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Repeated habitat mapping data reveal gains and losses of plant species

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Abstract

Detecting species trends across different habitat types and larger regions is required to generate a general and reliable foundation for conservation planning. While direct monitoring data covering a large spatial and temporal extent are mostly lacking, data collected for other purposes than monitoring can be considered to detect trends. Here we analyzed both habitat type and plant species trends over several decades (1979–2017), using repeated habitat survey data from the habitat mapping program of the city and federal state of Hamburg. Next to transitions between habitat types, we looked for differences between winner and loser species, considering also their habitat type preference, red list, and non-native status. Furthermore, we assessed the consistency between trends of habitat types and species that are characteristic of those habitat types. We found declines in habitat area of semi-natural (semi-)dry grasslands and semi-ruderal vegetation and increases in habitat area of species-poor grasslands, pioneer forests, and human settlements. More species showed positive than negative trends over time, with winners including many forest and scrub as well as non-native species, while losers were represented mostly by endangered and ruderal species. Most habitat types included a mixture of both winner and loser species. Habitat type trends were mostly not reflected in trends of species that were characteristic of a particular habitat, such as semi-natural (semi-)dry grasslands. This can be explained, on the one hand, by species extinction debts, and on the other hand, by a low habitat specificity of some species that find refuges also in secondary habitats. Our study not only shows the difficulties but also offers methods on how to use repeated habitat mapping data to detect trends for habitat types and plant species. In contrast to monitoring programs focusing on individual endangered habitats, results from repeated habitat surveys allow the identification of those secondary habitats of a species that might contribute the most to preserving populations of their primary habitat.

KEYWORDS
biodiversity change, Germany, habitat change, habitat mapping, Hamburg, resurvey, species trends, vegetation

INTRODUCTION

Humankind has reshaped the world's landscapes to an extent that by 2017 more than 80% of the terrestrial area had been modified (Ellis et al., 2021). Those habitat transformations, which include increasing urbanization and intensification in land use, come at the expense of a loss of natural habitats (Williams et al., 2020). The European red list of habitats now classifies 73 habitat types as vulnerable to critically endangered, which corresponds to 31% of all evaluated habitat types (Janssen et al., 2016). For Germany, especially open habitats as species-rich dry or wet grasslands show negative trends (Finck et al., 2017).

Habitat loss and degradation are believed to be the key driver of declines in species diversity worldwide (Díaz et al., 2019; Kerr & Deguise, 2004; Newbold et al., 2015; Pereira et al., 2012). For Germany, declines have been observed for plant species typical of several different habitat types, including grasslands (Diekmann et al., 2014; Wesche et al., 2012), arable fields (Meyer et al., 2013, 2015), and bogs (Sperle & Bruelheide, 2021). While many habitat types show declines for numerous species, there are also winners from changes in the landscape, especially nutrient demanding (Bruelheide et al., 2020; Jandt et al., 2011; Reinecke et al., 2014; Wesche et al., 2012) and non-native species (Eichenberg et al., 2021; Staude et al., 2020). In consequence, the species composition of many habitats has already undergone considerable changes (Dornelas et al., 2014; Finderup Nielsen et al., 2019; Hillebrand et al., 2018), even when overall species richness at the local scale might remain unaffected (Dornelas et al., 2014; Vellend et al., 2013). There are indications that the changes in species composition favor more widespread cosmopolitan species while rare habitat specialists become locally extinct (Diekmann et al., 2014, 2019; Jansen et al., 2020; Staude et al., 2020). Thus, detecting those changes in species composition might be more important for management decisions than species numbers per se (Hillebrand et al., 2018; Magurran, 2016). However, we have a data gap on biodiversity change at the landscape scale, as we do not know to which degree secondary habitats might compensate for primary habitat loss.

To witness general trends of species, surveys with both a large spatial as well as temporal extent are necessary. However, for Germany, long time analyses are rare and focus on the plot level or small regions (e.g., Diekmann et al., 2014; Hüllbusch et al., 2016; Strubelt et al., 2017). While those studies provide information on local trends, their representativeness might be restricted to specific habitat types and regions (Cardinale et al., 2018; Gonzalez et al., 2016). By contrast, studies with a broad spatial extent, covering large regions and several habitat types, have to rely on combining disparate data sources for temporal comparisons (Eichenberg et al., 2021; Jansen et al., 2020). As nationwide or region-wide monitoring programs for vascular plant species have only been initialized in the last two decades (e.g., for Switzerland, see Weber et al., 2004; for United Kingdom, see Pescott et al., 2019; and for a worldwide review, see Lee et al., 2005), it is necessary to use past data collected for other purposes than monitoring.

As in many other countries, habitat mapping programs (in German "Biotopkartierungen") have been implemented at the level of the federal states of Germany, with the aim of landscape planning and nature conservation (Kaiser et al., 2013; Sukopp et al., 1979). In many cases, the first habitat surveys were conducted more than 40 years ago, and since then, in some countries or regions, the surveys were repeated. Besides assigning habitat types for each habitat in a region, many programs have also involved recording the plant species that occurred in those habitats. The resulting datasets are readily available and could be used to identify trends of habitat types and species over large spatial and temporal extents. However, the incompleteness of species lists represents a challenge for analyses, and so far, this approach has only been applied to the federal state of Schleswig-Holstein and not in the combination with changes in habitat types (Bruelheide et al., 2020). Although all federal states in Germany carry out habitat mapping, these surveys are often incomplete, while some states have an excellent data basis.

Here, we present a unique dataset that covers the entire city and federal state of Hamburg, with data reaching back as far as 40 years. Although Hamburg is a special case for a European region because of a high proportion of land covered with built-up structures, it can also be considered representative of the ongoing worldwide urbanization trend. At the same time, while Hamburg is one of the smallest federal states in Germany, it harbors a diverse set of habitats, ranging from heathlands to forests, from bogs to arable fields. Thus, Hamburg can serve as an example for other regions in the northern hemisphere. As the present dataset includes information on habitat types, habitat areas, and plant species lists and is completely digitized, it offers a chance to analyze area-based trends for both habitat types as well as plant species over several decades.

In this study, we aim to overcome challenges concerning the inherent heterogeneous quality of habitat mapping data and difficulties in spatial comparisons to identify the winners and losers of both habitat types and plant species in Hamburg. We asked the following questions:

1. Which habitat types have suffered from losses and which benefited from gains? We hypothesized that semi-natural habitats have been replaced by anthropogenic habitats.
2. How do losing species differ from the winning ones? Here, we tested two hypotheses, that red-listed species suffered more from losses than those that were not red-listed and that native species tended to decline while non-native species increased.
3. Are trends for habitat types and species consistent? We expected that changes in habitat types are reflected in trends of species that are characteristic of these habitat types.

MATERIALS AND METHODS

Data preparation

The habitat mapping program from the federal state of Hamburg, Germany, started in 1979 and was accompanied by the Natura 2000 monitoring program of the European Union from 2004 onwards. In the following, we define a habitat as a parcel of land that has been surveyed for biodiversity. All habitats are digitized in GIS and have information available about habitat type(s) and size of habitat. Habitat sizes range from 12 m^2 to 387.29 ha, with a mean and median of 3 and 1 ha, respectively. Linear (<5 m width, e.g., rivers) and point habitats (e.g., single trees) were excluded from the analysis. Implications of this decision for the analysis can be found in Appendix S1: Table S1 along with several other challenges and solutions concerning the analysis of habitat mapping data. Each habitat has been assigned to one main habitat type, but can additionally contain several other habitat types. Within a habitat, plant species may have been recorded for each habitat type. Species lists were only mandatory for most semi-natural habitats and all Natura 2000 habitat types. All habitat types corresponding to habitats that were mapped before 2011 and/or through the Natura 2000 program were related to the habitat identification key from 2011 (Brandt & Engelschall, 2011). Based on the guideline, habitat types can be described using a hierarchical system of three levels, which is coded by a reference key of one, two, or three letters. The number of letters is an indicator of the level of detail with which a habitat type is described, for example, G: grassland (Level 1); GM: species-rich grassland, moist to semi-dry (Level 2); and GMW: species-rich pasture, moist (Level 3). Since habitats in early surveys have been often assigned to more broadly defined habitat types than in the more recent surveys, all assigned Level 3 habitat types were converted to the broader corresponding Level 2 habitat types. For some analyses, we further converted the Level 2 habitat types to the corresponding Level 1 habitat types. In the following, we use the term habitat types referring to the Level 2 habitat types, if not stated otherwise.

Data covered the years 1979–2017, and because surveys were not repeated before 1995, data were separated into two time periods: t_1 (1979–1994) and t_2 (1995–2017). Polygons from both time periods were overlaid with each other in ArcGIS 10.5 (ESRI, 2016), resulting in intersections between all habitats. Intersections covering less than 5% of the area of either habitat were considered as mapping and digitization inaccuracies and excluded from all further analyses. All t_1 habitats whose area was not remapped to at least 95% in t_2 and all t_2 habitats whose area was not previously mapped to at least 95% in t_1 were excluded as well. For each habitat from t_1 (i.e., before 1995), all most recent intersecting polygons were selected for comparison. This resulted in heterogeneous time spans between t_1 and t_2 (Appendix S1: Figure S1). Mean time spans further differed between habitat types (Appendix S1: Figure S2a). However, the mean time span per habitat type showed only a weak positive correlation with habitat type trends (Appendix S1: Figure S2b; Spearman rank correlation $r_s = 0.21$, $p = 0.04$). Similarly, the mean time span per species showed only a weak positive correlation with species trends (Spearman rank correlation $r_s = 0.11$, $p < 0.001$ for all species; $r_s = 0.50$, $p < 0.001$ for species with a significant trend) and with the strength of all species' trends (regardless of the direction of trends; $r_s = 0.15$, $p < 0.001$).

Different procedures for habitat comparisons

Depending on the type of analysis, we employed different procedures (Figure 1). As the assignment of a habitat to a particular habitat type changed over time, the size and borders of polygons often changed toward t_2. Therefore, most habitats from t_1 and t_2 overlapped only partially. This resulted in one-to-many, many-to-one, and many-to-many intersections, for example, one habitat from t_1 intersecting with two habitats from t_2. One way to compare habitats from both time periods would be to use these intersections individually (e.g., as done in Bruelheide et al., 2020), for both habitat type (change in total area) and species (change in frequency) analyses. In our study, this intersection method (IM) was used to analyze changes in the total area of habitat types. However, to calculate both the mean change in area per habitat type and species mean changes in occupied area, we used the recorded habitat areas instead of the intersection areas. We did so because the sizes of habitats can vary considerably and therefore (1) the use of intersection areas is prone to underestimate the mean size of area changed, as it would result in many small changes instead of fewer large changes and (2) using

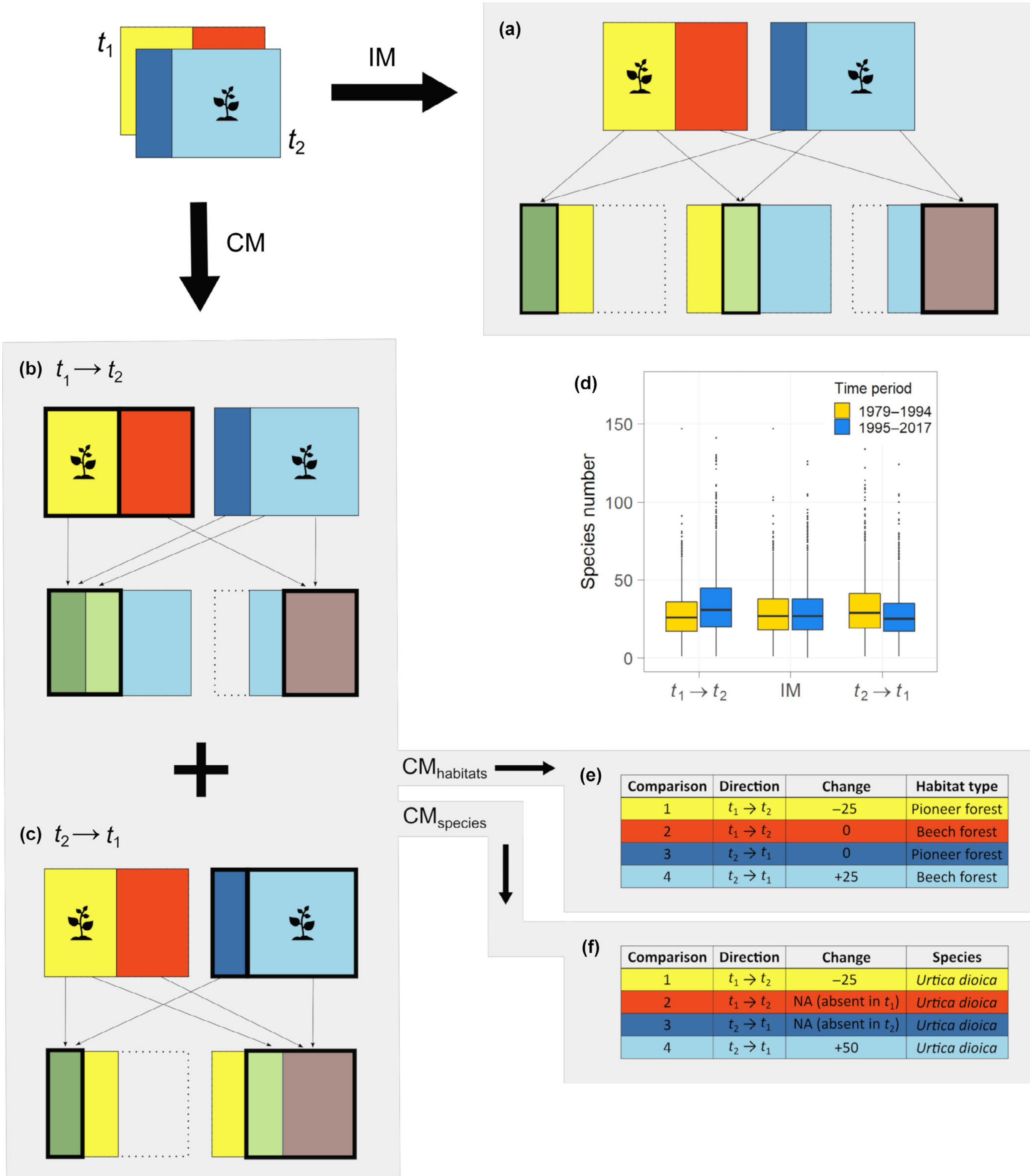

FIGURE 1 Legend on next page.

unweighted species frequencies gives the same weight to occurrences irrespective of the size of the habitat in which the species is found. While the data do not offer information on the actual habitat area occupied by a species, the area of a habitat in which a species occurs does mostly represent the available space for that species, and thus, is a measure of potential habitat space. The distinction between potential habitat area and occupied area is similar to the difference between extent of occurrence (EOO) and area of occupancy (AOO) in macroecology, or, in this study, more precisely between area of habitat (AOH) and AOO. While we are not able to provide AOO-type assessments, the AOH approach is also highly meaningful (Brooks et al., 2019), as in most cases the area occupied by a species will be linearly related to the area of the suitable habitat type. We therefore used this potential habitat space as a surrogate for the area occupied by a species. To calculate species trends based on this area and habitat type trends, we used a combination method (CM), for which all intersecting habitats must be joined. This can be done by including information from all habitats in t_2 that intersect with a habitat in t_1 ($t_1 \rightarrow t_2$) or by including information from all habitats from t_1 that intersect with a habitat from t_2 ($t_2 \rightarrow t_1$). To balance bias resulting from either of those two methods (Figure 1d), CM combines both methods ($t_1 \rightarrow t_2 + t_2 \rightarrow t_1$). This is performed separately to analyze the overall trend for each species ($CM_{species}$) or habitat type ($CM_{habitats}$). The fact that a particular habitat and the corresponding species list can take part in multiple comparisons was accounted for by decreasing the degrees of freedom for the statistical tests accordingly where it was appropriate.

Changes in habitat types

In addition to the main habitat type, habitats can contain several minor habitat types, for example, reed surrounding standing water. Only the habitats' main habitat type was used for the analysis and habitats were excluded if this main type covered only 50% or less of the whole habitat area. Habitat areas were weighted using the proportion covered by the main habitat type. Cases in which weighting was not possible were excluded. Habitats used for habitat type analysis were mainly located in the suburban and peri-urban parts of Hamburg (Appendix S1: Figure S3a).

To test for the mean change in area for each habitat type, analyses were performed using the combination method ($CM_{habitats}$). For $t_1 \rightarrow t_2$, the area of the habitat type of t_1 that was lost toward t_2 was used as a measure of change. Hence for $t_1 \rightarrow t_2$ only decreases (at least part of the habitat area changed into a different habitat type) or no change (complete habitat area still covered by the same habitat type) in the habitat area was possible. For $t_2 \rightarrow t_1$, the area of the habitat type of t_2 that was gained since t_1 was used as a measure of change. Hence for $t_2 \rightarrow t_1$ only increases (habitat area was at least partly covered by a different habitat type before) or no change (complete habitat area was covered by the same habitat type before) in habitat area was possible. By adding the comparisons from both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$, changes for each habitat type were analyzed using a Wilcoxon rank sum test. In addition to the Level 2 habitat type changes, changes per Level 1 habitat type (e.g., all forests) were analyzed using Wilcoxon rank sum tests as well, by averaging changes for all corresponding Level 2 habitat types.

To visualize total changes in the area of habitat types and conversion between habitat types, the IM was used, as it assumes the same sum of area for t_1 and t_2 and real habitat areas are not needed. For each intersection, changes in area and habitat type from t_1 to t_2 were visualized.

Given the changes in the mapping keys over time, the trends of some Level 2 habitat types cannot be expected to be reliable. We have highlighted those habitat types in all relevant figures and tables and will concentrate only on the reliable trends.

FIGURE 1 Scheme showing the two ways used to analyze changes in habitat types and species trends. Two habitats from time period 1 (t_1) are overlapping with two habitats from time period 2 (t_2). (a) The intersection method (IM) compares each intersection and its area, ignoring actually observed habitat areas. This method was used to visualize transitions between habitat types. (b–f) Changes in mean area per habitat type and in mean area occupied by each species were calculated using the combination method (CM), which combines outcomes from using either the habitats from t_1 as a baseline ($t_1 \rightarrow t_2$) or the habitats from t_2 as a baseline ($t_2 \rightarrow t_1$), that is, CM: $t_1 \rightarrow t_2 + t_2 \rightarrow t_1$. For species analysis ($CM_{species}$), (b) using $t_1 \rightarrow t_2$: For each habitat from t_1, match all habitats from t_2 that intersect with it and join their species lists; and (c) $t_2 \rightarrow t_1$: For each habitat from t_2, match all habitats from t_1 that intersect with it and join their species lists. (d) This results in, on average, more species in t_2 compared to t_1 for $t_1 \rightarrow t_2$ and fewer species in t_2 than in t_1 for $t_2 \rightarrow t_1$. Next, for each species, calculate the change in occupied area for all comparisons in both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ separately. (e) Finally, comparisons from both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ are combined in one table and used together to calculate species trends. For habitat type analysis ($CM_{habitats}$), (b) using $t_1 \rightarrow t_2$: For each habitat from t_1, match all habitats from t_2 that intersect with it and calculate the area of the respective t_1 habitat type that was lost; and (c) $t_2 \rightarrow t_1$: For each habitat from t_2, match all habitats from t_1 that intersect with it and calculate the area of the respective t_2 habitat type that was gained. (f) The final step here also is combining changes from $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ in one table and using it to calculate habitat type trends.

Species trends

Species lists were available for 35% of habitats. Species level comparisons were performed only for cases where a species list was available for both time periods. Habitats used for the species trend analysis were mainly located in the suburban and peri-urban parts of Hamburg (Appendix S1: Figure S3b). For habitats with several habitat types, there were sometimes several species lists available, which were merged for analysis. The taxonomy of species names was harmonized according to GermanSL 1.4 (Jansen & Dengler, 2008). Mosses, lichen, and algae were excluded from the analyses as they are often only recorded by specialists. Some species that are known to be difficult to differentiate in the field were merged. The final dataset included 1322 species including vascular plants and ferns.

Given the incompleteness of species lists, there is some potential observer bias toward red-listed (rare) species, while more common plants might be less intensively recorded. Thus, we compared species frequencies in all habitats used for analysis with species frequencies on a grid cell scale in Hamburg, including a 25 km^2 radius around the city (number of 5 × 5 km grid cells occupied, data derived from the German plant distribution database Florkart: www.floraweb.de). However, instead of a higher recording of relatively rare species in habitats, we found the most common species to be represented best by the habitat mapping data, indicated by the highest accordance with the grid cell frequency (Appendix S1: Figure S4).

The calculation of species trends was based on differences in the area occupied between the two time periods, using the combination method ($CM_{species\_area}$). Change in area per species and comparison was calculated for both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ using the $\log_{10}$ ratio of the area occupied by the species from both time periods (Equation 1)

$$\log_{10}\frac{\text{area}_{t_2}+1}{\text{area}_{t_1}+1}, \tag{1}$$

with area in square meters and adding 1 m^2 to allow for calculating the log ratio under complete habitat loss. Comparisons resulting from $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ were merged. This was considered to balance overestimation of increases in species for method $t_1 \rightarrow t_2$ and overestimation of decreases in species for method $t_2 \rightarrow t_1$ (Figure 1d). Wilcoxon rank sum tests were applied to test for trends for each species. Holm adjustment of significance levels was applied to account for the fact that all species were tested for change in occupied habitat area.

In addition to the changes in area occupied, species trends were analyzed using their frequency change ($CM_{species\_freq}$, ranging from −1 to 1) and their change in probability of occurrence by applying the Beals' index of sociological favorability ($CM_{species\_beals}$; Beals, 1984). Beals' index accounts for incomplete species observations by using co-occurrences of species to calculate occurrence probabilities for every species in every habitat, regardless of whether a species was observed in a specific habitat (Equation 2).

$$p_{pi} = \frac{1}{N_p}\sum_{j}^{N_p}\frac{M_{ij}}{M_j}. \tag{2}$$

The probability p_{pi} for species i to occur in a habitat p is calculated from joint occurrences M_{ij} with all species j of the total number of species in that habitat N_p, divided by the number of habitats M_j in which the species j is present. The co-occurrence matrix M_{ij} was based on all habitats from all years from Hamburg that had the species lists available. For an in-depth discussion on the Beals' index and its implications for temporal comparisons, see Bruelheide et al. (2020), Bruelheide et al. (2021). Change in frequency and probability of occurrence were analyzed using binomial and t-tests, respectively. Degrees of freedom were adjusted according to multiple use of habitats for $CM_{species\_freq}$ and $CM_{species\_beals}$ and Holm adjustment was applied.

Species habitat type preference

To assign habitat type preference to each plant species, their occurrence in all habitats from the Hamburg mapping program that contained species lists was used. In contrast to the other species analyses, species lists from habitats that contained several habitat types were not merged and cases in which those habitats did not contain separate species lists for each type were excluded. The Φ coefficient used calculates the fidelity for each species × habitat type combination (Equation 3; Chytrý et al., 2002).

$$\Phi = \pm\sqrt{\frac{\chi^2}{N}} = \frac{a \times d - b \times c}{\sqrt{(a+b)\times(c+d)\times(a+c)\times(b+d)}}, \tag{3}$$

χ^2 is the χ^2 statistic for a 2 × 2 contingency table, with N being the total number of observations, a is the number of occurrences of a species in a particular habitat type, b is the number of occurrences outside that habitat type, c is the number of times the species is absent in that habitat type, and d is the number of times the species is absent in all other habitat types. Φ ranges from −1 to 1 for species that perfectly avoid a particular habitat type or are perfectly confined to a particular habitat type, respectively. The habitat type with the maximum fidelity for a species was taken as the preferred type. For each habitat type, linear models were used to test if species that occur preferably in that type rather increased or decreased in their area occupied from t_1 to t_2 ($CM_{species\_area}$). Models were calculated without intercepts. Additional models were run with Level 1 habitat types as a predictor. Note that the Level 1 habitat types G and H were not normally distributed according to a Shapiro–Wilk normality test (but $p > 0.01$) and that there were many cases of fewer than three species per Level 2 habitat type.

Red list and non-native status

To assess differences between winner and loser species concerning their red list and non-native status, information on species status in Hamburg as well as in Germany was retrieved from Poppendieck et al. (2010).

Species trends per habitat type

Species trends were additionally analyzed separately by habitat type. Habitat types for each comparison were assigned according to the main habitat type from t_1, regardless of whether the habitat type changed toward t_2. The main habitat type had to cover more than 50% of the habitat area. For $t_2 \rightarrow t_1$ and in cases of one-to-many intersections, there were several habitat types from t_1 that matched with one habitat from t_2. In that case, the species was assigned to that habitat type from t_1, which covered most of the habitat from t_2 (min. 50%). To test for species changes in occupied area per habitat type, Wilcoxon rank sum tests were applied, with significance levels adjusted by Holm adjustment. In addition, to assess the amount of change within habitats that was not caused by transition between habitat types, species trends per habitat types were also calculated using only habitats that showed no change in habitat type from t_1 to t_2.

All analyses were conducted in R 4.0.3 (R Core Team, 2021), using the packages rgdal, sp, rgeos, maptools, data.table, dplyr, vegdata, reshape2, ggplot2, and yarrr. Maps were produced using QGIS 3.10.14 (QGIS Development Team, 2021).

RESULTS

Changes in habitat types

The $CM_{habitats}$ analysis showed numerous significant trends for changes in the area of habitat types from t_1 to t_2. On the broad habitat type Level 1, those included decreases in heathlands and nutrient-poor grasslands (T) and ruderal and semi-ruderal vegetation

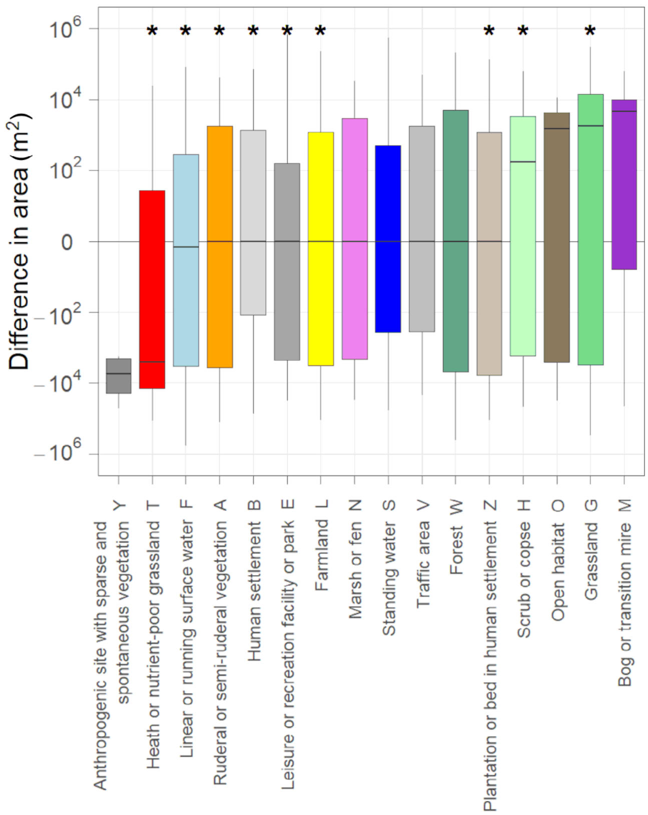

FIGURE 2 Difference in area in square meters between t_1 (1979–1994) and t_2 (1995–2017) for all Level 1 habitat types with calculation based on $CM_{habitats}$. The *y*-axis is on a $\log_{10}$ scale. Significant differences according to a Wilcoxon rank sum test are labeled with an asterisk.

(A) (mean change = −11,010 m^2, $p < 0.001$; and mean change = −2582 m^2, $p = 0.008$, respectively; Figure 2; Appendix S1: Table S2) as well as an increase of grasslands (G, mean change = +4479 m^2, $p < 0.001$; Figure 2), scrubs and copses (H, mean change = +277 m^2, $p = 0.029$), human settlements (B, mean change = +378 m^2, $p = 0.008$), and leisure and recreation facilities and parks (E, mean change = +2165 m^2, $p = 0.029$). On the finer Level 2 of categorization, semi-natural (semi-)dry grasslands (TM), species-rich wet or moist grasslands (GF), and arable fields (LA) significantly decreased in area over time (mean change = −15,783 m^2, −8262 m^2, and −7315 m^2, respectively; all $p < 0.001$; Appendix S1: Figure S5, Table S3). In contrast, species-poor grasslands (GI) and pioneer woodlands (WP) showed significant increases in area (mean change = +16,565 m^2 and + 10,303 m^2, respectively; both $p < 0.001$; Appendix S1: Figure S5).

Transitions between habitat types based on the IM showed that many of the semi-natural (semi-)dry grasslands (TM) have transitioned into species-rich moist to semi-dry grasslands (GM) and that the gain in species-poor grasslands (GI) was associated with

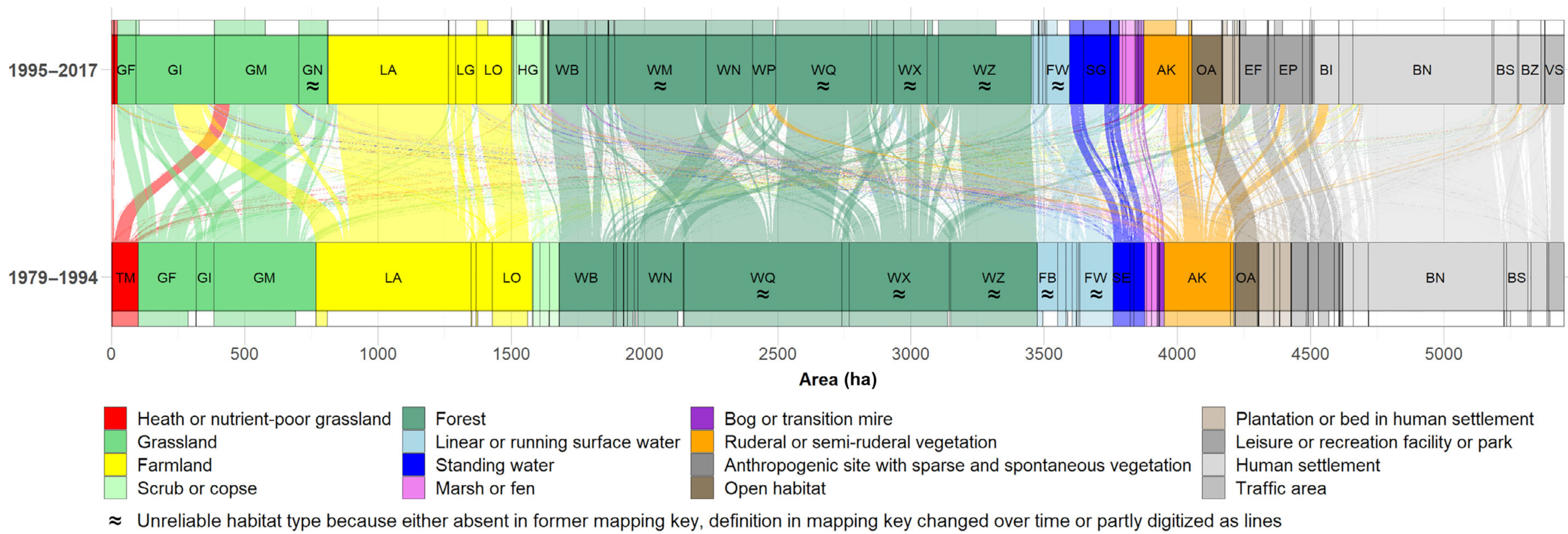

FIGURE 3 Alluvial plot showing total areas of and transitions between Level 2 habitat types from t_1 (1979–1994) to t_2 (1995–2017) for all habitat types with calculation based on the intersection method. Thin bars above and below the main bars represent the total area for each habitat type that has plant species lists attached in semi-transparent color and total area without species lists attached in white. Habitat type abbreviations according to the Hamburg identification key. Only habitat types with a total area >65 ha are labeled. Unreliable habitat types are marked with an approximation symbol (≈).

losses of species-rich moist to semi-dry grasslands (GM) and arable fields (LA; Figure 3). Species-rich wet or moist grasslands (GF) have turned into several other grassland categories, including wet grasslands with sedges, rushes, and tall forbs (GN). Pioneer forests (WP) have gained in area stemming from several other habitat types. The loss in semi-ruderal vegetation (AK) was associated with increases in anthropogenic habitats, especially industrial or commercial sites (BI).

Species trends

Spearman correlation between the trend methods ($CM_{species\_freq}$, $CM_{species\_area}$, and $CM_{species\_beals}$) revealed a high correlation between $CM_{species\_freq}$ and $CM_{species\_area}$ trends ($r_s = 0.997$, $p < 0.001$), but only moderate correlations of $CM_{species\_beals}$ with $CM_{species\_freq}$ and $CM_{species\_area}$ trends ($r_s = 0.43$ and 0.42, respectively, both $p < 0.001$). In the following, mainly the $CM_{species\_area}$ trends are presented, while the corresponding trends for the other methods are found in Appendix S1: Figures S6–S7, Table S4.

In total, 159 plant species showed significant trends regarding changes in occupied area ($CM_{species\_area}$) from t_1 to t_2, with 96 species increasing and 63 species decreasing (Figure 4; Appendix S1: Figure S8, Table S5). Species preferring forests (W) or scrubs and copses (H) increased in occupied area on average by a factor of 10 and 28, respectively (exponential estimate $= +0.98$ with $p < 0.001$ and estimate $= +1.44$ with $p = 0.001$, respectively; Appendix S1: Table S6), while species predominantly occurring in (semi-) ruderal vegetation (A) decreased in area on average by a factor of 33 (estimate $= -1.52$, $p = 0.002$; Appendix S1: Table S6; see Appendix S1: Table S7 for Level 2 habitat types).

The top winners derived from $CM_{species\_area}$ and $CM_{species\_freq}$ included non-native species such as *Rubus armeniacus* and *Senecio inaequidens*, some of which are known to be frequently planted (e.g., *Amelanchier lamarkii*). Species with the highest increases in Beals' occurrence probabilities ($CM_{species\_beals}$) were typical forest and scrub species, for example, *Acer pseudoplatanus*, *Corylus avellana*, and *Quercus robur*. The top losers according to $CM_{species\_area}$ and $CM_{species\_freq}$ included Hamburg red list species such as *Senecio sylvaticus* and *Elymus caninus*. The top losers derived from $CM_{species\_beals}$ were mainly common typical grassland species such as *Holcus lanatus*, *Trifolium repens*, and *Rumex acetosa* agg. Overall, endangered species rather decreased in their occupied area (Figure 5a,b), while non-native species rather increased in their occupied area (Figure 5c).

Species trends per habitat type

Analyzing species trends separately per former habitat type showed a mix of increasing and decreasing species for most habitat types (Figure 6; Appendix S1: Table S8). Significant trends per habitat type were found mainly for uncharacteristic species, that is, species that were assigned to prefer a different habitat type. Analyzing only habitats that had not undergone a transition in habitat type revealed only nine species with significant trends, which were all positive (Appendix S1: Figure S9).

DISCUSSION

Although the initial purpose of habitat mapping was to provide a basis for landscape planning and conservation, our study shows that these data can be used to detect biodiversity change. This can be performed both on the level of habitat types, revealing which habitat types suffered from a loss or gained in area, and species, identifying the losers and winners of biodiversity change.

Changes in habitat types

Habitat type analysis revealed overall decreases in area covered by nutrient-poor semi-natural (semi-)dry grasslands, which were mainly replaced by the more nutrient-rich species-rich moist to semi-dry grasslands. Dry and nutrient-poor grasslands have substantially decreased all over Europe and Germany over the last decades and show ongoing negative trends (Finck et al., 2017; Janssen et al., 2016). Those developments are mainly caused by eutrophication, leading to nutrient-rich sites, and the abandonment of management, in particular of grazing, leading to succession stages of scrubs and pioneer forests (Finck et al., 2017; Janssen et al., 2016). However, our analysis showed that pioneer forests did not only develop from semi-natural (semi-)dry grasslands but also from several different unmanaged habitat types. In these cases, the increase in woodland in urban and peri-urban areas can be beneficial on several levels, for example, by regulating the (micro)climate and air quality (Baro et al., 2014; Dobbs et al., 2011).

Although the overall area of grasslands increased, changes within grasslands showed a shift from

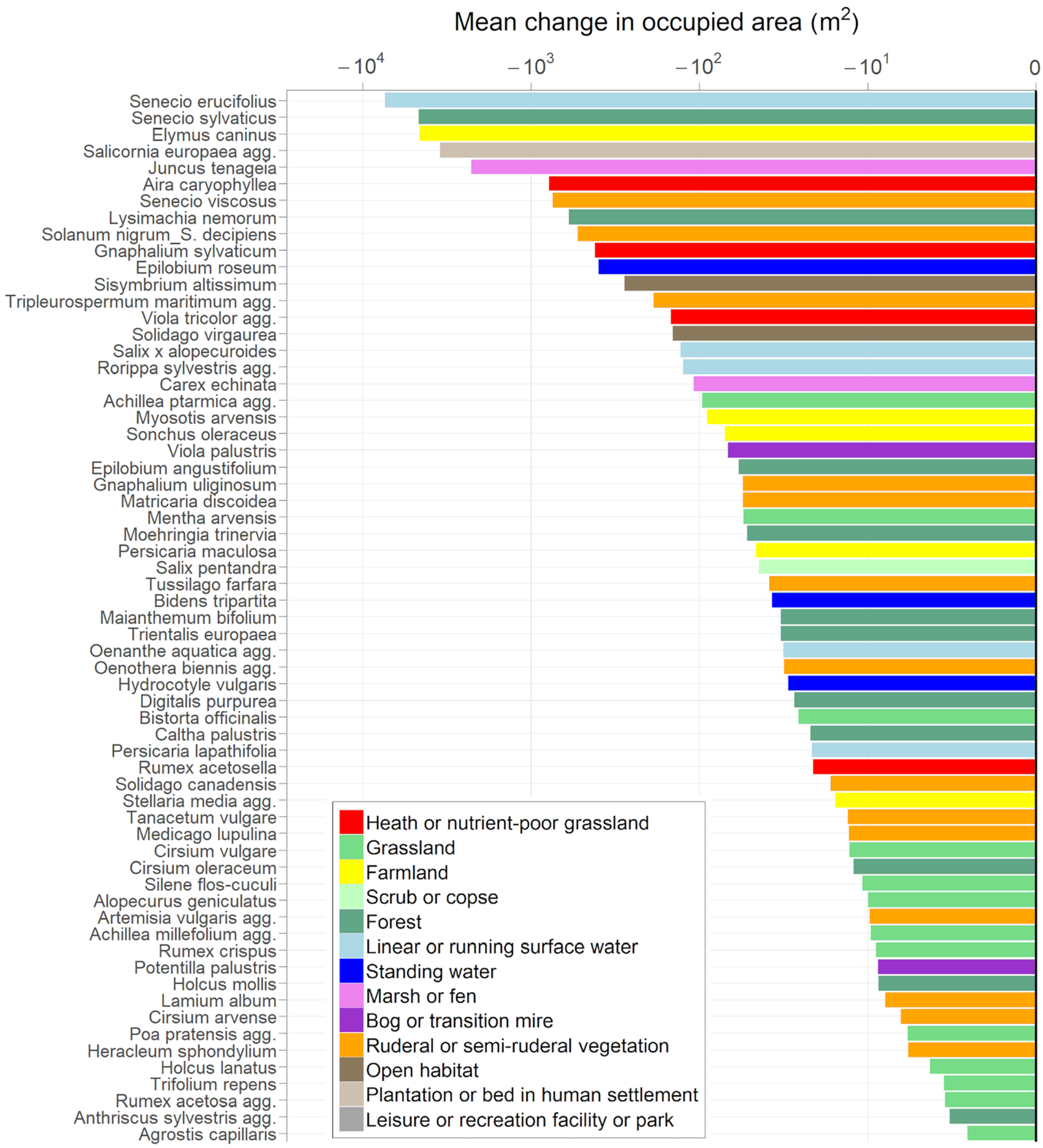

FIGURE 4 Mean change in occupied area in square meters from t_1 (1979–1994) to t_2 (1995–2017) for all species with significant trends. Change in occupied area was calculated as $\log_{10}(\text{area}_{\text{time period 1}} + 1/\text{area}_{\text{time period 2}} + 1)$ using $\text{CM}_{\text{species\_area}}$ and is shown on the $\log_{10}$ scale. Colors show the preferred Level 1 habitat type of the species, as assessed by the highest fidelity (Φ) of all habitat types for that species. Species that are known to be difficult to differentiate in the field were merged and are separated by an underscore. Figure 4 continues on next page.

species-rich moist to semi-dry grasslands toward species-poor grasslands, with the latter additionally gaining area from former arable fields. This trend reflects the increase in land use globally, which has led to severe decreases in species diversity in grasslands and arable fields (Meyer et al., 2013; Newbold et al., 2015; Wesche et al., 2012). This example also illustrates the value of the habitat type detail that habitat mapping data offers, which allows the observation of changes within broad categories, as grasslands, which are otherwise missed.

Next to the intensification of land use, the current progress in urbanization of the landscape represents another important pressure on habitats (Seto et al., 2013). In Hamburg, the observed increases in human settlements did mainly stem from ruderal sites, which also showed a general decrease in area. With Hamburg being a special case of a city state, urbanization is accompanied by a high turnover of land use, which is mostly driven by politics and economy. We also have to consider that a large part of ruderal habitats in Hamburg might have been missed in our analysis because the habitat mapping program only covered the inner part of Hamburg after 1995, which was thus not included in the analysis. This is also the reason why the majority of Hamburg's anthropogenic habitats is not well represented in Appendix S1:

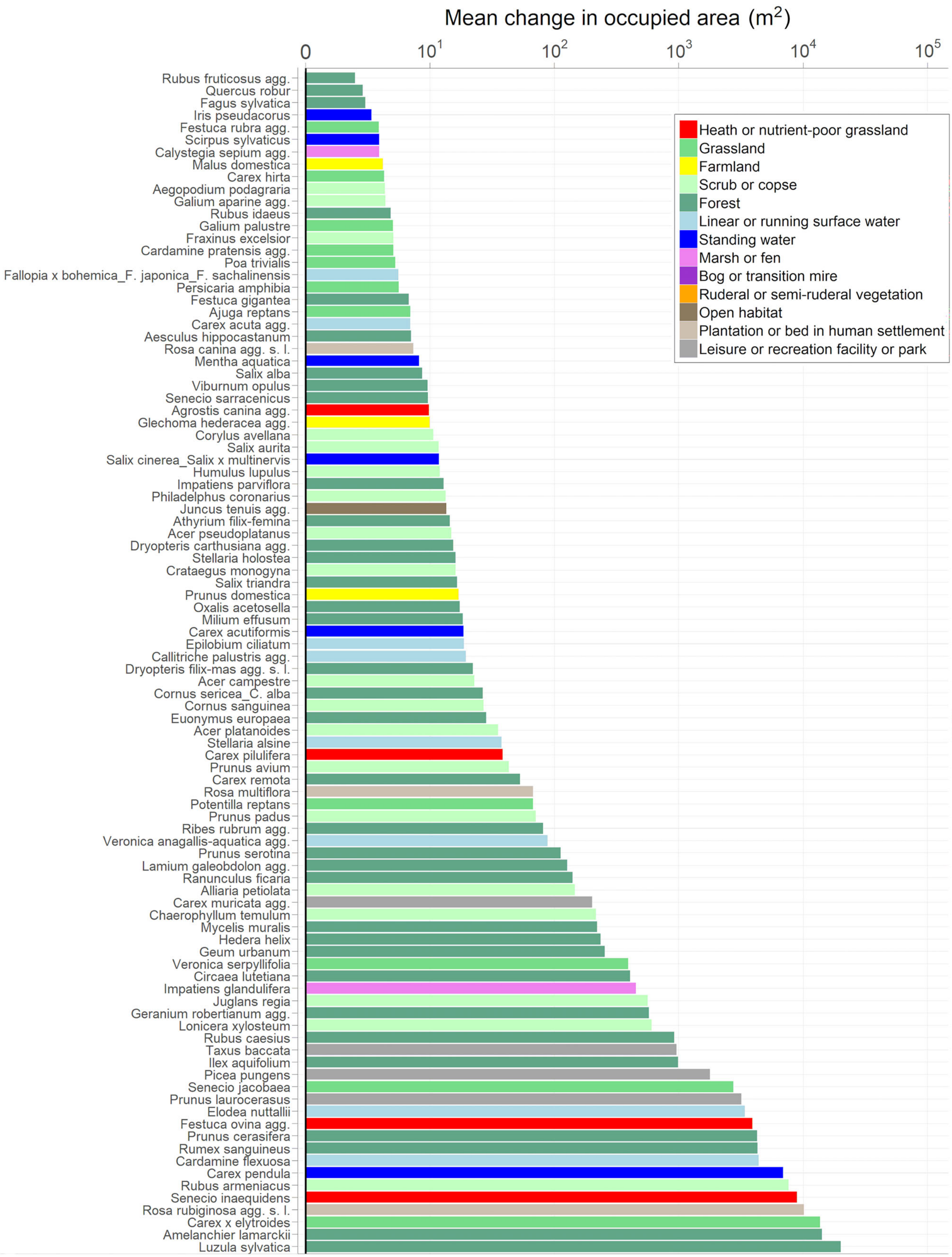

FIGURE 4 (Continued)

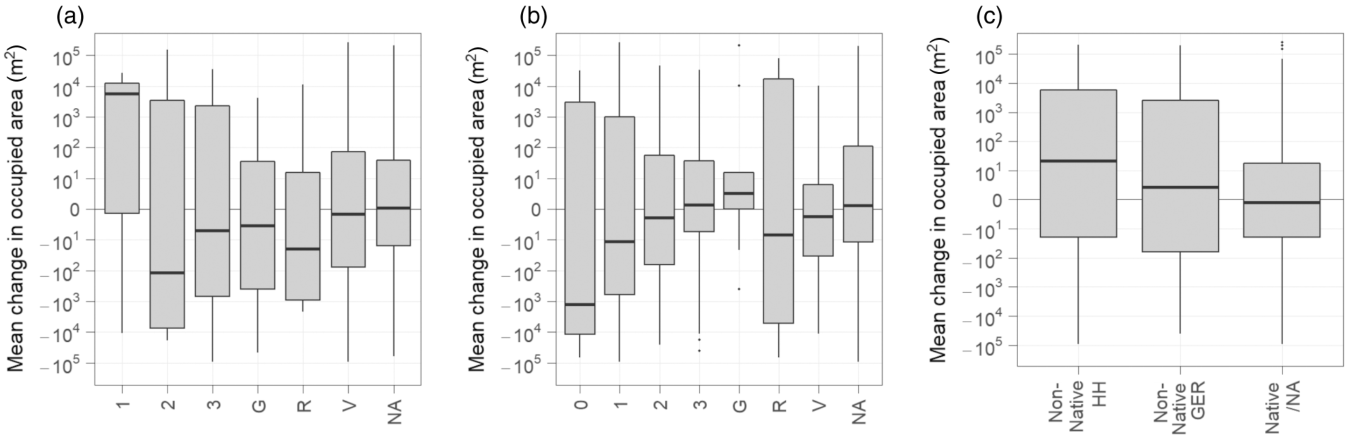

FIGURE 5 Mean change in occupied area in square meters from t_1 (1979–1994) to t_2 (1995–2017) for all species grouped by (a) red list status in Germany, (b) red list status in Hamburg, and (c) non-native status. Red list categories: 0 = extinct or lost, 1 = threatened with extinction, 2 = highly endangered, 3 = endangered, G = threatened, unknown extent, R = extremely rare, V = early warning, and NA = not threatened or not evaluated. Note that for (a) only three species with each only one occurrence across Hamburg were included for red list category 1. Species non-native to Germany (Non-Native GER) and Hamburg (Non-Native HH) are shown as separate categories, with Native/NA including native species, non-established non-natives and species for which no information was available.

Figure S5. Therefore, the observed transitions might mainly represent the current progress in urbanization of the suburban and peri-urban areas in Hamburg, reflecting overall urbanization trends in Germany (World Bank, 2021).

While we hypothesized that Hamburg's semi-natural habitats have been replaced by anthropogenic habitats, this was only partly the case, especially for species-rich grasslands. Many other transitions occurred between different semi-natural habitats and between different anthropogenic habitats.

Finally, some transitions between habitat types can only be interpreted as artifacts brought about by differences in the identification keys that could not be adjusted by the translation of habitat types. This is especially true for more detailed Level 2 habitat types in recent keys that did not exist in former times, which probably led to transitions such as from species-rich wet or moist grasslands toward wet grassland with sedges, rushes, and tall forbs. Despite those difficulties, most of the observed trends seem to reflect the situation of habitat type change in Germany and Europe.

Species trends

While species trends were similar for $CM_{species\_area}$ and $CM_{species\_freq}$, $CM_{species\_beals}$ ranked the sets of losers and winners differently than the other two methods. Beals' index includes differences in habitat quality as it incorporates the state of the habitat based on the species reported, which means that a habitat that already lost most of its typical species can be expected to be less suitable (and have a lower occurrence probability) even for the species that still occur there. In this way, Beals' occurrence probabilities reflect the extinction debt for species (Bruelheide et al., 2021). For example, the decrease in occurrence probability of typical grassland species reflects the loss of species-rich grasslands that was detected in the comparison of habitat area. However, based on the $CM_{species\_area}$ and $CM_{species\_freq}$ analyses, these species did not show much decrease in frequency and area, but can be expected to do so in the future. Commonly co-occurring species seem to have already decreased, pointing to habitat degradation and a decrease in habitat suitability for most species in these grassland habitats.

While we found more winners than losers overall, we identified several differences between those two groups. Winners included many non-native species, which was in line with our expectations and worldwide trends of increase in introductions of non-native species (Seebens et al., 2017), which especially affects urban areas (Pyšek et al., 2010). Hamburg with its large harbor is prone to receive many non-native species through international trade, which make up a high proportion of the flora, especially in the city center (Schmidt et al., 2014). With our species analysis not considering the inner part of Hamburg, the detected positive trends for non-native species might be even more severe and numerous in those more anthropogenic areas.

As expected, losers rather included red list species. However, locally rare species, which are often endangered, might not be very well captured in the habitat mapping data. Thus, the reliability of the trend for these species decreases with their rarity. Statistically, species with fewer than five occurrences would not show a significant trend,

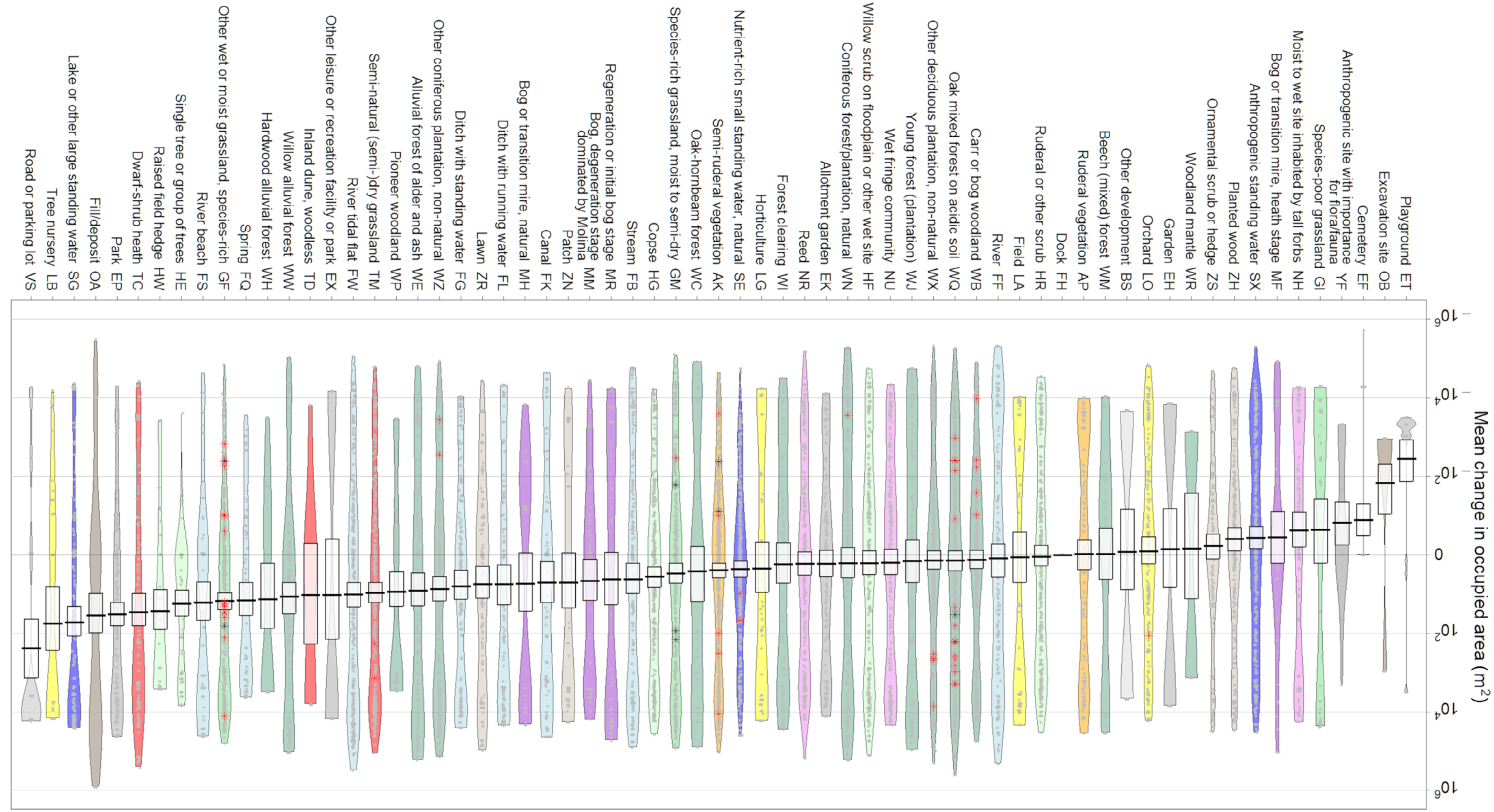

FIGURE 6 Mean change in occupied area in square meters from t_1 (1979–1994) to t_2 (1995–2017) for all species in all Level 2 habitat types in which they occurred in t_1. Assignment to habitat types regardless of whether habitat type changed toward t_2. Change in occupied area was calculated as $\log_{10}(\text{area}_{\text{time period }1} + 1/\text{area}_{\text{time period }2} + 1)$ using $CM_{\text{species\_area}}$ and is shown on the $\log_{10}$ scale. Colors according to the Level 1 habitat types in Figure 2. Species with a significant trend in a particular habitat type are shown as asterisks, which are colored black for species that prefer the respective habitat type and colored red for species that prefer a different habitat type. Species with insignificant trends are shown as gray dots.

even when they all disappeared (see also Sperle & Bruelheide, 2021). Given the incompleteness of species lists, trends derived from habitat mapping data cannot be confidently interpreted for rare species or those that only recently arrived. Trends for such species described by us have to be checked by experts. Nevertheless, we can assume that endangered species were especially sought out in surveys, also because species lists of preceding mapping events were made available to the surveyors. Thus, the decline of these species is realistic. Our observed trends are also in line with the decreasing trends for many red list species in Germany (Metzing et al., 2018).

One common trend across all applied methods was the increase in species typical of scrubs, copses, and forests, which reflects the increases discovered in area of the habitat types scrubs, copses, and pioneer forests. This finding is also consistent with European-wide trends of increasing succession in abandoned habitats (European Environment Agency, 2017; Navarro & Pereira, 2015). The opposite trend was the decline of typical (semi-) ruderal species, which reflects the decrease in area of ruderal habitat types in Hamburg. Although most of these species are not considered valuable with respect to nature conservation (Prach, 2003; Taft et al., 2006), they might have important functions in the urban environment. For example, many of the ruderal species are important providers of nectar and pollen for bees (Martins et al., 2017; Robinson & Lundholm, 2012).

It must be noted that in all our analysis, we always took a conservative approach (Appendix S1: Table S1), and the nature of the data might underestimate the actual species trends. First, the exclusions of habitats, which only had species lists available for one time period, can be assumed to reduce the detection of species losses. This is because the species analysis excluded many transitions of previously semi-natural habitats into anthropogenic and intensively managed habitats as the latter very rarely had species lists attached. Overall, it can be expected that species lists were less likely compiled for species-poor habitats. Second, at least since 1997, the old species lists have been made available to the surveyors, which has minimized the chance of missing previously observed species. This can be expected to have reduced negative trends caused by overlooked species in the resurvey. However, this underestimation of negative trends in our analysis gives more reliability to those trends we actually found.

Inconsistency of habitat and species trends

We had hypothesized a consistent trend both for habitat types and species characteristic of these habitat types. While trends of ruderal sites, scrubs, and copses as well as leisure or recreation facilities or parks were reflected in their associated species trends, this was not the case for the other six Level 1 habitat types. For those habitat types, habitat and species trends seemed to be mostly independent from each other so that our last hypothesis could not be confirmed. This implies that both types of analyses provide different information on trends and that surveying only habitat types or only plant species is not sufficient to capture the overall change in biodiversity.

This lack of consistency between habitat and species trends was also observed on the finer habitat type level, such as for semi-natural (semi-)dry grassland species. While the area of those grasslands decreased, their characteristic species did not show an overall significant trend, which was surprising as their decline in Germany has been observed in several studies and a high proportion of them are listed as red list species (Diekmann et al., 2014, 2019; Jandt et al., 2011; Metzing et al., 2018). This inconsistency can have different causes. First, habitat categories are crisp, while species trends are continuous. Thus, the nature of habitat mapping allows for abrupt changes in the assignment of habitat types, and in consequence, losses of habitat types occur suddenly, while reduction in species population occurs more gradually. A habitat that is in a transition stage might already be assigned to a new habitat type, while many once characteristic species might still occur, even when abundances are low (Jackson & Sax, 2010). In this case, species trends might be lagging behind habitat change trends, and these discrepancies could be considered impending extinction risks. Then, habitat changes might be indicators of species extinction debts (Kuussaari et al., 2009). Second, it is probable that those semi-natural (semi-)dry grassland species have a low habitat specificity and were also generally found outside their preferred habitat. This interpretation is supported by the absence of negative trends in those species within their respective former habitat types. Third, differences in habitat and species trends could have methodological reasons. For example, more complete species lists in the second compared with the first time period would result in underestimating the decline in species population.

In general, species trends per habitat type showed a mix of losers and winners for most habitat types, indicating a biodiversity change irrespective of the initial habitat type. Again, different reasons might be responsible for this finding. One of them might be that habitats have not yet transitioned into other habitat types but have already shown a considerable change in species composition. This could be considered a warning signal for an expected future transition of these habitat types into other types. Under this assumption, species trends per habitat type might indicate a "habitat extinction debt," as opposed to the extinction debts at the species level described above (Kuussaari et al., 2009). However, the evidence for habitat extinction debt is only weak. This is seen in our additional analysis including only habitats that have not changed in their assigned type, as significant trends were encountered only for nine species. This implies that species change within habitats is not the main driver of species change, but instead habitat change is the main driver of species change. In most cases, habitats have already transitioned into another habitat type and show a concomitant change in species composition. This would explain why habitat types showed significant increases mainly for uncharacteristic species of the habitat in question. Still, part of the change in species composition seems to be lagging behind. As mentioned before, the lack of negative trends of species per overall decreasing habitat type, for example, semi-natural (semi-)dry grasslands, point to those species seeking refuge in those newly emerged habitats. It is an open question whether these secondary habitats are only sink populations and provide acceptable site conditions only for a short time or whether they may ensure viable population sizes in the long run. These questions can only be answered by further species- and habitat-specific analyses. Other reasons for the mix of losers and winners per habitat type might be incomplete species lists, differences between former and recent habitat keys, and the inclusion of species from the minor habitat types of a habitat into the list of the main habitat. In any case, the combination of monitoring both species and habitats informs each other, and thus, can provide a more comprehensive picture of biodiversity change.

Management implications

Conservation management can only take place in an effective manner if we have information available about the past and recent developments in the landscape (Lindenmayer & Likens, 2009). Trends of habitat types and plant species derived from habitat mapping surveys offer useful information as their regional spatial scale of change matches that of regional conservation management. Therefore, our findings can directly be used for (1) the assessment of past conservation efforts for species and habitats, (2) for developing future conservation schemes, also adjusting for current actions, (3) assisting updating red lists of plants, which in turn will also influence conservation schemes, (4) identifying declining species and habitat types that are not in the focus of conservation measures yet and take actions to counteract negative trends early on, and (5) identifying species and habitat types that need further investigation, for example, about reasons for decrease. Close collaborations between governmental agencies and external researchers in making use of those habitat mapping data can thus enhance successful conservation effort.

CONCLUSIONS

Data from repeated habitat mapping programs are available both for several German states as well as for other countries. Mobilizing these data would allow to detect biodiversity change across those other regions as well, serving as a basis for effective conservation management. Although we acknowledge that there is bias arising from the heterogeneous quality of habitat mapping data, especially from incomplete species lists, our analysis showed that it can be used to detect biodiversity change for both habitat types and for plant species. While many monitoring programs focus on single endangered habitats, regional analyses across habitat types, which are based on repeated habitat mapping data, can identify the habitat types that might contribute most to species conservation. Those might also comprise secondary habitats of a species that could play a major role in preserving populations of their primary habitat. However, uncertainties in trends of less common species, which stem from incomplete species lists, clearly call for complete recordings of plant species across all habitat types in the future. While budget limits make this currently unfeasible for habitat mapping programs, a subset of surveys with complete plant species lists could serve as a benchmark for the detection biases in incomplete lists.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The raw data of the surveys are available in a database of the Ministry of Environment, Climate, Energy and Agriculture (BUKEA), Free and Hanseatic City of Hamburg, Germany: https://suche.transparenz.hamburg.de/dataset/biotopkataster-hamburg9. Data used for analyses (Lüttgert et al., 2022) are available on Figshare: https://doi.org/10.6084/m9.figshare.20201117.v1.

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REFERENCES

Baro, F., L. Chaparro, E. Gomez-Baggethun, J. Langemeyer, D. J. Nowak, and J. Terradas. 2014. “Contribution of Ecosystem Services to Air Quality and Climate Change Mitigation Policies: The Case of Urban Forests in Barcelona, Spain.” *Ambio* 43: 466–79.

Beals, E. W. 1984. “Bray-Curtis Ordination: An Effective Strategy for Analysis of Multivariate Ecological Data.” *Advances in Ecological Research*. Elsevier 14: 1–55.

Brandt, I., and B. Engelschall. 2011. “Kartieranleitung und Biotoptypenschlüssel für die Biotopkartierung in Hamburg.” Behörde für Stadtentwicklung und Umwelt.

Brooks, T. M., S. L. Pimm, H. R. Akcakaya, G. M. Buchanan, S. H. M. Butchart, W. Foden, C. Hilton-Taylor, et al. 2019. “Measuring Terrestrial Area of Habitat (AOH) and its Utility for the IUCN Red List.” *Trends in Ecology & Evolution* 34: 977–86.

Bruelheide, H., F. Jansen, U. Jandt, M. Bernhardt-Römermann, A. Bonn, D. Bowler, J. Dengler, et al. 2020. “Using Incomplete Floristic Monitoring Data from Habitat Mapping Programmes to Detect Species Trends.” *Diversity and Distributions* 26: 782–94.

Bruelheide, H., F. Jansen, U. Jandt, M. Bernhardt-Römermann, A. Bonn, D. Bowler, J. Dengler, et al. 2021. “A Checklist for Using Beals’ Index with Incomplete Floristic Monitoring Data.” *Diversity and Distributions* 27: 1328–33.

Cardinale, B. J., A. Gonzalez, G. R. H. Allington, and M. Loreau. 2018. “Is Local Biodiversity Declining or Not? A Summary of the Debate over Analysis of Species Richness Time Trends.” *Biological Conservation* 219: 175–83.

Chytrý, M., L. Tichý, J. Holt, and Z. Botta-Dukát. 2002. “Determination of Diagnostic Species with Statistical Fidelity Measures.” *Journal of Vegetation Science* 13: 79–90.

Díaz, S., J. Settele, E. S. Brondízio, H. T. Ngo, J. Agard, A. Arneth, P. Balvanera, et al. 2019. “Pervasive Human-Driven Decline of Life on Earth Points to the Need for Transformative Change.” *Science* 366: eaax3100.

Diekmann, M., C. Andres, T. Becker, J. Bennie, V. Blüml, J. M. Bullock, H. Culmsee, et al. 2019. “Patterns of Long-Term Vegetation Change Vary between Different Types of Semi-Natural Grasslands in Western and Central Europe.” *Journal of Vegetation Science* 30: 187–202.

Diekmann, M., U. Jandt, D. Alard, A. Bleeker, E. Corcket, D. J. G. Gowing, C. J. Stevens, and C. Duprè. 2014. “Long-Term Changes in Calcareous Grassland Vegetation in North-Western Germany—No Decline in Species Richness, but a Shift in Species Composition.” *Biological Conservation* 172: 170–9.

Dobbs, C., F. J. Escobedo, and W. C. Zipperer. 2011. “A Framework for Developing Urban Forest Ecosystem Services and Goods Indicators.” *Landscape and Urban Planning* 99: 196–206.

Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. “Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss.” *Science* 344: 296–9.

Eichenberg, D., D. E. Bowler, A. Bonn, H. Bruelheide, V. Grescho, D. Harter, U. Jandt, R. May, M. Winter, and F. Jansen. 2021. “Widespread Decline in Central European Plant Diversity across Six Decades.” *Global Change Biology* 27: 1097–110.

Ellis, E. C., N. Gauthier, K. Klein Goldewijk, R. Bliege Bird, N. Boivin, S. Diaz, D. Q. Fuller, et al. 2021. “People Have Shaped Most of Terrestrial Nature for at Least 12,000 Years.” *Proceedings of the National Academy of Sciences of the United States of America* 118: e2023483118.

ESRI. 2016. *ArcGIS*. Redlands: Environmental Systems Research Institute.

European Environment Agency. 2017. “Landscapes in Transition: An Account of 25 Years of Land Cover Change in Europe.” Copenhagen.

Finck, P., S. Heinze, U. Raths, U. Riecken, and A. Ssymank. 2017. “Rote Liste der gefährdeten Biotoptypen Deutschlands.” Bundesamt für Naturschutz.

Finderup Nielsen, T., K. Sand-Jensen, M. Dornelas, and H. H. Bruun. 2019. “More Is Less: Net Gain in Species Richness, but Biotic Homogenization over 140 Years.” *Ecology Letters* 22: 1650–7.

Gonzalez, A., B. J. Cardinale, G. R. H. Allington, J. Byrnes, K. Arthur Endsley, D. G. Brown, D. U. Hooper, F. Isbell, M. I. O’Connor, and M. Loreau. 2016. “Estimating Local Biodiversity Change: A Critique of Papers Claiming No Net Loss of Local Diversity.” *Ecology* 97: 1949–60.

Hillebrand, H., B. Blasius, E. T. Borer, J. M. Chase, J. A. Downing, B. K. Eriksson, C. T. Filstrup, et al. 2018. “Biodiversity Change Is Uncoupled from Species Richness Trends: Consequences for Conservation and Monitoring.” *Journal of Applied Ecology* 55: 169–84.

Hüllbusch, E., L. Brandt, P. Ende, and J. Dengler. 2016. “Little Vegetation Change during Two Decades in a Dry Grassland Complex in the Biosphere Reserve Schorfheide-Chorin (NE Germany).” *Tuexenia* 36: 395–412.

Jackson, S. T., and D. F. Sax. 2010. “Balancing Biodiversity in a Changing Environment: Extinction Debt, Immigration Credit and Species Turnover.” *Trends in Ecology & Evolution* 25: 153–60.

Jandt, U., H. von Wehrden, and H. Bruelheide. 2011. “Exploring Large Vegetation Databases to Detect Temporal Trends in Species Occurrences.” *Journal of Vegetation Science* 22: 957–72.

Jansen, F., A. Bonn, D. E. Bowler, H. Bruelheide, and D. Eichenberg. 2020. “Moderately Common Plants Show Highest Relative Losses.” *Conservation Letters* 13: e12674.

Jansen, F., and J. Dengler. 2008. "GermanSL—Eine universelle taxonomische Referenzliste für Vegetationsdatenbanken in Deutschland." *Tuexenia* 28: 239–53.

Janssen, J. A. M., J. S. Rodwell, M. García Criado, S. Gubbay, T. Haynes, A. Nieto, N. Sanders, et al. 2016. "European Red List of Habitats." Part 2. Terrestrial and Freshwater Habitats. Brussels.

Kaiser, T., H. Schlumprecht, P. Finck, and U. Riecken. 2013. "Biotopkartierungen in den deutschen Bundesländern—aktueller Stand und Methodenvergleich." *Natur und Landschaft* 88: 97–102.

Kerr, J. T., and I. Deguise. 2004. "Habitat Loss and the Limits to Endangered Species Recovery." *Ecology Letters* 7: 1163–9.

Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Ockinger, et al. 2009. "Extinction Debt: A Challenge for Biodiversity Conservation." *Trends in Ecology & Evolution* 24: 564–71.

Lee, W., M. McGlone, and E. Wright. 2005. "Biodiversity Inventory and Monitoring: A review of national and international systems and a proposed framework for future biodiversity monitoring by the Department of Conservation." Landcare Research contract report LC0405/122.

Lindenmayer, D. B., and G. E. Likens. 2009. "Adaptive Monitoring: A New Paradigm for Long-Term Research and Monitoring." *Trends in Ecology & Evolution* 24: 482–6.

Lüttgert, L., Heisterkamp, S., Jansen, F., Klenke, R., Kreft, K.-A., Seidler, G., Bruelheide, H. 2022. "Data Used to Analyze Temporal Habitat Type and Plant Species Trends in Hamburg." Figshare. Dataset. https://doi.org/10.6084/m9.figshare.20201117.v1.

Magurran, A. E. 2016. "How Ecosystems Change." *Science* 351: 448–9.

Martins, K. T., A. Gonzalez, and M. J. Lechowicz. 2017. "Patterns of Pollinator Turnover and Increasing Diversity Associated with Urban Habitats." *Urban Ecosystem* 20: 1359–71.

Metzing, D., N. Hofbauer, G. Ludwig, and G. Matzke-Hajek. 2018. "Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands." Band 7—Pflanzen. Bundesamt für Naturschutz, Bonn-Bas Godesberg.

Meyer, S., E. Bergmeier, T. Becker, K. Wesche, B. Krause, and C. Leuschner. 2015. "Detecting Long-Term Losses at the Plant Community Level—Arable Fields in Germany Revisited." *Applied Vegetation Science* 18: 432–42.

Meyer, S., K. Wesche, B. Krause, and C. Leuschner. 2013. "Dramatic Losses of Specialist Arable Plants in Central Germany since the 1950s/60s—a Cross-Regional Analysis." *Diversity and Distributions* 19: 1175–87.

Navarro, L. M., and H. M. Pereira. 2015. "Rewilding Abandoned Landscapes in Europe." In *Rewilding European Landscapes*, edited by H. M. Pereira and L. M. Navarro, 3–23. Cham: Springer International Publishing.

Newbold, T., L. N. Hudson, S. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Borger, et al. 2015. "Global Effects of Land Use on Local Terrestrial Biodiversity." *Nature* 520: 45–50.

Pereira, H. M., L. M. Navarro, and I. S. Martins. 2012. "Global Biodiversity Change: The Bad, the Good, and the Unknown." *Annual Review of Environment and Resources* 37: 25–50.

Pescott, O. L., K. J. Walker, F. Harris, H. New, C. M. Cheffings, N. Newton, M. Jitlal, J. Redhead, S. M. Smart, and D. B. Roy. 2019. "The Design, Launch and Assessment of a New Volunteer-Based Plant Monitoring Scheme for the United Kingdom." *PLoS One* 14: e0215891.

Poppendieck, H.-H., H. Bertram, I. Brandt, K.-A. Kreft, H. Kurz, A. Onnasch, H. Preisinger, J. Ringenberg, J. von Prondzinski, and D. Wiedemann. 2010. "Rote Liste und Florenliste der Gefäßpflanzen von Hamburg." In *Der Hamburger Pflanzenatlas von a bis z*, edited by H. H. Poppendieck, I. Bertram, B. E. Brandt, and J. V. Prondzinski. München: Dölling und Galitz Verlag.

Prach, K. 2003. "Spontaneous Succession in Central-European Man-Made Habitats: What Information Can Be Used in Restoration Practice?" *Applied Vegetation Science* 6: 125–9.

Pyšek, P., S. Bacher, M. Chytrý, V. Jarošík, J. Wild, L. Celesti-Grapow, N. Gassó, et al. 2010. "Contrasting Patterns in the Invasions of European Terrestrial and Freshwater Habitats by Alien Plants, Insects and Vertebrates." *Global Ecology and Biogeography* 19: 317–31.

QGIS Development Team. 2021. "QGIS Geographic Information System." Open Source Geospatial Foundation Project.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Reinecke, J., G. Klemm, and T. Heinken. 2014. "Vegetation Change and Homogenization of Species Composition in Temperate Nutrient Deficient Scots Pine Forests after 45 Yr." *Journal of Vegetation Science* 25: 113–21.

Robinson, S. L., and J. T. Lundholm. 2012. "Ecosystem Services Provided by Urban Spontaneous Vegetation." *Urban Ecosystem* 15: 545–57.

Schmidt, K. J., H.-H. Poppendieck, and K. Jensen. 2014. "Effects of Urban Structure on Plant Species Richness in a Large European City." *Urban Ecosystem* 17: 427–44.

Seebens, H., T. M. Blackburn, E. E. Dyer, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Pagad, et al. 2017. "No Saturation in the Accumulation of Alien Species Worldwide." *Nature Communications* 8: 14435.

Seto, K. C., S. Parnell, and T. Elmqvist. 2013. "A Global Outlook on Urbanization." In *Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities: A Global Assessment*, edited by T. Elmqvist, M. Fragkias, J. Goodness, B. Güneralp, P. J. Marcotullio, R. I. McDonald, S. Parnell, M. Schewenius, M. Sendstad, K. C. Seto, and C. Wilkinson, 1–12. Netherlands: Springer.

Sperle, T., and H. Bruelheide. 2021. "Climate Change Aggravates Bog Species Extinctions in the Black Forest (Germany)." *Diversity and Distributions* 27: 282–95.

Staude, I. R., D. M. Waller, M. Bernhardt-Romermann, A. D. Bjorkman, J. Brunet, P. De Frenne, R. Hedl, et al. 2020. "Replacements of Small- by Large-Ranged Species Scale up to Diversity Loss in Europe's Temperate Forest Biome." *Nature Ecology and Evolution* 4: 802–8.

Strubelt, I., M. Diekmann, and D. Zacharias. 2017. "Changes in Species Composition and Richness in an Alluvial Hardwood Forest over 52 Yrs." *Journal of Vegetation Science* 28: 401–12.

Sukopp, H., W. Trautmann, and J. Schaller. 1979. "Biotopkartierung in der Bundesrepublik Deutschland." *Natur und Landschaft* 54: 63–5.

Taft, J. B., C. Hauser, and K. R. Robertson. 2006. "Estimating Floristic Integrity in Tallgrass Prairie." *Biological Conservation* 131: 42–51.

Vellend, M., L. Baeten, I. H. Myers-Smith, S. C. Elmendorf, R. Beausejour, C. D. Brown, P. De Frenne, K. Verheyen, and S. Wipf. 2013. "Global Meta-Analysis Reveals no Net Change in Local-Scale Plant Biodiversity over Time." *Proceedings of the National Academy of Sciences of the United States of America* 110: 19456–9.

Weber, D., U. Hintermann, and A. Zangger. 2004. "Scale and Trends in Species Richness: Considerations for Monitoring Biological Diversity for Political Purposes." *Global Ecology and Biogeography* 13: 97–104.

Wesche, K., B. Krause, H. Culmsee, and C. Leuschner. 2012. "Fifty Years of Change in Central European Grassland Vegetation: Large Losses in Species Richness and Animal-Pollinated Plants." *Biological Conservation* 150: 76–85.

Williams, B. A., O. Venter, J. R. Allan, S. C. Atkinson, J. A. Rehbein, M. Ward, M. Di Marco, et al. 2020. "Change in Terrestrial Human Footprint Drives Continued Loss of Intact Ecosystems." *One Earth* 3: 371–82.

World Bank. 2021. "Urbanisierungsgrad: Anteil der Stadtbewohner an der Gesamtbevölkerung in Deutschland in den Jahren von 2000 bis 2020 [Graph]." Statista. https://de.statista.com/statistik/daten/studie/662560/umfrage/urbanisierung-in-deutschland/.

SUPPORTING INFORMATION

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

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