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Modelling the response of urban lichens to broad-scale changes in air pollution and climate☆

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A B S T R A C T

To create more resilient cities, it is important that we understand the effects of the global change drivers in cities. Biodiversity-based ecological indicators (EIs) can be used for this, as biodiversity is the basis of ecosystem structure, composition, and function. In previous studies, lichens have been used as EIs to monitor the effects of global change drivers in an urban context, but only in single-city studies. Thus, we currently do not understand how lichens are affected by drivers that work on a broader scale. Therefore, our aim was to quantify the variance in lichen biodiversity-based metrics (taxonomic and trait-based) that can be explained by environmental drivers working on a broad spatial scale, in an urban context where local drivers are superimposed. To this end, we performed an unprecedented effort to sample epiphytic lichens in 219 green spaces across a continental gradient from Portugal to Estonia. Twenty-six broad-scale drivers were retrieved, including air pollution and bio-climatic variables, and their dimensionality reduced by means of a principal component analysis (PCA). Thirty-eight lichen metrics were then modelled against the scores of the first two axes of each PCA, and their variance partitioned into pollution and climate components. For the first time, we determined that 15% of the metric variance was explained by broad-scale drivers, with broad-scale air pollution showing more importance than climate across the majority of metrics. Taxonomic metrics were better explained by air pollution, as expected, while climate did not surpass air pollution in any of the trait-based metric groups. Consequently, 85% of the metric variance was shown to occur at the local scale. This suggests that further work is necessary to decipher the effects of climate change. Furthermore, although drivers working within cities are prevailing, both spatial scales must be considered simultaneously if we are to use lichens as EIs in cities at continental to global scales.

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1. Introduction

Cities are becoming more densely populated, with 80% of the European population estimated to live in them by 2050 (UN, 2019). Thus, the government-led transition to more sustainable and resilient cities must be hastened (Cartalis, 2014). Together with increased anthropic pressure, a city's sustainability and resilience is threatened by both local drivers (i.e. having a spatial scale of action at the city level), such as the heat island effect (Tam et al., 2015) or the gradual conversion of land from non-urban to urban uses (Romero et al., 1999), and broad-scale drivers (e.g. climate change, which has a broad spatial range of action) (Dawson et al., 2017). However, we currently do not understand the effects of drivers working on a broad spatial scale in cities. Therefore, cities' responses to these drivers must be compared at the continental level and not only within cities. Although this is more commonly done by examining physicochemical parameters (e.g. temperature, precipitation, and pollutants concentration), these parameters are unable to quantify the effects of drivers in ecosystems.

Epiphytic lichens have long been used as ecological indicators (EIs) of the effects of global change drivers on ecosystems (Aptroot et al., 2021; Asta et al., 2002; Brunialti et al., 2012). Consequently, lichen biodiversity-based metrics (taxonomic and trait-based) can be associated with particular environmental drivers (Branquinho et al., 2015). Taxonomic-based diversity metrics (e.g. species richness or total species abundance) respond to high-intensity drivers, such as air pollution (Hauck et al., 2013; Lättman et al., 2014), whereas less intense drivers cause shifts in species composition rather than species loss (Ellis and Coppins, 2006). Thus, taxonomic metrics should be complemented by trait-based diversity metrics as these are better at detecting compositional shifts in the communities, are potentially more universal as they are not linked to species identity, and are better indicators of ecosystem function in response to global change drivers (Van Der Plas, 2019).

EIs should quantify the effects of broad-scale drivers, even when local-scale drivers are present. However, this task is particularly challenging as i) the effects of local-scale drivers can overshadow broad-scale effects (Branquinho et al., 2019); and ii) the same environmental driver (e.g. temperature) works at both spatial scales (e.g. climate change and the urban heat island effect) (Jenerette et al., 2007). Lichens have been used as the EI of drivers working at the local scale in cities, which include urbanisation (Lättman et al., 2014), air quality (McCarthy et al., 2009), and the urban heat island effect (Munzi et al., 2014). In studies at the continental level, they have also been used to track broad-scale drivers, such as pollution (Mccune et al., 1997) and climate (Phinney et al., 2021), but only in natural and semi-natural ecosystems. Thus, it is still not known whether lichen biodiversity-based metrics can monitor the effects of broad-scale drivers on urban ecosystems. This could potentially be tested by looking into epiphytic lichen communities across multiple cities along a continental gradient of climate and air pollution for example, but this has not yet been tested.

The aim of this study was to quantify the variance in lichen biodiversity-based metrics (taxonomic and trait-based) that is explained by environmental drivers working on a broad spatial scale, in an urban context where local-scale drivers are also present and can potentially overshadow their effects. To do so, we sampled epiphytic lichens, to an extent that has never before been done in cities. We also calculated several taxonomic and trait-based metrics, and tested them as the EI of broad-scale air pollution and climate. This was done across a large spatial gradient in Europe (in seven cities from Lisbon to Tartu), representing a continental gradient of climate and pollution. Based on the existing knowledge, we expect part of the metric variance to be related to local-scale drivers. Nevertheless, we believe that by exploring such a large continental gradient, lichen metrics will also reflect the influence of broad-scale urban drivers. Additionally, broad-scale air pollution intensity is expected to surpass that of climate, as urban pollutants present a more deleterious effect on lichens than climate (Evju and Bruteig, 2013; Molina and Molina, 2004). For this reason, we expect taxonomic metrics to better reflect the effects of high-intensity drivers, such as broad-scale air pollution, whereas trait-based metrics are expected to be more responsive to less intense drivers, such as climate.

2. Materials and methods

2.1. Sampling sites

Lichen communities were sampled across seven European cities in 2018, under the BIOVEINS project (BiodivERsA32015014). Almada and Lisbon (Portugal), Paris (France), Zurich (Switzerland), Antwerp (Belgium), Poznan (Poland), and Tartu (Estonia) were chosen to represent a large continental gradient of air pollution, climate, and local city characteristics (Fig. S1). Cities present distinct spatial extensions, namely at local administrative unit level 2 (LAU-2 Level) (http://ec.europa.eu/eurostat/web/nuts/local-administrative-units). Thus, for consistency in the spatial extent, only one section was used for very large cities (e.g. Paris). In all the cities, the sampling sites represented a gradient of urban density. Sampling sites were selected within the "Green Urban Area" class of the pan-European land-cover classification from the European Urban Atlas (EEA, 2018), to confirm the land-use typology and intensity. Stratification was performed using a patch size and connectivity index to randomly select up to 36 patches per city (219 sites in total). See the supplementary material for further details.

2.2. Field sampling

Epiphytic lichen diversity was sampled following the European standard method (Asta et al., 2002; Cristofolini et al., 2014) (Fig. S2). The four trees closest to the centroid were sampled while following the method selection criteria (see Supplementary Material for more details). A sampling grid (50 cm × 10 cm, divided into five squares) was placed on the four main aspects, and all lichens inside the grid were registered. Species abundance was determined on the basis of the number of squares in which they occurred (max. 20). One hundred and forty species were identified, nine of which were classified to the genus level only (Table S1).

2.3. Biodiversity-based metrics

The taxonomic and trait-based metrics were then computed. Eight taxonomic metrics were calculated including species richness, number of rare species, the Shannon diversity index, Inverse-Simpson index, total species abundance; and, to quantify community dissimilarity, the Bray–Curtis, Jaccard, and Morisita–Horn dissimilarity indices were used. The R software (Team, 2020) was used to calculate the taxonomic diversity metrics using the functions *diversity* and *vegdist* from the Vegan package (Oksanen et al., 2011). Regarding the trait-based metrics, indices representing both functional diversity and functional structure were computed, accounting for the abundance of species identified to the species level (Table S1). This was performed based on seven categorical traits known to respond to climate and/or air pollution (Table S2); these are growth form, main photobiont type (green algae other than *Trentepohlia*, *Trentepohlia*, and cyanobacteria), species substrate pH tolerance, tolerance to solar irradiation, tolerance to aridity, tolerance to eutrophication, and poleotolerance. Trait information was retrieved from the ITALIC database (Nimis and Martellos, 2021), and the maximum value for each species was used (trait classification is ordinal in the ITALIC database). Regarding functional diversity metrics, we calculated functional richness and Rao's quadratic entropy (RaoQ), and for functional structure, we calculated the community weighted mean (CWM). Trait-based metrics were calculated using the R software (Team, 2020) function *dbFD* from the FD package (Laliberté et al., 2014). See the Supplementary Material for details on the metrics calculation and justification of the selected metrics. Some metrics were omitted in the main text because of their high similarity with the other presented results (see Supplementary Material).

2.4. Environmental variables

A set of 26 environmental variables representing air pollution and climate (Harlan and Ruddell, 2011) was extracted for each sampling site (the average values per city are shown in Table S3). Both pollution and climate were derived from models working at a continental scale, thus, climate and air pollution values show little variance within each city site; this means that they represent environmental gradients working at the continental scale. In addition, in this study, scale refers to the spatial extent to which variables work (i.e. where the variance in the environmental variables between sampling sites can be found), and not to the geographical spatial extent of the study or to the quantification of variables.

For abroad-scale climate, 19 bioclimatic variables representing air temperature and precipitation were retrieved from the CHELSA database (Karger et al., 2017) (average 1979–2013) at the maximum available spatial resolution of 1 km (Table S4). For broad-scale air pollution, redN and OxN deposition (mg·m $^{-2}$), as well as NH_3, SO_2, NO_x, PM2.5, and PM10 concentrations in the air (μg·m^{-3}) for the year 2018 were retrieved from the EMEP (Fagerli et al., 2019) at the maximum available spatial resolution (11 km). We tested pollutants data from several years (2000–2018). Because all years performed similarly, only 2018 was used for further analysis (See details on "Use of temporal pollution data" chapter in Supplementary Material). Owing to their spatial resolution, all extracted environmental variables present minimal variation at the local scale (e.g. within each city). To account for the remaining broad-scale variability not represented by climate and air pollution, an additional factor was added to the analysis. This factor is "Other", which corresponds to city identity and is meant to represent all other potential drivers working at the broad scale, aside from air pollution and climate. This factor is expected to represent the remaining city characteristics that vary on a broad scale (i.e. differentiating cities), such as city size, air pollution legacy, and management policies.

2.5. Data analysis

All analyses were performed with R software v. 4.0.3 (Team, 2020) using RStudio v. April 1, 1103 (Team, 2021). Two principal component analyses (PCAs) were performed, one on the set of 19 climate variables and another on the set of seven air pollution variables. This was done to reduce the number of variables to two dimensions each (two axes), while representing most of the variance in the original datasets. The site scores were used as climate and air pollution variables in subsequent analyses. The second axis of the climate PCA isolated Zurich in the precipitation gradient, suggesting the use of a log-transformation of precipitation variables (Table S4). However, the resulting PCA was similar to the non-log-transformed variable (data not shown); thus, the transformations were discarded. The PCAs were computed using the *prcomp* function from the stats package.

Spearman correlations were used to make a preliminary assessment of the relationships between air pollution, macroclimate PCA axes, and biodiversity metrics (Fig. S4), as well as to reduce the number of biodiversity metrics shown to prevent overcrowding.

The inter-quartile range (25–75), minimum, maximum, average, and median of each taxonomic, functional diversity, and functional structure metric were calculated by city and presented as boxplots.

Linear regressions were used to model the response of each biodiversity metric to the four climate and air pollution variables (the site scores of the first two axes of each driver's PCA). To ensure that the linear model approach was adequate, we checked the residual distribution (normality) and homogeneity of distribution (quantile-quantile and density plots) of the linear models (Figs. S5–S9). The residuals showed good distribution in terms of normality and homogeneity, thus confirming the adequacy of the linear models. The potential interactions between the four broad-scale pollution and climate variables (by means of multiplicative linear models) were not tested here, as our focus was on the individual effect of each broad-scale driver on each lichen biodiversity-based metric.

A categorical variable named "Other", coded as the city name, was also tested both as a fixed and random factor in the linear models. First, it was tested as a fixed factor, along with the four climate and air pollution variables, in an attempt to represent the remaining drivers other than pollution and climate acting at the broad scale (Biodiversity metric ~ Climate PCA1 + Climate PCA2 + Pollution PCA1 + Pollution PCA2 + Other). The variable "Other" was highly collinear with the remaining four variables (VIF >150,000), and the resulting model was not better in terms of fit; thus, this variable was excluded as a fixed predictor. This result suggests that all broad-scale variance could be accounted for by looking only at climate and pollution, and the city did not bear any extra information. The remaining four variables (climate and pollution) presented low collinearity (VIF <1.5) (Zuur et al., 2010), and were kept in the model. Second, "Other" was also fitted as a random term in a linear model [(Biodiversity metric ~ Climate PCA1 + Climate PCA2 + Pollution PCA1 + Pollution PCA2 + (1|Other)]. Across all modelled metrics, the variable "Other" explained the majority of the variance that was previously explained by air pollution and climate, thereby effectively cancelling their effect without adding new information. Because doing so would not allow us to separate the effect of broad-scale drivers without providing us with any new information, we proceeded with linear modelling variance partitioning. Thus, the linear models used to quantify the response of biodiversity metrics to broad-scale drivers did not include "Other" [(Biodiversity-based metric ~ Climate PCA1 + Climate PCA2 + Pollution PCA1 + Pollution PCA2].

For each model, the total R^2 variance was partitioned to assess the proportion of variance explained by each predictor working at the broad scale. The remaining variance (= 1 - R^2) was interpreted as unaccounted variance associated with drivers working at a local scale, without further detail. In other words, local-scale drivers were not investigated as this was not the focus of the study. Variance partitioning is presented for each biodiversity metric, and averaged by group (taxonomic, functional diversity, and functional structure for each trait) and main broad-scale driver to summarise the variance explained by each, thereby facilitating clarification of the study expectations. This was done assuming that all metrics had the same value. To prevent overcrowding, metrics with very similar responses were omitted from Fig. 3. The results of the remaining metrics are presented in the Supplementary Material (Fig. S10). The models were considered statistically significant at $p < 0.05$. Models were performed using the *lm* function from the stats package, and the variance partition corresponded to the sum of squares of each predictor divided by the total (i.e. sum of squares of all predictors). As previously stated, the remaining unexplained variance in the model, which is that not explained by any of the variables working at a broad scale, was interpreted as being most likely driven by variables working at the local scale (acting at the city spatial scale). We are confident of this interpretation of variance partitioning between the broad and local scales. The results (see above) of using "Other" as a fixed term in the model allowed us to assume that city identity represents all possible sources of variance at the broad scale (e.g. climate and pollution, but also geology, other climate variables, day length, city age or city environmental policies). Thus, although we did not include other broad-scale drivers, the fact that city identity accounted for the same amount of variance in lichen biodiversity metrics as pollution and climate (data not shown) gives us confidence that the four broad scale variables used are, in fact, the most important ones acting on a broad scale. In this way, we were able to extract most of the variance that could be accounted for at the broad scale, and the remaining unexplained variance in lichen metrics could be attributed to the local scale (e.g. caused by local air pollution or surrounding land-use, park, or tree characteristics).

3. Results

3.1. Summarizing the climate and air pollution continental scale gradients

The PCA of climate variables (Fig. 1a) showed a main gradient of temperature on the first axis (58.8%) and a gradient of precipitation on the second axis (21.6%). Together, they represented most of the variance in climate (80.4%), with sampling sites clustered in cities along the temperature axis. Almada and Lisbon overlapped over the side with the warmest temperature of the continental-scale climate gradient, as expected, given their close geographic proximity. Paris and Antwerp followed in the middle part of the temperature gradient, with Zurich and Poznan next to them. Tartu stood on the opposite side of the temperature gradient as the coldest city in the dataset. In relation to the precipitation gradient (second axis), Zurich was the wettest city in our dataset, whereas the remaining cities presented similar precipitation levels that were on the driest part of the gradient.

The PCA of air pollution variables (Fig. 1b) showed a clear main gradient of overall increasing air pollution loads on the positive side of the first axis (57.6%), and a second one (20.8%) representing a gradient of pollutant types. Together, they represented most of the variance in air pollution (78.4%). The second axis can generally be interpreted as representing a gradient of sites dominated by N-based compounds (corresponding to eutrophication), and sites dominated by sulphur dioxide and particulate matter (corresponding to acidification, although particles can also be associated with eutrophication). The cities did not appear to be as distinctly clustered by pollution as they did by climate. In terms of the overall broad-scale air pollution load, Paris, Antwerp, and Zurich were the most polluted cities, followed by Poznan, Lisbon, and Almada, with Tartu representing the least polluted part of the gradient. In terms of pollutant types, Paris, Antwerp, and Zurich appeared to be more dominated by N compounds, whereas Almada, Lisbon, and Poznan seemed to have more sulphur dioxide and particulate matter.

3.2. Characterization of taxonomic and trait-based metrics in lichen

In total, 140 species of lichen were identified across all cities (Table S1). We found that Lisbon, Tartu, and Zurich harboured more species-rich lichen communities, whereas Poznan had the least rich communities (Fig. 2). The values for the Shannon diversity index was also the highest (i.e. more diverse) in Lisbon, Tartu, and Zurich; and so was the total abundance of lichens in these three cities. Meanwhile, the lowest total abundance was observed in Almada and Poznan (Fig. 2). All cities showed high spatial dissimilarity values. On average, Almada was the most dissimilar, whereas Lisbon, Paris, and Zurich showed the lowest spatial dissimilarity (Fig. 2).

In terms of functional structure, foliose narrow-lobed lichens were the dominant growth form in all cities, whereas crustose and foliose broad-lobed lichens were present in lower and similar proportions (Fig. 2). The exception was Almada, where crustose lichens co-dominated with foliose narrow-lobed lichens, followed in abundance by foliose broad-lobed lichens. Fruticose lichens represented a small proportion across all cities (<5% abundance). Communities were also dominated by lichens tolerant to high solar radiation in all cities, with those with the highest tolerance level accounting for more than 75% of the total lichen abundance (Fig. 2). The exception was, again, Almada, where medium-tolerant species accounted for 25% of the abundance. However, the aridity pattern was different (Fig. 2). Species less tolerant to arid conditions (i.e. those that were more hygrophytic) were nearly absent from all cities, except Almada (13%). Poznan was completely dominated by species with medium-high tolerance to aridity, with Antwerp, Lisbon, Paris, and Zurich also presenting high abundances of these species (>60%). In Almada and Tartu, medium-tolerant species dominated. Lichens more tolerant to eutrophication were clearly dominant (usually representing more than 50% of the total) in Paris, Zurich, Poznan, and Lisbon (Fig. 2). These were also the cities where species with lower eutrophication tolerance was scarce. However, in Antwerp, highly tolerant but especially medium-high eutrophication-tolerant lichens dominated. Tartu and Almada showed a more uniform distribution of species abundance between the different levels of eutrophication tolerance (Fig. 2). Similar to species richness, functional richness values were also highest in Tartu and lowest in Poznan, while the remaining cities ranked in the middle with similar values (Fig. 2). Regarding functional dispersion, Almada showed the highest values and Poznan showed the lowest (Fig. 2).

3.3. Partitioning the proportion of variance in biodiversity metrics explained at the broad and local scale

The vast majority of the models (Fig. 3 and S10) were found to be highly significant, showing p-values lower than 0.001, thereby strongly supporting their use for interpreting the data. Across all biodiversity metrics (Fig. 3), the four broad-scale drivers explained an average of 15%. The remaining unexplained variance was on average 85%, and was assumed to represent all drivers that are not working at the broad scale. This can thus be interpreted as local-scale variation (i.e. acting at the city scale). For six biodiversity metrics, broad-scale drivers explained more than 20% of the variance. Only the Jaccard, low tolerance to irradiation, and high tolerance to aridity models were not significant.

Considering the main broad-scale drivers (pollution and climate) and

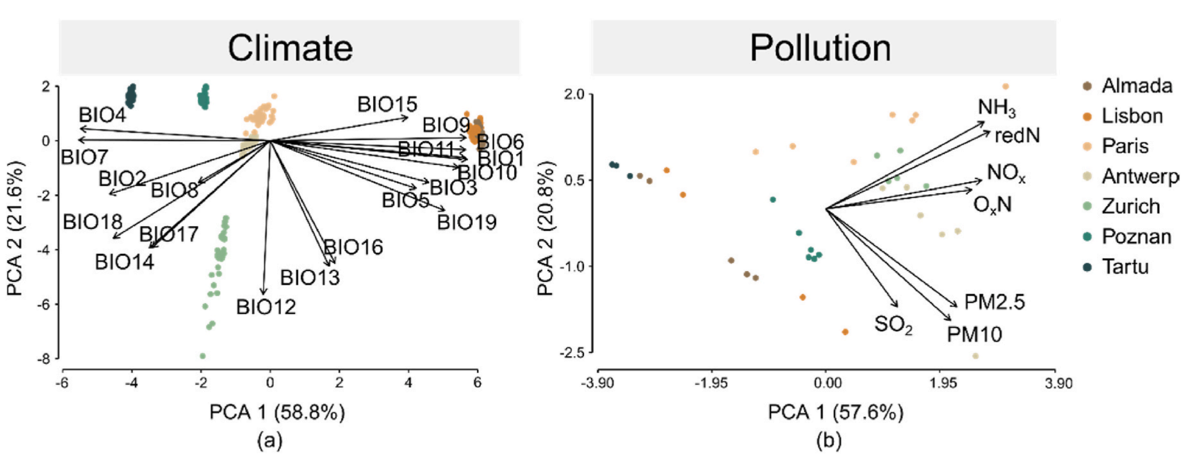

Fig. 1. Principal Components Analysis showing the ordination of sampling sites (N = 219) along climate (a) and air pollution (b) gradients. Decoding of pollution variables can be seen in Table S3. Decoding of bioclimatic variables can be seen in Table S4. Sites overlap in PCA (b) due to the lower spatial resolution of air pollution variables.

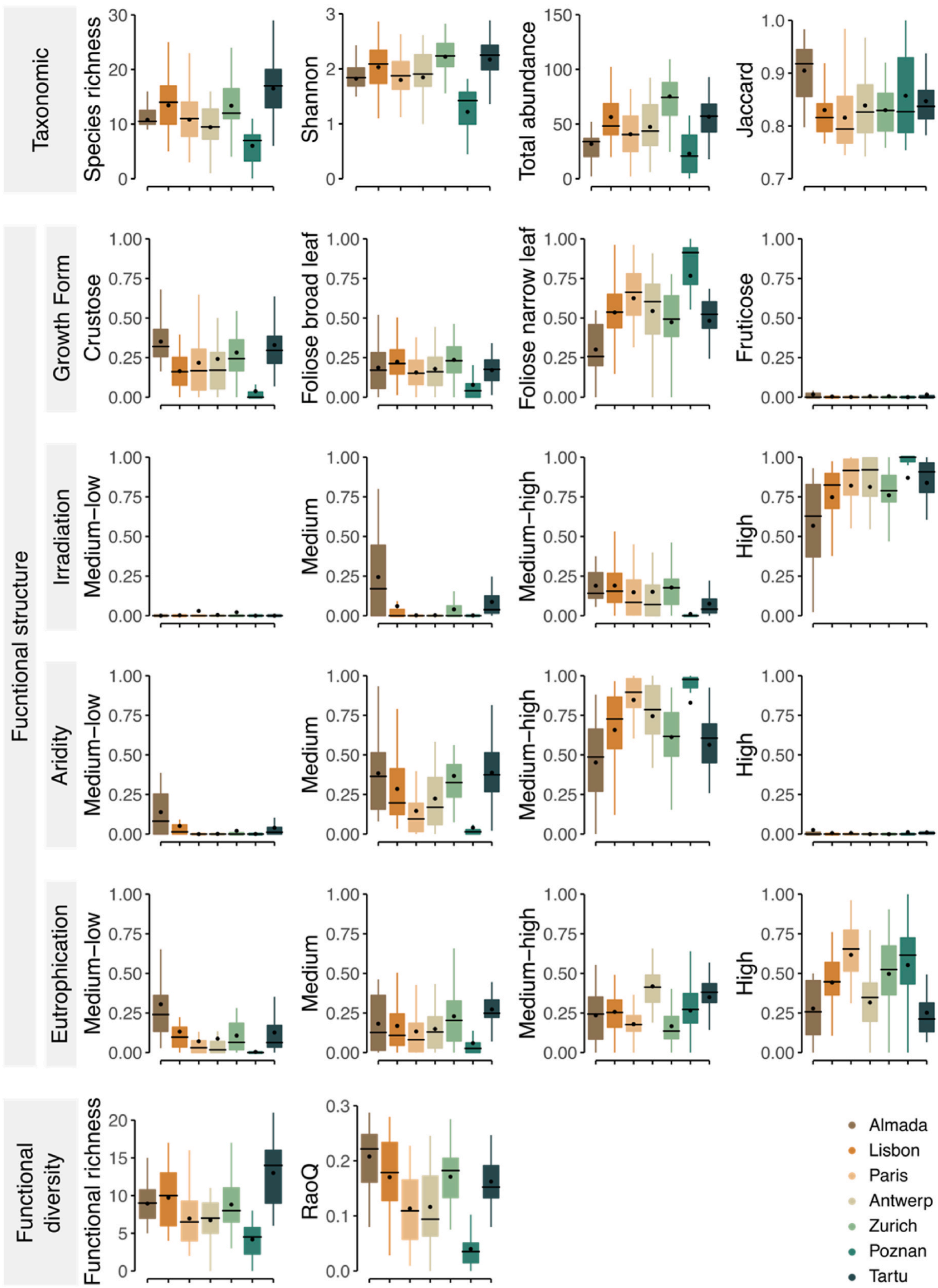

Fig. 2. Boxplots representing the distribution of taxonomic, functional structure and functional diversity metrics in the seven European cities, ordered here from the warmest (Almada to the coldest (Tartu), as indicated in the first axis of the PCA. Shannon, Jaccard and Rao's Q indices values range from 0 to 1. The functional structure, represented here by the CWM of each functional group (Table S2) belonging to the same trait (growth form, tolerance to irradiation, tolerance to aridity, tolerance to eutrophication) ranges also from 0 to 1 (the sum of all functional groups from the same trait is 1 at site level). Boxes display the interquartile range (25th and 75th percentiles), the black lines the median, the dots the average, and the whiskers the maximum and minimum (N = 219).

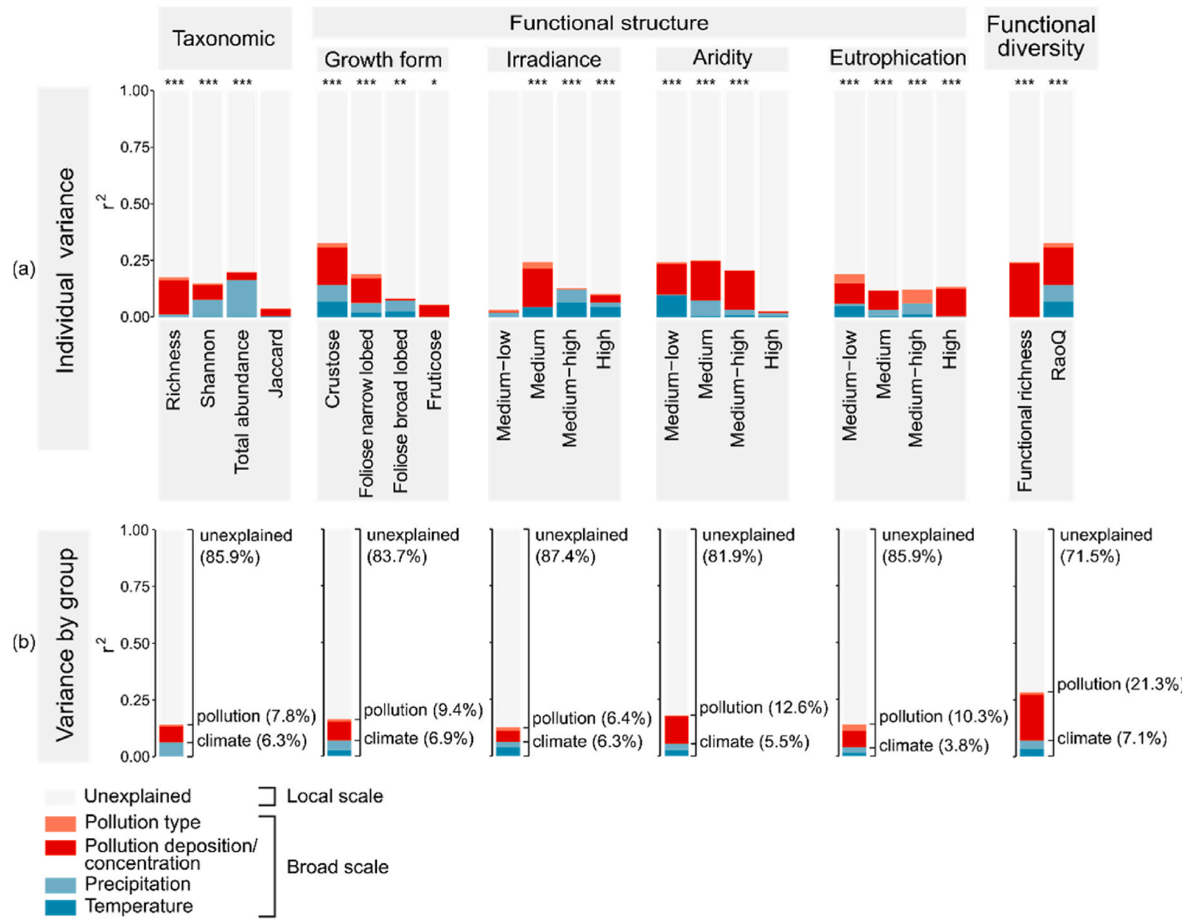

Fig. 3. Variance partitioning of broad scale drivers for each (a) lichen biodiversity metrics and (b) the average variance partitioning for each group of metrics. Metrics are grouped into taxonomic and trait-based, the latter sub-divided into functional diversity and functional structure by trait (growth form and tolerance to irradiance, aridity and eutrophication). Significance of the model is indicated in superscript: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$. Averaged variance (%), per spatial scale and metric group, was calculated assuming all metrics to value the same when evaluating changes in lichens community structure.

all the biodiversity metrics together, air pollution accounted for most of the variance found at the broad scale; it explained, on average, 11.3% of the variance, while climate explained 6.7% (Fig. 3b). When the metrics were grouped into taxonomic and functional structures or according to functional diversity (i.e. by the metric type, Fig. 3b), broad-scale pollution surpassed climate across the three metric groups. When considering each metric individually, air pollution also surpassed climate across 14 of the 22 biodiversity-based metrics.

Within the taxonomic metrics group, which is composed of the species richness, Shannon index, total abundance, and Jaccard dissimilarity index, air pollution explained more variance (7.8%) in comparison to climate (6.3%). However, not all taxonomic metrics responded equally (Fig. 3a). Within the significant models, species richness responded almost exclusively to the broad-scale air pollution gradient (17.5%), the Shannon index responded similarly to both pollution and climate (7.6% and 7.5%, respectively), and the total abundance responded mainly to climate (16.3% out of 19.9%).

Air pollution also explained the majority of the variance in functional diversity metrics (21.3% on average; Fig. 3b). Nevertheless, similar to the taxonomic diversity, each functional diversity metric responded differently. While the functional richness variance was almost exclusively explained by broad-scale air pollution (24.3%), for the RaoQ metric, both pollution and climate were equally relevant (18.4% and 14.2%, respectively; forming a total of 32.6%).

Regarding the functional structure, the relevance of each broad-scale driver was also different depending on the trait considered, and even among functional groups within the same trait (Fig. 3b). The variance explained by growth form was mostly attributed to the air pollution gradient (7.2% versus 4.3% of climate). Considering each growth form (Fig. 3a), air pollution was more important than climate for crustose and foliose narrow-lobed lichens (9.7% in 13.4%, and 12.8% in 19%, respectively), and it was the only driver explaining variance for fruticose (5.4%). For foliose broad-lobed lichens, climate was the most important driver (7.1% out of 8.1%). For the irradiance trait (Fig. 3a), the variance explained was almost equally divided between the two broad-scale drivers when the average of all functional groups of the trait was considered. Within the significant models, the medium irradiance tolerance metric was mainly explained by air pollution (19.9% in 24.3%) and was one of the six models in which broad-scale drivers jointly explained more than 20% of the variance. Contrarily, in both the medium-high and high metrics, variance was more satisfactorily explained by climate (19.9% in 24.3%, and 6.4% in 10.2%, respectively). For the aridity trait, air pollution explained, on average, twice as much as climate (12.6% versus 5.5%, Fig. 3b). In the medium-low, medium, and medium-high metric variances, air pollution surpassed climate (14.4% in 22.2%, 17.9% in 25.1%, and 17% in 20.4%, respectively). Finally, for the eutrophication trait, most of the variance was also explained by broad-scale pollution (10.3% versus 3.8% for climate, Fig. 3b). Within the medium-low and medium metrics, air pollution was in fact the main broad-scale driver (13.2% in 19%, and 8.7% in 11.8%, respectively), while in the medium-high metric, the importance of air pollution was similar with that of climate (5.6% and 6.1%, respectively).

4. Discussion

For cities adaptation and compliance with the United Nations' Sustainable Development Goals (SDGs) (UN, 2015), we must focus on a key aspect of urban areas, namely urban ecosystems (Maes et al., 2019). Therefore, it is fundamental to evaluate the effects of global change drivers at the ecosystem level, and this can only be fulfilled by comparing cities across large areas (i.e. continental to global) and looking at drivers working at the broad scale using EIs (Hák et al., 2016). To the best of our knowledge, this is the first time that lichen biodiversity-based metrics have been used as an EI to quantify the importance of broad-scale drivers in an urban context. Our study found that broad-scale drivers accounted for an average of 15% of all variance among lichen metrics. Furthermore, within the broad-scale drivers studied, air pollution (10%) was more important than climate (5%) across all metric groups. Consequently, and as expected, taxonomic metrics were better explained by the broad-scale air pollution drivers. However, contrary to our expectations, broad-scale climate was less important than broad-scale air pollution for trait-based metrics.

Broad-scale drivers (nearly homogeneous within the city and, thus, have little variance between sampling sites) accounted for an average of 15% in lichen metric variance, and reached a maximum of 33% in the RaoQ metric. Although the relevant studies were conducted only in natural or semi-natural environments, the effects of broad-scale drivers on lichen communities are well-documented (Geiser et al., 2021; Phinney et al., 2021). Therefore, we expected the variance partitioning among urban lichen metrics to reflect, to some extent, the influence of these broad-scale drivers. Although broad-scale drivers play a role in shaping urban lichen diversity, the unexplained variance suggests that drivers acting at the local scale may overshadow this effect. These local-scale drivers are known to act as high-intensity drivers and are well-documented in cities, albeit only for single-city studies (Davies et al., 2007; Koch et al., 2019; Munzi et al., 2007). Along with the urbanisation process, lichen communities are driven towards species that are more tolerant to the effects of high-intensity local drivers (Hawksworth, 1990; LiŠKa and Herben, 2008), to a point where the effects of other less intense drivers (i.e. broad-scale climate) are overshadowed. Thus, one potential solution to better isolate the effects of broad-scale drivers on lichen communities is to have standardisation for such local-scale effects. This could be done, for example, by homogenising the characteristics of the sampling sites (e.g. green areas of the same size). Another possibility is to include more cities with broader gradients of broad-scale pollution and climate. However, because the effects of broad-scale drivers are statistically significant across the majority of metrics, both spatial scales must be considered simultaneously to interpret lichen data derived from multi-city studies.

Within the broad scale, and as expected, the air pollution gradient was overall more significant (10% out of 15% of the total broad scale variance) to lichen metrics than climate. Air pollution has long been a high-intensity driver in urban areas due to the presence of local industrial and traffic pollutants within nearby cities (Babiy et al., 2003; Fenger, 1999), which translates to increased pollutant concentration or deposition (Krzyzanowski et al., 2014; Riga-Karandinos and Saitanis, 2005). Although the role of specific pollutants has been observed in several local-scale studies (Llop et al., 2017; Varela et al., 2018), our results suggest that on a broad scale, when multiple pollutants are superimposed, lichens respond to pollution overall rather than to specific pollutants. Because lichens absorb pollutants from wet and dry atmospheric deposition (Van Der Wat and Forbes, 2015), increased air pollution levels translate to an overall harmful effect on most lichen species, and result in consequent species loss, as reported by several authors in single-city studies (Gary, 2010; Koch et al., 2016; Munzi et al., 2007). Here, we confirm that this pattern is also visible at the broad scale, as the influence of broad-scale air pollution largely surpassed that of climate on species richness, one of the largest across all metrics. Meanwhile, for both the Shannon index and total abundance metrics, the importance of pollution in relation to climate decreased. In contrast to our initial expectations, air pollution was also the main broad-scale driver across both functional structure and functional diversity metric groups, reaching a maximum of 24% with the functional richness metric. These results reinforce the idea that high-intensity drivers, such as pollution, act as filters for lichens, promoting both species loss and the overall narrowing of functional groups. Thus, metrics based on presence (i.e. species richness or functional richness) are more suitable for tracking the effects of high-intensity drivers, regardless of them being taxonomic or trait-based in nature. Based on our results, we can also suggest that air pollution in Europe is still above the critical level and load for lichens (Cape et al., 2009); in other words, pollution levels are above the threshold for causing shifts in lichen communities. These shifts can either be due to overall negative effects of pollution or to a fertilizing effect on more tolerant lichen species (Fig. S4), although our data does not allow to disentangle their effects as they co-occur. This is in accordance with what was observed in other studies (Llop et al., 2012; Llop et al., 2017), but was observed for the first time in multiple cities and with broad-scale air pollution. The air pollution model used (EMEP MSC-W) includes not only pollution sources and concentrations, but also climatic information. Thus, the broad-scale air pollution data are expected to be richer than the climate data, which could help explain why it surpassed climate across all metric groups. This cannot be avoided, as it represents both broad-scale pollution and climate as accurately as possible. However, if climate alone had no effect on lichens, we would not have retrieved models based mostly on pollution. This reinforces the interpretation that air pollution is the main driver of lichen community composition on a broad scale, although it is very likely that climate has an indirect effect by affecting pollutant dispersion and deposition (Fiore et al., 2015; Kinney, 2008). Although not tested here, future studies should aim to assess the effects of the interactions between both broad-scale drivers on urban ecosystems. Still, to do that, sampling must be extended to a larger number of cities, which may be unfeasible. The effects of the broad-scale climate were, as expected, lower than those of pollution across all metrics and metric groups (average of 5% out of 15%). Despite the large continental gradient representing a broad range of climatic conditions (mean annual temperature and annual precipitation ranging from a maximum of 17 °C and 1071 mm to a minimum of 5 °C and 517 mm, respectively), its importance to all lichen metrics was still low. The response of lichens to broad-scale climate change has been well-documented (Concostrina-Zubiri et al., 2014; Di Nuzzo et al., 2021; Hurtado et al., 2020; Matos et al., 2015); however, those studies were mostly conducted in natural and semi-natural environments. Nevertheless, our work suggests that, in urban contexts, air pollution is probably still the most limiting factor for lichens, overshadowing climate effects. In fact, the two least polluted cities, Almada and Tartu, showed a high abundance of lichens that were more sensitive to aridity, suggesting that climate can become an important driver of lichen diversity when air pollution is not prevalent. Such phenomenon has already been detected in a previous study in Almada (Munzi et al., 2014), where the effects of the urban heat island were only detected when air pollution was low. The effects of climate on lichens are expected to be of lower intensity than those on air pollution, primarily inducing compositional shifts in lichen communities, which should be reflected more in trait-based metrics than in taxonomic ones (Ellis and Coppins, 2006). For this reason, we expected a higher contribution of the broad-scale climate across the trait-based metrics, particularly in climate-related traits (e.g. irradiance, aridity). Nevertheless, broad-scale air pollution surpassed the contribution of climate in these metrics groups also, emphasising the still prevalent role of other high-intensity drivers, such as air pollution, in cities. Furthermore, low-to intermediate-intensity drivers, such as climate, are expected to lead to changes in the abundance of lichen species (Branquinho et al., 2019), rather than species loss. Here we confirm that view, as metrics based on abundance (i.e. total abundance, RaoQ) reflected a high contribution from broad-scale climate. However, to develop EIs for the effects of climate in cities, future research must also focus on either proposing alternative metrics or developing statistical methodologies to disentangle the effects of the prevailing environmental drivers (e.g. air pollution) before examining the effects of climate. Such a need has already been raised (Branquinho et al., 2015), but remains unanswered. Although this problem is foreseen to decrease in the future, with the increasing importance of climate change together with a decrease in air pollution loads across Europe (Ortiz et al., 2020), disentangling climate from the remaining urban global change drivers is fundamental to establishing a baseline of effects on a broad scale (Ellis and Coppins, 2010; Nascimbene et al., 2012).

In the urban areas studied, the importance of local-scale drivers across all tested metrics, assumed here to represent the proportion of variance not explained by the broad-scale drivers, averaged at 85%. These could include local pollution sources (e.g. industrial, or from facilities or traffic), green urban area management and history (e.g. parks created from existing woodlands), and phorophyte species and age (although this last one was partially controlled through field sampling phorophyte restrictions), all of which have been seen to impact urban lichen communities (Matos et al., 2019; McDonald et al., 2017; Munzi et al., 2014). These results show the need to further detail the local drivers and their sources. To do so, one requires the use of local environmental data, which should be derived from common methods, rather than local information sources, such as city-specific cartography or single-city studies. Furthermore, other methods, such as lichen elemental analysis, can complement the application of lichens as ecological indicators because they possess the capacity to detail local pollution sources and origins (Jeran et al., 2002; Van Der Wat and Forbes, 2015). However, this is a more costly approach, contrary to the method of using ecological indicators, and cannot reflect the effects of environmental drivers at the ecosystem level. Thus, these findings emphasise that, for future European (EU) and global (UN - 11th SDG) efforts towards more sustainable and resilient cities, the development of indicators to monitor the effects of global change drivers on urban ecosystems must be able to detect the effects of drivers working at both scales and be applied over wide continental to global gradients (Hák et al., 2016; Klopp and Petretta, 2017). Despite all limitations and future challenges, biodiversity-based EIs are a valuable tool for quantifying the effects of broad-scale drivers on the structure and properties of urban ecosystems. As they are based on biodiversity, the backbone of ecosystem functioning, they can reflect the effects of these global change drivers on urban ecosystem services and functioning, which analytical methods (i.e. pollutant concentration, air temperature, precipitation, and humidity level monitoring) alone are not capable of translating. Furthermore, their cost-effectiveness allows for extensive monitoring of these effects over multiple cities.

5. Conclusions

For the first time, we quantified the amount of variance in lichen biodiversity metrics explained by broad-scale drivers associated with pollution and climate in urban areas. Overall, broad-scale drivers explained 15% of variance in lichen metrics, suggesting these were overshadowed by the effects of local drivers. Thus, our work supports the need to quantify the effects of drivers working at a local scale, even in multi-city studies. On a broad scale, air pollution was more important than climate, suggesting that urban lichen communities are primarily driven by pollution. Prior to this study, this has only been shown for single-city studies, but now it is also shown here in a multi-city design. The results also suggest that the effects of climate change can be detected only when pollution decreases. In our study, the effects of broad-scale drivers had a statistically significant effect on lichen metric variances, and thus must be considered alongside local drivers. From an ecological indicator perspective, the overall low contribution of broad-scale drivers across most metrics suggests that the tested lichen biodiversity-based metrics and statistical approaches are difficult to apply directly, that is, independently of the local context, when characterizing the effects of broad-scale drivers. However, the capacity of EIs to reflect the effects at the ecosystem level makes them valuable tools for achieving UN conventions goals in urban areas, such as those goals related to air pollution (CLRTAP) and climate change (UNFCCC). Their application can help overcome the lack of baseline characterization of pollution and climate effects, especially in southern European cities. In so doing, they can help create more resilient cities to face future climate change effects, as well as strategies to measure the efficacy of adopted measures. However, metrics must first be compared across cities, and for that, the effects of broad- and local-scale drivers must be simultaneously considered. Thus, to use them to evaluate the effects of broad-scale drivers in urban ecosystems, alternative sampling designs or statistical approaches must first be considered.

Author contributions

Bernardo Rocha: conceptualization, methodology, formal analysis, writing—original draft preparation, writing—review and editing and visualization; Paula Matos: conceptualization, methodology, formal analysis, writing—original draft preparation, writing—review and editing and visualization; Paolo Giordani: conceptualization, methodology, formal analysis, writing—original draft preparation and writing—review and editing; Lõhmus Piret: data curation and writing—review and editing; Cristina Branquinho: sampling design, formal analysis, writing—review and editing and funding acquisition; Joan Casanelles Abella: sampling design and writing—review and editing; Cristiana Aleixo: sampling design and writing—review and editing; Nicolas Deguines: writing—review and editing; Tiit Hallikma: sampling design and data curation; Lauri Laanisto: sampling design, conceptualization and writing—review and editing; Marco Moretti: sampling design, writing—review and editing and funding acquisition; Marta Alos Orti: data curation and writing—review and editing; Roeland Samson: writing—review and editing and funding acquisition; Piotr Tryjanowski: sampling design, data curation and writing—review and editing; and Pedro Pinho: sampling design, conceptualization, methodology, formal analysis, data curation, writing—original draft preparation, writing—review and editing, visualization project administration and funding acquisition. All authors have read and agreed to the published version of the manuscript.

Declaration of competing interest

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

Data availability

The authors are unable or have chosen not to specify which data has been used.

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Appendix A. Supplementary data

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