Global Change Biology

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Global Change Biology

RESEARCH ARTICLE

Towards a New Interpretative Framework for Air Quality and Climate Biomonitoring With Lichens: A Meta-Analysis of Surveys Using the European Protocol

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Received: 7 July 2025 | **Revised:** 20 September 2025 | **Accepted:** 14 November 2025

Keywords: air pollution | climate change | European protocol | lichen | meta-analysis | NH_3 | NO_x | sensitivity scales | SO_2

ABSTRACT

Air pollution and climate change remain critical environmental challenges, particularly in urban areas, where conventional monitoring networks are often too sparse to capture fine-scale exposure gradients due to their high operational costs. Epiphytic lichen biomonitoring provides a valuable complementary approach, as these organisms are sensitive to both air pollutants and climate conditions. Despite the existence of a standardized European protocol, large-scale implementation is hindered by the absence of a robust interpretative framework and incomplete knowledge of species-specific responses to pollutants and climate variables. This study initiated the development of a standardized interpretative framework for European lichen biomonitoring data by identifying a core set of indicator species with clear responses to major air pollutants and climate variables. To achieve this, we compiled and harmonized raw lichen data from 58 studies that applied the European protocol and modeled the response of 43 lichen species to dominant air pollutants (NH_3, NO_x, and SO_2) and climate variables (mean air temperature, mean relative humidity, and temperature seasonality). While confirming established trends, our models allowed us to decouple species responses to reduced (NH_3) vs. oxidized (NO_x) nitrogen compounds, a distinction rarely achievable in local studies due to insufficient contrast in pollutant gradients. We also provided actionable recommendations to enhance comparability, such as prioritizing widespread, well-studied tree species and standardizing lichen taxa groupings. Our study established a foundation for a harmonized European interpretative framework by identifying low-bias, ecologically meaningful indicator species. Future efforts should focus on translating sensitivity classifications into actionable air quality indices and refining regional-scale assessments.

1 | Introduction

Air pollution and climate change are among the most pressing environmental challenges of the 21st century, particularly in urban areas, where three-quarters of Europe's population resides (Richardson et al. 2023; Targa et al. 2024). While monitoring air pollution and climate is crucial for mitigating their adverse effects, conventional physical and chemical sensors face several limitations. Their high cost, in particular, restricts extensive deployment, reducing spatial resolution and coverage. Biomonitoring, which utilizes living organisms to assess environmental quality, offers a complementary

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approach by providing a direct assessment of the impact of both pollution and climate stressors on ecosystems. When implemented as a first step, biomonitoring can identify priority areas for sensor deployment, optimizing resource allocation and reducing unnecessary costs. Furthermore, it provides a means to evaluate ecosystem services, such as air quality regulation, thereby supporting evidence-based environmental management (Matos et al. 2019). Epiphytic lichens are extensively used as bioindicators of atmospheric pollution due to their morphological and physiological traits (e.g., absence of roots and protective barriers), which make them especially sensitive to air pollutants (Abas 2021; Conti and Cecchetti 2001). Beyond air pollution, lichens also respond strongly to climate variables, such as temperature and water availability, making them valuable indicators of both global climate change (Stapper and John 2015) and local phenomena like urban heat islands (Munzi, Correia, et al. 2014). Due to their ubiquity and perennial growth, they also integrate environmental conditions over space and time, offering a valuable complement to point-based sensors (Niepsch et al. 2022).

In this context, various methodologies have been developed to use epiphytic lichens as air quality bioindicators. The first category includes qualitative approaches focusing on the presence–absence of indicator species with contrasted sensitivities (Hawksworth and Rose 1970; Lallemant et al. 1996). However, these methods were developed within specific regional contexts and in environments where pollution was dominated by a single pollutant (i.e., SO_2), thus limiting their applicability in contemporary scenarios characterized by low concentrations of multiple pollutants (van Herk 2001). In parallel, quantitative approaches were introduced to better describe lichen communities by estimating species cover. These methods operate on the assumption that dominant species reflect prevailing environmental pressures. Cover estimation is typically performed using either semi-quantitative scales, such as the Braun-Blanquet coefficient (LeBlanc and De Sloover 1970; van Herk 1999) or grid-based methods, which yield a frequency score corresponding to the proportion of grid cells in which the species is detected (ANPA 2001; Asta et al. 2002; Kricke and Loppi 2002; Verein Deutscher Ingenieure 2005). To ensure repeatable and comparable results across studies, the European lichen biomonitoring community developed a common protocol (EN16413; CEN 2012) that standardizes both sampling site selection (i.e., the location where one or more trees are surveyed) and species frequency estimation.

For data interpretation, the European protocol relies on the lichen diversity value (LDV), calculated as the mean sum of species frequencies per tree. This metric serves as a general proxy for overall environmental quality, where a higher LDV indicates lower anthropogenic pressure from factors such as air pollution and habitat disturbance. However, this metric does not allow distinguishing between the types of environmental disturbances involved, limiting the comparability of LDV values across regions (Loppi et al. 2002). To overcome this limitation, researchers have complemented the LDV with trait-based indicators, which rely on species groupings defined by shared ecological traits (e.g., affinity for acidity or eutrophication), to calculate the proportion of functionally similar species within a community (e.g., Llop et al. 2012; Rocha et al. 2022). While promising, this approach also faces important limitations: the ecological databases used are typically compiled at the national level, such as Italy (Nimis 2025) or Germany (Wirth 2010) reducing their applicability in other bioclimatic contexts. Furthermore, the associated traits are not directly linked to specific pollutants, making it difficult to disentangle the effects of co-occurring pressures such as reduced (e.g., NH_3) versus oxidized (e.g., NO_2) nitrogen compounds (Frati et al. 2006; Gadsdon et al. 2010; Greaver et al. 2023; Manninen et al. 2023), or to account for interactions with climatic factors. In the absence of a unified interpretative framework, the large-scale implementation of this standardized protocol remains limited, undermining the credibility of lichen-based biomonitoring among both policymakers and the scientific community (Loppi 2019; Louis-Rose and Galsomiès 2011).

In this context, we aimed to initiate the development of a standardized interpretative framework for European lichen biomonitoring data by identifying a core set of indicator species with clear responses to major air pollutants and climate variables. To achieve this, we: (1) conducted a meta-analysis using the raw data of all available studies (i.e., 58 studies) that applied the European protocol; and (2) modeled the response of individual epiphytic lichen species to dominant air pollutants (NH_3, NO_x, and SO_2) and climate variables.

2 | Materials and Methods

2.1 | Database Constitution

2.1.1 | Lichen Data

A systematic literature review was conducted, encompassing both scientific and gray literature. For the scientific literature, the search was performed in Scopus using the query “lichen AND biomonitoring”, restricted to articles published between January 2000 and June 2024, yielding 1700 articles. For gray literature, reports were collected from consulting firms and environmental agencies (e.g., the ATMO network in France or ARPA in Italy) through targeted Internet search. Additionally, national lichenological societies across Europe were contacted, as identified via the International Association for Lichenology website.

From this initial set of sources, we only retained studies conducted in European countries that followed the standardized European protocol for lichen biomonitoring. This protocol involves placing a grid consisting of five vertical quadrats (10 cm × 10 cm) at each of the four cardinal directions around the tree trunk, at a height of 1 m. The frequency of each species is then assessed by counting the number of quadrats in which it is present, yielding a score out of 5 per exposure side or out of 20 per tree (Asta et al. 2002).

When raw lichen data were not publicly available, we contacted the authors directly to obtain: raw lichen frequencies (at the tree or sampling site level), GPS coordinates of each sampling site, survey year, and phorophyte-related data (i.e., the host tree species and girth, when available).

Lichen taxa names were standardized using the *Index Fungorum* database (Index Fungorum 2025), and unidentified taxa were excluded. Due to variability in the number of sampled trees per site across studies, we calculated the mean frequency (between 0 and 20, as defined by the European protocol) of each lichen species per sampling site. When trees of different species were sampled within the same site, the data were partitioned into separate sites (i.e., one per tree species) to account for phorophyte-related effects.

2.1.2 | Environmental Data

We considered broad-scale pollution data from the EMEP MSC-W model (Simpson et al. 2012), which provides annual mean concentration estimates for major atmospheric pollutants across Europe at an 11 km^2 resolution. For each sampling site, we extracted the modelled concentrations corresponding to the survey year, as concentrations varied only slightly between successive years, making multi-year averaging unnecessary. From the available pollutants, we first selected compounds with documented phytotoxic effects on lichens: SO_2, NH_3, NO_x, O_3, and particulate matter (PM) (Geebelen and Hoffmann 2001; Gombert et al. 2006; Pinho et al. 2012; Sebald et al. 2022). This focus on atmospheric concentrations, rather than deposition fluxes, was motivated by the high multicollinearity among deposition variables (see Figure S1), which would prevent disentangling pollutant-specific effects. This approach offers clearer targets for emission reduction strategies than total deposition metrics, which amalgamate multiple sources and pathways. To further limit multicollinearity, we performed a correlation analysis and retained only variables with pairwise Spearman correlation coefficients below 0.6. This led to the exclusion of PM and O_3 due to their strong correlations with other pollutants (see Figure S1 for the complete correlation matrix).

In parallel, climate variables were extracted from the CHELSA database (Karger et al. 2023), which provides high-resolution (1 km^2) bioclimatic data based on long-term mean values (1979–2013). We selected three ecologically relevant parameters known to impact species distribution: mean air temperature, mean relative humidity, and temperature seasonality (i.e., the standard deviation of monthly mean temperatures, used here as a proxy for continentality). These variables are consistently employed in established bioindication systems for both vascular plants (Dengler et al. 2023) and lichens (Wirth 2010).

2.2 | Data Processing

All analyses were performed using R 4.4.1 (R Core Team 2024).

2.2.1 | Lichen Data Filtering for Species Response Modeling

While all available data were used for the protocol implementation description, the modeling of species-environment relationships required specific data refinements to ensure reliable and interpretable sensitivity characterization. First, we restricted the analysis to sites located in open environments (i.e., non-forested environments such as urban parks, agricultural areas, roadside habitats), as identified from available site metadata, to avoid forest-associated biases and account for distinct lichen communities. Second, we consolidated taxonomically challenging species commonly grouped in biomonitoring studies (e.g., *Physcia adscendens* and *Physcia tenella* as *Physcia* gr. *adscendens*; *Candelariella reflexa* and *Candelariella xanthostigma* as *Candelariella* gr. *xanthostigma*) to reduce false negatives due to identification uncertainties. This option does not reduce their value as indicators, as they share common characteristics regarding climate and pollution tolerance (Nimis 2025). Third, to reduce substrate-related variability (e.g., bark pH, texture, water-holding capacity), we exclusively retained sites where phorophytes belonged to EU groups 1 and 2 (i.e., acid to subneutral bark; CEN 2012), as these were the most frequently sampled and were widely distributed across the study area. This allowed us to more accurately isolate the true responses of species to environmental gradients, rather than confounding them with substrate preference. Fourth, studies limited to macrolichens (i.e., foliose or fruticose species, typically easier to identify) were excluded from the microlichen-specific models (focused on crustose and other small-bodied taxa) to ensure consistent taxonomic resolution. Finally, our analysis was restricted to species occurring in at least 5% of sampling sites to ensure robust model fitting and limit outliers.

2.2.2 | Species Response Modelling

We used quantile regression (*quantreg* R package; Koenker 2024) to identify key environmental factors influencing lichen distribution patterns, particularly suited to zero-inflated data (i.e., with a high proportion of zero values; species absence rates ranging from 22% to 99.9% in our dataset). By focusing on the upper 95th quantile (Q_{95}), we aimed to identify optimal environmental conditions while accounting for unmeasured constraints (Cade et al. 1999; Schröder et al. 2005). For each individual lichen species, we developed a model using logit-transformed frequencies (Bottai et al. 2010), constraining model predictions within the 0–20 range defined by the European standardized protocol (i.e., the number of occupied quadrats out of 20). To account for unequal sampling effort across studies, we weighted each site proportionally to the number of trees surveyed.

The quantile regression models incorporated the six explanatory variables: three pollution parameters (NH_3, NO_x, and SO_2) and three climate parameters (mean annual air temperature, mean relative humidity, and temperature seasonality). To capture potential non-linear relationships, quadratic terms were considered for each climate variable, while they were not included for pollution variables due to their coarse spatial resolution (11 km^2), which could potentially lead to unreliable or ecologically implausible model fits. To optimize goodness-of-fit while limiting model complexity, we systematically tested all eight possible combinations of the quadratic climate terms (i.e., including or excluding each of the three squared terms) and selected the model with the lowest Akaike Information Criterion (AIC; Akaike 1974). Collinearity among predictors was evaluated by calculating Variance Inflation Factors (VIF) from an equivalent linear model including the three quadratic climate terms; all VIF values were below 3, indicating no substantial multicollinearity.

2.2.3 | Model Quality Assessment and Species Classification

To evaluate generalizability and limit study-specific bias, we implemented a resampling procedure over 500 iterations. At each step, we: (1) randomly excluded 5% of studies, a threshold chosen because higher exclusion rates caused the 95th percentile quantile to be zero for the less frequent species; (2) repeated model selection (i.e., based on AIC) and calculated species response curves for each environmental variable (keeping other variables at their mean value); and (3) identified the predicted optimum (i.e., the value of the environmental variable where the species reaches its maximum frequency) for each variable.

We then examined the distribution of optima across iterations: species consistently (i.e., $\geq 99\%$ of iterations) reaching their optimum in the lowest tercile of the environmental gradient were considered negatively associated with the variable, while those in the highest tercile were considered positively associated. When predicted frequencies remained low across the entire variable range (i.e., $< Q_{95}/2$), we treated this as noise rather than ecological signal. This conservative approach minimized the risk of overinterpreting spurious patterns and ensured that only strong and consistent responses were retained for classifying lichen species. Data S1 includes a schematic overview of the resampling and classification method (Figure S2).

3 | Results

3.1 | Description of Compiled Data

We gathered data from 58 studies (corresponding to 2932 sampling sites and 9064 sampled trees) conducted between 2001 and 2023, covering 15 European countries (Figure 1a,b; see Data S2 for the complete list). The dataset covered a wide range of climate conditions (including Mediterranean, temperate, oceanic, and continental climates), as well as pollution gradients, including both large urban areas (e.g., Paris, Hamburg, Rome, and Marseille) and remote rural regions. Italy (22 studies) and France (13 studies) were the most represented countries, with contributions from multiple institutions across many regions. In contrast, although well-established lichen biomonitoring programs exist in Germany (Kirschbaum et al. 2012), Switzerland (Herzig et al. 2020), and the Netherlands (Van Dobben and De Bakker 1996; van Herk et al. 2002), we retrieved fewer datasets from these countries because different sampling methods

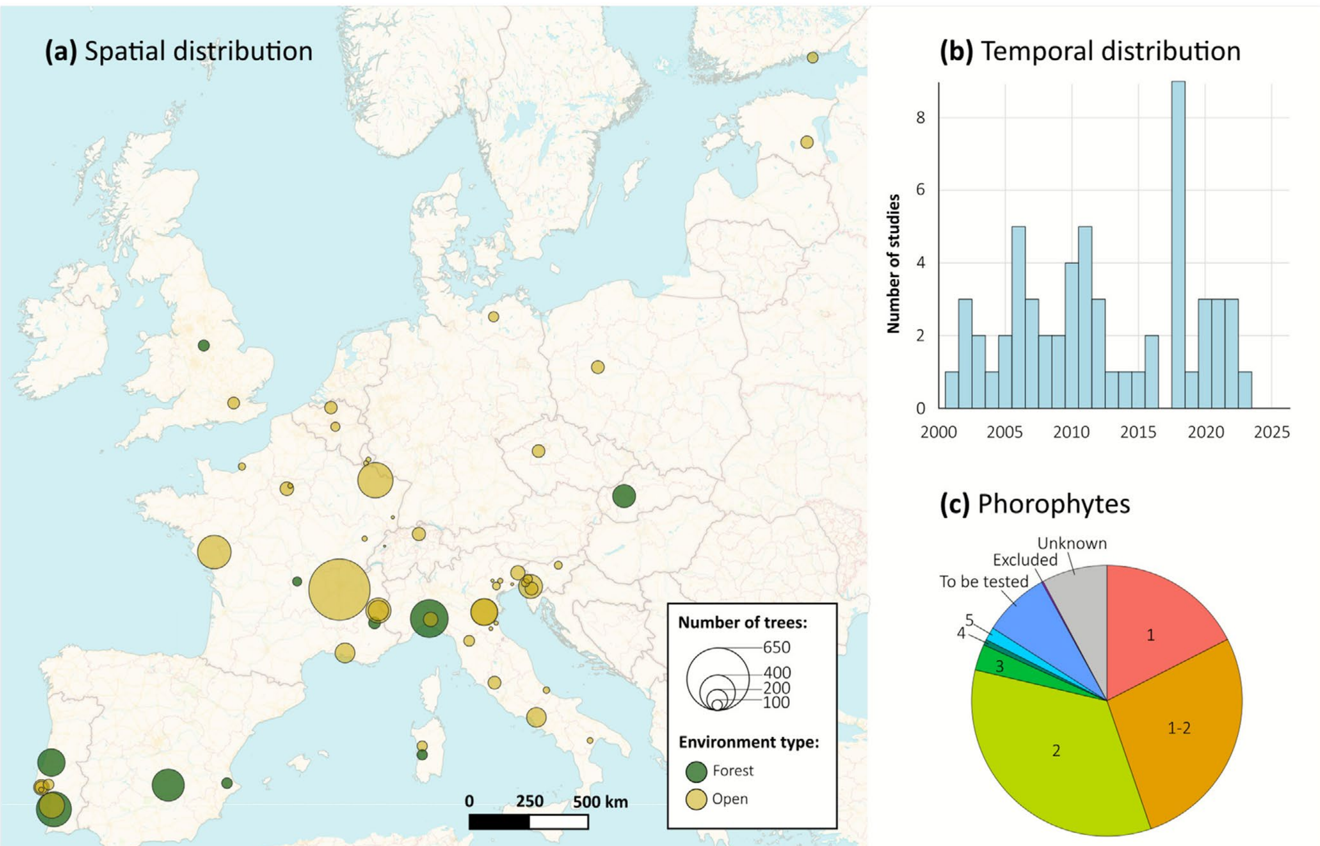

FIGURE 1 | Spatial, temporal, and methodological overview of lichen biomonitoring studies included in the analysis: Geographic distribution of studies (a), number of studies conducted per sampling year (b), proportions of tree species groups surveyed across studies (c). Tree species groups follow the European protocol classification: Group 1 (broadleaved species with subneutral bark, mainly *Acer* spp. and *Fraxinus* spp.); group 2 (broadleaved acid barked species, mainly *Quercus* spp.); intermediate group 1–2 (mainly *Tilia* spp.); group 3 (mostly conifers); group 4 (*Alnus glutinosa* and *Betula pendula*); and group 5 (mainly *Fagus sylvatica* and *Carpinus betulus*). The "excluded" group includes species that should not be sampled due to exfoliating bark, while the "to be tested" group includes species not yet classified. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

were used, such as the German VDI protocol (Verein Deutscher Ingenieure 2005).

Most studies were conducted by researchers (66%), while the remainder originated from gray literature sources (i.e., mostly environmental agencies). Even though all studies retained in our database applied the European protocol, notable differences remained in terms of monitoring objectives (e.g., local pollution assessment for source identification, regional air quality mapping, or biodiversity assessment for conservation purposes) and habitat type. For example, 10 studies (i.e., 16% of sampled sites) were conducted in forests, while others focused on open environments. This led to variations in the protocol implementation, including differences in sampling density and in the number of trees surveyed per site. For instance, more trees were sampled in forests (mean: 5.6 ± 2.2) than in open habitats (mean: 3.3 ± 1.3).

In our dataset, the most represented phorophyte categories defined by the European protocol (CEN 2012) were group 1 (mainly *Acer* spp. and *Fraxinus* spp.), group 2 (mainly *Quercus* spp.), and the intermediate 1–2 group (mainly *Tilia* spp.), accounting for 17%, 34%, and 27% of sampled trees, respectively (Figure 1c). In contrast, other tree groups collectively accounted for only 13% of sampled trees and were unevenly distributed (e.g., *Olea* spp. restricted to Mediterranean areas). Among them, the "to be tested" group (8% of sampled trees) included a wide range of species, such as exotic trees (e.g., *Robinia pseudoacacia* or *Ginkgo biloba*).

Our lichen database contains 511 taxa (Data S2), representing 477 species across 175 genera. Of these, only 26 (5%) were reported in at least half of the studies (Figure 2b), encompassing species with diverse ecological traits, such as eutrophic species (e.g., *Physcia adscendens*, *Xanthoria parietina*, and *Phaeophyscia orbicularis*), alongside mesotrophic and oligotrophic species (e.g., *Parmelia sulcata*, *Flavoparmelia caperata*, and *Hypogymnia physodes*). Besides this, the majority of taxa was observed in only one (192 taxa, 38%) or two studies (87 taxa, 17%; Figure 2a). Among the most frequently encountered taxa, several morphologically and ecologically similar species pairs were not reported consistently across studies. For instance, *Physcia adscendens* was recorded in all 58 studies (100%), whereas the closely related *P. tenella* appeared in only 40 studies (69%; Figure 2b). Similar inconsistencies were observed in other species pairs, such as *Candelariella xanthostigma*/*C. reflexa* and *Punctelia subrudecta*/*P. borreri*. Additionally, 34 taxa (6.7%) were identified solely at the genus level. The most frequently genus-level reported taxa were *Lepraria* (30 studies), *Lecanora* (14), *Usnea* (13), and *Cladonia*

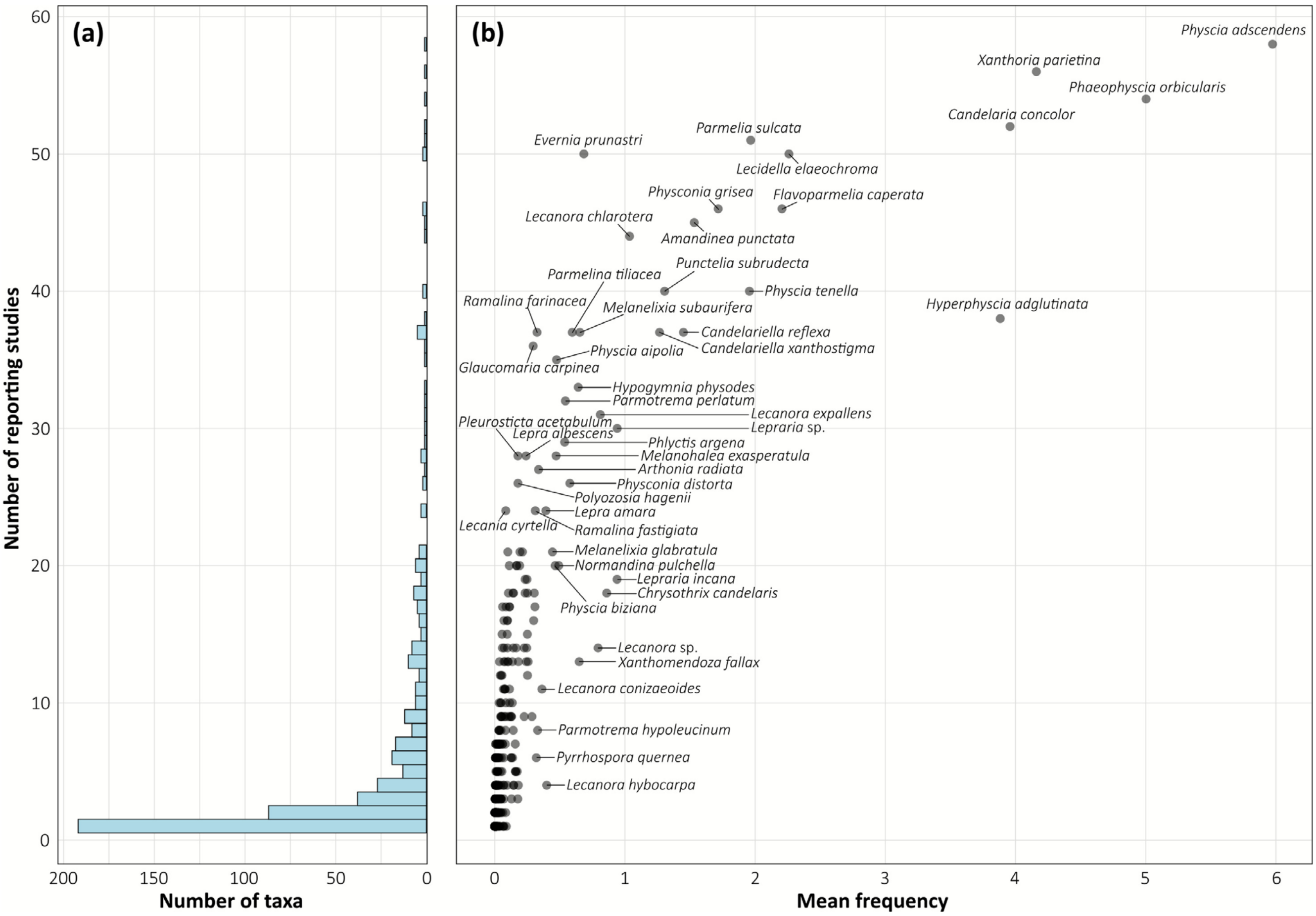

FIGURE 2 | Observed distribution of species in lichen biomonitoring studies: Number of taxa reported by a given number of studies (a) and relationship between number of reporting studies and mean frequency (0–20) for individual species (b). Both panels share the same y-axis. Panel (a) helps visualize the distribution of points along the y-axis in panel (b), where many species with similar values are superimposed. For clarity, species names in panel (b) are labeled only for those reported in at least 24 studies or with a mean frequency > 0.32.

(11). A total of 141 taxa (28%) was exclusively observed in forested environments. For this reason, our analyses were restricted to open habitats, where lichen communities are more directly shaped by climate and air pollution.

3.2 | Quantile Regressions

To characterize species-specific responses to key pollutants and climate variables, we used a subset of the full lichen database, restricting the analysis to the species observed in at least 5% of the sampling sites in open environments. This selection yielded 43 species (or species groupings) that collectively accounted for 89% ± 17% of the total recorded sum of frequencies per site, suggesting that this subset is broadly representative of lichen communities in open environments across Europe. Most response curves derived from the Q_{95} models showed biologically plausible patterns, including monotonic increases or decreases, sigmoidal trends, or unimodal responses (Figure 3a–c). A few U-shaped responses were also observed for climate variables, but these involved species with very low predicted frequencies across all the values of the environmental variable, making any ecological interpretation unreliable due to a lack of signal. A summary of the modeling results is presented in Data S3.

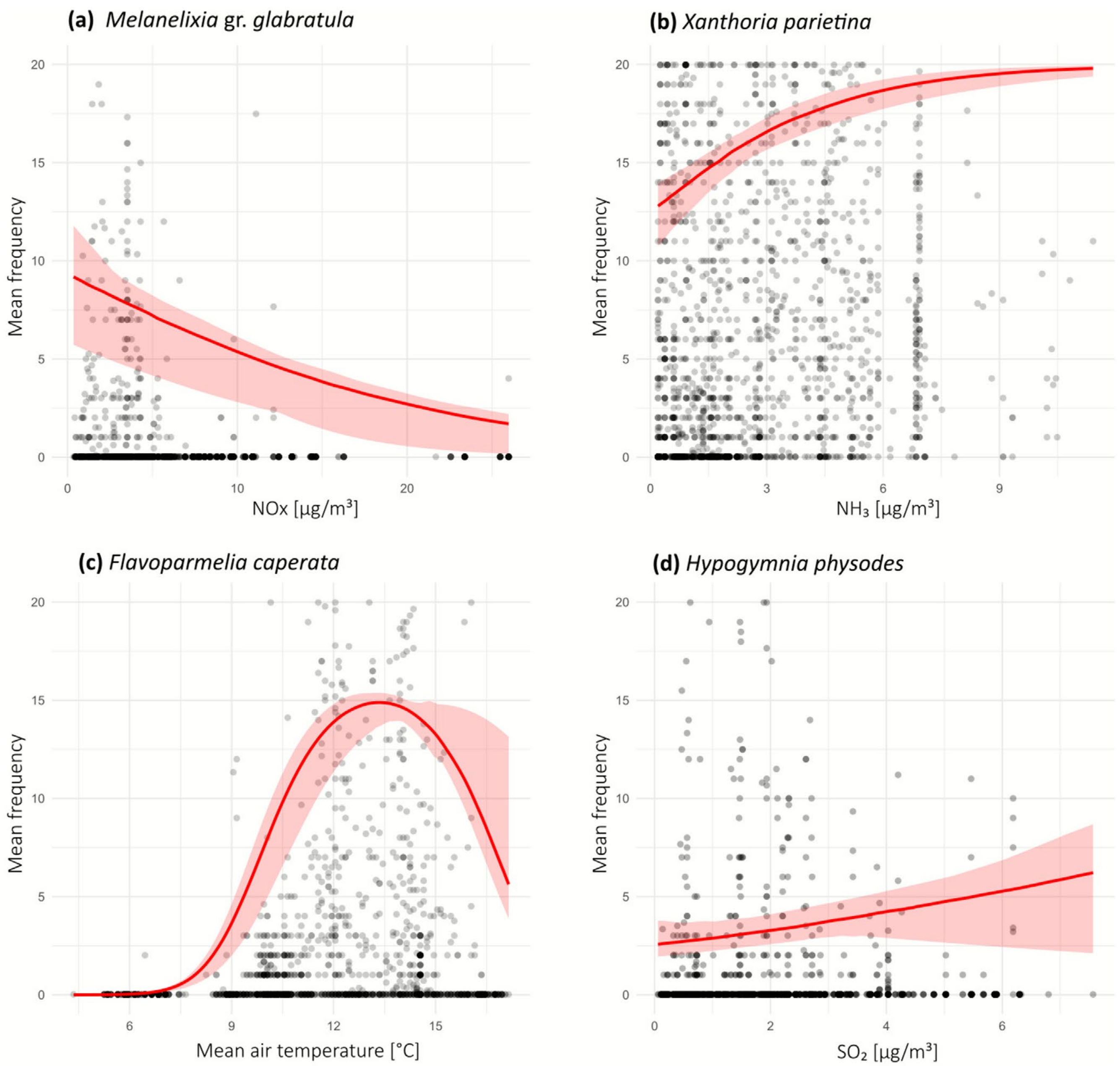

FIGURE 3 | Examples of 95th quantile response curves generated by the multivariate model, with all other predictors held at their mean values: Negative response of *Melanelixia* gr. *glabratula* to NO_x concentrations (a), positive response of *Xanthoria parietina* to NH_3 concentrations (b), unimodal response of *Flavoparmelia caperata* to mean air temperature (c), and unstable positive response of *Hypogymnia physodes* to SO_2 concentrations (d). The red line represents the median prediction across 500 resampling iterations, while the light red shading indicates the 95% prediction envelope (2.5th–97.5th percentiles).

Overall, negative responses to pollutants were more frequent than positive ones, with only 16, 12, and 9 positive responses out of 43 models for NH_3, NO_x, and SO_2, respectively (Figure 4a–c). For climate variables, most response curves were unimodal, indicating that many species reach their ecological optimum under intermediate conditions and are less frequent/abundant at climatic extremes (Figure 4d–f). However, some monotonic responses were also observed, including increasing trends (e.g., *Hypogymnia physodes* with mean relative humidity; Figure 4e) and decreasing trends (e.g., *Polycauliona candelaria* with mean air temperature; Figure 4d). Finally, although temperature seasonality (used here as a proxy for continentality) was not the main driver for most species, some showed strong monotonous responses to this variable (e.g., *Parmelia sulcata* with positive response or *Diploicia canescens* with negative response; Figure 4f).

4 | Discussion

4.1 | Protocol Implementation and Potential Biases

Results demonstrate the broad adoption of the European biomonitoring protocol, extending its application beyond academic research into operational monitoring programs. However, this widespread implementation has revealed methodological variations that may influence detection probabilities and species frequency estimates (Poličnik et al. 2008). These inconsistencies can bias biodiversity assessments and community composition metrics, potentially affecting the reliability of air quality assessment based on lichen indicators (Counoy et al. 2023; Ferretti et al. 2004).

A key issue is that applying the same protocol across highly divergent environments (e.g., open habitats vs. forests) introduces significant interpretive challenges. Open environments are generally more suitable for pollution monitoring, as lichens are directly exposed to atmospheric pollutants. In contrast, although the European protocol can be applied in forest areas to assess anthropogenic pressures (e.g., agriculture, wildfires, forest management; Garrido-Benavent et al. 2015; Guttová et al. 2017; Svoboda et al. 2010), forests introduce ecological complexity. Natural variability in stand structure, microclimate, and bark properties can obscure anthropogenic signals (Frati and Brunialti 2023; Poličnik et al. 2008). Furthermore, the limited number of forest studies in our dataset (10 out of 58) and their heterogeneous distribution across European forest types preclude a robust analysis of lichen sensitivity in these habitats. Developing a dedicated forest interpretative framework will require larger, standardized datasets, such as those from the ICP Forests network (Lorenz 1995; Stofer et al. 2012), to account for these confounding factors (Frati and Brunialti 2023).

Additionally, strict adherence to the protocol's tree selection criteria (e.g., species, trunk straightness, bryophyte cover) is often challenging, particularly in open habitats where trees meeting all those criteria are generally scarce (e.g., Svoboda 2007). The results indicate that over three-quarters of surveys were conducted on trees from groups 1 and 2 defined by the European protocol (CEN 2012). These groups—comprising widely distributed species with similar bark properties (e.g., pH, roughness, and water-holding capacity)—improve cross-regional comparability by minimizing the influence of bark on lichen communities (Buba and Danmallam 2019; Spier et al. 2010; van Herk 2001). Focusing on these groups also helps to avoid potential biases associated with rare or exotic tree species, whose suitability for native lichen communities has yet to be validated (Möller et al. 2021). Although this selection somewhat restricts the number of locations where the protocol can be applied, the phorophytes of groups 1 and 2 are among the most widespread in European urban areas (Pauleit et al. 2002). This represents a key strength of the current protocol implementation, ensuring reliable biomonitoring outcomes across diverse regions.

Our findings reveal several observer-related reporting biases that compromise data consistency in lichen biomonitoring. A key issue is the inconsistent reporting of morphologically and ecologically similar species. These discrepancies are often linked to field identification challenges, particularly when using grid-based frequency estimates or when taxonomic tools are limited. For instance, *Physcia tenella* was frequently underreported compared to the closely related *P. adscendens*, despite their co-occurrence and morphological similarity. Additionally, the frequent use of genus-level identifications (e.g., *Lepraria*, *Lecanora*, and *Usnea*) highlights limitations in taxonomic resolution, reflecting differences in surveyor expertise and access to advanced identification techniques, such as microscopy or thin-layer chromatography.

These inconsistencies directly affect key biomonitoring metrics by influencing estimates of species richness and ecological indicator values, which in turn can distort air quality assessments. This presents a critical challenge for biomonitoring programs: while precise species-level identification is essential for biodiversity conservation, it can reduce comparability across studies and increase the complexity of data collection. To address this, we recommend the formal grouping of cryptic and hard-to-identify species into aggregates (e.g., *Physcia* gr. *adscendens*). This approach not only facilitates fieldwork but is also essential for protocol standardization and ensuring reliable, large-scale comparisons in European lichen biomonitoring initiatives.

4.2 | Species Responses to Air Pollutants and Climate Variables

The response curves obtained from the resampling procedure allowed us to classify each species according to its response to the six environmental variables (Table 1). This classification approach only considers species showing consistent responses across the majority of calibration subsets (i.e., datasets with 5% of studies excluded). Species with unstable responses to a given variable (e.g., Figure 3d) were not classified as positively or negatively impacted.

4.2.1 | Response to NH_3

For NH_3, our classification identified eight species as positively impacted, while a negative effect was detected for 22 species (Table 1). Among the positively affected taxa, we found several well-known nitrophilous species (e.g.,

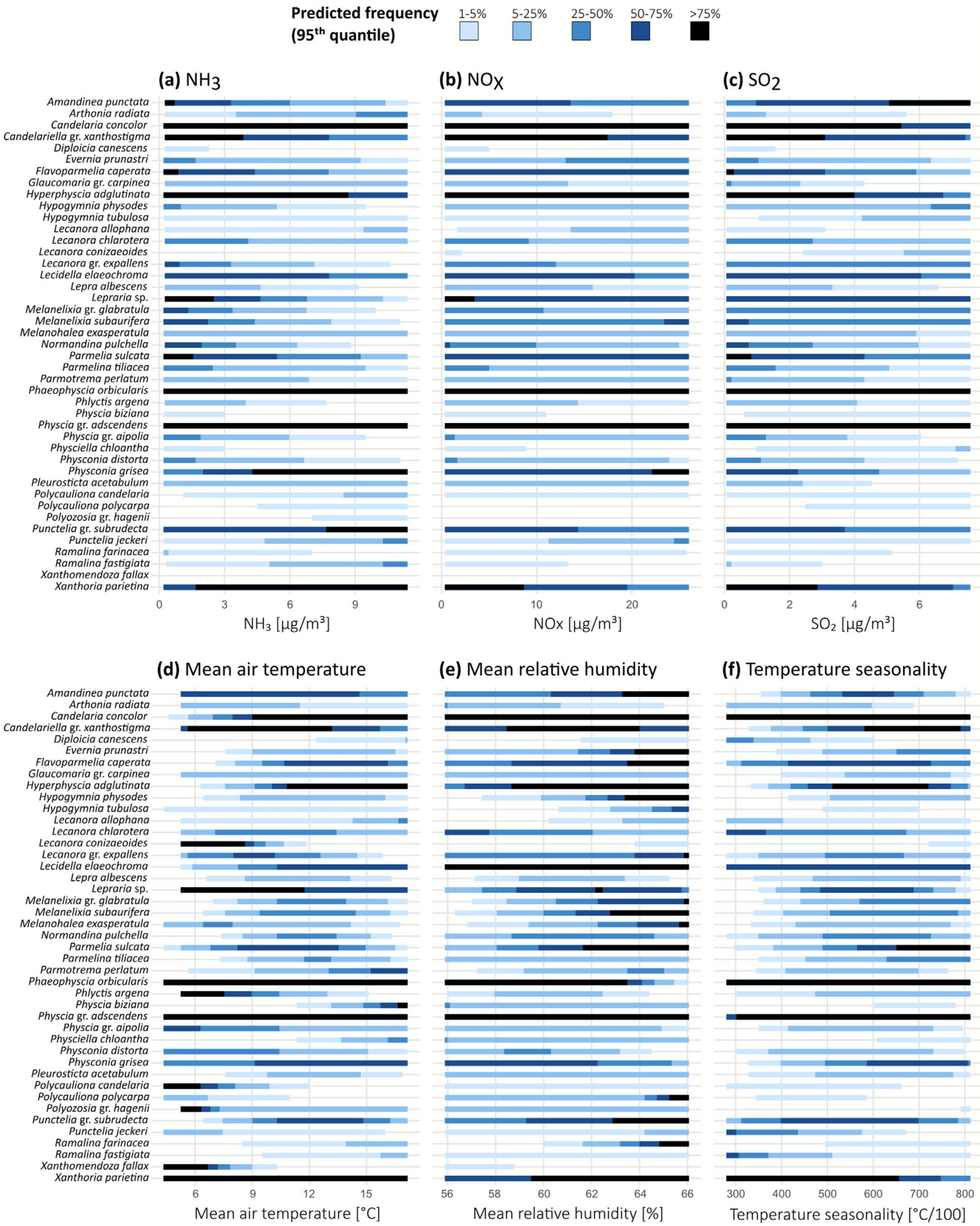

FIGURE 4 | Response curves of the 95th quantile models for the 43 lichen species in relation to the six environmental variables considered, based on the full dataset (without resampling): NH_3 (a), NO_x (b), SO_2 (c), mean air temperature (d), mean relative humidity (e) and temperature seasonality (f). Colors represent the predicted normalized frequency, expressed as a percentage, with 100% corresponding to a frequency of 20 according to the European protocol (CEN 2012).

TABLE 1 | Summary of species sensitivity classification based on model responses to pollutants and climate variables: NH_3, NO_x, SO_2, mean air temperature (MAT), mean relative humidity (RH), and temperature seasonality (TS). A "+" indicates a positive association with the variable, whereas a "−" indicates a negative association. Empty cells correspond to cases where the model did not yield a stable trend across the 500 resampling iterations, or where the species showed a consistent unimodal response peaking in the intermediate tercile of the environmental variable. The reliability of each classification is discussed using two criteria adapted from von Hirschheydt et al. (2024): Conspicuousness (Consp.), referring to whether a species can be easily spotted in the field, and identifiability (Identif.), referring to whether it can be reliably distinguished from similar taxa.

Species	Number of sites	NH_3	NO_X	SO_2	MAT	RH	TS	Consp.	Identif.
Amandinea punctata	517	−		+	−				
Arthonia radiata	101	+	−	−	−			×	×
Candelaria concolor	917	+		−			+	×	×
Candelariella gr. *xanthostigma*	819	−		−			+		×
Diploicia canescens	145				+		−	×	×
Evernia prunastri	381	−		−		+	+	×	×
Flavoparmelia caperata	575	−		−	+	+		×	×
Glaucomaria gr. *carpinea*	186		−	−				×	
Hyperphyscia adglutinata	679	−		−	+	+			×
Hypogymnia physodes	245	−				+	+	×	×
Hypogymnia tubulosa	104			+		+		×	×
Lecanora allophana	106			−				×	
Lecanora chlarotera	430	−	−	−		−	−	×	
Lecanora conizaeoides	92			+	−			×	×
Lecanora gr. *expallens*	332	−	−	+					
Lecidella elaeochroma	688	−	−	−				×	×
Lepra albescens	98	−	−	−				×	×
Lepraria sp.	471	−						×	×
Melanelixia gr. *glabratula*	207	−	−			+		×	×
Melanelixia subaurifera	299	−				+		×	×
Melanohalea exasperatula	301			−	−	+		×	×
Normandina pulchella	139	−	−	−				×	×
Parmelia sulcata	768	−		−		+	+	×	×
Parmelina tiliacea	266	−		−			+	×	×
Parmotrema perlatum	208	−		−	+	+		×	×
Phaeophyscia orbicularis	1239	+	+	−	−			×	×
Phlyctis argena	192	−	−	−	−			×	×
Physcia biziana	176				+	−		×	×
Physcia gr. *adscendens*	1501		+	−		+		×	×
Physcia gr. *aipolia*	252	−	−	−	−			×	×
Physciella chloantha	119	−			+			×	
Physconia distorta	225	−	−	−	−			×	×
Physconia grisea	550	+	+	−				×	×
Pleurosticta acetabulum	161			−		+		×	×

(Continues)

TABLE 1 | (Continued)

Species	Number of sites	NH_3	NO_X	SO_2	MAT	RH	TS	Consp.	Identif.
Polycauliona candelaria	123	+			−			×	×
Polycauliona polycarpa	178				−	+		×	×
Polyozosia gr. *hagenii*	149	+			−				×
Punctelia gr. *subrudecta*	626		−	−		+		×	×
Punctelia jeckeri	109	+		−	−	+		×	
Ramalina farinacea	152	−	−	−	+	+		×	×
Ramalina fastigiata	198		−	−	+	+	−	×	×
Xanthomendoza fallax	175				−			×	×
Xanthoria parietina	1284	+	−	−				×	×

Candelaria concolor, *Phaeophyscia orbicularis*, *Physconia grisea*, *Polycauliona candelaria*, *Polyosozia* gr. *hagenii*, and *Xanthoria parietina*). Conversely, negatively impacted species included well-established nitrophobic lichens (e.g., *Evernia prunastri* and *Hypogymnia physodes*), as well as others often considered intermediate in their response (e.g., *Flavoparmelia caperata* and *Parmelia sulcata*). These trends are consistent with the literature on lichen sensitivity to ammonia (Delves et al. 2023; Geiser et al. 2021; Lallemant et al. 1996; Munzi, Cruz, et al. 2014; Van Dobben 1999) and demonstrate that our model is able to capture ecologically meaningful large-scale patterns.

Despite this overall agreement with the literature, some discrepancies also emerged. Indeed, some species were unexpectedly classified as nitrophilous (e.g., *Arthonia radiata* and *Punctelia jeckeri*), while others, known to be favored by high nitrogen levels, were not (e.g., *Polycauliona polycarpa* and *Glaucomaria* gr. *carpinea* classified as neutral, while *Hyperphyscia adglutinata*, *Amandinea punctata*, *Lecanora chlarotera*, and *Lecidella elaeochroma* classified as sensitive). These inconsistencies may stem from missing predictors since most of the misclassified species are early-successional crustose lichens preferring smooth bark or young trees (e.g., *Lecidella elaeochroma*, *Arthonia radiata*, *Lecanora chlarotera*, and *Glaucomaria* gr. *carpinea*; Van Haluwyn 2010), a factor that we did not include in our models due to lack of available data, but that is known to significantly impact epiphytic lichen communities (e.g., Cristofolini et al. 2008; Sebald et al. 2022). Those species could also be affected by observer bias, due to their small size or identification challenges (e.g., the identification of *Lecanora chlarotera* requires microscopy, *Punctelia jeckeri* was only recently separated from *P. subrudecta*; Crespo et al. 2004). Indeed, several studies have demonstrated that detection and identification difficulty significantly influence lichen species reporting (Brunialti et al. 2012; Counoy et al. 2023; Munzi et al. 2023). To account for this, we reported conspicuousness and identifiability of each species (Table 1), as estimated by von Hirschheydt et al. (2024). Conspicuousness reflects how easy a species can be detected in the field, while identifiability quantifies the ease of accurate identification based on: (1) the clarity of its taxonomic delimitation; and (2) the magnitude of morphological differences from similar species. Thus, results for species with low conspicuousness or identifiability should be interpreted cautiously, as they may reflect limitations in data quality rather than true ecological responses. Their inconsistent classification suggests that they may be less reliable indicators for large-scale biomonitoring due to susceptibility to phorophyte- and observer-related biases.

4.2.2 | Response to NO_x

Regarding NO_x, a clear negative effect was detected for 15 species, while only three responded positively: *Phaeophyscia orbicularis*, *Physconia grisea*, and *Physcia* gr. *adscendens*. This pattern aligns with literature suggesting that NO_x may have a more pronounced negative effect on overall lichen diversity than NH_3 (Greaver et al. 2023). The fact that the three positively responding species are among the most widespread (Figure 2b) and are widely recognized as nitrophilous and pollution-tolerant further supports our classification. Nonetheless, direct comparison with existing literature remains challenging, as very few studies have assessed species-level sensitivity to NO_x alongside NH_3 and SO_2 (Davies et al. 2007; Van Dobben 1999). In addition, given that NO_x concentrations can vary sharply at fine spatial scales (e.g., < 100 m; Hewitt 1991; Richmond-Bryant et al. 2017), our analysis based on predictors at a coarser resolution (~11 km^2) can only capture broad-scale trends rather than localized effects. It therefore remains unclear whether the observed increase in frequency for these three species reflects a true ecological preference or indirect mechanisms, such as competitive release following the disappearance of larger foliose species (Armstrong and Welch 2007; Connell 1961; Munzi, Cruz, et al. 2014).

Interestingly, we found contrasting responses for NO_x and NH_3. While several species responded positively (e.g., *Phaeophyscia orbicularis* and *Physconia grisea*) or negatively (e.g., *Lepra albescens* and *Ramalina farinacea*) to both forms of nitrogen, others showed divergent responses. For example, *Xanthoria parietina* was positively impacted by NH_3 but negatively by NO_x, whereas *Parmelia sulcata* and *Evernia prunastri* appeared sensitive to NH_3 without showing a clear trend in response to NO_x (Figure 4a,b and Table 1). These findings further suggest that lichens may exhibit distinct sensitivities to different nitrogen compounds, rather than responding uniformly to total nitrogen loads. Although physiological studies have long suggested that lichens may respond differently to NO_x and NH_3 (Greaver et al. 2023), such distinctions have rarely been explored in field studies, with few exceptions based on stable nitrogen isotope analyses (Gerdol et al. 2014). This gap likely arises because most local studies are conducted in areas where one nitrogen form predominates, complicating the isolation of compound-specific effects (Frati et al. 2006; Gadsdon et al. 2010). However, in large-scale studies spanning a broad gradient of environments (i.e., from rural to highly urbanized areas), separating the effects of NO_x and NH_3 becomes both more feasible and ecologically meaningful. This underscores the need to develop more refined bioindicator indices that distinguish between NO_x and NH_3 sensitivity. In parallel, further experimental research (e.g., fumigation) is required to clarify the underlying physiological mechanisms, which remain poorly understood.

4.2.3 | Response to SO_2

Among the three pollutants examined, SO_2 had the strongest negative effect on lichen species, with 28 out of 43 species (65%) showing a consistent decline in frequency across the 500 resampling iterations. This aligns with the well-documented toxicity of SO_2, which affects nearly all lichen species and leads to marked reductions in overall biodiversity. Only four species (i.e., *Amandinea punctata*, *Hypogymnia tubulosa*, *Lecanora conizaeoides*, and *Lecanora* gr. *expallens*) were positively associated with higher SO_2 concentrations. While *Hypogymnia* species are known to prefer acidic substrates (Geiser et al. 2021; Nimis 2025; Wirth 2010) and exhibit moderate resistance to SO_2, the three other species are among the most SO_2-tolerant taxa (Hawksworth and Rose 1970) and widely reported as dominant during the 1970s, when SO_2 pollution was still widespread (Kirschbaum et al. 2012). In particular, *Lecanora conizaeoides* is a well-known indicator species of SO_2-polluted environments and was virtually restricted to such conditions during peak industrial emissions. However, as previously mentioned, the model for *Amandinea punctata* may be biased due to observer-related issues linked to its inconspicuousness and difficulties in identification. These findings indicate that, despite the substantial decline in SO_2 emissions over recent decades, its ecological impact remains detectable, at least in certain areas where emissions are still significant, such as major port cities (e.g., Antwerp, Marseille) and industrial regions of northern Italy, which correspond to the highest SO_2 levels in our dataset.

4.2.4 | Response to Climate Variables

Contrasting responses were observed for temperature, with 13 species associated with cooler conditions (e.g., *Melanohalea exasperatula*, *Polycauliona polycarpa*, and *Polycauliona candelaria*) and eight showing affinities for warmer environments (e.g., *Parmotrema perlatum*, *Flavoparmelia caperata*, and *Hyperphyscia adglutinata*; Figure 4d and Table 1). Apart from inconspicuous or taxonomically challenging species, this classification showed an overall good agreement with the current knowledge of species ecology and distribution, most of those species exhibiting changes in frequency associated with spatial or temporal temperature gradients (Aptroot and Van Herk 2007; Kirschbaum et al. 2012).

Despite this high contrast in temperature affinity, most species appeared to be favored by intermediate or high mean relative humidity levels. Only two species were classified as negatively impacted (*Physcia biziana* and the taxonomically challenging *Lecanora chlarotera*; Figure 4e), while 17 were considered positively impacted, including species associated with both warmer and cooler conditions. This suggests that most widespread epiphytic lichens tend to be negatively affected by dry climates, whether warm or cold. These results are consistent with studies conducted in dry environments, where communities tend to display lower cover and diversity compared to those in more temperate or humid regions (Loppi et al. 2002).

Finally, a few species showed robust frequency variations linked to temperature seasonality (Figure 4f), reflecting adaptation to either oceanic (e.g., *Ramalina fastigiata* and *Diploicia canescens*) or continental (e.g., *Evernia prunastri* and *Hypogymnia physodes*) climates. Consequently, large-scale biomonitoring programs need to account for these climatic preferences to avoid misattributing species frequency changes solely to pollution or other environmental stressors.

4.3 | Selecting Indicator Species for the European Protocol

Despite the coarse resolution of the environmental data used, several broad-scale trends were detected, consistent with existing knowledge of lichen species sensitivities and ecological requirements. Notably, all 43 species examined responded to at least one pollutant or climate variable, with most responding to both. To our knowledge, this represents the first large-scale assessment at the European level, making a significant advance in understanding how widespread and easily recognizable epiphytic species respond to multiple environmental pressures.

Some species models, however, showed inconsistencies with existing literature. These discrepancies were limited to species affected by observer-related biases—due to challenges in detection or identification—and/or those strongly influenced by tree species characteristics, particularly bark roughness. While further standardization of phorophyte traits remains difficult, given limitations in finding suitable trees across regions, these findings suggest that the selection of indicator lichen species may need to be reconsidered.

Although the European protocol requires identification of all lichen species present, substantial observer bias has been documented, even among experienced lichenologists (Brunialti et al. 2012, 2019; Cristofolini et al. 2014; Vondrák et al. 2016), especially for inconspicuous or taxonomically complex taxa (von Hirschheydt et al. 2024). We therefore recommend excluding such species from large-scale biomonitoring analyses to reduce observer- and phorophyte-related biases and improve indicator reliability. Nonetheless, these species should still be recorded where feasible, especially in biodiversity conservation efforts (Giordani et al. 2009) or local-scale monitoring where observer consistency is higher (Brunialti et al. 2019). At broader spatial scales, focusing on lichen species that are easy to detect and consistently identified offers a more reliable basis for biomonitoring.

In support of this, Bergamini et al. (2007) demonstrated that macrolichens (i.e., non-crustose species), which are generally easier to identify, can serve as a proxy for total lichen diversity across several European countries. While their ecological indicator value was not assessed in that study, the findings support the approach of prioritizing easily identifiable species. However, this does not imply the exclusion of all crustose lichens; species such as *Phlyctis argena* and *Lepra albescens* are readily recognizable and can serve as robust indicators.

Interestingly, we also found responses to pollutants often assumed to have similar ecological effects (i.e., NH_3 and NO_x as eutrophying compounds, or SO_2 and NO_x as acidifying ones). This suggests that lichen communities have the potential not only to indicate overall nitrogen or acidity levels, but also to differentiate between specific nitrogen compounds. These results move beyond the traditional nitrophilous/acidophilous dichotomy and open the door to more nuanced environmental assessments.

Our analyses identified several species as potential climate change indicators, including taxa associated with warmer (e.g., *Flavoparmelia caperata*) or cooler conditions (e.g., *Polycauliona* spp.). Shifts in their frequencies have been documented in long-term studies from temperate regions such as Germany (Kirschbaum et al. 2012) and the Netherlands (van Herk et al. 2002), supporting their relevance for tracking rising air temperatures. However, as climate change is also projected to increase the frequency and duration of droughts (Calvin et al. 2023), species sensitivity to relative humidity should also be considered. While some drought-tolerant species (e.g., *Physcia biziana*) may increase in response to declining humidity, the general scarcity of such species suggests that drought is more likely to lead to a widespread decline in epiphytic lichen abundance rather than a distinct increase in drought-favored taxa.

Although our study did not determine species-specific tolerance thresholds, it identified robust, large-scale response patterns that offer a solid foundation for developing standardized biomonitoring indicators across Europe. Prioritizing widespread and easily identifiable species not only reduces observer-related bias but also facilitates broader protocol adoption, potentially expanding biomonitoring efforts to new regions and increasing public participation. Simplified approaches, such as those used in the French citizen science networks Lichens GO (38 taxa; Counoy et al. 2023) and VOCE (4 taxa; Dauphin et al. 2018), demonstrate how inclusive and accessible monitoring can support widespread data collection while maintaining ecological relevance. Our list of indicator species enables the creation of tailored tools—such as functional group classifications (e.g., Llop et al. 2012), community-weighted mean indices (e.g., Simijaca et al. 2023), or composite scores (Herzig et al. 2020; Will-Wolf et al. 2015; Wolseley et al. 2009)—that can translate species-specific responses into actionable air quality and climate assessments.

5 | Conclusions

This study represents the first compilation and analysis of 58 datasets from across Europe using the standardized lichen biomonitoring protocol. By examining protocol adoption patterns and identifying key implementation divergences (i.e., variation in phorophyte selection and lichen species groupings), we conducted a large-scale assessment of lichen responses to air pollutants and climate variables. Most findings were consistent with existing literature, while new insights emerged, notably the contrasting sensitivities of lichen species to reduced (NH_3) vs. oxidized (NO_x) nitrogen compounds. Thus, this study establishes the foundation for a new interpretative framework by providing a standardized list of indicator species with quantified responses to major pollutants and climate variables.

Our results demonstrate that data collected by different surveyors can yield ecologically meaningful insights, provided that taxa prone to observer- or phorophyte-related biases are treated with caution. These taxa, particularly those with pioneer behavior or low detectability, showed weaker agreement with established knowledge, likely due to identification challenges and variable tree species characteristics.

To improve comparability across studies, we propose the following recommendations: (1) prioritize phorophyte from genera *Acer*, *Quercus*, *Tilia* and *Fraxinus* (i.e., groups 1 and 2 defined by the European protocol), as their widespread distribution and their bark properties minimize substrate-related biases; (2) standardize the grouping of morphologically similar taxa (e.g., *Physcia adscendens* and *P. tenella*) to reduce reporting inconsistency; and (3) exclude pioneer and inconspicuous species from large-scale biomonitoring analyses to minimize observer- and phorophyte-related biases.

Looking ahead, two priorities emerge to advance lichen biomonitoring: (1) developing actionable air quality indices based on our species sensitivity classification to support a unified interpretative framework across Europe; this will enable consistent pollution mapping and climate impact tracking using lichen frequency data from reliably identifiable species; and (2) refining regional-scale analyses, particularly for NO_x, to capture spatial heterogeneity and improve resolution. By addressing methodological disparities while maintaining ecological rigor, our study reinforces the value of lichens as robust bioindicators and supports their integration into evidence-based environmental policy across Europe.

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Laure Turcati: supervision, writing – review and editing. **Franc Batič:** writing – review and editing. **Miris Castello:** writing – review and editing. **Cristina Branquinho:** writing – review and editing. **Claire Boucheron:** writing – review and editing. **Gregory Agnello:** writing – review and editing. **Lisa Brancaleoni:** writing – review and editing. **Immacolata Catalano:** writing – review and

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Acknowledgements

We would like to thank all those who generously contributed data that made this work possible: Mathieu Bagard and Jacques Mersch (Biomonitor), Eve Chretien and Jonathan Signoret (Atmo Grand-Est), Anne François (Atmo Normandie), Claude Remy (Arnica Montana), Nathan Martin (CPIE), and Patricia Wolseley. We sincerely thank the five anonymous reviewers for their insightful comments, which improved this manuscript.

Funding

This work was supported by Fonds pour la Formation à la Recherche dans l'Industrie et dans l'Agriculture (FRIA) from the Fonds de la Recherche Scientifique (F.R.S.-FNRS).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study is available in Data S1–S3 of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Selection of environmental variables and overview of the methodological framework. **Data S2:** Studies considered in the meta-analysis and reported lichen taxa. **Data S3:** Summary of modeling results.