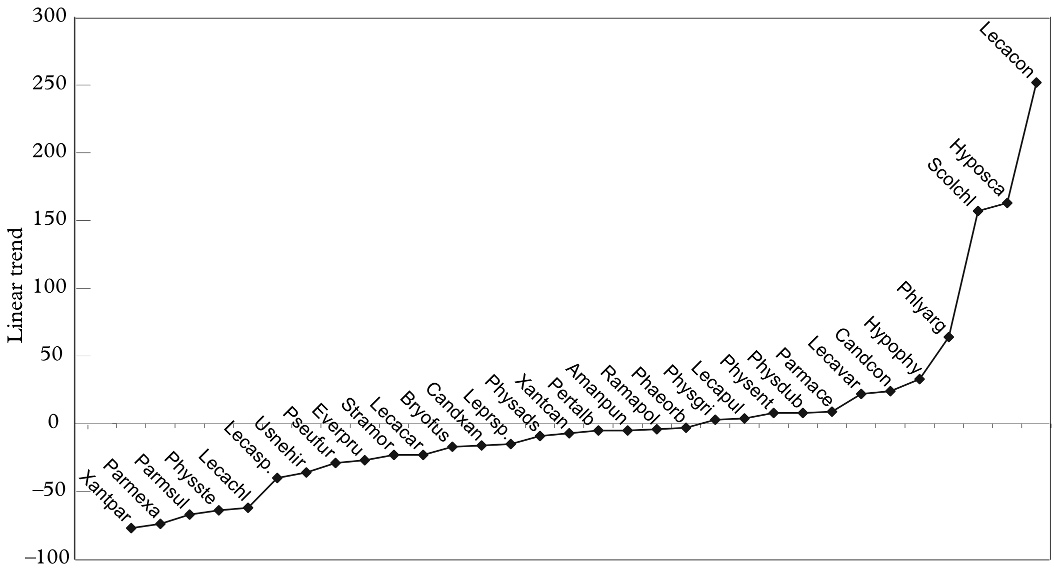

FIG. 5. Species trends over time expressed using contrast coefficients: negative scores mean decrease and positive scores mean increase over time. Numeric scaling is arbitrary. For species abbreviations see Fig. 2. Only species with mean frequencies ≥5 are shown.

expallens vs. *Lepraria* sp.) or a high risk of being overlooked (*Rinodina pyrina*), might also have affected the data.

Species that increased most include nitrophobous species typically occurring on bark with a low pH (e.g. *Parmeliopsis ambigua*, *Parmelia saxatilis*, *Lecanora expallens*) as well as nitrophilous species growing on bark of higher pH (e.g. *Physcia dubia*, *Physconia enteroxantha*, *Ramalina fastigiata*). The first group of species also represent species of humid habitats (ombrophilous, hygrophilous, skiophilous). A possible interpretation is that a local change of conditions (increased eutrophication) can increase frequency. However, some species mentioned here have a low frequency (under 5) and therefore trends for these species are difficult to interpret (e.g. *Parmeliopsis ambigua*, *Parmelia saxatilis*, *Xanthoria fallax*). Species with high frequency that increased in abundance are acidophytic lichens known to tolerate air pollution (*Hypocenomyce scalaris*, *Lecanora conizaeoides*, *L. expallens*, *Scoliciosporum chlorococcum*).

TABLE 5. *Tests of response of lichen community composition to individual parameters of trees using canonical correspondence analysis. Axis 1, Axis 2 (position of the tree on the first and second principal axes of DCA of the 1974 data set, respectively); time (recording time); distance [distances from the pollution sources in Tábor and Sezimovo Ústí (SÚ)]. For comparison, results of detrended correspondence analysis of the same data are in the first row*

Variable tested*	Covariables	Randomization of recordings within trees	Randomization of trees (sets of recordings)	Variance explained by canonical axes (%)	*F*-ratio	*P*
None	Tree	N/A	N/A	15·2†	N/A	N/A
Time	Tree	Yes	No	4·7	20·4	0·002
Altitude × Time	Tree, Time	No	Yes	0·6	2·70	0·014
Distance to Tábor × Time	Tree, Time	No	Yes	0·7	3·00	0·01
Distance to SÚ × Time	Tree, Time	No	Yes	0·6	2·68	0·016
Axis 1 × Time	Tree, Time	No	Yes	1·2	5·13	0·002
Axis 2 × Time	Tree, Time	No	Yes	1·2	4·95	0·006
Axis 1 × Time, Axis 2 × Time	Tree, Time	No	Yes	2·3	4·84	0·002
Altitude × Time, Distance to Tábor × Time	Tree, Time	No	Yes	1·5	3·16	0·002

* × Indicates interaction.

†Variance explained by the first ordination axis.

TABLE 6. *Stepwise analyses of the effects of individual tree variables on change in lichen community composition. Axis 1, Axis 2 – position on the tree at the first and second principal axes of DCA for the 1974 data set, respectively; time – recording time, distance – distances from the pollution sources in Tábor and in Sezimovo Ústí (SÚ)*

Predictor variables used for selection	Covariables	Step	Variable to-enter	*F*-ratio	Significance
Analysis 1					
Altitude × Time, Distances × Time	Tree, Time	0	**Distance to Tábor × Time**	3·00	0·01
		1	**Altitude × Time**	3·33	0·002
		2	Distance to SÚ × Time	1·56	n.s.
Analysis 2					
Altitude × Time, Distances × Time, Axis 1 × Time, Axis 2 × Time	Tree, Time	0	**Axis 1 × Time**	5·13	0·002
		1	**Axis 2 × Time**	4·52	0·008
		2	**Altitude × Time**	2·85	0·016
		2	Distance to Tábor × Time	2·36	n.s.

Bold indicates significant ($P<0{\cdot}05$) effects, n.s.—indicates not significant.

Species showing a maximum decrease are mainly nitrophilous species of subneutral bark or of habitats affected by dust (*Rinodina pyrina*, *Physconia distorta*, *Physcia caesia*). Some of these lichens are typically present on trunk bases strongly influenced by dust; these habitats were excluded from the data processing owing to standardization (see Methods). Nonetheless, even the results for these species were probably influenced by a local change of conditions (decreased eutrophication).

Interestingly, the rates of change of lichen community composition shows interactions with several tree parameters; i.e. ecologically or geographically defined groups of trees showed very unequal rates of change over the observation period. Primarily, trees affected by eutrophication seem to be more resistant to change in pollution, indicating that

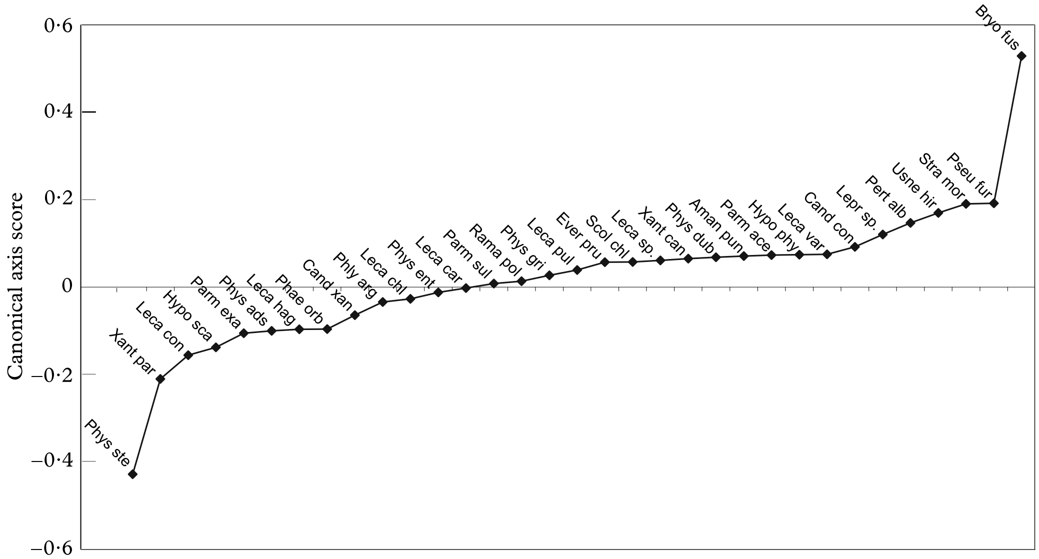

FIG. 6. Species ordination using canonical correspondence analysis of the species composition of all recordings. Tree (subject) and recording time are used as covariates; interaction between time and tree ordination score in 1974 (i.e. initial species composition) is used as predictor. Position along the first (canonical) axis indicates type of change over time: positive scores indicate species that increased on eutrophicated trees and/or decreased on acidic trees, and negative scores indicated species that decreased on eutrophicated trees and/or increased on acidic trees. Numeric scaling is arbitrary. Only species with mean frequencies ≥5 are shown. For species abbreviations see Fig. 2.

eutrophication may ameliorate the deleterious effect of air pollution. This is clearly demonstrated by the species canonical ordination with time and eutrophication. Essentially, this is an effect of bark pH: air pollution promotes acidification of bark and eutrophication is very often connected with increasing pH (cf. van Dobben & ter Braak 1999). Through this mechanism, eutrophication can act as a buffer effect against the effect of air pollution, so the toxic effect of SO_2 is weaker in the higher pH range (Türk & Wirth 1975). However, there is a complicating factor in this argument, since the species complements on eutrophicated and non-eutrophicated trees are almost entirely different. As a result of this, the effect of environmental change acts on two very different species pools whose mean response need not be the same.

On the other hand, distance from pollution sources did not have a particularly strong impact on the rate of change of community composition. This contrasted with our original expectation that trees further from the pollution source(s) would be affected much more since their vegetation was much less damaged at the beginning of the observation period than of those close to the pollution source. This indicates that the change is gradual and tends to affect all trees irrespective of the initial state of their lichen vegetation. A further complicating factor is the considerable community component that is unrelated to proximity to the town. Not all trees close to the pollution sources are impoverished (particularly trees in sheltered or more humid positions); on the other hand, some trees at higher altitudes tend to be impoverished more, probably due to some long-distance transport of pollutants. However, the effect of altitude *per se* is rather weak. First, there is little variation in altitude (390–570 m a.s.l., with a mean of 461 m); second, there is a positive correlation of altitude and distance to the pollution source (higher altitudes are as a rule, farther from the pollution sources).

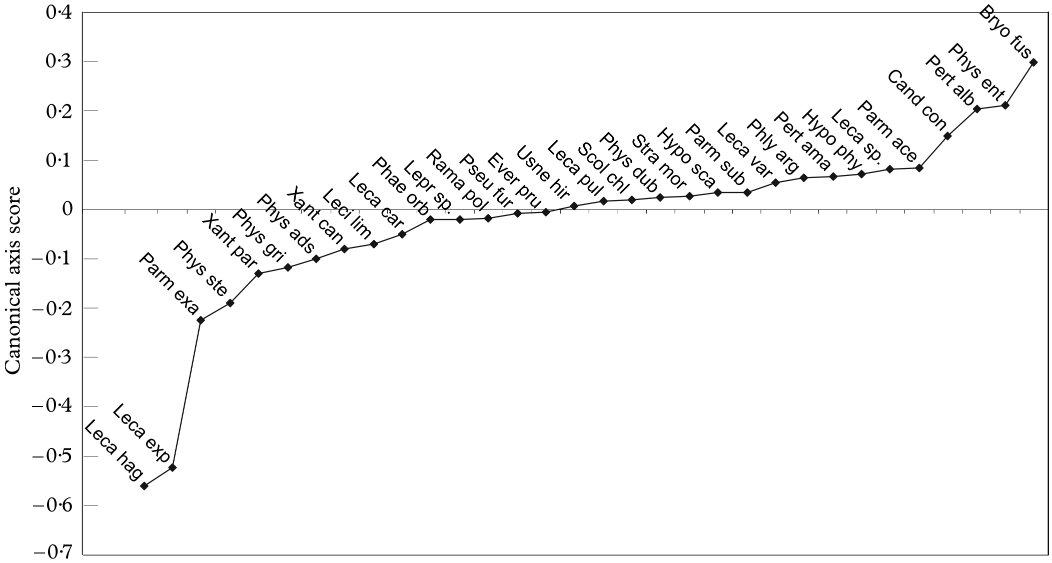

FIG. 7. Species ordination using canonical correspondence analysis of the species composition of all recordings. Tree (subject) and recording time are used as covariates; interaction between time and distance to Tábor is used as a predictor. Position along the first (canonical) axis indicates type of change over time: negative scores indicate species that increased on trees close to Tábor and/or decreased on trees far away from it, and positive scores indicate species that decreased on trees close to Tábor and/or increased on trees far away from it. Numeric scaling is arbitrary. Only species with mean frequencies ≥5 are shown. For species abbreviations see Fig. 2.

As a result, the overall heterogeneity of the species composition decreases over time. This means that one of the effects of air pollution is also a general homogenization of the lichen vegetation on the solitary trees (and under extreme pollution stress, the final stage is a tree without lichens). This is mainly due to the fact that change in more distant trees was relatively larger and their species composition thus became closer to that of trees polluted earlier. It remains to be seen how the system will develop in the future under changing pollution levels since sulphur dioxide emissions reduced markedly in the whole country during the 1990s.

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