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Congruent responses of epiphytic bryophyte communities to air pollution on two species of trees differing in bark chemistry

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Abstract: Epiphytic bryophytes are susceptible to air pollution. The disappearance of sensitive species from highly polluted areas and their recovery after a decrease in pollution were recorded in the second half of the 20th century in Europe. However, the effect of current air pollution on the composition of epiphytic communities and the associated role of host-tree bark chemistry have not been sufficiently studied. Here, the effects of acidifying air pollution on the structure of epiphytic bryophyte communities hosted by tree species with different bark pH are assessed. Due to the higher acid-buffering capacity of basic substrates, a smaller difference between communities on host trees with high bark pH in areas with different pollution loads was expected. Epiphytic bryophytes were studied at 50 sites with similar climate but contrasting levels of SO_2 and NO_x air pollution in central Europe. As a proxy for the current pollution load at each site, in addition to SO_2 and NO_x atmospheric concentrations, tissue N concentration was measured in *Hypnum cupressiforme*. Abundances of species of bryophytes were recorded on trunks of oaks (*Quercus robur* and *Q. petraea*, low bark pH expected) and ash (*Fraxinus excelsior*, high pH expected). Ninety species of bryophytes were recorded. Acidifying air pollution still influences the structure of epiphytic bryophyte communities in Europe, despite the lower levels of pollutants than previously. Atmospheric concentration of SO_2 was found to be a significant environmental variable affecting structure of epiphytic bryophyte communities. Ash with high bark pH hosted more diverse communities, including sensitive species, but were just as affected by SO_2 pollution as oaks. Species richness, occurrence of epiphytic specialists, and diversity of epiphytic bryophyte communities decrease with increasing SO_2 pollution, both on oak and ash. However, it is likely that acidifying air pollution is not the sole driver of the structure of current epiphytic communities in central Europe.

Keywords: epiphytic bryophytes, epiphytic communities, SO_2, NO_x, air pollution, host tree bark pH

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Introduction

Bryophytes are poorly protected against the harmful effects of the atmosphere (Hallingbäck & Hodgetts 2000) due to their poikilohydric type of metabolism and that they obtain all the nutrients and water they need through the entire surface of their body (Proctor 2009). Bryophytes also have an extremely high capacity for accumulation, including some toxicants (e.g. metals, radioisotopes, organic pollutants) (Bates 2009). Presence of particular species of bryophytes indicates specific environmental conditions (e.g. pH, type of bedrock, humidity) as well as the presence of toxic substances (Hallingbäck & Hodgetts 2000). Due to these facts, together with the wide distribution of the majority of species, and their narrow ecological amplitudes, bryophytes are used as bioindicators and biomonitors (e.g. Markert et al. 2003, Proctor 2009, Harmens et al. 2011, 2012, Plášek et al. 2014, Mahapatra et al. 2019) and indicators of ecosystem change (Pakeman et al. 2019).

Some pollutants are toxic for bryophytes. High levels of especially nitrogen and sulphur compounds have a negative effect on bryophyte tissue (Gilbert 1970, LeBlanc & Rao 1973, Rao 1982). Negative changes in physiological functions (Nash & Nash 1974, Mitchell et al. 2004), growth and biomass (Greven 1992, Shi et al. 2017) and changes in bryophyte community structure (Mitchell et al. 2005, Zechmeister et al. 2007) are the most common responses to increasing levels of pollution. The uptake of large quantities of nitrogen and sulphur can adversely affect photosynthesis (Coker 1967, Song et al. 2012) and sulphur and nitrogen oxides can also cause acidification of the environment. The biomass of forest bryophytes experimentally exposed to acid precipitation decreased with decreasing pH (Hutchinson & Scott 1988). In addition, the germination of bryophyte diaspores is adversely affected by low pH (Löbel & Rydin 2010). Changes in reproduction, especially, may be the first response of sensitive bryophytes, which is manifested long before visible signs of damage to adult plants (LeBlanc & DeSloover 1970, Rao 1982). The changes in community structure caused by sulphur and nitrogen compounds are long-lasting, and the recovery of epiphytic communities in previously heavily polluted areas appears to be slow (Zechmeister et al. 2007). Song et al. (2012) emphasize that the increase in pollution load not only causes physiological damage to bryophyte plants or even extinction of sensitive species, but also the risk of a global loss of biodiversity. In addition, the toxic substances in the air can spread over long distances, disregarding the boundaries of protected areas, national borders, or continents, and are even at high concentrations in areas without local sources of pollution (Hallingbäck & Hodgetts 2000).

Epiphytic species of bryophytes tend to be more sensitive to air pollution than species growing on other substrates due to their more direct exposure to toxicants (e.g. Leith et al. 2008). Epiphytes also gain nutrients from stemflow (Bates 2009), which contains pollutants from dry and wet deposition on the entire surface of the crown of a tree. The concentration of pollutants in the stemflow can be much higher than in rain (Farmer et al. 1991). In the second half of the 20th century, European bryologists reported the disappearance of some species of epiphytic bryophytes from highly polluted areas and their recovery after a decrease of pollution levels (e.g. Gilbert 1968, Müller 1993, Bates et al. 1997, Richter et al. 2009, Kučera et al. 2012). Hutsemékers et al. (2023) report great temporal shifts in epiphytic bryophyte communities caused by changing levels of air pollution. Lack of epiphytic bryophytes was reported in polluted industrial areas (e.g. Sim-Sim et al. 2000).

Different species of trees differ in the characteristics of their bark, including its chemistry. Tree identity, therefore, determines the abundance and structure of epiphytic communities (e.g. Cleavitt et al. 2009, Fritz et al. 2009, Becker et al. 2019, Mitchell et al. 2021). In pristine conditions, both acidic and alkaline bark host bryophyte species sensitive to air pollution (Barkman 1958, Bates & Brown 1981). Sensitive species of epiphytic bryophytes, such as the *Orthotrichaceae* family, however, were predominantly collected from trees that have alkaline bark, i.e. a high pH (e.g. *Fraxinus*, *Juglans*, *Malus*) during the period of heavy sulphur pollution in the Ostrava region (Czech Republic) in the 1970s and 1980s. Farmer et al. (1991) report that epiphytic bryophytes are affected by acid pollution, which reduces bark buffering capacity and increases its acidity. In addition, Gilbert (1968) reports that high levels of pH and its acid buffering capacity can mitigate the harmful effects of pollutants. Therefore, some species of trees may act as refugia for sensitive species due to the buffering effect of their alkaline bark.

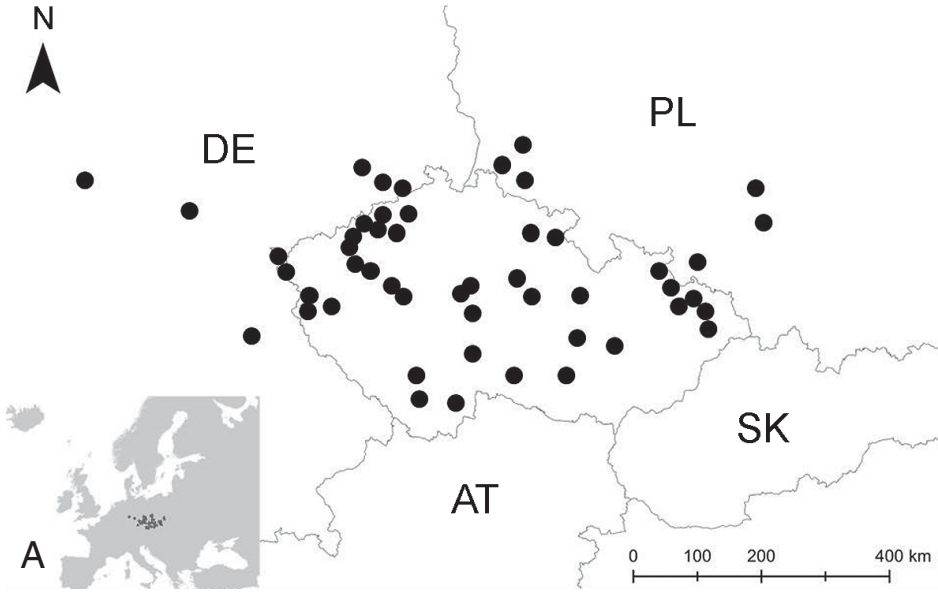
This study aims to determine the effect of acidifying air pollution on the structure of bryophyte communities on trees with bark of different levels of pH in central Europe. It is hypothesized, that the effect of pollution on bryophyte communities will vary depending on the pH of their bark in areas with a similar climate. It is likely, that the detrimental effect of pollutants will be less severe on trees with high bark pH levels.

Methods

Areas with a similar climate and different levels of acidifying air pollution were selected in the Czech Republic, Poland and Germany (central Europe, Fig. 1A). Information on climate and air pollution levels is that predicted by an atmospheric concentration model based on mean annual precipitation (500–850 mm, Fig. 1B), mean annual temperature (6.5–8.5 °C) (WorldClim; Hijmans et al. 2005), as well as five-year (2006–2010) average NO_x (Fig. 1C) and SO_2 (Fig. 1D) (1 km grid, EEA 2015; GIS analyses in ArcMap version 10; ESRI 2011). Fifty woodlands in which both oaks (*Quercus petraea* or *Q. robur*) and ash (*Fraxinus excelsior*) occurred were selected, with 25 in the areas with 8.0–12.0 $\mu g \cdot m^{-3}$ NO_x and 0.5–4.5 $\mu g \cdot m^{-3}$ SO_2 together (= low pollution), and 25 in areas with 12.5–16.5 $\mu g \cdot m^{-3}$ NO_x and 5.0–10.5 $\mu g \cdot m^{-3}$ SO_2 (= high pollution).

Nitrogen (N) content in the tissue of *Hypnum cupressiforme* and bark pH were measured as proxy variables of air pollution to assess its actual level at each of the sites studied (e.g. Harmens et al. 2011). Specimens of *H. cupressiforme* were collected from three of the trees studied at each site, 130 cm high above ground. For N determination, about 1.50 mg of ball-milled green tissue was Kjeldahl-digested with concentrated sulphuric acid and analysed calorimetrically as NH_4^+ using flow injection analysis. Bark pH was measured using a flat electrode for measuring surfaces (WTW SenTix Sur, Vario pH meter) of small pieces of bark in the laboratory after spraying the bark with 0.1 M KCl (Farmer et al. 1990).

One of the authors (J.P.) did the field sampling for consistency. Five oak and five ash trees were selected by stratified random sampling at each study site that met the following criteria: trees with straight trunks, DBH at least 15 cm, position within the forest at least 10 m from the forest edge and at least 10 m from other sampled trees. All species of bryophytes and their abundance (three-point scale: 1 = up to 1 cm^2; 2 = 1–400 cm^2; 3 = over 400 cm^2) were recorded from the ground to 2 m height on the trunks of the selected



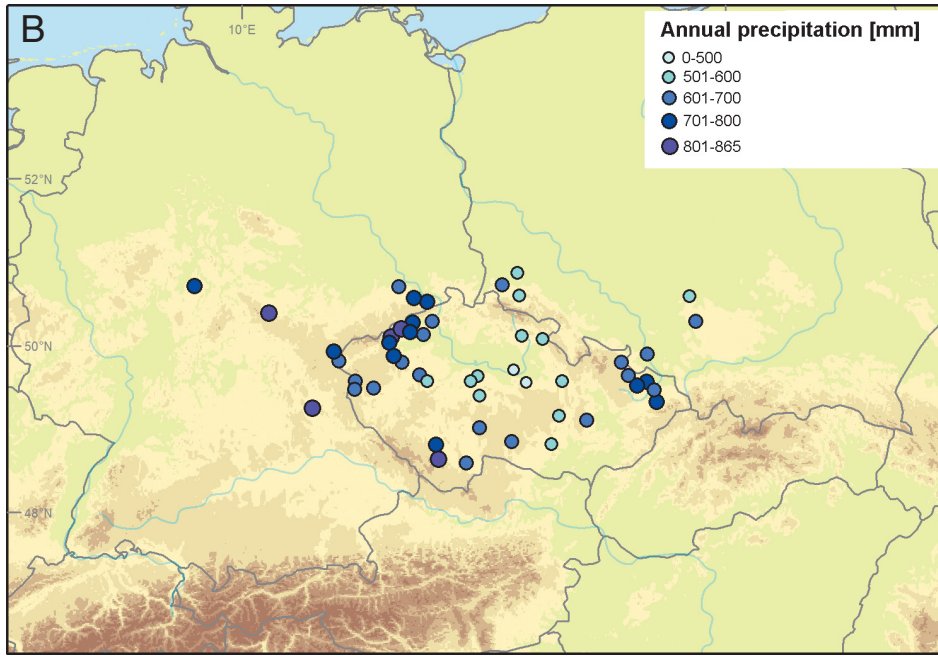
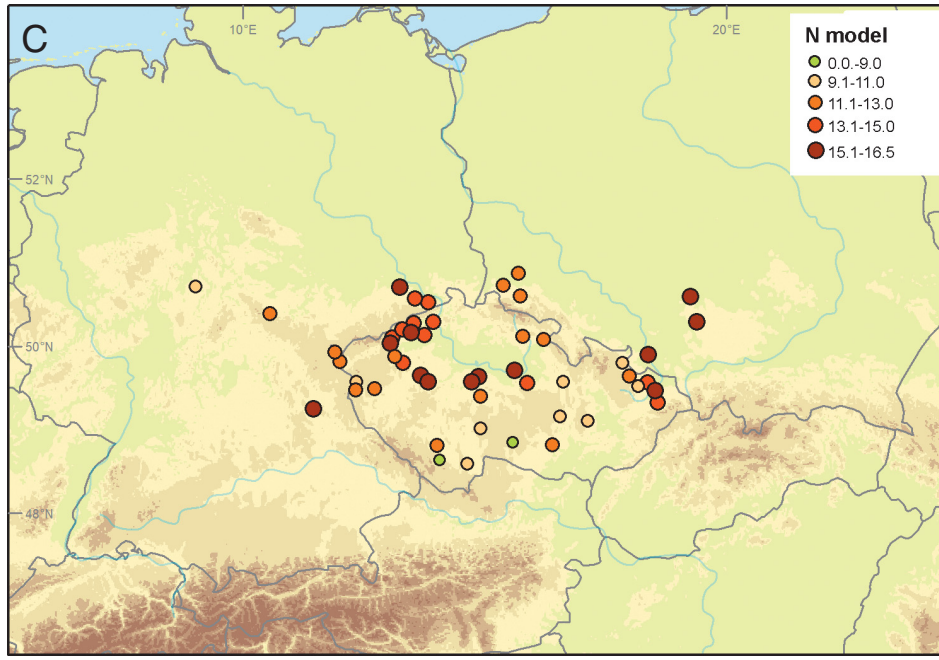
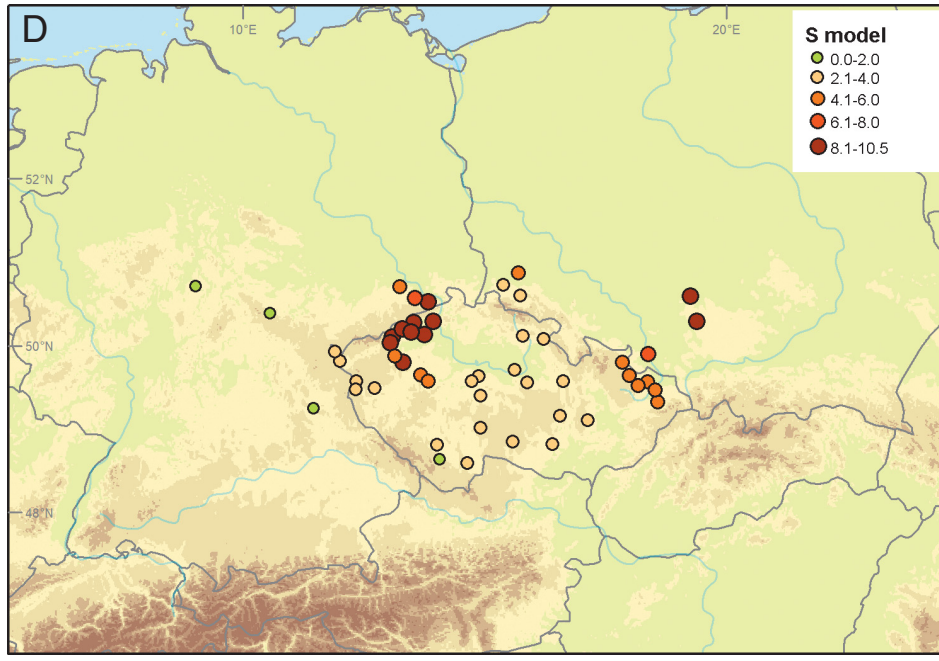


Fig. 1. Map showing the location of the sites studied (A), along with the mean annual precipitation (B) and model-predicted mean atmospheric NO_x (C) and SO_2 (D) concentrations characteristic for the sites. For C and D see next page.


C
10°E
20°E
52°N
50°N
48°N
N model
0.0.-9.0
9.1-11.0
11.1-13.0
13.1-15.0
15.1-16.5


D
10°E
20°E
52°N
50°N
48°N
S model
0.0-2.0
2.1-4.0
4.1-6.0
6.1-8.0
8.1-10.5

trees. Tree size (DBH) had a significantly different effect on epiphytic community richness on oak and ash (Poisson generalized linear mixed model with site ID as random factor, tree species × DBH interaction: $z = -2.7$, $P < 0.01$). Therefore, separate univariate and multivariate models were fitted for each tree species. DBH was also used as a covariate in these models.

The field work was done in 2016 and 2017. The environmental variables used in statistical analyses (Supplementary Table S1) included: model mean NO_x and SO_2 concentration (EEA 2015), mean annual temperature, temperature maxima and minima, mean annual precipitation, mean precipitation in the wettest and the driest month of the year, temperature annual range, average altitude, N concentration in *Hypnum cupressiforme* tissue, mean bark pH (for oak and ash separately, square-root transformed in statistical models), mean host tree diameter at breast height (DBH, for oak and ash separately) and legal protection status of the site (binary variable). All climatic variables came from WorldClim2 (Fick & Hijmans 2017). The list of epiphytic specialists (Supplementary Table S2) was compiled by analysing data in the Bryoatt database (Hill et al. 2007). For each species, an index of its affinity for particular trees were calculated. The Bryoatt database presents the affinity for each bryophyte species for particular substrates on a three-point scale (0–2). The ratio between the indicator value for living on trees and the sum of all indicator values referring to other substrates, but with all types of rocky substrates merged into a single indicator value using the highest occurrence frequency point on rocky substrates, were calculated. The species of bryophytes with an index value higher than 1 were considered as epiphytic specialists. One exception was *Hypnum andoi*, which had an index value of 1. Based on field experience, this moss was not considered an epiphytic specialist as it grows on other substrates in the area studied.

A paired t-test was used to determine differences in bark pH between ash and oak trees at the sites studied and Pearson correlation to test the association between ash and oak bark pH between sites. A Spearman rank correlation matrix was computed in order to evaluate the associations between the N content of *Hypnum*, bark pH, NO_x and SO_2 atmospheric concentration as proxies of air pollution level, and climatic variables (Supplementary Fig. S1). Poisson generalized linear models were computed to test which environmental factors determine the total and specialist species richness of epiphytic communities separately on ash and oak. The models were built from candidate environmental predictors using the stepwise selection procedure and retaining only the significant terms ($P < 0.05$) in the models. The full tables summarizing analyses of the differences are provided in Supplementary Table S3.

Distance-based redundancy analyses (db-RDA) with square-rooted Bray-Curtis dissimilarity, based on presence-absence data of bryophytes for particular sites, were used to identify drivers of community composition. Separate db-RDA analyses were constructed for oak and ash. In the db-RDAs, the effects of NO_x, and SO_2 atmospheric concentrations was determined in order to determine whether they are drivers of bryophyte community composition, using a forward stepwise predictor selection. In this model, DBH and additional environmental covariates (average altitude, temperature maxima and minima, mean annual temperature, temperature annual range, mean annual precipitation, mean precipitation in the wettest and the driest month of the year) were used to remove possible confounding effects between environmental gradients and pollution level. To test the significance of predictors and the final model, a Monte-Carlo permutation test with

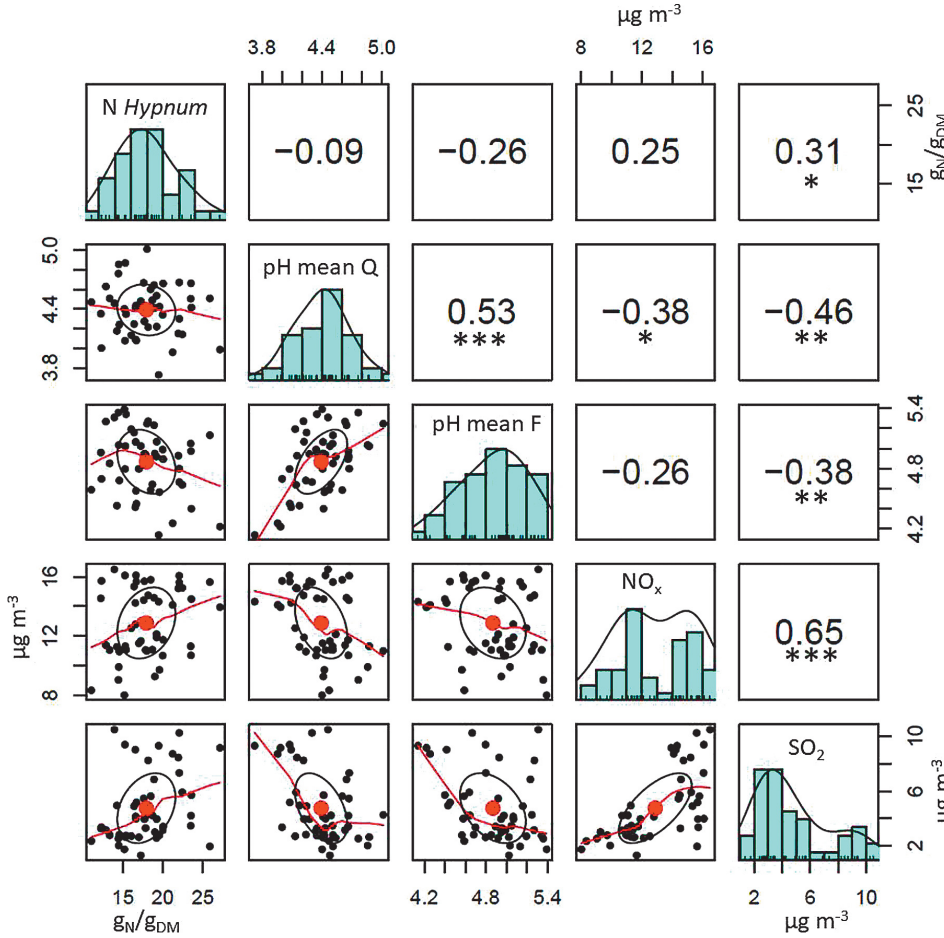


Fig. 2. The air pollution proxies. Pair panel plot showing the distribution and pair correlations of environmental predictors used in this study, with correlation ellipses and their centroids (narrower ellipse = stronger correlation), and with smoothed fit through LOESS regression. The upper triangle shows the values of the Spearman's rank correlation coefficient. The pH of oak bark (pH mean Q) correlated with data on SO_2 and NO_x atmospheric concentrations, whereas the pH of ash bark (pH mean F) correlated only with SO_2 data. The N concentration in *Hypnum* tissue (N *Hypnum*) correlated only with SO_2 data. *** $P < 0.001$, ** $P < 0.001$, * $P < 0.01$

999 permutations was used. Additional unconstrained ordinations (Principal Coordinate Analysis) with passively projected atmospheric SO_2 concentration were conducted. These analyses of community composition based on total differences were further supplemented by analyses focusing on the turnover and nestedness components of beta-diversity. Dissimilarity matrices based on (qualitative) turnover and nestedness pairwise beta-diversity components were computed. These matrices were subsequently subjected to the same db-RDA analyses supplemented by Monte-Carlo permutation tests as the Bray-Curtis dissimilarity matrix. All statistical analyses were done in R, ver. 4.2.2 (R Core Team 2022); multivariate community composition and beta-diversity analyses were computed in R packages vegan (Oksanen et al. 2022) and betapart (Baselga et al. 2023)

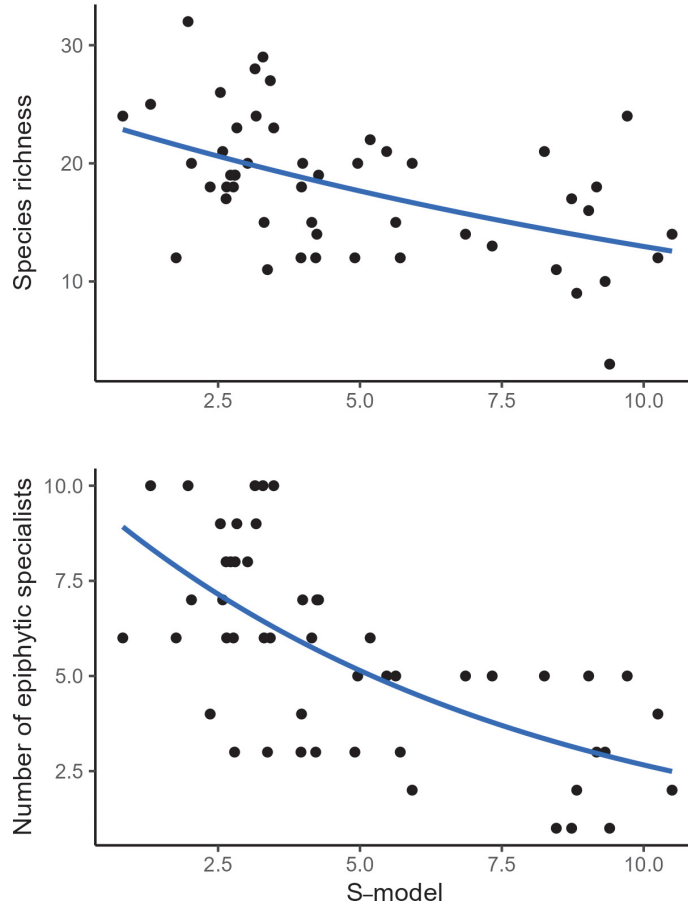


Fig. 3. Dependence of total species richness and the number of epiphytic specialists growing on *Fraxinus excelsior* on model predicted air SO_2 concentration (S-model; μg/mł). The regression lines correspond to Poisson GLM fits.

Nomenclature of bryophyte taxa is according to Hodgetts et al. (2020). Species *Ulota crispa* (Hedw.) Brid., *U. crispula* Bruch and *U. intermedia* Schimp. were grouped as *Ulota crispa* s. lat. The genus level was used in analyses when specimens lacked necessary parts for species identification (in the case when there was no determined species of that genus occurring on the same study site); taxon *Orthotrichum* sp. s. lat. includes *Lewinskya* and *Orthotrichum* genera in that case.

Results

A total of 90 species of bryophytes were recorded, including 81 species of mosses and 9 liverworts; 17 species were considered to be epiphytic specialists (Supplementary Table S2). The most frequently encountered species were mosses *Pylaisia polyantha* and *Brachytheciastrum velutinum* (found on 373 and 362 trees of the 500 host trees studied, respec-

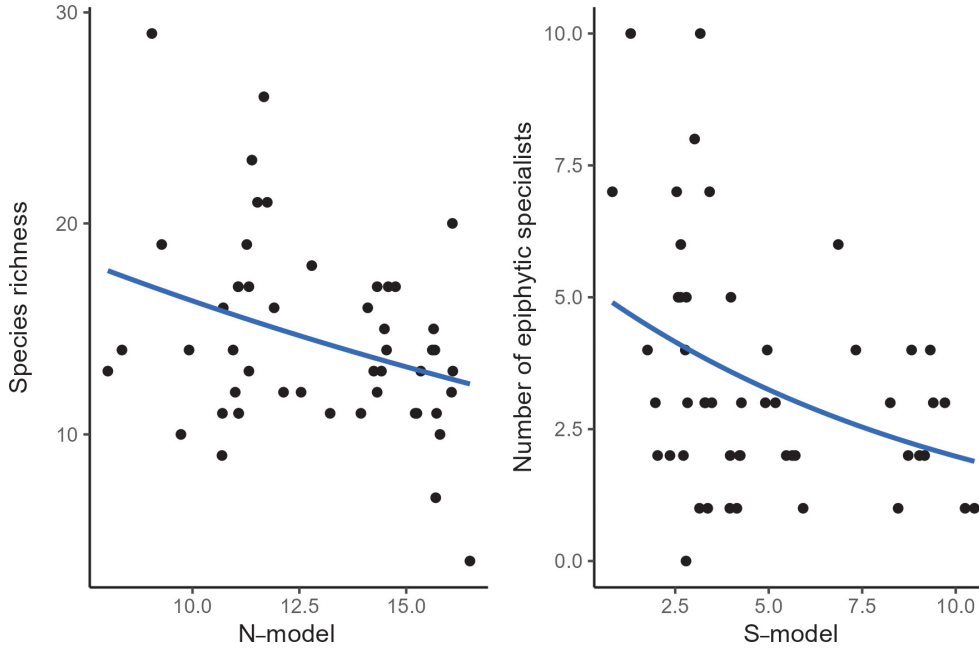


Fig. 4. Dependence of total species richness and the number of epiphytic specialists growing on *Quercus* sp. on significant air-pollution predictors (N-model for all species, S-model for specialists; NO_x and SO_2 concentrations in μg/mł). The regression lines correspond to Poisson GLM fits.

tively). Epiphytic communities on particular host trees consisted of 1–25 species (with a median of 7 species). Per study site, 13–37 species (with a median of 23), were recorded.

The assumption that the pH of the bark of ash is higher than that of oak was confirmed (paired t-test within study sites: $t_{49} = -11.9$, $P < 0.001$), but the pH values recorded for the two trees were correlated (Pearson $r = 0.544$, $t_{48} = 4.5$, $P < 0.001$). Ash pH value ranged from 4.10 to 5.39, with a median of 4.93; oak pH value ranged from 3.72 to 5.01, with a median of 4.39. The proxies for air pollution were weakly correlated (Fig. 2). Data on SO_2 atmospheric concentration were significantly correlated with both ash and oak bark pH, while NO_x data correlated only with oak bark pH. The N concentration in *Hypnum* tissue was only correlated with SO_2 data.

The SO_2 atmospheric concentration (variance accounted for = 0.24, $z = -3.8$, $P < 0.01$; Fig. 3), DBH (variance accounted for = 0.15, $z = 3.8$, $P < 0.01$), and precipitation in the driest month (variance accounted for = 0.07, $z = 0.0095$, $P < 0.01$) were found to be significant drivers of species richness of epiphytic communities on ash; NO_x atmospheric concentration (variance accounted for = 0.11, $z = -2.5$, $P = 0.01$; Fig. 4) and precipitation in the driest month (variance accounted for = 0.07, $z = 2.2$, $P < 0.05$) significantly influenced species richness on oak. The occurrence of epiphytic specialists was significantly associated with the model prediction of SO_2 atmospheric concentration (variance accounted for = 0.43, $z = -5$, $P < 0.001$; Fig. 3) on ash and also on oak (variance accounted for = 0.14, $z = -3.1$, $P < 0.01$; Fig. 4), where the number of specialists was furthermore associated with the mean precipitation in the driest month (variance accounted for = 0.10, $z = 2.7$, $P < 0.01$).

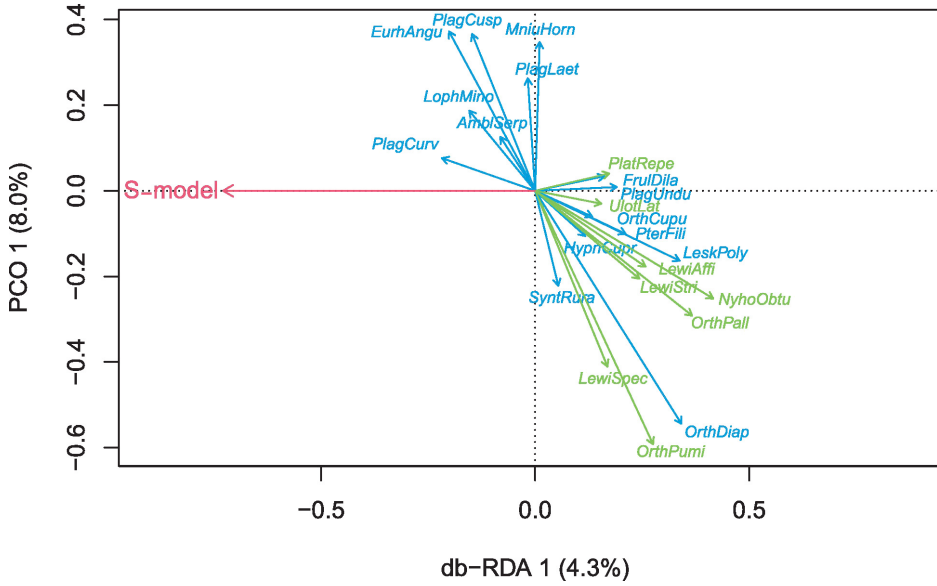


Fig. 5. A db-RDA diagram showing the association between the model prediction of SO_2 atmospheric concentration (S-model) and bryophyte communities growing on *Fraxinus*. Green arrows and labels highlight epiphytic specialists. Species abbreviations are listed in Supplementary Table S4.

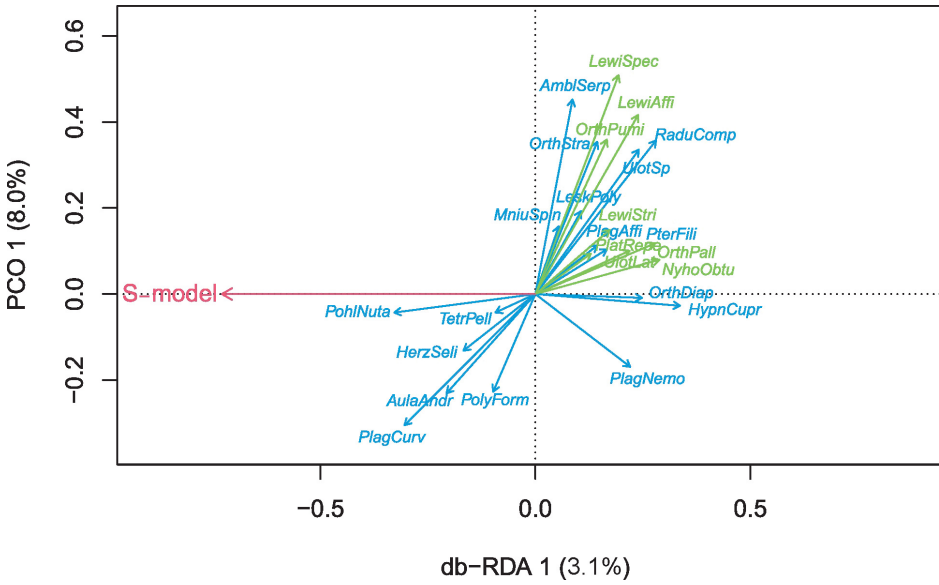


Fig. 6. db-RDA diagram showing the association between the model prediction of SO_2 atmospheric concentration (S-model) and bryophyte communities growing on *Quercus*. Green arrows and labels highlight epiphytic specialists. Species abbreviations are listed in Supplementary Table S4.

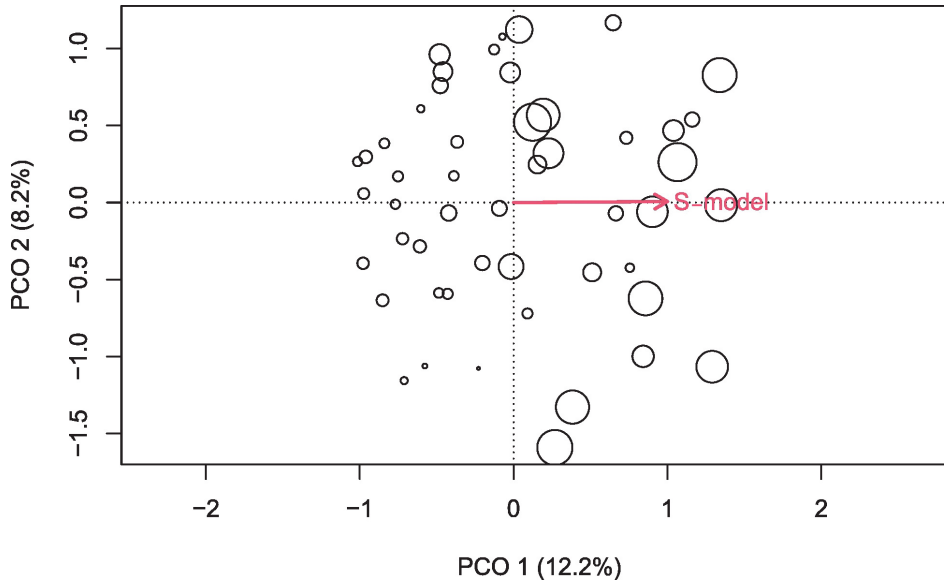


Fig. 7. PCoA diagram of site scores based on the differences in the bryophyte communities on *Fraxinus*. Symbol size indicates S-model variable at individual sites. The red arrow displays passively projected trend in SO_2 atmospheric concentration. Correlation of SO_2 atmospheric concentration with the first two axes: $R^2 = 0.39$, $P < 0.001$ (Monte-Carlo permutation test with 999 permutations).

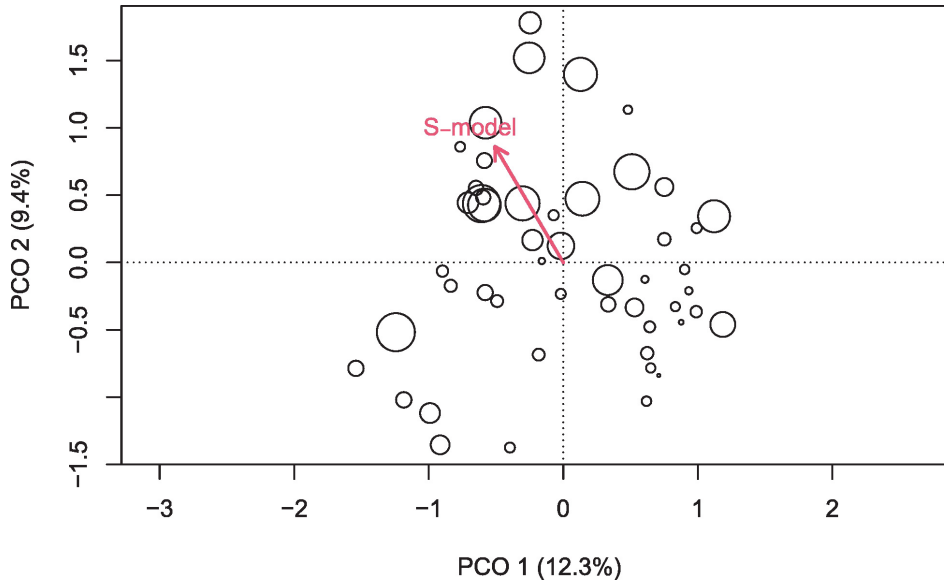


Fig. 8. PCoA diagram of site scores based on differences in the bryophyte communities on Quercus. Symbol size indicates S-model variable at individual sites. The red arrow displays passively projected trend in SO_2 atmospheric concentration. Correlation of SO_2 atmospheric concentration with the first two axes: $R^2 = 0.22$, $P = 0.002$ (Monte-Carlo permutation test with 999 permutations).

The model prediction of SO_2 and NOx atmospheric concentrations were significantly correlated with the bryophyte community on ash (SO_2: $P < 0.001$, NOx: $P = 0.03$; db-RDA – simple effects tested using Monte-Carlo permutation tests). However, only SO_2 was retained in the model built by stepwise selection, which accounted for 4.3% of the variability (pseudo-$F_{1,39} = 2.3$, $P = 0.001$; Fig. 5). SO_2 was the only pollution predictor having a significant association with bryophyte communities growing on oak (explained 3.1% of variability, pseudo-$F_{1,39} = 1.6$, $P = 0.01$; Fig. 6). Epiphytic specialists, especially *Lewinskya striata*, *Nyholmiella obtusifolia*, *Orthotrichum pallens*, *Platygyrium repens* and *Ulota crispa* s. lat. were negatively associated with the SO_2 concentration gradient in both ordination diagrams (Figs 5–6). On the other hand, species that thrive in acidic environments, such as *Tetraphis pellucida* and *Herzogiella seligeri*, which are predominantly epixylic and grow on decaying wood, as well as the generalist *Plagiothecium curvifolium* and *Pohlia nutans*, were recorded growing even under high concentrations of SO_2 (Figs 5–6). In addition, unconstrained PCoA analyses indicated, that SO_2 concentration was associated with the most important gradient in community composition (PCo 1) on ash (Fig. 7) and the second most important gradient (PCo 2) on oak (Fig. 8).

Analysis of beta diversity revealed that the significant impact of SO_2 on species composition was given by its effect on species turnover (ash: pseudo-$F_{1,40} = 2.1$, $P = 0.004$; oak: pseudo-$F_{1,40} = 1.63$, $P = 0.012$). The association with bryophyte community nestedness was not significant.

Discussion

Our results indicate that even with lower concentrations of pollutants than in the second half of 20th century, the current air pollution levels of SO_2 and NO_x still affect epiphytic bryophyte communities in present-day central Europe. This conclusion assumes that the communities of bryophytes reflect current rather than past pollution levels due to their potential for rapid dispersal.

SO_2 concentrations at most sites were in the high pollution levels of 8–10 μg/m^3. These values correspond to the critical SO_2 load of 10 μg/m^3 defined for lichens (bryophytes were not assessed), which is only slightly lower than that of 15 μg/m^3 for natural vegetation (CLRTAP 2024). Our results indicate that the critical SO_2 load, i.e. concentration below which significant harmful effects do not occur according to present knowledge, is below 10 μg/m^3 for epiphytic bryophytes. This reduction in the critical load is consistent with the patterns reported for plant sensitivity to other pollutants such as NH_3 (CLRTAP 2024).

Acidifying pollutants can result in a decrease in bark pH (Stetzka & Werthschütz 2008). As initially expected, the pH of ash bark was higher than that of oak bark. Bark pH was correlated with both SO_2 and NO_x model atmospheric concentration in oaks, while ash bark pH was correlated only with SO_2 data, presumably due to its greater acidifying effect than NO_x. Nevertheless, bark pH can be influenced by various factors, making it challenging to establish a clear relationship between air pollution levels and bark pH (Larsen et al. 2007). For instance, atmospheric ammonia, which was not included in this study, may have the opposite effect of acidifying pollutants and increase bark pH (Pescott et al. 2015). The effects of air pollution and bark pH on bryophytes may be complementary, even if these variables are not directly correlated (e.g. Mitchell et al. 2005, Zechmeister et al. 2007).

The N concentration in *Hypnum* tissue did not correlate with the NO_x model-predicted atmospheric concentration data. This could be attributed to sampling design. The aim was to obtain an accurate image of NO_x influence on the communities studied, so *Hypnum* was collected directly from the host trees. However, canopy drip can substantially influence the measured concentration of NO_x (Harmens et al. 2015), which is higher under canopies (Kluge et al. 2013, Skudnik et al. 2014). This methodology enabled the development of a proxy for pollution with real effect on the communities studied. On the other hand, NO_x is not the only source of nitrogen for epiphytic mosses, as ammonia and ammonium may be the predominant forms of reactive N in rural areas (Tang et al. 2021).

The epiphytic communities are clearly more species-rich in areas with low SO_2 pollution. Increasing loss of bryophyte species with increasing deposition of pollutants is also reported by e.g. Larsen et al. (2007) and Fritz et al. (2009). The tolerance of bryophytes to pollutants varies (e.g. Smith 2004). In this study, epiphytic specialists were mostly found in areas with low SO_2 concentrations and absent in those with high air pollution. The overall composition of epiphytic bryophyte communities also changes along an air pollution gradient (Song et al. 2012, Hutsemékers et al. 2023). It is mainly generalists and acidophilous species that thrive even in polluted areas. Replacement of epiphytic communities of mosses in the family *Orthotrichaceae* by more acidophilic community is also reported in the British Isles (Bates et al. 1997).

However, the spread of some bryophyte species may also reflect the level of pollution by ammonia (Sheppard et al. 2011), affecting trophic levels and pH of host tree bark (Pescott et al. 2015). Also processes during recolonization after a period with very high levels of acidifying air pollution are not recorded. The high proportion of unexplained variability may indicate that current air quality levels are not the sole driver of the current communities. Other environmental factors and past pollution events may also have played a role.

Bryophyte communities on oak and ash trees differed. Communities on ash were rich in species and contained more epiphytic specialists. Ash hosted also a higher number of the species recorded in Database of Lichens and Bryophytes in the Czech Republic (Man et al. 2022). Löbel et al. (2006) and Mežaka et al. (2012) report that tree species and bark pH are the most important variables determining the structure of epiphytic communities, species composition, as well as species richness. On the other hand, e.g. Palmer (1986) takes the view that the host tree is not as important as the set of conditions associated with the tree. Frahm (1992) draws attention to the fact that the degree of association with a specific type of host tree decreases with increasing air humidity. The results indicate that air pollution affects communities more on host trees with more acidic bark, as was initially hypothesized. Both the communities on oak and ash were associated with the level of air pollution.

Conclusions

Level of acidifying air pollution is associated with species composition and richness of epiphytic communities of bryophytes in central Europe in spite of the relatively low recent concentrations of pollutants. Ash with a high bark pH hosted more diverse communities with frequent presence of sensitive species, but also communities the presence of which was determined by a high SO_2 atmospheric concentration. Species richness, occurrence of epiphytic specialists and diversity of epiphytic bryophytes communities decreased with increasing SO_2 level, both on oak and ash. Effect of acidifying air pollution on bryophyte communities did not vary depending on the host tree.

Supplementary materials

Fig. S1. Pair panel plot showing the distribution and pair correlations of environmental predictors (climate variables and pollution proxies) used in this study.
Table S1. Summary of all environmental data used in the statistical analyses.
Table S2. The list of bryophyte species and frequencies of their occurrence recorded on particular host trees and study sites.
Table S3. Analysis of different tables of species richness GLM models.
Table S4. Species abbreviations used in db-RDA diagrams.

Supplementary materials are available at https://www.preslia.cz

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References

Barkman J. J. (1958) Phytosociology and ecology of cryptogamic epiphytes. – Van Gorcum, Assen.
Baselga A., Orme D., Villeger S., De Bortoli J., Leprieur F., Logez M., Martinez-Santalla S., Martin-Devasa R., Gomez-Rodriguez C. & Crujeiras R. (2023) Betapart: partitioning beta diversity into turnover and nestedness components. R package version 1.6. – URL: https://CRAN.R-project.org/package=betapart.
Bates J. W. (2009) Mineral nutrition and substratum ecology. – In: Goffinet B. & Shaw A. J. (eds), Bryophyte biology, p. 299–356, Cambridge University Press, Cambridge.
Bates J. W. & Brown D. H. (1981) Epiphyte differentiation between *Quercus petraea* and *Fraxinus excelsior* trees in a maritime area of South West England. – Vegetatio 48: 61–70.
Bates J. W., Proctor M. C. F., Preston C. D., Hodgetts N. G. & Perry A. R. (1997) Occurrence of epiphytic bryophytes in a 'tetrad' transect across southern Britain. 1. Geographical trends in abundance and evidence of recent change. – Journal of Bryology 19: 685–714.
Becker D., Dobson A. & Klitgaard K. (2019) Bark characteristics affect epiphytic bryophyte cover across tree species. – California Ecology and Conservation Research 2019: 1–8.
Cleavitt N. L., Dibble A. C. & Werier D. A. (2009) Influence of tree composition upon epiphytic macrolichens and bryophytes in old forests of Acadia National Park, Maine. – Bryologist 112: 467–487.
CLRTAP (2024) Mapping critical levels for vegetation. Chapter 3 of Manual on methodologies and criteria for modelling and mapping critical loads and levels and air pollution effects, risks and trends. – UNECE Convention on Long-range Transboundary Air Pollution, URL: https://www.umweltbundesamt.de/en/cce-manual.
Coker P. D. (1967) The effects of sulphur dioxide pollution on bark epiphytes. – Transactions of the British Bryological Society 5: 341–347.
EEA (2015) European Environmental Agency, data and maps. – URL: https://www.eea.europa.eu/data-and-maps.
ESRI (2011) ArcGIS Desktop: release 10. – Environmental Systems Research Institute, Redlands.
Farmer A. M., Bates J. W. & Bell J. N. B. (1990) A comparison of methods for the measurement of bark pH. – Lichenologist 22: 191–194.
Farmer A. M., Bates J. W. & Bell J. N. B. (1991) Seasonal variations in acidic pollutant inputs and their effects on the chemistry of stemflow, bark and epiphyte tissues in three oak woodlands in N.W. Britain. – New Phytologist 118: 441–451.
Fick S. E. & Hijmans R. J. (2017) Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. – International Journal of Climatology 37: 4302–4315.
Frahm J.-P. (1992) Untersuchungen zur epiphytischen Moosvegetation der Vogesen. – Herzogia 9: 213-228.
Fritz Ö., Brunet J. & Caldiz M. (2009) Interacting effects of tree characteristics on the occurrence of rare epiphytes in a Swedish beech forest area. – Bryologist 112: 488–505.
Gilbert O. L. (1968) Bryophytes as indicators of air pollution in the Tyne Valley. – New Phytologist 67: 15–30.

Gilbert O. L. (1970) Further studies on the effect of sulphur dioxide on lichens and bryophytes. – New Phytologist 69: 605–627.

Greven H. C. (1992) Changes in the moss flora of the Netherlands. – Biological Conservation 59: 133–137.

Hallingbäck T. & Hodgetts N. (eds) (2000) Mosses, liverworts, and hornworts. Status survey and conservation action plan for bryophytes. – IUCN/SSC Bryophyte Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Harmens H., Ilyin I., Mills G., Aboal J. R., Alber R., Blum O., Coskun M., De Temmerman L., Fernández J. Á., Figueira R., Frontasyeva M., Godzik B., Goltsova N., Jeran Z., Korzekwa S., Kubin E., Kvietkus K., Leblond S., Liiv S., Magnússon S. H., Maňkovská B., Nikodemus O., Pesch R., Poikolainen J., Radnovi D., Rühling Å., Santamaria J. M., Schröder W., Spiric Z., Stafilov T., Steinnes E., Suchara I., Tabors G., Thöni L., Turcsányi G., Yurukova L. & Zechmeister H. G. (2012) Country-specific correlations across Europe between modelled atmospheric cadmium and lead deposition and concentrations in mosses. – Environmental Pollution 166: 1–9.

Harmens H., Norris D. A., Cooper D. M., Mills G., Steinnes E., Kubin E., Thöni L., Aboal J. R., Alber R., Carballeira A., Coskun M., De Temmerman L., Frolova M., González-Miqueo L., Jeran Z., Leblond S., Liiv S., Maňkovská B., Pesch R., Poikolainen J., Rühling Å., Santamaria J. M., Simončič P., Schröder W., Suchara I., Yurukova L. & Zechmeister H. G. (2011) Nitrogen concentrations in mosses indicate the spatial distribution of atmospheric nitrogen deposition in Europe. – Environmental Pollution 159: 2852–2860.

Harmens H., Norris D. A., Sharps K., Mills G., Alber R., Aleksiayenak Y., Blum O., Cucu-Man S.-M., Dam M., De Temmerman L., Ene A., Fernández J. A., Martinez-Abaigar J., Frontasyeva M., Godzik B., Jeran Z., Lazo P., Leblond S., Liiv S., Magnússon S. H., Maňkovská B., Pihl Karlsson G., Piispanen J., Poikolainen J., Santamaria J. M., Skudnik M., Spiric Z., Stafilov T., Steinnes E., Stihi C., Suchara I., Thöni L., Todoran R., Yurukova L. & Zechmeister H. G. (2015) Heavy metal and nitrogen concentrations in mosses are declining across Europe whilst some "hotspots" remain in 2010. – Environmental Pollution 200: 93–104.

Hijmans R. J., Cameron S. E., Parra J. L., Jones P. G. & Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. – International Journal of Climatology 25: 1965–1978.

Hill M. O., Preston C. D., Bosanquet S. D. S. & Roy D. B. (2007) BRYOATT: attributes of British and Irish mosses, liverworts and hornworts. – Centre for Ecology and Hydrology, Cambridge.

Hodgetts N. G., Söderström L., Blockeel T. L., Caspari S., Ignatov M. S., Konstantinova N. A., Lockhart N., Papp B., Schröck C., Sim-Sim M., Bell D., Bell N. E., Blom H. H., Bruggeman-Nannenga M. A., Brugués M., Enroth J., Flatberg K. I., Garilleti R., Hedenäs L., Holyoak D. T., Hugonnot V., Kariyawasam I., Köckinger H., Kučera J., Lara F. & Porley R. D. (2020) An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. – Journal of Bryology 42: 1–116.

Hutchinson T. C. & Scott M. (1988) The response of the feather moss *Pleurozium schreberi* (Brid.) Mitt. to five years of simulated acid precipitation in the Canadian boreal forest. – Canadian Journal of Botany 66: 82–88.

Hutsemékers V., Mouton L., Westenbohm H., Collart F. & Vanderpoorten A. (2023) Disentangling climate change from air pollution effects on epiphytic bryophytes. – Global Change Biology 29: 3990–4000.

Kluge M., Pesch R., Schröder W. & Hoffmann A. (2013) Accounting for canopy drip effects of spatiotemporal trends of the concentrations of N in mosses, atmospheric N depositions and critical load exceedances: a case study from North-Western Germany. – Environmental Sciences Europe 25: 26.

Kučera J., Váňa J. & Hradílek Z. (2012) Bryophyte flora of the Czech Republic: updated checklist and Red List and a brief analysis. – Preslia 84: 813–850.

Larsen R. S., Bell J. N. B., James P. W., Chimonides P. J., Rumsey F. J., Tremper A. & Purvis O. W. (2007) Lichen and bryophyte distribution on oak in London in relation to air pollution and bark acidity. – Environmental Pollution 146: 332–340.

LeBlanc F. & DeSloover J. (1970) Relation between industrialization and the distribution and growth of epiphytic lichens and mosses in Montreal. – Canadian Journal of Botany 48: 1485–1496.

LeBlanc F. & Rao D. N. (1973) Effects of sulphur dioxide on lichen and moss transplants. – Ecology 54: 612–617.

Leith I. D., Mitchell R. J., Truscott A.-M., Cape J. N., van Dijk N., Smith R. I., Fowler D. & Sutton M. A. (2008) The influence of nitrogen in stemflow and precipitation on epiphytic bryophytes, *Isothecium myosuroides* Brid., *Dicranum scoparium* Hedw. and *Thuidium tamariscinum* (Hedw.) Schimp. of Atlantic oakwoods. – Environmental Pollution 155: 237-246.

Löbel S. & Rydin H. (2010) Trade-offs and habitat constraints in the establishment of epiphytic bryophytes. – Functional Ecology 24: 887–897.

Löbel S., Snäll T. & Rydin H. (2006) Species richness patterns and metapopulation processes – evidence from epiphyte communities in boreo-nemoral forests. – Ecography 29: 169-82.

Mahapatra B., Dhal N. K., Dash A. K., Panda B. P., Panigrahi K. C. S. & Pradhan A. (2019) Perspective of mitigating atmospheric heavy metal pollution: using mosses as biomonitoring and indicator organism. – Environmental Science and Pollution Research 26: 29620–29638.

Man M., Malíček J., Kalčík V., Novotný P., Chobot K. & Wild J. (2022) DaLiBor: Database of Lichens and Bryophytes of the Czech Republic. – Preslia 94: 579–605.

Markert B. A., Breure A. M. & Zechmeister H. G. (2003) Bioindicators and biomonitors. Principles, concepts and applications. – Elsevier, Oxford.

Mežaka A., Brūmelis G. & Piterāns A. (2012) Tree and stand-scale factors affecting richness and composition of epiphytic bryophytes and lichens in deciduous woodland key habitats. – Biodiversity and Conservation 21: 3221–3241.

Mitchell R. J., Hewison R. L., Beaton J. & Douglass J. R. (2021) Identifying substitute host tree species for epiphytes: the relative importance of tree size and species, bark and site characteristics. – Applied Vegetation Science 24: e12569.

Mitchell R. J., Sutton M. A., Truscott A. M., Leith I. D., Cape J. N., Pitcairn C. E. R. & van Dijk N. (2004) Growth and tissue nitrogen of epiphytic Atlantic bryophytes: effects of increased and decreased atmospheric N deposition. – Functional Ecology 18: 322–329.

Mitchell R. J., Truscott A. M., Leith I. D., Cape J. N., van Dijk N., Tang Y. S., Fowler D. & Sutton M. A. (2005) A study of the epiphytic communities of Atlantic oak woods along an atmospheric nitrogen deposition gradient. – Journal of Ecology 93: 482–492.

Müller F. (1993) Studien zur Moos- und Flechtenflora der Stadt Halle/S. – Limprichtia 1: 1–167.

Nash T. H. & Nash E. H. (1974) Sensitivity of mosses to sulphur dioxide. – Oecologia 17: 257–263.

Oksanen J., Simpson G., Blanchet F., Kindt R., Legendre P., Minchin P., O'Hara R., Solymos P., Stevens M., Szoecs E., Wagner H., Barbour M., Bedward M., Bolker B., Borcard D., Carvalho G., Chirico M., De Caceres M., Durand S., Evangelista H., FitzJohn R., Friendly M., Furneaux B., Hannigan G., Hill M., Lahti L., McGlinn D., Ouellette M., Ribeiro Cunha E., Smith T., Stier A., Ter Braak C. & Weedon J. (2022) Vegan: community ecology package. R package version 2.6-4. – URL: https://CRAN.R-project.org/package=vegan.

Pakeman R. J., Brooker R. W., O'Brien D. & Genney D. (2019) Using species records and ecological attributes of bryophytes to develop an ecosystem health indicator. – Ecological Indicators 104: 127–136.

Palmer M. W. (1986) Pattern in corticolous bryophyte communities of the North Carolina Piedmont: do mosses see the forest or the trees? – Bryologist 89: 59-65.

Pescott O. L., Simkin J. M., August T. A., Randle Z., Dore A. J. & Botham M. S. (2015) Air pollution and its effects on lichens, bryophytes, and lichen-feeding lepidoptera: review and evidence from biological records. – Biological Journal of the Linnean Society 115: 611–635.

Plášek V., Nowak A., Nobis M., Kusza G. & Kochanowska K. (2014) Effect of 30 years of road traffic abandonment on epiphytic moss diversity. – Environmental Monitoring and Assessment 186: 8943–8959.

Proctor M. C. F. (2009) Physiological ecology. – In: Goffinet B. & Shaw A. J. (eds), Bryophyte biology, p. 237–268, Cambridge University Press, Cambridge.

R Core Team (2022) R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, URL: https://www.R-project.org.

Rao N. D. (1982) Responses of bryophytes to air pollution. – In: Smith A. J. E. (ed.), Bryophyte ecology, p. 445–471, Chapman & Hall, London.

Richter S., Schütze P. & Bruelheide H. (2009) Modelling epiphytic bryophyte vegetation in an urban landscape. – Journal of Bryology 31: 159–168.

Sheppard L. J., Leith I. D., Mizunuma T., Neil Cape J., Crossley A., Leeson S., Sutton M. A., van Dijk N. & Fowler D. (2011) Dry deposition of ammonia gas drives species change faster than wet deposition of ammonium ions: evidence from a long-term field manipulation. – Global Change Biology 17: 3589–3607.

Shi X.-M., Song L., Liu W.-Y., Lu H.-Z., Qi J.-H., Li S., Chen X., Wu J.-F., Liu S. & Wu C.-S. (2017) Epiphytic bryophytes as bio-indicators of atmospheric nitrogen deposition in a subtropical montane cloud forest: response patterns, mechanism, and critical load. – Environmental Pollution 229: 932–941.

Sim-Sim M., Carvalho P. & Sérgio C. (2000) Cryptogamic epiphytes as indicators of air quality around an industrial complex in the Tagus valley, Portugal. Factor analysis and environment variables. – Cryptogamie Bryologie 21: 153–170.

Skudnik M., Jeran Z., Batič F., Simončič P., Lojen S. & Kastelec D. (2014) Influence of canopy drip on the indicative N, S and $\delta^{15}N$ content in moss *Hypnum cupressiforme*. – Environmental Pollution 190: 27–35.

Smith A. J. E. (2004) The moss flora of Britain and Ireland. – Cambridge University Press, Cambridge.

Song L., Liu W.-Y., Ma W.-Z. & Qi J.-H. (2012) Response of epiphytic bryophytes to simulated N deposition in a subtropical montane cloud forest in southwestern China. – Oecologia 170: 847–856.

Stetzka K. M. & Werthschütz C. (2008) Veränderungen der epiphytischen Moos- und Flechtenflora im Nationalpark „Sächsische Schweiz" Ergebnisse von Dauerbeobachtungsflächen von 1999 bis 2005. – Sauteria 15: 529–543.

Tang Y. S., Flechard C. R., Dämmgen U., Vidic S., Djuricic V., Mitosinkova M., Uggerud H. T., Sanz M. J., Simmons I., Dragosits U., Nemitz E., Twigg M., van Dijk N., Fauvel Y., Sanz F., Ferm M., Perrino C., Catrambone M., Leaver D., Braban C. F., Cape J. N., Heal M. R. & Sutton M. A. (2021) Pan-European rural monitoring network shows dominance of NH_3 gas and NH_4NO_3 aerosol in inorganic atmospheric pollution load. – Atmospheric Chemistry and Physics 21: 875–914.

Zechmeister H. G., Dirnböck T., Hülber K. & Mirtl M. (2007) Assessing airborne pollution effects on bryophytes – lessons learned through long-term integrated monitoring in Austria. – Environmental Pollution 147: 696–705.

Společenstva epifytických mechorostů na dvou druzích stromů lišících se chemickým složením kůry reagují shodně na znečištění ovzduší

Epifytické mechorosty jsou citlivé na znečištění ovzduší. Ústup některých druhů z oblastí s vysokou mírou imisní zátěže a jejich postupný návrat po snížení koncentrací polutantů byl zaznamenán v druhé polovině 20. století na mnoha místech Evropy. Vliv současného znečištění ovzduší na složení epifytických společenstev a související role chemismu borky hostitelských dřevin však nebyly dostatečně prozkoumány. V této studii hodnotíme vliv kyselého znečištění ovzduší na strukturu epifytických společenstev mechorostů na stromech s rozdílným pH borky. Vzhledem k vyšší pufrační kapacitě bazických substrátů jsme v oblastech s různou mírou imisní zátěže očekávali menší rozdíly mezi společenstvy na stromech s vyšším pH borky. Epifytické mechorosty byly studovány na 50 lokalitách ve střední Evropě s podobnými klimatickými podmínkami, avšak s rozdílnou úrovní znečištění ovzduší SO_2 a NO_x. Jako zástupná proměnná současné imisní zátěže byl na každé lokalitě kromě modelovaných atmosférických koncentrací SO_2 a NO_x měřen obsah dusíku v mechu *Hypnum cupressiforme*. Mechorosty byly studovány na kmenech dubů (*Quercus robur* a *Q. petraea*, s očekávaným nižším pH borky) a jasanů (*Fraxinus excelsior*, s očekávaným vyšším pH borky). Celkem bylo zaznamenáno 90 druhů mechorostů. Zjistili jsme, že znečištění ovzduší ovlivňuje epifytická společenstva i v současné Evropě, přestože je míra imisní zátěže nižší než dříve. Koncentrace SO_2 v ovzduší měla signifikantní vliv na strukturu společenstev epifytických mechorostů. Jasany s vyšším pH borky hostily rozmanitější společenstva zahrnující citlivé druhy, avšak i ony byly ovlivněny SO_2, podobně jako společenstva na dubech. Druhová bohatost, výskyt epifytických specialistů a rozmanitost společenstev epifytických mechorostů klesaly s rostoucím znečištěním SO_2, a to jak na dubech, tak na jasanech. Znečištění ovzduší je však pravděpodobně jen jedním z řady faktorů ovlivňujících strukturu současných epifytických společenstev ve střední Evropě.

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