Resurvey studies of terricolous bryophytes and lichens indicate a widespread nutrient enrichment in German forests

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Abstract

Questions: Vegetation resurveys, both single studies and meta-analyses, have predominantly been based on vascular plant data while bryophytes and lichens have largely been neglected. Our study aims to fill this gap and addresses the following research questions: has the overall species richness of terricolous bryophytes and lichens in forests changed over time? Which are the winners and losers among single species and ecological species groups? Do the results give a signal of the impact of nutrient enrichment, of changes in the light regime and of climate change?

Location: Deciduous and coniferous forests in Germany.

Methods: We compiled 35 single resurvey data sets, including 1096 plots in total (each sampled twice). The time interval between initial surveys and resurveys ranged from 10 to 65 years. The differences between old and new plots were analysed with respect to the frequency of single species, total species richness, and the absolute and relative numbers of taxa in the species groups. Trend scores of species were related to ecological indicator values to identify the main environmental drivers behind the observed changes.

Results: Total species richness did not systematically change, while pleurocarpous mosses had increased at the expense of acrocarpous mosses and, in coniferous forests, of lichens. Weak changes were generally observed in deciduous forests on base-rich soils. In coniferous forests and in deciduous forests on acid soils, species with high nitrogen demand and high shade tolerance had increased, whereas those being typical for more infertile and open forest sites had decreased. There were trends towards a larger share of taxa with a more oceanic distribution.

Conclusions: The changes in the vegetation of terricolous bryophytes and lichens in the studied forests indicate nutrient enrichment and increasingly shady conditions in forests on acid soils, likely caused by nitrogen deposition and shrub layer closure.

Keywords
acrocarpous mosses, bryophytes, Ellenberg indicator values, lichens, liverworts, nitrogen deposition, pleurocarpous mosses, shrub layer, species trend scores, tree layer
1 | INTRODUCTION

Species composition and diversity change over time, caused by various processes. These include stochastic events such as succession, temporal fluctuations of weather and soil conditions, as well as directed changes of environmental, including anthropogenic, drivers. It is an important task of vegetation science to disentangle the ‘natural’ and ‘human-induced’ parts of these processes for taking measures in time to counteract anthropogenic change and to halt biodiversity loss.

Whereas most field monitoring surveys and experiments are short-term and do not capture changes acting over several decades, long-term observations have the potential to detect also slower changes and their underlying drivers. In vegetation science, resurveys—comparing historical plot records with current data from the same sites—have become an important and popular tool (Hédé et al., 2017; Kapfer et al., 2017). Especially when such time series data are analysed across larger spatial scales and different habitat types (Verheyen et al., 2017) and are complemented by measured environmental data (Litz & Diekmann, 2017; Peppler-Lisbach et al., 2020; Mazalla et al., 2021), resurveys offer general insights into the regional dynamics of plant communities. At present, most vegetation resurvey studies are available from forests, owing to the high number of past vegetation records and the relative simplicity to install permanent markings on trees or to draw detailed maps with woodland plot locations. Apart from a large number of single resurvey studies mainly from northern temperate regions in Europe and North America, several meta-analyses have lately examined the general patterns of forest vegetation change across larger areas or whole continents (Verheyen et al., 2012, 2017; Bernhardt-Römermann et al., 2015). In general, these studies have suggested a turnover of understorey communities towards a higher share of more nutrient-demanding and shade-tolerant species, while total species richness has remained largely unchanged. More recently, also other habitat types have been subject to resurveys, for example seminatural grasslands (see meta-analysis by Diekmann et al., 2019) and arable fields (e.g., Meyer et al., 2013).

The evidence from the above-mentioned publications almost exclusively relies on the examination of vascular plants, namely in forests the herbaceous layer that is more species-rich and less affected by management than the woody layers. In contrast, much less is known about bryophytes and lichens in the ground layer, with the exception only of pine forests on sandy, acid soils (Reinecke et al., 2011, 2014; Fischer et al., 2015; Stefańska-Krzaczez et al., 2018). This is also true for epiphytic species. There are three main reasons for this knowledge gap: (1) in many habitat types, including most types of deciduous forest and grassland, terricolous (epigeic) bryophytes and lichens are clearly less species-rich than vascular plants; (2) many plant ecologists consider them as more difficult to identify and traditionally tend to neglect them; (3) in habitat types such as forests, bryophytes and lichens are perceived as ecologically less relevant than vascular plants (Ewald, 2009), and their ecological optima and tolerances towards environmental factors are less well known (but see Schönhar, 1996). As a consequence, bryophytes and lichens have often been or are still ignored, both in the sampling of vegetation plots and in reviews, although bryophytes have received increasing attention lately (e.g., Cacciatori et al., 2022; Stefańska-Krzaczez et al., 2022). Accordingly, to our knowledge, bryophytes and lichens have not been treated in previous resurvey meta-analyses. Here, we argue that they should receive more attention in long-term studies, as they may offer additional information to or other insights than the evidence obtained from vascular plants. The thallus of bryophytes does not have a cuticle (comparable to that of vascular plants), causing the plants to be predominantly ectohydric, that is, they (with the exception of e.g. Polytrichum) lack an internal vascular tissue and take up water and nutrients through the surface of the whole gametophyte (thalli, stems and leaves) (Buch, 1947; Hosokawa et al., 1964). Lichens also do not possess a thallus with an efficient protection against desiccation. Both are thus highly exposed to the (changing) environment and have since long served as excellent indicators of the levels of air pollution, especially sulphur or nitrogen deposition (Skye, 1979; Slack, 2011). Many bryophytes and lichens are also fast colonizers and may track environmental changes more rapidly than vascular plants (e.g., Becker Scarpitta et al., 2017). An example is the recovery of many epiphytic bryophyte and lichen species resulting from drastically reduced SO2 emissions since the 1990s (Pescott et al., 2015; Krause et al., 2017; Koperski, 2018).

To put a stronger focus on cryptogams in the study of long-term vegetation changes, we systematically collected resurveyed vegetation plots including complete records of terricolous bryophytes and lichens. Apart from giving some general information about the species richness of bryophytes and lichens in the forests, our main research questions are: (1) has the overall species richness of terricolous bryophytes and lichens in forests changed over time? (2) Are there consistent trends of increase or decrease in the major groups of species, such as lichens and the main growth forms of bryophytes? (3) Which are the winners and losers among single species, and do the ecological requirements and traits of these species allow us to identify the environmental factors that drive the vegetation change? More specifically, (4) does an altered species composition of bryophytes and lichens give an indication of the impact of nutrient enrichment that differs from that observed in vascular plants? (5) Is there a signal of a changing light regime or climate change on the long-term dynamics of the species?

2 | METHODS

2.1 | Data search

The compilation of data sets started with a search in the ISI Web of Science, using different combinations of search terms [resurvey OR revisitation OR (semi-)permanent plot* AND forest OR woodland AND vegetation AND cryptogam* OR bryophyte* OR lichen*]. Papers were only retrieved if they included, usually in the form of appendices, full vegetation tables with single plots. The papers were
also screened for secondary publications that included resurvey plots. If the papers did not report the detailed information for single plots, authors were contacted and asked to contribute to the database. In addition, data sets were searched for in regional journals and also obtained from colleagues. Several of the data sets have their origin in Bachelor and Master theses conducted at the University of Bremen and other universities in Germany.

To be included in the database, some pre-conditions had to be met: (a) for reasons of data availability, the current study focuses on forests in Germany, located mainly in the northern parts of the country where especially coniferous and deciduous forests on acid, nutrient-poor soils are widespread and well-studied. (b) Studies were only retained if the resurveyed plots represented truly permanent or semi- (quasi-)permanent plots as defined by Kapfer et al. (2017). (c) There had to be sufficient information about sampling years, plot sizes, and the approximate location of the study sites. (d) Studies were kept only if the methods and results tables indicated that a complete list of terricolous bryophytes and lichens was sampled in all plots. For the final data analysis, a total of 35 data sets were used (Appendix S1). These differed largely with respect to the number of plots (varying between 10 and 78) and to the time interval between initial survey and resurvey (ranging from 10 to 65 years). The total number of plots was 1096 (each sampled twice resulting in 2192 plot records).

### 2.2 Data handling

Prior to the statistical analysis, all data sets were transformed and standardized. As the cover abundance scales for the species differed widely between data sets and in some cases were not explicitly detailed, only presence/absence values were used for all species-specific analyses. An important first step was the harmonization of species lists and taxonomy, for which we applied the reference lists for German bryophytes (Koperski et al., 2000) and lichens (Wirth et al., 2011). In some cases—when different taxonomic concepts were applied in the initial survey and resurvey, or in different data sets, and when authors indicated that species identification was difficult—taxa were merged to aggregates, such as *Hypnum cupressiforme* (mainly *H. cupressiforme*, on acid soils especially in coniferous forests also *H. julandinicum*), *Leucobryum glaucum* (mainly *L. glaucum*, rarely in the south *L. juniperoides*) and *Plagiothecium laetum* (mainly *P. laetum*, including *P. curvifolium*). Most authors distinguished *Brachythecium* to the species level, but as the genus includes several forest-inhabiting taxa that are difficult to identify, records of *B. rubrotinctum* may in some cases include also *B. oedipodium* and *B. salebrosum*. No species were distinguished in the lichen aggregates *Cladonia arbuscula*, *C. furcata*, *C. gracilis* and *C. pyxidata*.

Plot sizes varied considerably between the data sets. While 400 m² was the most frequently used plot size, being applied in 11 studies, values ranged from 12 to 900 m². In most initial data sets, plot sizes were not held constant, while the resurveys in all cases except one (data set 34) applied the same area as for the corresponding initial plot. Whereas information about plot sizes was available for all plots, percentage values for the total cover of vegetation layers (tree, shrub, herb, and cryptogams) were missing in several of the older studies. However, we kept the cover data when they were given for old and new plots, because we assumed that there is a one-sided effect of the changes in the cover of tree and shrub layer on the species composition of bryophytes and lichens on the ground.

Based on a literature review and preliminary examination of the data sets, we expected that species composition and richness would strongly differ between different site and forest types. For example, in contrast to relatively open pine forests on dry soils with a dense carpet of bryophytes and lichens, beech forests with a closed canopy and a thick leaf litter layer contain only a sparse and species-poor bryophyte layer. We therefore divided the data sets into three broad forest types: (1) coniferous forests (*Vaccinio-Picetalia*), mostly dominated by Scots pine (*Pinus sylvestris*) and assigned to the alliance *Dicroano-Pinion sylvestris* (Mucina et al., 2016); (2) deciduous forests on acid, nutrient-poor soils, in the tree layer predominantly composed of pedunculate oak (*Quercus robur*) or European beech (*Fagus sylvatica*), or of a mixture of the two species (*Quercetalia roboris* and *Luzulo-Fagion sylvaticae*); (3) deciduous forests on more base- and nutrient-rich soils, including beech forests (*Fagetalia sylvaticae*), oak-hornbeam forests rich in *Carpinus betulus* (*Carpinetalia betuli*), mixed broadleaved forests with European ash (*Fraxinus excelsior*) and elm (*Ulmus spp.* *Aceretalia platani*), and, more rarely, black alder (*Alnus glutinosa*) forests (*Alnetea glutinosae*). This coarse division resulted in groups with 9, 14 and 12 data sets, respectively, and allowed us to examine broad trends.

### 2.3 Data analysis

With few exceptions, no environmental measurements were available in any of the data sets, which applied especially to the initially sampled plots. Like in many other resurvey studies, we therefore relied on Ellenberg indicator values to assess the climatic and edaphic conditions in the plots and to compare the old and more recent surveys. The following variables were assessed: light (L), temperature (T), and continentality (K), as well as soil moisture (F), soil reaction (pH, R), and soil nitrogen/nutrients (N). Values were obtained from Ellenberg et al. (2001), except for the N scores that were extracted from the recently published list of Simmel et al. (2021). Unlike in most other (resurvey) studies, we did not calculate mean plot values for the six variables, because a large number of plots did not contain bryophytes and lichens at all, or contained only species lacking indicator values for some of the variables. Instead, we calculated trend scores for each species, separately for the three forest types. For each data set of a forest type, we evaluated whether there was an increase or decrease in a species, irrespective of the extent of change, and then summed up all increases and decreases. For example, a species with higher numbers of occurrences in the resurveyed plots.
compared to the initial plots in five data sets and lower numbers of occurrences in the resurveyed plots compared with the initial plots in three other data sets obtained a trend score of +2. By not considering the different numbers of plots in the various data sets, we thereby downweighted the influence of data sets with a large number of plots.

Four main (partly systematic) groups of bryophytes and lichens were distinguished (Hallingbäck, 1985): three bryophyte groups (pleurocarpous and acrocarpous mosses, liverworts) and lichens (nearly all of them fruticose). To examine the different temporal trends of species with different traits, we used the recently published trait database of Bernhardt-Römermann et al. (2018) and related the previously calculated trend scores to a selection of traits. We included traits related to growth and reproduction that we assumed to play a role for the dispersal to new sites and for the competitive strength at the sites where the species have established. These included growth form (categorical; orthotrophic or plagiotropic), life form (categorical; annual, turf, cushions, mat, weft, dendroid, rosette), shoot length (numerical), mean size of spores (numerical), fruiting frequency (six categories, from very rare to very common), and vegetative dispersal traits (tubers, gemmae, branches, leaves; each coded as unknown (0) or occurring (1)).

All statistical analyses were conducted with the program R version 3.4.2 (R Core Team, 2020). Changes in the percentage cover of the layers of vascular plants (tree, shrub, and herb) and cryptogams between initial and resurveyed plots were assessed by generalized linear mixed models (GLMMs; package lme4; Bates et al., 2015), assuming a binomial error distribution (function ‘glmer’). While time (old, new) served as a fixed, categorical variable, the data set and plot ID (nested in data set) were used as random factors. Changes in species richness were analysed in a similar manner, but with a Poisson error distribution. These analyses were carried out separately for the three forest types. Changes in species richness across time in single data sets were examined with the Wilcoxon signed-rank test (for paired data). The same test was used in the analysis of the temporal changes in the frequency of life forms (pleurocarpous and acrocarpous mosses, liverworts, lichens). Here, we did not apply a correction for multiple testing such as the one named after Bonferroni (Miller, 1966), because we were mainly interested here in the broad trends in the three forest types and not specifically in the changes in single data sets. For the analysis of the overall patterns of temporal change in species richness and in the absolute numbers and relative numbers (proportion of species of a group relative to the total number of species) of the main groups of bryophytes and lichens between initial and resurveys, we applied a Holm–Bonferroni correction (Holm, 1979).

The species’ trend scores were correlated with the corresponding Ellenberg values to find out the environmental drivers of change, using linear regression analysis. Differences in the species’ trend scores between traits were analysed with Spearman rank correlation (numeric variables), the Wilcoxon test for unpaired data (categorical with two outcomes) and the Kruskal–Wallis test (categorical with more than two outcomes).

3 | RESULTS

3.1 | General data set properties

The database contained a total of 168 bryophytes and 29 lichens (Appendix S2). Across all data sets and forest types (Appendix S3), bryophytes showed an approximately equal share of pleurocarpous and acrocarpous mosses, while liverworts were clearly less frequent. Lichens were prominent only in coniferous forests, namely pine forests.

Across all data sets, there was a significant effect of plot size on total species richness, from an average of ca three species at the smallest plot size (12 m²) to ca five species at 900 m². Importantly, there were no clear differences in mean plot size between the forest types (coniferous forests: 353 m²; deciduous forests on acid soils: 375 m²; deciduous forests on base-rich soils: 372 m²) that would explain differences in species richness between the types. The mean number of terricolous bryophytes and lichens per plot was higher in coniferous forests than in deciduous forests on acid and base-rich soils. In the coniferous forests, the mean values for single data sets ranged from 1.8 to 12.7 species (mean across data sets with old and new plots: 5.8; Appendix S3) and were in some cases even slightly higher than those for the vascular plants, namely in Cladonio-Pinetum woodlands. Mean numbers in deciduous forests on acid soils varied between 0.6 and 5.7 (mean: 3.65), with generally higher richness in oak- than in beech-dominated stands. A similar variation was observed in deciduous forests on base-rich soils (0.8–7.4; mean: 3.75) that showed particularly high values in alder forests and low values in beech- and hornbeam-dominated forests.

The cover of the woody layers in forests on acid soils changed in consistent ways: negative changes were observed in the tree and herb layers, positive ones in the shrub layer (Table 1). No significant changes were found in deciduous forests on base-rich soils. Overall, the cover changes did not give clear evidence for altered light conditions at the forest floor.

3.2 | Temporal changes in the cover and species richness of bryophytes and lichens (research question 1)

In coniferous forests, the mean cover of bryophytes and lichens increased from 36.3% in the old plots to 49.9% in the recent plots (Table 1). The increasing cover was not accompanied by an overall higher species richness [old plots: mean 5.2, new plots: mean 5.4; GLMM: n (no. of old and new plots) = 554, p = 0.347]. While the number of species had increased significantly in four studies, it had decreased in three and remained stable in two studies (Figure 1a).

In deciduous forests on acid soils, the mean cover of bryophytes and lichens was considerably lower than in coniferous forests and did not change over time (old plots: 6.4%; new plots: 6.1%). In contrast, there was a weak but significant increase in species richness from 3.8 to 4.1 (GLMM: n = 924, p = 0.008). In the single studies,
species numbers increased and decreased in three data sets each, while they remained unchanged in eight data sets (Figure 1b).

The cover of bryophytes (lichens were almost absent) in the deciduous forests on base-rich soils varied considerably between sites and did not differ significantly between time periods despite an overall lower mean value in the old (3.2%) compared to the new plots (6.6%). Species richness increased from an average of 3.2–3.9 (GLMM: n = 714, p < 0.001). Accordingly, there was a surplus of single studies with significant increases in species number (Figure 1c). Across all 35 data sets, there was no significant change in the total richness of bryophytes and lichens (Table 2).

### 3.3 | Temporal changes in the frequency of species groups (research question 2)

Pleurocarpous mosses increased significantly in seven out of nine data sets of coniferous forests and in seven out of 12 data sets of deciduous forests on base-rich soils (Appendix S4). In deciduous forests on acid soils, the number of pleurocarps was stable in eight data sets, while there was a significant increase in five data sets. Across all data sets there was an increase in pleurocarps both in absolute and relative numbers (Table 2). For acrocarpous mosses, no significant changes were observed in eight data sets, while three data sets each showed positive and negative changes, a pattern similar to the one found for total species richness (Appendix S4). While the number of acrocarps remained unchanged across all data sets, the proportion decreased over time (Table 2). Liverworts were the least frequent group of bryophytes, with an average of less than one species per plot, resulting also in a low number of significant, either positive or negative, changes in single studies and no change in number or proportion across all data sets. Lichens in the coniferous forests declined over time in four out of nine studies, in the other data sets they were absent or remained stable. Overall, lichens showed significant declines in both absolute and relative numbers (Table 2).

When examining the temporal trends of species with different growth forms or reproductive strategies, no significant relationships were observed, the only exception being the more positive trend of plagiotropic species compared to the orthotropic species, in accordance with the increase in pleurocarpous taxa (Appendix S5).

Finally, the temporal dynamics of the species increased with the time interval between initial and recent survey: The sum of the species gains and losses per plot increased with an increasing number of years between surveys (r_t = 0.359, p = 0.034), and—as time interval and the year of the first survey were highly correlated (r_t = −0.947) — was higher the earlier the first survey was done (r_t = 0.379, p = 0.025).

### 3.4 | Temporal trends of single species and their environmental drivers (research question 3)

Some bryophyte species showed a consistent and partly pronounced increase in frequency in all forest types, namely Brachythecium rutabulum (a net increase in 28 out of 35 data sets), Eurhynchium praelongum (18), Hypnum cupressiforme (17), Dicranella heteromalla (16), Plagiothecium affine (15), and Mnium hornum (12). Other species increased strongly in two of the types, but decreased (albeit weakly) in the third (Atrichum undulatum, Polytrichum formosum, and Scleropodium purum).

Loser species differed more strongly between the forest types. In coniferous forests, declining trends were mostly observed in Cladonia lichens, but also in light-demanding acrocarpous species with low nutrient demands, such as Dicranum polysetum, D. spurium and Leucobryum glaucum, and in the liverwort Pilidium ciliare. Various Dicranum species also decreased in deciduous forests on acid soils, together with Pleurozium schreberi and Pohlia nutans. In deciduous forests on base-rich soils, declines were observed in Plagiothecium spp., Rhodobryum roseum and Thuidium tamariscinum.

Ellenberg light values were negatively correlated with the species’ trend scores in coniferous forests and deciduous forests on base-rich soils, suggesting an increase of shade-tolerant species at the expense of more light-demanding species (Appendix S6, Figure 2). There was no systematic temporal change of species...
FIGURE 1  Changes in species richness of bryophytes and lichens in (a) coniferous forests (nine data sets), (b) deciduous forests on acid soils (14 data sets), and (c) deciduous forests on base-rich soils (12 data sets). The boxplots (with median, interquartile range, whiskers and in some cases outliers) show the differences in the number of species between resurvey and initial survey, with values above the zero line reflecting an increase and values below the zero line reflecting a decrease in species richness. The symbols above the bars denote whether the temporal change in species richness was significantly positive (+) or negative (−) according to Wilcoxon signed-rank tests.
TABLE 2 Changes in absolute and relative numbers of the main growth forms of bryophytes and lichens between initial survey and resurvey across all 35 data sets

<table>
<thead>
<tr>
<th>Absolute species number</th>
<th>Relative species number (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median initial survey</td>
</tr>
<tr>
<td>All species</td>
<td>4.0</td>
</tr>
<tr>
<td>Pleurocarpous mosses</td>
<td>1.1</td>
</tr>
<tr>
<td>Acrocarpous mosses</td>
<td>2.3</td>
</tr>
<tr>
<td>Liverworts</td>
<td>0.1</td>
</tr>
<tr>
<td>Lichens (all forests)</td>
<td>0</td>
</tr>
<tr>
<td>Means</td>
<td>0.4</td>
</tr>
<tr>
<td>(only coniferous)</td>
<td>0.3</td>
</tr>
</tbody>
</table>

Note: The relative number was calculated as the ratio of the number of species of a given life form divided by the total number of species. Statistical differences between initial and resurvey were analysed with Wilcoxon signed-rank tests, applying a Holm–Bonferroni correction of p-values for multiple testing. The higher median values (in lichens also the means) in significant comparisons are shown in bold.

with respect to the climatic temperature values. However, we found a negative correlation of species trend scores with continentality in coniferous forests, as well as a marginally significant effect in deciduous forests on acid soils, indicating an increase in species with a more oceanic distribution. Among the soil variables, no trends were found for moisture and only one significant trend for pH, with a positive correlation with the trend scores in deciduous forests on acid soils. In the latter as well as in coniferous forests, there were highly significant correlations between temporal change and the Ellenberg values for nitrogen, suggesting an increase in nutrient-demanding species (Appendix S6, Figure 2). Two of three mosses with the highest change in frequency in coniferous forests were among the taxa with the highest Ellenberg N values, Brachythecium rutabulum (N = 8) and Scleropodium purum (N = 6). In deciduous forests on acid soils, B. rutabulum again was among the species with the most pronounced temporal increase, together with Eurhynchium praelongum and Plagiomnium affine, both also having relatively high N values (7 and 5, respectively). B. rutabulum and E. praelongum again were among the strongest winners in deciduous forests on base-rich soils, together with Hypnum cupressiforme (N = 5). However, here also two species with low N values (N = 3) had increased in most data sets, the acrocarpous taxa Dicranella heteromalla and Polytrichum formosum.

Across all species, there was a significantly negative correlation between the Ellenberg indicator values for light and nitrogen, both when analysed separately for the three forest types and in the whole data set (Spearman rank correlation, p < 0.001).

4 | DISCUSSION

In the following, we will first look at the overall species richness of bryophytes and lichens, discuss the winner and loser species in more detail and then try to identify the main environmental drivers of changes in species composition in comparison to vascular plants.

4.1 | Species richness

There was no clear change in the species richness of bryophytes and lichens in any of the forest types, which coincides with the observations of Delgado and Ederra (2013) from Southwest Europe. In a floristic resurvey study in North German forests over a much longer time period (1900–2013), in contrast, a decline in terricolous bryophytes was observed (Ditrich et al., 2016). The authors attribute this to the promoted competitive strength of vascular plants owing to increased nitrogen levels. However, in our study, there was only a weak, non-significant relation between the species richness of bryophytes and lichens and the cover of the herb layer (results not shown). In addition, there may also be a reverse effect, that is, a dense moss carpet may hamper the regeneration of vascular plants and thereby cause a decrease in cover and species richness of herbaceous species (Økland et al., 2023). Likely, the changes in total species richness of bryophytes and lichens in forests are highly variable, depending on region and forest type, the dominant tree species, forest management, changes in the cover of woody and herb layers, and abiotic drivers such as nutrient enrichment or climate change (see also below).

4.2 | Winners and losers

The list of winner species coincides well with results from the study by Becker Scarpitta et al. (2017) from a deciduous forest in northwestern France, where Brachythecium rutabulum and Eurhynchium praelongum showed the strongest increase in absolute frequency. Both species also increased in frequency in spruce forests of a low mountain range in Central Germany. Brachythecium rutabulum had become more common also in acidic beech forests (Weckesser & Schmidt, 2004). Some taxa appear to increase in forests on acid soils, especially coniferous woodlands, at the expense of lichens (see below), but show a reversed trend in more base-rich forests, such as Hylocomium splendens and Pleurozium schreberi. It is noticeable that several of the above-mentioned taxa are among the most
**FIGURE 2** Relationship between the temporal trend scores (difference between the number of studies with increasing and decreasing frequencies) of species and their corresponding Ellenberg indicator values. For reasons of clarity, overlapping data points (species with the same trend scores and indicator values) were slightly shifted in their position in the diagrams. Upper panels: coniferous forests on acid soils (nine data sets), middle panels: deciduous forests on acid soils (14 data sets), lower panels: deciduous forests on base-rich soils (12 data sets). Left: Ellenberg nitrogen values, right: Ellenberg light values.
frequent species in at least one forest type (see Appendix S2), and were so already at the initial survey. They represent forest generalists and are at the same time geographically widespread: *B. rutabulum* is the most abundant of all bryophyte species in the country and is present in all grid squares (Meinunger & Schröder, 2007). *Dicranum heteromalla*, *E. praelongum*, *Hypnum cupressiforme*, *Mnium hornum*, *Polytrichum formosum*, and *Scleropodium purum* are also very widespread. Among the winners, there is a surplus of pleurocarpous species, whereas most bryophytes with negative trends represent acrocarpous taxa, including *Dicranum* spp., *Leucobryum glaucum*, and *Pohlia nutans* (Fischer et al., 2015). The latter were found to decrease also in a resurvey study of pine forests in Poland (Stefaniska-Krzaczek et al., 2018). The increase in pleurocarpous taxa may be explained by their superior ability to spread laterally under improved nutrient conditions, which likely leads to a higher competitive strength against acrocarpous mosses (Heinen & Zipper, 2004).

Correspondingly, a recent monitoring study from Norwegian spruce forests showed the replacement of small-growing bryophytes such as many liverworts by large, often mat-forming, species such as *Hylocomium splendens* and *Sphagnum* spp. (Økland et al., 2023). Liverworts generally showed low numbers and no consistent changes, but due to their small size and inconspicuousness, they may sometimes be overlooked in the surveys.

Lichen species regularly occur only in acid and nutrient-poor forests, especially pine woodlands, and have shown a dramatic decline in frequency and abundance, which has already been emphasized in several publications from both Germany (Reinecke et al., 2011, 2014; Fischer et al., 2014, 2015; Dittmann et al., 2018; Günther et al., 2021) and other countries in central and northern Europe (Finland: Mäkipää & Heikkinen, 2003; Poland: Stefaniska-Krzaczek et al., 2018). The decline concerns the large reindeer lichens (e.g., *Cladonia arbuscula* and *C. rangiferina*), many smaller *Cladonia* species and other terricolous taxa such as *Cetraria* spp. The process is mainly driven by the higher competitive ability of bryophytes, especially large species (Tonteri et al., 2022; Økland et al., 2023).

4.3 | Environmental drivers

The main environmental drivers of the changes appear to be nutrient enrichment and altered light conditions (Figure 2), although the relationships between trend scores and Ellenberg values were not significant in all forest types. Most species with a strong and more or less consistent increase over time were indicators of high levels of nitrogen (N), those with declines had mostly low N values. This observation is consistent with the results from other resurvey studies of terricolous bryophytes in Europe (Delgado & Ederra, 2013; Becker Scarpitta et al., 2017; Stefaniska-Krzaczek et al., 2018) and also with the floristic resurvey in Germany by Dittrich et al. (2016). As bryophytes and lichens are largely independent of soil mineralization for their nutrient supply, this nutrient enrichment is likely driven by N deposition (Weldon et al., 2022), which has remained high in Central Europe since more than four decades (e.g., Dentener et al., 2006). However, the cessation of historical land use, especially litter raking, may also contribute to nutrient enrichment (see Vild et al., 2015), and these soil nutrients may increasingly diffuse from the soil surface into the bryophytes and lichens, or be transported to the thalli during heavy rains by splashes. The recognition of eutrophication as the main driver of changes in species composition is also supported by fertilization experiments where N addition resulted in a decrease in lichens as well as some mosses (*Hylocomium splendens*, *Pleurozium schreberi*) and an increase in other bryophyte species such as *Brachythecium* spp. (Van Dobben et al., 1999; Olsson & Kellner, 2006). In coniferous forests, the widely applied amelioration limiting may also drive composition changes, increasing the microbial activity and thereby promoting nutrient availability in favour of more N-demanding species (Weckesser & Schmidt, 2004; Baumann et al., 2019). Bates (1994) showed that especially *Brachythecium rutabulum* relies on nutrient supply from the substratum.

At the same time, the changes in species composition suggest that most forests tend to have become darker, again coinciding with observations from other countries (Delgado & Ederra, 2013; Stefaniska-Krzaczek et al., 2018). However, this change does not coincide with the analysis of changes in the canopy cover of trees and shrubs (Table 2). Whereas many resurvey studies have pointed out that forests often have developed a denser tree canopy over the past decades (Verheyen et al., 2012), our results show the opposite, simultaneously indicating the formation of a denser shrub layer (see also Förster et al., 2017). It is difficult to judge whether these changes result in more or less light transmission to the forest floor, and we cannot exclude pronounced observer differences between initial survey and resurvey in the estimation of canopy cover. Likely, forest structure changes in an idiosyncratic way: some forests may recover from the former coppice or coppice with standards management. Especially in conifer (pine) forests, also nutrient enrichment during the recovery from litter raking may result in denser canopies, often associated with the regeneration of deciduous tree species such as *Quercus* spp. and *Prunus serotina*. Less intensive logging activities due to longer rotation periods may also result in canopy closure (Delgado & Ederra, 2013). Other forests may be opened up by shelterwood management or get sparser in their canopy due to diseases and storm damage (Verheyen et al., 2012), or as a result of increasing drought stress exposure of trees (Leuschner & Ellenberg, 2017; Schulte et al., 2020). Our own observations indicate that many open-canopy forests have developed a much denser shrub layer, as happened, for example, in many forest stands on acid soils as a result of the invasion of *Prunus serotina* (see also Halarewicz & Pruchniewicz, 2015), but also of *Fagus sylvatica*, *Quercus* spp., *Frangula alnus* and *Sorbus aucuparia*. This would also explain the decrease in cover of the herb layer in the forests on acid soils (Table 2). Lichens are particularly sensitive to the increasing shade.

There is only weak evidence of an effect of soil acidity on the changes in species composition, pointing at an increase in pH in forests on acid soils (Appendix S6). This coincides with observations of a
recent pH recovery of forest soils in Germany (Jansone et al., 2020). However, in an ancient forest in the northwest German lowlands, increasing soil pH was only observed in acidic forests, whereas forests on base-rich substrate showed an opposite trend, probably caused by a lowering of the ground water table (Strubelt et al., 2019). An increase in bryophyte community affinity to pH was also shown by Becker Scarpitta et al. (2017). However, our results are not based on pH measurements, but on species indicator values, and there is a highly significant positive correlation between the indicator scores for R and N (data not shown), rendering the interpretation difficult. There was no sign of an increase in more temperature-demanding species in our resurvey, in contrast to some other studies on terricolous bryophytes (Delgado & Ederra, 2013; Becker Scarpitta et al., 2017; Økland et al., 2023). An eastward spread of bryophytes with an oceanic distribution in Central Europe (Bomble, 2014) may also be attributed to an altered temperature regime towards lower climate continentality, most likely driven by higher winter temperatures. This is in line with the indicated trends of a decrease of continental taxa in the forests on acid soils (Appendix S5).

5 | CONCLUSIONS

Bryophytes and lichens do not only fill the gaps between vascular plants on the forest floor, but are a component of forests with species filling habitat niches and showing responses to environmental changes just as vascular plants. Therefore, resurvey studies should pay more attention to this group of species, the more so as these species with their high exposure to the atmosphere and potentially often faster dispersal might be the better indicators for environmental changes, especially those driven by atmospheric pollution (Becker Scarpitta et al., 2017). This holds especially true in forest types with a relatively low number of vascular plant species. Our results, largely coinciding with those from the few other resurvey studies on terricolous forest species, show that there are important parallels in the temporal trends of bryophytes/lichens and vascular plants (as shown by meta-analyses: Verheyen et al., 2012; Bernhardt-Römermann et al., 2015) and cross-regional surveys (Hedwall & Brunet, 2016): (a) plot-based species richness has remained stable; (b) in contrast, the number and proportion of some single and groups of species have changed; (c) the ecology of loser and winner species suggests, at least for some forest types, a eutrophication signal and points at lower light availability at the forest floor. Thus, our study results support the main conclusions drawn from most resurveys of vascular plant vegetation. We still do not know much about the changes in the composition of forest bryophytes and lichens in deciduous forests on very wet soils, such as alder–ash or black alder forests, as these types were underrepresented in our database. Here, drainage or a drought-induced lowering of the water table may be important environmental drivers of vegetation change (Leuschner & Ellenberg, 2017) by affecting both water and nutrient supply, especially in the lowlands (Strubelt et al., 2019).

AUTHOR CONTRIBUTIONS

MD collected the resurvey studies and compiled the data tables, carried out the statistical analysis and led the writing. All authors contributed to the discussion and revised the manuscript.

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DATA AVAILABILITY STATEMENT

The data sets of plots from the original and resurveyed forests are stored at the working group of the corresponding author, Institute of Ecology, University of Bremen, Germany.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Data sources of the 35 resurvey data from German forests

Appendix S2. Frequencies of bryophytes and lichens in the resurvey studies of the three forest types

Appendix S3. Mean numbers of bryophyte and lichen species in the 35 data sets

Appendix S4. Changes in the number of species of different cryptogam species groups

Appendix S5. Relationships between the species’ change scores and Ellenberg indicator values

Appendix S6. Relationships between the species’ change scores and their trait values

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