

RESEARCH ARTICLE

Disentangling climate change from air pollution effects on epiphytic bryophytes

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Abstract

At the interface between atmosphere and vegetation, epiphytic floras have been largely used as indicators of air quality. The recovery of epiphytes from high levels of SO₂ pollution has resulted in major range changes, whose interpretation has, however, been challenged by concomitant variation in other pollutants as well as climate change. Here, we combine historical and contemporary information on epiphytic bryophyte species distributions, climatic conditions, and pollution loads since the 1980s in southern Belgium to disentangle the relative impact of climate change and air pollution on temporal shifts in species composition. The relationship between the temporal variation of species composition, climatic conditions, SO₂, NO₂, O₃, and fine particle concentrations, was analyzed by variation partitioning. The temporal shift in species composition was such, that it was, on average, more than twice larger than the change in species composition observed today among communities scattered across the study area. The main driver, contributing to 38% of this temporal shift in species composition, was the variation of air quality. Climate change alone did not contribute to the substantial compositional shifts in epiphytic bryophyte communities in the course of the last 40 years. As a consequence of the substantial drop of N and S loads over the last decades, present-day variations of epiphytic floras were, however, better explained by the spatial variation of climatic conditions than by extant pollution loads. The lack of any signature of recolonization delays of formerly polluted areas in the composition of modern floras suggests that epiphytic bryophytes efficiently disperse at the landscape scale. We suggest that a monitoring of epiphyte communities at 10-year intervals would be desirable to assess the impact of raising pollution sources, and especially pesticides, whose impact on bryophytes remains poorly documented.

KEYWORDS

air quality, ammonia, bryophytes, climate change, epiphytes, fine particles, nitrogen oxides, ozone, sulfur dioxide

1 | INTRODUCTION

Since the beginning of the industrial era, terrestrial ecosystems have experienced anthropogenic disturbance, involving complex factors such as land use changes, pervasive levels of air pollution from fossil fuel combustion, and climate change. Disentangling how these factors, or the combination thereof, affect ecosystem functioning and diversity remains, however, challenging (Esseen et al., 2022; Mathias & Thomas, 2018; Suleiman et al., 2022).

Anthropogenic emissions of the main air pollutants, including oxidized (NO_x) and reduced (NHy) forms of nitrogen, fine particulate matter, and sulfur oxides (SO_x), contribute to air quality problems, with damaging effects on human health, vegetation, and ecosystems (Bobbink et al., 2010; Castellanos & Boersma, 2012; Hilboll et al., 2013; Stern, 2005).

In Europe, changes in fuel usage and combustion technology, as well as commitments to reducing air pollution under the Convention on Long-Range Transboundary Air Pollution (1979) and, subsequently, the European Union National Emissions Ceiling Directive (Directive 2001/81/EC), have resulted in a substantial decline of SO_2 concentrations following a peak in the late 1980s (Stern, 2005) and, subsequently, of NO_x concentrations in the late 1990s (Castellanos & Boersma, 2012; Hilboll et al., 2013). NHy deposition, which mostly originates from fertilizer and manure and thus peak in rural areas, experienced a less sharp decrease (about 20% since the 1980s in the UK, Pescott et al., 2015) and even increased in some areas, potentially offsetting the benefits of NO_x deposition reduction (Tan et al., 2020).

While the spectacular forest decline in industrial countries during the 1980s and the 1990s focused the attention on the dramatic impact of acidic mists and rains (Pitelka & Raynal, 1989), the impact of global change on less obvious, but highly sensitive organisms such as cryptogams was already recognized since the 19th century, when bryophytes and lichens disappeared from the immediate vicinities of industrial areas during the Industrial Revolution (Lee et al., 1998; Pescott et al., 2015). Bryophytes are in fact the “canaries in the coal mine” for exhibiting a series of traits that make them particularly vulnerable to pollution (Slack, 2011), and hence, sensitive indicators of air quality (see Pescott et al., 2015 for review). In particular, bryophytes absorb water and nutrients directly through leaf surfaces from the immediate environment, resulting in an equilibrium with their water environment that makes them particularly susceptible to atmospheric pollution (Pescott et al., 2015). Bryophyte leaves further tend to be one-cell thick, thereby enhancing exposure to pollutants, while the absence of stomata in leaf tissues prevents the regulation of gas exchanges, especially under stress conditions (Bates, 2000). At the interface between atmosphere and vegetation, epiphytic floras are a case in point. They have, by a considerable margin, undergone the most dramatic change out of any of the groups analyzed in the United Kingdom (Pescott et al., 2015).

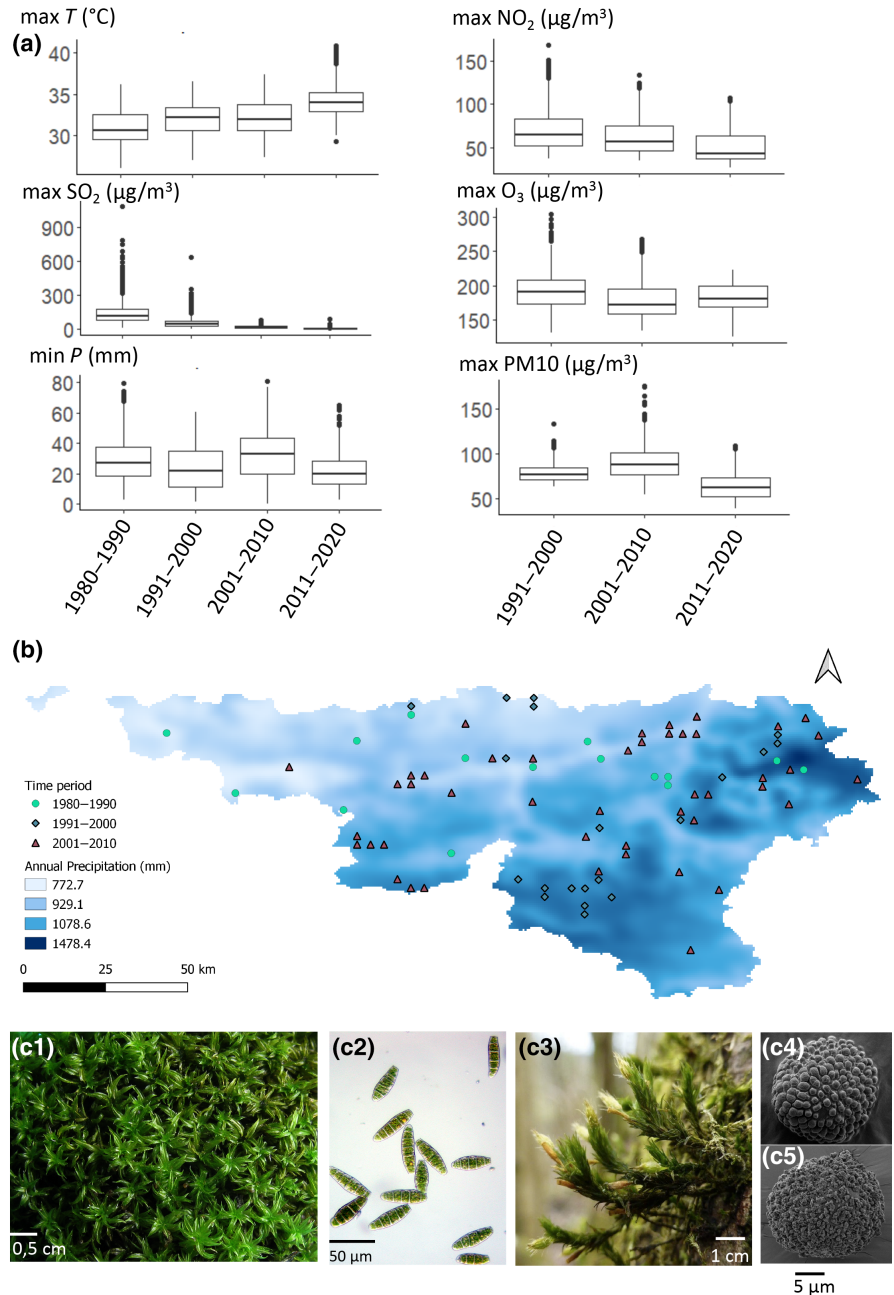
Since the 1990s, a massive back-colonization of acid-sensitive and a decline of acidophilous species have been recurrently reported (Bates et al., 1997; Duckett & Pressel, 2010; Pescott et al., 2015;

Purvis et al., 2010; Sérgio et al., 2016; Stebel & Fojcik, 2016). Identifying which factors, or combination of factors, account for this back-colonization is, however, not straightforward. In fact, changes in air quality have been largely concomitant with climate change, which is likely to affect epiphytic bryophytes in two ways. On the one hand, milder winters may benefit to species that previously had a hyper-oceanic range (e.g., *Myriocolea minutissima*, *Plenogemma phyllantha*) and that have expanded inland for the last few decades (Bates & Preston, 2011). On the other hand, bryophytes rely on atmospheric precipitation for water uptake and temperate species are highly sensitive to moderately warm temperatures (He et al., 2016). Even relatively slight temperature increase (1.5°C) and relative humidity decrease impact on growth rates and photosynthetic performance (Hao & Chu, 2021; Song et al., 2012). Many temperate species die when kept hydrated continuously at temperatures above 30°C (Furness & Grime, 1982). Although the vulnerability to climate change varies across species and habitats (Barbé et al., 2020; Hespanhol et al., 2022), increased summer temperature and drought are therefore expected to impact the composition of epiphytic communities, as suggested by dramatic projections of future species distributions under climate change in Europe (Zanatta et al., 2020).

While the relative importance of extant climate conditions and pollution loads on epiphytic bryophyte and lichen distributions has been assessed (Ellis & Coppins, 2009), disentangling the contribution of the historical variation of climatic conditions and air pollution on the observed recolonization of epiphyte floras during the last decades has been challenging. Bates and Preston (2011) concluded that “there are problems in attributing changes to climate change as opposed to other causal factors, always assuming that the changes are actually the result of single factors (rather than of interactions between factors). In particular, the recovery of epiphytes and possibly other species from high levels of SO_2 pollution, has resulted in major range changes, which may be masking the effects of climate change.”

Furthermore, the extent to which extant species composition reflects extant conditions, suggesting that species are at equilibrium with their environment or reflect past pollution loads due to delays in recolonization caused by dispersal limitations, remains to be assessed. In epiphytic lichens, historical (19th century) woodland structure significantly contributed to explain extant distribution patterns, pointing to a strong habitat specialization and a time lag between changes in habitat conditions and extant species distributions caused by dispersal limitations (Ellis & Coppins, 2009). Bryophytes disperse by spores and specialized vegetative diaspores (Figure 1c), which exhibit high long-distance dispersal capacities (see Patiño & Vanderpoorten, 2018 for review). This is especially true for epiphytes, which need to track patches of suitable trees in a dynamic landscape for persistence (Snäll et al., 2005). Despite this, epiphytic bryophyte distributions are typically clustered (Löbel et al., 2006a, 2006b) and some exhibit strong fine-scale genetic structures (Snäll et al., 2004), pointing to dispersal limitations. This raises the question whether current epiphytic bryophyte distributions reflect current patterns in air quality and climatic conditions or are still constrained by past pollution events.

FIGURE 1 Spatiotemporal variation of the epiphytic bryophyte flora, climatic conditions, and air pollution in southern Belgium. (a) Boxplots (showing the first and third quartiles (upper and lower bounds), second quartile (center), 1.5* interquartile range (whiskers), and minima–maxima beyond the whiskers) of the spatiotemporal variation of annual maximal temperature (max T), minimum precipitation (min P), and maximum air pollutant loads (max NO_2 , SO_2 , O_3 , particle matter with an aerodynamic diameter smaller than $10\ \mu\text{m}$ PM_{10}) across 81 $16\ \text{km}^2$ pixels in southern Belgium per decade (see [Figure S1](#) for annual average variations). (b) Map of the survey area, location, and decade of first survey of epiphytic bryophytes in the 81 $16\ \text{km}^2$ selected pixels. (c). Epiphytic mosses: *Zygodon conoideus* (c1) and its vegetative gemmae (c2); *Lewinskya speciosa* (c3); spores of *Ulota bruchii* (c4); and *Syntrichia laevipila* (c5). c1. photo A. Mora. c2–3 photo A. Sotiaux. c4–5 photo M. De Haan.



Here, we take advantage of the availability of epiphytic bryophyte species distributions, climatic data, and an air pollution monitoring program since the 1980s in southern Belgium to characterize temporal shifts in species frequencies and community composition in the epiphytic bryophyte flora. In particular, we assess whether (i) shifts involve a decrease of the acidophilous flora and an increase of the nitrophilous flora (Q1a) and (ii) changes in species composition have been more important within the same community through time, as a response to environmental change, or among communities under present conditions due to the spatial variation of environmental conditions (Q1b). We then disentangle the relative impact of climate change and temporal variation of air pollution on temporal shifts in species composition (Q2). We finally determine the relative contribution of past and present climatic conditions and pollution

loads on present patterns of species composition to assess whether species distributions are at equilibrium with present conditions or reflect past conditions, pointing to a recolonization delay (Q3).

2 | METHODS

2.1 | Study area and data collection

This study took place in southern Belgium, thanks to the availability of spatiotemporal data of air quality and climatic conditions, and of complete floristic inventories of the bryophyte flora since the 1980s. The atlas of bryophyte species distributions in southern Belgium (Sotiaux & Vanderpoorten, 2015) originated from the systematic

survey, during two complete days at different seasons to take potential phenological differences into account and by the same team of three recorders, of all 1139 pixels of 16 km² constitutive of the area. In the framework of the present study, we resurveyed 81 of those pixels between 2016 and 2020 using the same protocol (Figure 1b). Initially, we focused on pixels that include one of the 23 stations of the network of measuring stations of air quality in southern Belgium. We then extended the sampling to 81 pixels, selecting additional pixels to maximize the spatial cover of the study area and have comparable numbers of pixels surveyed before and after 2000 ($n=36$ and 45, respectively).

Epiphytes were recorded up to 2.5 m, which, in temperate forests, is sufficient to capture the bulk of epiphytic bryophyte diversity. Boch et al. (2013) in fact reported that, after thorough plot sampling, only 4% of the bryophyte species were overlooked if the tree crown was not surveyed. All analyses were based on a dataset (Hutsemékers et al., 2022) documenting the distribution of 51 species (nomenclature of Hodgetts et al., 2020), which are either strict epiphytes or are preferentially found on living trees in southern Belgium, in the 81 selected pixels.

Data on the variation of air pollutant concentrations through time were obtained for NO₂, SO₂, O₃, and fine particles (Particle Matter, hereafter PM) with an aerodynamic diameter smaller than 10 μm (PM₁₀), which are among the major pollutants in southern Belgium. Data have been collected across the area since 1980 for SO₂, since 1990 for NO₂ and O₃, and since 1996 for PM₁₀, and stored by the Belgian Interregional Environment Agency (IRCEL–CELINE). These data have been recorded hourly from the 23 measuring stations in southern Belgium, complemented by data from an additional 73, 18, 26, and 51 measuring stations of the Belgian official network (thus including stations from the Brussels area and Flanders) for NO₂, SO₂, O₃, and PM₁₀, respectively. These data served to calibrate the RIO model. RIO is an interpolation 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. Based on the interpolated data, the maximum hourly concentration and annual average concentration of each pollutant were computed every year for each pixel. For NH₃, only concentrations recorded by 32 passive samplers were available between mid-April and mid-May 2021, that is, during the peak season of fertilizer spreading in the area. Using a simple inverse distance weighting method, we interpolated these data to generate values at each of the 81 pixels.

Climatic data were provided daily since 1980 at the centroid of each pixel by the Royal Meteorological Institute of Belgium (RMI). Precipitations were recorded daily from the manual rain gauges of the climatological network and from the automatic rain gauges from the RMI network of automatic weather stations. Temperature data include daily extreme observations from the climatological network and from the RMI network of automatic weather stations at 10' intervals. These data are subsequently spatially interpolated by kriging methods, taking geographic distance, elevation, and remote

sensing data into account (<https://opendata.meteo.be>). These daily data served to compute total annual precipitation, minimum precipitation of the driest month and maximum precipitation of the wettest month, average annual temperature, annual maximum temperature of the warmest month, and annual minimum temperature of the coldest month.

All air pollution loads and climatic data are available from Hutsemékers et al. (2022).

2.2 | Data analysis

To summarize the temporal variation of species frequencies, we computed species frequencies for three time periods (i.e., 1980–1999, $n=36$; 2000–2015, $n=45$; 2016 to present, i.e., the present re-survey, $n=81$), as the number of occupied pixels divided by the number of pixels surveyed during that time period. To visualize whether the observed temporal changes of species frequencies involve a decrease in acidophilous species and an increase in nitrophilous species (Q1a), we characterized the observed changes in species frequencies by shifts in the proportions of acid-sensitive to acidophilous species and N-sensitive to nitrophilous species, as defined by species Ellenberg indicator values (Hill et al., 2007 with updates for N from Simmel et al., 2021). We thus computed, for each time period, the proportion of species depending on their Ellenberg indicator values for pH (indR, ranging in the southern Belgian flora from acid (3) to strongly basic (7)) and the proportion of species depending on their Ellenberg indicator values for N (indN, ranging from infertile (2) to richly fertile (8)) substrates.

Differences among epiphytic communities within the same pixel at two time periods (temporal variation between the initial survey and the resurvey) and between pairs of pixels under present conditions (spatial variation based on resurvey between 2016 and 2020) were characterized by beta diversity. Beta diversity can be split into two components reflecting different phenomena (Baselga, 2010). Nestedness occurs when the poorest assemblages are subsets of the richest assemblages, reflecting the orderly loss (or gain) of species that may occur, for example, along chronosequences due to dispersal limitations or changes in environmental conditions. Species turnover reflects the replacement of some species by others among communities, which typically occurs along ecological gradients (Baselga, 2010). Here, we employed Baselga's nestedness-resultant dissimilarity (β_{sne}) and Simpson's dissimilarity index (β_{sim}) among pixel pairs:

$$\beta_{sim} = \frac{\min(b, c)}{a + \min(b, c)}$$

$$\beta_{sne} = \frac{\max(b, c) - \min(b, c)}{2a + \min(b, c) + \max(b, c)} \times \frac{a}{a + \min(b, c)}$$

where a is the number of species common to both pixels, b is the number of species that occur in the first pixel but not in the second one,

and c is the number of species that occur in the second pixel but not in the first one.

These metrics were computed with the command `beta.pair` in the R package `betapart` (Baselga et al., 2021) in R version 4.2.1. We focused on β_{sne} as a means to characterize spatiotemporal differences among pixels, because this metric best correlated with variations in air quality through time, and presented results based on β_{sim} as an appendix.

To determine whether changes in species composition have been more important within the same community through time, as a response to environmental change, or among communities under present conditions due to environmental variation at the landscape scale (Q1b), we compared the spatial differences among communities between pairs of pixels for the 2016–2020 period ($\beta_{sne-spat}$ and $\beta_{sim-spat}$) with the differences among communities from the same pixel at two time periods ($\beta_{sim-temp}$ and $\beta_{sne-temp}$). This comparison involves the inclusion of the same observation multiple times (the same species occurrences in a pixel serving to compute the pairwise $\beta_{sim-spat}$ and $\beta_{sne-spat}$ with all the other pixels), violating the assumption that the observations are independent from each other. We therefore computed, for each pixel, the average $\beta_{sim-spat}$ and $\beta_{sne-spat}$ values with all the other pixels. We thus obtained 81 comparisons, each involving the average values of $\beta_{sim-spat}$ and $\beta_{sne-spat}$ of a pixel and all the other pixels for the 2016–2020 period on the one hand, and the temporal variation ($\beta_{sim-temp}$ and $\beta_{sne-temp}$) between communities of the same pixel at the two time periods on the other. Because the distributions of average values of $\beta_{sim-spat}$ and $\beta_{sne-spat}$ significantly departed from a normal distribution (Shapiro test, $p < .001$ in both cases), we employed nonparametric paired Wilcoxon tests.

To help visualizing the spatiotemporal changes in species composition, a classical (metric) multidimensional scaling (MDS) based on the Sørensen distance matrix was performed.

To determine the extent to which temporal changes in climatic conditions and pollutant loads contributed to variations of species composition through time (Q2), we implemented variance partitioning as implemented by the `varpart` function of the `vegan` package (Oksanen et al., 2022). The dependent variable was either $\beta_{sne-temp}$ or $\beta_{sim-temp}$. Predictors included two matrices: M1 included the difference in average and maximum concentrations in O_3 , PM10, SO_2 , and NO_2 between the two time periods of floristic survey for the same pixel. M2 included the difference in minimum, maximum, and average temperature; annual precipitation; precipitation of the driest and of the wettest month between the two time periods of floristic survey for the same pixel. Because NO_2 and O_3 concentrations were available from 1990, and PM10 concentrations from 1996, the analyses were performed three times, first with all floristic data but using only SO_2 in the M1 matrix ($n=81$); second with the floristic data starting in 1990 and including SO_2 , NO_2 , and O_3 in the M1 matrix ($n=68$); and third with the floristic data starting in 1996 and including SO_2 , NO_2 , O_3 , and PM10 in the M1 matrix ($n=64$). To further disentangle the impact of the main pollutants, we repeated the analyses, using average and maximum concentrations in O_3 , SO_2 , and NO_2 as predictors.

Finally, to determine whether extant or historical variation in climatic conditions and air quality shape current species composition patterns (Q3), we implemented variation partitioning extended to several predictor matrices with the `rdacca.hp` package (Lai et al., 2022). The Y matrix documented the presence/absence of all 51 species in each pixel. X matrices included two matrices describing the climatic conditions and pollution loads, respectively, which prevailed in 1990–1994, and two matrices describing the climatic conditions and pollution loads, respectively, which prevailed in 2016–2020. Extant climatic conditions included the average annual temperature and precipitation, maximum temperature of the warmest month and minimum temperature of the coldest month between 2016 and 2020. Extant pollution loads included the annual average and hourly maximum concentrations of SO_2 , NO_2 , and O_3 between 2016 and 2020. Past climatic conditions and pollution loads involved the average annual temperature and precipitation, maximum temperature of the warmest month and minimum temperature of the coldest month, annual average and hourly maximum concentrations in SO_2 , NO_2 , and O_3 between 1990 and 1994. To analyze the impact of extant NH_3 concentrations among other pollutants, we performed a last variation partitioning analysis, using the same predictors as above, but also including average NH_3 concentrations during the Spring 2021.

3 | RESULTS

The annual maxima and average temperature, precipitation, NO_2 , O_3 , SO_2 , and PM10 concentrations at the investigated sites in southern Belgium are represented in Figure 1a and Figure S1, respectively. There was a clear trend for an increase of average temperature over the past four decades, from $8.56 \pm 1.08^\circ C$ during the 1980–1990 period to $9.86 \pm 1.14^\circ C$ after 2010 (Figure S1). Maximum temperatures followed the same trend (Figure 1a), while precipitation did not exhibit any temporal trend. SO_2 concentrations exhibited a continuous decrease, from annual average and hourly maximum concentrations of 14.1 ± 10.8 and $1083.0 \mu g/m^3$ during the 1980–1990 period to 1.1 ± 0.1 and $87.0 \mu g/m^3$ after 2010, respectively. NO_2 concentrations tended to decrease from annual average and hourly maximum concentrations of 16.7 ± 7.8 and $168.0 \mu g/m^3$ during the 1991–2000 period to 10.3 ± 5.8 and $107.5 \mu g/m^3$ after 2010, respectively. O_3 annual average concentrations increased from $45.4 \pm 7.0 \mu g/m^3$ during the 1991–2000 period to $49.8 \pm 5.8 \mu g/m^3$ after 2010, but hourly maxima exhibited the reverse trend, decreasing from $303.8 \mu g/m^3$ in 1991–2000 to $223.2 \mu g/m^3$ after 2010. Minimum, average ($\pm SD$), and maximum NH_3 average concentrations across pixels in Spring 2021 ranged between 7.71, 11.29 ± 1.31 and $16.12 \mu g/m^3$, respectively.

On average, species frequencies increased since 1980, from 0.29 ± 0.25 in 1980–1999, 0.37 ± 0.11 in 2000–2015 to 0.49 ± 0.09 in 2016–2020 (Figure 2a). These trends reflect the sharp increase in frequency for the bulk of the species (81%), while three species (*Ptychostomum moravicum*, *Ptilidium pulcherrimum*, *Sanionia uncinata*) exhibited the reverse trend, four species (*Dicranoweisia*

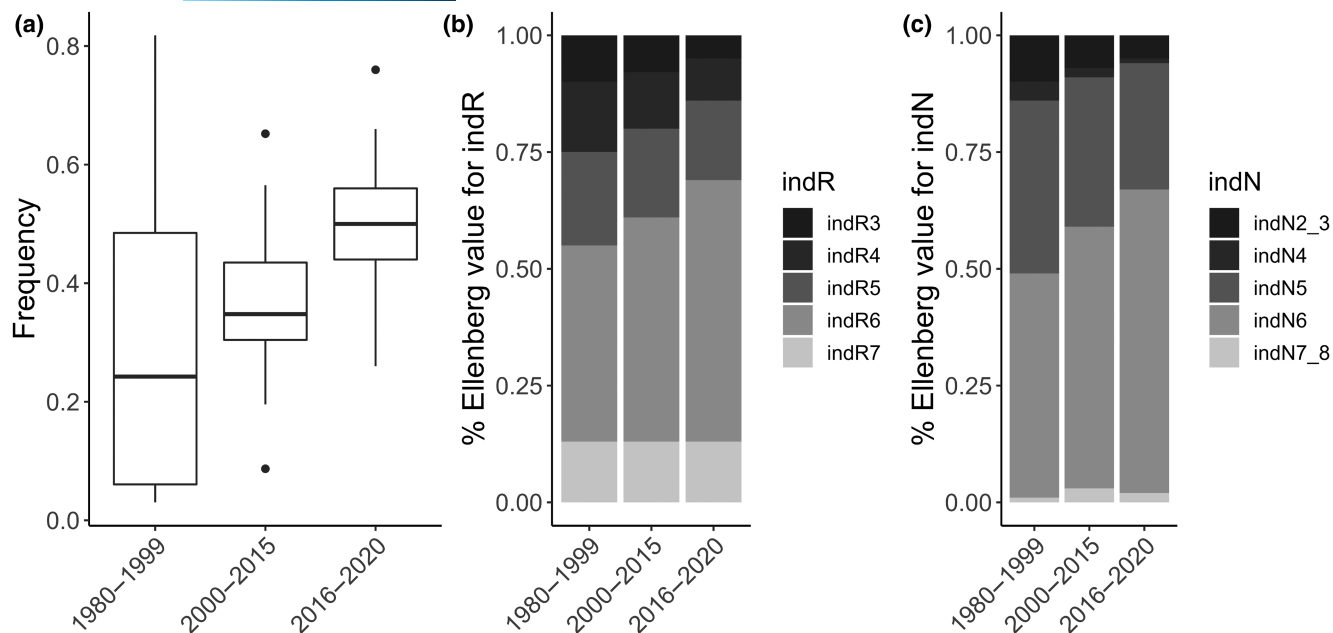


FIGURE 2 Temporal variation of (a) the frequency of epiphytic bryophyte species, (b) the proportion of species depending on their Ellenberg indicator values for pH (indR, ranging from acid (3) to strongly basic (7)) and (c) for N (indN, ranging from infertile (2) to richly fertile (8)) substrates. The frequencies are computed for three time periods (1980–1999, $n=36$; 2000–2015, $n=45$; 2016–2020, $n=81$). The boxplots (showing the first and third quartiles (upper and lower bounds), second quartile (center), 1.5* interquartile range (whiskers), and minima–maxima beyond the whiskers) show the frequencies of all 51 species (see Table S1 for species-specific trends) per time period.

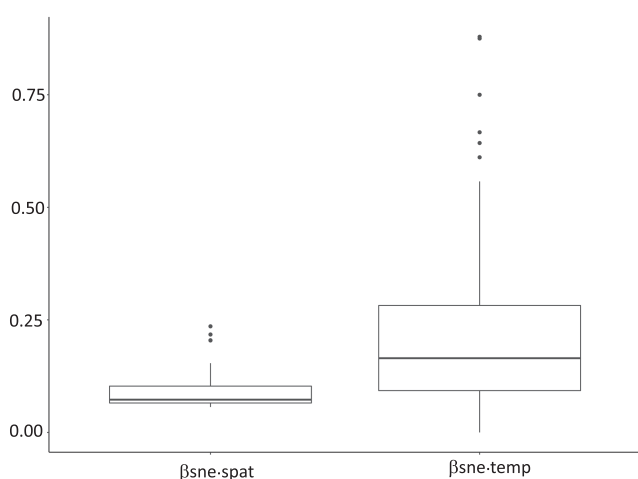


FIGURE 3 Spatiotemporal differences among communities of epiphytic bryophyte floras in southern Belgium. Boxplot (showing the first and third quartiles (upper and lower bounds), second quartile (center), 1.5* interquartile range (whiskers), and minima–maxima beyond the whiskers) represent the (spatial differences under present conditions, β sne-spat) across 81 16 km^2 pixels and the temporal variation (comparisons among assemblages of the same pixel at two time periods, β sne-temp).

cirrata, *Dicranum tauricum*, *Microlejeunea ulicina*, *Orthotrichum diaphanum*) exhibited a peak of frequency during the end of the 20th century, and the frequency of two species (*Frullania tamarsici*, *Leskea polycarpa*) did not exhibit any marked temporal trend (Table S1).

These changes in species frequencies were paralleled by shifts in the proportion of acidophilous and nitrophilous species through time. Thus, the proportions of acidophilous (Figure 2b) species decreased, while the proportions of acid-sensitive species (Figure 2b) and nitrophilous (Figure 2c) species increased.

Differences in community composition were significantly larger among communities from the same pixel through time than among communities from different pixels at present time (β sne-temp = 0.22 ± 0.19 , β sne-spat = 0.09 ± 0.08 , $p < .001$; Figure 3; see Figure S2 for differences among communities expressed as β sim).

These spatiotemporal variations among epiphytic bryophyte assemblages are illustrated by the MDS ordination of the 81 investigated 16 km^2 pixels based on a Sorensen distance matrix of their composition in epiphytic bryophytes under present and past (<2010) conditions, showing that floristic assemblages tend to segregate depending on the period of record (Figure 4). Some pixels resurveyed during the 2016–2020 period (see arrows in Figure 4), however, had coordinates, and hence, floristic compositions that were more similar to those of pixels surveyed during previous decades.

The variation partitioning analysis showed that temporal changes in air pollution loads accounted for 38% of the observed temporal differences among communities from the same pixel at different time periods (β sne-temp). Climate change did not contribute to this pattern (Figure 5a). Among pollutants, NO_2 and SO_2 together explained 25% of the variance of β sne-temp against 9% for O_3 alone (Figure 5b). Analyses based on climatic variation and SO_2 concentrations since 1980, and including PM10 after 1996, revealed the same

FIGURE 4 MDS ordination of 81 16 km² pixels in southern Belgium based on a Sorensen distance matrix of their composition in epiphytic bryophytes in 1980–1990, 1991–2000, 2001–2010, and 2016–2020. Each dot represents an individual pixel, with a color reflecting the time (decade) or record. Arrows identify the position of a specific pixel (G447) at two different time periods, the dot corresponding to the present record (in mauve) being closely located to the dot corresponding to the 2000–2009 record (in turquoise), indicating little floristic change between the two records and pointing to locally persisting high air pollution loads.

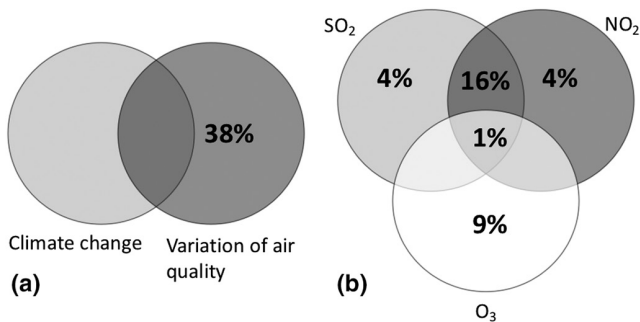
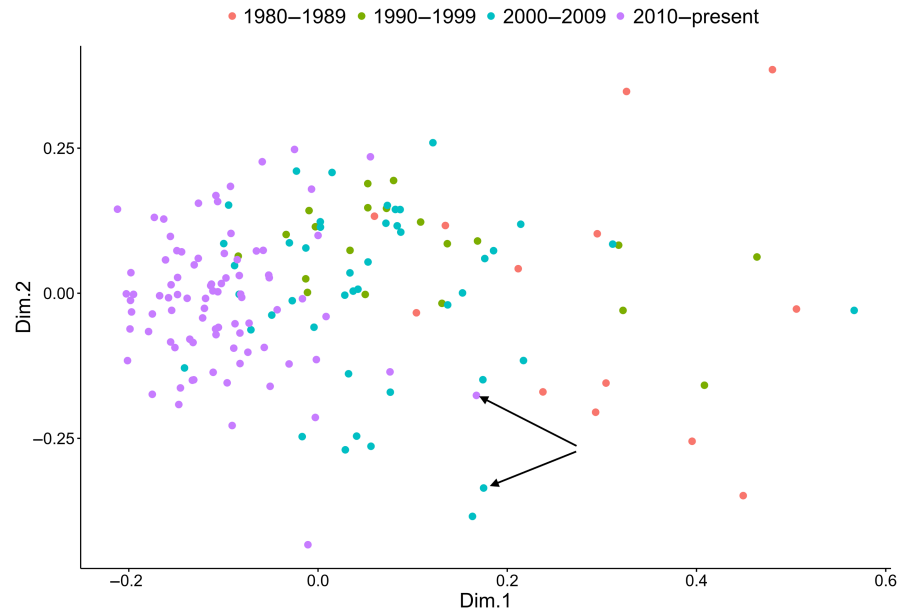


FIGURE 5 Venn diagram representing the contribution (in %variance explained) of the temporal variation in air pollutant concentrations (SO₂, NO₂, O₃) and climate change (precipitation and temperature; a) and of each pollutant individually (b) to temporal differences among epiphytic bryophyte communities (expressed as β sne-temp) since 1990 in southern Belgium.

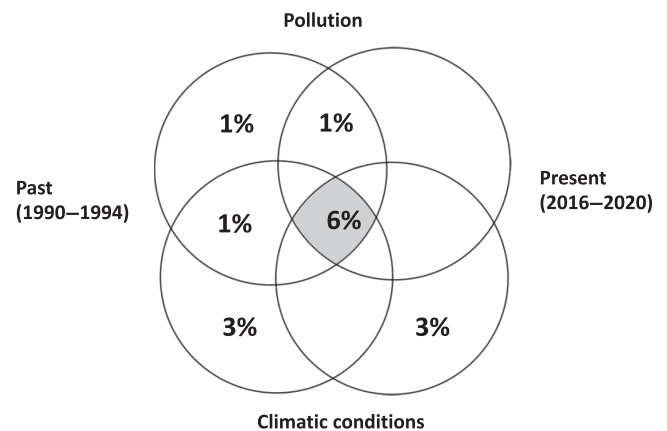


FIGURE 6 Venn diagram representing the contribution (in %variance explained) of past (1990–1994) and present (2016–2020) variation in climatic conditions (annual minimum, maximum, and average temperature *T* and precipitation *P*) and air pollutant loads (hourly maximum and average SO₂, NO₂, O₃) on the present variation of the epiphytic bryophyte species composition in 81 16 km² pixels in southern Belgium.

trend (Figures S3 and S4), although climate change and temporal changes in pollution levels jointly contributed to 7% of the variance of β sne-temp in the analysis involving SO₂ concentrations and climate change since 1980 (Figure S3). Similar trends were observed for turnover, but with a lower proportion of variance explained (Figure S3–S5).

Fifteen percent of the species composition of the present epiphytic bryophyte floras could be explained in terms of past and present climatic conditions and pollution loads. The factors that, alone, most contributed to this explained floristic variation were past (1990–1994) and present (2016–2020) climatic conditions (6%), with a marginal contribution of past pollution loads and no contribution of current pollution loads (Figure 6).

Analyses including NH₃ on extant patterns of species composition revealed that NH₃ alone marginally further contributed to the variation in species composition at 0.1%.

4 | DISCUSSION

4.1 | Temporal shifts in epiphytic bryophyte communities and their relationships with changes in climatic conditions and air pollution loads

The comparative analysis of epiphytic bryophyte floras in southern Belgium since 1980 revealed that on average, species frequencies increased from 0.29 ± 0.25 in 1980–1999, 0.37 ± 0.11 in 2000–2015 to 0.49 ± 0.09 in 2016–2020, contributing to a growing bulk of evidence for the massive recolonization of formerly polluted areas by epiphytes since the end of the 20th century (Bates et al., 1997; Duckett & Pressel, 2010; Pescott et al., 2015; Purvis et al., 2010;

Sérgio et al., 2016; Stebel & Fojcik, 2016). The increase in species frequencies was paralleled by an increase of species richness through time, with the emergence of “newcomers” in the flora (*Habrodon pusillus*, *Lewinskya shawii*, *Myriocoleopsis minutissima*, *Orthotrichum consimile*, *O. rogeri*, *O. scanicum*, *Plenogemma phyllantha*, *U. rehmannii*) since the late 1990s and the beginning of the 21st century (Sotiaux & Vanderpoorten, 2015) that represent 15% of the current flora of strict and preferential epiphytes. These shifts were also characterized by a decrease of acidophilous species (e.g., *Dicranoweisia cirrata*, *Dicranum* spp.) and an increase of acid-sensitive (e.g., *Pyralisia polyantha*) and of nitrophilous (e.g., *Syntrichia* spp.) species.

The differences between communities from the same pixel through time were such that they were, on average, more than twice larger than the differences observed today among communities scattered across the study area. Therefore, epiphytic communities are more similar among pixels recorded at the same time period than among geographically close pixels recorded at different periods of time. Similar patterns were observed in the aquatic bryophyte flora (Vanderpoorten, 1999), emphasizing the strength of the temporal variation in species composition as a response to the dramatic changes in their environmental conditions since the past four decades. Locally, however, present-day communities exhibited a composition that was closer to that observed during previous decades than to other extant communities (see, e.g., pixel G447 in Figure 4, which, with 82 and 209 $\mu\text{g}/\text{m}^3$ of NO_2 and O_3 , respectively, is among the most polluted pixels), suggesting that pollution loads may still, in some areas, prevent a complete back-colonization of the epiphytic flora.

Our spatiotemporal analysis of the variation in species composition, climate conditions, and pollutant loads allowed us to determine that the main driver, contributing alone to 38% of the temporal variation of differences in epiphytic bryophyte communities, is the variation of air quality. Among pollutants, SO_2 and NO_2 contributed to about three times as much as O_3 to the observed changes in bryophyte communities. Beginning in the late-18th and early-19th century, large-scale SO_2 and NO_2 pollution resulting from the industrial and residential burning of fossil fuels and associated acidification of substrata decimated epiphytic floras (Pescott et al., 2015). If fully grown gametophytes proved to tolerate SO_2 concentrations beyond $2500\mu\text{g}/\text{m}^3$, which were reached only during the most acute pollution waves, such as the dramatic fog in London of 1952, younger developmental stages, and in particular, protonemata, are killed beyond concentrations of $500\mu\text{g}/\text{m}^3$ (see Lee et al., 1998 for review). In lichens, fumigation experiments revealed that SO_2 , interacting with low bark pH, may play a role at even much lower concentrations (Bates et al., 1996). Annual means of $30\mu\text{g}/\text{m}^3$ are sufficient to eradicate the most sensitive taxa (World Health Organization, 2000), and community changes were observed at average concentrations below $10\mu\text{g}/\text{m}^3$ around a newly established rural point source (Will-Wolf, 1981). Hence, even modest SO_2 levels have still inhibited recolonization of trees by epiphytes in major European cities in the early 2000s (Batty et al., 2003). In southern Belgium, concentration peaks higher than $200\mu\text{g}/\text{m}^3$ have not been reported since

the early 1990s. The substantial decrease in SO_2 concentrations, currently of about $1\text{--}2\mu\text{g}/\text{m}^3$, have allowed SO_2 -sensitive species to back-colonize areas where they previously had suffered extinction, in line with the decrease of acidophilous species and increase of acid-sensitive species mentioned above. In the United Kingdom similarly, the rise and fall of acidophilous epiphytic bryophytes has been clearer, or larger in magnitude, in areas exposed to high SO_2 pollution, consistent with the interpretation that these species were favored by acidic air pollution until the 1980s (Pescott et al., 2015).

In the context of decreasing NO_2 pollution, however, the global increase in nitrophilous species since the 1980s, also reported in epiphytic lichens (Ellis & Coppins, 2009) and non-epiphytic bryophytes (Pakeman et al., 2022), is more puzzling. One interpretation is that other N sources than NO_2 have played a role in the increase of nitrophilous species. In particular, it has been suggested in lichens that atmospheric NH_3 caused the increase of the nitrophilous flora, while the rise of bark pH due to NH_3 pollution has caused the decrease of the acidophilous flora (Van Herk, 2001). This would invalidate the notion that the decline of acidophilous species mirrors an improvement of air quality, while in fact, an increase of NH_3 may be the main cause (Van Herk, 2001). Such an interpretation is, however, not consistent with the fact that, in southern Belgium, NH_3 emissions have, like NO_2 , decreased, dropping by 25% between 1990 and 2020 (<http://etat.environnement.wallonie.be/contents/indicatorsheets/AIR%202.html>). Furthermore, although a long-term monitoring of NH_3 concentrations in southern Belgium would be desirable, our preliminary analyses based on NH_3 concentration measurements in Spring 2021 suggest that extant NH_3 concentrations do not account to differences in species composition among pixels.

Altogether, these results therefore suggest that the observed differences in species composition are linked with decreasing air pollution loads. In this context, past SO_2 pollution levels could have masked the impact of eutrophication, which is now progressively revealed as SO_2 concentrations have been decreasing, leading to the observed spread of nitrophilous species. Past NO_2 concentrations themselves could have been toxic, even for the nitrophilous flora. In fact, while bryophyte growth is initially boosted by moderate N supplies (Armitage et al., 2012), wet N deposition beyond $10\text{--}15\text{ kg}/\text{ha}/\text{year}$ is sufficient to impact epiphytic bryophyte community composition and richness (Mitchell et al., 2005; Song et al., 2012; Shi et al., 2017; Wilkins & Aherne, 2016). In this context, nitrophilous species may have increased in frequency since the 1990s as N levels would have shifted from toxic to enhancing growth. It is tempting to see in the most recent decline of the highly nitrophilous *Orthotrichum diaphanum* (Simmel et al., 2021), the signature of a forthcoming global decline of nitrophilous species as N deposition continues to decrease.

Another pollutant that could have played a role in the temporal variation of epiphytic floras is O_3 , whose average (but not maxima) concentrations have been increasing. Reduction of photosynthetic activity and membrane leakage was reported in four of 22 species exposed to concentrations of $300\mu\text{g}/\text{m}^3$ (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 & Coppins, 2009), calling for further experimental work. In fact, this pollutant could have a growing impact on epiphytic floras in the future, given that O_3 concentrations tend to increase with global warming and with the decrease of NO_x emissions.

The contribution of climate change alone to the observed temporal shifts in community composition ranged between 0 and 7% depending on the analysis performed. This suggests that the dramatic compositional shifts in epiphytic bryophyte communities observed in the study area, and recurrently reported across Europe, cannot be attributed to climate change. Experimentally increased temperatures up to +3°C, combined with various moisture regimes, similarly showed modest impacts on the bryophyte layer of limestone grasslands (Bates et al., 2005). The impact of climatic conditions in our study may even be overestimated, as the climatic conditions employed in the present analyses were obtained from meteorological stations, which are typically located in open areas. Epiphytes, the bulk of which occur on the lower trunk and in areas exposed to high air humidity (Ellis, 2020; Ellis & Eaton, 2021), experience microclimatic conditions under the canopy that are substantially buffered as compared to the ones prevailing in open areas (see De Frenne et al., 2021 for review), so that their variation since the 1980s is likely to have been even less important than that documented from available meteorological data.

4.2 | Factors accounting for the extant composition of epiphytic communities

Present-day variations of epiphytic floras were better explained by the spatial variation of climatic conditions than by extant air pollution loads. This suggests that, as a result of air quality improvement in southern Belgium, spatial variation in climatic conditions is now the main driver of the composition of epiphytic communities. No signature of past pollution events could be detected in modern floras, as suggested by the marginal contribution of past pollution loads to extant patterns of species composition. Although epiphytes need to track patches of suitable trees for persistence (Snäll et al., 2005), epiphytic bryophytes typically exhibit spatially clustered distributions (Löbel et al., 2006a, 2006b) and their fine-scale patterns of genetic variation are significantly spatially structured (Ledent et al., 2020; Vanderpoorten et al., 2019), pointing to dispersal limitations. The lack of any signature of recolonization delay of formerly polluted areas reported here thus suggests that efficient dispersal occurs at the landscape scale, in line with similar observations on the efficient colonization of newly available substrates by bryophytes within a few decades (Hutsemékers et al., 2008). This does not undermine the value of some species, such as *Antitrichia curtipendula*, *Frullania fragilifolia*, *F. tamarisci*, or *Microlejeunea ulicina*, which did not increase or even decreased in frequency during the past decades in southern Belgium, as bioindicators of ancient forests. Such species, which are long-lived and

seldom produce sporophytes, can only colonize suitable habitats quickly if they are found in the immediate vicinity (Baumann et al., 2022), and their distribution patterns are mostly explained by forest continuity (Wierzycholska et al., 2020).

5 | CONCLUSION

Epiphytic bryophyte communities experienced dramatic compositional shifts in the course of the past four decades, larger than their extant spatial patterns of variation. While the concomitant global warming and shifts in air pollution have long blurred the interpretation of the dramatic changes in epiphytic floras (Bates & Preston, 2011), our analyses revealed that the temporal shifts in epiphytic communities result from variation of air pollution loads. The minimal role played by climate change to the observed patterns was unexpected because bryophytes are globally sensitive to moderately high temperatures and drought.

The lack of climatic impact on epiphytic floras reported here does, however, not suggest that such floras are resilient to climate change. While, in line with the inconclusive trends reported across central Europe (Gudmundsson & Seneviratne, 2016), no temporal trends in the precipitation regime were observed in the course of the past four decades in southern Belgium, anthropogenic climate change has already increased drought risk and number of dry days in southern and northern Europe, respectively (Gudmundsson & Seneviratne, 2016). Furthermore, Europe has been experiencing its worst drought in at least 500 years in the course of the past couple of years (European Drought Observatory, <https://edo.jrc.ec.europa.eu/edov2/php/index.php?id=1000>). This, together with record-breaking temperatures in Europe during the 2022 summer (Witze, 2022), suggests that climate change impacts on bryophytes will start to become apparent during the next decades. Epiphytic floras proved to globally efficiently recover from past pollution events, but these have a local to regional impact. In contrast, climate change occurs at a much larger scales, especially in lowland areas that, as southern Belgium, are characterized by high velocities of climate change (Dobrowski & Parks, 2016), raising the question of the ability of species to efficiently track the shift of climatically suitable areas across large distances (Zanatta et al., 2020).

In addition, other pollutants than those investigated here, and especially pesticides, whose impact on bryophytes remains poorly documented, may play a potentially increasing role. Given the fast response of epiphytic communities to environmental change, we suggest that a monitoring of epiphyte communities at 10-year intervals would be desirable to accurately assess the threats that they will face in the course of the next decades.

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DATA AVAILABILITY STATEMENT

The data employed in the present study are openly available in Figshare at DOI: [10.6084/m9.figshare.21630179](https://doi.org/10.6084/m9.figshare.21630179).

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SUPPORTING INFORMATION

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