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DOES AIR POLLUTION STILL IMPACT EPIPHYTIC BRYOPHYTES IN THE POST ACIDIC RAIN ERA? INSIGHTS FROM SPATIAL VARIATION OF COMMUNITY COMPOSITION IN SOUTHERN BELGIUM☆

Lea Mouton[a,*] , Virginie Hutsemekers [b], Flavien Collart [a] , Alain Vanderpoorten [a]

a University of Liège, Institute of Botany, Liège, Belgium
b Belgian Interregional Environment Agency, Brussels, Belgium

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** Corresponding author. E-mail address: Lea.Mouton@uliege.be (L. Mouton).*

KEYWORDS

SO_2 – Pesticides – Nitrogen - Fine particulate matter Bioindication - Ozone

ABSTRACT

Since the dramatic air pollution peaks that prevailed in the course of the 20th century in Europe, effective environmental policies, along with major shifts in fuel usage, resulted in the substantial decrease of SO_x and NO_x pollution. At the interface between atmosphere and vegetation, epiphytic bryophyte floras responded by massive back-colonisation of formerly polluted areas. Whether extant concentrations of these pollutants are indeed too low to impact species distributions, and whether other pollutants today play a more important role remains, however, an open question. Taking advantage of an air quality monitoring network for a wide range of pollutants in southern Belgium, we implement here variation partitioning and embedded covariate selection to assess the contribution of current air pollutant loads to variations in epiphytic community composition relative to that of background environmental factors. Factors accounting for variation in species composition included, by decreasing order of importance, background environmental factors, major air pollutants (SO_x, NO_x, O_3, fine particle matter), pollutants of agricultural origin (NH3, pesticides), and heavy metals. The substantially larger role played by background environmental factors over air pollution points to the efficiency of air pollution reduction policies, even for such sensitive organisms as epiphytic bryophytes. Ozone was the most important pollutant. Its ecophysiological impact on cryptogamic epiphytes remains poorly known, and the difference of its

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concentrations between urban and rural areas suggests that it may actually be interpreted as a land-use marker. Pesticides, whose impact on epiphyte floras was not previously assessed, marginally contributed to community composition and species distributions.

Introduction

In the course of the industrial era in Europe, air concentrations in oxidized forms of nitrogen (NO_x) and sulfur (SO_x), largely resulting from coal and fuel combustion, peaked in the 1950s-1980s (Stern, 2005; Castellanos and Boersma, 2012; Hilboll et al., 2013). These pollution peaks had a substantial impact on the environment, such as the spectacular forest decline caused by acidic rains (Pitelka and Raynal, 1989), and on public health, as best exemplified by the great smog of London in 1952 (Polivka, 2018). The global eutrophication trend that peaked in the 1990s, with 79 % of the ecosystem area having exceedances (i.e., the difference between the deposition loads of acidifying and/or eutro- phying airborne pollutants and the critical loads) (European Environment Agency, 2014), resulted in shifts in plant species community composition (Bahr et al., 2012; Karlsmo et al., 2023). Westwards shifts in plant distributions caused by eutrophication took place at faster rates than northward range shifts in response to climate change (Sanczuk et al., 2024).

Several environmental policies aiming at improving air quality, such as the Convention on Long-Range Transboundary Air Pollution (1979), the Ambiant Air Quality Directive (2008/50/CE) and the European Union National Emissions Ceiling Directives (Directive, 2001/81/EC), have therefore been implemented. These policies, together with concomitant changes in fuel usage and combustion technology, resulted in a substantial and global decrease of NOx and SOx pollution since the 1990s onwards (Stern, 2005; Jyethi, 2016; Chen et al., 2024; Syrek-Gerstenkorn et al., 2024). Five pollutants, namely NO_x, non-methane volatile organic compounds, SO_2, NH_3, and fine particulate matter with a diameter <2.5 µm (hereafter, $PM_{2.5}$) have, however, been identified for still contributing to poor air quality and leading to negative impacts on human health and the environment. It is further estimated that 96 % of the EU's urban population remains exposed to unsafe concentrations of black carbon (here after BC) (Bycenkiene et al., 2022; Chen et al., 2024), and ozone, whose long-term concentrations even tend to increase in Europe, especially in the south (Chen et al., 2024). In 2022, almost one third of Europe's agricultural lands were exposed to ground-level ozone concentrations above the threshold value set for protection of vegetation in the EU's Ambient Air Quality Directive

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(https://www.eea.europa.eu/en/analysis/publications/impacts-of-air- pollution-on-ecosystems-in-europe). The NEC Directive (2016/2284/EU) therefore sets 2020 and 2030 emission reduction commitments for these five main pollutants to reduce the health impacts of air pollution by half compared with 2005. This Directive also introduces a number of reporting requirements on emissions of a number of pollutants including, in addition to the five precited ones, PM_{10} (fine particulate matter with a diameter <10 µm), BC, total suspended particulate matter, several heavy metals, and persistent organic pollutants.

At the interface between atmosphere and vegetation, epiphytic bryophyte floras are particularly exposed to air pollution. Their ecophysiological features, and in particular, direct reliance on atmospheric precipitation for water and nutrient uptake and lack of stomates to regulate gas exchanges, make them particularly vulnerable to variations in environmental conditions (Bates, 2000). As a consequence, they have undergone the most dramatic change out of any of the groups analysed as a response to global change since the past decades by a considerable margin (Pescott et al., 2015). Since the 1990s, a massive back-colonisation of acid-sensitive and a decline of acidophilous species have been recurrently reported (Bates et al., 1997; Duckett and Pressel, 2010; Pescott et al., 2015; Purvis et al., 2010; Sergio et al., 2016; Stebel and Fojcik, 2016). The temporal shift in species composition due to changes in air pollutant concentrations was such that it was, on average, more than twice larger than the spatial change in species composition observed today among communities (Hutsemekers et al., 2023). The extent to which major pollutants such as NO_x and SO_x still drive extant species distributions, and whether other pollutants, either emerging or whose effects were historically masked by the impact of major pollutants, play a role in contemporary species distribution patterns, remain, however, open questions. This is particularly the case for pesticides, whose extensive application has led to growing concerns about their impact on ecosystems and population health, but whose impact remains difficult to assess due to the lack of quantitative data on their spreading and concentrations in the environment (Habran et al., 2022).

Here, we take advantage of the official network of air quality monitoring stations for a wide range of pollutants and spatially-explicit estimates of agricultural pesticide use (Habran et al., 2022) in southern Belgium to address the following questions: what is the contribution of current air pollutant loads to variations in epiphytic community composition relative to that of background environmental factors of climatic conditions, topography and vegetation (Q1)? Which pollutants, if any, still account for variations in community composition and species distribution patterns (Q2a)?

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In particular, what is the relative role played by heavy metals, pollutants of agricultural origin and other major pollutants (Q2b)?

Materials and methods

DATA COLLECTION

We assembled three datasets to analyse the relationships between pollution loads, environmental factors and epiphytic bryophytes (Table 1). Datasets 1and 2 were based on complete species inventories of selected areas at two spatial resolution levels, suitable for analyses of the environmental drivers of community composition. Dataset 3included species occurrence data across the entire study area, suitable for analyses of the environmental drivers of individual species distributions.

The factors that affect epiphytic bryophyte distributions vary depending on the degree of spatial resolution and extent (Medina et al., 2014). At the level of individual trees, tree identity, age, and size (Mitchell et al., 2021) drive bark texture and physico-chemistry, and hence, the composition of epiphytic communities (Tyler & Olsson, 2016; Kovarova et al., 2022; Shao et al., 2023). At increasing spatial resolution and geographic extent, site characteristics, such as microclimate, air quality, and vegetation type, increasingly prevail (Medina et al., 2014; Hutsemekers et al., 2023). The present data were collected at the level of epiphyte communities and therefore included site-specific characteristics rather than features of individual trees. The dataset at the finest spatial resolution (dataset 1) included, however, information on host-tree identity, an integrative factor accounting for bark texture and physico-chemistry shown to explain more the variation in epiphytic species distributions than bark pH (Spier et al., 2010).

Dataset 1included local species frequencies of all epiphytic bryophytes recorded between 2016 and 2020 across the 20 nearest phor- ophytes with a DBH (diameter at breast height) > 20 cm surrounding the 20 air quality monitoring stations. Data on atmospheric pollutants originated from actual hourly measurements at the 20 stations and stored by the Belgian Interregional Environment Agency (IRCEL—CELINE).

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***Table 1**. Datasets of epiphytic bryophyte species, air pollutant concentrations, and environmental background (climate, topography, vegetation) in southern Belgium.*

	Dataset 1	Dataset 2	Dataset 3
Sampling units	Air pollution measuring stations (n = 20)	16 km^2 pixels (n = 43)	16 km^2 pixels (n = 633)
Floristic data	frequency of all epiphytic bryophyte species recorded on 20 phorophytes surrounding the station (n = 74)	presence/absence of all epiphytic bryophyte species per pixel (n = 140)	occurrence of only strict epiphytic bryophyte species per pixel (n = 51)
Topographic data	Elevation, northness, slope	Elevation, northness, slope, averaged across each 16 km^2 pixel	idem
Climatic data	Annual mean air temperature (mean T), annual range of air temperature (range T), annual total precipitation, mean relative humidity of the driest month, (meanRH_driest), annual range of radiations at 1 km^2 resolution (Rangersrad)	Idem, averaged across each 16 km^2 pixel	idem
Pollutants	Measured concentrations at n = 20 stations: - Heavy metals (arsenic, cadmium, chromium, nickel, lead, zinc) - Other major pollutants (NO_2, O_3, SO_2, black carbon (BC), fine particles with an aerodynamic diameter < 10 µm (Particle Matter, PM10) and 2.5 µm (PM2.5)	Interpolated concentrations - Pollutants of agricultural origin (NH_3 and modelled loads of herbicides, insecticides, fungicides, all pesticides) - Other major pollutants (NO_2, O_3, SO_2, black carbon (BC), fine particles with an aerodynamic diameter < 10 µm (Particle Matter, PM10) and 2.5 µm (PM2.5)	idem
Forest	Frequency of host tree species, % broadleaf forest cover (% BLForest), % mixed forest cover (% MixForest) in a 50m (1ha) and 200m (10ha) radius around the station	% broadleaf forest cover (%BLForest), % mixed forest cover (%MixForest) per pixel	idem

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For each pollutant, we computed annual mean and maximum concentrations for the same period of time as the floristic data, i.e., 2016–2020. These pollutants included heavy metals (arsenic, cadmium, chromium, nickel, lead, zinc) and other major pollutants (SO2, NO2, O3, PM_{10} and $PM_{2.5}$). Climatic data included annual mean air temperature, annual range of air temperature, annual total precipitation, mean relative humidity of the driest month, annual range of solar radiation, derived from CHELSA 1.2 (Karger et al., 2017, 2018) at 30 arc-second (~1 km) resolution for the 1981–2010 time period. Topographic data included elevation, northness and slope at 30 arc-second resolution from Amatulli et al. (2018). Vegetation data included species identity of the 20 selected trees, as well as % forest cover, % broadleaf forest cover, % mixed forest cover in a 50m (1ha) and 200m (10ha) radius around the station, retrieved from Bolyn et al. (2022). Altogether, dataset 1included 37 variables (appendix 1).

Dataset 2included complete inventories of all epiphytic bryophyte species recorded between 2016 and 2020 in 43 pixels of 16 km^2 (Hutsemekers et al., 2023), background environmental factors, and air pollutant concentrations. Background environmental factors also included percentages of broadleaf forest cover (%BLForest) and of mixed forest cover (%MixForest) per pixel. These variables at 30 arc-second resolution were averaged to 16 km^2 resolution using the raster package (Hijmans, 2024) in R 4.2.1. Pollutants included major pollutants (SO2, NO2, O3, PM10 and PM2.5) as well as pollutants of agricultural origin. Concentrations of the major pollutants were obtained for each pixel of 16 km^2 resolution by interpolation. The interpolation was performed using the RIO model based on land use, a semivariogram based on the distances to the nearest measuring stations and the levels of air pollution, which was employed to compute, on an hourly basis, the background concentrations at the centroid of all the investigated pixels. Pollutants of agricultural origin included NH_3, which originates at >90 % from agriculture in the study area (Regional Air Pollutant Inventories, 2023), but to which traffic emissions also contribute (Cape et al., 2004; Manninen et al., 2023) and pesticides. NH_3 was measured at 32 passive samplers during the peak season of fertilizer spreading (between mid-April and mid-May 2021) and interpolated using a simple inverse distance weighting method. Data for pesticides included estimated amounts of total active ingredients (in kg/ha/year) for herbicides, insecticides, fungicides and all active substances (composed of herbicides, insecticides, fungicides and growth regulators) across the period 2015–2017 (Habran et al., 2022). These estimates were obtained by quantifying the amount of pesticides yearly applied to particular crops based on a reference sample (around 4 % of farms in southern Belgium) and then extrapolating these figures for each crop field across the area depending on crop type (Habran et al., 2022). Based on these estimated application loads per crop field, we derived mean and maximum values for each 16 km^2 pixel. Heavy metals, which are characterized by limited airborne spread (Kovacik et al., 2023) and whose concentrations cannot be interpolated, were excluded from this analysis. Altogether, dataset 2included 30 variables (appendix 2).

Dataset 3 included occurrence data for 51 strict epiphytic bryophyte species recorded after 2016 from the atlas of bryophyte species distributions in southern Belgium (Sotiaux and Vanderpoorten, 2015, updated in www.Biogeonet.ulg.ac.be) across 633 pixels of 16 km^2 and the same set of pollutants and environmental factors as in Dataset 2.

DATA ANALYSIS

Variation partitioning, as implemented by the varpart function of the vegan package (Oksanen et al., 2022), was used to disentangle the role of pollution loads from that of background environmental factors on the composition of bryophyte communities (Q1). For dataset 1, the Y matrix included species frequencies across 20 nearest phorophytes to the measuring stations. We also implemented a second analysis where species frequencies were converted into presence/absence data to assess the relevance of frequency vs presence-absence data in such analyses. Predictor matrices included heavy metals (X1), other major pollutants (X2) and background environmental factors (X3) listed in Table 1. To reduce the number of predictors and avoid multicollinearity, a Principal Component Analysis (PCA) was performed to summarize the information included within each of the three predictor matrices. For each PCA, the first two axes were retained. For Dataset 2, the Y matrix included species presence/absence per 16 km^2 pixel. Predictor matrices included interpolated concentrations of pollutants of agricultural origin (X1), other major pollutants (X2) and background environmental factors (X3) listed in Table 1. To visualize how species respond to these factors, we presented the species x environment plots of the Redundancy Analyses (RDA) underlaying the variation partitioning analyses for both datasets. To help interpreting the gradients in species composition, species scores on the first two RDA axes were correlated with species ecological traits, including ecological indicator values and species habitat preference (van Zuijlen et al., 2023). Ecological indicator values included light (indL), temperature (indT), continentality (indK), moisture (indF), acidity (indR), nutrient availability (indN), as well as an additional indicator value for heavy metals (indHM). Habitat preference traits included whether species are classified as epiphytes, epixylic (on rocks), how strongly species are bound to forest habitats (forest), and hemeroby, i.e., whether a species is largely restricted to close-to-nature habitats, largely restricted to man-made

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habitats, or indifferent.

To determine which factors account for variations in species distribution patterns (Q2), we implemented the embedded covariate selection procedure of Adde et al. (2023). Based on three algorithms (Generalized Linear Model (GLM), Generalized Additive Model (GAM) and Random Forest), the embedded covariate selection procedure was used to identify the best predictors of each of 51 strict epiphytes (dataset 3) among 30 predictors at 16 km^2 resolution. We implemented this analysis for each species in two ways: (i) keeping only variables jointly selected by the three algorithms, and (ii) fixing the total number of variables in the model to 4. This number of four variables was determined, based on the rule-of-thumb according to which the addition of a variable in a model requires the addition of >10 observations (Peduzzi et al., 1996; Harrell et al., 1996), to the size of the datasets with the lowest numbers of occurrences. We then assessed the importance of each variable as a function of the proportion of models, in which it was included, weighted by its ranking during the selection procedure. For the analysis consistently keeping the four best variables, the first variable to be selected had a weight of 1, the second variable a weight of 0.75, 0.5 for the third variable, 0.25 for the fourth and 0 for the variables that have not been selected. The variable importance corresponded to the sum of its weights across species. For the analyses retaining the variables selected by all three algorithms, the number of variables retained varied among species, and the weight was thus rescaled between 0 and 1 depending on the number of variables selected (total number of selected variables – variable rank + 1/total number of selected variables). To help visualizing and interpreting the results, and in particular, take the correlation among variables into account, we computed the correlation among variables and generated a dendrogram of similarity using Ward's algorithm (Murtagh and Legendre, 2014).

Results

Background environmental conditions, measured concentrations of heavy metals and other major pollutants uniquely accounted for 30 %, 1 % and 9 %, respectively, of the total explained variance in epiphytic bryophyte species frequencies at the level of air pollution measuring stations (dataset 1) (Fig. 1a). When species presence-absence instead of frequencies were employed as dependent variables, these proportions dropped to 8 %, <1 % and 3 %, respectively (Fig. 1b). At the level of 16 km^2 pixels (dataset 2), background environmental conditions, interpolated concentrations in pollutants of agricultural origin and other major pollutants uniquely accounted for 7 %, <1 % and 2 %, respectively, of the total explained variance in species composition (Fig. 1c).

The results of the Redundancy Analyses between epiphytic bryophyte community composition, air pollution and background environmental factors using datasets 1and 2 are displayed in Fig. 2. In both analyses, the main gradient involved a shift from forest oligotrophic specialist epiphytes (e.g., *Frullania tamarisci, Tetraphis pellucida*) to nitrophilous (*Syntrichia* spp., *Orthotrichum diaphanum*), primarily epi- xylic species (*Grimmia pulvinata*, *Tortula muralis*) (see Fig. S1 for the correlation between species ecological traits and their scores on the RDA axes).

The results of the embedded covariate selection procedure determining the importance of individual variables accounting for species distributions (dataset 3) yielded similar results when keeping the four best variables per model (Fig. 3) vs all the variables consistently selected by the three algorithms per model (Fig. S2). The three first most important variables were maximum O_3 concentrations, mixed forest cover, and elevation. These variables belonged to a cluster of highly correlated variables that, except for O3, characterize background environmental conditions. The fourth most important variable was mean annual temperature. Mean annual temperature belonged to a cluster of highly correlated variables that mostly included major air pollutants. The fifth most important variable was NH_3, which belonged to a group of correlated pollutants of agricultural origin (group3).

Discussion

The results from different datasets at different spatial resolutions and based on different analytical approaches congruently evidence that current epiphytic bryophyte distribution patterns in southern Belgium are, in an increasing order of importance, explained by heavy metals and pollutants of agricultural origin, then by other major pollutants, and finally by background environmental factors. While the importance of macroclimatic variation on species distribution patterns is indeed expected to increase with spatial extent (Siefert et al., 2012), change in air pollutant concentrations has been, in the course of the past decades, the major factor of the temporal variation of epiphytic bryophyte community composition at regional scales (Pescott et al., 2015). This change was such, that the temporal shift in species composition has been, on average, more than twice larger than the spatial change in species composition observed today

(Hutsemekers et al., 2023). The larger role played by background environmental factors over air pollution reported here thus points to the efficiency of air pollution reduction policies and their impact on biodiversity patterns, even for such highly sensitive organisms as epiphytic bryophytes. This pattern is consistent with previous reports on the partitioning of environmental drivers of lichen species composition at a regional scale, highlighting the role of climatic variation over air pollution loads (Ellis and Coppins, 2010). Several studies reported, however, departures from this pattern. Concentrations in major air pollutants still significantly impact epiphytes in large cities (Rocha et al., 2022; Sebald et al., 2022) and in central Europe (Prochazkova et al., 2025), highlighting that, despite ongoing overall improvements in air quality, current EU standards are still not met across Europe (European Environment Agency, 2024).

SO_x and NO_x, which have driven the spectacular shifts in species composition in the course of the past decades (Hutsemekers et al., 2023), marginally contributed to explain spatial variation in community composition and distribution, suggesting that these pollutants reached concentrations levels below critical levels for epiphytic floras. In fact, SO_2 concentrations between 2015 and 2020 reached, on average across the study area, 1 µg/m^3, i.e., well-below the concentrations shown to impact bryophytes and lichens (Lee et al., 1998; Bates et al., 1996). In urban epiphytic lichens, the contribution of contemporary concentrations of SO_2 to current patterns of diversity and composition was similarly shown to be minimal (Sebald et al., 2022). Regarding NO_x, the shift from species with low to high (*Syntrichia* spp., *Orthotrichum diaphanum*) nitrogen preference along the main pollution gradient retrieved here is, at first sight, consistent with similar trends reported in epiphytic lichens (Ellis and Coppins, 2009) and non-epiphytic bryophytes (Pakeman et al., 2022), and with previous reports on the impact of NO2 on the composition of epiphytic communities in urban environments (Sebald et al., 2022). In the context of decreasing NO_2 pollution, and given that shifts in species composition also involved a shift towards species with high pH preferences, whereas NO_2 deposition leads to substrate acidification however, this trend is puzzling. One interpretation is that other N sources than NO_2 have played a role in the increase of nitrophilous species.

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Fig. 1. *Venn diagrams of the variation partitioning analysis between epiphytic bryophyte species composition, air pollutant concentrations and background environmental factors. (a). Species frequencies at 20 trees surrounding the measuring stations vs measured concentrations of heavy metals (X1), other major pollutants (X2, including SO_2, NO_2, O_3, PMs), and background environmental factors (X3, including topography, climate, vegetation). (b). idem, but with species frequencies converted into presence/absence. (c). Species presence/absence at 43 pixels of 16 km^2 vs interpolated measured concentrations of pollutants of agricultural origin (X1, including NH_3, herbicides, insecticides, fungicides), other major pollutants (X2), and background environmental factors (X3).*

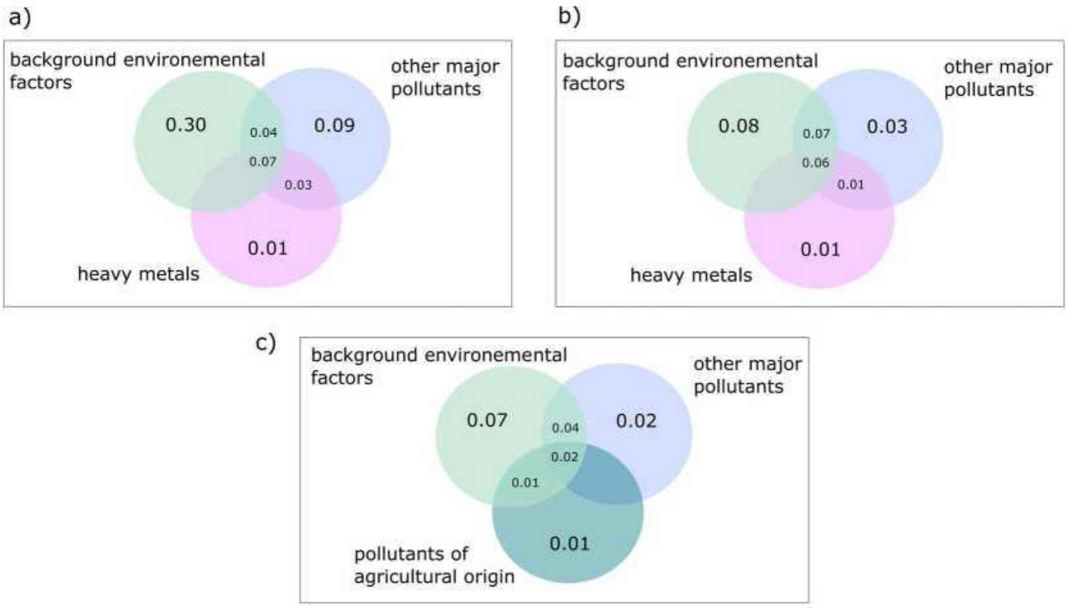

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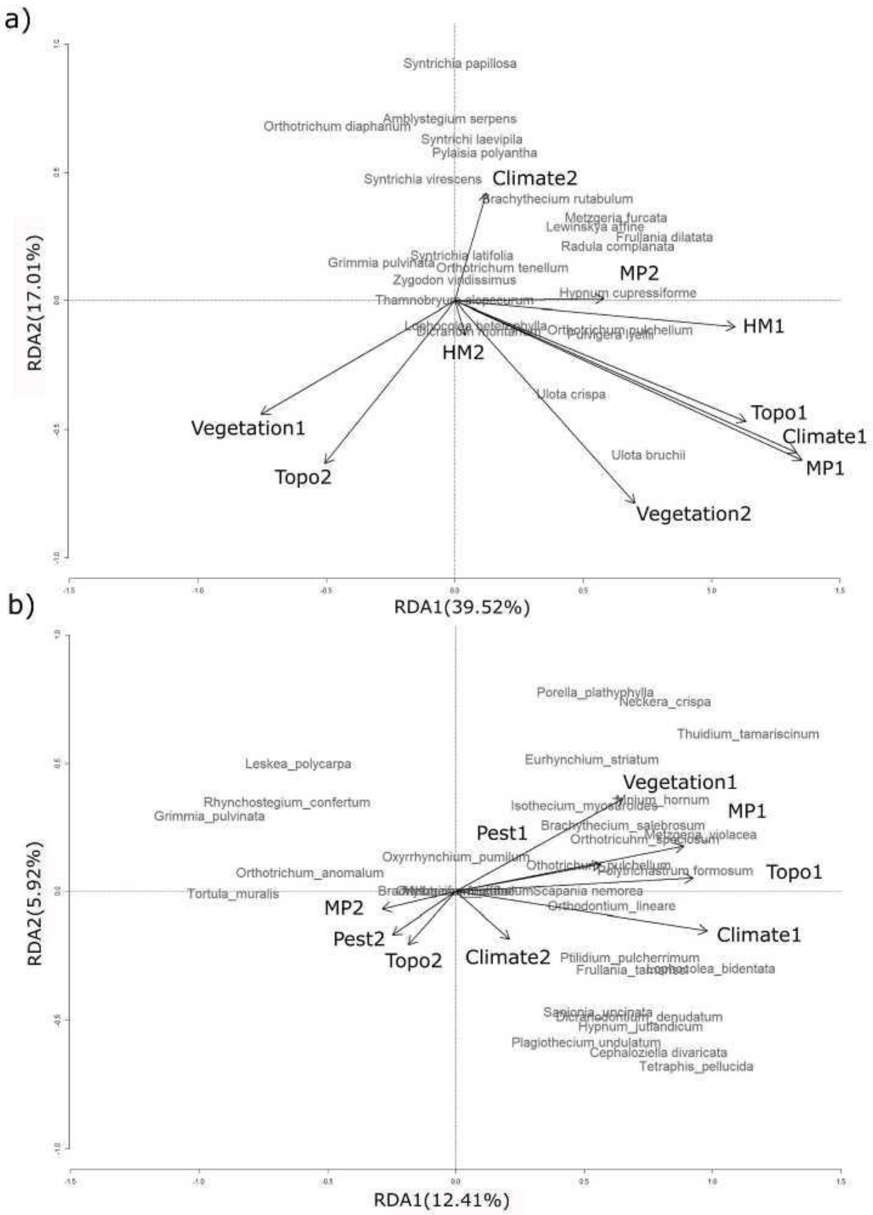
Fig. 2. *Redundancy analysis of the variation in epiphytic bryophyte community composition, background environmental variables and air pollutant concentrations. (a). Species frequencies at 20 trees surrounding the measuring stations vs measured concentrations of heavy metals (arsenic, cadmium, chromium, nickel, lead, zinc, summarized by the first two axes of their principal component analysis, labelled as HM1 and 2), other major pollutants (SO_2, NO_2, O_3, Particle Matters, summarized by the first two axes of their principal component analysis, labelled as MP1 and 2), and background environmental factors (topography, climate, vegetation). (b). Species presence/absence at 43 pixels of 16 km^2 vs interpolated measured concentrations of pollutants of agricultural origin (NH_3, herbicides, insecticides, fungicides, all pesticides, summarized by the first two axes of their principal component analysis, labelled as PEST1 and 2), other major pollutants (see above), and background environmental factors.*



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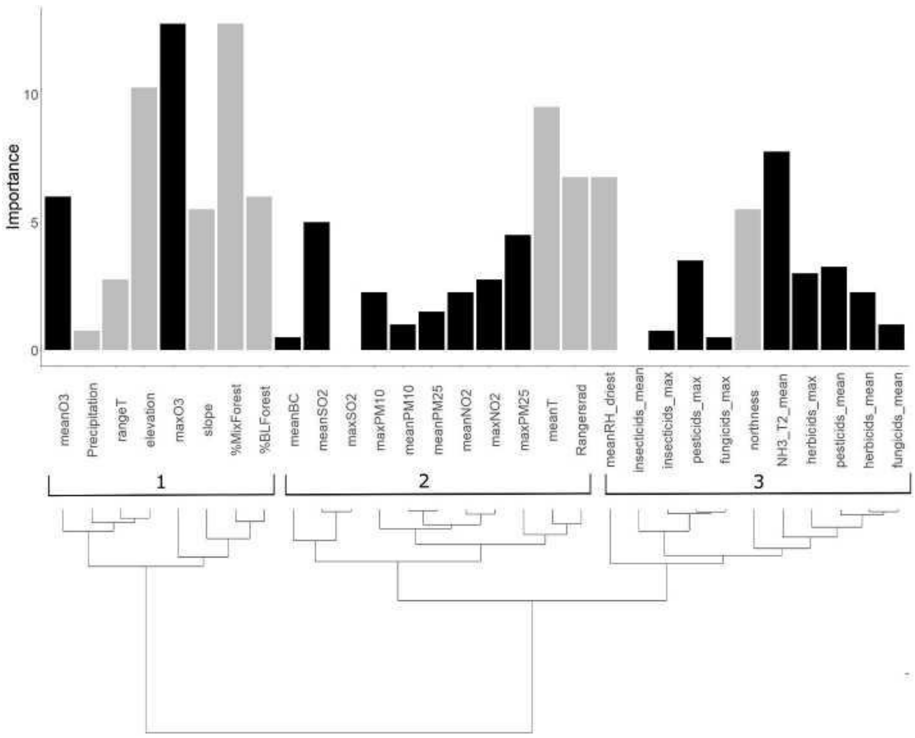
In particular, NH_3 was the fifth most important variable and second pollutant in terms of predictor of species occurrences. Experimental evidence in fens exposed to different sources of N pollution suggests that NHy impacts bryophyte vegetation much more severely than NOx. NHy may have both direct and indirect effects on epiphytic bryophytes communities. Indirect effects would result from increased competition due to eutrophication. On trees, fast spreading, thick mats of colonies formed by dendroid growth forms, such as *Isothecium*, whose creeping primary shoots rapidly spread over the surface and whose erect secondary shoots overarch underlying species, are considered as typical examples of effective competitors (Peck & Frelich, 2008).

Fig. 3. *Importance of environmental variables (black: air pollutants, grey: background environmental conditions, see Table 1 for abbreviations) accounting for the distribution of strictly epiphytic bryophytes in southern Belgium. The importance of each variable is a function of the proportion of models, in which it was included by the embedded covariate selection (keeping the four best variables per model), weighted by its ranking during the selection procedure. The panel below is a dendrogram of similarity among variables based on the correlation coefficient among variables and using Ward's algorithm as the clustering criterion.*



The role of competition among bryophyte communities has, however, remained an area of controversy (Ma et al., 2024, and references therein). Co-occurrence analyses suggested that, in epiphytic communities, biotic interactions play a secondary role as compared to environmental filtering, with a very marginal contribution of competitive exclusion (Shen et al., 2023), supporting the notion that competitive exclusion is a rare process in bryophyte communities (Steel et al., 2004; Malson & Rydin, 2009; Udd et al., 2016).

Direct effects of NHy, which accumulates beyond the N-saturation point, include impacts on photosynthesis performance and C fixation, uptake regulation of P and K, and oxidative stress, causing the production of reactive oxygen species whose accumulation can lead to the deterioration of cell membranes (Izquieta-Rojano et al., 2018). In addition, NH3 deposition results in an increase of bark pH (Van Herk, 2001; Manninen et al., 2023), resulting in a decrease of the acidophilous lichen flora (Manninen et al., 2023; Gauslaa, 2024) and most likely contributing to the decrease of the acidophilous bryophyte flora over the past decades (Hutsemekers et al., 2023). The increase of bark pH due to NH3 pollution could explain the observed trend for calciphilous epixylic species typically found on concrete (e.g., *Grimmia pulvinata*, *Orthotrichum anomalum*, *Tortula muralis*) to grow as epiphytes in the most polluted areas. Altogether, bark pH and NHy concentration in the stemflow therefore appeared as the main drivers of the regional variation in epiphytic bryophyte and lichen communities (Mitchell et al., 2005).

Among pollutants whose variations in concentrations best correlated with epiphytic bryophyte species distributions, ozone was identified as the most important one. O_3 is a strong oxidizing agent that damages plant internal structure and impacts physiological functions, accelerating senescence and decreasing photosynthesis (see Zhao et al., 2020 and references therein). The substantial increase of O3 since the pre-industrial era (Young et al., 2013) is such, that current concentrations are sufficiently high to impact crop yield (Du et al., 2024) and forest primary production (Sorrentino et al., 2025). In bryophytes, reduction of photosynthetic activity and membrane leakage was reported in four of 22 species exposed to concentrations of 300 µg/m^3 (Lee et al., 1998), which are almost in the range of the maxima currently recorded in southern Belgium. The ecophysiological impact of O_3 on cryptogamic epiphytes remains, however, poorly known (Ellis and Coppins, 2009). In addition, the fact that O_3 concentrations are higher in rural than urban areas (Paoletti et al., 2014), together with the fact that O_3 concentrations were highly correlated with background environmental factors, and not with other pollutants, suggests that O_3 may actually be interpreted as a land-use marker rather than a factor actually impacting epiphytic floras. This suggests that the contribution of air pollutants as compared to that of other background environmental factors reported above may even be overestimated.

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Among other investigated pollutants, pesticides, whose impact on ecosystems has been widely acknowledged (Albaseer et al., 2025 and references therein), marginally contributed to explain variations in epiphytic bryophyte community composition and species distributions. Several herbicides, some of which are specifically used against bryophyte development in, e.g., golf courses (Fausey, 2003; Post et al., 2016), have an effective impact on bryophyte ecophysiology. For example, bryophytes suffer detrimental effects after exposure to widely used herbicides such as asulam at concentrations similar to those that affect bracken, against which they are implemented (Rowntree et al., 2003). The response of bryophytes varies, however, among species and depending on the kind of pesticide implemented (Newmaster et al., 1999; Rowntree et al., 2003; Rowntree et al., 2005; Fuselier and Carreiro, 2022). Detailed information on pesticide concentrations in the air, as well as further experimental investigations on the impact of pesticides on bryophyte ecophysiology, would be necessary for a more accurate evaluation of the impact of pesticides on bryophyte floras.

Another family of pollutants whose impact was not revealed by the present analyses are heavy metals. In contrast to angiosperms, which tend to develop specialized tolerant strains, bryophytes tend to exhibit 'all-purpose' genotypes and a high intrinsic tolerance to metals through physiological acclimatization (Shaw, 2000). Mounting evidence points to the role played by metabolites such as allantoin, which have increasingly been identified as important mediators of stress, enhancing tolerance to metals (Dresler et al., 2023). Nevertheless, the limited amount of data on heavy metals in the present study due to the impossibility to accurately interpolate their concentrations in the air, calls for further research on their potential impact.

Substantial variations in species composition along a gradient of air pollution were retrieved here, with a shift from oligotrophic assemblages comprised of true epiphytes to eutrophic assemblages comprised of generalist species. This supports the notion that individual species exhibit different 'indicator values' for air pollution, underlaying the implementation of air-monitoring schemes that have been widely developed to survey spatio-temporal changes in air quality (Zechmeister et al., 2007; Sergio et al., 2016; Jiang et al., 2020). There was, however, a substantial drop of the percent explained variance of the bryophyte community when using species presence absence vs relative frequencies. Beyond actual species composition, species relative frequencies thus yield important information regarding environmental factors and should be recorded in epiphytic vegetation surveys.

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In conclusion, our survey reveals that background environmental factors prevail over air pollution to explain extant epiphytic bryophyte community composition and species distributions at a regional scale. Major pollutants such as SOx and NOx, which prevailed a few decades ago, now seem to marginally impact epiphyte floras. The impact of pesticides, which was, to our knowledge, not previously assessed on epiphyte floras, was marginal as well. Since pesticides were experimentally shown to impact bryophyte ecophysiology, we suggest that further empirical studies on the role of pesticides in the wild would be necessary to assess whether our findings are generalizable. Ultimately, while bryophytes have been efficiently used as biomonitors of atmospheric deposition of heavy metals (Harmens et al., 2010), they have not been the focus of long-term community composition survey programmes as vascular plants, which revealed substantial shifts in species distributions associated with global environmental change in general and N deposition in particular (Sanczuk et al., 2024). Given the extreme sensitivity of bryophytes to air pollution and climate change, we suggest that a network of permanent plots surveyed on a regular basis, following standardized protocols across a range of geographical regions and habitats (e.g., Cateau et al., 2024), should be implemented to disentangle the role played by individual drivers of global change on biodiversity patterns.

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CREDIT AUTHORSHIP CONTRIBUTION STATEMENT

Lea Mouton: Writing - review & editing, Methodology, Formal analysis, Data curation, Conceptualization.

Virginie Hutsemekers: Validation, Data curation.

Flavien Collart: Methodology, Formal analysis.

Alain Vanderpoorten: Writing - review & editing, Supervision, Conceptualization.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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SUPPLEMENTARY DATA

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