Biodiversity trends for Germany using repeated habitat mapping data

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“*We abuse land because we regard it as a commodity belonging to us. When we see land as a community to which we belong, we may begin to use it with love and respect.*”

Aldo Leopold, *A Sand County Almanac*, 1949

Table of contents

Summary

The world is experiencing an ongoing decline in many aspects of biodiversity, including natural and semi-natural habitat types as well as their characteristic species. To understand the extent and possible drivers of this biodiversity crisis, it is essential to identify its winners and losers. Since systematic monitoring data is rare, many studies make use of heterogeneous data to derive temporal trends of habitat types or species. One example of such data, which have rarely been used so far to analyze trends, are data from habitat mapping programs, which typically aim at mapping all protected habitat types in a region while also recording plant species on site. In Germany, such mapping is organized by the federal states and has often been repeated.

In this thesis, I used repeated habitat mapping data spanning the years 1977-2021 from the German federal states Hamburg (chapters 2, 4), Baden-Württemberg (chapters 3, 4), and Schleswig-Holstein (chapter 4) to derive biodiversity trends. I calculated trends of habitat types (chapters 2, 3), of plant species across all habitat types (chapters 2, 3, 4), and of plant species within different habitat types (chapters 2, 3, 4). Habitat type trends were based on mean changes in area while also looking at transitions between habitat types. For species trends, I used three change metrics: change in frequency, occupied area, and probability of occurrence (Beals' index), with the latter accounting for the incomplete species lists of the data. I then tested if specific species groups declined or increased by grouping species by their preferred habitat type, Red List status, and non-native status.

In the first study (chapter 2), I found that Hamburg experienced the highest mean losses in area for the groups of heaths and semi-natural grasslands as well as for ruderal and semi-ruderal vegetation. In contrast, mesic to wet grasslands, scrubs, copses and field hedges, and human settlements increased in area. However, the increases in mesic to wet grasslands were driven by species-poor grasslands while many species-rich grassland types declined, emphasizing the importance of considering trends of detailed habitat types for the interpretation of broader habitat type trends.

In the second study (chapter 3), I analyzed trends for Baden-Württemberg. I explicitly looked for consistencies between trends in habitat types with trends of their characteristic species across the state and with mean trends of all species within those habitat types. While most of the protected habitat types decreased in area, dry to moderately moist forests showed positive trends. Trends of habitat types and their characteristic species were mostly consistent. However, mean species trends within habitat types were generally negative, also for habitat types that showed increases in their area, i.e. deciduous forests.

The third study (chapter 4) focused on species trends in Hamburg, Baden-Württemberg, and Schleswig-Holstein, comparing trends for individual species and species groups between these three states. Consistently in all states, I found negative trends for species of heaths and semi-natural grasslands, moist to wet grasslands, and coastal and marine habitats as well as for endangered species. In contrast, positive trends were found for species of scrubs, copses and field hedges, and for non-native species. Within habitat types, characteristic species mostly declined. While some individual species trends varied among states, the overall patterns of winners and losers were highly similar.

In conclusion, my work reveals declines in many protected habitat types, and points to ongoing habitat degradation, implied by losses of characteristic species and a woody encroachment in many habitat types. Similar trend patterns between the states imply that species are affected by similar drivers in different parts of Germany. These drivers include water drainage, climate change, eutrophication, and abandonment of extensive management.

This thesis represents an important contribution towards analyzing heterogeneous biodiversity data by providing a blueprint and many considerations on how to confront such data. It further provides biodiversity trends across federal states, improving the knowledge on biodiversity change in Germany. Still, systematic monitoring programs for habitats, species, and drivers of change are needed, and more urgently, intensified action to stop the biodiversity crisis, including better protection and restoration of nature.

Zusammenfassung

Der weltweit anhaltende Rückgang vieler Aspekte der Biodiversität betrifft sowohl natürliche und naturnahe Biotoptypen als auch ihre charakteristischen Arten. Um die Ausmaße und möglichen Treiber dieser Biodiversitätskrise besser zu verstehen, braucht es Kenntnisse darüber, wer ihre Gewinner und Verlierer sind. Da systematische Monitoringprogramme selten sind, verwenden viele wissenschaftliche Studien heterogene Daten, um zeitliche Trends von Biotoptypen und Arten zu erstellen. Ein Beispiel für solche Daten, die bislang nur selten für Trendberechnungen verwendet wurden, stellen Daten aus Biotopkartierungen dar. Bei Biotopkartierungen werden üblicherweise alle geschützten Biotoptypen in einer bestimmten Region kartiert, wobei auch die in den Biotopen vorkommenden Pflanzenarten aufgenommen werden. In Deutschland werden großflächige Biotopkartierungen von den Bundesländern koordiniert und liegen oft wiederholt vor.

In meiner Dissertation habe ich wiederholte Biotopkartierungen aus den Jahren 1977-2021 der Bundesländer Hamburg (Kapitel 2, 4), Baden-Württemberg (Kapitel 3, 4), und Schleswig-Holstein (Kapitel 4) verwendet, um Biodiversitätstrends zu erstellen. Dabei habe ich Trends von Biotoptypen (Kapitel 2, 3), von Pflanzenarten über alle Biotoptypen hinweg (Kapitel 2, 3, 4) und von Pflanzenarten innerhalb verschiedener Biotoptypen (Kapitel 2, 3, 4) berechnet. Die Trends der Biotoptypen beruhen auf den mittleren Flächenänderungen, wobei ich zusätzlich Umwandlungen zwischen Biotoptypen betrachtet habe. Für die Trends der Arten verwendete ich drei metrische Maßzahlen: Änderung in der Frequenz, der besetzten Fläche und der Vorkommenswahrscheinlichkeit (Beals‘ index), wobei letztere die unvollständigen Artenlisten der Kartierungen berücksichtigt. Mithilfe dieser Trends testete ich dann, ob bestimmte Artengruppen zu- oder abnahmen, wobei ich die Arten anhand ihres präferierten Biotoptypen, ihres Rote Liste- und Neophyten-Status gruppierte.

In der ersten Studie (Kapitel 2) zeigte sich, dass in Hamburg vor allem Heiden und nährstoffarme Grasländer, aber auch ruderale und halbruderale Krautfluren in ihrer mittleren Fläche zurückgingen. Im Gegensatz dazu nahmen mesische bis nasse Grünländer, Gebüsche, Feldgehölze und Feldhecken, ebenso wie Siedlungsflächen zu. Es zeigte sich jedoch, dass die Zunahmen der mesischen bis nassen Grünländer auf Zunahmen von artenarmem Grünland beruhten, wohingegen viele artenreiche Grünlandtypen abnahmen. Dies verdeutlicht, wie wichtig die

Berücksichtigung der Trends der detaillierten Biotoptypen bei der Interpretation der Trends gröberer Biotoptypen ist.

In der zweiten Studie (Kapitel 3) berechnete ich Trends für Baden-Württemberg und prüfte explizit die Übereinstimmungen der Trends der Biotoptypen mit den bundesweiten Trends ihrer charakteristischen Arten als auch mit den mittleren Trends aller Arten innerhalb der jeweiligen Biotoptypen. Während die meisten der geschützten Biotoptypen in ihrer Fläche abnahmen, nahmen trockene bis mäßig feuchte Wälder zu. Die Trends der Biotoptypen und ihrer charakteristischen Arten stimmten in ihrer Richtung größtenteils miteinander überein. Allerdings waren die mittleren Trends aller Arten innerhalb von Biotoptypen generell negativ, so auch für Biotoptypen, die in ihrer Fläche zunahmen, wie Laubwälder.

Die dritte Studie (Kapitel 4) befasste sich mit Artentrends innerhalb Hamburgs, Baden-Württembergs und Schleswig-Holsteins, wobei explizit die Trends zwischen den Bundesländern verglichen wurden, sowohl von einzelnen Arten als auch von Artgruppen. Konsistent in allen Bundesländern zeigten sich negative Trends von Arten der Heiden und nährstoffarmen Grasländer, der feuchten bis nassen Grünländer und Küsten- und Meeresbiotope, als auch von gefährdeten Arten. Dagegen zeigten Arten der Gebüsche, Feldgehölze und Feldhecken, und Neophyten positive Trends. Innerhalb der Biotoptypen nahmen vor allem charakteristische Arten ab. Während einige einzelne Artentrends zwischen den Bundesländern variierten, waren die grundsätzlichen Trendmuster von Gewinnern und Verlieren sehr ähnlich.

Zusammenfassend zeigt meine Arbeit Rückgänge vieler geschützter Biotoptypen und weist auf eine Verschlechterung des Zustandes vieler Biotoptypen hin, impliziert vor allem durch den Rückgang vieler charakteristischer Arten als auch die Verbuschung in vielen Biotoptypen. Die ähnlichen Trendmuster zwischen den Bundesländern deuten darauf hin, dass Arten von ähnlichen Treibern in verschiedenen Gebieten Deutschlands betroffen sind. Diese Treiber beinhalten die Entwässerung der Landschaft, den Klimawandel, die Eutrophierung der Landschaft und die Aufgabe von extensiver Landnutzung.

Die vorliegende Dissertation liefert einen wichtigen Beitrag zur Analyse heterogener Biodiversitätsdaten, indem sie eine Blaupause solcher Analysen bereitstellt und dabei die vielseitigen Probleme der Daten berücksichtigt und diskutiert. Weiterhin liefert sie Biodiversitätstrends für mehrere Bundesländer und verbessert somit den Wissensstand bezüglich Biodiversitätsveränderungen in Deutschland. Nichtsdestotrotz braucht es systematische Monitoringprogramme für Biotoptypen, Arten und Treiber des Wandels, sowie vor allem verstärkte Bemühungen, die Biodiversitätskrise zu stoppen, inklusive besseren Schutzes und einer Renaturierung der Natur.

Chapter 1

General introduction

THE BIODIVERSITY CRISIS – TRENDS, THEIR DRIVERS, AND SCALE DEPENDENCE

The world is in a biodiversity crisis (Ceballos et al., 2015; Johnson et al., 2017). This human-induced crisis is characterized by the decline in many aspects of biodiversity, most prominently of natural and semi-natural habitat types as well as their inhabiting species (Díaz et al., 2019; IPBES, 2019; Isbell et al., 2023; Pereira et al., 2012). While common trends and change drivers have been observed across the world and taxonomic groups, in the following I will focus on the situation in Germany. Here, the habitat types that experienced the most drastic losses in area and quality over the last decades and sometimes centuries have been bogs, (species-rich) arable fields, as well as wet and dry grasslands (Finck et al., 2017; Wirth et al., 2024). In contrast, forests and shrublands have showed overall increases in area over the past decades (European Environment Agency, 2017; Fuchs et al., 2013).

For plant species, many individual temporal trends have been reported for Germany (Eichenberg et al., 2021; Jandt et al., 2022). To understand why some species increase and others decrease, they are often grouped by their characteristics, e.g., their traits, sensitivity to different environmental conditions, geographic distributions, or environmental niches. Species can also be grouped by their affiliation to specific habitat types (Büttner et al., 2022). Studies using this information have shown that mainly habitat types' characteristic species have declined, often being replaced by generalists and common species (Diekmann et al., 2019; Heinrichs & Schmidt, 2017; Meyer et al., 2013; Staude et al., 2020). Overall, trends of different species groups can hint at specific drivers of biodiversity change, e.g., increases in nutrient demanding species indicate eutrophication. This is especially important since driver information at the local scale is usually scarce.

Among the main reasons for the ongoing biodiversity decline in Germany are the intensification of land use (e.g., eutrophication, drainage) and the destruction and fragmentation of habitats (e.g., urbanization), followed by climate change, pollution, and invasive species (Finck et al., 2017; Marx et al., 2024; Metzing et al., 2018). These factors can also reinforce or mitigate each other (Brook et al., 2008; Isbell et al., 2023; Komatsu et al., 2019; Oliver & Morecroft, 2014) and differ depending on the habitat type (Tyler et al., 2018). Thus, it is necessary to analyze trends and/or their drivers also separately by habitat type.

Biodiversity change can be analyzed on different temporal and spatial scales. Concerning temporal scales, longer time periods usually lead to stronger changes and are less sensitive to fluctuations (Gonzalez et al., 2016; Magurran et al., 2010). Further, data that reaches further back into the past is capable of detecting changes caused by anthropogenic pressures that already started many decades ago, while recent short-term studies start at an already shifted baseline (Gonzalez et al., 2023; Mihoub et al., 2017; Montras-Janer et al., 2024). Further, extinction debts, i.e. slow responses of species to habitat change or loss, lead to an initial underestimation of species declines after habitat change, which only become evident after maybe decades, especially for long-lived species such as trees (Essl et al., 2015a; Essl et al., 2015b). However, long-term studies spanning several decades are rare.

The observed biodiversity change further depends on the spatial scale, which caused some debate on whether species net numbers on a local scale are overall decreasing or not (Dornelas et al., 2014; Gonzalez et al., 2016; Vellend, Baeten, et al., 2013; see Cardinale et al. (2018) and Primack et al. (2018) for a summary). Current literature suggests that on a local scale species richness trends are variable, depending on the site and whether habitat conversion occurred, while on a landscape/regional scale usually more species are gained than lost, and on a global scale way more species are lost than gained (Chase et al., 2019; Dornelas et al., 2023; Primack et al., 2018; Vellend et al., 2017). Increases of species numbers on the local to regional scale are often caused by gains in a few widespread or non-native species outpacing losses of native species, with sites then becoming more similar to each other concerning their species composition (Finderup Nielsen et al., 2019; Hillebrand et al., 2018; Montras-Janer et al., 2024). Thus, instead of looking at changes in species numbers, on a local to regional scale, analyzing changes in the composition of sites or identifying groups of winners vs. losers seems more insightful (Hillebrand et al., 2018; Magurran, 2016; Santini et al., 2017; Timmermann et al., 2015; Wiegmann & Waller, 2006). The spatial level of habitats at the scale of a few hundred square meters to hectares, lies between the local plot and landscape scale. Compared with the local scale, trend analyses on the habitat scale have a lower power to detect changes and are more likely to observe colonizations compared to extinctions, even though this imbalance is even greater on the landscape scale (Chase et al., 2019; Jarzyna et al., 2015). In contrast to the local scale, however, the habitat scale offers relatively stable trends, as fluctuations are averaged in space. Still, only few studies on biodiversity change are conducted on this scale so far.

BIODIVERSITY TREND DATA

For analyzing biodiversity trends, availability of data is the most limiting factor. Trends of habitat types on large scales are mostly based on satellite data, using broad land cover/use categories (e.g., MODIS, Landsat, Corine Land Cover; e.g., Fuchs et al., 2013; Radwan et al., 2021; Song et al., 2018; Winkler et al., 2021). On smaller scales, such data are often complemented or substituted by data stemming from aerial photographs, (historical) maps, and/or field surveys, allowing for more detailed habitat categories and/or to reach further back in time (e.g., Bender et al., 2005; Biró et al., 2018; Bryn & Hemsing, 2012; Cousins et al., 2015; Tomaselli et al., 2023). However, habitat changes on a more detailed level remain mostly unanalyzed for larger regions due to a lack of data (but see Biró et al., 2018). This is particularly unfortunate because changes on this finer habitat type level offer information on drivers that cause changes other than extreme habitat transitions, for example land use intensification.

Trends of plant species are mostly based on vegetation plot data, thus local data covering usually an area of several square meters in open habitats and several hundred square meters in forests (Vellend et al., 2017). However, most plot time series are short and/or cover only specific habitat types (Cardinale et al., 2018; Gonzalez et al., 2016). An alternative for large scales is aggregating species occurrence records per grid-cells, regions, or countries, including data from herbaria, floristic atlas surveys, and individual mapping projects (Eichenberg et al., 2021; Franklin et al., 2017; Vellend et al., 2017). Analyses based on such data, however, are not able to distinguish between trends in different habitat types. This would only be possible with data from the intermediate scale, i.e. from data collected at the resolution of habitats, but such data is scarce and rarely analyzed (but see Bruelheide et al., 2020). Overall, systematic monitoring data for both habitat types and plants species that cover long time periods, several habitat types, and are geographically representative are still scarce (Kühl et al., 2020; Mihoub et al., 2017).

Given the sparse amount of data stemming from systematic monitoring programs, more and more studies are making use of heterogeneous data (Büttner et al., 2022; Isaac et al., 2014; Vellend, Brown, et al., 2013). So far, little attention has been paid to the potential of habitat mapping programs to provide information for trends not only for habitat types but also for plant species. Worldwide, many countries conduct these surveys of habitat types to provide information for nature conservation, landscape planning, and policy decisions (European Environment Agency & Museum national d'Histoire naturelle, 2014; Hearn et al., 2011). In the European Union, monitoring of protected habitat types is mandated by the European Habitats Directive (92/43/EEC; Council of the European Union, 1992). Many European countries run additional monitoring programs, for example Germany, where mapping is conducted on the level of the federal states (in German "Biotopkartierungen"; European Environment Agency & Museum national d'Histoire naturelle, 2014; Kaiser et al., 2013). Mapping is usually conducted via field surveys, sometimes supplemented by remote sensing. In addition to mapping protected habitat types, some programs also include recording of plant species on site, for example in most German federal states (European Environment Agency & Museum national d'Histoire naturelle, 2014; Kaiser et al., 2013).

POTENTIAL MEASURES OF BIODIVERSITY CHANGE FOR HABITAT MAPPING DATA

Like other heterogeneous data, habitat mapping data comes with challenges for trend analyses. For trends of habitat types, this concerns mainly spatially inconsistent and incomplete mapping over time (discontinued or newly established mapping), changes in mapping keys and observer bias. Most other research on habitat type trends report net or proportional changes for rather broad habitat types, sometimes aided by maps of change (e.g., Cousins et al., 2015; Fuchs et al., 2013; Radwan et al., 2021). Trends of detailed habitat types across Hungary have been analyzed using changes in relative frequencies (Biró et al., 2018). What is rarely reported, however, are mean changes in the area of habitat types, which would offer more robust trends than net changes, and which can be tested for significance. This could give insights into if habitat-specific net changes are based on reoccurring patterns throughout a region instead of solely being caused by a few large habitats that underwent change.

For plant species trends, especially the incomplete species occurrence data of habitat mapping programs pose a problem, since most programs require only the recording of dominant, characteristic, and endangered species (European Environment Agency & Museum national d'Histoire naturelle, 2014; Kaiser et al., 2013). Thus, such data is not suitable to derive assemblage-level biodiversity metrics like species richness or community change, as those rely on the complete sampling of communities and are sensitive to sampling effort (Dornelas et al., 2019; Roswell et al., 2021). Instead, habitat mapping data can be used to derive trends for individual species (e.g., Bruelheide et al., 2020). Still, also for trends of individual species, the incomplete species occurrence data poses challenges (Bruelheide et al., 2020).

A simple measure of species change that studies commonly use is the (relative) change in frequency in local sites/plots (e.g., Britton et al., 2009; Heinrichs & Schmidt, 2017; Jandt et al., 2011; Meyer et al., 2015; Meyer et al., 2013; Wesche et al., 2012; Wiegmann & Waller, 2006). Similarly, also abundance estimates such as cover are often used as a measure of change (e.g., Britton et al., 2009; Diekmann et al., 2014; Heinrichs & Schmidt, 2017; Jandt et al., 2022; Meyer et al., 2015; Naaf & Wulf, 2011; Reinecke et al., 2014; Timmermann et al., 2015). An alternative to those change measures, that have not been explored in this context before, is the change in the area of a habitat site that is occupied by a specific species. This can be calculated as the average change in the size of such a site, with the underlying assumption that such a site represents a species' potential habitat space, which is similar to the concept of Area of Habitat (AOH; Brooks et al., 2019). Overall, however, none of these measures account for incomplete species lists. To do so, several metrics have been applied in past studies. For data on the grid scale, occupancy-detection models can be used, which estimate the occupancy of a species while incorporating detection probabilities (e.g., Bowler et al., 2021; Isaac et al., 2014; Klinkovská et al., 2024). Another option for grid cell data is the Frescalo algorithm (FREquency SCAling using Local Occupancy; Hill, 2012), which calculates species occurrence probabilities while accounting for varying recorder effort by using information on species recorded occurrences and ecological similarity from neighboring cells (e.g., Eichenberg et al., 2021; Isaac et al., 2014). For data collected on the plot or habitat level, an option to account for incomplete species lists is to use Beals' index (Beals, 1984), which measures the probability of occurrence of a species based on all other species occurring at a site (e.g., Bruelheide et al., 2020; Trindade et al., 2021). While Beals' index has been found to be a suitable measure to capture temporal species trends (Bruelheide et al., 2020), it has rarely been used for this purpose so far.

THESIS OBJECTIVES AND OUTLINE

The main aim of this thesis is to identify which habitat types and which plant species have been the winners and losers (i.e., showed positive and negative trends, respectively) over the last decades in Germany. For this, I used repeated habitat mapping data from three German federal states (hereinafter "states"), recorded over the past four decades, to derive temporal trends of both habitat types and plant species in all protected habitat types. Trends were analyzed separately for the states Hamburg, Baden-Württemberg, and Schleswig-Holstein. I chose those states because they had repeated mapping data available, spanning two time periods in a rather high quality/detail, and because they are representative of the German landscape. As measures of habitat type change I mainly used mean changes in area. I also identified common transitions between habitat types. As measures of species change I used three metrics: frequency, occupied area, and probability of occurrence (Beals), with varying emphasis in each chapter 2-4. I grouped species by their preferred habitat types, Red List status, and non-native status and calculated mean trends per group. In addition to species changes across each state, I also derived species trends within each habitat type. Throughout the chapters, I further provided a blueprint for analyzing habitat mapping data. For a graphical outline of chapters 2-4 see Figure 1.

Explicitly, in **chapter 2**, I derived habitat type and species trends for the state of Hamburg, using data from 1979-2017. I used all three measures of species change, with an emphasis on trends in species occupied area. In contrast to the other chapters, the data used here included also non-protected habitat types for the recent mapping.

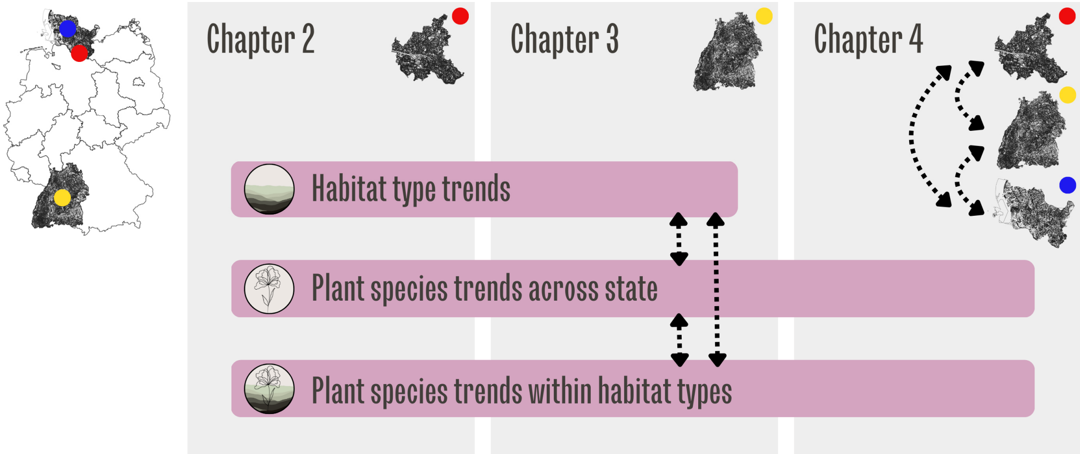

Figure 1 Overview of the three core chapters (2-4) of this thesis. Given for each chapter are the federal state(s) used (Hamburg, Baden-Württemberg, Schleswig-Holstein) and which trends were analyzed (Habitat type trends, Plant species trends across state, Plant species trends within habitat types). Arrows for chapters 3 and 4 indicate which trends were compared, i.e. in chapter 3 the three different types of trends were compared to each other and in chapter 4 the same type of trend was compared between states.

In **chapter 3**, I again derived both habitat type and species trends, but this time for the state of Baden-Württemberg from 1989-2021. Here, I explicitly compared trends in habitat types with 1) trends of their affiliated species across the state and 2) mean trends of all species within those habitat types, to see if they are consistent. The species analysis focused on frequency and Beals change.

Chapter 4 focused on trends of species only and combined trends from the states Hamburg, Baden-Württemberg, and Schleswig-Holstein (the latter with data from 1977-2021). In this chapter, I focused on Beals trends and explicitly compared those trends between the three states, concerning individual species as well as species groups. Further, I investigated if characteristic species rather declined within their preferred habitat types.

In **chapter 5**, I then synthesize the results from the previous chapters, before diving deeper into the consistent and varying trends found and their possible drivers. After discussing methods for analyzing the heterogeneous data of habitat mapping programs, the last section of this chapter focuses on the way forward, discussing applications of my thesis results, and future research ideas. I end my thesis with ideas on how to bring nature conservation forward, concerning both biodiversity monitoring and conservation measures to halt the biodiversity decline.

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Chapter 2

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., 2015; Meyer et al., 2013), 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., 2019; Diekmann et al., 2014; 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

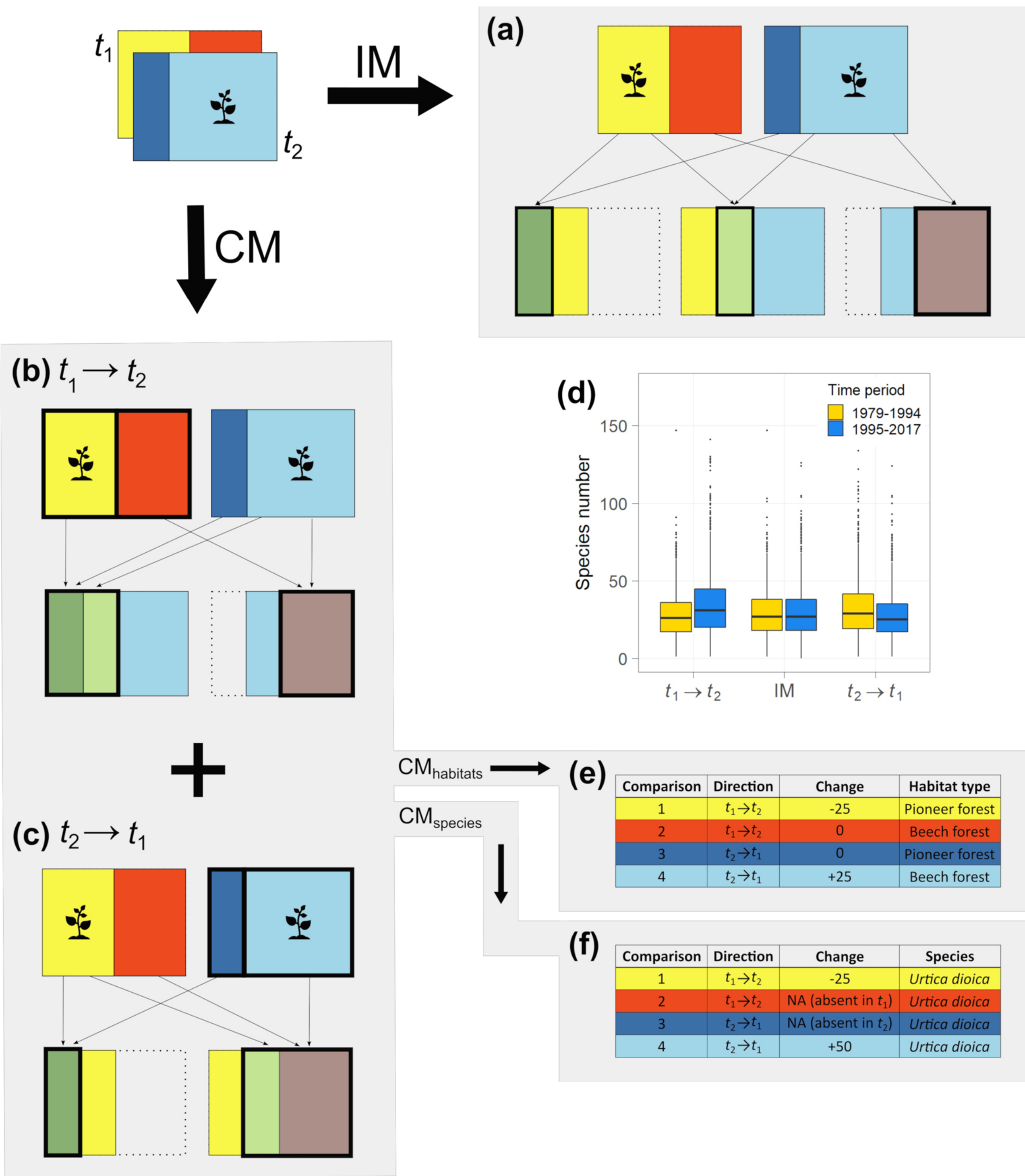

Figure 1 Scheme showing the two ways used to analyze changes in habitat types and species trends. Two habitats from time period 1 (t_1) are overlapping with two habitats from time period 2 (t_2). **(a)** The intersection method (IM) compares each intersection and its area, ignoring actually observed 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.

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 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.

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 x 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)

$$log_{10}\frac{area_{t2}+1}{area_{t1}+1} \qquad (1)$$

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).

$$p_{pi} = \frac{1}{N_p}\sum_{j}^{N_p}\frac{M_{ij}}{M_j} \qquad (2)$$

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, 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 x habitat type combination (Equation 3; Chytrý et al., 2002).

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

X^2 is the X^2 statistic for a 2 x 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 (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 losses of species-rich moist to semi-dry grasslands (GM) and arable fields (LA; Figure 3). Species-rich wet or moist grasslands

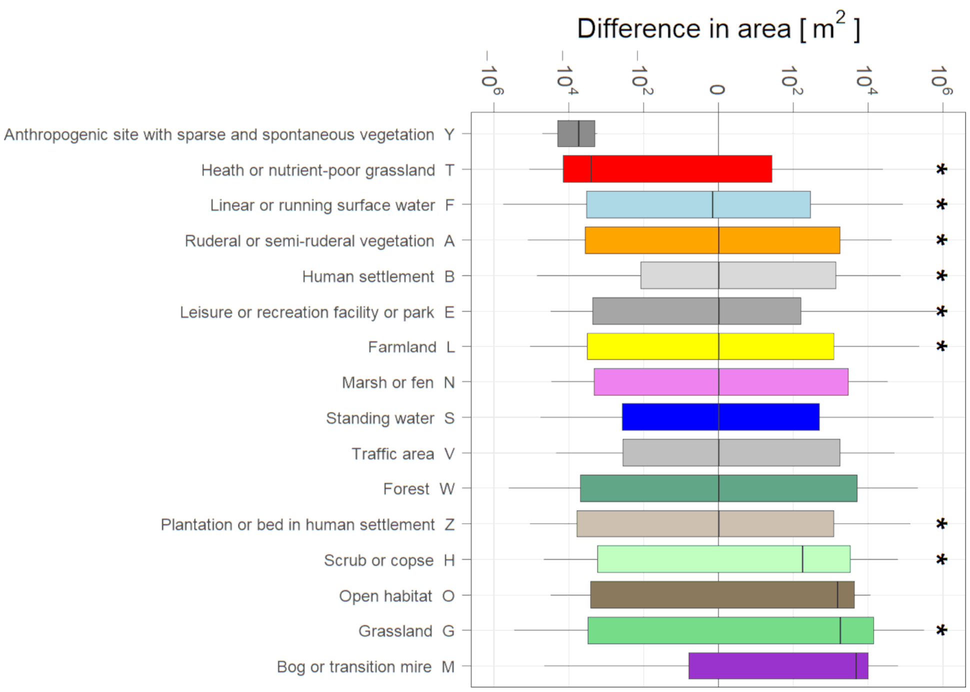

Figure 2 Difference in area in square meters between t_1 (1979–1994) and t_2 (1995–2017) for all Level 1 habitat types with calculation based on $CM_{habitats}$. The y-axis is on a $\log_{10}$ scale. Significant differences according to a Wilcoxon rank sum test are labeled with an asterisk.

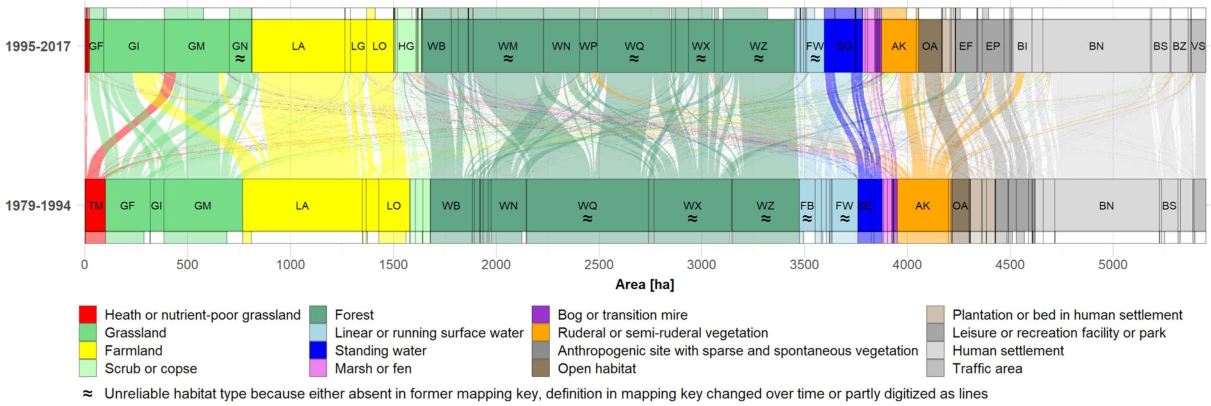

Figure 3 Alluvial plot showing total areas of and transitions between Level 2 habitat types from t_1 (1979–1994) to t_2 (1995–2017) for all habitat types with calculation based on the intersection method. Thin bars above and below the main bars represent the total area for each habitat type that has 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 (≈).

(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 ($\text{CM}_{\text{species\_freq}}$, $\text{CM}_{\text{species\_area}}$, and $\text{CM}_{\text{species\_beals}}$) revealed a high correlation between $\text{CM}_{\text{species\_freq}}$ and $\text{CM}_{\text{species\_area}}$ trends ($r_s = 0.997$, $p < 0.001$), but only moderate correlations of $\text{CM}_{\text{species\_beals}}$ with $\text{CM}_{\text{species\_freq}}$ and $\text{CM}_{\text{species\_area}}$ trends ($r_s = 0.43$ and 0.42, respectively, both $p < 0.001$). In the following, mainly the $\text{CM}_{\text{species\_area}}$ 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 ($\text{CM}_{\text{species\_area}}$) 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 $\text{CM}_{\text{species\_area}}$ and $\text{CM}_{\text{species\_freq}}$ 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 ($\text{CM}_{\text{species\_beals}}$) were typical forest and scrub species, for example,

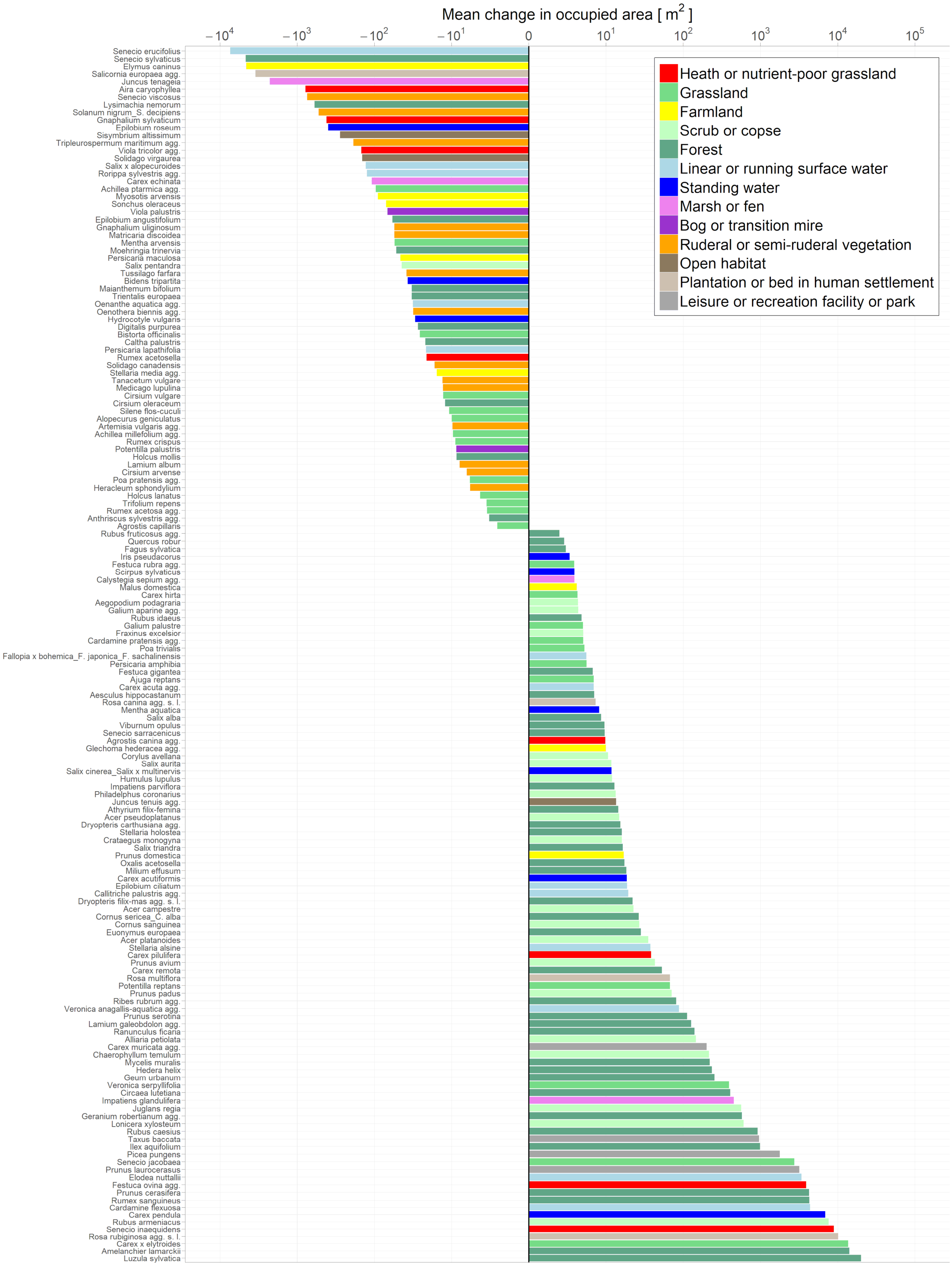

Figure 4 Mean change in occupied area in square meters from t_1 (1979–1994) to t_2 (1995–2017) for all species with significant trends. Change in occupied area was calculated as $\log_{10}(\text{area}_{\text{time period 1}} + 1/\text{area}_{\text{time period 2}} + 1)$ using $CM_{\text{species\_area}}$ 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.

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.

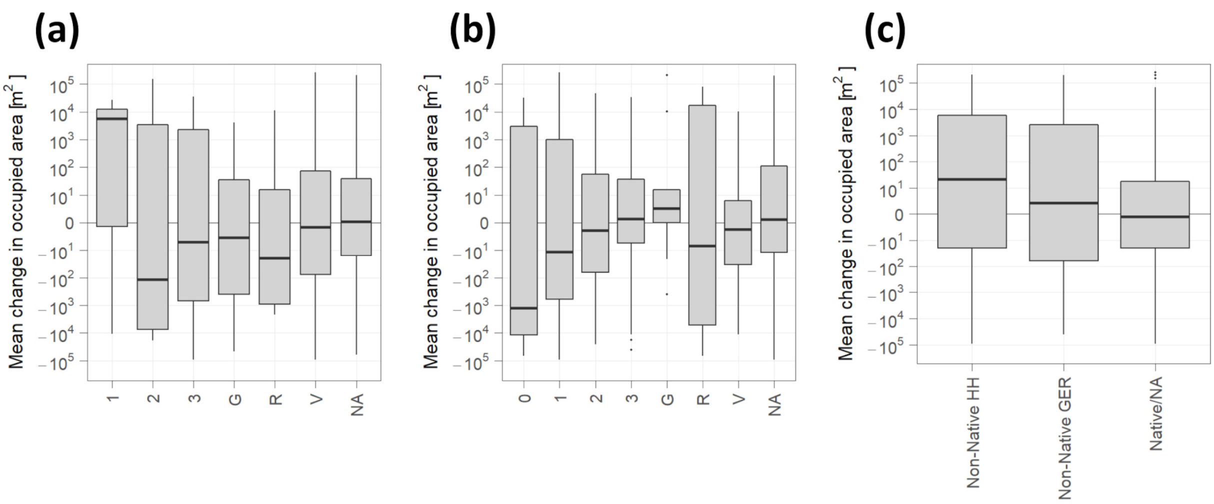

Figure 5 Mean change in occupied area in square meters from t_1 (1979–1994) to t_2 (1995–2017) for all species grouped by **(a)** red list status in Germany, **(b)** red list status in Hamburg, and **(c)** non-native status. Red list categories: 0 = extinct or lost, 1 = threatened with extinction, 2 = 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.

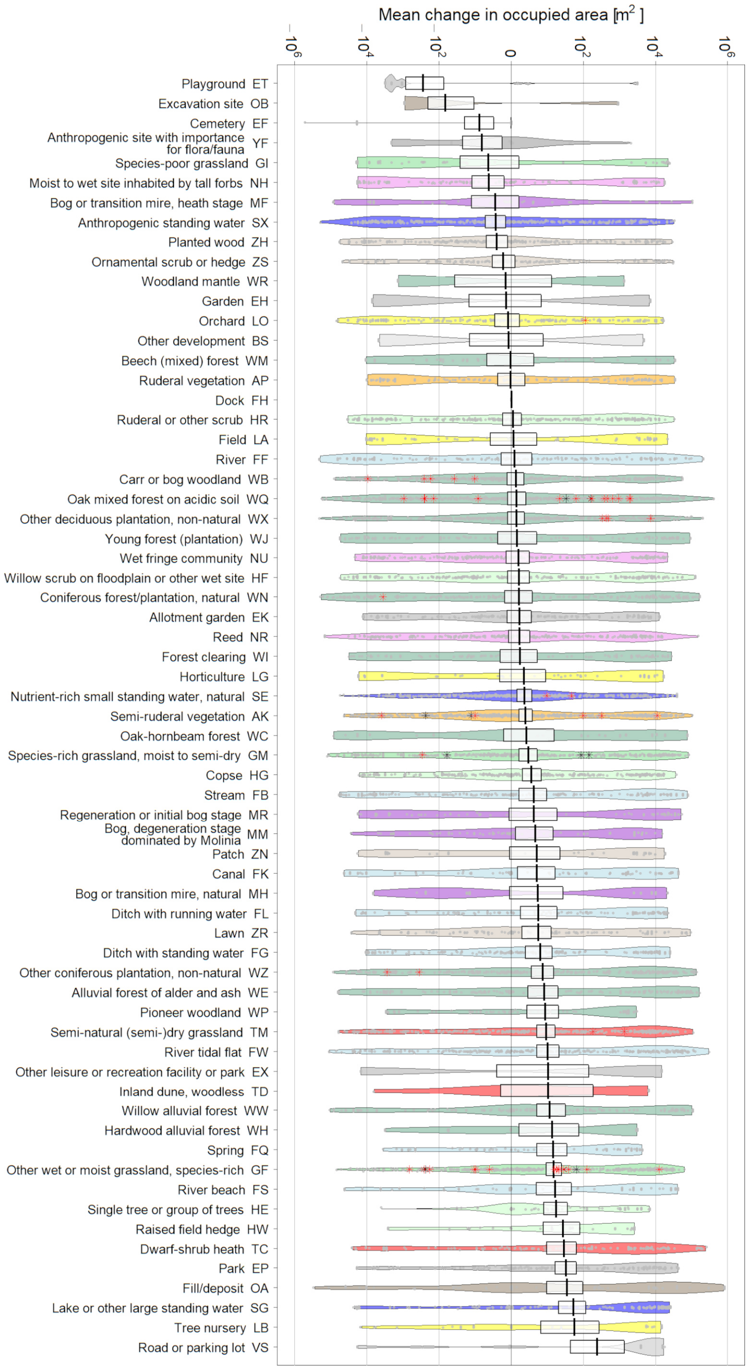

Figure 6 Mean change in occupied area in square meters from t_1 (1979–1994) to t_2 (1995–2017) for all species in all Level 2 habitat types in which they occurred in t_1. Assignment to habitat types regardless of whether habitat type changed toward t_2. Change in occupied area was calculated as $\log_{10}(\text{area}_{\text{time period 1}} + 1/\text{area}_{\text{time period 2}} + 1)$ 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.

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 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 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, 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., 2019; Diekmann et al., 2014;

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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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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APPENDIX S1

Due to the length of tables S4 and S5 they can only be found online in the Supporting Information section at: https://doi.org/10.1002/ecs2.4244

Table S1 Challenges and solutions concerning the analysis of habitat mapping data.

Challenge	Chosen solution	Results/Implications	Concerning methods
How to divide data into two time periods (t_1 & t_2)	Year of first repeated mapping: 1995	Longer time span for t_2	All
Habitats from several years of t_2 intersect with one habitat from t_1	Use most recent habitat(s) from t_2	Heterogenous time spans	All
Changes in habitat sizes and borders lead to bias for $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$	Use changes from both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ to calculate trends (CM)	Balanced trends	$CM_{habitats}$ $CM_{species}$
Habitats mapped as lines (e.g., rivers with width < 5m) and points (e.g., single trees) geographically not reliable	Exclude habitats digitized as lines or points	Commonly linear habitats (rivers, ditches, hedges) not reliable for analysis	IM $CM_{habitats}$ Species trends per habitat type
Changes in habitat identification keys	Use broader level of definitions (level 3 to level2)	Might miss changes in nutrient or water levels; some problems remain because of new groups in recent key and changes in habitat type definitions	$CM_{habitats}$ Species trends per habitat type
Different habitat sizes are not reflected in species frequencies	Use change in area instead of frequency change ($CM_{species\_area}$)	Similar trends of $CM_{species\_freq}$ and $CM_{species\_area}$	$CM_{species\_area}$
Incomplete species lists	Beals' index ($CM_{species\_beals}$)	Different trends than $CM_{species\_freq}$ and $CM_{species\_area}$	$CM_{species\_beals}$
Several species lists per habitat in case of several habitat types	Merge lists	A species might not actually occur in the main habitat type for which its trend is calculated	Species trends per habitat type

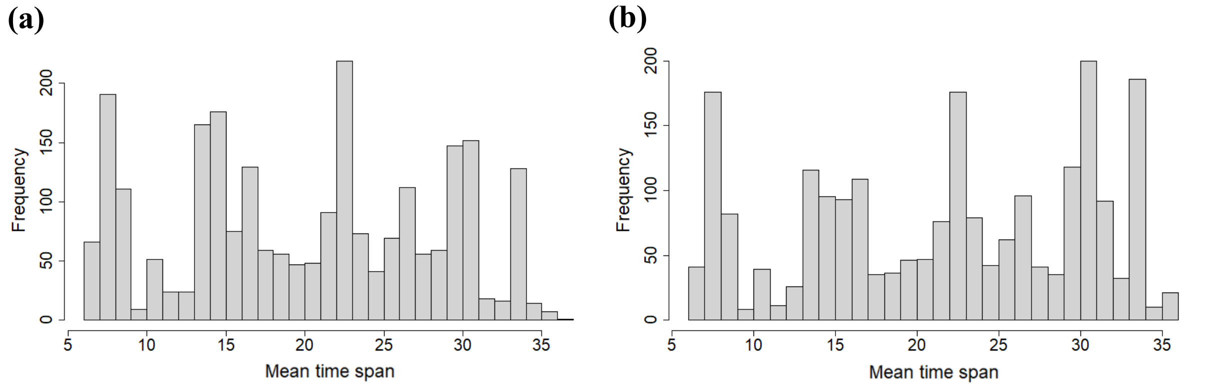

Figure S1 Histogram of the mean time span between habitat surveys for the comparisons used for species analysis for **(a)** $t_1 \rightarrow t_2$ and **(b)** $t_2 \rightarrow t_1$.

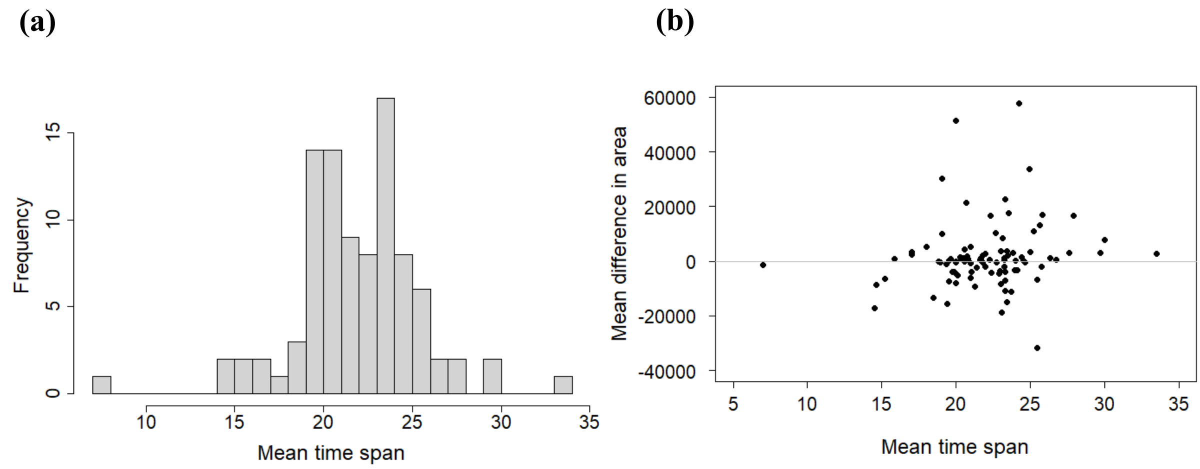

Figure S2 Mean time span between t_1 and t_2 for all level 2 habitat types, **(a)** showing their frequencies in a histogram and **(b)** plotted against mean difference in area, with a horizontal line at zero in gray.

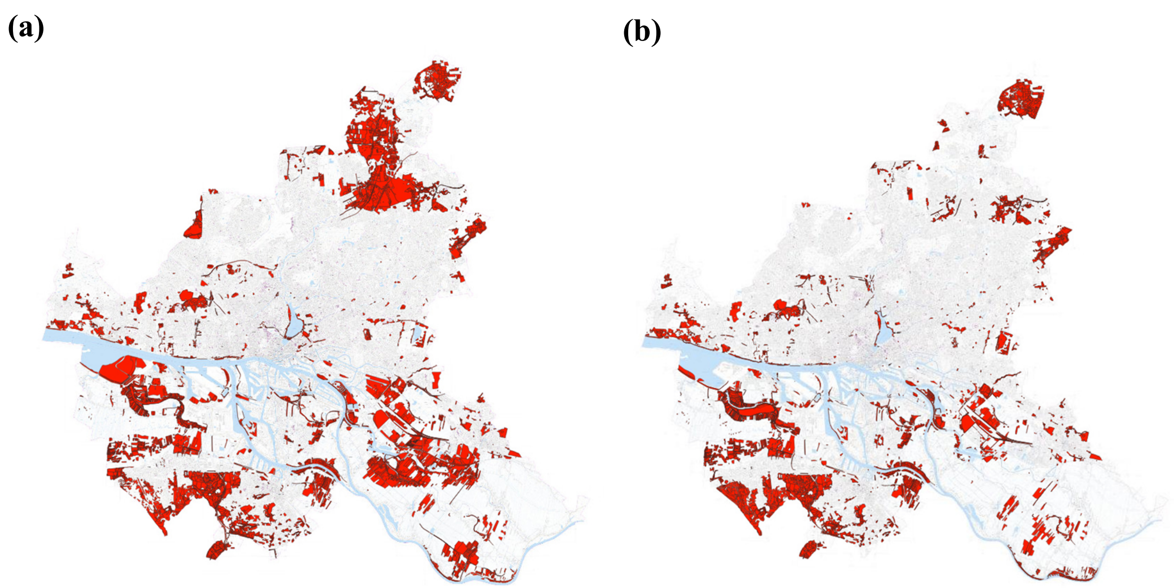

Figure S3 Habitats in Hamburg indicated in red were used for **(a)** habitat type analysis and **(b)** species trend analysis.

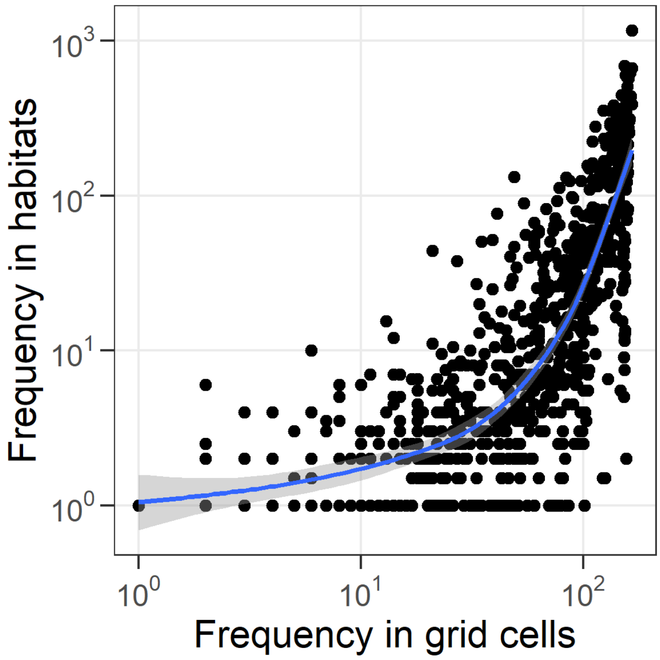

Figure S4 Frequency of species in the habitats of the mapping program of Hamburg as a function of grid cells of the German plant distribution database Florkart. Data is shown on the $\log_{10}$ scale. In blue a smoothed regression line, derived via GAM smoothing.

Table S2 Level 1 habitat types which showed a significant trend in their mean difference in area in m^2 between time period 1 (1979-1994) and time period 2 (1995-2017) with calculations based on $CM_{habitats}$. Significant differences according to Wilcoxon rank sum tests. *n* represents the number of comparisons per habitat type.

Habitat type	n	Mean difference in area	p value	Habitat type English	Habitat type German
T	75	-11010.05	<.001	Heath or nutrient-poor grassland	Heiden, Borstgrasrasen, Magerrasen
F	138	-10087.31	0.029	Linear or running surface water	Lineare und Fließgewässer
Z	141	-4476.05	<.001	Plantation or bed in human settlement	Vegetationsbestimmte Habitatstrukturen besiedelter Bereiche
A	371	-2581.47	0.008	Ruderal or semi-ruderal vegetation	Ruderale und halbruderale Krautflur
L	512	-1121.12	0.05	Farmland	Biotope landwirtschaftlich genutzter Flächen
H	308	276.88	0.029	Scrub or copse	Gebüsche und Kleingehölze
B	524	378.51	0.008	Human settlement	Biotopkomplexe der Siedlungsflächen
E	248	2165.29	0.029	Leisure or recreation facility or park	Biotopkomplexe der Freizeit-, Erholungs-, Grünanlagen
G	697	4479.39	<.001	Grassland	Grünland

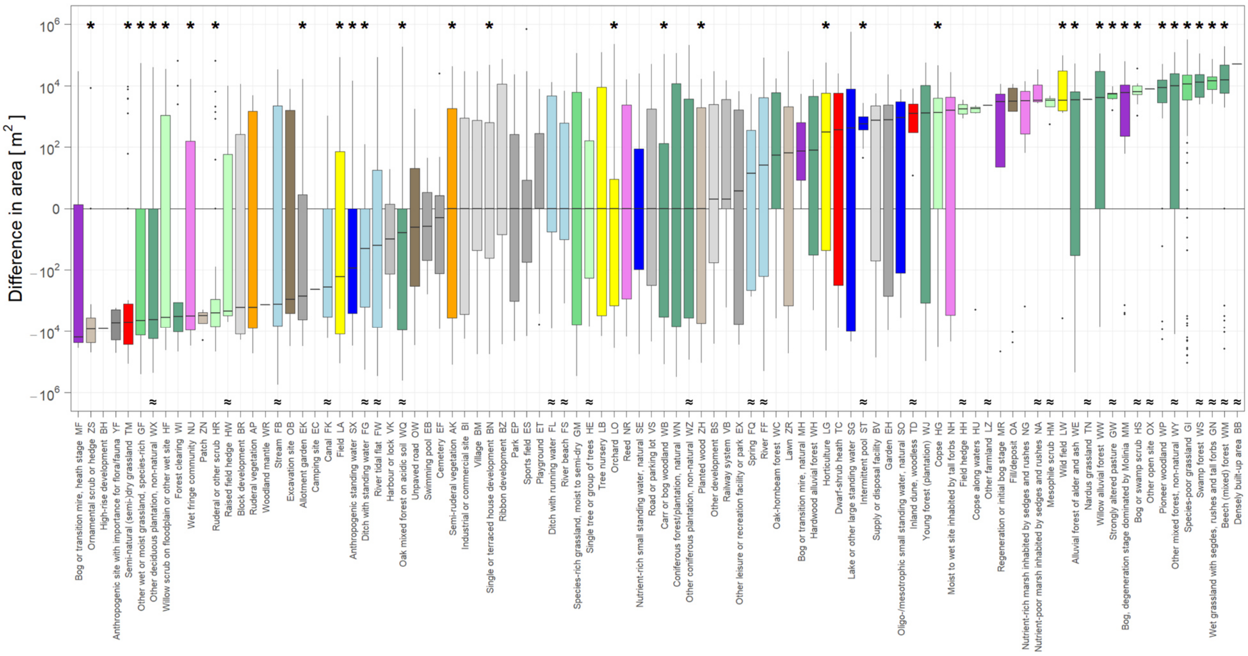

Figure S5 Difference in area in m² between t_1 (1979-1994) and t_2 (1995-2017) for all level 2 habitat types with calculation based on $CM_{habitats}$. The y-axis is on a log_{10} scale. Significant differences according to a Wilcoxon rank sum test are labelled with an asterisk. Colors according to the level 1 habitat types in Figure 2. Unreliable habitat types are marked with an approximation symbol (≈).

Table S3 Level 2 habitat types which showed a significant trend in their mean difference in area in m² between time period 1 (1979-1994) and time period 2 (1995-2017) with calculations based on $CM_{habitats}$. Significant differences according to Wilcoxon rank sum tests. n represents the number of comparisons per habitat type. Unreliable habitat types are marked with an approximation symbol (≈).

Habitat type	n	Mean difference in area	p value	Habitat type English	Habitat type German	Unreliable ≈
WX	161	-18812.22	<.001	Other deciduous plantation, non-natural	Sonstiger Laubforst, naturfern	≈
TM	56	-15782.54	<.001	Semi-natural (semi-)dry grassland	Trocken- oder Halbtrockenrasen	
ZS	20	-15148.50	<.001	Ornamental scrub or hedge	Zier-Gebüsch, -Hecke	
WQ	233	-10871.41	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	≈
FG	25	-8647.44	0.005	Ditch with standing water	Graben mit Stillgewässercharakter	≈
GF	159	-8261.53	<.001	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	
LA	179	-7315.13	<.001	Field	Acker	
HR	41	-6001.71	<.001	Ruderal or other scrub	Ruderal- und sonstiges Gebüsch	
NU	26	-5230.23	0.015	Wet fringe community	Feuchte Staudensäume	
ZH	76	-3978.20	0.021	Planted wood	Gepflanzter Gehölzbestand	

HF	39	-3949.33	0.004	Willow scrub on floodplain or other wet site	Weidengebüsch der Auen, Ufer und sonstigen Feuchtstandorte	
WB	165	-3615.10	<.001	Carr or bog woodland	Bruchwald und Moorwälder	
AK	360	-2372.36	0.013	Semi-ruderal vegetation	Halbruderale Gras- und Staudenflur	
SX	61	-2091.23	0.001	Anthropogenic standing water	Naturfernes Stillgewässer	
WE	31	-2027.52	0.046	Alluvial forest of alder and ash	Erlen- und Eschenwald	
EK	75	-2021.92	<.001	Allotment garden	Kleingartenanlage	
LO	173	662.29	0.002	Orchard	Obstpflanzung	
BN	264	688.15	0.014	Single or terraced house development	Einzel- und Reihenhausbebauung	
ST	21	703.38	<.001	Intermittent pool	Tümpel	≈
LG	126	1383.83	0.01	Horticulture	Erwerbsgartenbauflächen	
HG	161	1976.12	<.001	Copse	Feld-, Stadt- und Kleingehölz	
GW	6	5163.83	0.031	Strongly altered pasture	Stark veränderte Weidefläche	≈
HS	19	8255.53	<.001	Bog or swamp scrub	Moor- und Sumpfgebüsch	≈
WP	60	10302.52	<.001	Pioneer woodland	Pionierwald/ Vorwald	
MM	15	11060.87	0.005	Bog, degeneration stage dominated by Molinia	Pfeifengras-Degenerationsstadium	
GN	73	16539.73	<.001	Wet grassland with segdes, rushes and tall forbs	Seggen-, binsen- und hochstaudenreiche Nasswiese	≈
GI	196	16565.24	<.001	Species-poor grassland	Artenarmes Grünland	
WW	30	16887.43	0.001	Willow alluvial forest	Weiden-Auwald	
WY	16	17696.81	0.024	Other mixed forest, non-natural	Sonstiger Mischwald, naturfern	≈
LW	10	21202.00	0.02	Wild field	Wildacker	
WS	10	22476.60	0.002	Swamp forest	Sumpfwald	≈
WM	69	33568.28	<.001	Beech (mixed) forest	Buchenwald	≈

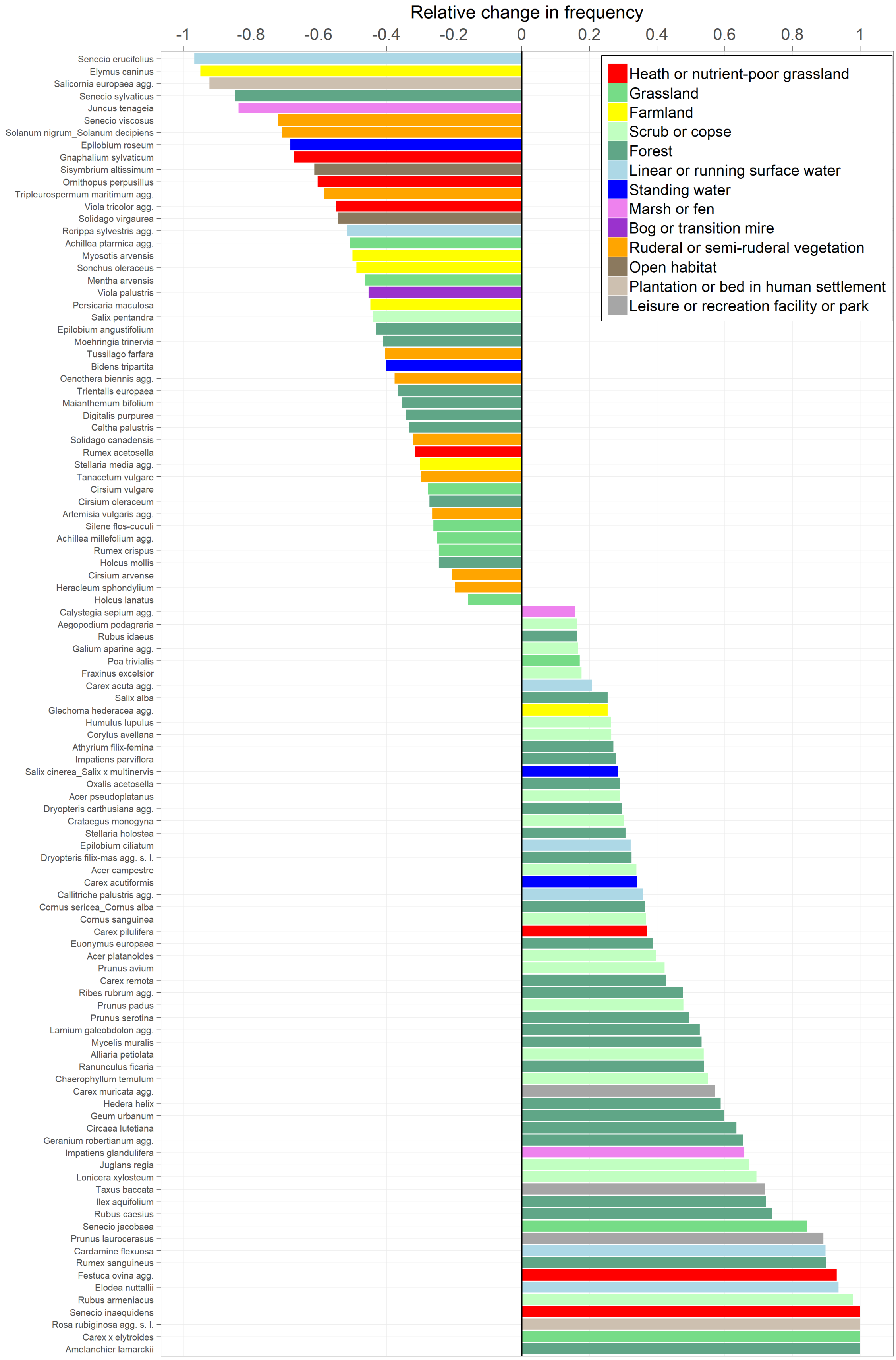

Figure S6 Mean change in frequency from time period 1 (1979-1994) to time period 2 (1995-2017) for all species with significant trends. Change in frequency ranges from −1, with a species disappearing from all habitats previously occupied, to 1, with a species showing only new appearances in habitats. Changes were derived using $CM_{species\_freq}$. Significant trends according to sign tests. 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 which are known to be difficult to differentiate in the field were merged and are separated by an underscore.

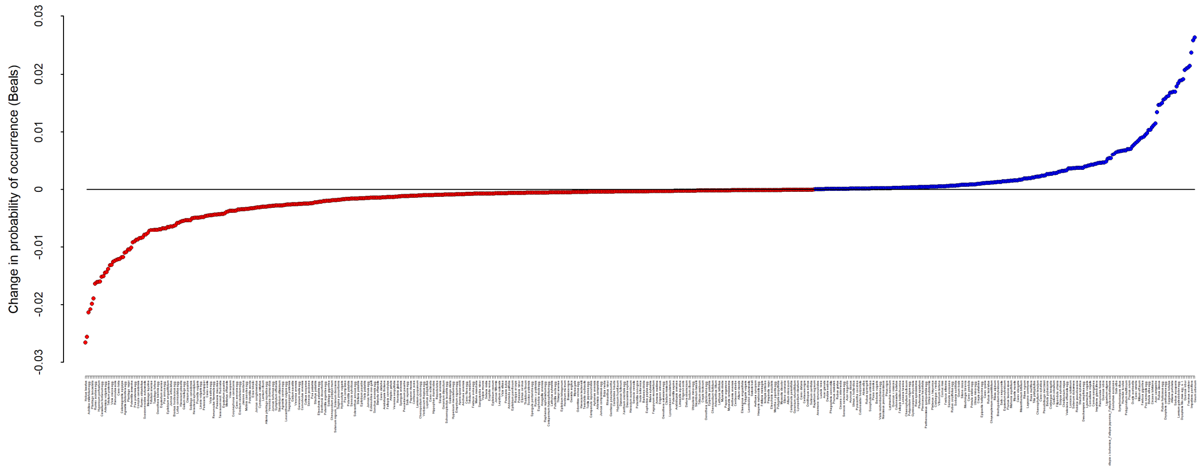

Figure S7 Mean change in occurrence probability (Beals' index) from time period 1 (1979-1994) to time period 2 (1995-2017) for all species with significant trends. Changes based on $CM_{species\_beals}$. Red dots represent negative trends, whereas blue dots represent positive trends. Significant trends according to *t* tests. Note that not all species names appear on the x-axis. Species which are known to be difficult to differentiate in the field were merged and are separated by an underscore.

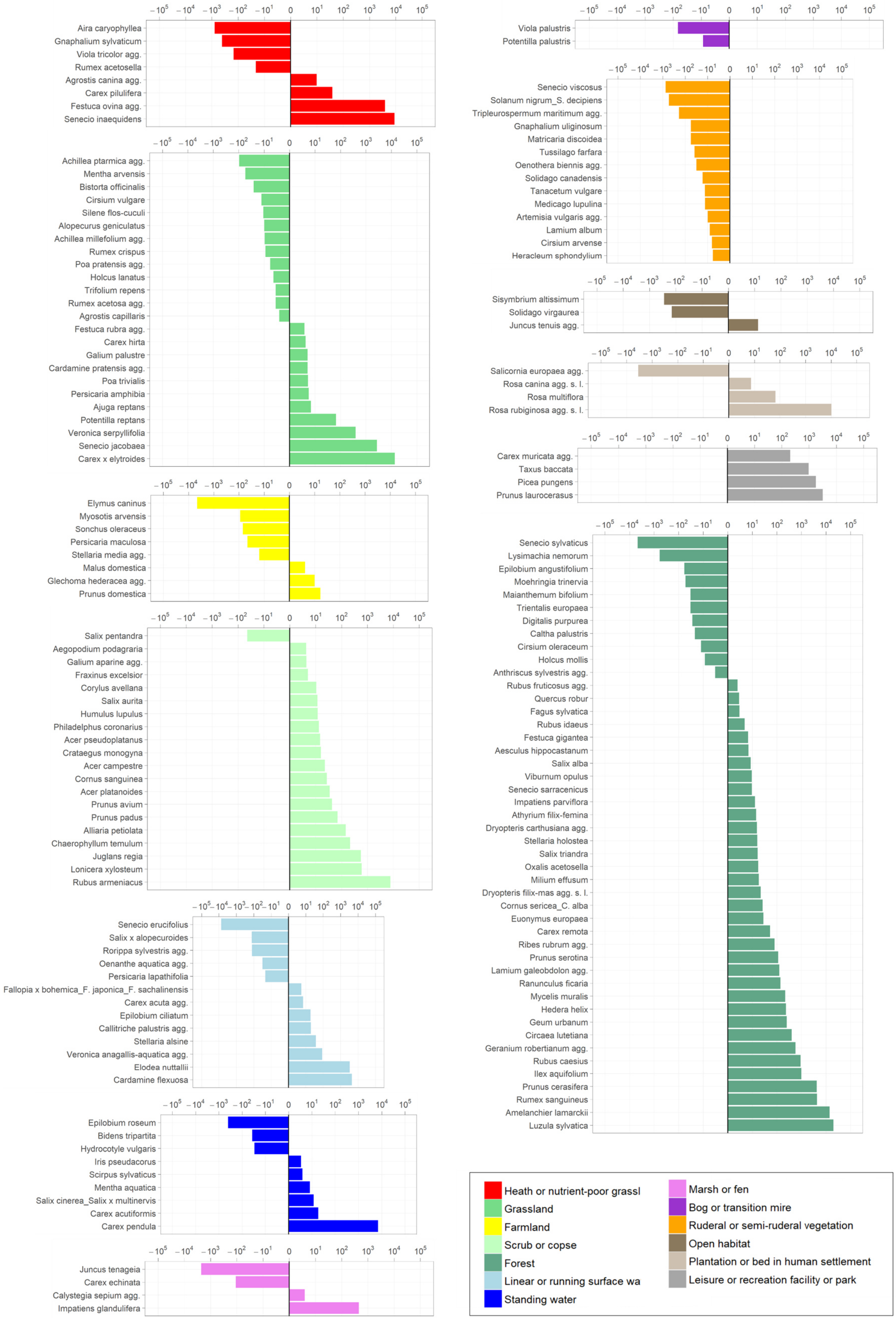

Figure S8 Mean change in occupied area in m² from time period 1 (1979-1994) to time period 2 (1995-2017) for all species with significant trends, with plots separated by species preferred level 1 habitat type. Change in occupied area was calculated as $\log_{10}(\text{area}_{\text{time period 1}} + 1\ /\text{area}_{\text{time period 2}} + 1)$ using $CM_{\text{species\_area}}$ and is shown on the $\log_{10}$ scale. Preferred habitat type of a species was assessed by the highest fidelity (Φ) of all habitat types for that species. Species which are known to be difficult to differentiate in the field were merged and are separated by an underscore.

Table S4 Species trends according to $CM_{species\_area}$ (difference $\log_{10}$(area)), $CM_{species\_freq}$ (difference frequency), and $CM_{species\_beals}$ (difference beals) for all species with significant trends for at least one of the methods (690 species). *n* refers to the uncorrected number of comparisons used for $CM_{species\_area}$ and *n* corrected refers to the corrected number of comparisons used for $CM_{species\_freq}$. Species which are known to be difficult to differentiate in the field were merged and are separated by an underscore.

This table can be found in the Supporting Information section at: https://doi.org/10.1002/ecs2.4244

Table S5 Mean change in occupied area in m² (difference $\log_{10}$(area)) from time period 1 (1979-1994) to time period 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 $CM_{species\_area}$. *n* represents the number of comparisons per species. Habitat type preferred represents the level 2 habitat type with the highest fidelity value (Φ) of all habitat types for that species. Species which are known to be difficult to differentiate in the field were merged and are separated by an underscore.

This table can be found in the Supporting Information section at: https://doi.org/10.1002/ecs2.4244

Table S6 Outcomes of a linear model (calculated without intercept, i.e. means parameterization of ANOVA) which tested if species that occur preferably in a specific level 1 habitat type rather increased or decreased in their area occupied from t_1 to t_2 ($CM_{species\_area}$). Shown are the preferred habitat types as predictors, the number of species as *n*, the mean change as estimates, confidence intervals and *p* values. As the model used $\log_{10}$ transformed mean changes, taking 10 at the power of the estimate gives the factor by which the occupied area changed from t_1 to t_2. Note that Shapiro-Wilk normality tests were not possible for the habitat type M due to the small sample size ($n = 2$) and that the habitat type G was not normally distributed (but $p > 0.01$).

Predictors	n	Estimates	CI	p
pref habitat [A]	14	-1.52	-2.46 – -0.58	**0.002**
pref habitat [E]	4	3.01	1.25 – 4.77	**0.001**
pref habitat [F]	13	0.30	-0.67 – 1.28	0.538
pref habitat [G]	24	0.16	-0.56 – 0.88	0.657
pref habitat [H]	20	1.44	0.65 – 2.22	**<0.001**
pref habitat [L]	8	-0.93	-2.17 – 0.31	0.140
pref habitat [M]	2	-1.38	-3.87 – 1.10	0.273
pref habitat [N]	4	-0.53	-2.29 – 1.22	0.549
pref habitat [O]	3	-1.16	-3.18 – 0.87	0.262
pref habitat [S]	9	0.29	-0.88 – 1.46	0.629
pref habitat [T]	8	0.14	-1.10 – 1.38	0.823
pref habitat [W]	46	0.98	0.46 – 1.50	**<0.001**
pref habitat [Z]	4	0.79	-0.96 – 2.55	0.375
Observations			159	
R^2 / R^2 adjusted			0.276 / 0.211	

Table S7 Outcomes of a linear model (calculated without intercept, i.e. means parameterization of ANOVA) which tested if species that occur preferably in a specific level 2 habitat type rather increased or decreased in their area occupied from t_1 to t_2 ($CM_{species\_area}$). Shown are the preferred habitat types as predictors, the number of species as *n*, the mean change as estimates, confidence intervals and *p* values. As the model used $\log_{10}$ transformed mean changes, taking 10 at the power of the estimate gives the factor by which the occupied area changed from t_1 to t_2. Note that Shapiro-Wilk normality tests were not possible for all types with $n < 3$ and that GM, HG, TM, WM and WZ were not normally distributed.

Predictors	n	Estimates	CI	p
pref habitat [AK]	10	-1.22	-2.18 – -0.27	**0.012**
pref habitat [AP]	4	-2.27	-3.78 – -0.76	**0.004**
pref habitat [EF]	1	3.25	0.23 – 6.27	**0.035**
pref habitat [EP]	2	3.24	1.11 – 5.38	**0.003**
pref habitat [ET]	1	2.31	-0.71 – 5.33	0.133

pref habitat [FG]	3	0.21	-1.54 – 1.95	0.815
pref habitat [FH]	1	0.75	-2.27 – 3.77	0.626
pref habitat [FL]	2	2.41	0.28 – 4.55	**0.027**
pref habitat [FQ]	2	2.61	0.47 – 4.75	**0.017**
pref habitat [FS]	1	-2.11	-5.13 – 0.91	0.169
pref habitat [FW]	4	-1.34	-2.85 – 0.17	0.082
pref habitat [GF]	3	-0.74	-2.49 – 1.00	0.401
pref habitat [GM]	14	0.28	-0.53 – 1.08	0.497
pref habitat [GN]	7	0.32	-0.83 – 1.46	0.584
pref habitat [HG]	17	1.59	0.86 – 2.32	**<0.001**
pref habitat [HS]	2	-0.29	-2.42 – 1.85	0.790
pref habitat [HW]	1	2.34	-0.68 – 5.36	0.128
pref habitat [LA]	2	-1.81	-3.94 – 0.33	0.096
pref habitat [LB]	1	-3.66	-6.68 – -0.64	**0.018**
pref habitat [LO]	5	-0.04	-1.39 – 1.31	0.957
pref habitat [MH]	1	-1.83	-4.85 – 1.19	0.233
pref habitat [MR]	1	-0.94	-3.96 – 2.08	0.540
pref habitat [NA]	1	-2.03	-5.05 – 0.99	0.185
pref habitat [NP]	1	-3.35	-6.37 – -0.33	**0.030**
pref habitat [NR]	1	0.59	-2.43 – 3.61	0.698
pref habitat [NU]	1	2.66	-0.36 – 5.68	0.084
pref habitat [OA]	1	-2.44	-5.46 – 0.58	0.112
pref habitat [OK]	1	-2.16	-5.18 – 0.87	0.160
pref habitat [OW]	1	1.13	-1.89 – 4.15	0.460
pref habitat [SE]	8	0.51	-0.56 – 1.57	0.349
pref habitat [SO]	1	-1.47	-4.49 – 1.55	0.336
pref habitat [TC]	1	1.59	-1.43 – 4.61	0.300
pref habitat [TD]	2	-0.59	-2.72 – 1.55	0.586
pref habitat [TM]	5	0.14	-1.21 – 1.49	0.834
pref habitat [WB]	1	-2.77	-5.79 – 0.25	0.072
pref habitat [WE]	6	1.95	0.72 – 3.18	**0.002**
pref habitat [WI]	2	-2.72	-4.85 – -0.58	**0.013**
pref habitat [WM]	10	1.69	0.73 – 2.64	**0.001**
pref habitat [WN]	2	4.23	2.09 – 6.36	**<0.001**
pref habitat [WP]	2	3.30	1.16 – 5.43	**0.003**
pref habitat [WQ]	8	0.97	-0.10 – 2.04	0.075
pref habitat [WW]	8	0.33	-0.74 – 1.39	0.546
pref habitat [WX]	1	0.85	-2.17 – 3.87	0.579
pref habitat [WZ]	6	-0.26	-1.49 – 0.97	0.678
pref habitat [ZH]	4	0.79	-0.72 – 2.30	0.301
Observations			159	
R^2 / R^2 adjusted			0.584 / 0.419	

Table S8 Species with their significant trends per level 2 habitat type, using $CM_{species\_area}$ with separation per habitat type of time period 1. Significant trends according to Wilcoxon rank sum tests. Species preferred habitat type with the corresponding fidelity (Φ) value are given as well as the number of comparisons (*n*) and the mean change in area of species per habitat type (difference $\log_{10}$(area)).

Habitat type	Species	n	Difference $\log_{10}$(area)	p value	Habitat type English	Habitat type German	Habitat type preference	Φ value
AK	*Senecio viscosus*	22	-3.59	0.018	Semi-ruderal vegetation	Halbruderale Gras- und Staudenflur	AP	0.03
AK	*Tripleurospermum maritimum* agg.	60	-2.37	0.011	Semi-ruderal vegetation	Halbruderale Gras- und Staudenflur	AK	0.03

AK	*Tanacetum vulgare*	156	-1.11	0.003	Semi-ruderal vegetation	Halbruderale Gras- und Staudenflur	AK	0.06
AK	*Agrostis capillaris*	141	-1.00	0.011	Semi-ruderal vegetation	Halbruderale Gras- und Staudenflur	GM	0.04
AK	*Crataegus monogyna*	84	1.99	0.009	Semi-ruderal vegetation	Halbruderale Gras- und Staudenflur	HG	0.04
AK	*Impatiens parviflora*	44	2.51	0.023	Semi-ruderal vegetation	Halbruderale Gras- und Staudenflur	WQ	0.05
AK	*Rubus armeniacus*	26	4.05	<.001	Semi-ruderal vegetation	Halbruderale Gras- und Staudenflur	HG	0.02
GF	*Achillea millefolium* agg.	78	-2.82	<.001	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GM	0.05
GF	*Cirsium oleraceum*	76	-2.41	<.001	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	WW	0.03
GF	*Achillea ptarmica* agg.	82	-2.36	0.008	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GF	0.03
GF	*Anthriscus sylvestris* agg.	96	-2.25	<.001	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	WW	0.02
GF	*Bistorta officinalis*	67	-1.03	0.019	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GN	0.05
GF	*Urtica dioica*	208	-0.98	0.006	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	HG	0.02
GF	*Holcus lanatus*	249	-0.59	<.001	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GM	0.04
GF	*Juncus effusus*	222	1.20	0.002	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	SE	0.04
GF	*Agrostis stolonifera* agg.	197	1.26	0.003	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	FG	0.03
GF	*Cerastium fontanum* agg.	138	1.31	0.034	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GM	0.06
GF	*Poa trivialis*	184	1.34	<.001	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GM	0.02
GF	*Carex acuta* agg.	170	1.34	<.001	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	FG	0.04
GF	*Potentilla anserina*	143	1.46	0.041	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GF	0.03
GF	*Cardamine pratensis* agg.	167	1.46	<.001	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GN	0.05
GF	*Festuca rubra* agg.	148	1.60	<.001	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GM	0.04
GF	*Persicaria amphibia*	116	1.81	<.001	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GF	0.02
GF	*Carex disticha*	71	2.11	0.008	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GN	0.04
GF	*Carex x elytroides*	62	4.10	<.001	Other wet or moist grassland, species-rich	Sonstiges Feucht- und Nassgrünland	GN	0.06
GM	*Stellaria media* agg.	58	-2.46	0.042	Species-rich grassland, moist to semi-dry	Artenreiches Grünland frischer bis mäßig trockener Standorte	LO	0.02
GM	*Bellis perennis*	92	-1.78	0.006	Species-rich grassland, moist to semi-dry	Artenreiches Grünland frischer bis mäßig trockener Standorte	GM	0.07
GM	*Carex hirta*	73	1.94	0.044	Species-rich grassland, moist to semi-dry	Artenreiches Grünland frischer bis mäßig trockener Standorte	GM	0.03
GM	*Festuca rubra* agg.	75	2.16	0.008	Species-rich grassland, moist to semi-dry	Artenreiches Grünland frischer bis mäßig trockener Standorte	GM	0.04
LO	*Taraxacum* sect. *Ruderalia*	57	2.05	0.02	Orchard	Obstpflanzung	GM	0.04
SE	*Urtica dioica*	183	0.99	<.001	Nutrient-rich small standing water, natural	Naturnahe, nährstoffreiche Kleingewässer	HG	0.02
SE	*Glechoma hederacea* agg.	89	1.68	0.034	Nutrient-rich small standing water, natural	Naturnahe, nährstoffreiche Kleingewässer	LO	0.02

TM	*Plantago lanceolata*	63	2.27	0.003	Semi-natural (semi-)dry grassland	Trocken- oder Halbtrockenrasen	GM	0.05
TM	*Crataegus monogyna*	46	3.14	0.006	Semi-natural (semi-)dry grassland	Trocken- oder Halbtrockenrasen	HG	0.04
WB	*Lysimachia thyrsiflora*	23	-3.97	0.003	Carr or bog woodland	Bruchwald und Moorwälder	FG	0.05
WB	*Peucedanum palustre*	63	-2.40	0.004	Carr or bog woodland	Bruchwald und Moorwälder	SO	0.03
WB	*Cirsium palustre*	72	-2.23	0.039	Carr or bog woodland	Bruchwald und Moorwälder	GN	0.04
WB	*Holcus lanatus*	96	-1.58	0.035	Carr or bog woodland	Bruchwald und Moorwälder	GM	0.04
WB	*Urtica dioica*	149	-1.01	0.039	Carr or bog woodland	Bruchwald und Moorwälder	HG	0.02
WN	*Epilobium angustifolium*	35	-3.55	0.018	Coniferous forest/plantation, natural	Nadelwald/-forst, naturnah	WI	0.03
WQ	*Cirsium arvense*	55	-2.97	0.002	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	AK	0.05
WQ	*Trientalis europaea*	75	-2.41	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	WZ	0.06
WQ	*Digitalis purpurea*	79	-2.40	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	WZ	0.04
WQ	*Maianthemum bifolium*	98	-2.15	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	WM	0.04
WQ	*Deschampsia flexuosa*	194	-0.91	0.003	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	WZ	0.06
WQ	*Glechoma hederacea* agg.	126	1.35	0.046	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	LO	0.02
WQ	*Lamium galeobdolon* agg.	139	1.52	0.004	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	WQ	0.04
WQ	*Acer platanoides*	111	1.80	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	HG	0.04
WQ	*Prunus serotina*	120	2.21	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	WQ	0.03
WQ	*Hedera helix*	148	2.24	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	WM	0.05
WQ	*Geum urbanum*	156	2.59	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	WM	0.03
WQ	*Ilex aquifolium*	107	2.67	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	WM	0.04
WQ	*Alliaria petiolata*	81	2.82	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	HG	0.02
WQ	*Taxus baccata*	74	2.98	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	EP	0.03
WQ	*Circaea lutetiana*	68	3.27	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	WM	0.05
WQ	*Geranium robertianum* agg.	52	3.30	<.001	Oak mixed forest on acidic soil	Bodensaurer Eichen-Mischwald	WM	0.02
WX	*Hedera helix*	57	2.53	0.001	Other deciduous plantation, non-natural	Sonstiger Laubforst, naturfern	WM	0.05
WX	*Geum urbanum*	93	2.64	<.001	Other deciduous plantation, non-natural	Sonstiger Laubforst, naturfern	WM	0.03
WX	*Lamium galeobdolon* agg.	52	2.69	0.01	Other deciduous plantation, non-natural	Sonstiger Laubforst, naturfern	WQ	0.04
WX	*Ilex aquifolium*	42	3.87	<.001	Other deciduous plantation, non-natural	Sonstiger Laubforst, naturfern	WM	0.04
WZ	*Senecio sylvaticus*	39	-3.44	0.012	Other coniferous plantation, non-natural	Sonstiger Nadelforst, naturfern	WI	0.03
WZ	*Epilobium angustifolium*	57	-2.55	0.025	Other coniferous plantation, non-natural	Sonstiger Nadelforst, naturfern	WI	0.03

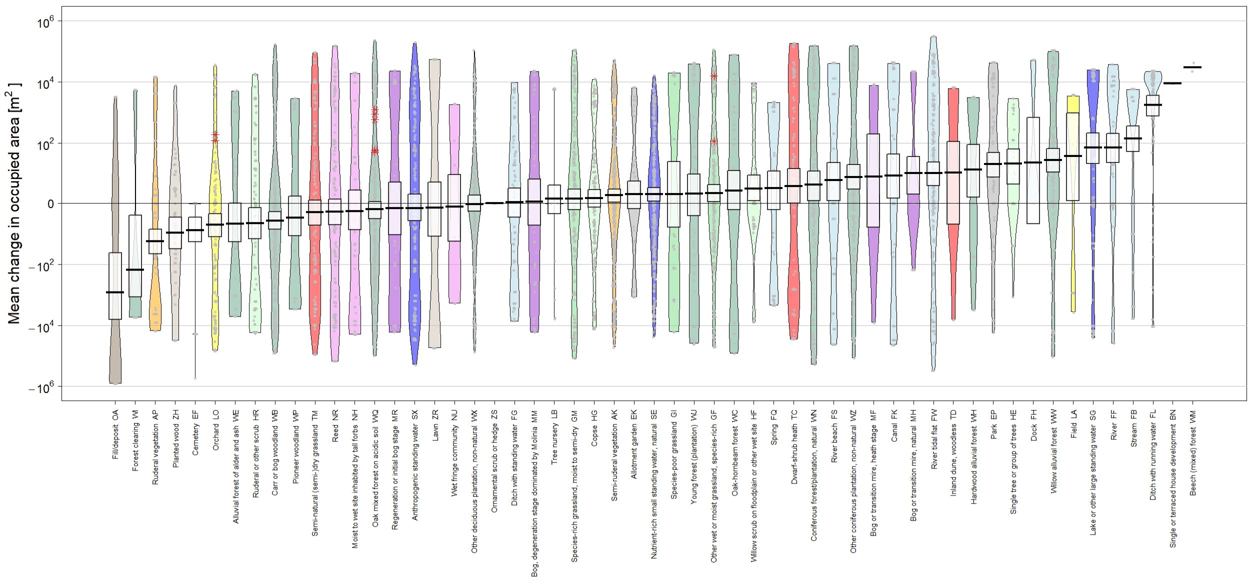

Figure S9 Mean change in occupied area in m² from t_1 (1979-1994) to t_2 (1995-2017) for all species in all level 2 habitat types. Only including habitats which habitat type did not change towards t_2. Change in occupied area was calculated as $\log_{10}(\text{area}_{\text{time period 1}} + 1 / \text{area}_{\text{time period 2}} + 1)$ using $\text{CM}_{\text{species\_area}}$ 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 which prefer the respective habitat type and colored red for species which prefer a different habitat type. Species with insignificant trends are shown as grey dots.

Chapter 3

Linking trends of habitat types and plant species using repeated habitat mapping data

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ABSTRACT

Aims: Trends in the extent of habitat types and species frequencies might not follow a simple pattern. However, data that are able to link those trends are scarce. Here, we use data from a repeated habitat mapping program to test consistency between habitat type and species change.

Location: Federal state of Baden-Württemberg, Germany.

Methods: We derived temporal trends over several decades concerning: (a) the extent of all protected habitat types across the state, (b) plant species across the state, and (c) plant species within habitat types. We tested the consistency between trends in the extent of every protected habitat type with trends of those species that prefer that particular habitat type, as well as with mean trends of all species that occur within that particular habitat type.

Results: We found that, on average, most protected habitat types decreased in area, with the exception of forests, which showed positive trends. Species analysis showed positive trends for species preferring the habitat types scrubs, copses and field hedges, as well as bog, carr, swamp and alluvial forests. By contrast, negative trends were found for species preferring the habitat types heaths and semi-natural grasslands, meadows and pastures. While non-native species increased, species that were considered endangered decreased. A species' trend across Baden-Württemberg mostly followed the trend of the species' preferred habitat type. However, within some habitat types, the mean species' trend did not follow the trend of those habitat types' extent. Decreasing species within habitat types were especially those that preferred each particular habitat type.

Conclusions: Our results point to an ongoing turnover of floristic composition, and thus to changes in habitat quality within habitat types. This implies that future monitoring programs should track temporal trends of both habitat types and the species occurring in these habitat types as a measure of habitat quality, because they can show diverging trends.

KEYWORDS

biodiversity, Germany, habitat mapping, habitat types, habitats, monitoring, plants, repeated surveys, temporal trends, vegetation

INTRODUCTION

Both (semi)natural habitat types and species are facing ongoing human-induced pressures leading to habitat loss and species declines worldwide (Díaz et al., 2019; Williams et al., 2020). Habitat loss and habitat degradation are two of the main drivers of species declines themselves (Díaz et al., 2019; Jaureguiberry et al., 2022; Pereira et al., 2012). This holds true across habitat types and taxonomic groups (Isbell et al., 2023). Given these alarming declines, tracking temporal trends of both habitat types and species is crucial to assess their current status to counteract biodiversity changes. Moreover, it is important to analyze the relationship between trends in the extent of habitat types and species frequencies, because they may not follow a simple linear correlation (Pereira & Daily, 2006). Moreover, changing site conditions may be especially detrimental to specialist species and favor more generalists (Diekmann et al., 2019; Rooney et al., 2004).

Although systematic monitoring of both habitat types and species across regions is still scarce, there are attempts to establish such programs; for example, at the European scale (Moersberger et al., 2022). However, for past trends there is the possibility of using existing data from opportunistic surveys (Eichenberg et al., 2020). For habitat types, such data are available from habitat mapping programs, which have been carried out for decades in many countries with the goal of both nature conservation and landscape planning (European Environment Agency & Museum national d'Histoire naturelle, 2014). These programs often collect detailed information on habitat types via field surveys, sometimes aided by remote sensing. Prominent examples of nationwide habitat mapping programs come from Hungary and the Czech Republic (Divíšek et al., 2014; Molnár et al., 2007). Extensive mapping has also been carried out on a regional scale for Catalonia in Spain (Carreras & Ferré, 2017) and in many small-scale programs (European Environment Agency & Museum national d'Histoire naturelle, 2014; Winkler & Wrbka, 1995).

Although some programs have been established only recently and have not yet repeated their mappings, others have data available for at least two time periods (European Environment Agency & Museum national d'Histoire naturelle, 2014). These data have been used to detect habitat type change in the United Kingdom (UK; Carey et al., 2008), Norway (Bryn & Hemsing, 2012), Hungary (Biró et al., 2018), Italy (Tomaselli et al., 2021) and Spain (Bou et al., 2020). A survey on habitat mapping programs in Europe showed that about half of the programs include the recording of plant species on-site (European Environment Agency & Museum national d'Histoire naturelle, 2014). However, there have been only a few attempts to make use of these data to derive species trends over time. Exceptions come from analyses concerning species change inside a German federal state (Bruelheide et al., 2020) and the Countryside Survey in the UK, which is, however, explicitly targeted at capturing vegetation change (Thomas & Palmer, 2015; Wood et al., 2017).

A reason why much of the habitat mapping data remain unanalyzed is that analyzing this kind of data presents several challenges. One challenge derives from the nature of habitat type complexes, which are comprised of several habitat types occurring in close proximity. To map these, some programs treat common types of complexes as their own groups alongside all other habitat types (European Environment Agency & Museum national d'Histoire naturelle, 2014). Another approach is to map these habitat type complexes as separate units and digitize them as one polygon, but treat them as unique habitat type combinations by adding information on the cover of each (or only the most prominent) habitat type that the complex is built of (European Environment Agency & Museum national d'Histoire naturelle, 2014; Kaiser et al., 2013). However, because spatial information within this complex is not provided, it is not known which habitat type is located in which part of the polygon, posing a challenge for detecting habitat type change over time. Furthermore, habitat type boundaries may shift over time making it difficult to intersect polygons from subsequent time steps. This problem is exacerbated by varying precision between repeated habitat mappings, resulting in multiple detailed habitat types being superimposed on one broadly defined habitat type. In some cases, it may not even be clear whether a polygon that does not overlap with any resurveyed polygon was lost or simply not remapped. For the analysis of species trends, an additional problem is the incompleteness of species lists recorded at a site, because full recordings are mostly non-compulsory. This is especially problematic if mapping keys change over time. For more challenges of data analysis and options on how to overcome them see Appendix S1: Table 1.

Despite these challenges, the unique combination of information across regions on both habitat types and the plant species occurring in them has great potential to detect biodiversity change at the scale of single countries or provinces. In particular, it allows us to test whether habitat type change and species change go hand in hand and whether this relationship differs between habitat types. Species trend analyses based on other kinds of data are usually not able to differentiate between different habitat types and can therefore only provide trends across habitat types (Eichenberg et al., 2021; Rich & Woodruff, 1996) or only focus on one specific habitat type (Diekmann et al., 2014; Strubelt et al., 2017). Furthermore, although time series of vegetation-plot records offer detailed species lists, they usually miss sites that have undergone habitat type change (Gonzalez et al., 2016; Jandt et al., 2022). However, species trends within these transitioned sites can be derived from repeated habitat mapping data, closing an important scale gap in species monitoring (Chase et al., 2019). Although some attempts have been made to use repeated habitat mapping data to derive biodiversity trends for regions of Germany (Bruelheide et al., 2020; Lüttgert et al., 2022), a comprehensive description of the necessary steps is missing so far.

The aim of this study is to provide such a blueprint, which would allow to apply the approach to other countries and regions where similar data are available. We use the case of the federal state of Baden-Württemberg in Germany, for which the data from mapping programs are very detailed and reach back more than three decades. In Baden-Württemberg, habitat mapping has been carried out for all protected habitat types and includes records of plant species occurrences within those habitat types (German: "Biotopkartierung"). We used these data to derive temporal trends of: (a) habitat types, (b) plant species across the state and (c) plant species within different habitat types. We tested the consistency of trends of habitat types with trends of those species that prefer that particular habitat type, as well as with the mean trends of all species that occur within that particular habitat type.

Although it is not feasible to formulate precise hypotheses for trends for every habitat type, based on the report on the state of nature of the European Union (European Environment Agency, 2020) we expected to encounter negative trends for semi-natural grasslands, mesic meadows, and bogs and mires. By contrast, we expected positive trends for shrub vegetation and forests. Furthermore, we expected habitat type trends to be reflected in trends of those species that prefer the respective habitat type. Therefore, we hypothesized that we would encounter decreases in species of grasslands and bogs and mires, and increases in species of shrub vegetation and forests across the state. In addition, we expected declines in these characteristic species also to occur within their preferred habitat type, which would indicate a deterioration in habitat quality. At the same time, we would anticipate an increase in non-characteristic species of that habitat type. Finally, given the reported declines in many endangered species and increases in many non-native species in Germany (Eichenberg et al., 2021; Metzing et al., 2018), we expected negative trends for endangered and positive trends for non-native species.

METHODS

Habitat mapping

In Germany, regional habitat mappings are carried out at the scale of the federal states and are coordinated by the federal agencies (Kaiser et al., 2013; Sukopp et al., 1979). Baden-Württemberg is the third largest federal state in Germany, covering ca. 10% of the country's area. The habitat mapping program of Baden-Württemberg is separated into two subprojects: mapping of open land, which includes all non-forested habitat types; and mapping of wooded land. Both programs cover only protected habitat types, which is ca. 3.5% of the area of Baden-Württemberg. In the past, hay meadows of Natura 2000 habitat types 6510 and 6520 were mapped in a separate program in designated Natura 2000 sites (areas protected based on the European Habitats Directive, HD, Council Directive 92/43/EEC) before their mapping was integrated into the open land mapping across the whole state of Baden-Württemberg. Habitat mapping started in 1989 for wooded land, in 1992 for open land and in 2003 for hay meadows. Whereas open land has been surveyed in specified time intervals, wooded land has been mapped continuously. At the time of analysis, the open land was not yet completely remapped, with some districts missing (Appendix S1: Figure S1). Some sites have been mapped by different projects in different years, because of changes in habitat types, but also changes in administrative mapping assignments. The definitions of habitat types are mostly consistent between the different mapping programs. In cases in which the vegetation at a site changed so much that the site lost its protection status, mapping of sites was either completely discontinued (mostly for forests) or sites were mapped as "lost" without any further information on the recent habitat type (mostly for open land). At each visit to a site, not only habitat types were mapped, but for most sites also plant species were recorded. However, complete plant species lists were not mandatory and recording focused mostly on species that were mentioned in the mapping keys as being characteristic for a particular habitat type, dominant or endangered. Species lists are therefore often incomplete. Furthermore, owing to administrative changes in the federal agencies, the mapping of wooded land shifted towards later in the year over time (Appendix S1: Figures S3-S4).

All data were digitized as polygons and in the following, we refer to the mapped units as polygons. Polygon areas ranged from 2 m^2 to 3,305 ha, with a mean of 20,254 m^2 and a median of 3,010 m^2. Based on mapping periods for open land and peaks in mapping years of the different projects (Appendix S1: Figure S2), data were divided into two time intervals: t_1 (1989–2005) and t_2 (2006–2021). In the following, we only report the main methods, but additional information on data cleaning and processing can be found in the Appendix S1.

Approach for trend analyses

Polygons from both time intervals were intersected in ArcGIS version 10.5 (ESRI, 2016). Poorly overlapping polygons were excluded from further analysis. A main challenge of the data is the overlapping of several polygons with each other. To capture all changes using all intersecting polygons per polygon, we first compared each polygon from t_1 with all its intersecting polygons from t_2 ($t_1 \rightarrow t_2$ hereon), and then compared each polygon from t_2 with all its intersecting polygons from t_1 ($t_2 \rightarrow t_1$ hereon). Comparisons from both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ were then taken together to calculate trends. This approach was used for both the habitat type and the species analyses (Figure 1).

Habitat type data

Habitat types can be described with different levels of detail, often using a hierarchical system that uses a code of two, three or four digits. In Baden-Württemberg, the level of detail increased with the number of digits; for example, 33: meadows and pastures, 332: wet meadow, and 3323: wet meadow on base-poor soils. Level 4 habitat types were converted to the broader corresponding level 3 habitat types and for most analyses further grouped into 10 broad habitat types. Those included a category for polygons that were not remapped because they lost their protection status. Those polygons were available only for open land. We were not able to include previously non-protected habitat sites into the analysis, because we could not assume that "not mapped at t_1" equals "not protected" because hay meadows and field hedges in particular were more intensively mapped in the second time period. In the following, we use the term habitat type to refer to the broad habitat type groups, unless stated otherwise. Each polygon had either one or several habitat types assigned to it. In the latter case, those habitat type complexes have information on the coverage (%) of each habitat type in the total polygon area. For each habitat type of a polygon, we weighted the polygon area by the cover of the respective habitat type.

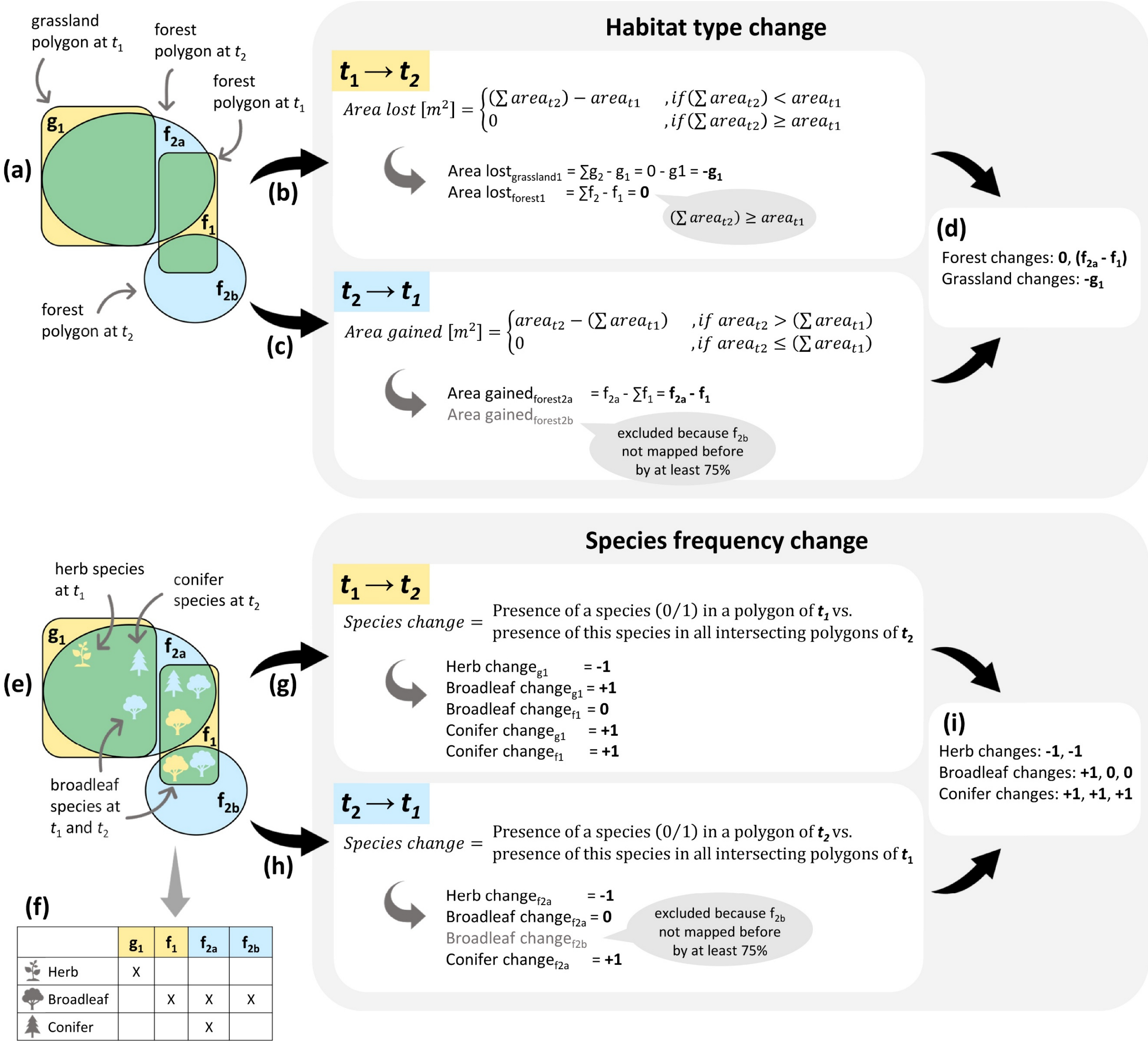

Figure 1 Approaches used to calculate habitat type change **(a–d)** and species frequency change **(e-i)**. **(a)** Two polygons g_1 and f_1 from t_1 are intersecting with two polygons f_{2a} and f_{2b} from t_2. For simplicity each polygon here contains only one habitat type (grassland or forest). To calculate habitat type change, **(b)** losses and **(c)** gains in area are calculated separately. **(b)** For each polygon and its habitat type from t_1, we compared its initial area with the area of all intersecting polygons from t_2 that have the same habitat type. **(c)** For each polygon and its habitat type from t_2, we compared its current area with the area of all intersecting polygons from t_1 that have the same habitat type. Only t_2 polygons were used that have been previously mapped by at least 75%, which excludes polygon f_{2b}. **(d)** Losses and gains calculated in **(b)** and **(c)** were then taken together per habitat type to later calculate their mean trends. **(e)** The same polygons are here used to calculate frequency changes of an herb, a broadleaf and a conifer species. Species in yellow are from t_1 and species in blue from t_2 and their occurrences are further displayed in the table in **(f)**. We calculated frequency change by first comparing all species' presences in a polygon of t_1 with all species' presences in all intersecting polygons from t_2 **(g)** and then comparing all species' presences in a polygon of t_2 with all species' presences in all intersecting polygons from t_1 **(h)**. Each change of a species in frequency from t_1 towards t_2 was assigned a value of either −1, 0, or 1, meaning loss, no change or gain of that species. To cancel out biases resulting from merging species lists of several polygons in each approach, we then combined the changes of both approaches per species to later calculate their relative change in frequency **(i)**.

Change in mean habitat type area

To calculate the change in area of each habitat type of a given polygon, we checked how much of the area of this type was also present in the overlapping polygons from the other time interval. Changes per polygon and habitat type were calculated using both approaches $t_1 \rightarrow t_2$ (comparing a polygon of t_1 with all intersecting polygons from t_2) and $t_2 \rightarrow t_1$ (comparing a polygon of t_2 with all intersecting polygons from t_1). This was necessary because of polygon clusters in which one or several t_1 polygons intersected with one or several t_2 polygons, some containing the same broad habitat type. Because those clusters were sometimes very large, they were hard to compare as a whole. Losses and gains in area could not be calculated in the same step, but always had to be in relation to a target habitat type, either at t_1 or t_2. Thus, losses were only calculated based on the target polygon of t_1, whereas gains were only calculated based on the target polygon of t_2. For example, a polygon that was grassland in t_1 and forest in t_2 leads to a loss of all grassland area via $t_1 \rightarrow t_2$ and to a gain in all forest area via $t_2 \rightarrow t_1$. Explicitly, $t_1 \rightarrow t_2$ calculates the area of a habitat type that was lost from t_1 toward t_2 (Equation 1).

$$Area\ lost\ [m^2] = \begin{cases} (\sum area_{t2}) - area_{t1} & , if\ (\sum area_{t2}) < area_{t1} \\ 0 & , if\ (\sum area_{t2}) \geq area_{t1} \end{cases} \quad (1)$$

All intersecting areas of the target habitat type at t_2 were summed to take into account that a habitat type mapped as a single polygon at t_1 might be represented by one or more polygons at t_2. The area lost was set to zero if area loss was negative because area gains were calculated separately in the next step. Conversely, for $t_2 \rightarrow t_1$ the area of a polygon that was gained from t_1 toward t_2 was calculated (Equation 2).

$$Area\ gained\ [m^2] = \begin{cases} area_{t2} - (\sum area_{t1}) & , if\ area_{t2} > (\sum area_{t1}) \\ 0 & , if\ area_{t2} \leq (\sum area_{t1}) \end{cases} \quad (2)$$

Here, all intersecting areas of the target habitat type at t_1 were summed, and the area gained was set to zero if area gain was negative, because area losses were calculated in the previous step. Mean change per habitat type was calculated using all losses and gains per habitat type, i.e. $t_1 \rightarrow t_2$ + $t_2 \rightarrow t_1$. Note that this approach is conservative and leads to a bias toward detecting zero change because setting gains to zero in Equation 1 and setting losses to zero in Equation 2 decreased the mean area change. However, this conservative approach made sure that spurious gains or losses were not reported if intersecting polygons from t_2 extended far beyond the area of that habitat type at t_1 and vice versa. In consequence, any changes reported can be more reliably interpreted as being real and not the consequence of intersecting artifacts. To test whether the area changes differed from zero, Wilcoxon signed rank tests were used, which discard the zero changes. This was done for all habitat type groups and for all level 3 habitat types separately. Because we wanted to report mean trends, we tested their robustness by excluding all outliers that fell outside the range between the 1st and 99th percentile per habitat type. The few cases in which those outlier exclusions led to a change in the direction of the mean trend of a habitat type are marked in the respective trend figures.

For habitat types that showed a significant trend over time, we extrapolated the trends 200 years into the future. We did so by using their mean proportional change in area per year and calculated their t_{50}; i.e., the time until half of the habitat type area was lost or the area doubled in size.

Change in total habitat type area

We additionally calculated the sum of all polygon areas per habitat type for each time interval. We then calculated the difference of the summed areas between the two time intervals. Although this calculation does not allow a statistical evaluation, it provides a clear expectation of total changed area. This simple approach might contradict the trends calculated from comparing single polygons. This is because some districts and sites have not been remapped, specific habitat types have been mapped more intensely in t_2, and small errors in estimating the proportion of habitat type cover within polygons with habitat type complexes might add up. Thus, we corrected the summation approach by summing the area of only those polygons that were used in both $t_1 \rightarrow t_2$ and in $t_2 \rightarrow t_1$, i.e. those that intersected with polygons of the other time interval.

Transitions between habitat types

We visualized the change in the assignment of a polygon to another habitat type in the intersecting polygons at t_2 to reveal the pathways of change. Here, we focused only on the main habitat type of each polygon because there was no information on the location of a habitat type within a polygon of a habitat type complex, and therefore no information which types from a t_1 and a t_2 polygon are overlapping in reality. The main habitat type used was the type that covered more than 50% of the polygon area.

Processing of plant species data

Species lists were available for the polygons of both open land and wooded land, except for the Natura 2000 hay meadows. We excluded mosses, lichen and algae from the analysis because they were usually only recorded by a few specialist surveyors. Furthermore, hybrids and cultivated forms, as well as some species that were known to have been falsely identified, were excluded. Plant species were harmonized in their nomenclature and aggregated up to the section level according to the taxonomic reference list GermanSL 1.5 (Jansen, 2022). Further information on the processing of the species data (Jansen & Dengler, 2010) can be found in Appendix S1. The final complete species list contained 1,865 species. Some of these species were expected to show unreliable trends because their preferred habitat types (e.g., arable fields) were not included in the mapping program or because they were only sporadically recorded in general. Thus, we conducted an additional analysis only for species that were mentioned in the mapping keys of the mapping programs, in the following referred to as "key species" (FVA, 2017; LUBW, 2014). Mapping keys included the names of species that are characteristic or endangered for each habitat type, resulting in more consistent coverage of these species, and thus more reliable trends over time. These key species represented 46% of the plant species used for the main analysis. We still focused our main analysis on all species to provide information about their trends in secondary habitat types and added expert information on how to interpret the trends in the table with significant species trends.

Species trends across the federal state

For the main analysis, we applied two different metrics to calculate species trends: change in frequency and change in probability of occurrence (Beals' index). For both metrics of change, we compared the species list of each polygon (= target polygon) with the merged species lists from all overlapping polygons from the respective other time interval. Similar to the habitat type trend analysis, we again applied both $t_1 \rightarrow t_2$ (comparing a polygon of t_1 with all intersecting polygons from t_2) and $t_2 \rightarrow t_1$ (comparing a polygon of t_2 with all intersecting polygons from t_1).

To calculate the relative change in frequency, each change of a species in frequency from t_1 towards t_2 was first assigned a value of either −1, 0, or 1, meaning loss, no change or gain of that species. These changes were biased due to the comparison of single species lists with the merged species lists of all intersecting polygons, which contained more species than single lists. Specifically, for $t_1 \rightarrow t_2$ there was a higher chance of a positive change in species frequency, whereas for $t_2 \rightarrow t_1$ there was a higher chance of a negative change in species frequency. That is why we combined both approaches, thus canceling out their respective biases. The relative change in frequency was therefore computed by taking the mean of all changes per species, i.e. of $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$. Values ranged between −1 and 1, with a value of −1 indicating that a species was lost in all polygons previously occupied, and 1 indicating that a species was new to all its polygons. To test whether the trend of a species was significantly different from zero, we used a two-tailed binomial test (a sign test), accounting for the duplicated use of polygons in $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ by reducing the degrees of freedom. Furthermore, we applied Holm adjustment of significance levels for testing of multiple species.

For the second metric of change, we applied the Beals' index of sociological favorability (hereafter called "Beals"; Beals, 1984; for an in-depth discussion see Bruelheide et al., 2021), which calculates species probabilities of occurrence (Equation 3). This index accounts for incomplete species observations by using co-occurrences of species to calculate occurrence probabilities for every species in every polygon, regardless of whether a species was observed in that polygon.

$$p_{pi} = \frac{1}{N_p} \sum_j^{N_p} \frac{M_{ij}}{M_j} \qquad (3)$$

The probability p_{pi} of species i occurring in polygon p is calculated from the joint occurrences M_{ij} with all species j of the total number of species in that polygon N_p, divided by the number of polygons M_j in which species j is present. The species co-occurrence matrix M_{ij} was created by using the species records across all polygons from both time intervals. Changes in occurrence probabilities for every species in every polygon from t_1 to t_2 were again calculated for both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$. Mean changes were tested for significance using t tests and Holm adjustment. Even though we compared occurrence probabilities across all polygons for each species, the degrees of freedom for each species were taken from the actual number of occurrences across all polygons.

We explored species change in the occupied area as another metric of change, but because results were very similar to the frequency analysis we only report on those methods and results in Appendix S1.

Because it is difficult to reliably detect trends for very rare species with habitat mapping data, we only report trends for species with at least n = 50 occurrences in the cleaned data set. This also applies to any further analyses based on these trends.

Species habitat type preference, endangerment and native status

We assigned preferred habitat types to all species by using their occurrences in all habitat types. To do so, we applied the Φ coefficient, which calculates the fidelity for each species x habitat type combination (Equation 4; Chytrý et al., 2002).

$$\Phi = \pm\sqrt{\frac{X^2}{N}} = \frac{a \cdot d - b \cdot c}{\sqrt{(a+b)\cdot(c+d)\cdot(a+c)\cdot(b+d)}} \tag{4}$$

The fidelity Φ of a species to a specific habitat type is calculated using the X^2 statistic for a 2 x 2 contingency table and is dependent on the total number of observations N, with a being the number of occurrences of the species in the habitat type, b being the number of occurrences of the species outside the habitat type, c being the number of absences of the species in the habitat type, and d being the number of absences of the species in all other habitat types. The value of Φ ranges from −1 to 1 for species perfectly avoiding a habitat type or species perfectly bound to a habitat type. The preferred habitat type of a species was defined as the habitat type for which the species showed the highest fidelity. To be typical of a certain habitat type, a species had to have a minimum Φ value, otherwise no preferred habitat type was assigned to that species. This was particularly the case for species with too few observations to make a reliable assignment. Therefore, only species with a maximum Φ value to any habitat type that was equal or higher than the median Φ value of all species (0.006) were considered to be preferential for a certain habitat type.

We tested for each habitat type if it was preferred by either loser or winner species. We did so by calculating the mean frequency trend for all species that showed a significant trend across both metrics and that preferred the respective habitat type. The significance of these trends from zero was tested using *t* tests. Note that not all groups were normally distributed but Wilcoxon signed rank tests resulted in the same species groups showing significant trends. Furthermore, we tested whether endangered species that showed a significant trend across both metrics rather increased or decreased over time. We also tested whether the (non-) native status of species in Germany had an influence on the mean trends of species. Red list and native status were retrieved from Breunig and Demuth (1999) and Biolflor (Klotz et al., 2002) respectively. For further information on data processing see Appendix S1. The mean trends per red list category as well as per native status category were tested using *t* tests, again confirming results of non-normally distributed groups with Wilcoxon signed rank tests.

Species trends within habitat types

In addition to species trends across all habitat types, we calculated species trends within habitat types. This was done (a) for all polygons, and (b) only for those polygons that did not change in their main habitat type from t_1 toward t_2. This main habitat type was always assigned according to the habitat type of the respective t_1 polygon with the highest cover. We excluded all polygons that did not have any habitat type covering at least 50%. Changes were calculated using both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$. For approach $t_2 \rightarrow t_1$ there can be several t_1 polygons with their respective habitat types intersecting with a polygon from t_2. To assign the habitat type of t_1 for comparison, we always selected the habitat type of the polygon of t_1 that covered most of the polygon from t_2 (minimum 50%).

We again calculated species changes in terms of both their frequency and probability of occurrence. To test frequency trends for significance, we used two-tailed binomial tests (sign tests) while accounting for duplicated usage of polygons and applying the Holm adjustment of significance levels. Even though Beals trends were available for all species x habitat type combinations, we used only those combinations that were also observed at least once during the mapping programs. We additionally used the number of actual occurrences per species x habitat type combination as degrees of freedom when testing for the significance of changes in occurrence probability with *t* tests. Again, we applied the Holm adjustment of significance levels. We furthermore tested for each habitat type if the mean species trend across all species occurring in that habitat type differed from zero. We calculated these mean trends using trends in probability of occurrence instead of trends in species frequency because for the latter there were only a few significant species trends for some habitat types. Finally, we tested for significance using *t* tests, confirming the results of non-normally distributed groups with Wilcoxon signed rank tests. Again, we used and report only trends for species with at least n = 50 occurrences in the cleaned data set.

Consistency of trends

We compared the area trends of habitat types with: (a) the overall trends across Baden-Württemberg of species that preferred the respective habitat types; and (b) the mean trends of all species that showed a significant trend within the respective habitat types. For the species trends we used changes in probability of occurrence.

All analyses except for the intersection of polygons were conducted in R version 4.1.2 (R Core Team, 2021), using the packages *broom*, *BSDA*, *data.table*, *dplyr*, *egg*, *ggalluvial*, *ggplot2*, *grid*, *officer*, *reshape2*, *rgdal*, *sf*, *sjPlot*, *stringr*, *terra* and *vegdata*.

RESULTS

Habitat type change

Analysis of habitat type trends showed significant increases in the polygon area of coniferous forests (mean change per polygon = +2,773 m^2, p < 0.001; Figure 2) and of deciduous forests (mean change = +913 m^2, p < 0.001). Negative trends were shown for meadows and pastures (mean change = −492 m^2, p < 0.001; Figure 2), heaths and semi-natural grasslands (mean change = −338 m^2, p < 0.001), ruderal, fringe and tall forb communities and clearings (mean change =

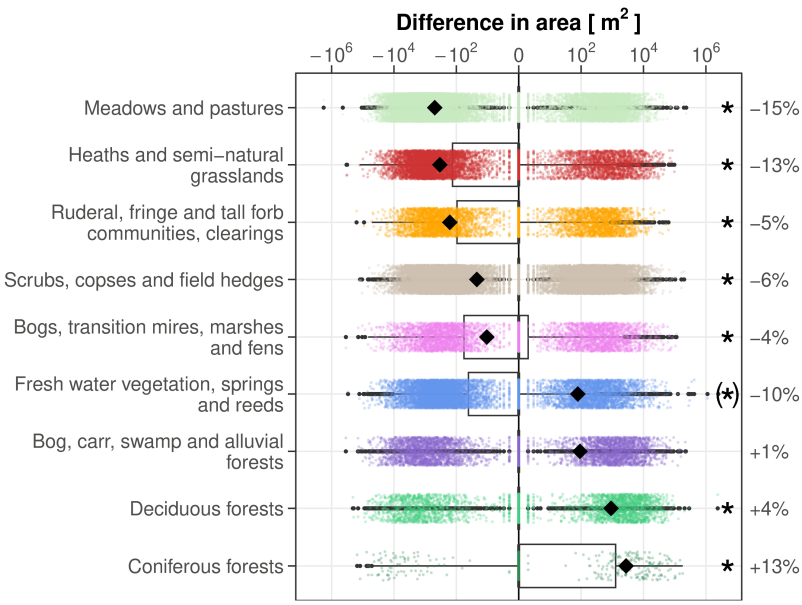

Figure 2 Difference in polygon area in m^2 between t_1 (1989–2005) and t_2 (2006–2021) for all protected habitat types. The x-axis is on a $\log_{10}$ scale. Note that all medians are at 0. Mean differences per habitat type are indicated by a diamond symbol. Significant differences according to Wilcoxon signed rank tests are labeled with an asterisk. Brackets around one asterisk indicate that excluding outliers (observations that fall outside the range between the 1st and 99th percentile per habitat type) led to a reversal in the direction of the mean trend. Percentages on the right site of the plot indicate the mean proportional change in area between t_1 and t_2 of each habitat type.

−161 m^2, $p < 0.001$), scrubs, copses and field hedges (mean change = −21 m^2, $p < 0.001$), as well as for bogs, transition mires, marshes and fens (mean change = −10 m^2, $p = 0.001$). The finer level 3 habitat types showed numerous significant trends. The highest mean gains occurred in mountainous spruce forests on base-poor soils (mean change = +8,582 m^2, $p < 0.001$), dry oak-linden forests (mean change = +4,902 m^2, $p < 0.001$) and mixed pioneer forests (mean change = +4,657 m^2, $p < 0.001$). The highest mean losses occurred in oak forests on sandy plains (mean change = −5,865 m^2, $p = 0.047$), raised bogs (mean change = −4,359 m^2, $p = 0.01$) and *Molinia* meadows (mean change = −3,571 m^2, $p = 0.021$; Appendix S2: Figure S1, Table S1).

When comparing the sums of all polygons per habitat type in t_1 and t_2, increases followed the mean trends. The biggest increases in area were observed for coniferous forests (change = +1,503,483 m^2, $n = 422$), deciduous forests (change = +1,227,800 m^2, $n = 5{,}986$) and fresh water vegetation, springs and reeds (change = +843,178 m^2, $n = 11{,}664$; Appendix S2: Table S2). The biggest decreases in total area were displayed by meadows and pastures (change = −39,428,206 m^2, $n = 55{,}825$), heaths and semi-natural grasslands (change = −4,957,188 m^2, $n = 10{,}037$) and scrubs, copses and field hedges (change = −3,002,371 m^2, $n = 35{,}420$).

Visualization of the changes between habitat types revealed that the majority of mapped areas did not show a change in habitat type (Appendix S2: Figure S2). Most of the polygons that were no longer considered protected in t_2, and therefore not remapped, were previously assigned to the habitat types meadows and pastures, followed by scrubs, copses and field hedges, as well as heaths and semi-natural grasslands. Transitions between habitat types occurred mainly within the main groups of habitat types, but also between different groups (Figure 3). In the following we discuss the most relevant changes between level 3 habitat types that happened between habitat type groups.

All scrubs, copses and field hedges gained area from semi-natural grasslands. The largest transition of copses (411) into another habitat type group was toward riverine woodland (523). The biggest part of mixed pioneer forests (582) developed into spruce bog forests (512). Deciduous and coniferous forests gained mostly from the group of bog, carr, swamp, and alluvial forests. Spruce bog forests (512) turned to some extent into mountainous spruce forests on base-poor soils (572), whereas riverine woodland (523) turned to a smaller extent into moist to wet Tilio-Acerion forest of slopes, screes and ravines (541). In addition, swamp forests (522) turned to some extent into oak–hornbeam forests (561). One large polygon led to a well visible change from raised bog area (311) towards mixed pioneer forest (582) in t_2. A considerable amount of semi-natural grasslands on calcareous substrates (365) turned into lowland hay meadows (651), although this change also happened in the opposite direction.

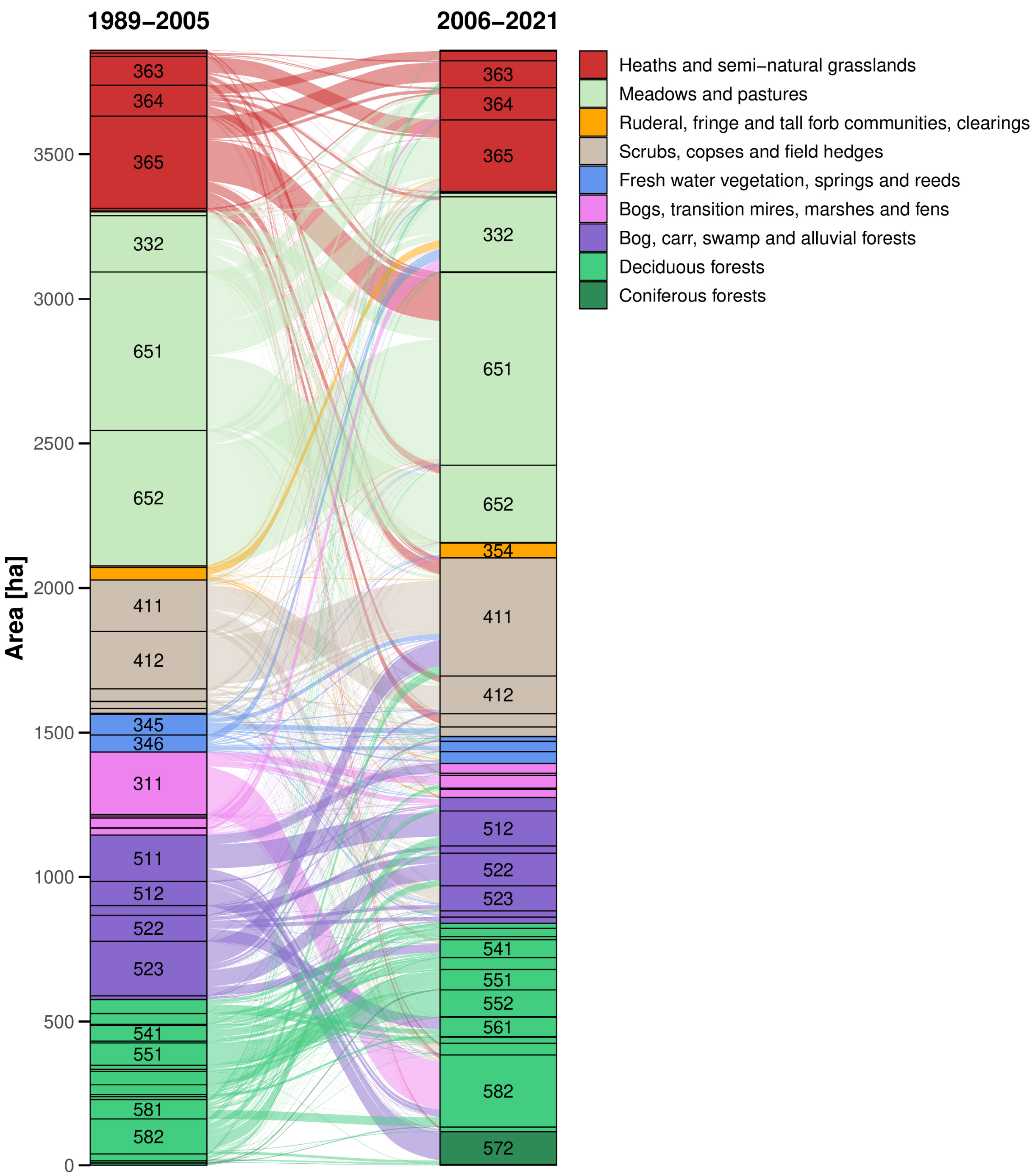

Figure 3 Transitions between protected level 3 habitat types from t_1 (1989–2005) to t_2 (2006–2021). For visibility, only polygons are included that changed in their habitat type over time. Note that this also excludes polygons that have not been remapped because they lost their protection status. See Appendix S2: Figure S2 for all transitions. Habitat type abbreviations according to the Baden-Württemberg identification key. Only habitat types with a total area of >50 ha are labeled. Colors refer to the groups of habitat types.

Extrapolation of trends

Extrapolation of habitat type trends into the future showed that, under the assumption that habitat types continue their trends from past decades, meadows and pastures will lose approximately half of their area in the next 59 years (mean proportional change per year = −0.012, SE = 0.0001, $t = -102.95$, $p < 0.001$; Figure 4). Heaths and semi-natural grasslands will lose half of

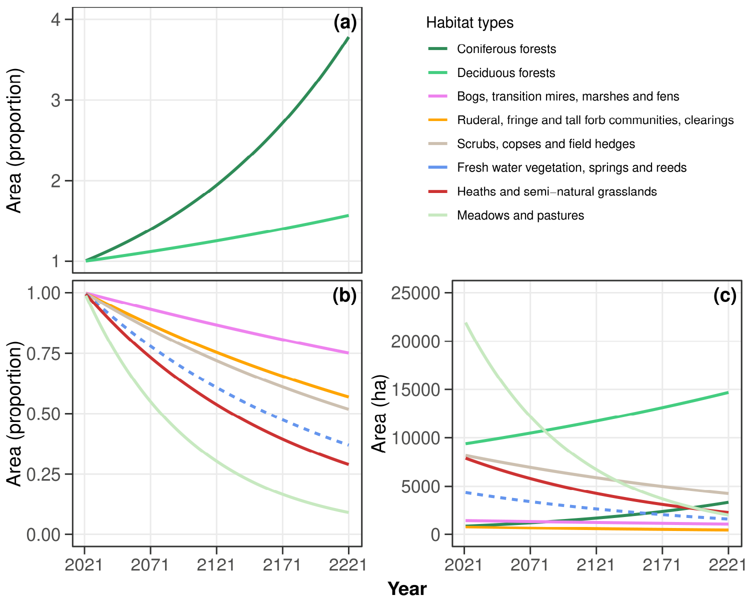

Figure 4 Extrapolation of the mean proportional trends in area of the protected habitat types for the next 200 years. **(a,b)** Proportional **(a)** increases for habitat types with positive trends and **(b)** decreases for habitat types with negative trends. **(c)** Total change in area for all habitat types. Note that the scales of the plots differ. The group of "Fresh water vegetation, springs and reeds" is only plotted with a dashed line as outliers led to different directions of trends concerning the mean proportional area, making the extrapolation unreliable.

their area in the next 112 years (mean proportional change per year = −0.006, SE = 0.0002, t = −27.73, p < 0.001). Assuming no increase-limiting factors, coniferous forests will approximately double their area in the next 104 years (mean proportional change per year = +0.007, SE = 0.0012, t = 5.80, p < 0.001; Figure 4). For the other habitat types it would take more than 200 years to halve or double their size (Appendix S2: Table S3).

Species trends across the federal state

Focusing species analysis on key species led to the same direction in trends per species group for almost all analyses. Therefore, we report trends for all species here, but results for the reduced species list can be found in the extended results in Appendix S3.

Frequency analysis showed significant trends for 374 species, with 197 species increasing and 177 species decreasing. Analysis based on changing co-occurrence probability according to Beals showed significant trends for 845 species, with 169 species increasing and 676 species decreasing. Among the 868 species that showed significant trends for at least one of the metrics (Appendix S2: Table S4), Spearman rank correlations showed rather low correlations between frequency and Beals trends (r_s = 0.250, p < 0.001; Appendix S2: Figure S3). This correlation was higher for the 344 species that showed a significant (but not necessarily consistent) trend for both metrics (r_s = 0.33, p < 0.001).

In total, 272 species displayed significant and consistent trends for both metrics (either significant positive or negative trends), with 112 species showing positive trends and 160 species showing negative trends (Figure 5 and Appendix S2: Table S5). The correlation coefficient between the trend metrics for this set of species was higher compared with the coefficient across all species (r_s = 0.532, p < 0.001).

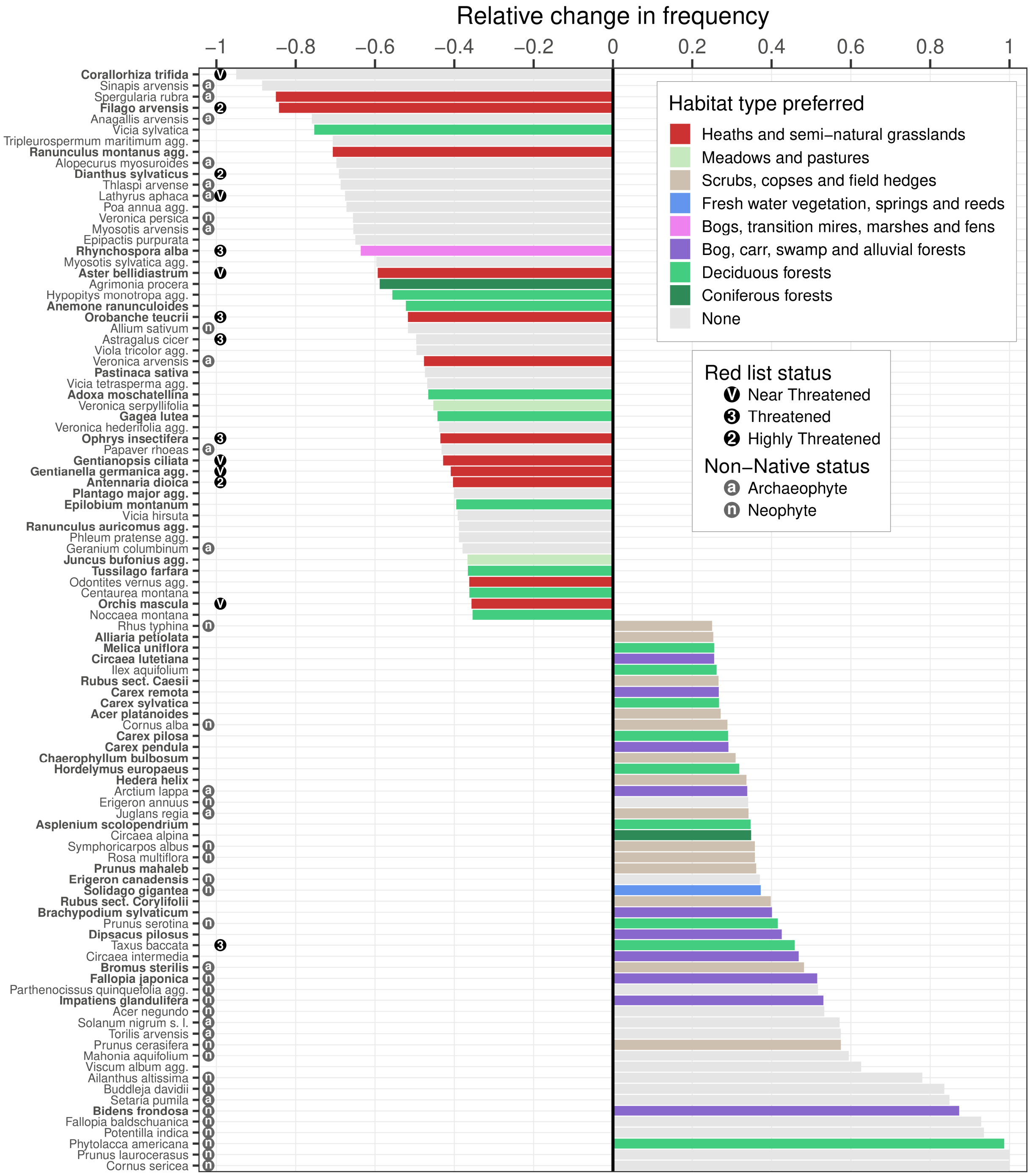

Figure 5 Relative change in frequency from time interval t_1 (1989–2005) to time interval t_2 (2006–2021) for species that showed significant trends across the two change metrics. Of those 272 species only the 50 top losers and 50 top winners are shown. Colors refer to the preferred habitat type of each species, based on the fidelity (Φ) of species to habitat types. The category "None" refers to species that showed a fidelity lower than the median of all species of Φ = 0.006 to their most preferred habitat type. Names of species that were mentioned in the mapping keys of the mapping programs of Baden-Württemberg are displayed in bold.

In the following, only the trends in frequency of species that showed also significant trends for Beals are discussed in detail, but see Appendix S2: Figure S4 for all trends in probability of occurrence. The three top loser species were *Vicia sylvatica*, *Tripleurospermum maritimum* agg. and *Ranunculus montanus* agg., of which only *Ranunculus montanus* agg. was a key species, and therefore expected to be more consistently recorded (bold in Figure 5). The next two loser key species were *Dianthus sylvaticus* and *Rhynchospora alba*. The three top winner species were *Prunus laurocerasus, Phytolacca americana* and *Buddleja davidii*, which were all not key species. The three top winner key species were *Impatiens glandulifera*, *Fallopia japonica* and *Bromus sterilis*. Losers were further represented especially by species of heaths and semi-natural grasslands (mean change = −0.25, t = −13.3, p < 0.001) and by species of meadows and pastures (mean change = −0.18, t = −9.38, p <0.001). Winners were mostly species of bog, carr, swamp and alluvial forests (mean change = +0.15, t = 3.05, p = 0.005) and species of scrubs, copses and field hedges (mean change = +0.11, t = 4.64, p < 0.001). Comparing trends of species with different red list status showed that near-threatened and threatened (Red list categories V and 3, respectively) species were mostly decreasing (mean change = −0.24 and −0.29, t = −3.34 and −3.80, p = 0.004 and p < 0.001, respectively; Figure 6a). Comparing trends with respect to the native status, we found that neophytes showed positive trends (mean change = +0.32, t = 4.56, p < 0.001), whereas native species showed overall negative trends (mean change = −0.10, t = −5.66, p < 0.001; Figure 6b).

Species trends within habitat types

Analyzing species trends within habitat types resulted in very similar trends for analyses including or excluding polygons that changed in their habitat type over time (Figure 7, Appendix

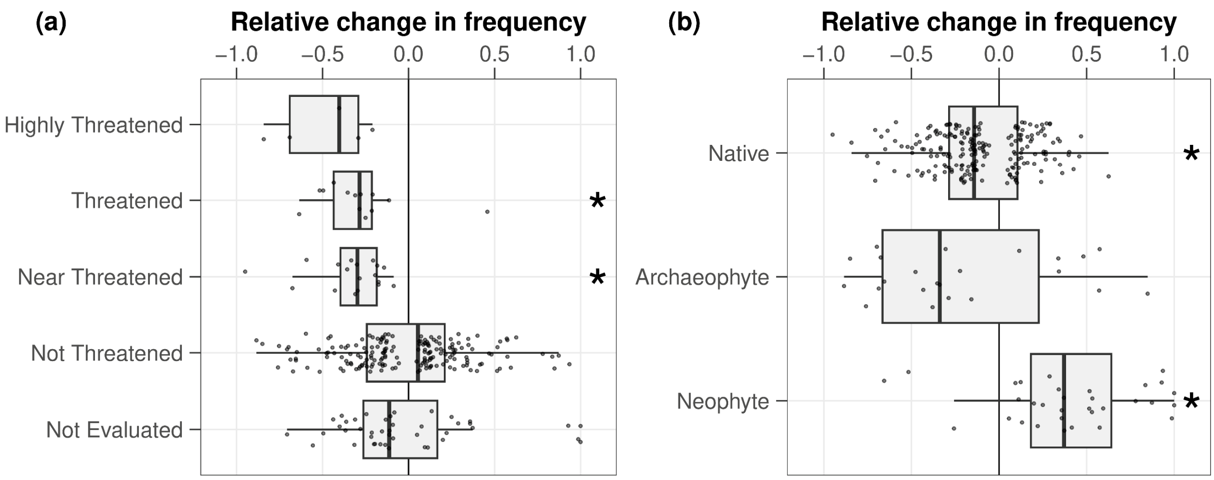

Figure 6 Relative change in frequency from time interval t_1 (1989–2005) to time interval t_2 (2006–2021) for species of different **(a)** red list categories of Baden-Württemberg and **(b)** non-native status in Germany. Only species are plotted that showed significant trends across the two change metrics. **(a)** Group categories according to Breunig and Demuth (1999): Highly Threatened (=Category 2), Threatened (=Category 3), Near-Threatened (=Category V), Not Threatened (=Category *), Not Evaluated (=Categories D and ^). **(b)** Non-native status according to Biolflor (Klotz et al., 2002). Significant differences from zero according to t tests are labeled with an asterisk.

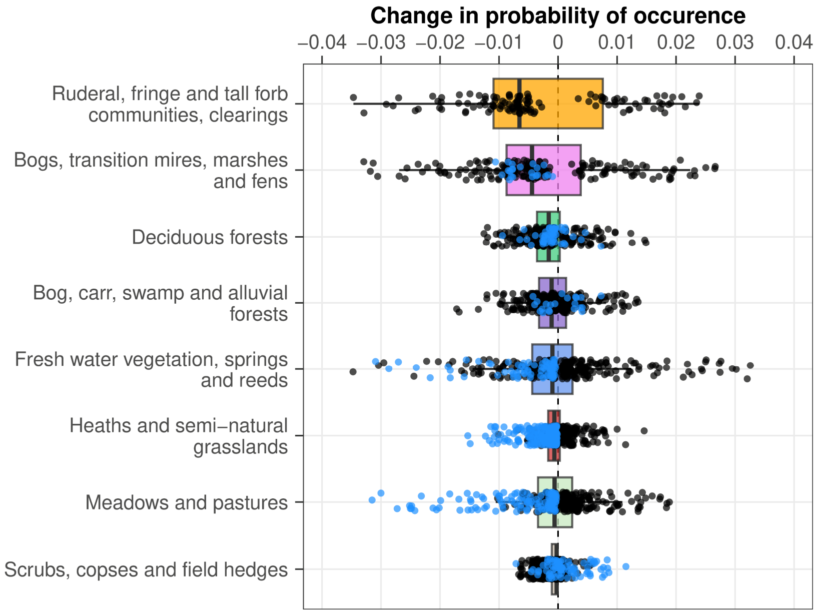

Figure 7 Mean changes in species' probabilities of occurrence within different habitat types. Only significant trends are shown. Polygons that transitioned in their habitat type over time are included. Blue dots represent species that prefer the respective habitat type in which they show a trend, black dots represent all species that prefer another type or which fidelity lies below the median of all species (Φ = 0.006). Blue dots are plotted on top of black dots for visibility.

S2: Figure S5). Thus, we here present the results only for the analysis that included all polygons.

Most habitat types had more species increasing than species decreasing in frequency over time (Appendix S2: Figure S5a). By contrast, there were more species with decreasing than species with increasing occurrence probabilities in all habitat types (Figure 7, Appendix S4: Table S1). The highest mean decreases in occurrence probability were found for species in bogs, transition mires, marshes and fens (mean change = −0.003, t = −3.31, p = 0.001), for species in deciduous forests (mean change = −0.001, t = −5.29, p < 0.001) and for species in heaths and semi-natural grasslands (mean change = −0.001, t = −6.53, p < 0.001). The mean trends of the habitat types meadows and pastures, heaths and semi-natural grasslands, and fresh water vegetation, springs and reeds were especially driven by species that preferred the respective habitat type. Therefore, here, especially specialist species showed negative trends in their preferred habitat types. The opposite was observed for scrubs, copses and field hedges, where typical species seemed to increase rather than decrease in their occurrence probability (Figure 7). Species of scrubs, copses and field hedges showed increases in probability of occurrence in almost all other habitat types over time (Appendix S2: Figure S6).

Consistency of trends

Trends of species mostly followed the trend of the habitat type that they prefer (Figure 8a). However, the mean trend of all species within a habitat type did not necessarily follow the mean area trend of the respective habitat type (Figure 8b). All mean species trends within habitat types were negative, which contradicted the positive trend in area of deciduous forests.

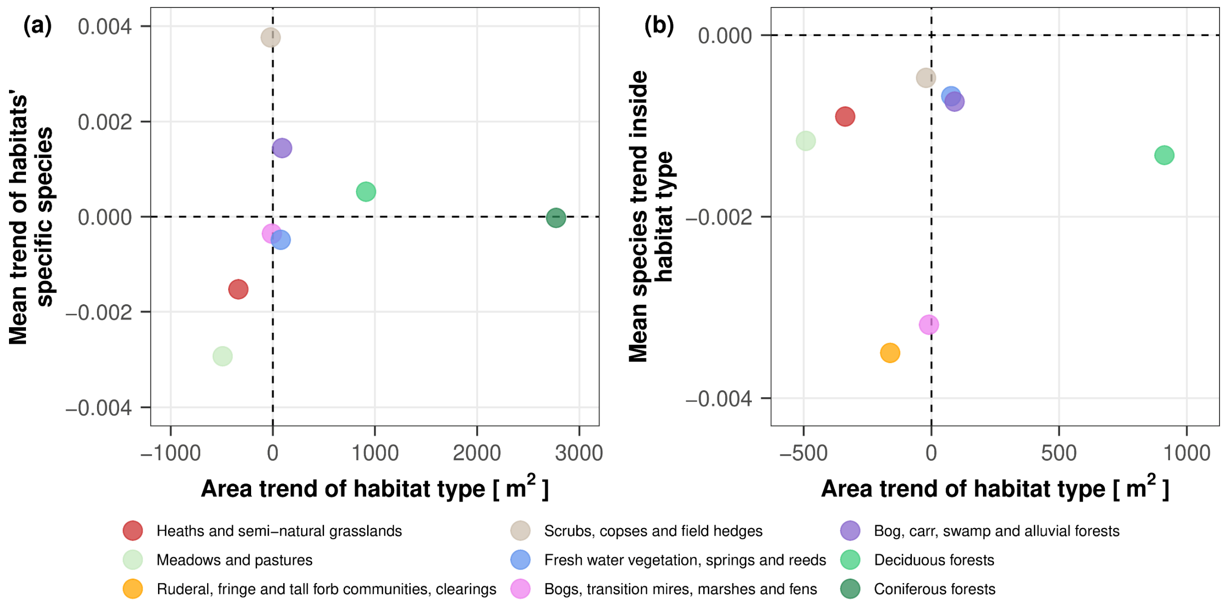

Figure 8 Comparison of mean trends for habitat type area with **(a)** mean trends of habitat types' specific species and **(b)** mean species trends within habitat types. **(a)** Species trends refer to the trends in occurrence probability across all habitat types in Baden-Württemberg. **(b)** Species trends refer to the trends in occurrence probability. Area trends of habitat types are in m^2. Colors according to the habitat types. Note that also habitat types are included that did not show a significant trend over time (fresh water vegetation, springs and reeds; bog, carr, swamp and alluvial forests). Only species that showed significant trends over time were used to compute the mean species trends for **(a)** and **(b)**. There were no species with a significant trend that belonged to ruderal, fringe and tall forb communities (plot a) and no species with a significant trend within coniferous forests (plot b).

DISCUSSION

This study demonstrates how opportunistic data originating from habitat mapping programs can be used to derive temporal trends of both habitat types and plant species. As a showcase, we used data from Baden-Württemberg and reported temporal trends of all protected habitat types and most plant species, while looking for consistency between these trends.

Habitat type trends confirm expectations

In total, 18% of polygon area was assigned to a different habitat type in the second survey, indicating considerable biodiversity change. Studies on habitat type change in parts of Norway and in the UK showed even slightly higher turnover rates of around 25% over the past decades (Bryn & Hemsing, 2012; Carey et al., 2008).

Although many natural habitat types in Europe have experienced severe decreases in area, wooded land seems to be the winner over the past decades (European Environment Agency, 2017; Fuchs et al., 2013; Kimberley et al., 2021; Kuemmerle et al., 2016). These positive trends are mainly driven by afforestation and the natural expansion of forests through succession, mainly because of abandoned land uses (European Environment Agency, 2017; Navarro & Pereira, 2015). Therefore, we expected positive trends for forests as well as scrubs, copses and field hedges. Indeed, trend analysis of habitat types showed increases in both deciduous and coniferous forests.

Although some of those increases can be attributed to succession from copses, a greater amount stems from transitions from wet forest types, such as swamp forests and riverine woodland. These changes might be attributed to an increased intensity of forest management, human-induced lowering of groundwater levels, altering of riverbeds, and climate change (Čížková et al., 2013; Demuth et al., 2021). Against our expectations and local expert assessments, the area of scrubs, copses and field hedges showed negative trends. Although some of these losses were due to ongoing succession into forests, the majority stemmed from transitions into sites that were no longer protected. This stresses the need to continue the mapping of sites that have undergone transition to non-protected habitat types, because otherwise habitat loss is underestimated.

Scrubs, copses and field hedges, however, also gained a considerable amount of area from semi-natural grasslands. Semi-natural grasslands in Europe are usually affected by encroachment with woody species when abandoned (Buitenwerf et al., 2018; Janssen et al., 2016). We found that those grasslands overall lost area in Baden-Württemberg, mirroring negative trends across Germany and Europe and confirming our expectations (Finck et al., 2017; Janssen et al., 2016). Another type of protected grassland that decreased was the meadows and pastures group. In particular, those protected under the European habitats directive Natura 2000 showed high losses in area, with their majority turning into no longer protected habitat types. The sites used for analyses compromise ca. 30% of the total amount of Natura 2000 meadows and pastures in Baden-Württemberg and are mostly located inside designated Natura 2000 habitat regions. Our analysis revealed that many of those meadows did vanish. Additional information for some of the no longer protected meadows and pastures revealed intensification of land use and succession as main threats (data not shown), which confirms assessments of natural grasslands worldwide (Janssen et al., 2016; Newbold et al., 2015). Our extrapolation of trends showed that – should these threats continue – meadows and pastures will lose approximately half of their area in the next 59 years and semi-natural grasslands will lose half of their area in the next 112 years. Although we acknowledge that these extrapolated trends are only rough estimates of the future development and unrestrained growth of, for example, coniferous forests is not realistic, they do demonstrate the severity of the changes we have observed over the past decades and how they could further develop in the future.

Finally, bogs and mires have severely suffered in number and quality over the past centuries in Europe and Germany, mainly because of peat extraction, drainage, and conversion to agriculture and forestry, and further accompanied by nutrient input and climate change (Finck et al., 2017; IPBES, 2018; Kosonen et al., 2019). Thus, we hypothesized that they would also be seen to decline in Baden-Württemberg. Indeed, we found consistently negative trends for the group of bogs, transition mires, marshes and fens, with particularly high losses for raised bogs. Most of these raised bogs transitioned to pine bog forests, and the regeneration and heath stages of bogs (data not shown). The largest transition in terms of area lost was into a mixed pioneer forest, with the former bog mapped by the open land project and the latter forest mapped by the forest project. Although this could generally imply a case of succession, this particular site has always been mapped as forest by the forest project, but the respective old polygon was excluded for analysis because of poor overlapping with recent polygons. This is a prominent example of cases in which differences between mapping practices between projects or over time, or changes in the mapping keys, could not be accounted for by grouping or adjusting the habitat types and led to only apparent transitions between protected habitat types. Another example are the transitions between semi-natural grasslands and meadows and pastures. Although some of these changes might be attributed to changes in management intensity, others are brought about by different mapping practices between the periods and the integration of former, already protected, habitat types of semi-natural grasslands into Natura 2000 meadows and pastures.

Species trends partly reflect habitat type trends

We expected habitat type trends to be reflected in the trends of species that prefer the respective habitat type. This was indeed the case for species of semi-natural grasslands and species of meadows and pastures, which both showed mainly negative trends, mirroring the area losses of semi-natural grasslands and meadows and pastures. This reflects Germany-wide species trends derived in other studies (Diekmann et al., 2014; Jandt et al., 2022). It should be noted that although we used methods to overcome biases in species trends that are caused by the aggregation of polygons, some other methodological difficulties could not be accounted for and resulted in a bias toward positive species trends. This included the lack of species occurrence lists for sites that were no longer protected. Because these sites no longer met the criteria for protection, it can be expected that those sites in particular have experienced (specialist) species losses. Those sites went into the habitat type analysis but could not be used for species analysis, hence excluding potentially severe losses.

Winner species did not especially prefer habitat types that were increasing in area overall. Despite a negative trend of scrubs, copses and field hedges, species that usually occur in those habitat types showed positive trends. This indicates an encroachment with woody species across different habitat types, whereas the transition into wooded (non-forest) land is not completed yet. Winners also included species of bog, carr, swamp and alluvial forests, although their habitat types did not show significant area trends. Despite the observed increases in the area of deciduous and coniferous forests, their typical species did not show a significant trend. This also contradicts findings from a study across 7,738 vegetation plots in Germany, which found overall increases in forest species across all habitat types during the past decades (Jandt et al., 2022). Species of oligotrophic forests, however, have also shown decreases in Germany (Günther et al., 2021). Furthermore, despite decreases in the area of their respective habitat types, species of bogs, transition mires, marshes and fens, as well as species of ruderal, fringe and tall forb communities and clearings mostly showed no significant trends. This was particularly surprising for bogs and mires, because a study that analyzed species trends within 124 sites of bogs and mires of the Black Forest of Baden-Württemberg revealed significant temporal trends in the occupancy of many characteristic plant species (Sperle & Bruelheide, 2021). However, population trends within sites were not considered and may show even more drastic changes. Furthermore, bog species belong to the most endangered plant groups in Germany (Metzing et al., 2018). Overall, as expected, endangered species showed negative trends in Baden-Württemberg and are thus conform with the red list assignments for Baden-Württemberg (Breunig & Demuth, 1999). However, more than half of the non-threatened species showed negative trends as well. Because the focus of conservation efforts and monitoring does not focus on those not (yet) threatened species, most of their decreases usually go unnoticed. This includes moderately common plant species, which showed the highest relative losses in a study for northeast Germany (Jansen et al., 2020). Our analysis also showed overall negative and positive trends of native and non-native plants, respectively, reflecting Germany-wide trends (Eichenberg et al., 2021).

Although species trends in frequency and area showed more winners than losers overall, co-occurrence probability trends showed many more losers than winners. This pattern was similar for trends per habitat type, with more negative trends in co-occurrence probability compared with trends in frequency. Because Beals' index accounts for incomplete species lists, it assesses occurrence probability on the basis of all other species of a site (Bruelheide et al., 2021) and can thus be taken as a forecast for future conditions, foreshadowing future species trends. Here, the observed differences between species trend metrics point to habitat degradation, which is captured by Beals, but not by the frequency trends. Thus, there seems to be an extinction debt present for many species. These species appear to still be present at their sites, but can be expected to decline in the future, because their probability of occurrence at the sites has already shown to be declining. Extinction debts often occur when habitat degradation makes sites less suitable for many species, but the responses of the concerned species are lagging (Kuussaari et al., 2009). In this context it is important to point out that these calculations excluded rare specialist species because Beals trends for species with only a few records, and thus, only a few co-occurrences with other species, are not significant. Furthermore, we excluded very rare species from the analyses. Including rare species would probably have reinforced the observed trend (Finderup Nielsen et al., 2019; Kempel et al., 2020). However, in cases where species lists are incomplete, we generally recommend calculating the probabilities of occurrence in addition to frequency changes to confirm species trends. This is also helpful in cases of seasonal shifts in mapping.

We ran additional analyses restricting the species pool to species that appear in the mapping keys, because those species are quite consistently recorded and therefore may offer more reliable trends. They represent mainly native species and species characteristic of their respective habitat types while excluding many non-native and generalist species. Therefore, this approach describes trends for the most relevant species for habitat type distinction, while missing trends for common species. It also excludes trends for species that are typical of non-protected and therefore not mapped habitat types, e.g., of arable fields like *Alopecurus myosuroides* or *Veronica persica*. Trends of those species derived in the current study are only representative for their secondary habitat types and cannot reflect their overall trends across Baden-Württemberg. However, analyses that focused on the restricted species pool did not change the direction of species group trends across analyses. We can conclude from this that common and characteristic species seem to generally be impacted in similar ways by changes of the past decades.

Habitat types' characteristic species less likely to occur than in the past

More species decreased rather than increased in their probability of occurrence within all habitat types. This was especially the case for species that preferred the respective habitat type, which implies some degree of habitat degradation. Although many species might still persist on the sites, conditions seem to have already changed in favor of non-typical species, resulting in an ongoing turnover of floristic composition. This is in line with studies that found declines in specialists while more widespread and generalist species were increasing (Britton et al., 2009; Diekmann et al., 2019; Heinrichs & Schmidt, 2017). In the specific case of scrubs, copses and field hedges, the observed decrease in non-typical species can be explained by decreases in, for example, species of semi-natural grasslands, lowering the diversity inside scrubs and field hedges. Prominent across almost all habitat types was an increase in the probability of occurrence of species of scrubs, copses and field hedges, pointing toward encroachment with woody species. For grasslands, this is probably caused by the abandonment of management, allowing woody plants to grow (Janssen et al., 2016). For bogs and mires, this implies a lowering of groundwater levels and increases in nutrient availability over time, enabling woody plants to establish (Demuth et al., 2021; Gunnarsson et al., 2002).

Lack of agreement between habitat type and species trends point to habitat degradation

Although trends of species generally followed the trends of their preferred habitat type, only some of these species' trends were significant and some were even reversed for the habitat type and species of scrubs, copses and field hedges. Furthermore, although deciduous forests increased in area, they had more species with negative trends than species with positive trends within their habitat type. Given the general positive bias for species trends in our study, the negative trends of characteristic forest species point to a decrease in habitat quality without a loss of habitat type area. Particularly characteristic species might still be decreasing even if their habitat type area is mostly increasing (Finderup Nielsen et al., 2021). However, losing characteristic species also makes assignments to habitat types more difficult, and ultimately, will result in forfeiture of the site's protection status. Mismatches between habitat type and plant species trends have also been found by a study across Denmark, especially for mires and forests (Finderup Nielsen et al., 2021). Results from the Countryside Survey in the UK showed some inconsistencies between habitat type and species trends as well (Carey et al., 2008). These inconsistencies demonstrate that monitoring only one aspect of biodiversity change is not sufficient to capture the whole picture, especially considering habitat degradation and extinction debts (Kühl et al., 2020; Kuussaari et al., 2009). Although monitoring of both habitat types and species across regions is costly, an alternative would be to restrict the complete species sampling to a manageable amount of vegetation plots inside different habitat types (Pescott et al., 2019). Monitoring schemes that sample vegetation plots within different habitat types have already been implemented by the UK Countryside Survey (Wood et al., 2017) and the National Plant Monitoring Scheme in the UK (Pescott et al., 2019).

CONCLUSIONS

Our study has shown that data from habitat mapping programs can be used to derive biodiversity trends. We hope that this study can serve as a blueprint for analyzing similar data from other countries and regions. If the data are thoroughly cleaned and the challenges addressed, the approach has the potential to detect biodiversity change across regions. In particular, the presence of information on both habitat types and plant species makes it possible to link trends. Because we have shown that these trends can diverge, future monitoring programs should track temporal trends of both habitat types and the species that inhabit them. Thus, we should strive for complete species lists within habitat types because they provide additional information on habitat quality beyond habitat extent. Continued monitoring of areas that are no longer protected habitat types is crucial to track all changes, including those into species-poor and anthropogenic habitat types. Therefore, it is recommended that in re-surveys all sites be remapped, including those that have lost their protection status. We further recommend that changes in mapping keys and the mapping of complexes should be avoided wherever possible because they make it difficult to detect habitat type changes. In this way, habitat mapping, which has very different purposes in landscape planning and conservation, can serve an additional purpose in providing valuable data on biodiversity trends.

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DATA AVAILABILITY STATEMENT

All polygon data from the current mappings are publicly available via https://udo.lubw.baden-wuerttemberg.de/public/index.xhtml. As all data belong to the federal state agencies of Baden-Württemberg, publication of the rest of the data is in part restricted. This concerns data from previous mappings for the open land and observations of endangered species. All other data are archived in the iDiv Biodiversity Data Portal (iBDP) (Lüttgert et al., 2024, https://doi.org/10.25829/IDIV.3558-y2sd63).

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APPENDIX S1

This Methodological Appendix provides additional information on the data processing specific for the case of the habitat mapping program of Baden-Württemberg. The more general methods can be found in the main script.

Table S1. Options for analyses of repeated habitat mapping data. For each issue several options are given with their pros and cons. Generally, the best option always depends on the specific habitat mapping program and can therefore vary for different kind of data. Not all options are exclusive but can be combined. In light grey the options which were chosen for the analyses in this paper.

Issue	Option	Pro	Contra
Overlapping of polygons	Exclude polygons that are not overlapping to some specific extent, e.g., 75%	Avoid pseudoturnover resulting from comparing different locations	Lose some data
	Include all polygons	Keep all data	Risk of pseudoturnover
Weigh polygon area	Weigh polygon area by percent overlapping with other time interval	Exclude area that has not been remapped/previously mapped	Miss some potential gains and losses
Select from overlapping polygons of the same time interval	Select intersections of polygons, in the following order, that are both protected, come from the same project, result in the largest time span, have the largest overlap	Selection of intersections that lead to the smallest bias, that might arise by different mapping projects, poor overlapping etc.	Polygons from the same project and protection status favor the detection of no change

Set time intervals	Same time window for all mapping projects	Trends are comparable across projects	Lose some data
	Different time windows depending on mapping project	Keep all data	Not as comparable
Select habitat types	Keep morphological types in addition to types defined by their vegetation	Keep data on sites that are only defined by their morphological features, e.g., rivers	For sites with both morphological and vegetation-defined habitat types, it is difficult to define a main habitat type, which is necessary for some analyses
	Exclude morphological types	Mostly easy to define a main habitat type, as sites with overlapping morphological and vegetation-defined types are excluded	Lose data on sites that are only defined by their morphological features, e.g., rivers
	Keep types that are usually mapped as lines	Report trends of commonly linear habitat types, e.g., rivers and hedges	Linear types of different time intervals are mostly not well overlapping, excluding many polygons and making their mean habitat type trends not representative
	Exclude types that are usually mapped as lines	No reports on unrepresentative trends of commonly linear habitat types	No reports on trends of commonly linear habitat types, which might still be valid
	Keep polygons with no information on habitat type (unprotected types)	Include most cases of habitat losses and habitat degradations	Bias towards losses, as gains on previously not mapped area are generally not captured
	Exclude polygons with no information on habitat type	Prevent possible bias towards losses	Exclude most cases of habitat losses and habitat degradations, probably bias towards positive change as gains in protected habitat type areas from unprotected types are generally rare
	Keep types that are not mapped in both time intervals	Might be an option if anthropogenic types are only mapped in recent times	Trends are most likely mainly due to changing mapping practices
	Exclude types that are not mapped in both time intervals	No reports on unreliable trends for types that are not consistently mapped	If anthropogenic types are only mapped in recent times, some habitat loss will be missed
Level of habitat types	Finest level	Detect habitat type changes on finer level, especially habitat degradation (e.g., nutrient or water level)	Lose data on sites that have only broadly defined types assigned, bias from inconsistent mappings by different people, campaigns, and weather
	Intermediate level	Keep most data, still capture changes on a relatively fine level, minimized bias from inconsistent mapping	Lose some data, slight bias from inconsistent mappings, miss habitat type changes on the finer scale
	Coarse level	Keep all data, minimize bias from inconsistent mapping, less habitat type complexes (as they are combined by group)	Miss changes on intermediate and fine level and in consequence underestimating habitat type change
Habitat type complexes	Exclude complexes	Ensures that habitat types of polygons of different time intervals are overlapping	Lose some amount of data (depending on how commonly complexes were mapped)
	Only use the main type of a complex (e.g., that covers >50% of area)	Ensures that habitat types are more or less overlapping. Can be used for species analysis within habitat types	Lose data on sites with no habitat type covering >50%, lose information on especially habitat types that are typically small
	Use all types of a complex	Keep most data	Habitat types might not be overlapping in reality
	Create own groups of common complexes	Keep most data	Time intensive, subjective, maybe not feasible
Calculate habitat type changes	Difference of sum of area of all t_2 and all t_1 polygons	Easy to calculate	Pseudochanges when area not completely remapped or changes in the mapping procedure occurred, large polygons have a rather high influence, no statistics possible
	Difference of sum of area of all t_2 and all t_1 polygons that are intersecting	Relatively easy to calculate	Still some pseudochanges possible, large polygons have a rather high influence, no statistics possible

	Calculate change within each polygon separately	Only small possibility of pseudochanges in case of incomplete remapping, statistics possible	Bias towards no change as polygons might not have been remapped if they lost their protection status or only lately gained their protection status
Select plant species	All species	More complete picture of trends of plant groups	Trends of uncharacteristic species less reliable
	Species that were mentioned in mapping keys (mostly characteristic or endangered species)	More reliable trends as those species have been more consistently recorded	Ignores trends of common species and neophytes, higher bias towards endangered species
Compare species lists to calculate species change	$t_1 \rightarrow t_2$, i.e. the species list of a t_1 polygon is compared with the joined species list from all intersecting t_2 polygons		Underestimates species declines, as there are by chance more species in the joined species list of t_2 than in the single species list of t_1
	$t_2 \rightarrow t_1$, i.e. the species list of a t2 polygon is compared with the joined species list from all intersecting t_1 polygons		Overestimates species declines, as there are by chance more species in the joined species list of t_1 than in the single species list of t_2
	$t_1 \rightarrow t_2 + t_2 \rightarrow t_1$, i.e. combine the results of the two approaches above	Bias minimized (balanced trends)	Duplicated use of changes that are captured in both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ gives those cases more weight, which are often completely overlapping polygons and cases of zero change
	Compare species lists of only the two polygons of each intersection	Relatively easy to calculate	In cases where one polygon intersects with many other polygons, many changes for the same polygon are reported, not possible to accurately calculate changes in occupied area
Species change metric	Frequency	Easy to calculate	Same weighting of different sized polygons, does not account for incomplete species lists
	Occupied area	Accounts for different polygon sizes	Species usually not present in whole polygon area (too much weight to large polygons), does not account for incomplete species lists
	Probability of occurrence (Beals' index)	Accounts for incomplete species lists, captures future trends	Does not work well for very rare species, bit computing-intensive for large data sets

Data cleaning of intersections

All data were digitized as polygons, including linear, but not point-like habitat types, as the latter were only represented by springs, which were excluded in general as they are not defined by their vegetation. Many of those linear polygons, however, dropped out of analyses because of poor overlay with polygons from other years. Overlaying the polygons from both time intervals resulted in numerous small intersections. Intersections covering less than 5% of either of the two intersecting polygons' areas were excluded from further analysis. Polygons intersecting less than 75% with polygons from the other time interval were excluded as well. This was done to ensure that all sites used were mapped in both intervals. At the time of analysis, the open land was not yet completely remapped, with some districts missing (Figure S1). Based on mapping periods of open land and peaks in mapping years of the different projects (Figure S2), data was divided into two time intervals: t_1 (1989-2005) and t_2 (2006-2021). Some sites were mapped more than once in each time period (polygon overlap of at least 10%). To exclude those duplicates per time period, those polygons were selected, in the following order, which were 1) still mapped as protected (might be not remapped by open land because now mapped by wooded land project), 2) mapped

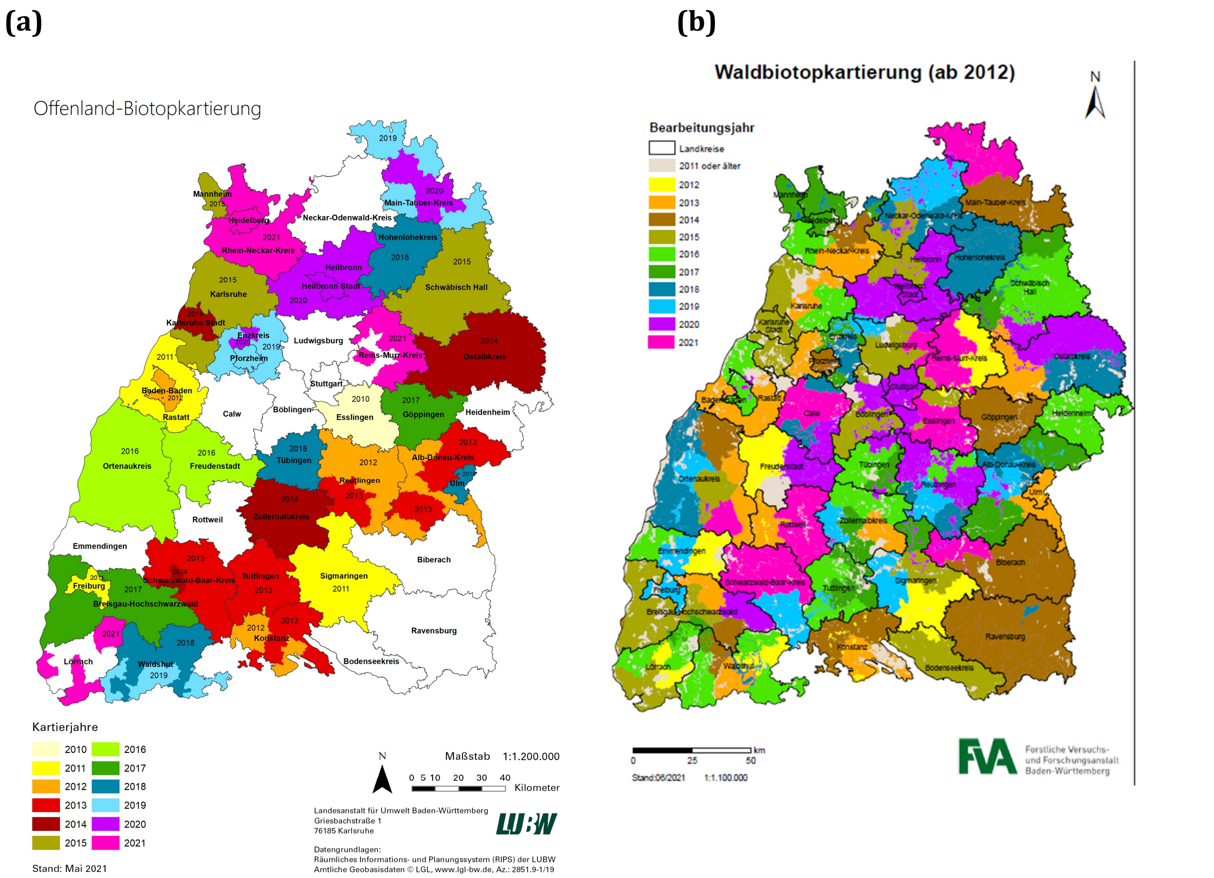

Figure S1 Status of remapping at the time of analysis of **(a)** open land ("Offenland-Biotopkartierung") and **(b)** wooded land ("Wald-Biotopkartierung"). Colors indicate the year of remapping for each district, white districts have not been remapped by the end of 2021, i.e. when analyses started. Wooded land **(b)** has been completely remapped by the time of analysis. Map **(a)** originating from LUBW (Landesanstalt für Umwelt Baden-Württemberg), an updated version can be found at https://www.lubw.baden-wuerttemberg.de/natur-und-landschaft/offenland-biotopkartierung. Map **(b)** originating from FVA (Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg), an updated version can be found at https://www.fva-bw.de/daten-tools/geodaten/wbk-waldbiotopkartierung/aktuelles.

within the same mapping project (open land, wooded land, hay meadows), 3) resulted in the largest time span between resurveys or 4) in the case of mappings during the same year, resulted in the largest overlay between resurveys.

Habitat types

Habitat types of level 4 were converted to the broader corresponding level-3 habitat types and for most analyses further grouped into 10 broad habitat types ("Heaths and semi-natural grasslands", "Meadows and pastures", "Ruderal, fringe and tall forb communities, clearings", "Scrubs, copses and field hedges", "Fresh water vegetation, springs and reeds", "Bogs, transition mires, marshes and fens", "Bog, carr, swamp and alluvial forests", "Deciduous forests", "Coniferous forests", "Not remapped"). These simplifications were done to be able to keep polygons which were not mapped with the detail of level 4 but also to reduce bias arising from the circumstance that mapping was carried out in different projects, different time periods and by different people, which can lead to pseudo-differences in habitat types between mapping events. Polygons which were not mapped

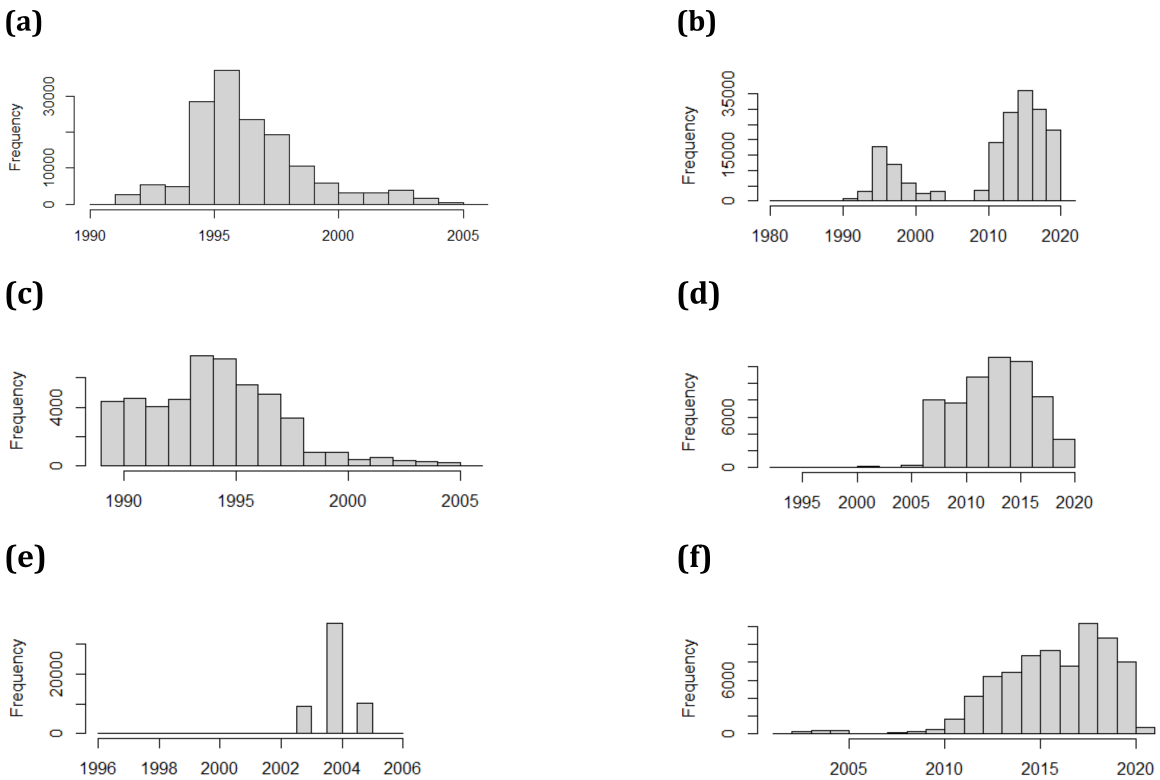

Figure S2. Number of polygons (habitats) mapped per year for **(a)** open land as of 2006, **(b)** open land as of 2021, **(c)** wooded land as of 2006, **(d)** wooded land as of 2021, **(e)** Natura 2000 meadows and pastures as of 2006, and **(f)** Natura 2000 meadows and pastures as of 2021. The data as of 2021 still includes polygons that were mapped before 2006 in case they have not yet been remapped.

with a minimum of detail of level 3 were excluded for habitat type analysis. Polygons of the level-3 type “Mixed pioneer forest” were converted to the level-2 type “Deciduous forest”, as the mapped forests of this category were mainly deciduous tree species-dominated.

In cases where a polygon had multiple habitat types assigned, the sum of cover of all those habitat types could generally exceed 100%. This is because habitat types could overlap when they were based on different criteria such as vegetation type and morphological structures, e.g., fresh water vegetation in a lake. For our analysis of the Baden-Württemberg data, only habitat types which were based on vegetation types were used. Polygons in which the sum of the cover of all habitat types still exceeded 100% were excluded. Habitat types that were only mapped in t_1 or only in t_2 were excluded, too.

In total, 18% of polygon area was not assigned to the same habitat type anymore, with 10% having not been remapped because the sites were not classified as protected anymore and with only 8% of polygon area that underwent a known transition between habitat types. Out of the polygons that have not been remapped, 68% were previously mapped as meadows and pastures and 20% as scrubs, copses and field hedges.

Change in mean habitat type area

To calculate the change in area of each habitat type of a given polygon, we checked how much of the area of this type was also present in the overlapping polygons from the other time interval. Theoretically, for two overlapping polygons of habitat type complexes it would be possible that the area of a certain habitat type is not located inside the intersection area. However, as no information about the location of each habitat type inside a polygon with a habitat type complex was available, we made the general assumption that the intersection always contained the same proportions of habitat types as the intersecting polygons.

Across all habitat types, 54% of all mapped polygons from t_1 were used for the mean trend analysis (120,949 out of 222,285), representing 68 % of the total polygon area from t_1. The remaining polygons of t_1 did not have a match with those in t_2 mostly because they were either not yet remapped, mapping was discontinued due to total habitat loss, because of poor overlay of linear polygons, or because the area still protected has shrunken to less than 75% of its original area and was therefore deleted in the cleaning step described above. Best represented were deciduous forests (69% of polygons and 80% of polygon area) and meadows and pastures (71% of polygons and 78% of polygon area) and worst represented were scrubs, copses and field hedges (41% of polygons and 48% of polygon area) and fresh water vegetation, springs and reeds (43% of polygons and 55% of polygon area). For the visualization of changes between habitat types, only 47% out of all t_1 polygons could be used, with a corresponding area of 41% of the total polygon area of t_1.

Transitions between habitat types

For the visualization of transitions between habitat types, each polygon had to have a habitat type assigned that covered at least 50% of the polygons area. Thus, we excluded habitat type complexes with none of their habitat types covering at least 50%. Intersection areas were weighted by the minimum of the habitat type area of the two intersecting polygons. Intersections were used for visualization if at least one of the polygons intersected by at least 75% with polygons of the other time interval (present in $t_1 \rightarrow t_2$ or $t_2 \rightarrow t_1$).

Plant species

Species records at the genus level were excluded (which especially concerned *Rosa* spec., *Rubus* spec.), except for the genus *Crataegus*, for which all species were merged at the genus level. Some other species taxonomies were manually changed to the aggregation level, based on known difficulties to differentiate them in the field. Appendix S1: List S1 provides information on all additional changes and exclusions of species.

The time intervals differed from those in the habitat type analysis and were shorter for the species analysis, as species mapping was inconsistent for wooded land for a specific time period (between

List S1 Information on all additional **(a)** exclusions of species and **(b)** changes of species taxonomies.

(a) Additional exclusion of species

- Species that are known to have been falsely identified:
    - *Thymus vulgaris*
    - *Galium verrucosum*
    - *Equisetum pratense*
    - *Glycine max*
    - *Luzula luzulina*
    - *Cirsium erucagineum*
    - *Prunus cerasus* agg.
    - *Salix meyeriana*
- Species which taxonomy did not match the reference list in case they had less than 11 occurrences across the whole state

(b) Additional changes of species taxonomies to the aggregation level, based on known difficulties to differentiate them in the field

- Crataegus
    - *Crataegus crus-galli*
    - *Crataegus laevigata* s. l.
    - *Crataegus macrocarpa* s. l.
    - *Crataegus media*
    - *Crataegus monogyna*
    - *Crataegus rhipidophylla* s. l.
    - *Crataegus subsphaerica*
- Rosa canina agg.
    - *Rosa canina* s. l.
    - *Rosa corymbifera* s. l.
- Rosa rubiginosa agg.
    - *Rosa elliptica*
    - *Rosa micrantha*

2001 and 2012) and for open land for years not included in the main official mapping campaigns. Therefore, in the case of wooded land, t_1 was reduced to 1989-2000 and t_2 to 2013-2020 and for open land t_1 was reduced to 1992-2004 and t_2 to 2010-2021 (= official mapping campaigns of open land). In some cases, species records were added to species lists a year after the field survey, which were kept in the analyses. We tested for seasonal differences in mapping periods between the former and recent mapping campaigns. While for the open land mapping we did not find major shifts in the mapping seasons, wooded land mappings shifted towards later months in the second time period (Figure S3 & S4).

Red list status of endangered species in Baden-Württemberg was retrieved from Breunig & Demuth (1999). For species aggregates without a clear red list status, we assigned the status from the name-giving taxon, e.g., from *Dactylorhiza incarnata* for *Dactylorhiza incarnata* agg. For exceptions see Appendix S1: List S2. We also tested if the (non-)native status of species in Germany had an influence on the mean trends of species. Data on native status was retrieved from Biolflor (Klotz et al., 2002). For species without a clear native status, we used additional information from Floraweb, especially for status of aggregates (www.floraweb.de; Buttler et al., 2018, Wisskirchen & Haeupler, 1998).

Species aggregates were assigned as key species if at least one of the species inside the aggregate was mentioned in the mapping keys.

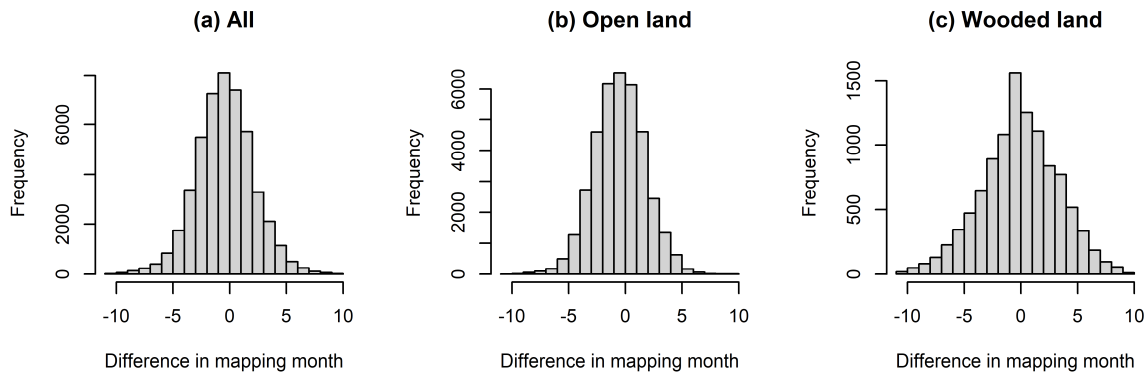

Figure S3 Differences in mapping months of remapped polygons for: **(a)** all polygons, **(b)** open land, and **(c)** wooded land. Difference in mapping month was calculated by subtracting the month of the t_1 mapping from the month of the t_2 mapping, i.e. positive values indicate a later mapping month in t_2 compared to t_1 and vice versa. Only includes polygons that were used for species analysis ($t_1 \rightarrow t_2$).

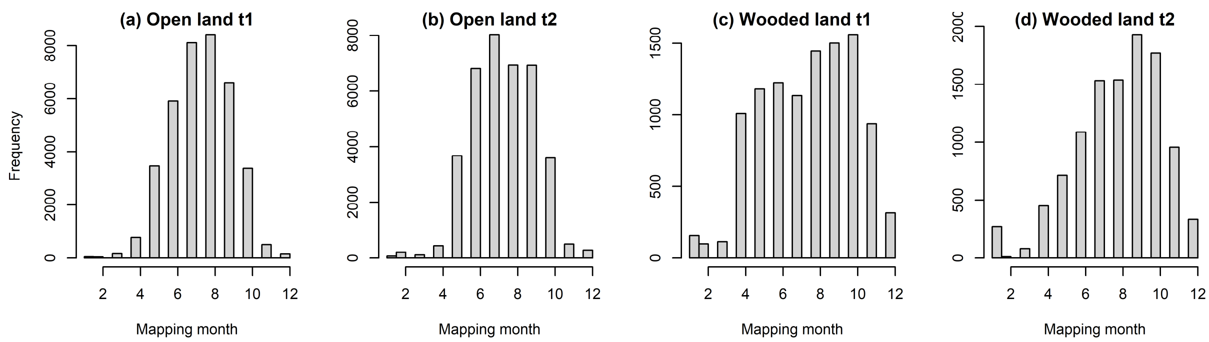

Figure S4 Mapping months of polygons for: **(a)** open land in t_1, **(b)** open land in t_2, **(c)** wooded land in t_1, and **(d)** wooded land in t_2. Months from January to December are represented by numbers from 1 to 12. Only includes polygons that were used for species analysis ($t_1 \rightarrow t_2$).

List S2 Red list status assignment for species aggregates where assigning status according to the name-giving taxon (e.g., from *Dactylorhiza incarnata* for *Dactylorhiza incarnata* agg.) was not possible.

Species (aggregate)	**Red list status (assigned)**
Arabis alpina agg.	Highly Threatened (= Category 2)
Centaurea paniculata agg.	Not Threatened (= Category *)
Centaurea phrygia agg.	Not Evaluated
Elymus repens s. str.	Not Threatened (= Category *)
Malva sylvestris	Not Threatened (= Category *)
Microthlaspi perfoliatum	Not Threatened (= Category *)
Oenothera-biennis-Gruppe	Not Threatened (= Category *)
Rosa rubiginosa agg.	Not Threatened (= Category *)
Rosa tomentella agg.	Near Threatened (= Category V)
Rubus sect. *Corylifolii*	Not Threatened (= Category *)
Rubus sect. *Rubus*	Not Threatened (= Category *)
Vaccinium uliginosum s. l.	Near Threatened (= Category V)

Additional change metric: Species change in occupied area

As a third metric of species change we calculated species change in occupied area by using the polygons area where a species was present instead of simply species occurrences. We assumed that a species can occupy the whole area of a polygon it was recorded in. We used all intersections where a species was present in either or both t_1 and t_2. We compared the area of the target polygon (if species was present, otherwise set to zero) with the sum of the intersecting areas of all overlapping polygons where a species was present. The target polygon was weighted by how much was covered by polygons of the other time interval. Per species and polygon, we calculated the $\log_{10}$ ratio of area occupied by the species from both time intervals (Equation 1) as

$$log_{10} \frac{area_{t2}+1}{area_{t1}+1} \tag{1}$$

with area in square meters and adding 1 m^2 to allow for calculating the log ratio in cases of species absences. Similar to the frequency change, we calculated these changes for the approaches $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ and used all changes per species to derive mean changes. Species trends were tested for departure from zero with Wilcoxon signed rank tests. We applied Holm adjustment of significance levels for testing of multiple species.

450 species showed significant trends in their occupied area over time, with 249 species increasing and 201 species decreasing. Trends in species occupied area were very similar to trends in species frequency among the 461 species that showed significant trends for at least one of the metrics (spearman rank correlation $r_s = 0.997$, $p < 0.001$). All significant trends in species occupied area are included in Appendix S2: Table S4.

APPENDIX S2

Due to the length of tables S4 and S5 they can only be found online in the Supporting Information section at: https://doi.org/10.1111/avsc.12799.

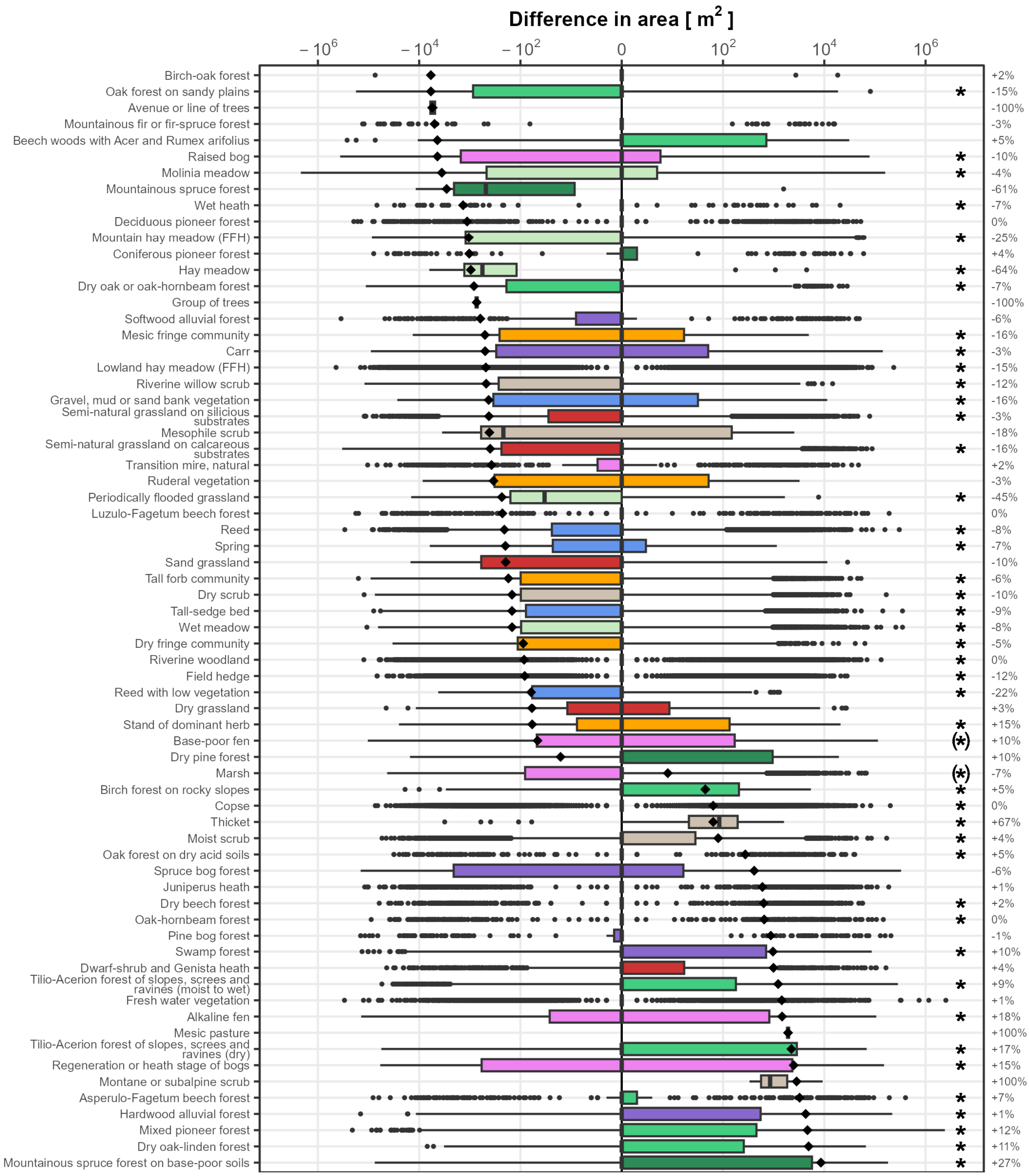

Figure S1 Difference in polygon area in m² between t_1 (1989-2005) and t_2 (2006-2021) for all protected level-3 habitat types. The x-axis is on a $\log_{10}$ scale. Note that most medians are at 0. Mean differences per habitat type are indicated by a diamond symbol. Significant differences according to Wilcoxon signed rank tests are labelled with an asterisk. Brackets around asterisks indicate that excluding outliers (observations that fall outside the range between the 1st and 99th percentile per level-3 habitat type) led to a reversal in the direction of the mean trend. Percentages on the right site of the plot indicate the mean proportional change in area between t_1 and t_2 of each habitat type.

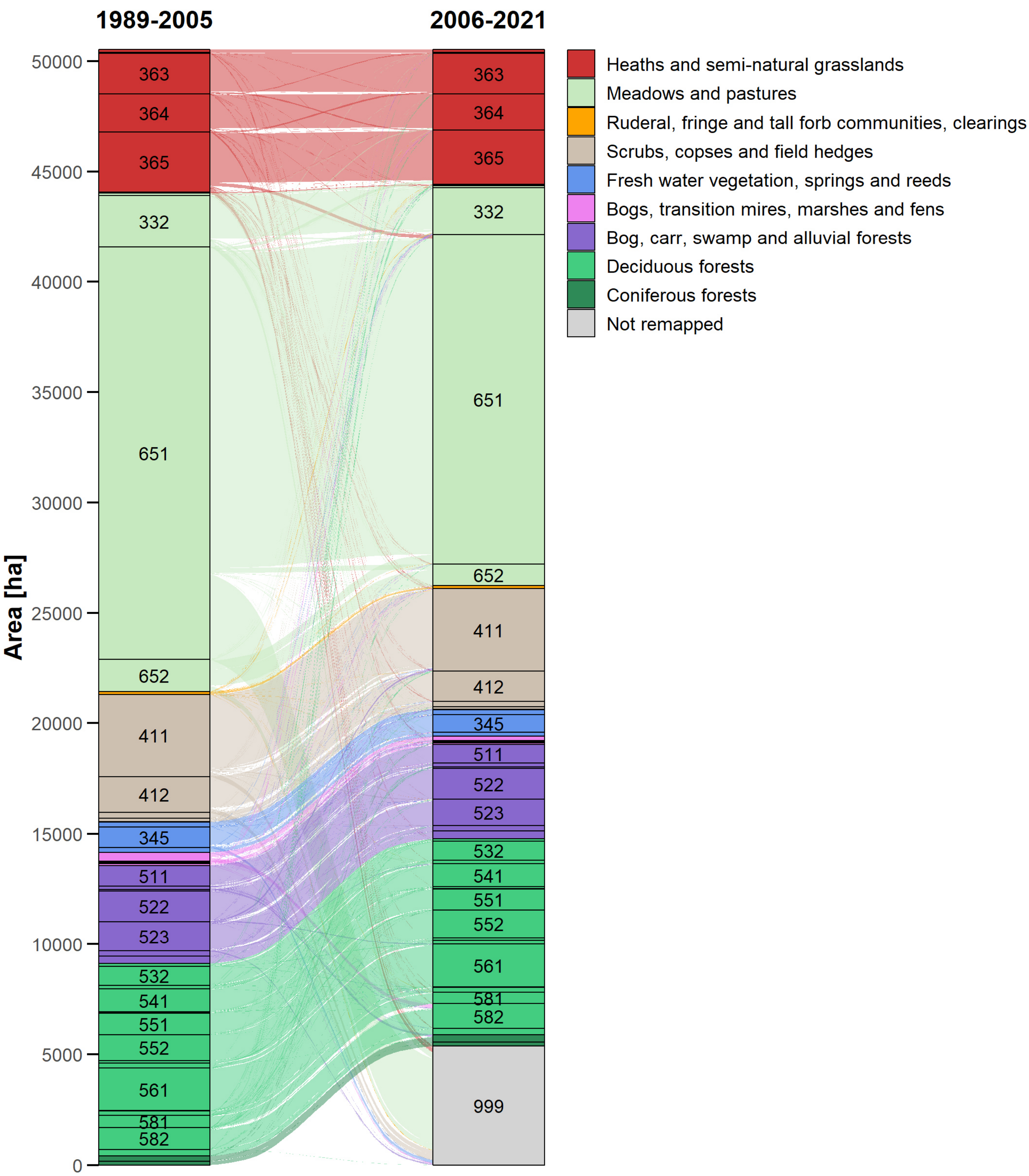

Figure S2 Transitions between level-3 habitat types from t_1 (1989-2005) to t_2 (2006-2021). Habitat type abbreviations according to the Baden-Württemberg identification key. Only habitat types with a total area of >500 ha are labeled. Colors refer to the groups of habitat types. The level-3 habitat type "999" refers to polygons which have not been remapped because they were not classified as protected habitat types at t_2.

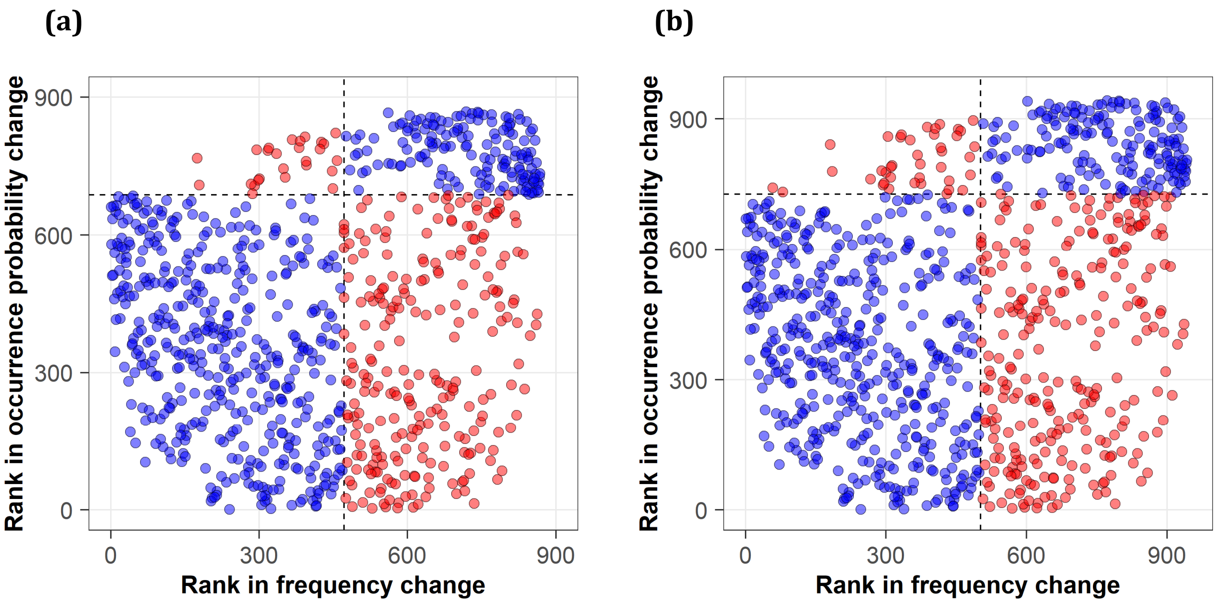

Figure S3. Comparison of species ranks regarding their changes in frequency and probability of occurrence (Beals' index), including **(a)** only species which show a significant trend for either trend metric and **(b)** all species. Species at rank 0 represent species with the most negative trend and species at the maximum rank (rank 868 for **(a)** and rank 942 for **(b)**) represent the species with the most positive trend. Dashed lines represent the rank of each metric that represents zero change. Blue dots represent species that show the same trend direction for the two metrics and red dots represent species that show opposing trend for the two metrics. All red colored species were removed from further analysis, in addition to species that did not show a significant trend across both trend metrics.

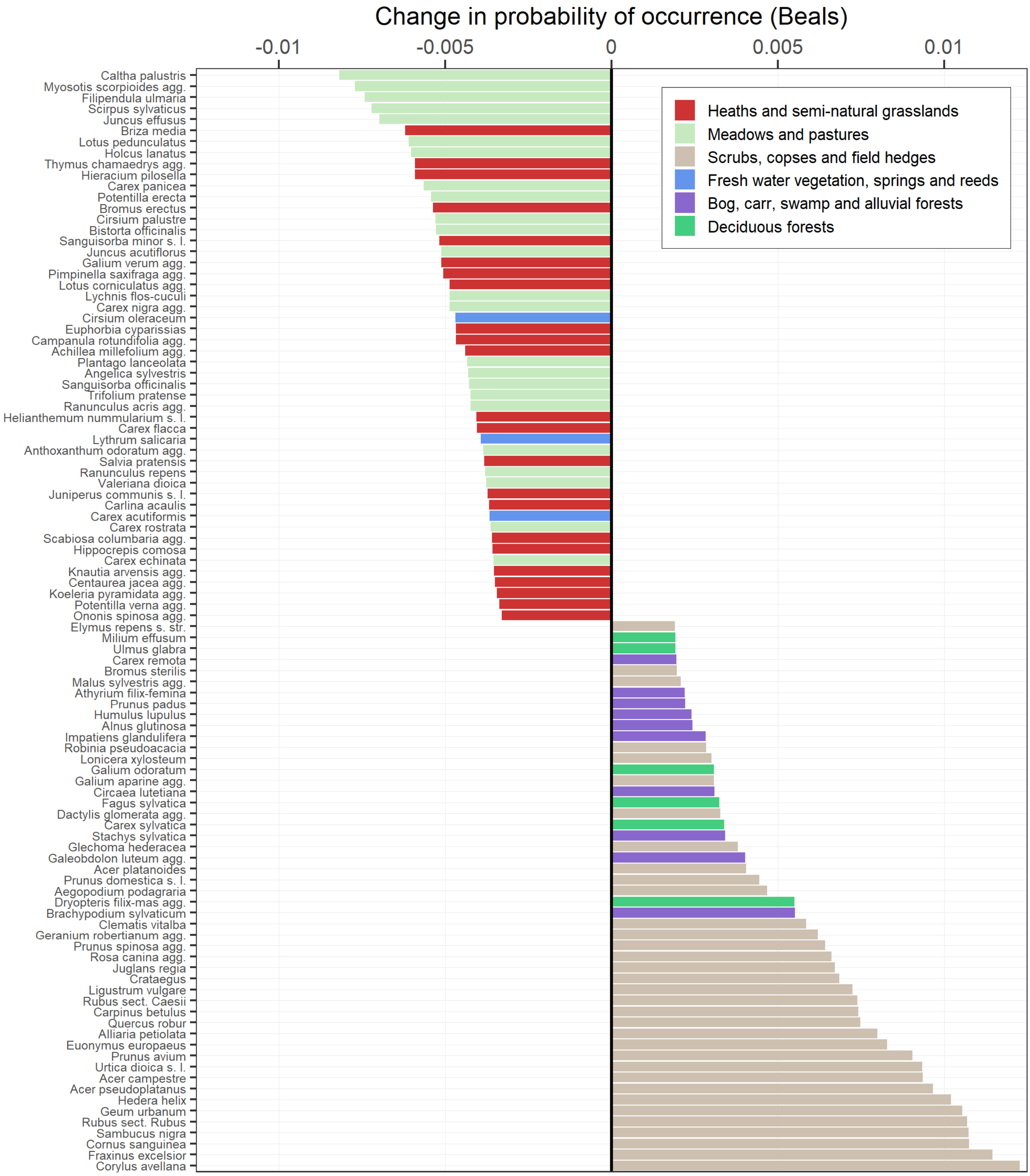

Figure S4. Change in probability of occurrence (Beals' index) from time interval t_1 (1989-2005) to time interval t_2 (2006-2021) for species that showed a significant trend for this metric. Out of those 845 species only the 50 top losers and 50 top winners are shown. Colors refer to the preferred habitat type of each species, based on the fidelity (Φ) of species to habitat types.

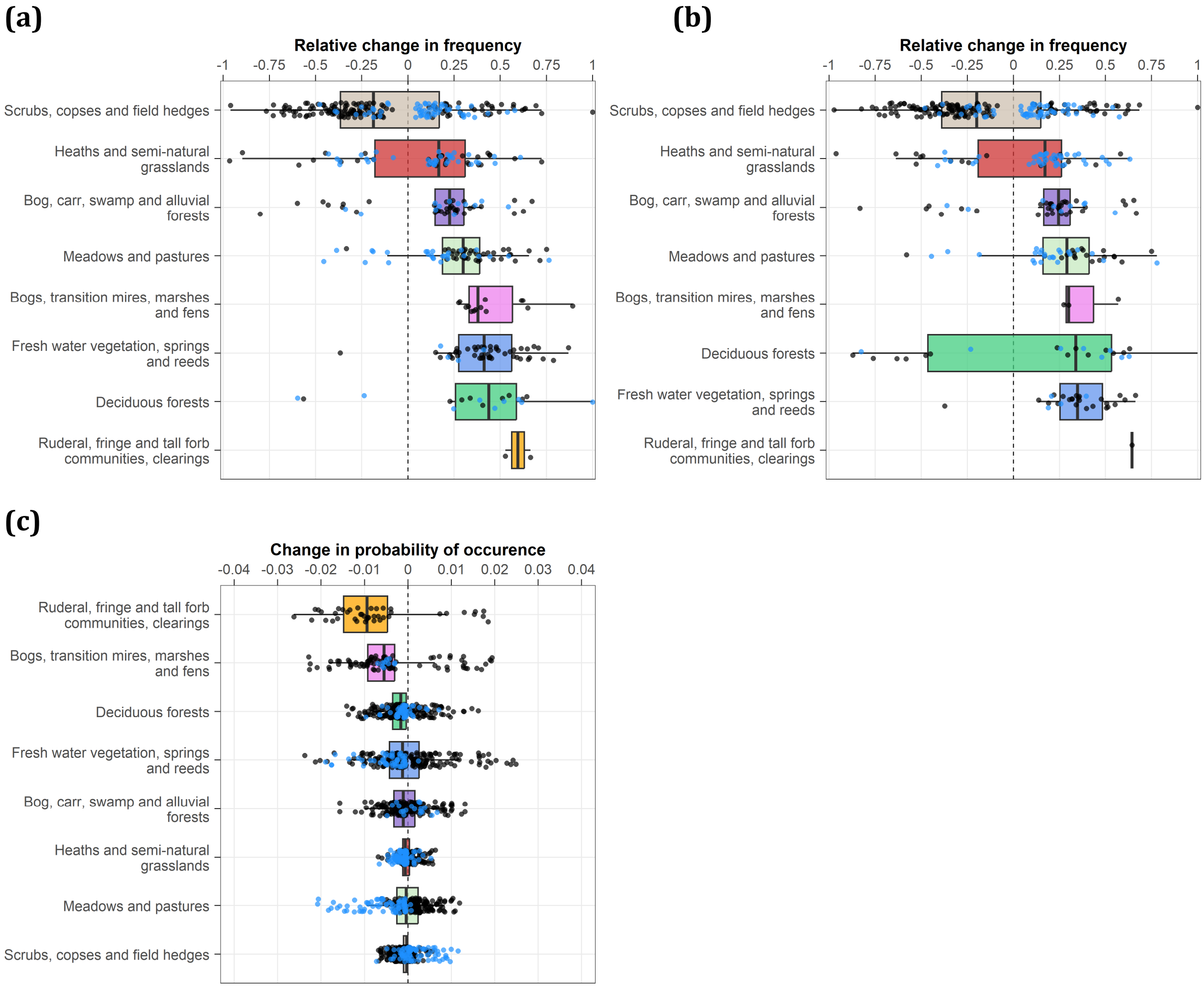

Figure S5 Trends of species within different habitat types. **(a)** Relative change in frequency including polygons that transitioned in their habitat type over time, **(b)** Relative change in frequency excluding polygons that transitioned in their habitat type over time, **(c)** Mean changes in species' probabilities of occurrence (Beals' index) excluding polygons that transitioned in their habitat type over time. For all plots, only significant trends are shown. Blue dots represent species that prefer the respective habitat type in which they show a trend, black dots represent all species that prefer another type or which fidelity lies below the median of all species (Φ = 0.006). Blue dots are plotted on top of black dots for visibility.

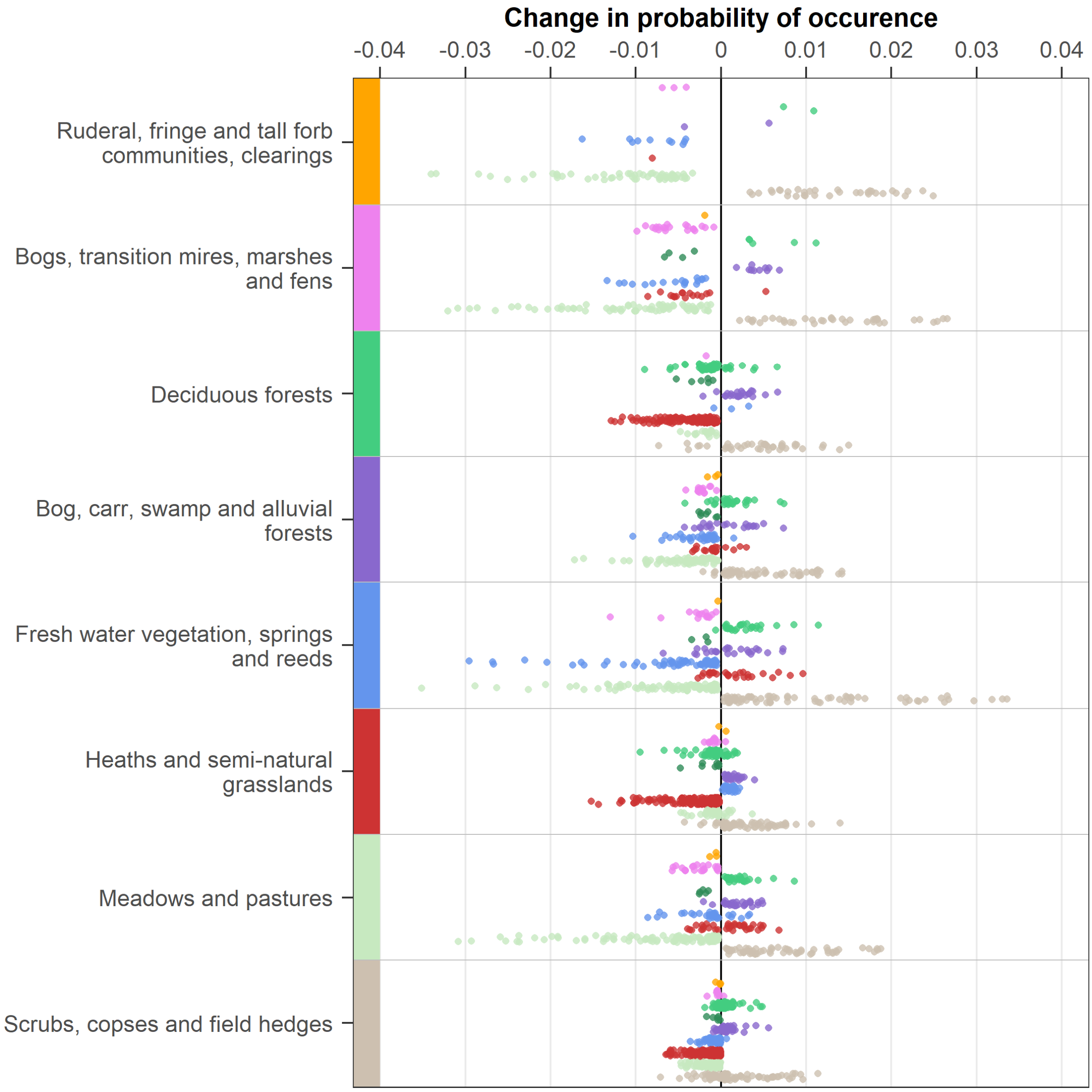

Figure S6 Mean changes in probability of occurrence (Beals' index) of species with different habitat type preferences within different habitat types. Only significant trends are shown. Only species with a fidelity (Φ) value above or at the median of all species (Φ = 0.006). Polygons that transitioned in their habitat type over time are included. Color of dots refer to the preferred habitat type of each species, according to the color code of the habitat types on the left side of the plot. There were no significant species trends within coniferous forests, however species that prefer coniferous forests are represented as dark green dots.

Table S1 Mean changes in polygon area in m² between t_1 (1989-2005) and t_2 (2006-2021) for all protected level-3 habitat types. *n* represents the number of comparisons per habitat type. *p* values are based on Wilcoxon signed rank tests for deviation of changes from zero.

Habitat type	n	Mean change in area	p value	Habitat type English	Habitat type German
562	9	-5879	1	Birch-oak forest	Birken-Stieleichen-Wald mit Pfeifengras
555	75	-5865	0.047	Oak forest on sandy plains	Traubeneichen-Buchen-Wald
451	2	-5535	0.5	Avenue or line of trees	Allee oder Baumreihe
573	119	-4976	0.132	Mountainous fir or fir-spruce forest	Tannen- oder Fichten-Tannen-Wald
554	88	-4371	0.104	Beech woods with Acer and Rumex arifolius	Hochstaudenreicher Ahorn-Buchen-Wald

311	183	-4359	0.01	Raised bog	Hochmoor
331	657	-3571	0.021	Molinia meadow	Pfeifengras-Streuwiese
544	4	-2867	0.625	Mountainous spruce forest	Fichten-Blockwald
361	127	-1358	0.014	Wet heath	Feuchtheide
581	912	-1129	0.325	Deciduous pioneer forest	Sukzessionswald aus Laubbäumen
652	3481	-1048	<.001	Mountain hay meadow (FFH)	Berg-Mähwiese
584	134	-1026	0.858	Coniferous pioneer forest	Sukzessionswald aus Nadelbäumen
334	22	-955	0.008	Hay meadow	Wirtschaftswiese mittlerer Standorte
531	589	-828	<.001	Dry oak or oak-hornbeam forest	Eichen- oder Hainbuchen-Eichen-Wald trockenwarmer Standorte
452	1	-732	1	Group of trees	Baumgruppe
524	347	-619	0.753	Softwood alluvial forest	Silberweiden-Auwald (Weichholz-Auwald)
351	125	-501	0.022	Mesic fringe community	Saumvegetation mittlerer Standorte
521	483	-497	0.021	Carr	Bruchwald
651	55341	-481	<.001	Lowland hay meadow (FFH)	Magere Flachland-Mähwiese
424	630	-474	<.001	Riverine willow scrub	Uferweiden-Gebüsch (Auen-Gebüsch)
342	113	-424	0.04	Gravel, mud or sand bank vegetation	Vegetation einer Kies-,Sand- oder Schlammbank
364	3718	-419	<.001	Semi-natural grassland on silicious substrates	Magerrasen bodensaurer Standorte
422	12	-410	0.197	Mesophile scrub	Gebüsch mittlerer Standorte
365	10425	-395	<.001	Semi-natural grassland on calcareous substrates	Magerrasen basenreicher Standorte
312	731	-371	0.461	Transition mire, natural	Natürliches Übergangs- oder Zwischenmoor
356	49	-340	0.318	Ruderal vegetation	Ruderalvegetation
333	90	-232	<.001	Periodically flooded grassland	Flutrasen
551	508	-227	0.724	Luzulo-Fagetum beech forest	Buchen-Wald basenarmer Standorte
345	12186	-207	<.001	Reed	Röhricht
343	201	-197	0.004	Spring	Quellflur
366	102	-195	0.068	Sand grassland	Sandrasen
354	6329	-172	<.001	Tall forb community	Hochstaudenflur
421	4480	-146	<.001	Dry scrub	Gebüsch trockenwarmer Standorte
346	8577	-146	<.001	Tall-sedge bed	Großseggen-Ried
332	10554	-145	<.001	Wet meadow	Nasswiese
352	1376	-87	<.001	Dry fringe community	Saumvegetation trockenwarmer Standorte
523	8154	-84	0.004	Riverine woodland	Auwald der Bäche und kleinen Flüsse
412	31609	-81	<.001	Field hedge	Feldhecke
344	487	-61	<.001	Reed with low vegetation	Kleinröhricht
367	1050	-58	0.052	Dry grassland	Trockenrasen
353	588	-58	0.005	Stand of dominant herb	Dominanzbestand
321	2128	-45	0.013	Base-poor fen	Kleinseggen-Ried basenarmer Standorte
534	34	-15	0.704	Dry pine forest	Kiefern-Wald trockenwarmer Standorte
323	5492	7	<.001	Marsh	Waldfreier Sumpf
543	96	44	0.008	Birch forest on rocky slopes	Birken-Blockwald
411	28291	63	0.003	Copse	Feldgehölz
431	48	63	<.001	Thicket	Gestrüpp
423	6415	79	<.001	Moist scrub	Gebüsch feuchter Standorte
563	557	275	0.025	Oak forest on dry acid soils	Hainsimsen-Traubeneichen-Wald
512	240	412	0.143	Spruce bog forest	Rauschbeeren-Fichten-Moorrandwald
363	1360	599	0.06	Juniperus heath	Wacholderheide
532	1314	635	<.001	Dry beech forest	Buchen-Wald trockenwarmer Standorte
561	959	649	0.015	Oak-hornbeam forest	Hainbuchen-Wald mittlerer Standorte
511	255	878	0.825	Pine bog forest	Rauschbeeren-Kiefern-Moorwald
522	1659	968	<.001	Swamp forest	Sumpfwald (Feuchtwald)
362	856	991	0.138	Dwarf-shrub and Genista heath	Zwergstrauch- und Ginsterheide
541	2158	1227	<.001	Tilio-Acerion forest of slopes, screes and ravines (moist to wet)	Schlucht- Blockhalden- oder Hangschuttwald frischer bis feuchter Standorte
341	3763	1445	0.373	Fresh water vegetation	Tauch- oder Schwimmblattvegetation
322	418	1468	<.001	Alkaline fen	Kleinseggen-Ried basenreicher Standorte
335	1	1923	1	Mesic pasture	Weide mittlerer Standorte
542	377	2240	<.001	Tilio-Acerion forest of slopes, screes and ravines (dry)	Schlucht- oder Blockwald trockenwarmer Standorte

313	184	2491	0.042	Regeneration or heath stage of bogs	Regenerations- und Heidestadien von Hoch-, Zwischen- oder Übergangsmoor
425	4	2838	0.125	Montane or subalpine scrub	Gebüsch hochmontaner bis subalpiner Lagen
552	596	3251	<.001	Asperulo-Fagetum beech forest	Buchen-Wald basenreicher Standorte
525	147	4290	0.009	Hardwood alluvial forest	Stieleichen-Ulmen-Auwald (Hartholz-Auwald)
582	811	4657	<.001	Mixed pioneer forest	Sukzessionswald aus Laub- und Nadelbäumen
533	87	4902	<.001	Dry oak-linden forest	Seggen-Eichen-Linden-Wald
572	273	8582	<.001	Mountainous spruce forest on base-poor soils	Geißelmoos-Fichten-Wald

Table S2 Area changes in m² of all level-2 habitat types between t_1 (1989-2005) and t_2 (2006-2021). Shown per habitat type are the number of comparisons (*n*), the mean change in area, the significance of change according to a Wilcoxon signed rank test (*p* value), the sum of all polygon areas for each time interval (t_1 and t_2) while using only those polygons that were used for the mean change analysis (i.e. that were used in both $t_1 \rightarrow t_2$ and in $t_2 \rightarrow t_1$ and therefore have been mapped in both time periods), the difference of these two summed areas (i.e. change between the two time intervals).

Habitat type	n	Mean change in area	p value	Sum area t_1	Sum area t_2	Sum change in area
Meadows and pastures	69768	-491.70	<.001	191996149	152567944	-39428206
Heaths and semi-natural grasslands	15849	-337.59	<.001	67172409	62215221	-4957188
Ruderal, fringe and tall forb communities, clearings	8205	-161.48	<.001	6162340	4641658	-1520682
Scrubs, copses and field hedges	62502	-21.03	<.001	54380813	51378442	-3002371
Bogs, transition mires, marshes and fens	7938	-9.54	0.001	12551663	12152887	-398775
Fresh water vegetation, springs and reeds	17616	77.44	<.001	35853589	36696767	843178
Bog, carr, swamp and alluvial forests	10772	90.79	0.084	48495852	48076775	-419077
Deciduous forests	8052	912.53	<.001	86289488	87517288	1227800
Coniferous forests	555	2772.95	<.001	8196904	9700387	1503483

Table S3 Mean proportional changes per year for all habitat types that showed significant changes over time. Difference from zero was tested using *t* tests, with the results reported as standard errors, *t* values and *p* values. t_{50} indicates the half-life time, i.e. the time in years until half of a polygons' area will be lost (for negative mean proportional changes per year) or a polygons' area will we doubled (for positive mean proportional changes per year), under the assumption of an exponential decline/increase. Note that for the group of "Fresh water vegetation, springs and reeds" outliers led to different directions of trends concerning the mean proportional area, thus making the calcualtions here unreliable.

Habitat type	Mean proportional change per year	Standard Error	t value	p value	t50
Meadows and pastures	-0.0119	0.0001	-102.95	<.001	59
Heaths and semi-natural grasslands	-0.0062	0.0002	-27.73	<.001	112
Fresh water vegetation, springs and reeds	-0.0050	0.0002	-24.56	<.001	140
Scrubs, copses and field hedges	-0.0033	0.0001	-38.53	<.001	211
Ruderal, fringe and tall forb communities, clearings	-0.0028	0.0004	-7.16	<.001	246
Bogs, transition mires, marshes and fens	-0.0014	0.0004	-3.57	<.001	485
Deciduous forests	0.0023	0.0002	11.50	<.001	308
Coniferous forests	0.0067	0.0012	5.80	<.001	104

Table S4 Trends of all species that showed a significant trend for at least one of the three trend metrics (874). In addition to the trends and their significances for frequency change and change in probability of occurrence (Beals' index), also changes in occupied area (log_{10} area) are given as a third change metric (for more information see Appendix S1). Significances according to two-sided binomial tests (frequency change), Wilcoxon signed rank tests (occupied area), and *t* tests (Beals' index). *n* refers to the corrected number of comparisons used for analysis. Further the information is given if a species was mentioned in the mapping keys of the habitat mapping programs of Baden-Württemberg (Keyspecies).

This table can be found in the Supporting Information section at: https://doi.org/10.1111/avsc.12799.

Table S5 Trends of species that showed a significant trend for the two main trend metrics (272). Trends and their significances for frequency change and change in probability of occurrence (Beals' index). Significances according to two-sided binomial tests (frequency change) and *t* tests (Beals' index). *n* refers to the corrected number of comparisons used for analysis. Each species' preferred habitat type is given, as derived from the maximum Φ value of each species x habitat type combination. Only given for species with a Φ value equal or higher than the median Φ value of all species (0.006). Further the information is provided if a species was mentioned in the mapping keys of the habitat mapping programs of Baden-Württemberg (KS), is endangered in Baden-Württemberg (RL, according to Breunig & Demuth (1999)), and non-native in Germany (NN, according to Klotz et al., 2002). Red list categories: Highly Threatened (= Category 2), Threatened (= Category 3), Near Threatened (= Category V), Not Threatened (= Category *), Not Evaluated (= Categories D and ^). Non-native categories: I = Native (Indigen), A = Archaeophyte, N = Neophyte, NA = No information available. Expert information (EI) on species which trends might be unreliable for reasons given by the digits: 1: Species often falsely assigned; 2: Species typical of arable land (this habitat type was not mapped); 3: Species typical of other unprotected habitat types (again habitat types that have not been mapped). In addition, declared as digit 4: Cases in which species trends go against expert expectations or their personal observations.

This table can be found in the Supporting Information section at: https://doi.org/10.1111/avsc.12799.

APPENDIX S3

This Appendix presents the results of the analyses that were restricted to species that were mentioned in the mapping keys of the mapping programs of Baden-Württemberg (LUBW, 2014, FVA, 2017). In the following we will use the term "key species" for these species.

Frequency analysis showed significant trends for 269 key species, with 149 species increasing and 120 species decreasing. The analysis based on changing co-occurrence probability according to Beals showed significant trends for 604 species, with 119 species increasing and 485 species deceasing. Across the 623 species that showed significant trends for at least one of the metrics, Spearman rank correlations showed rather low correlations (r_s = 0.246, p < 0.001). In total, 188 species displayed significant and consistent trends for both metrics (that is either significant positive or negative trends), with 80 species showing positive trends and 108 species showing negative trends (Figure S1). The correlation coefficients of these species trends between the two metrics were higher compared to the coefficients across all species (r_s = 0.578, p < 0.001).

In the following, only the trends for frequency that showed also significant trends for Beals will be discussed in detail. Losers were represented especially by species of heaths and semi-natural grasslands (mean change = −0.24, t = −11.1, p < 0.001) and of species of meadows and pastures (mean change = −0.16, t = −9.97, p < 0.001). Winners were mostly species of bog-, carr-, swamp-

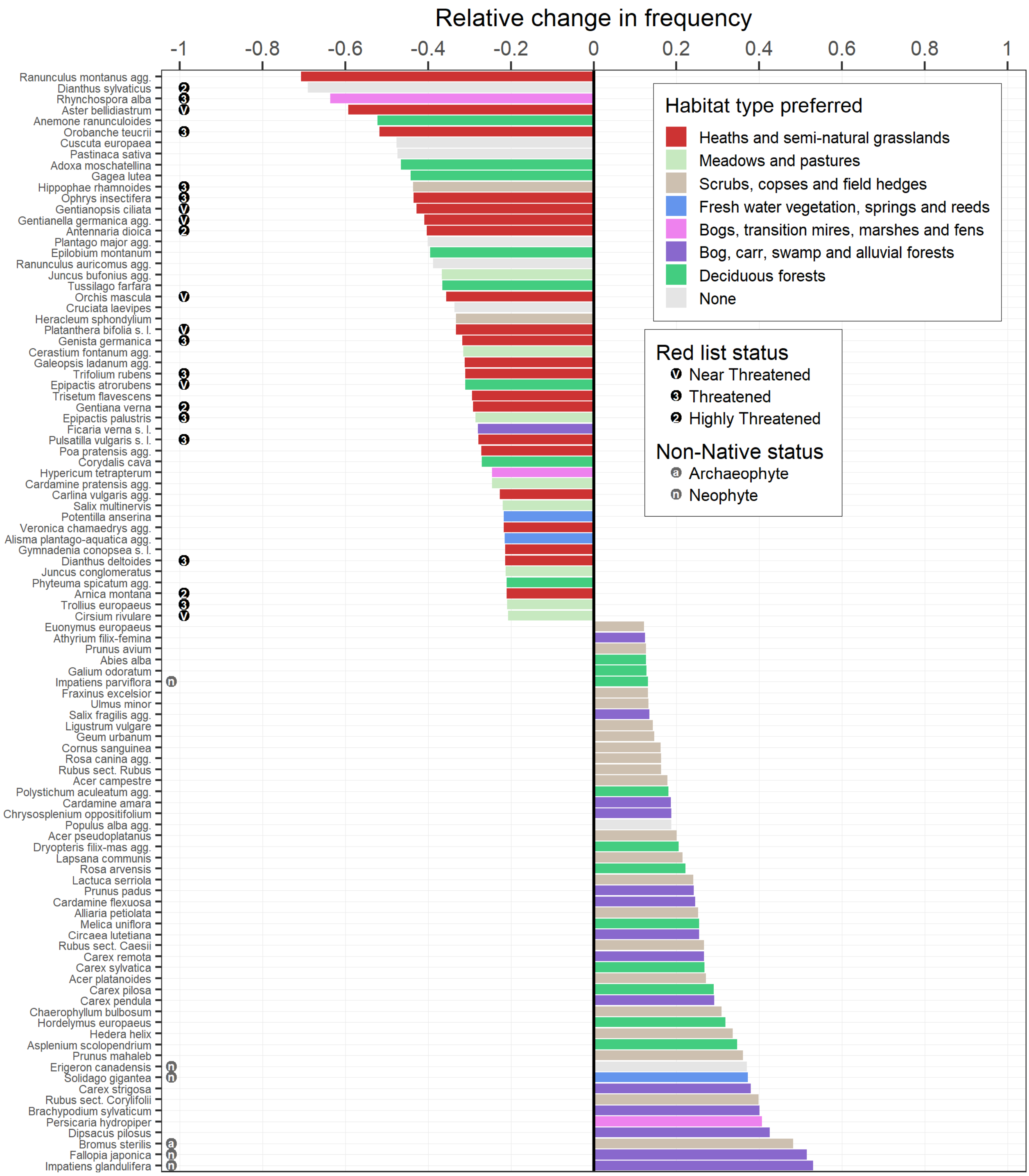

Figure S1 Relative change in frequency from time interval t_1 (1989-2005) to time interval t_2 (2006-2021) for key species that showed significant trends across both change metrics. Out of those 188 species only the 50 top losers and 50 top winners are shown. Colors refer to the preferred habitat type of each species, based on the fidelity (Φ) of species to habitat types. Category "None" refers to species that showed a fidelity lower than median of all species of Φ =0.006 to their most preferred habitat type.

and alluvial forests (mean change = +0.17, t = 3.85, p < 0.001) and species of scrubs, copses and field hedges (mean change = +0.10, t = 3.94, p < 0.001). Comparing trends of species with different red list status showed that near threatened, threatened and not yet evaluated (Red list categories V, 3, and NE respectively) species were mostly decreasing (mean change = −0.276, −0.316, and

−0.167 respectively, $t = −6.94$, $−7.48$, and $−4.48$ respectively, all $p < 0.001$; Figure S2a). Comparing trends with respect to the native status, we found that neophytes showed no overall significant trend, while native species showed overall negative trends (mean change = −0.07, $t = −3.81$, $p < 0.001$; Figure S2b).

Keypecies within habitat types

Most habitat types had more key species increasing than key species decreasing in frequency over time (Figure S3b). In contrast, there were more key species with decreasing than key species with increasing occurrence probabilities in all habitat types (Figure S3a). The highest mean decreases in occurrence probability were found for species in ruderal, fringe and tall forb communities and clearings (mean change = −0.003, $t = −2.37$, $p = 0.02$), for species in bogs, transition mires, marshes and fens (mean change = −0.003, $t = −3.36$, $p < 0.001$), and for species in deciduous forests (mean change = −0.001, $t = −5.02$, $p < 0.001$). The mean trends of the habitat types meadows and pastures, heaths and semi-natural grasslands, and fresh water vegetation, springs and reeds were especially driven by species that preferred the respective habitat type. Therefore, here especially specialists showed negative trends in their preferred habitat types. The opposite was observed for scrubs, copses and field hedges, where typical species seemed to rather increase than decrease in their occurrence probability.

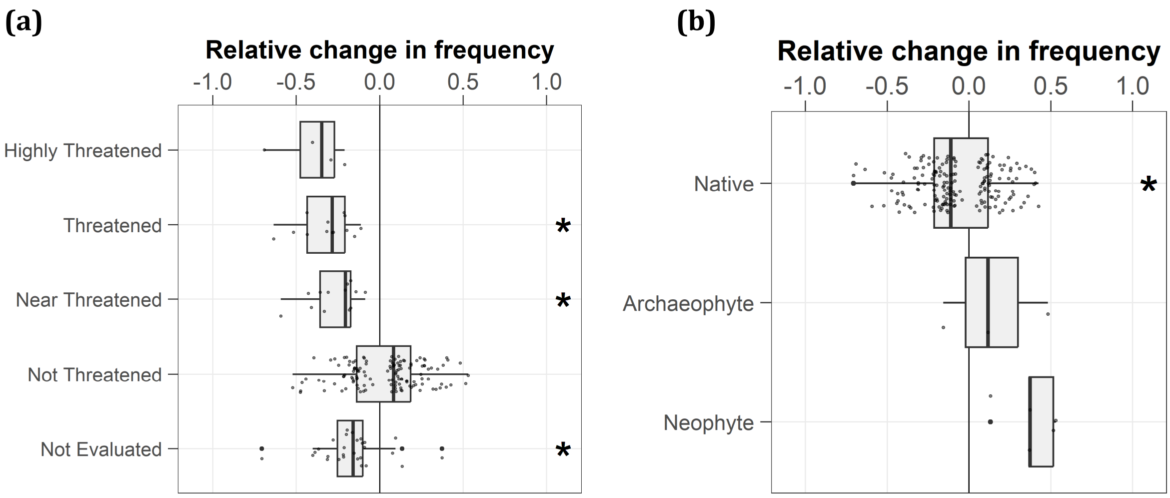

Figure S2 Relative change in frequency from time interval t_1 (1989-2005) to time interval t_2 (2006-2021) for key species of different **(a)** red list categories of Baden-Württemberg and **(b)** non-native status in Germany. Only species are plotted that showed significant trends across all change metrics. **(a)** Group categories according to the Red List key from Germany: Highly Threatened (= Category 2), Threatened (= Category 3), Threatened (unknown extent) (= Category G), Near Threatened (= Category V), Not Threatened (= Category *), Not Evaluated (= Categories D and ^), according to Breunig & Demuth (1999). **(b)** Non-native status according to Biolflor (Klotz et al., 2002). Significant differences from zero according to *t* tests are labelled with an asterisk.

Consistency key species

Trends of key species mostly followed the trend of the habitat type that they prefer (Figure S4a). However, the mean trend of all species within a habitat type did not necessarily follow the mean area trend of the respective habitat type (Figure S4b). All mean species trends within habitat types were negative, which contradicted with the positive trend in area of deciduous forests.

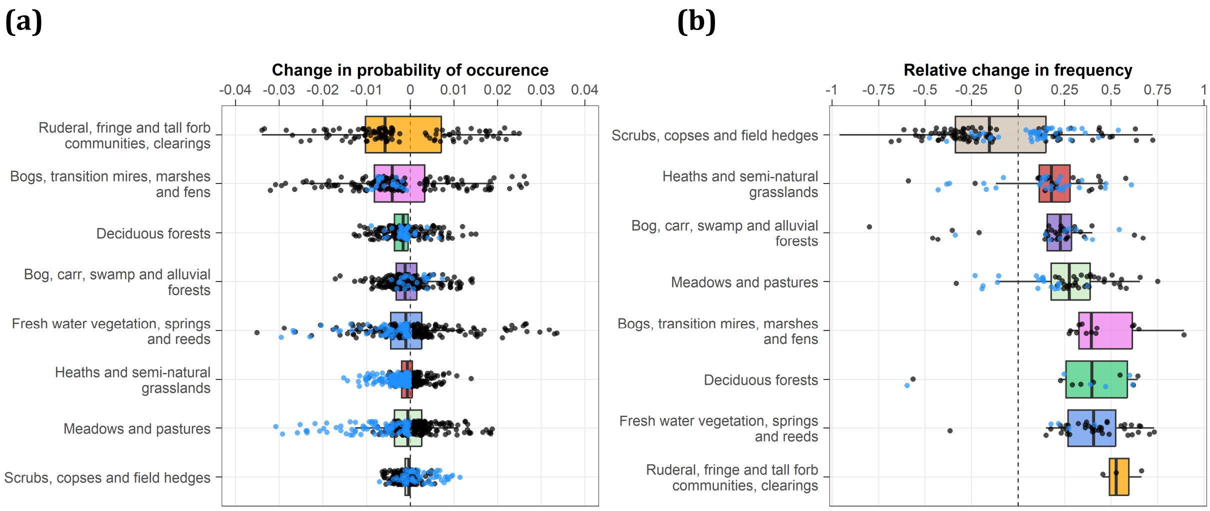

Figure S3. Trends of key species within habitat types. **(a)** Mean changes in species' probabilities of occurrence (Beals' index) within different habitat types. **(b)** Relative change in frequency of species within different habitat types. Only significant trends are shown. Polygons that transitioned in their habitat type over time are included. Blue dots represent species that prefer the respective habitat type in which they show a trend, black dots represent all species that prefer another type or which fidelity lies below the median of all species (Φ = 0.006). Blue dots are plotted on top of black dots for visibility.

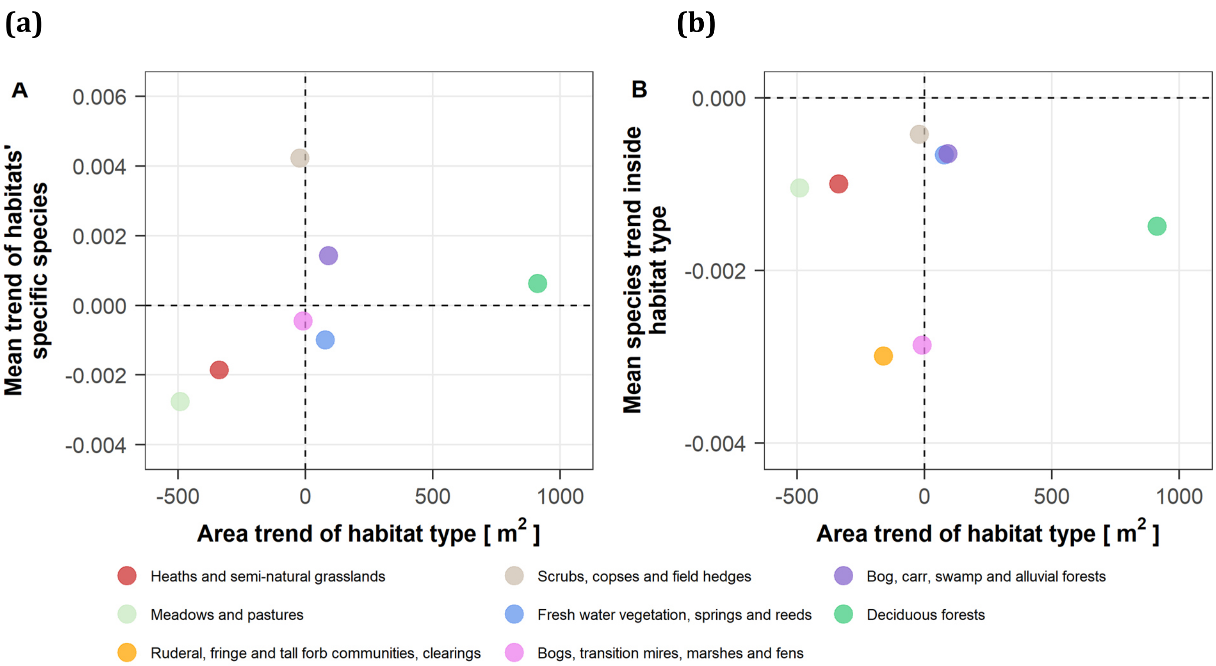

Figure S4 Comparison of mean trends of habitat type area with **(a)** mean trends of habitat types' specific key species and **(b)** mean key species trends within habitat types. **(a)** Species trends refer to the trends of occurrence probability (Beals' index) across all habitat types in Baden-Württemberg. **(b)** Species trends refer to the trends of occurrence probability (Beals' index). Area trends of habitat types are in m². Colors according to the habitat types. Note that also habitat types are included that did not show a significant trend over time (fresh water vegetation, springs and reeds; bog-, carr-, swamp- and alluvial forests). Only species that showed significant trends over time were used to compute the mean species trends for **(a)** and **(b)**. There were no species with a significant trend across the habitat types that belonged to ruderal, fringe and tall forb communities or coniferous forests **(plot a)** and no species with a significant trend within coniferous forests **(plot b)**.

APPENDIX S4

Due to the length of table S1 it can only be found online in the Supporting Information section at: https://doi.org/10.1111/avsc.12799.

Table S1 Mean changes in species' probabilities of occurrence (Beals' index) within different habitat types. Only significant trends are shown and only species x habitat type combinations that were observed at least once during the mapping program. Polygons that transitioned in their habitat type over time were included. *n* refers to the number of actual occurrences per species x habitat type combination. *p* values according to *t* tests, applying Holm adjustment. Habitat type preference is based on the fidelity (Φ) of species to habitat types. Category "None" refers to species that showed a fidelity lower than the median of all species of Φ =0.006 to their most preferred habitat type.

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Chapter 4

Loss of characteristic species across German federal states detected by repeated mapping of protected habitats

This chapter has been submitted to **Biological Conservation** as:

Lüttgert, L., Heisterkamp, S., Jansen, F., Kaufmann, R., Kellner, S., Klenke, R. A., Lütt, S., Seidler, G., Wedler, A., Wörmann, R., & Bruelheide, H. (2025). Loss of characteristic species of open habitats across Germany detected by repeated mapping of protected habitats.

Note that the version submitted to Biological Conservation differs slightly in the wording of the text but all results are exactly the same as in this thesis.

And has been published as a preprint on **bioRxiv** as:

Lüttgert, L., Heisterkamp, S., Jansen, F., Kaufmann, R., Kellner, S., Klenke, R. A., Lütt, S., Seidler, G., Wedler, A., Wörmann, R., & Bruelheide, H. (2025). Loss of characteristic species across German federal states detected by repeated mapping of protected habitats. *bioRxiv*. https://doi.org/10.1101/2025.02.27.640325

Note that this version is identical with the version of this thesis.

ABSTRACT

Identifying the winners and losers of biodiversity change within different habitat types requires systematic monitoring. While such data are still lacking in Germany, species trends could be derived from previously untapped sources. Here, we derive temporal trends in plant species from data of repeated habitat mapping programs of three German states from 1977-2021, both across all habitat types per state and within habitat types. Consistently negative trends were found across all states for species preferring heaths and semi-natural grasslands, moist to wet grasslands, and coastal and marine habitats, including many endangered species. Consistently positive trends were found for species preferring scrubs, copses and field hedges, and for non-native species. Trends within habitat types showed negative trends for species characteristic of those habitat types. While trends varied among states, the overall patterns were very similar. This points to ongoing habitat degradation and common drivers of biodiversity change in Germany.

KEYWORDS

Biodiversity change, characteristic species, Germany, habitat mapping, plants, resurvey, species trends, vegetation

INTRODUCTION

In response to the ongoing biodiversity loss and habitat degradation in Europe, with the EU Biodiversity Strategy and Nature Restoration Law the European Union set targets to protect 30% of its terrestrial and marine area and to restore at least 30% of degraded habitats by 2030 (European Commission, 2022; European Commission & Directorate-General for Environment, 2021). Further targets include halting or even reversing negative trends in both protected habitat types and plant species. To efficiently direct these nature conservation efforts, identifying degraded habitats as well as the winners and losers of habitat degradation is essential (Kühl et al., 2020).

Past decades' environmental change did not threaten species randomly, with especially habitat specialists showing declines (Britton et al., 2009; Diekmann et al., 2019; Heinrichs & Schmidt, 2017). For plants, these are often species typical of nutrient-poor habitats due to habitat loss and nutrient enrichment (Klinkovská et al., 2024; Sperle & Bruelheide, 2021). Losers are also often rare and endangered species (Kempel et al., 2020; Metzing et al., 2018). In contrast, the set of plant species that have benefited from environmental change includes common and widespread generalist, often nutrient-demanding species (Glaser et al., 2024; Hallman et al., 2022; Heinrichs & Schmidt, 2017; Kindlund & Tyler, 2023; Staude et al., 2023). Trends are particularly positive for woody species (Buitenwerf et al., 2018; Hallman et al., 2022; Wieczorkowski & Lehmann, 2022) and non-native species (Eichenberg et al., 2021; Hallman et al., 2022; Kindlund & Tyler, 2023).

How many and what type of species increase or decrease depends on the spatial and temporal scale the observations are made, the region and the habitat types studied (Eichenberg et al., 2021; Gonzalez et al., 2023; Prévosto et al., 2011; Vellend et al., 2017). While studies based on a fine spatial grain, such as permanent vegetation plots on a few square meters, are sensitive to detect changes, they are mostly not spatially representative and exclude sites that have experienced habitat type transition and destruction (Gonzalez et al., 2016; Jandt et al., 2022). In contrast, studies on a coarse spatial grain, for example based on grid-cells of several square kilometers, can only detect strong trends and do not allow to distinguish between habitat types (e.g., Eichenberg et al., 2021; Rich & Woodruff, 1996). It is the intermediate scale, i.e. of habitats within a landscape, that would provide sufficient sensitivity and representativeness. However, such studies at the regional scale are notoriously scarce (Chase et al., 2019; Naaf & Wulf, 2010). This is particularly unfortunate because at this scale most conservation measures are implemented (Erasmus et al., 1999; Ferrier, 2002; Naaf & Wulf, 2010). Similar to the spatial scale, the temporal scale will influence the trends observed, with short-term studies expected to result in different and/or weaker trends than long-term studies due to short-term fluctuations and time lags (Magurran et al., 2010; Skálová et al., 2022). Still, long-term studies are rare. Furthermore, we lack studies that allow comparing trends between different habitat types. Thus, in an ideal world, systematic plant monitoring would cover all habitat types, be geographically representative, and extend into the last century (Buckland & Johnston, 2017; Gonzalez et al., 2023). While such systematic data are not available in any country, some data sources may come close, although they are based on programs that were never intended to provide species trends.

Such data might be extracted from habitat mapping programs, which have been established decades ago in many countries with the goal of nature conservation and landscape planning (Bunce et al., 2012; European Environment Agency & Museum national d'Histoire naturelle, 2014; Lengyel et al., 2008). In Germany, mapping campaigns have been carried out by all federal states over the past decades, in some of them also repeatedly (Kaiser et al., 2013). They include wall-to-wall mapping of all protected habitat types through field surveys, including records of plant species occurrences in most habitat sites. The programs thus provide species occurrence information at the habitat scale across large regions and habitat types. More recently, these data have been used to derive species trends, but only to a limited extend for individual federal states (Bruelheide et al., 2020; Jansen et al., 2020; Lüttgert et al., 2022; Lüttgert et al., 2024). A main obstacle preventing data integration across federal states has been the federal structure of the nature conservation administration in Germany, which resulted in differences in mapping keys, habitat definitions and database structures. We also expected that conditions across states might be idiosyncratic due to differences in regional history of land use, habitat types, and environmental conditions (Hallman et al., 2022; Prévosto et al., 2011; Timmermann et al., 2015).

Here, we employ data from the habitat mapping programs of three federal states (hereafter states) in Germany to derive and compare their plant species trends. We chose the states Schleswig-Holstein, Hamburg, and Baden-Württemberg because they are representative of the German landscape but also because they had repeated mapping data available for at least two time periods within 1977-2021. We calculated species trends both across all habitat types of each state and within different habitat types, and tested whether specific species groups tended to increase or decrease over time. We then compared the consistency of trends among states based on both individual species trends and group trends.

While the three states differ in location (northern vs. southern, coastal vs. more continental), geography (lowland vs. upland) and urbanization level, they have all experienced intensification of agricultural land use, increases of build-up area, and abandonment of traditional land uses. Thus, we expected that these drivers would result in common patterns of species change. In particular, we hypothesized to encounter

1) a common set of losers across the states, including species of nutrient-poor habitats (bogs, semi-natural grasslands), and endangered species;
2) a common set of winners across the states, including shrubs, ruderals, and neophytes (non-native species introduced after 1492);
3) declines in habitat-characteristic species within their preferred habitat type across all states.

METHODS

Habitat mapping

The three German federal states Schleswig-Holstein (SH), Hamburg (HH), and Baden-Württemberg (BW) together cover an area of 52,307 km^2, which is 14.6% of Germany (Statistisches Bundesamt, 2024; SH: 15,804 km^2, HH: 755 km^2, and BW: 35,748 km^2; Appendix S1: Figure S1). All three states have been mapping their protected habitat types for decades, starting in the 1970s. While in BW only protected habitat types have been mapped, in SH also other “potentially valuable” sites were included, while in HH also non-protected habitat types have been mapped since the mid-1990s. Most habitat sites have been remapped at least twice by 2021 (except in some districts for the open land mapping in BW). Habitat mapping includes the recording of both habitat types and plant species at each site. However, complete species lists were not mandatory. Thus, species lists are mostly incomplete, with the focus on species that are endangered, characteristic for a particular habitat type, or dominant at a particular site.

Spatial data processing

All states have digitized at least one version of old and all new mapping data, with each habitat site represented by a polygon to which metadata and species lists were assigned. Hereafter, we refer to a mapped unit as a polygon, even if a mapped unit sometimes consists of several different polygons in proximity if they all belong to the same habitat type. The number and size of polygons differed between states and mapping periods (Appendix S1: Table S1). We processed the spatial data separately by federal state. For each state, we intersected polygons from the first digitally available mapping campaign with polygons from the most recent mapping campaign in ArcGIS 10.5 (ESRI, 2016). Only intersecting polygons were used for trend analyses. Thus, polygons that were either not remapped or not previously mapped were excluded. Further data cleaning was slightly adapted for each state, according to the underlying mapping schemes and data (see Supplementary Methods for SH, Lüttgert et al. (2022) for HH, and Lüttgert et al. (2024) for BW for explicit cleaning steps). Generally, we excluded small intersections considered as mapping and digitization inaccuracies (less than 5% of each or either polygon, depending on state), polygons which had not been remapped to a proportion of a set threshold (50% for SH, 95% for HH, and 75% for BW), and which were not accompanied by a species list. We divided data into two time intervals each, which differed slightly between the states depending on the available data: t_1: 1977-2005 and t_2: 2007-2021 for SH, t_1: 1979-1994 and t_2: 1995-2017 for HH, and t_1: 1989-2005 and t_2: 2006-2021 for BW. Time spans between resurveys of polygons ranged from 6 to 42 years, with a median of 32, 22, and 19 years for SH, HH, and BW, respectively (Appendix S1: Figure S2).

Plant occurrence data

Taxonomy was harmonized using GermanSL 1.5. (Jansen & Dengler, 2008, 2010), aggregating species to the section level and merging some taxa further onto the genus level. We excluded mosses, lichen, algae, most hybrids and cultivated forms, as well as some species known to have been falsely identified. 2212 species remained after harmonization, with 1301, 1287, and 1977 species recorded in SH, HH, and BW, respectively. 998 species were recorded in all states. Since the ratio of species to polygons was relatively high in HH, we drew species accumulation curves for all states, expecting slower accumulation of species for HH. However, while the curve was slightly steeper for HH, the asymptote was approached in all states (Appendix S1: Figure S3).

Habitat type data

We used information on habitat types per polygon to assign preferred habitat types to species and to calculate species trends within habitat types. Habitat type categories differed between states and mapping periods. Thus, we assigned all habitat types to 14 broadly defined habitat type groups in accordance with all habitat mapping keys, including 646, 475, and 248 detailed habitat types from SH, HH, and BW, respectively (Appendix S1: Tables S2 &S3). Some groups were only recorded in some states. Since a polygon could have multiple habitat types assigned to it, we only used the habitat type with the highest cover (at least 51%) of each polygon.

Preferred habitat types, Red List and non-native status

We assigned a preferred habitat type to each species by applying the Φ coefficient, i.e. the fidelity of each species x habitat type combination (Chytrý et al., 2002; Equation 1).

$$\Phi = \pm\sqrt{\frac{X^2}{N}} = \frac{a \cdot d - b \cdot c}{\sqrt{(a+b) \cdot (c+d) \cdot (a+c) \cdot (b+d)}} \tag{1}$$

The fidelity Φ of a species to a specific habitat type is calculated using the X^2 statistic for a 2 x 2 contingency table and is dependent on the total number of observations N, with a the number of occurrences of the species within the habitat type, b the number of occurrences of the species outside the habitat type, c the number of absences of the species within the habitat type, and d the number of absences of the species in all other habitat types. Φ ranges from −1 to 1 for species perfectly avoiding a habitat type or species perfectly bound to a habitat type, respectively. We used all polygons from all states together (including polygons that did not intersect) to calculate across-state fidelities for all species x habitat type combinations. Fidelities are therefore biased towards the larger states as they had more polygons available. We considered the habitat type showing the highest fidelity to each species as its preferred habitat type. Species that prefer a habitat type can also be seen as characteristic for that habitat type. However, we did not assign a type to species whose highest Φ value was below the median of all species' highest Φ value (0.0073). This resulted in the removal of species with only few observations from the list of habitat-specific species.

We assigned Red List (endangerment) and non-native status in Germany to all species, based on the Red List of Germany (Metzing et al., 2018) and BiolFlor (Klotz et al., 2002), respectively. Non-native species were separated into archaeophytes, i.e. non-natives introduced before 1492, and neophytes, i.e. non-natives introduced after 1492. We manually assigned a few species' non-native status based on information from Floraweb (www.floraweb.de; Buttler et al., 2018; Wisskirchen & Haeupler, 1998). We did not assign a status to species aggregates for which the lower taxonomic levels had different status.

Trend calculation and metrics

Polygons from one time interval were often overlapping with several polygons from the other time interval, caused by habitat change or changes in the detail in which habitat types were mapped. Thus, we compared each t_1-polygon's species list with the merged species lists of all its intersecting polygons from t_2 (hereinafter $t_1 \rightarrow t_2$), and each t_2-polygon's species list with the merged species lists of all its intersecting polygons from t_1 (hereinafter $t_2 \rightarrow t_1$). We derived species trends using both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ separately. Because we often compare one species list from one time period with several species lists from the other time period, changes derived from $t_1 \rightarrow t_2$ are biased towards species gains and changes derived from $t_2 \rightarrow t_1$ are biased towards species losses. Thus, to make sure to only report robust trends that can be compared between states, we here only report trends that were significant and consistent for both approaches $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$. For those cases, we report the mean trends derived from both approaches and common statistical values.

We calculated temporal species trends separately for each state, using two change metrics each: relative change in frequency and probability of occurrence. For frequency trends, we calculated the change in presence/absence for each species in all its previously and/or recently occupied polygons from t_1 towards t_2 (−1, 0, or 1). The mean of those changes per species represented the relative change across each state. Trends ranged from −1 to 1, with a value of −1 indicating that a species was lost in all previously occupied polygons and 1 that a species was new to all its polygons.

To account for incomplete species observations, we additionally estimated species change in probability of occurrence, using Beals' index of sociological favorability (Beals, 1984). We estimated the probability of each species to occur in each polygon, based on a species' co-occurrence information with all species that were recorded in that polygon (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 polygon p is calculated from its joint occurrences M_{ij} with all species j of the number of species in that polygon N_p, divided by the number of polygons M_j in which species j is present. M_{ij} values were derived from a co-occurrence matrix of all species across all polygons of a state (including polygons that did not intersect). We then calculated the change in probability of occurrence (hereinafter Beals) from t_1 to t_2 for each polygon p x species i combination and calculated each species' mean change across each state. Because Beals values are generally lower for co-occurrence matrices that are based on a higher number of polygons, the large state BW had lower Beals values, and hence, also Beals change values were lower than in the other states (Appendix S1: Figure S4). To make the values comparable between the states, we standardized the Beals trends per species and state by dividing them by the standard deviation of species' Beals trends of each state.

Trends within habitat types

In addition to deriving trends across a state, we also derived trends within different habitat types. We used the same habitat types that we used for assigning species to their preferred habitat types.

We grouped the data by using the habitat type of the first mapping of a habitat site, regardless of whether a polygon's habitat type changed over time. For each recorded habitat type and species combination, we derived trends in both frequency and in Beals as described above for the trends across the states. Again, we standardized the mean Beals change values per species, habitat type, and state by dividing them by the standard deviation of the mean trends of each state.

Statistical analyses

To test for significance of each species' frequency trend, we used two-tailed binomial tests (i.e. sign tests). We first tested significance for the approaches $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ separately while accounting for duplicated usage of polygons within $t_1 \rightarrow t_2$ and within $t_2 \rightarrow t_1$ by reducing the degrees of freedom accordingly. For species with significant trends for both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$, we calculated their mean trends as well as common p values from both approaches, also with two-tailed binomial tests. For this, we used the mean numbers of occurrences from both approaches, i.e. the mean number of increases, mean number of decreases, and mean number of cases without a change.

To test for significance of each species' Beals trend, we used two-tailed t tests, again first testing significance for the approaches $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$ separately. We corrected p values by using the number of polygons in which a species actually occurred instead of the number of all polygons. We corrected for duplicated usage of polygons within $t_1 \rightarrow t_2$ and within $t_2 \rightarrow t_1$ and additionally applied Holm adjustment of significance levels for testing of multiple species. For species with significant trends for both $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$, we calculated their mean trend as well as common p values and 95% confidence intervals from both approaches. For this, we used the mean trend, mean number of occurrences, and mean variance from both approaches to derive common standard errors and t values.

For each state, we used Spearman rank correlations to compare frequency and Beals trends using all species with a significant trend for both metrics. We additionally compared single species trends between two states each by using Spearman rank correlations for each metric.

Next, for each state and change metric, we tested if specific species groups rather increased or decreased. We grouped species based on their preferred habitat type, Red List, and non-native status. We only used species with a significant trend in the respective change metric and tested for significance using two-tailed Wilcoxon signed rank tests. We also produced trend heatmaps for species grouped by state and preferred habitat type, including dendrograms for states and for preferred habitat types.

We additionally calculated each species mean trend across all states by taking the average from the three state trends. Again, we did so for frequency and Beals trends. Based on those mean trends, we tested again if specific species groups (preferred habitat type, Red List, non-native status) rather increased or decreased using two-tailed Wilcoxon signed rank tests.

For frequency and Beals trends within habitat types, we used the same statistical approach as we did for the trends across the states. For each state and change metric, we then tested whether all species within a given habitat type tended to show positive or negative trends. We only used species x habitat type combinations with a significant trend in the respective change metric and tested for significance using two-tailed Wilcoxon signed rank tests.

The significance for all statistical tests was determined at $p < 0.05$.

If not stated otherwise, we used R 4.3.2 (R Core Team, 2023) for all analyses. We used the packages data.table, dplyr, ggdist, ggnewscale, ggplot2, ggpubr, gplots, reshape2, sf, sjPlot, stringr, and vegdata.

RESULTS

Trends across each state

We found significant Beals trends for 389, 319, and 809 species in SH, HH, and BW, respectively (Appendix S2: Table S1). Overall, 105 species displayed a significant Beals trend in all states (Appendix S1: Table S4). Significant trends in frequency were encountered for 136, 122, and 404 species in SH, HH, and BW, respectively (Appendix S3: Table S1). Only nine species showed a significant frequency trend in all states.

A total of 96, 93, and 307 species showed a significant trend in both frequency and Beals in SH, HH, and BW, respectively (Appendix S1: Figures S5-S7). Frequency and Beals trends in each state were only moderately correlated (Spearman rank correlation $r_s = 0.53$ for SH, $r_s = 0.53$ for HH, and $r_s = 0.26$ for BW, all $p < 0.001$).

Trends of species that were significant in two states were positively correlated between states. These Spearman rank correlations between states were generally higher for Beals trends, and highest for trends between SH and HH ($r_s = 0.82$ with $n = 137$ for SH and HH, $r_s = 0.68$ with $n = 251$ for SH and BW, $r_s = 0.71$ with $n = 237$ for BW and HH, all $p < 0.001$; Appendix S1: Figure S8 a-c). For frequency, Spearman rank correlations were lower, especially for trends between SH and BW ($r_s = 0.81$ with $p <0.001$ and $n = 23$ for SH and HH, $r_s = 0.39$ with $p = 0.011$ and $n = 42$ for SH and BW, $r_s = 0.58$ with $p < 0.001$ and $n = 58$ for BW and HH; Appendix S1: Figure S8 d-f).

Preferential habitat types

Species preferring scrubs, copses and field hedges mainly increased in their probability of occurrence in all states (Figure 1, Appendix S1: Table S5). By contrast, species preferring moist to wet grasslands, heaths, inland dunes and semi-natural grasslands, as well as coastal and marine habitats mostly decreased in their probability of occurrence in all states. For species preferring other habitat types, Beals trends were not significant in all states (Figure 1, Appendix S1: Table S5). Species of bogs, transition mires, marshes and fens showed negative trends in both SH and BW. Species of mesic grasslands as well as species of moist to wet forests showed negative trends in both HH and BW. Comparing the direction and magnitudes of significant Beals trends between states, based on their preferred habitat type, revealed no case of opposing trends (Figure 2).

Similarly, out of the 105 species with a significant Beals trend in all states, only very few showed opposing trends between states (Appendix S1: Figure S9). Mean species trends across states revealed relatively many winner species preferring scrubs, copses and field hedges, moist to wet forests and dry to moderately moist forests (Figure 3, Appendix S1: Table S5). In contrast, loser species often preferred moist to wet grasslands, heaths, inland dunes and semi-natural grasslands, and coastal and marine habitats. In contrast to the Beals trends, no clear species

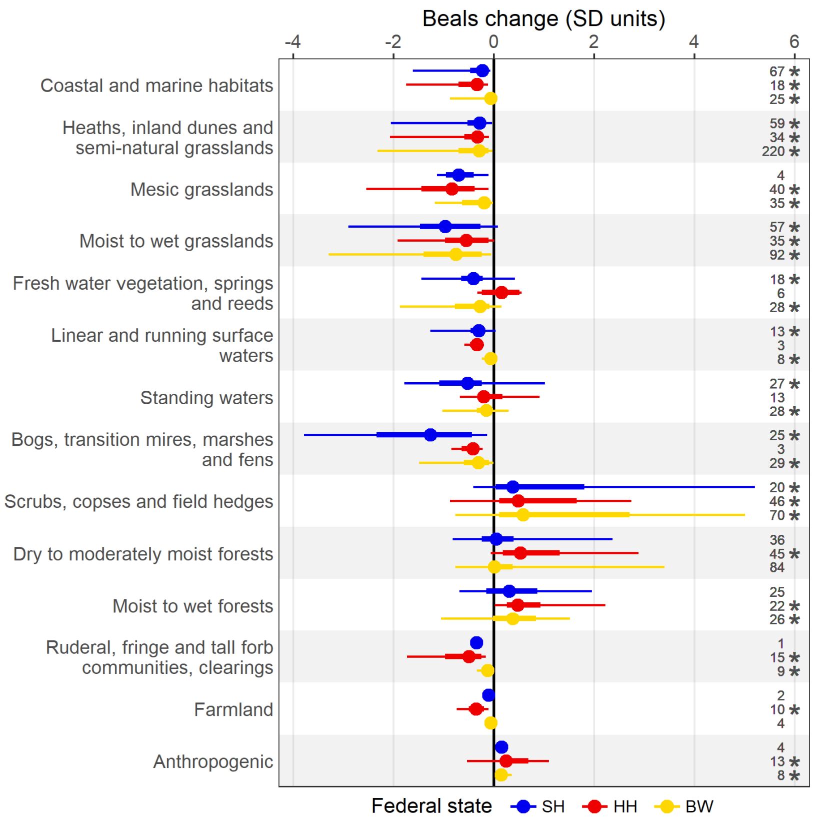

Figure 1 Beals trends of species grouped by their preferred habitat type separately by state. Points, thick and thin whiskers show the median, 50% and 95% data range. Only species are included per group that showed a significant trend and that had a preferred habitat type assigned. *n* is given for number of species with a significant trend that are included in each combination of state and preferred habitat type. Asterisks indicate whether a group's trend deviated from zero change according to Wilcoxon signed rank tests. Habitat types correspond to the following EUNIS habitat types (European Nature Information System; European Environment Agency; Moss, 2008; 2021 version if not stated otherwise): Coastal and marine habitats (N1, N2, N3), Heaths, inland dunes and semi-natural grasslands (S4, R1), Mesic grasslands (R2), Moist to wet grasslands (R3), Fresh water vegetation, springs and reeds (C3, D5; based on EUNIS 2012 version), Linear and running surface waters (C2, C3; based on EUNIS 2012 version), Standing waters (C1, C3; based on EUNIS 2012 version), Bogs, transition mires, marshes and fens (D1, D2, D4, D5; based on EUNIS 2012 version), Scrubs, copses and field hedges (S3, T4, V4), Dry to moderately moist forests (T1, T3, V6), Moist to wet forests (T1, T3), Ruderal, fringe and tall forb communities, clearings (V3, T4, R5), Farmland (V1, V5, V6), Anthropogenic (V2, V3).

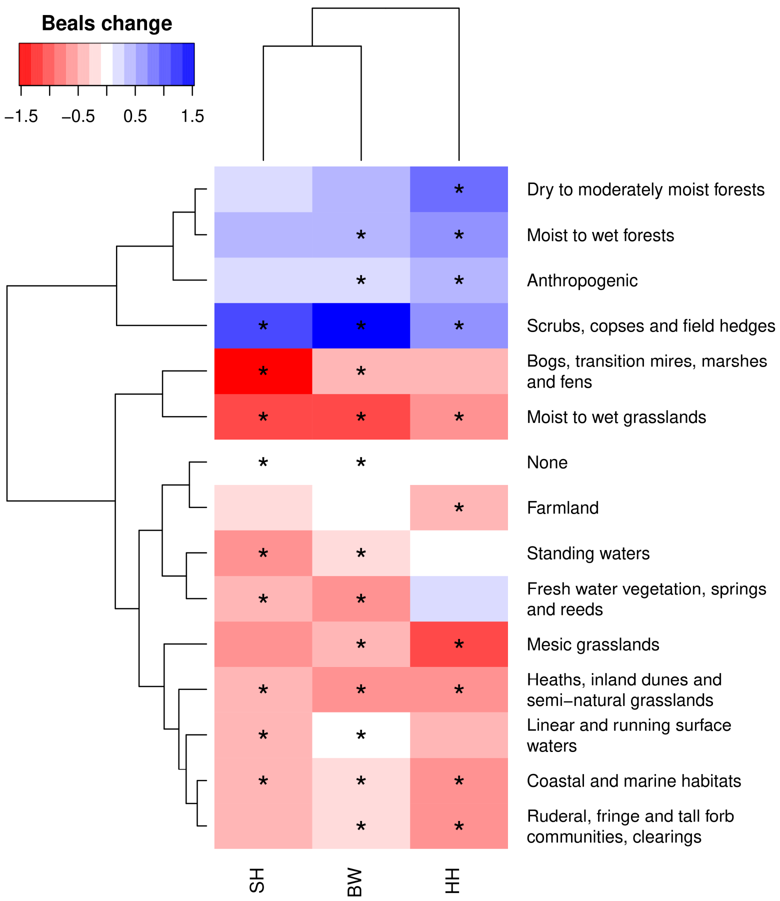

Figure 2 Mean Beals trends of species grouped by state and by their preferred habitat type. Only species were included in a group that showed a significant trend in the respective state (but not necessarily in all states). Asterisks indicate whether a group's trend deviated from zero change according to Wilcoxon signed rank tests.

frequency trend per preferred habitat type were encountered across all states (Appendix S1: Figure S10).

Non-native and Red List status

Neophytes increased in their occurrence probability in all states, however this was only significant for SH and BW (Figure 4a, Appendix S1: Table S6). Native species on average decreased in their occurrence probability in all states. Archaeophytes showed negative trends in both BW and HH while in SH no significant overall trend was found for this group. Trend patterns concerning those three status groups were generally similar for frequency and Beals (Figure 4a, Appendix S1: Figure S11a).

Regarding the Red List status, highly endangered, endangered, and near threatened species decreased in their occurrence probability in SH and BW (Figure 4b, Appendix S1: Table S7). In addition, non-threatened species decreased in their occurrence probability in all states. There were only very few significant group trends regarding endangered species' frequency (Appendix S1: Figure S11b).

Trends within habitat types

We found significant Beals trends for 1380, 67, and 1458 species x habitat type combinations for SH, HH, and BW, respectively. Frequency trends were significant for 600, 131, and 776 species x habitat type combinations for SH, HH, and BW, respectively. Only five combinations showed significant trends in all states, both concerning Beals and frequency trends.

Species trends within habitats types showed overall more positive trends for frequency compared with Beals (Figure 5, Appendix S1: Figure S12). We found a prevalence of species to significantly decrease in Beals within two, zero, and five habitat types in SH, HH, and BW respectively, while a

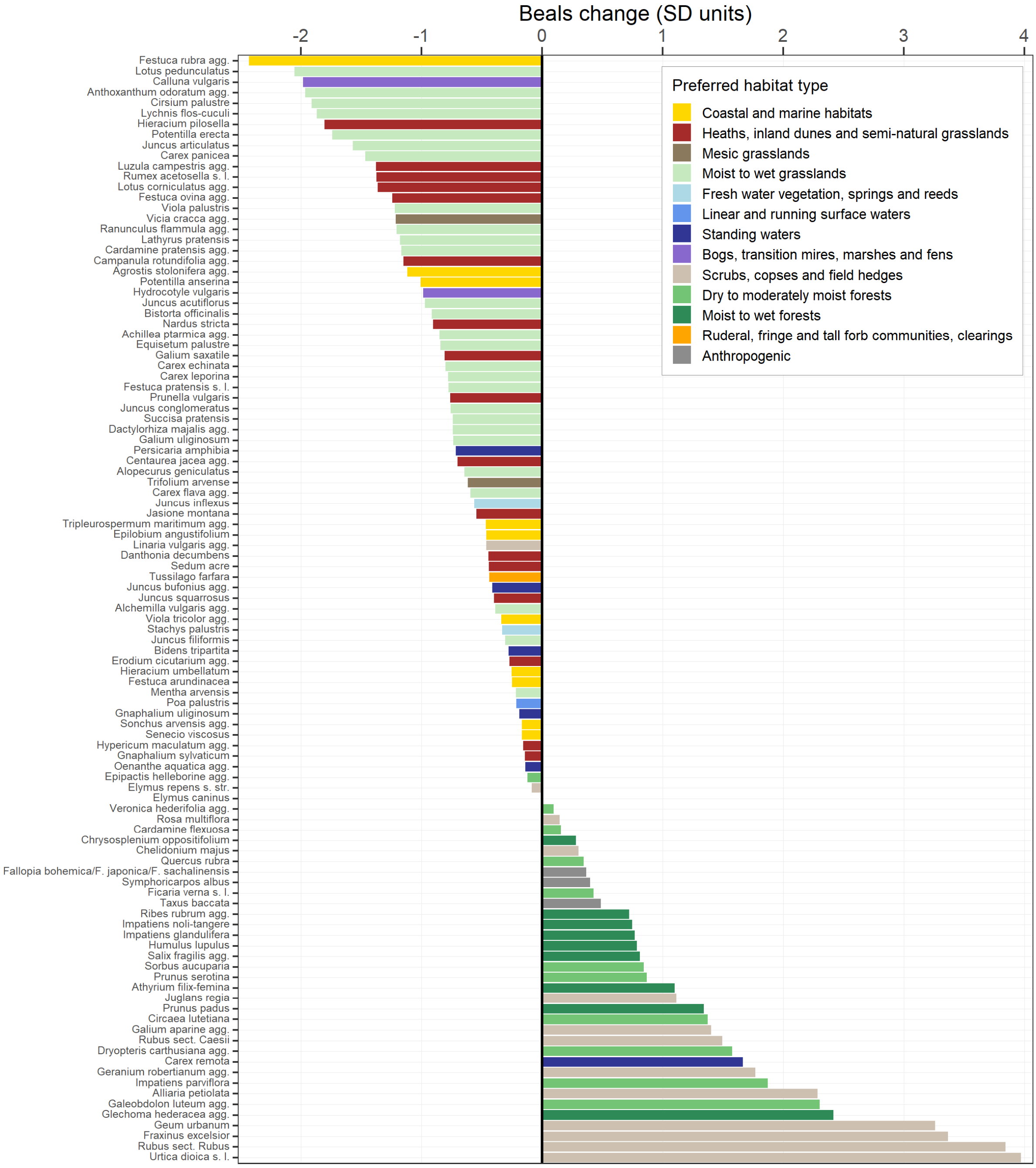

Figure 3 Mean Beals trend of species across all states, derived from the three trends of each state. Only species are included that showed a significant trend in all states (105). Colours indicate the species' preferred habitat type.

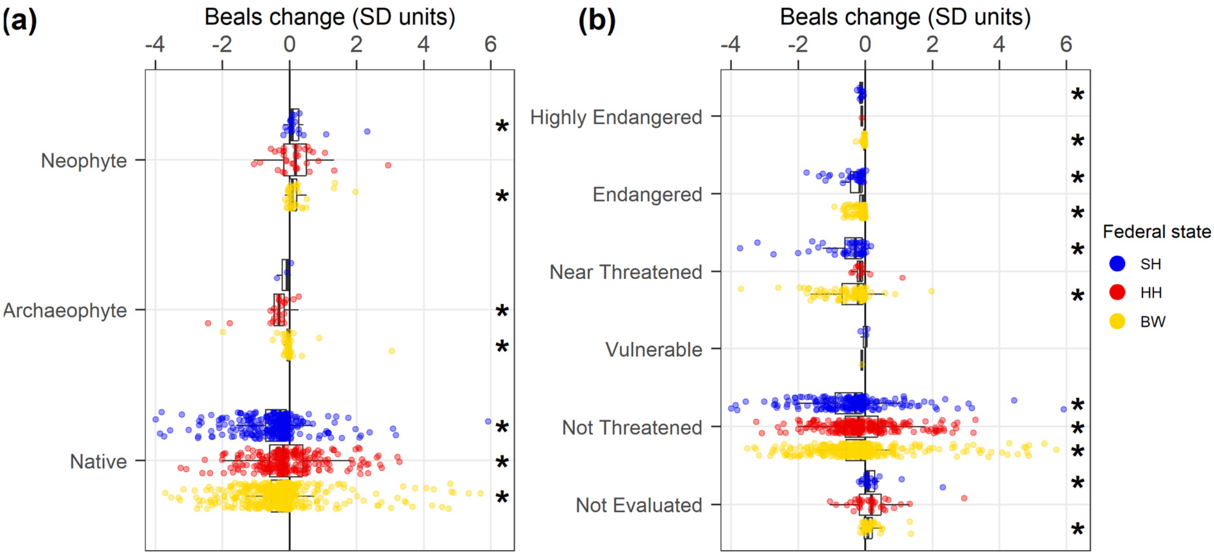

Figure 4 Beals trends grouped by states and **(a)** non-native and **(b)** Red List status. **(a)** Archaeophytes = non-natives introduced before 1492, neophytes = non-natives introduced after 1492. **(b)** There were no species with a significant trend of the Red List categories "extinct or lost" or "threatened with extinction". Asterisks indicate whether a group's trend deviated from zero change according to Wilcoxon signed rank tests. Status according to German wide lists (Buttler et al., 2018; Klotz et al., 2002; Metzing et al., 2018; Wisskirchen & Haeupler, 1998).

prevalence to significantly increase was only encountered within one habitat type in HH (dry to moderately moist forests). Concerning frequency, we found a prevalence of species to significantly decline only within one habitat type in BW and a prevalence of species to significantly increase within eight, six, and four habitat types in SH, HH, and BW, respectively. Especially species that preferred the respective habitat type showed decreases in their probability of occurrence in SH and BW (Figure 5). This pattern was not found for most trends in frequency or in HH (Appendix S1: Figure S12, Figure 5). Species of scrubs, copses and field hedges as well as forests increased

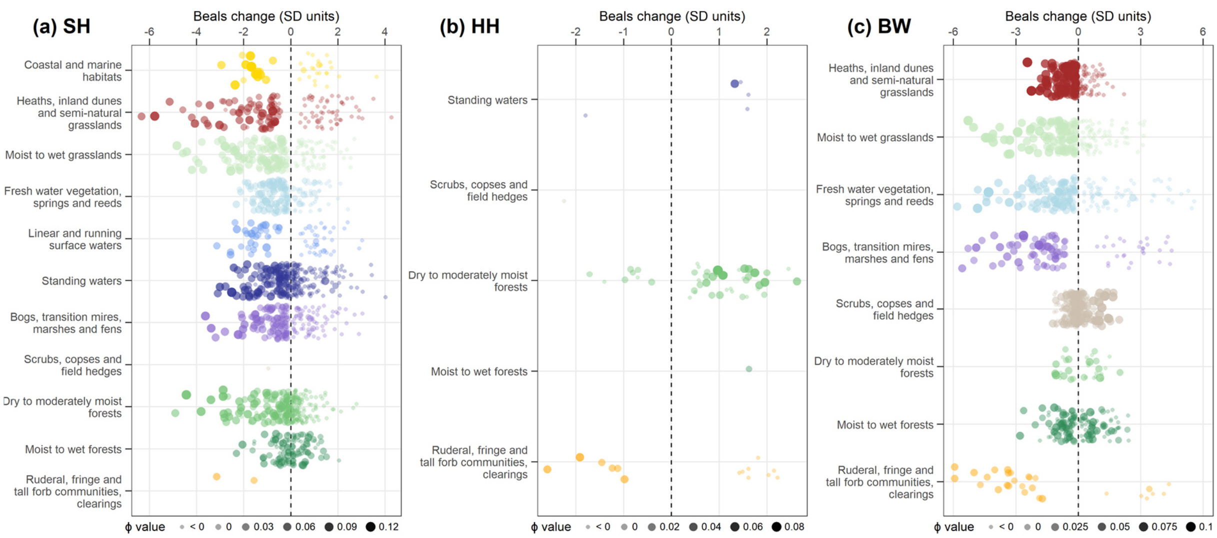

Figure 5 Beals trends within habitat types for **(a)** SH, **(b)** HH, and **(c)** BW. Species' preferences to each habitat type (Φ value) are indicated by size and opacity. All Φ values below 0 are grouped into the category "< 0". Only species are included that showed a significant trend. Note that not all habitat types were mapped in all states.

within several habitat types, especially in SH and BW (Appendix S1: Figures S13-S14). Within dry to moderately moist forests, species preferring these forest types showed mostly negative trends in SH, mixed trends in BW, and positive trends in HH (Figure 5).

DISCUSSION

We found consistent trends in probability of occurrence for most species groups across all three federal states. Similarly, the trends for the same species were largely consistent across states. Both approaches identified a set of loser species typically found in heaths, inland dunes and semi-natural grassland, wet to moist grassland, or coastal and marine habitats. In contrast, winners were species characteristic of scrubs, copses and field hedges.

Declines in species of heaths, inland dunes and semi-natural grasslands confirm our expectation that in particular species that favor nutrient-poor conditions are suffering from losses. These species have shown declines in many habitats across Europe and are typically threatened by management abandonment and increases in nutrients (Diekmann et al., 2014; Fagúndez, 2013; Jandt et al., 2011; Klinkovská et al., 2024; Tyler et al., 2020). Similarly, species characteristic of bogs, transition mires, marshes and fens, which where almost exclusively species of nutrient-poor habitat types, showed overall negative trends in BW and SH. However, this pattern was not significant in HH. This might be due to the limited number of bogs and mires remaining at the beginning of habitat mapping in this state, resulting in a rather small number of typical species present. Following habitat destruction, climate change, and eutrophication, declines of typical bog and mire species have also been found in the black forest region of Baden-Württemberg and elsewhere in Europe (Finderup Nielsen et al., 2021; Hallman et al., 2022; Kindlund & Tyler, 2023; Sperle & Bruelheide, 2021; Tyler et al., 2020).

Species of meadows and pastures may also be negatively affected by increases in nutrients and by an overall intensification of management (Newbold et al., 2015; Wesche et al., 2012). Indeed, the biggest losers included species of moist to wet grasslands in SH and BW and species of mesic grasslands in HH. These results are consistent with declines of these species in other regions of Germany (Diekmann et al., 2019; Wesche et al., 2012).

Dune and coastal habitats have one of the worst conservation statuses in Europe, with a similar situation in Germany (European Environment Agency, 2020; Finck et al., 2017; Hodapp et al., 2024). In SH, especially grey dunes, coastal dune heaths, and moist dune valleys are in a bad condition (Landesamt für Landwirtschaft Umwelt und ländliche Räume, 2020). Species characteristic of coastal and marine habitats generally declined in all states, including in HH and BW, which have no marine coastline and only few brackish water bodies. The latter was possible because this category included species common in both coastal and non-coastal habitat types, such as *Festuca rubra* agg. Those species were likely often assigned as coastal species because the protected coastal sites had more often complete species lists available, including non-characteristic species, compared with other habitat sites. However, these declining species share their tolerance to salt, drought, extreme temperatures, nutrient deficiency, and disturbance (Martínez et al., 2013). In the Netherlands, changes in drainage regimes, grazing pressure, and atmospheric nitrogen deposition led to a loss of characteristic species in coastal dunes over 50 years (Kuiters et al., 2009). Similar reasons for the decline of species characteristic of coastal and marine habitats are likely for Germany. In addition, human outdoor-activities (including trampling), pollution, and modifications of the coastline by recreational structures and dykes threat these species at the coast state SH (Heinze et al., 2019). As most saltmarshes had to be excluded from the analyses (Supplementary Methods), many coastal sites at the North Sea are missing from the analysis of SH. Trends in those mostly protected areas, which are generally in a good condition (Landesamt für Landwirtschaft Umwelt und ländliche Räume, 2020), might be more stable than in the sites used for our analysis.

Endangered species showed the most pronounced declines in BW and SH. The lack of significant negative trends for those species in HH can be explained by fewer endangered species left in the city. A key finding was the overall decrease in the occurrence probability of non-threatened species in all states. This underpins recent observations that biodiversity decline not only affects endangered plant species but also previously moderately common species (Jansen et al., 2020).

In accordance with our expectations, the set of across-states winner species included species of scrubs, copses and field hedges, with also forest species showing mostly positive trends. Furthermore, we found increases of woody plants within several different habitat types in SH and BW. These positive trends imply a woody encroachment across the landscape, which has also been observed in many other formerly extensively used habitats (mainly grasslands and heathlands) in Europe (Buitenwerf et al., 2018; European Environment Agency, 2017; Navarro & Pereira, 2015; Prévosto et al., 2011). Forest species have also been found to increase across Germany (Jandt et al., 2022) and in the German biodiversity assessment (Müller et al., 2024).

As expected, neophytes showed significant increases for BW and SH in accordance with positive trends of non-native species reported across Germany in other studies (Eichenberg et al., 2021). In HH, the lack of an overall significant trend might be due to a long history of neophyte introductions in HH, with some long-established neophyte species nowadays being similarly negatively affected by land use changes as native ones. The spread of neophytes might have been more pronounced in close-to-nature habitat types over the last decades, which are more abundant in BW and SH.

We found no opposing significant trends in occurrence probability of species groups in the different states. Furthermore, species showing a significant trend in two respective states had generally positively correlated trends. Overall, the largely consistent trends of species groups across the states suggest common drivers of biodiversity change across the studied parts of Germany. Thus, on a national scale, these common drivers appear to override regional and local differences in land use history, habitat types and environmental conditions. We expect other parts of Germany to show similar species trends, as despite some regional differences, they generally share a similar history of land use change, including agricultural intensification, shrub encroachment, climate change, nitrogen deposition, and urban expansion (Finck et al., 2017).

Consistent trends were also found for trait-based species groups within different regions and semi-natural habitat types in Denmark, indicating that common drivers led to more fertile and less disturbed conditions across the landscape (Timmermann et al., 2015). Similarly, mostly consistent trends were found across different parishes in Sweden, with some dissimilarities due to different environmental or land use changes (Hallman et al., 2022).

In line with our expectations, trends within habitat types in SH and BW showed that especially species that preferred a certain habitat type decreased in occurrence probability within that habitat type. The decline of characteristic species has been a common pattern found in many different habitat types across Europe over the past decades (Britton et al., 2009; Heinrichs & Schmidt, 2017; Klinkovská et al., 2023; Kuiters et al., 2009). However, this pattern was not encountered for trends in frequency or trends in HH. The latter is probably due to a limited amount of data for HH. Generally, we found higher losses indicated by the probability of species to occur compared with their actual losses in frequency. As frequencies are based on the raw number of observations, they suffer from a bias towards positive change brought about by the higher number of polygons in the second time interval. This bias was accompanied by uncertainties caused by incomplete species lists, which we tried to account for by only reporting robust trends. However, this conservative approach excluded many trends in frequency. Still, we included the frequency metric in our analysis to demonstrate its limits when being applied to habitat mapping data. Instead, Beals occurrence probabilities offer a more reliable change metric. In addition, as Beals occurrence probabilities are based on all present species at a site, they can be interpreted as an early warning of species loss in response to habitat degradation (Bruelheide et al., 2020). Thus, it seems that while a few characteristic species might still persist in degraded sites across the states (no frequency loss), conditions are not favorable anymore (negative Beals trends caused by the absence of typically co-occurring species) and species might after an extinction debt be completely lost from many sites (Hylander & Ehrlen, 2013; Kuussaari et al., 2009).

While forest species increased in many uncharacteristic habitat types in our investigated states, the situation of those species within dry to moderately moist forests seems to differ between states. We found mostly negative trends of those forest species in SH, mixed trends in BW, but positive trends in HH. Thus, while species turnover seems to occur in all states, the trend goes towards less characteristic species in dry to moderately moist forests in SH but indicates recovery of characteristic species in dry to moderately moist forests in HH from being more intensively used in the past. This could be further explained by a higher proportion of forests that are protected in HH (90%) compared with the other states (59% and 79% for SH and BW, respectively, based on the polygons used for analysis).

While common challenges of habitat mapping data for trend analysis can be overcome by appropriate data cleaning and applying metrics that account for incomplete species records, some limitations remain. First, we want to stress that frequency trends have to be taken with caution given their susceptibility to incomplete species recordings while Beals trends are generally more robust (Bruelheide et al., 2020). Second, while our study included sites that underwent habitat transition over the study period, those were almost exclusively sites that kept their protection status and had species lists available from both time intervals. Thus, severely degraded sites were mostly excluded. Third, it is not possible to derive trends for most rare species, given their incomplete representation in the co-occurrence matrices used for Beals (Bruelheide et al., 2021). In conclusion, given the bias towards positive trends, difficulties to detect trends for most rare species, and the exclusion of most severely degraded sites, our estimates are highly conservative and underestimate the amount and magnitude of negative trends in all states. The "true" trends can be expected to be even worse. Still, given the consistency of species group trends that were analyzed independently across the three federal states and with other studies, the overall trends we derived can be considered robust.

Despite its heterogeneous quality, we demonstrated that habitat mapping data can be used to determine the winner and loser species of last decades' biodiversity change. The mostly consistent trends of species groups we found across the three federal states point to common drivers of biodiversity change in different regions of Germany. Identifying those exact drivers for different habitat types needs so far unavailable fine-scale data for multiple drivers, especially concerning land management and interventions, nutrient enrichment, and hydrological changes. Furthermore, to analyze changes for very rare species or changes in species richness and composition, we need systematic monitoring efforts of species occurrences across habitat types and regions. Our trends are mostly consistent with findings from local-scale analyses derived from other data sources and regions in Europe. Our analyses demonstrate the importance of including the landscape scale and not only to rely on trends on coarser scales, as this is the relevant scale at which conservation measures are applied to achieve the goals set by, for example, the EU Biodiversity Strategy.

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DATA ACCESSIBILITY STATEMENT

Polygon data are publicly available via https://umweltanwendungen.schleswig-holstein.de/fachauswertungweb/ for the current mappings in SH, via https://suche.transparenz.hamburg.de/dataset/biotopkataster-hamburg9 for both old and current mappings in HH, and via https://udo.lubw.baden-wuerttemberg.de/public/index.xhtml for the current mappings in BW. As all data belong to the federal state agencies, the full dataset is in parts restricted to be published. This concerns data from previous mappings for the open land for BW and observations of endangered species in BW. All other data are currently in the process of being archived in the iDiv Biodiversity Data Portal (iBDP, https://idata.idiv.de/) and will be publicly available upon acceptance.

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APPENDIX S1

Supplementary Methods – Data cleaning of SH habitat mapping data

This part provides additional information on the data cleaning specific to the habitat mapping data of the federal state Schleswig-Holstein (SH).

Habitat mapping in SH was mainly carried out in two mapping campaigns, with the first one running from 1978-1993 and the recent one from 2014-2020. However, we also included data coming from side mapping projects, which resulted in a total time interval from 1977-2021. We divided the data into two time intervals: t_1 from 1977-2005 and t_2 from 2007-2021, with no data available for 2006.

While as for most federal states, the habitat mapping in SH includes mapping all protected habitat types, in SH also other “potentially valuable” and some other unprotected habitat types are mapped. However, species lists are usually only compiled for protected habitat types. Thus, only 45% of our intersecting polygons had a species list attached.

Next to the two main mapping campaigns, data was available from the additional mapping projects for saltmarshes (Salzwiesen-Kartierung), lakes (Seen-Kartierung), high-nature value grasslands (Wertgrünland-Kartierung) and islands (Inselkartierung). They all followed the same mapping keys and thus were generally included in our analysis. However, we excluded polygons from the saltmarshes project, as here often the same species list is attached to many polygons (>50) and thus we would have treated many different sites as if they were one.

After intersecting all (remaining) polygons, we excluded intersections covering less than 5% of the area of both polygons. This deviates from the methods for BW and HH, where only intersections covering less than 5% of the area of either polygon were excluded. However, for SH this stricter method would exclude many cases where one large t_1 polygon intersects with many small t_2 polygons.

For the same reason, we set the proportion of a polygon’s area that had to intersect with polygons from the other time interval to 50%. Since all habitat sites have been remapped, the risk to include not yet remapped polygons is negligible (in contrast to BW for example). For BW and HH we set this threshold to 75% and 95% respectively. Already using 50% as a threshold for SH excluded many intersections, especially since no longer protected sites mostly did not have a species list attached for the t_2 record. Thus, all once but no more protected habitats’ species lists could not be compared to anything in t_2 and thus those probable species losses could not go into analyses. For approach $t_1 \rightarrow t_2$, only 76% of intersections (and 66% of t_1 polygons) remained after deleting polygons that have not been remapped with a species list by at least 50% of their area. For approach $t_2 \rightarrow t_1$, 84% of intersections (and 83% of t_2 polygons) remained.

There were cases where a polygon of one time interval intersected with several neighbouring polygons from several years from the other time interval. This was the case because 1) some polygons (mainly from t_1) lay on the border of two districts and those districts were mapped in different years in the other time interval (mainly t_2); 2) of different mapping projects that ran in different years; and 3) case-specific remappings of sites. Thus, for those cases, we always compared a polygon from one year with several polygons from several years.

While for the species analysis across all polygons we included polygons with no or insufficient habitat type information, we had to reduce the dataset to polygons with sufficient habitat type information for trends within habitat types and the assignment of species' preferred habitat types. Habitat mapping keys changed over time, with formerly 69 and recently 577 habitat types (Landesamt für Landwirtschaft Umwelt und ländliche Räume des Landes Schleswig-Holstein, 2017; Landesamt für Naturschutz und Landschaftspflege Schleswig-Holstein, 1991). To make the types between time intervals, but also between all three states comparable, we aggregated all 646 detailed types to 12 broad habitat type groups. There were no species lists available for the two additional groups out of the 14 that were used for analysis, i.e. for anthropogenic habitats and farmland. See table S3 for all assignments. Generally, the mapping key includes two types of habitat types, one is based on the structure of a location and one is based on the vegetation of a site. Polygons that have habitat types from both categories assigned can have a summed cover of all habitat types of up to 200%. Cases with a summed cover of >200% were excluded if the mapped habitat types were from different broad habitat type groups, otherwise the cover was set to 100%. Polygons without a main habitat type covering min. 51% of its area had to be excluded.

For taxonomic harmonization, all species were aggregated to the section level and cleaned in accordance with the species lists from the other two states. For SH, this resulted in 1301 species.

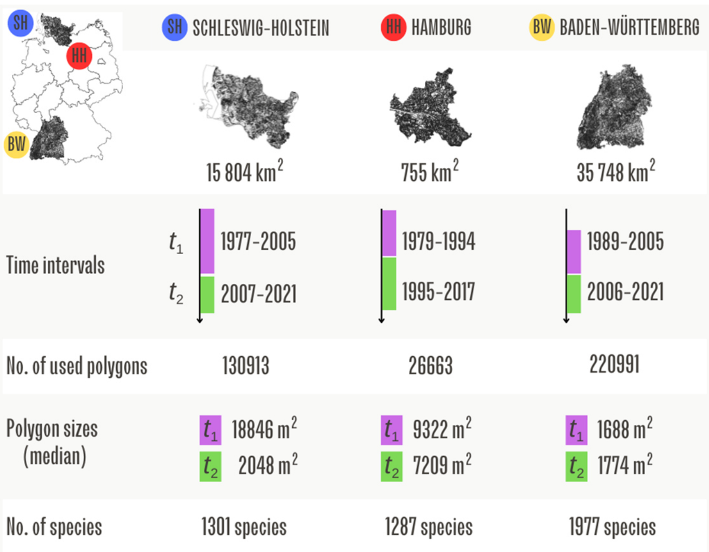

Figure S1 Overview of the three federal states used for analysis. Data for area of states is based on Statistisches Bundesamt 2023. All information on the mapping data is based on the adjusted data set.

Table S1 Polygon numbers and sizes for the three states and two time intervals. Based on the complete cleaned data set, which still includes non-intersecting polygons as they were included for the calculation of the Beals co-occurrence matrix and species' habitat type preferences.

Federal state	Time	Number polygons	Polygon area [m²] mean	median	min	max
SH	both	130913	18661	2547	1	29025586
	t_1	13435	105953	18846	2	28816471
	t_2	117478	8590	2048	1	29025586
HH	both	26663	21170	7421	1	2111000
	t_1	2769	30974	9322	1	2025152
	t_2	23894	20034	7209	12	2111000
BW	both	220991	6898	1731	2	7403074
	t_1	108865	7182	1688	5	6999119
	t_2	112222	6626	1774	2	7403074

(a) (b) (c)

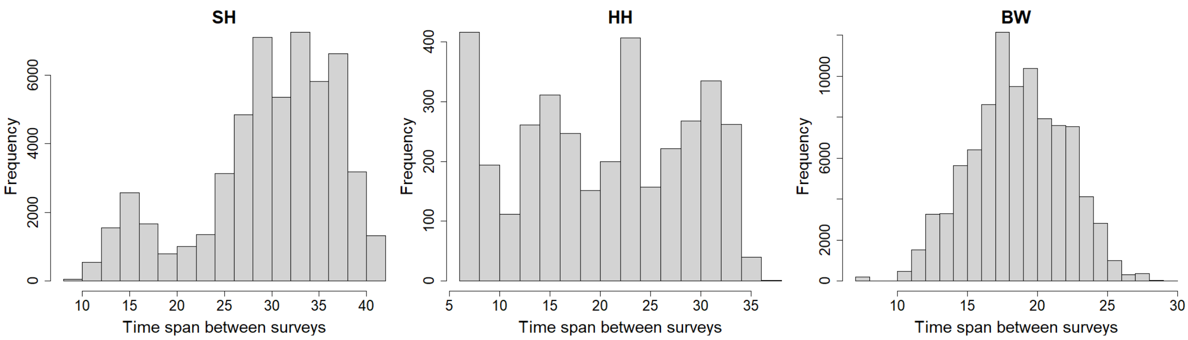

Figure S2 Time spans between surveys t_1 and t_2 for **(a)** SH, **(b)** HH and **(c)** BW. Based on intersection data used for trend analysis. For SH, in cases where polygons of several years intersected with one polygon of the other time interval, mean values of those mapped polygons' years were calculated.

(a) (b) (c) (d)

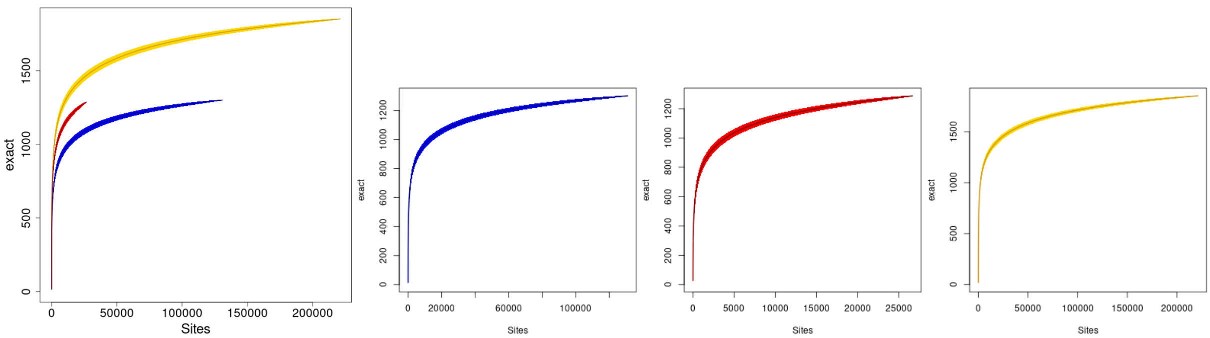

Figure S3 Accumulation curve of species recorded in polygons for **(a)** all states, separated by colour with SH in blue, HH in red and BW in yellow; and separately for **(b)** SH, **(c)** HH, **(d)** BW. Sites on the x-axis refer to the number of polygons sampled and exact on the y-axis refers to the number of species recorded.

Table S2 The 14 habitat type groups used for analysis. With "x" in the columns SH, HH, and BW indicating that a group was mapped in the respective federal state.

Habitat type group	SH	HH	BW
Coastal and marine habitats	x		
Heaths, inland dunes and semi-natural grasslands	x	x	x

Mesic grasslands	x	x	x
Moist to wet grasslands	x	x	x
Fresh water vegetation, springs and reeds	x		x
Linear and running surface waters	x	x	
Standing waters	x	x	
Bogs, transition mires, marshes and fens	x	x	x
Scrubs, copses and field hedges	x	x	x
Dry to moderately moist forests	x	x	x
Moist to wet forests	x	x	x
Ruderal, fringe and tall forb communities, clearings	x	x	x
Farmland		x	
Anthropogenic		x	

Table S3 All habitat types included per habitat type group in each state. The column "Code" indicates the state's specific habitat type code and corresponds to the German name of each habitat type. Groups correspond to the groups listed in table S2. NAs in this column indicate that the habitat type was not used for analysis, mainly because there were no species lists available. The column "Time" for the state SH indicates if this habitat type category was mapped during the first (1) or second (2) time interval.

Due to the length of table S3 it can only be found online in Appendix S1 in the Supplementary Material section as "Table S1.3" at: https://doi.org/10.1101/2025.02.27.640325

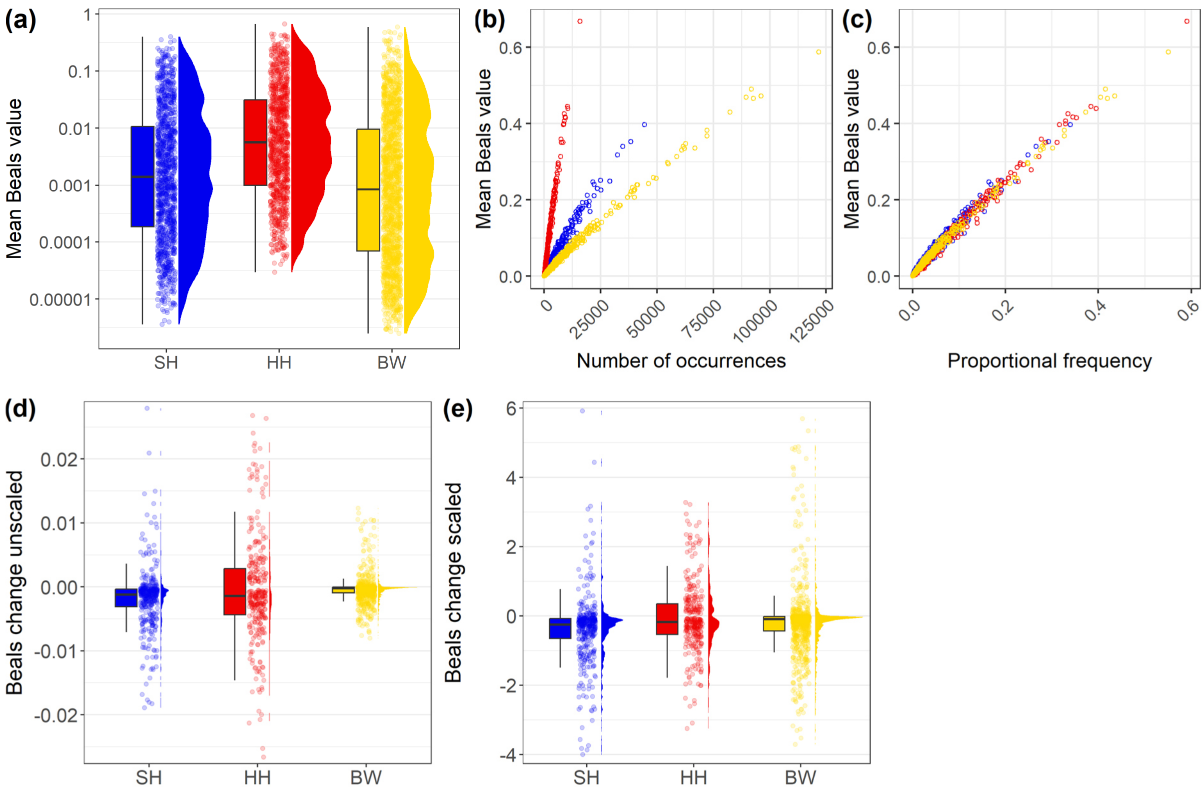

Figure S4 Mean Beals and Beals change values for each species across each state. **(a)** Species mean Beals values, **(b)** species mean Beals values in relation to the number of the species' occurrences in a state (polygons), **(c)** species mean Beals values in relation to the proportional frequency of each species in a state, **(d)** species mean Beals change values, and **(e)** standardized species mean Beals change values (mean Beals change/sd(mean Beals changes)). Dots for SH in blue, for HH in red, and for BW in yellow for all plots.

Table S4 Beals trends of all species that showed a significant trend in all states (105). Given are raw and scaled Beals trends of species within each state, including *n*, *t*, and *p* values (after Holm adjustment) according to *t* tests. In addition, each species' preferred habitat type and its mean scaled Beals trend across all states, derived from the three trends of each state, are given. Habitat type preferences are based on the fidelity (Φ) of species to habitat types in all states taken together. Beals trends were scaled per state as Beals trend/sd(Beals trends).

Species	n (SH)	Beals trend (SH)	t (SH)	p (SH)	Beals trend scaled (SH)	n (HH)	Beals trend (HH)	t (HH)	p (HH)	Beals trend scaled (HH)	n (BW)	Beals trend (BW)	t (BW)	p (BW)	Beals trend scaled (BW)	Habitat type preferred	Mean Beals trend
Festuca rubra agg.	2066	-0.0189	-31.73	<.001	-4.00	405	-0.0165	-11.83	<.001	-2.01	3200	-0.0028	-31.04	<.001	-1.28	Coastal and marine habitats	-2.43
Lotus pedunculatus	1538	-0.0109	-32.48	<.001	-2.30	254	-0.0087	-8.92	<.001	-1.07	3692	-0.006	-43.22	<.001	-2.79	Moist to wet grasslands	-2.05
Calluna vulgaris	1011	-0.0183	-46.43	<.001	-3.87	110	-0.0071	-7.31	<.001	-0.87	1834	-0.0026	-29.45	<.001	-1.21	Bogs, transition mires, marshes and fens	-1.98
Anthoxanthum odoratum agg.	1608	-0.0143	-32.57	<.001	-3.02	192	-0.009	-11.10	<.001	-1.10	2466	-0.0038	-44.67	<.001	-1.77	Moist to wet grasslands	-1.96
Cirsium palustre	2401	-0.0124	-34.91	<.001	-2.62	280	-0.0057	-6.17	<.001	-0.70	3916	-0.0052	-39.46	<.001	-2.41	Moist to wet grasslands	-1.91
Lychnis flos-cuculi	1180	-0.0127	-50.31	<.001	-2.70	154	-0.0056	-8.09	<.001	-0.68	2890	-0.0048	-43.79	<.001	-2.23	Moist to wet grasslands	-1.87
Hieracium pilosella	538	-0.0095	-31.78	<.001	-2.01	64	-0.0058	-10.12	<.001	-0.70	4046	-0.0058	-39.06	<.001	-2.70	Heaths, inland dunes and semi-natural grasslands	-1.80
Potentilla erecta	896	-0.0111	-63.15	<.001	-2.34	85	-0.0032	-9.68	<.001	-0.39	3204	-0.0054	-44.18	<.001	-2.49	Moist to wet grasslands	-1.74
Juncus articulatus	1290	-0.0125	-41.77	<.001	-2.64	176	-0.0067	-8.10	<.001	-0.82	1543	-0.0027	-44.16	<.001	-1.25	Moist to wet grasslands	-1.57
Carex panicea	486	-0.008	-69.78	<.001	-1.70	25	-0.0009	-6.91	<.001	-0.11	2702	-0.0056	-45.84	<.001	-2.59	Moist to wet grasslands	-1.47
Luzula campestris agg.	978	-0.011	-52.93	<.001	-2.33	134	-0.0056	-10.53	<.001	-0.69	1674	-0.0024	-36.51	<.001	-1.11	Heaths, inland dunes and semi-natural grasslands	-1.38
Rumex acetosella s. l.	866	-0.0099	-35.39	<.001	-2.09	221	-0.0144	-13.76	<.001	-1.76	965	-0.0006	-12.38	<.001	-0.27	Heaths, inland dunes and semi-natural grasslands	-1.37
Lotus corniculatus agg.	507	-0.0054	-33.28	<.001	-1.14	84	-0.0059	-11.45	<.001	-0.72	4168	-0.0048	-34.89	<.001	-2.22	Heaths, inland dunes and semi-natural grasslands	-1.36
Festuca ovina agg.	448	-0.0073	-39.01	<.001	-1.55	104	-0.0073	-10.04	<.001	-0.89	2152	-0.0028	-34.62	<.001	-1.30	Heaths, inland dunes and semi-natural grasslands	-1.24
Viola palustris	764	-0.0097	-66.83	<.001	-2.06	64	-0.0015	-6.30	<.001	-0.18	1558	-0.0031	-36.92	<.001	-1.42	Moist to wet grasslands	-1.22
Ranunculus flammula agg.	964	-0.0082	-38.13	<.001	-1.73	158	-0.0046	-6.06	<.001	-0.56	1685	-0.0029	-38.47	<.001	-1.33	Moist to wet grasslands	-1.21
Vicia cracca agg.	764	-0.0055	-32.07	<.001	-1.16	306	-0.0132	-13.87	<.001	-1.61	2634	-0.0019	-38.03	<.001	-0.87	Mesic grasslands	-1.21
Lathyrus pratensis	986	-0.0055	-26.70	<.001	-1.16	219	-0.0086	-10.20	<.001	-1.05	2433	-0.0029	-48.33	<.001	-1.33	Moist to wet grasslands	-1.18
Cardamine pratensis agg.	1324	-0.01	-25.69	<.001	-2.11	194	-0.005	-6.26	<.001	-0.61	1424	-0.0017	-37.34	<.001	-0.77	Moist to wet grasslands	-1.17
Campanula rotundifolia agg.	372	-0.005	-33.62	<.001	-1.06	37	-0.0021	-9.82	<.001	-0.26	4148	-0.0046	-36.24	<.001	-2.12	Heaths, inland dunes and semi-natural grasslands	-1.15
Agrostis stolonifera agg.	2554	-0.0063	-14.77	<.001	-1.33	558	-0.0115	-10.46	<.001	-1.41	1227	-0.0013	-27.79	<.001	-0.61	Coastal and marine habitats	-1.12
Potentilla anserina	1218	-0.0071	-22.57	<.001	-1.49	360	-0.0102	-10.91	<.001	-1.25	585	-0.0006	-25.28	<.001	-0.28	Coastal and marine habitats	-1.01
Hydrocotyle vulgaris	929	-0.0129	-68.22	<.001	-2.73	60	-0.0017	-6.85	<.001	-0.21	15	0	-12.42	<.001	-0.01	Bogs, transition mires, marshes and fens	-0.98
Juncus acutiflorus	197	-0.0018	-35.85	<.001	-0.38	48	-0.0015	-6.43	<.001	-0.19	2752	-0.0051	-40.61	<.001	-2.34	Moist to wet grasslands	-0.97
Bistorta officinalis	52	-0.0007	-28.39	<.001	-0.15	62	-0.0015	-6.14	<.001	-0.18	3288	-0.0052	-44.68	<.001	-2.41	Moist to wet grasslands	-0.91
Nardus stricta	264	-0.0043	-48.71	<.001	-0.92	35	-0.0031	-7.06	<.001	-0.38	1530	-0.0031	-34.45	<.001	-1.42	Heaths, inland dunes and semi-natural grasslands	-0.90
Achillea ptarmica agg.	515	-0.007	-68.97	<.001	-1.48	104	-0.0043	-13.79	<.001	-0.52	819	-0.0012	-34.58	<.001	-0.55	Moist to wet grasslands	-0.85
Equisetum palustre	1162	-0.004	-20.85	<.001	-0.85	263	-0.0049	-6.74	<.001	-0.60	1643	-0.0023	-40.81	<.001	-1.08	Moist to wet grasslands	-0.84
Galium saxatile	738	-0.0063	-41.16	<.001	-1.33	112	-0.0028	-6.26	<.001	-0.34	973	-0.0016	-28.33	<.001	-0.76	Heaths, inland dunes and semi-natural grasslands	-0.81
Carex echinata	201	-0.0032	-59.99	<.001	-0.67	21	-0.0009	-7.66	<.001	-0.11	1606	-0.0035	-37.46	<.001	-1.63	Moist to wet grasslands	-0.80

Carex leporina	490	-0.0049	-38.82	<.001	-1.03	107	-0.0048	-11.87	<.001	-0.58	982	-0.0016	-35.59	<.001	-0.72	Moist to wet grasslands	-0.78
Festuca pratensis s. l.	553	-0.0046	-27.75	<.001	-0.97	191	-0.0074	-10.64	<.001	-0.91	714	-0.001	-35.08	<.001	-0.45	Moist to wet grasslands	-0.78
Juncus conglomeratus	524	-0.0051	-52.89	<.001	-1.09	82	-0.0032	-10.24	<.001	-0.39	1048	-0.0017	-41.59	<.001	-0.79	Moist to wet grasslands	-0.76
Prunella vulgaris	378	-0.004	-39.41	<.001	-0.85	108	-0.0049	-12.40	<.001	-0.60	1226	-0.0018	-46.60	<.001	-0.83	Heaths, inland dunes and semi-natural grasslands	-0.76
Dactylorhiza majalis agg.	294	-0.0051	-67.22	<.001	-1.08	16	-0.0007	-6.24	<.001	-0.09	1059	-0.0023	-38.16	<.001	-1.04	Moist to wet grasslands	-0.74
Galium uliginosum	402	-0.0042	-51.90	<.001	-0.88	35	-0.0009	-5.88	<.001	-0.11	1536	-0.0026	-40.70	<.001	-1.22	Moist to wet grasslands	-0.74
Succisa pratensis	216	-0.0043	-68.17	<.001	-0.92	11	-0.0006	-8.21	<.001	-0.07	1353	-0.0027	-43.53	<.001	-1.23	Moist to wet grasslands	-0.74
Persicaria amphibia	1272	-0.0048	-22.20	<.001	-1.02	250	-0.0067	-8.52	<.001	-0.82	493	-0.0006	-24.46	<.001	-0.30	Standing waters	-0.72
Centaurea jacea agg.	146	-0.0017	-30.77	<.001	-0.36	12	-0.0012	-7.87	<.001	-0.14	3258	-0.0035	-34.94	<.001	-1.60	Heaths, inland dunes and semi-natural grasslands	-0.70
Alopecurus geniculatus	760	-0.0057	-24.91	<.001	-1.20	115	-0.0055	-10.88	<.001	-0.67	80	-0.0001	-12.15	<.001	-0.06	Moist to wet grasslands	-0.64
Trifolium arvense	268	-0.0042	-26.80	<.001	-0.90	59	-0.0071	-11.12	<.001	-0.87	107	-0.0002	-8.14	<.001	-0.08	Mesic grasslands	-0.61
Carex flava agg.	152	-0.0031	-60.16	<.001	-0.65	16	-0.0008	-8.98	<.001	-0.09	998	-0.0022	-41.60	<.001	-1.03	Moist to wet grasslands	-0.59
Juncus inflexus	326	-0.0017	-24.37	<.001	-0.36	29	-0.0008	-6.08	<.001	-0.10	1996	-0.0026	-36.67	<.001	-1.22	Fresh water vegetation, springs and reeds	-0.56
Jasione montana	238	-0.0052	-34.23	<.001	-1.11	24	-0.0035	-9.59	<.001	-0.42	120	-0.0002	-10.58	<.001	-0.10	Heaths, inland dunes and semi-natural grasslands	-0.54
Epilobium angustifolium	370	-0.0014	-20.04	<.001	-0.29	272	-0.0062	-11.97	<.001	-0.76	1104	-0.0007	-23.70	<.001	-0.33	Coastal and marine habitats	-0.46
Linaria vulgaris agg.	271	-0.0024	-27.86	<.001	-0.51	107	-0.005	-13.26	<.001	-0.61	1532	-0.0006	-14.51	<.001	-0.26	Scrubs, copses and field hedges	-0.46
Tripleurospermum maritimum agg.	130	-0.0012	-19.13	<.001	-0.26	102	-0.009	-14.75	<.001	-1.10	46	-0.0001	-16.06	<.001	-0.04	Coastal and marine habitats	-0.46
Danthonia decumbens	150	-0.0024	-40.47	<.001	-0.50	26	-0.0023	-6.76	<.001	-0.28	937	-0.0012	-25.62	<.001	-0.55	Heaths, inland dunes and semi-natural grasslands	-0.44
Sedum acre	130	-0.0022	-26.29	<.001	-0.46	20	-0.0024	-8.36	<.001	-0.30	745	-0.0012	-30.19	<.001	-0.57	Heaths, inland dunes and semi-natural grasslands	-0.44
Tussilago farfara	198	-0.0016	-24.27	<.001	-0.35	148	-0.0067	-15.28	<.001	-0.82	334	-0.0003	-15.33	<.001	-0.15	Ruderal, fringe and tall forb communities, clearings	-0.44
Juncus bufonius agg.	308	-0.0036	-43.62	<.001	-0.77	67	-0.0028	-9.26	<.001	-0.35	130	-0.0003	-23.44	<.001	-0.12	Standing waters	-0.41
Juncus squarrosus	176	-0.0031	-46.17	<.001	-0.67	24	-0.0018	-7.17	<.001	-0.21	284	-0.0007	-27.84	<.001	-0.32	Heaths, inland dunes and semi-natural grasslands	-0.40
Alchemilla vulgaris agg.	110	-0.0013	-42.43	<.001	-0.27	18	-0.0008	-7.96	<.001	-0.09	1198	-0.0017	-44.13	<.001	-0.79	Moist to wet grasslands	-0.39
Viola tricolor agg.	126	-0.0021	-27.45	<.001	-0.44	44	-0.0044	-12.53	<.001	-0.54	54	-0.0001	-14.85	<.001	-0.04	Coastal and marine habitats	-0.34
Stachys palustris	802	-0.0025	-23.02	<.001	-0.52	214	-0.0024	-4.48	<.001	-0.29	741	-0.0004	-13.91	<.001	-0.18	Fresh water vegetation, springs and reeds	-0.33
Juncus filiformis	180	-0.0027	-56.96	<.001	-0.58	17	-0.0007	-6.21	<.001	-0.08	272	-0.0005	-30.70	<.001	-0.25	Moist to wet grasslands	-0.30
Bidens tripartita	228	-0.0027	-46.44	<.001	-0.58	73	-0.0019	-7.10	<.001	-0.23	26	-0.0001	-11.71	<.001	-0.03	Standing waters	-0.28
Erodium cicutarium agg.	97	-0.0014	-25.63	<.001	-0.29	22	-0.0035	-9.90	<.001	-0.43	83	-0.0002	-8.35	<.001	-0.09	Heaths, inland dunes and semi-natural grasslands	-0.27
Festuca arundinacea	371	-0.0015	-19.07	<.001	-0.32	126	-0.0027	-8.66	<.001	-0.33	378	-0.0002	-11.74	<.001	-0.10	Coastal and marine habitats	-0.25
Hieracium umbellatum	93	-0.0025	-39.83	<.001	-0.53	20	-0.001	-8.01	<.001	-0.12	369	-0.0002	-13.78	<.001	-0.10	Coastal and marine habitats	-0.25
Mentha arvensis	84	-0.0008	-32.58	<.001	-0.16	82	-0.0031	-12.47	<.001	-0.37	234	-0.0003	-20.27	<.001	-0.12	Moist to wet grasslands	-0.22
Poa palustris	190	-0.0012	-30.71	<.001	-0.25	138	-0.0028	-8.16	<.001	-0.34	122	-0.0001	-10.86	<.001	-0.05	Linear and running surface waters	-0.21
Gnaphalium uliginosum	84	-0.0009	-23.99	<.001	-0.19	37	-0.0029	-11.43	<.001	-0.35	28	0	-8.94	<.001	-0.02	Standing waters	-0.19
Senecio viscosus	59	-0.0007	-17.42	<.001	-0.15	33	-0.0028	-11.10	<.001	-0.34	28	0	-8.39	<.001	-0.01	Coastal and marine habitats	-0.17
Sonchus arvensis agg.	290	-0.0014	-16.44	<.001	-0.30	30	-0.0014	-9.12	<.001	-0.18	48	0	-5.80	<.001	-0.02	Coastal and marine habitats	-0.17
Hypericum maculatum agg.	112	-0.0008	-35.56	<.001	-0.18	37	-0.0009	-6.81	<.001	-0.11	408	-0.0004	-22.52	<.001	-0.17	Heaths, inland dunes and semi-natural grasslands	-0.15
Gnaphalium sylvaticum	24	-0.0004	-20.50	<.001	-0.08	44	-0.0025	-14.07	<.001	-0.31	52	-0.0001	-14.62	<.001	-0.03	Heaths, inland dunes and semi-natural grasslands	-0.14
Oenanthe aquatica agg.	431	-0.001	-12.25	<.001	-0.21	68	-0.0015	-5.21	<.001	-0.18	22	0	-6.12	<.001	-0.02	Standing waters	-0.14
Epipactis helleborine agg.	194	-0.0014	-29.55	<.001	-0.29	18	0.001	9.15	<.001	0.13	872	-0.0004	-15.33	<.001	-0.20	Dry to moderately moist forests	-0.12

Elymus repens s. str.	727	0.0025	21.11	<.001	0.53	594	-0.0134	-11.34	<.001	-1.63	3962	0.0018	27.24	<.001	0.85	Scrubs, copses and field hedges	-0.09
Elymus caninus	48	-0.0004	-20.45	<.001	-0.08	18	-0.0006	-6.66	<.001	-0.07	616	0.0003	14.51	<.001	0.13	Moist to wet forests	-0.01
Veronica hederifolia agg.	196	0.0012	25.41	<.001	0.25	14	0.0009	8.86	<.001	0.11	209	-0.0001	-9.72	<.001	-0.07	Dry to moderately moist forests	0.10
Rosa multiflora	11	0.0001	16.51	<.001	0.03	36	0.0018	12.64	<.001	0.23	326	0.0004	25.10	<.001	0.19	Scrubs, copses and field hedges	0.15
Cardamine flexuosa	370	0.0011	19.97	<.001	0.23	18	0.0008	6.89	<.001	0.10	282	0.0003	16.31	<.001	0.14	Dry to moderately moist forests	0.16
Chrysosplenium oppositifolium	774	0.0014	11.90	<.001	0.30	7	0.0012	12.31	<.001	0.14	1250	0.0009	16.03	<.001	0.40	Moist to wet forests	0.28
Chelidonium majus	104	0.0009	30.05	<.001	0.19	41	0.0033	13.69	<.001	0.40	1488	0.0007	17.02	<.001	0.32	Scrubs, copses and field hedges	0.30
Quercus rubra	208	0.0013	26.60	<.001	0.27	105	0.0048	11.99	<.001	0.59	461	0.0004	21.35	<.001	0.18	Dry to moderately moist forests	0.35
Fallopia bohemica_Fallopia japonica_Fallopia sachalinensis	138	0.0008	21.52	<.001	0.16	208	0.0056	10.52	<.001	0.69	439	0.0005	32.12	<.001	0.25	Anthropogenic	0.37
Symphoricarpos albus	78	0.0006	28.23	<.001	0.13	122	0.007	14.45	<.001	0.85	400	0.0005	29.71	<.001	0.21	Anthropogenic	0.40
Ficaria verna s. l.	2319	0.0055	22.15	<.001	1.16	72	0.0046	15.85	<.001	0.56	2699	-0.0009	-12.18	<.001	-0.44	Dry to moderately moist forests	0.43
Taxus baccata	116	0.0008	30.14	<.001	0.17	100	0.0091	17.72	<.001	1.11	360	0.0004	14.16	<.001	0.18	Anthropogenic	0.49
Ribes rubrum agg.	1397	0.0041	32.59	<.001	0.87	98	0.0077	19.34	<.001	0.95	1218	0.0008	25.47	<.001	0.35	Moist to wet forests	0.72
Impatiens noli-tangere	1702	0.0053	29.71	<.001	1.13	54	0.0032	11.64	<.001	0.39	3682	0.0016	17.56	<.001	0.72	Moist to wet forests	0.75
Impatiens glandulifera	388	0.002	38.02	<.001	0.42	99	0.0044	14.20	<.001	0.54	3699	0.0029	38.41	<.001	1.35	Moist to wet forests	0.77
Humulus lupulus	1240	0.0018	14.86	<.001	0.39	193	0.007	13.67	<.001	0.86	3668	0.0024	41.05	<.001	1.11	Moist to wet forests	0.79
Salix fragilis agg.	1150	0.0054	38.60	<.001	1.14	208	0.0038	7.52	<.001	0.47	5566	0.0018	18.23	<.001	0.83	Moist to wet forests	0.81
Sorbus aucuparia	3506	0.0058	12.10	<.001	1.23	533	0.0171	10.35	<.001	2.09	6278	-0.0017	-18.38	<.001	-0.79	Dry to moderately moist forests	0.85
Prunus serotina	1558	0.0051	24.79	<.001	1.09	255	0.0108	13.13	<.001	1.32	360	0.0004	21.17	<.001	0.20	Dry to moderately moist forests	0.87
Athyrium filix-femina	1942	0.0052	24.98	<.001	1.10	189	0.0093	15.58	<.001	1.13	4008	0.0023	22.86	<.001	1.08	Moist to wet forests	1.10
Juglans regia	21	0.0002	20.12	<.001	0.03	32	0.0022	12.05	<.001	0.26	6497	0.0066	68.73	<.001	3.04	Scrubs, copses and field hedges	1.11
Prunus padus	1417	0.0042	26.59	<.001	0.89	208	0.017	20.27	<.001	2.08	4686	0.0023	32.55	<.001	1.06	Moist to wet forests	1.34
Circaea lutetiana	2698	0.0063	17.35	<.001	1.34	120	0.0108	19.00	<.001	1.32	3252	0.0032	44.64	<.001	1.47	Dry to moderately moist forests	1.38
Galium aparine agg.	2587	0.0093	42.40	<.001	1.97	466	0.0071	9.25	<.001	0.87	12650	0.003	23.39	<.001	1.38	Scrubs, copses and field hedges	1.40
Rubus sect. *Caesii*	724	0.0016	22.10	<.001	0.35	101	0.0062	17.43	<.001	0.76	9583	0.0073	65.89	<.001	3.38	Scrubs, copses and field hedges	1.49
Dryopteris carthusiana agg.	4632	0.0099	22.99	<.001	2.09	382	0.0151	12.31	<.001	1.84	3582	0.0017	18.03	<.001	0.81	Dry to moderately moist forests	1.58
Carex remota	2979	0.0145	43.87	<.001	3.08	104	0.008	17.11	<.001	0.98	1942	0.002	29.95	<.001	0.94	Standing waters	1.67
Geranium robertianum agg.	2120	0.0076	27.42	<.001	1.60	90	0.0065	17.62	<.001	0.80	11282	0.0063	47.14	<.001	2.92	Scrubs, copses and field hedges	1.77
Impatiens parviflora	1948	0.0109	45.78	<.001	2.31	483	0.0241	15.77	<.001	2.94	1208	0.0008	21.84	<.001	0.37	Dry to moderately moist forests	1.87
Alliaria petiolata	1180	0.0055	29.79	<.001	1.15	250	0.0167	19.67	<.001	2.05	9350	0.0079	68.08	<.001	3.66	Scrubs, copses and field hedges	2.29
Galeobdolon luteum agg.	3294	0.013	27.37	<.001	2.75	220	0.0184	20.16	<.001	2.25	5666	0.0041	38.89	<.001	1.92	Dry to moderately moist forests	2.31
Glechoma hederacea agg.	4288	0.015	49.83	<.001	3.17	782	0.0188	18.15	<.001	2.30	7063	0.0038	44.29	<.001	1.78	Moist to wet forests	2.42
Geum urbanum	2633	0.0083	23.78	<.001	1.75	348	0.0263	21.28	<.001	3.22	15057	0.0104	64.45	<.001	4.82	Scrubs, copses and field hedges	3.26
Fraxinus excelsior	3544	0.01	16.82	<.001	2.12	444	0.0216	18.70	<.001	2.64	22786	0.0115	64.85	<.001	5.34	Scrubs, copses and field hedges	3.37
Rubus sect. *Rubus*	5653	0.0209	36.33	<.001	4.43	796	0.0184	12.50	<.001	2.24	17402	0.0105	71.24	<.001	4.86	Scrubs, copses and field hedges	3.85
Urtica dioica s. l.	7535	0.0279	51.70	<.001	5.91	1270	0.014	10.65	<.001	1.72	28635	0.0093	45.61	<.001	4.29	Scrubs, copses and field hedges	3.97

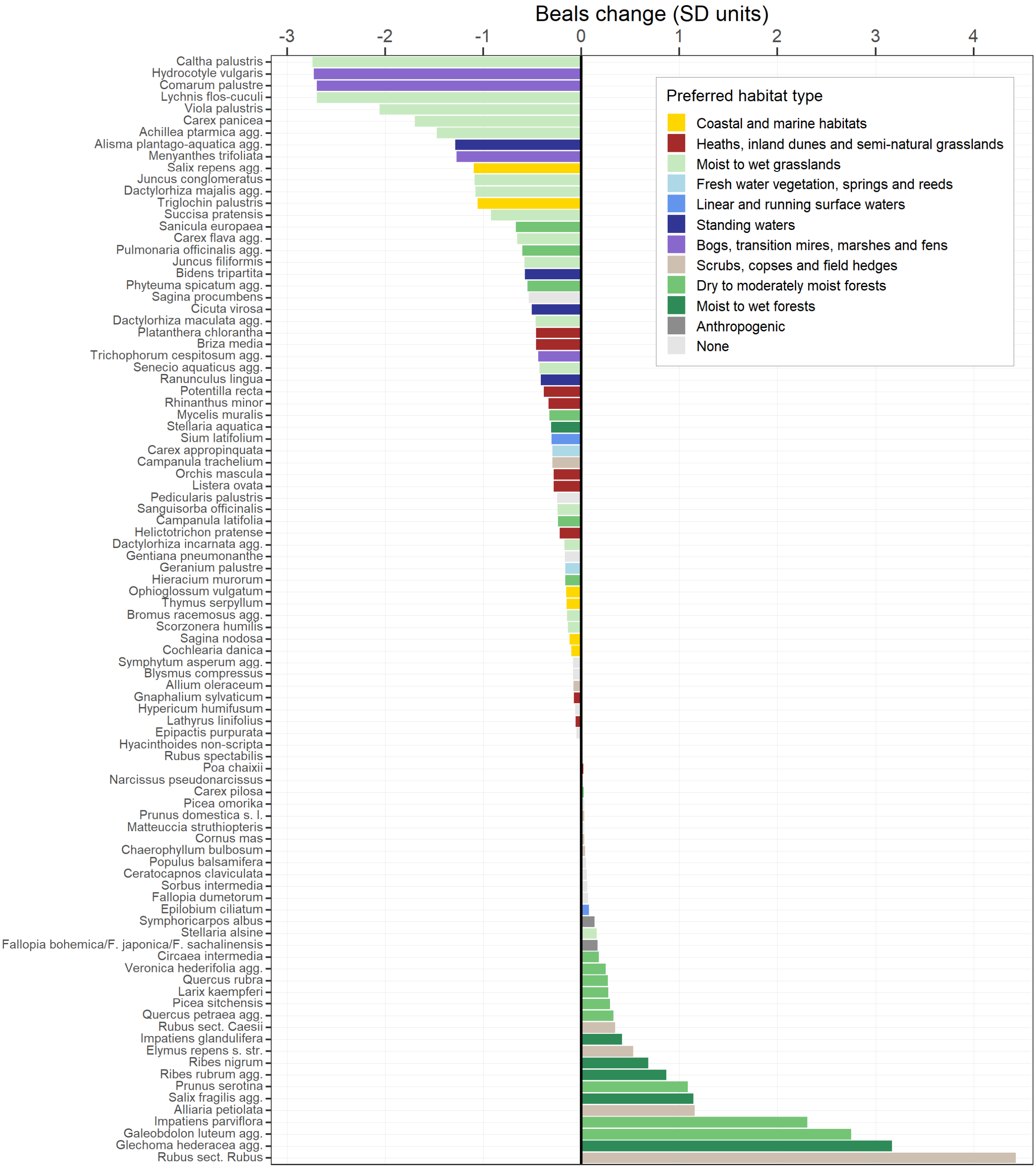

Figure S5 Beals trends of species that showed significant and consistent trends for Beals and frequency in SH (94 species). Colours indicate the species' preferred habitat type.

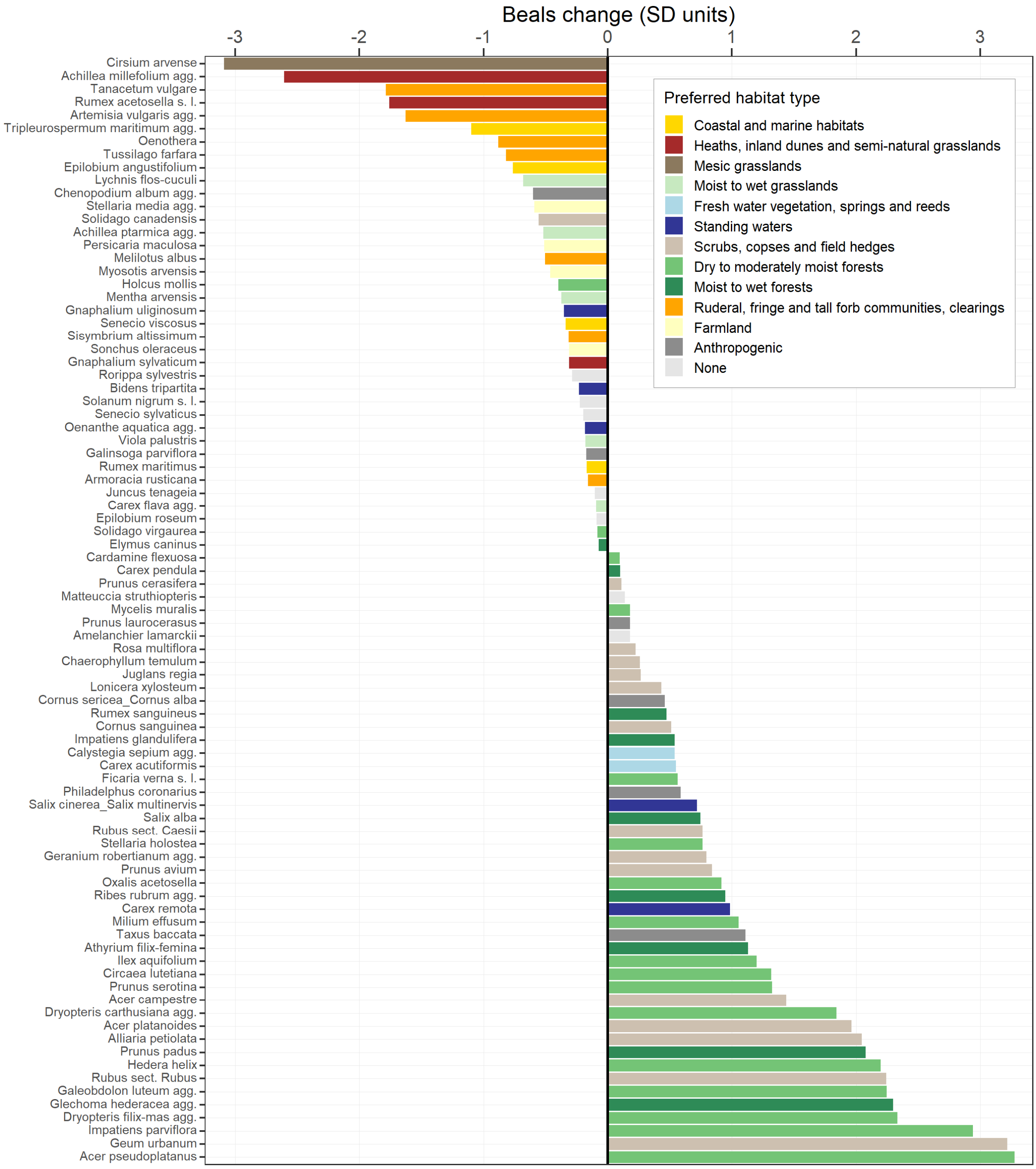

Figure S6 Beals trends of species that showed significant and consistent trends for Beals and frequency in HH (85 species). Colours indicate the species' preferred habitat type.

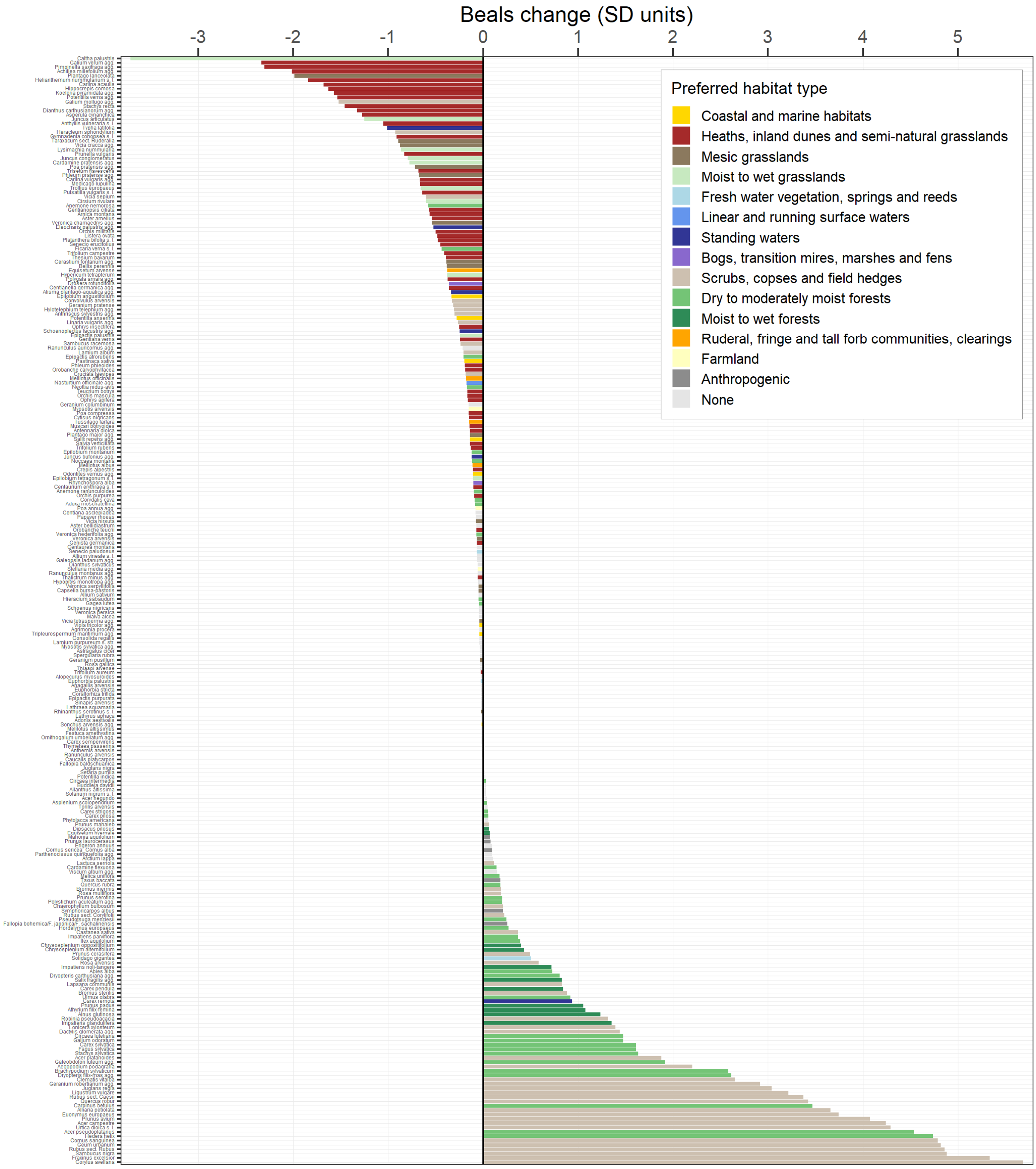

Figure S7 Beals trends of species that showed significant and consistent trends for Beals and frequency in BW (256 species). Colours indicate the species' preferred habitat type.

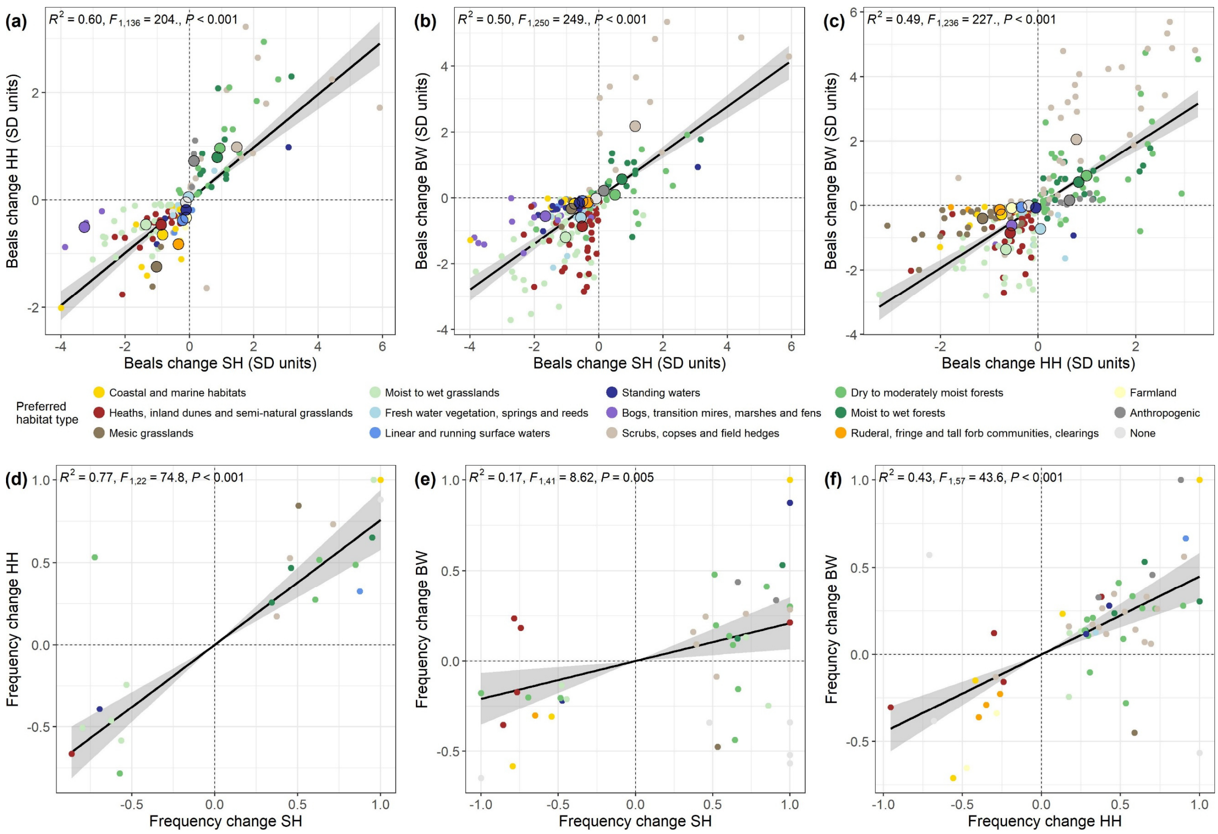

Figure S8 Comparison of species trends in two states each, concerning **(a-c)** Beals and **(d-f)** frequency. Species are coloured by their preferred habitat type. Thick dots in **(a-c)** represent mean trends per species of a preferred habitat type. Only species are included that showed a significant trend in both states each. Regression lines were obtained from a linear model, including 95% confidence intervals.

Table S5 Mean and Median Beals trends of species grouped by their preferred habitat type and by state. Only species were included per group that showed a significant trend in the respective state and that had a preferred habitat type assigned. The state category "Across" includes all species that showed a significant trend in all states and its values refer to the mean and median of those species mean trends across all states, derived from the three trends of each state. *n* is given for number of species with a significant trend that are included in each group. *p* values indicate whether a group's trend deviated from zero change according to Wilcoxon signed rank tests.

Habitat type preferred	State	n	Mean trend	Median trend	p
Anthropogenic	SH	4	0.136	0.149	0.125
Anthropogenic	HH	13	0.338	0.240	0.04
Anthropogenic	BW	8	0.163	0.140	0.008
Anthropogenic	Across	3	0.418	0.400	0.25
Bogs, transition mires, marshes and fens	SH	25	-1.531	-1.274	< 0.001
Bogs, transition mires, marshes and fens	HH	3	-0.503	-0.423	0.25
Bogs, transition mires, marshes and fens	BW	29	-0.463	-0.311	< 0.001
Bogs, transition mires, marshes and fens	Across	2	-1.484	-1.484	0.5
Coastal and marine habitats	SH	67	-0.427	-0.232	< 0.001
Coastal and marine habitats	HH	18	-0.576	-0.344	< 0.001
Coastal and marine habitats	BW	25	-0.161	-0.066	< 0.001
Coastal and marine habitats	Across	10	-0.665	-0.400	0.002
Dry to moderately moist forests	SH	36	0.267	0.038	0.315
Dry to moderately moist forests	HH	45	0.872	0.522	< 0.001
Dry to moderately moist forests	BW	84	0.339	0.002	0.06
Dry to moderately moist forests	Across	11	0.887	0.845	0.003

Farmland	SH	2	-0.106	-0.106	0.5
Farmland	HH	10	-0.379	-0.356	0.002
Farmland	BW	4	-0.078	-0.068	0.125
Fresh water vegetation, springs and reeds	SH	18	-0.469	-0.410	< 0.001
Fresh water vegetation, springs and reeds	HH	6	0.128	0.153	0.438
Fresh water vegetation, springs and reeds	BW	28	-0.523	-0.277	< 0.001
Fresh water vegetation, springs and reeds	Across	2	-0.445	-0.445	0.5
Heaths, inland dunes and semi-natural grasslands	SH	59	-0.469	-0.291	< 0.001
Heaths, inland dunes and semi-natural grasslands	HH	34	-0.530	-0.334	< 0.001
Heaths, inland dunes and semi-natural grasslands	BW	220	-0.546	-0.298	< 0.001
Heaths, inland dunes and semi-natural grasslands	Across	17	-0.816	-0.759	< 0.001
Linear and running surface waters	SH	13	-0.454	-0.305	< 0.001
Linear and running surface waters	HH	3	-0.379	-0.342	0.25
Linear and running surface waters	BW	8	-0.092	-0.063	0.008
Linear and running surface waters	Across	1	-0.213	-0.213	1
Mesic grasslands	SH	4	-0.661	-0.706	0.125
Mesic grasslands	HH	40	-1.017	-0.840	< 0.001
Mesic grasslands	BW	35	-0.391	-0.200	< 0.001
Mesic grasslands	Across	2	-0.914	-0.914	0.5
Moist to wet forests	SH	25	0.361	0.300	0.052
Moist to wet forests	HH	22	0.706	0.471	< 0.001
Moist to wet forests	BW	26	0.389	0.377	0.006
Moist to wet forests	Across	10	0.897	0.778	0.004
Moist to wet grasslands	SH	57	-1.036	-0.974	< 0.001
Moist to wet grasslands	HH	35	-0.660	-0.558	< 0.001
Moist to wet grasslands	BW	92	-1.020	-0.758	< 0.001
Moist to wet grasslands	Across	27	-1.051	-0.849	< 0.001
None	SH	31	-0.068	-0.063	0.001
None	HH	16	-0.089	-0.114	0.051
None	BW	143	-0.027	-0.025	< 0.001
Ruderal, fringe and tall forb communities, clearings	SH	1	-0.348	-0.348	1
Ruderal, fringe and tall forb communities, clearings	HH	15	-0.713	-0.503	< 0.001
Ruderal, fringe and tall forb communities, clearings	BW	9	-0.135	-0.123	0.004
Ruderal, fringe and tall forb communities, clearings	Across	1	-0.438	-0.438	1
Scrubs, copses and field hedges	SH	20	1.102	0.371	0.002
Scrubs, copses and field hedges	HH	46	0.712	0.482	< 0.001
Scrubs, copses and field hedges	BW	70	1.328	0.579	< 0.001
Scrubs, copses and field hedges	Across	13	1.725	1.495	0.002
Standing waters	SH	27	-0.568	-0.529	< 0.001
Standing waters	HH	13	-0.040	-0.206	0.497
Standing waters	BW	28	-0.234	-0.150	< 0.001
Standing waters	Across	6	-0.010	-0.233	0.438

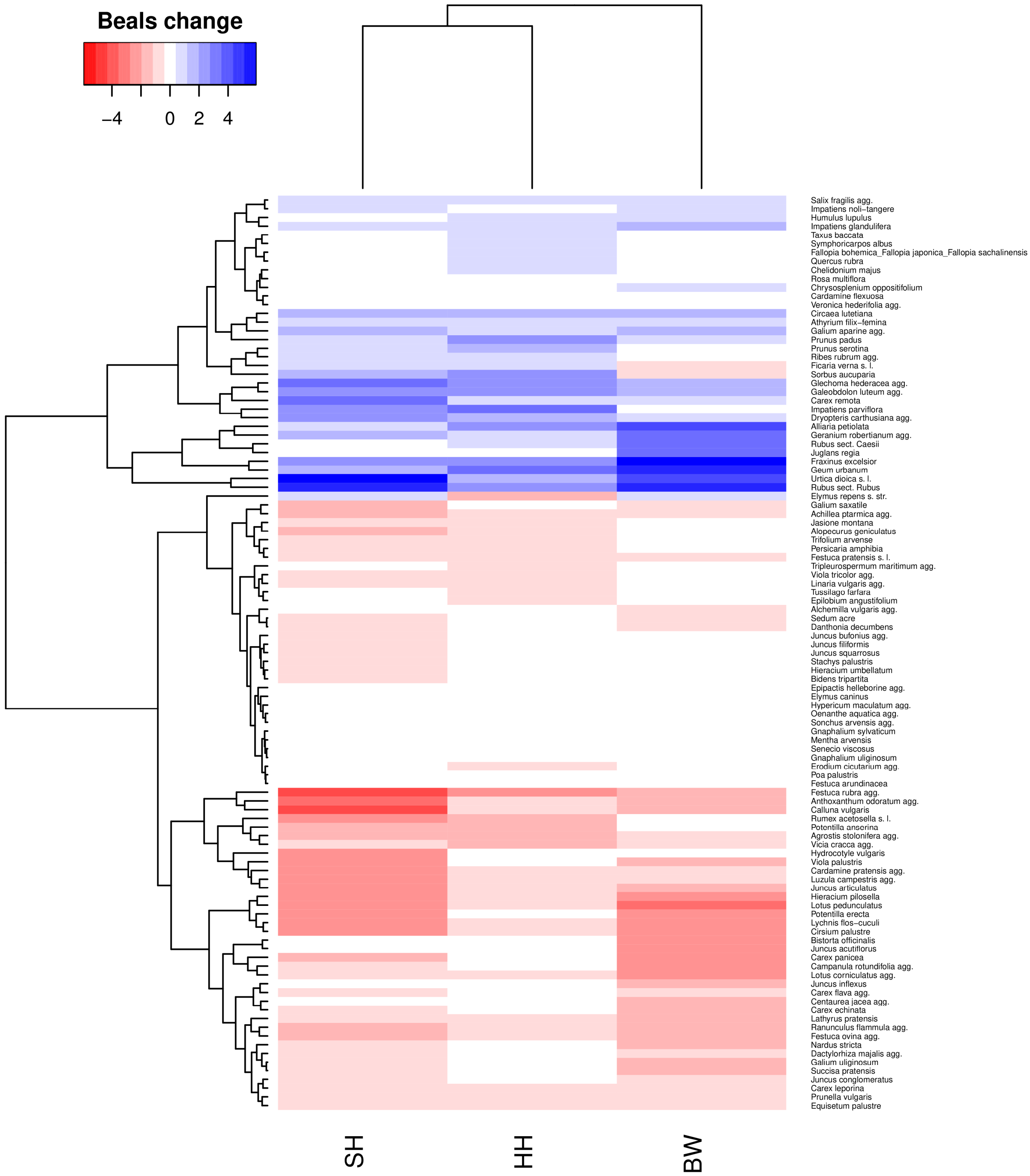

Figure S9 Beals trends in each state of the 105 species that showed a significant trend in all states. Beals trends were scaled per state as Beals trend/sd(Beals trends).

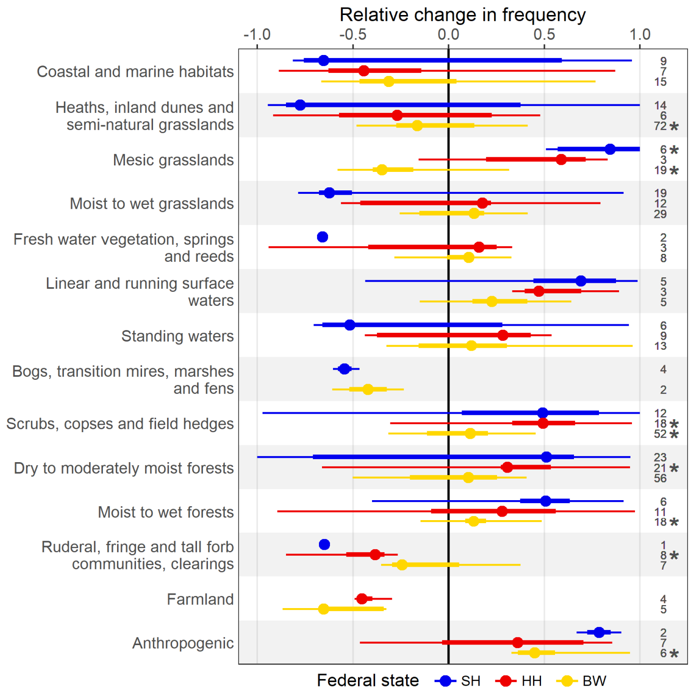

Figure S10 Frequency trends of species grouped by their preferred habitat type separately by state. Points, thick and thin whiskers show the median, 50% and 95% data range. Only species are included per group that showed a significant trend and that had a preferred habitat type assigned. *n* is given for number of species with a significant trend that are included in each combination of state and preferred habitat type. Asterisks indicate whether a group's trend deviated from zero change according to Wilcoxon signed rank tests. Habitat types correspond to the following EUNIS habitat types (European Nature Information System; European Environment Agency; Moss, 2008; 2021 version if not stated otherwise): Coastal and marine habitats (N1, N2, N3), Heaths, inland dunes and semi-natural grasslands (S4, R1), Mesic grasslands (R2), Moist to wet grasslands (R3), Fresh water vegetation, springs and reeds (C3, D5; based on EUNIS 2012 version) , Linear and running surface waters (C2, C3; based on EUNIS 2012 version), Standing waters (C1, C3; based on EUNIS 2012 version), Bogs, transition mires, marshes and fens (D1, D2, D4, D5; based on EUNIS 2012 version), Scrubs, copses and field hedges (S3, T4,V4), Dry to moderately moist forests (T1, T3, V6), Moist to wet forests (T1, T3), Ruderal, fringe and tall forb communities, clearings (V3, T4, R5), Farmland (V1, V5, V6), Anthropogenic (V2, V3).

Table S6 Mean and Median Beals trends of species grouped by their non-native status and by state. Only species were included per group that showed a significant trend in the respective state and that had a status assigned. *n* is given for number of species with a significant trend that are included in each group. *p* values indicate whether a group's trend deviated from zero change according to Wilcoxon signed rank tests.

Non-native status	State	n	Mean trend	Median trend	p
Native	SH	355	-0.452	-0.282	< 0.001
Native	HH	253	-0.066	-0.184	0.023
Native	BW	702	-0.223	-0.122	< 0.001
Archaeophyte	SH	3	-0.142	-0.079	0.5
Archaeophyte	HH	22	-0.440	-0.317	< 0.001
Archaeophyte	BW	54	-0.018	-0.038	< 0.001
Neophyte	SH	21	0.240	0.076	0.005
Neophyte	HH	34	0.190	0.174	0.138
Neophyte	BW	40	0.204	0.077	< 0.001

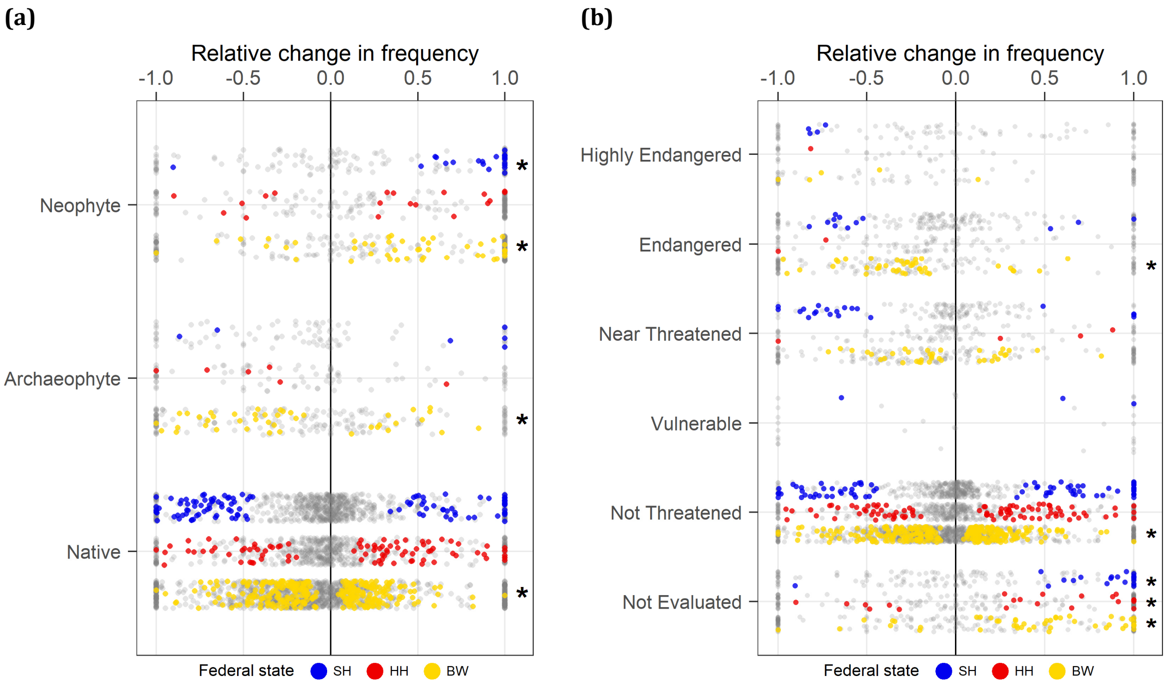

Figure S11 Frequency trends grouped by states and **(a)** non-native and **(b)** Red List status. **(a)** Archaeophytes = non-natives introduced before 1492, neophytes = non-natives introduced after 1492. **(b)** There were no species with a significant trend of the Red List categories 0 (extinct or lost) or 1 (threatened with extinction). Significant trends are coloured, non-significant trends are displayed in grey. Asterisks indicate whether a group's trend (only based on significant species trends) deviated from zero change according to Wilcoxon signed rank tests. Status according to German wide lists (Buttler et al., 2018; Klotz et al., 2002; Metzing et al., 2018; Wisskirchen & Haeupler, 1998).

Table S7 Mean and Median Beals trends of species grouped by their Red List status and by state. Only species were included per group that showed a significant trend in the respective state and that had a status assigned. Not all states had species with significant trends of each Red List group. *n* is given for number of species with a significant trend that are included in each group. *p* values indicate whether a group's trend deviated from zero change according to Wilcoxon signed rank tests.

Red List status	State	n	Mean trend	Median trend	p
Highly Endangered	SH	11	-0.126	-0.120	0.001
Highly Endangered	HH	1	-0.104	-0.104	1
Highly Endangered	BW	29	-0.045	-0.030	< 0.001
Endangered	SH	45	-0.360	-0.170	< 0.001
Endangered	BW	132	-0.151	-0.071	< 0.001
Near Threatened	SH	53	-0.586	-0.305	< 0.001
Near Threatened	HH	12	-0.069	-0.152	0.092
Near Threatened	BW	119	-0.447	-0.223	< 0.001
Vulnerable	SH	3	-0.023	0.018	1
Vulnerable	BW	1	-0.113	-0.113	1
Not Threatened	SH	256	-0.406	-0.305	< 0.001
Not Threatened	HH	270	-0.089	-0.209	0.005
Not Threatened	BW	486	-0.147	-0.129	< 0.001
Not Evaluated	SH	21	0.244	0.080	0.011
Not Evaluated	HH	36	0.177	0.174	0.162
Not Evaluated	BW	42	0.153	0.065	< 0.001

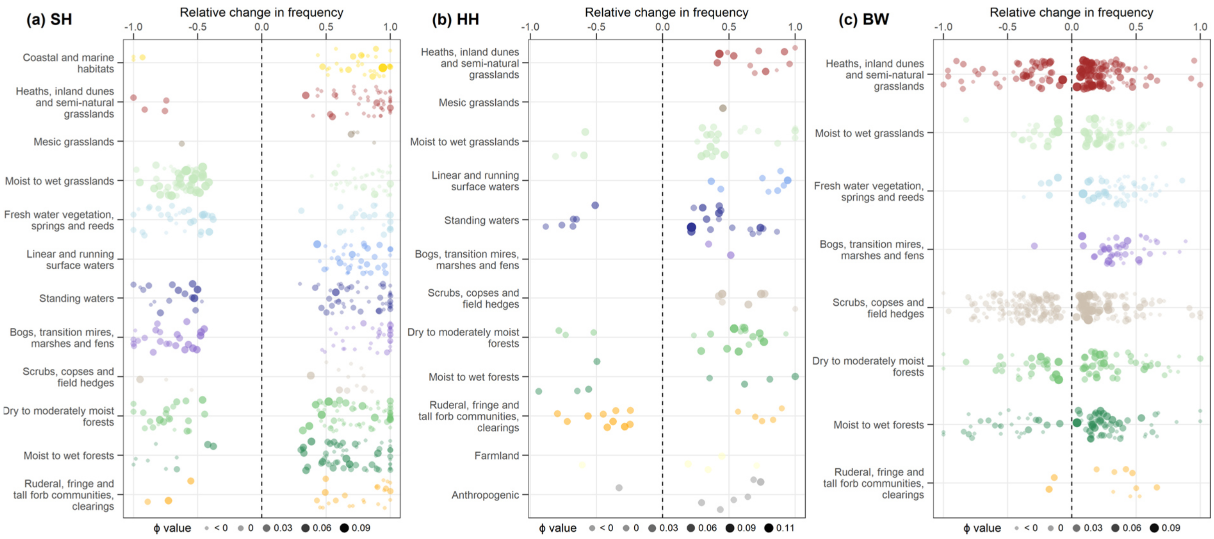

Figure S12 Frequency trends within habitat types for **(a)** SH, **(b)** HH, and **(c)** BW. Species' preferences to each habitat type (Φ value) are indicated by size and opacity. All Φ values below 0 are grouped into the category "< 0". Only species are included that showed a significant trend. Note that not all habitat types were mapped in all states.

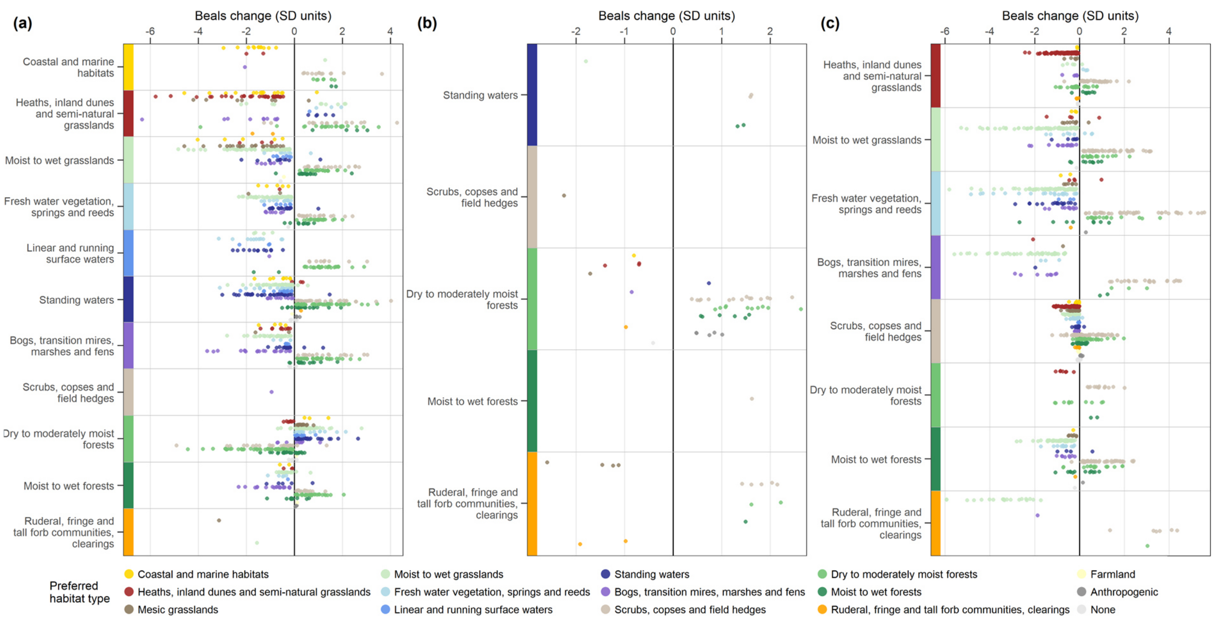

Figure S13 Beals trends within habitat types, separately by the species' preferred habitat type for **(a)** SH, **(b)** HH, and **(c)** BW. Colour bars on the left indicate the habitat type in which trends occurred (matches y-labels). Colours of points indicate the preferred habitat type of a species. Only species are included that showed a significant trend. Note that not all habitat types were mapped in all states.

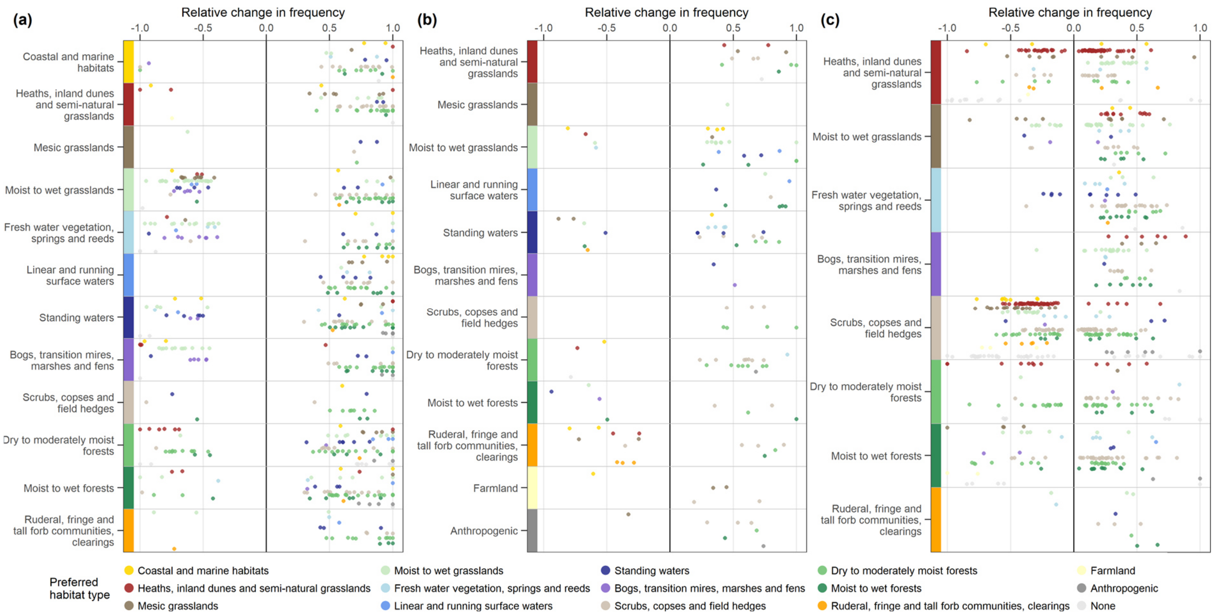

Figure S14 Frequency trends within habitat types, separately by the species' preferred habitat type for **(a)** SH, **(b)** HH, and **(c)** BW. Colour bars on the left indicate the habitat type in which trends occurred (matches y-labels). Colours of points indicate the preferred habitat type of a species. Only species are included that showed a significant trend. Note that not all habitat types were mapped in all states.

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APPENDIX S2

Table S1 Beals trends of all species that showed a significant trend in at least one state. Given are raw and scaled Beals trends of species within each state, including *n*, and *p* values (after Holm adjustment) according to *t* tests. In addition, each species preferred habitat type and its Red list (RL) and non-native (NN; I = Native (indigenous), N = Neophytes, A = Archaeophytes, NA = no status assigned) status in Germany are given. Habitat type preferences are based on the fidelity (Φ) of species to habitat types in all states taken together.

Due to the length of table S1 it can only be found online in Appendix S2 in the Supplementary Material section as "Table S2" at: https://doi.org/10.1101/2025.02.27.640325

APPENDIX S3

Table S1 Frequency trends of all species that showed a significant trend in at least one state. *n*, and *p* values according to two-tailed binomial tests. In addition, each species preferred habitat type and its Red list (RL) and non-native (NN; I = Native (indigenous), N = Neophytes, A = Archaeophytes, NA = no status assigned) status in Germany are given. Habitat type preferences are based on the fidelity (Φ) of species to habitat types in all states taken together.

Due to the length of table S1 it can only be found online in Appendix S3 in the Supplementary Material section as "Table S3" at: https://doi.org/10.1101/2025.02.27.640325

Chapter 5

Synthesis

In this thesis, I investigated individual trends and trend patterns of habitat types and plant species in three federal states of Germany over the last four decades. Based on those trends, I looked for consistencies between trends of habitat types and trends of their characteristic species as well as for common trend patterns across the three states. In the following, I briefly summarize each chapter's findings, before bringing those results together by comparing habitat type trends from chapters 2 and 3. Then I dive into a discussion on possible drivers of the trends found in this thesis, before reflecting on the analysis of the heterogeneous habitat mapping data and its limitations. Lastly, I discuss ways forward concerning future research ideas, biodiversity monitoring, and possible ways to halt further biodiversity decline.

SUMMARY OF RESULTS

In the **second chapter**, I showed that Hamburg (HH) experienced the highest mean losses in area for the groups of heaths and semi-natural grasslands (in this chapter called "heaths and nutrient-poor grasslands") as well as for ruderal and semi-ruderal vegetation. In contrast, mesic to wet grasslands (called "grasslands"), scrubs, copses and field hedges as well as human settlements showed some of the highest mean gains in area. Changes analyzed at a more detailed habitat type level revealed that the increase of mesic to wet grasslands was driven by species-poor grasslands while many species-rich grassland types declined. This demonstrated the importance of mapping habitats at a detailed level. Concerning species trends, especially species of (semi-)ruderal vegetation declined, while species of forests and scrubs, copses and field hedges increased. Overall, this chapter revealed prevalent land use intensification, woody encroachment, and urbanization in HH.

The **third chapter** focused on the question if trends of habitat types and their inhabiting and/or characteristic plant species are consistent in Baden-Württemberg (BW). The chapter revealed a considerable loss of protected habitat sites in BW, indicated by the relatively large amount sites of open land that have no longer been remapped in detail. While most protected habitat types decreased in area, dry to moderately moist forests (called "deciduous forests" or "coniferous forests") showed positive trends. Regarding species trends, species of heaths and semi-natural grasslands as well as meadows and pastures declined, while species of scrubs, copses and field hedges, and of bog-, carr-, swamp- and alluvial forests increased. Trends of habitat types and their characteristic species were mostly consistent. However, mean species trends within habitat types were generally negative, also for habitat types that showed increases in their area, i.e. deciduous forests. Together with the encountered trend of succession of scrubs, copses and field hedges in other habitat types, this implies an ongoing habitat degradation in some habitat types.

In the **fourth chapter**, I brought together species trends from the states HH, BW, and Schleswig-Holstein (SH). Consistently in all states, I found negative trends for species of heaths and semi-natural grasslands (called "heaths, inland dunes and semi-natural grasslands"), moist to wet grasslands, and coastal and marine habitats as well as for endangered species. In contrast, positive trends were found for species of scrubs, copses and field hedges, and for non-native species. Within habitat types, the species characteristic of the respective habitat type mostly declined. While some individual species trends varied among states, the overall patterns of winners and losers were highly similar. Thus, species seem to be affected by similar drivers and overall by habitat degradation in different parts of Germany.

OVERARCHING AND VARYING TRENDS AND THEIR POSSIBLE DRIVERS

Comparison of habitat type trends

Habitat type trends were analyzed in chapters two and three for HH and BW, respectively. In the following, I will compare those trends between the two states, first for the broad and then for the detailed habitat types. Because habitat type categories differ between the states, I will focus on types that are comparable in their definition.

When looking at the broad habitat types that were mapped in and showed significant trends for both states, two types showed trends in the same direction (heaths and semi-natural grasslands, ruderal habitats) and two types indicated trends in opposite directions (scrub or copse, grassland). However, the positive trend for grassland in HH stems mainly from increases in species-poor grasslands (in large parts from former farmland, see chapter 2: Figure 3), while this category was not mapped in BW. The group of scrubs, copses and field hedges showed positive trends in HH but negative trends in BW. These losses in BW mainly concerned field hedges, with many habitats haven been turned into unknown non-protected habitat types for uncertain reasons (chapter 3: Figures S1 & S2). Possible explanations include reallocations for agricultural land or urbanization, due to insufficient control or in exchange for compensation measures, and succession leading to scrub expansion, which mostly comprise habitat types that are not protected and thus not mapped (personal communication Thomas Sperle).

There were only a few detailed habitat types that were mapped in a comparable category and showed significant trends for both states. Those types showed mainly the same direction of trends in both states, with declines in semi-natural grasslands (in HH this category included semi-dry grasslands), carrs (in HH this category included bog forests), and willow scrubs. Increases were found in both states for different forest types (beech forests, swamp forests, copses), scrubs (bog or swamp scrubs, moist scrubs) as well as for bog degeneration stages. However, beech forests were mapped only in subcategories in BW, and not all those categories showed significant trends (significant for dry beech forest and Asperulo-Fagetum beech forest, but not for Luzulo-Fagetum beech forest and beech woods with *Acer* and *Rumex arifolius*). Also species-rich wet to moist grasslands were not directly comparable to each other, as they were divided into slightly different types in each state. In HH, wet grassland with sedges, rushes and tall forbs showed increases, while other wet or moist species-rich grasslands displayed decreases. In BW, all types of wet to moist grasslands decreased in area (*Molinia* meadows, periodically flooded grasslands, wet meadows). Similarly, while acidic oak mixed forests declined in HH, the most analogue category of this group increased in BW (oak forest on dry acidic soils), with however two other types that also partly correspond to the HH type declining in BW (oak forest on sandy plains, dry oak or oak-hornbeam forest).

Thus, while many types showed similar trends in the two states, some trends were opposing and many trends were not significant in both states. However, these differences are partly caused by different mapping schemes and subtypes included. Generally, different mapping keys make it difficult to compare habitat type trends between states and there have been several efforts to establish a common mapping key for Germany, which is however rarely implemented so far (Kaiser et al., 2013; Riecken et al., 2003; Riecken et al., 1993; Tschiche et al., 2024). At least making the states' mapping keys translatable to the EUNIS level 3 habitat types (EUNIS classification for habitats in Europe; European Environment Agency; Moss, 2008) would be an improvement for the usage of the resulting data.

Drivers of biodiversity change

The trends found in the three previous chapters point to similar drivers of habitat and species change in all states. Loss in wet habitats (chapters 2 & 3: carrs, most wet to moist grassland types, willow scrubs in HH and BW) and their characteristic species (chapter 4: negative Beals trends for species of moist to wet grasslands in all states; negative Beals trends for species of bogs, transition mires, marshes and fens, and species of fresh water vegetation, springs and reeds in SH and BW) reflect water drainage and climate change, which represent large threats to those habitats (Čížková et al., 2013; Janssen et al., 2016; Marx et al., 2024). Increases in a few other wet habitat types (chapters 2 & 3: bog or swamp scrubs, bog degeneration stages in HH and BW) are most likely caused by woody encroachment and an ongoing habitat degradation in bogs and other wet habitats, even though I only found a decrease of raised bogs in BW. The observed increases in swamp forests in both states were unexpected, but in BW and partly in HH stem mainly from riverine alluvial woodlands that are no longer periodically flooded, probably due to human-caused river regulations and climate change (Müller et al., 2024). Positive Beals trends for species of moist to wet forests in HH and BW reflect mainly increases within other habitat types, probably due to succession (chapter 4: Figure S9).

In the current discussion on reforestation for providing carbon sequestration, the found increases in woody species and forest area (chapters 2-4) could generally be seen positively (Aweto, 2024; Ding & Eldridge, 2024). However, if such increases stem from drained open bogs, carbon storage might decrease (Gregg et al., 2021; van der Velde et al., 2021), and also for species-rich grasslands, effects of woody encroachment on carbon sequestration are variable (Li et al., 2016). Further, woody gains within protected habitat types lead to losses of many characteristic and endangered species of e.g., bogs and semi-natural grasslands (chapter 4). At the same time, even with increasing forest area, characteristic forest plants can show decreases, as seen e.g., for *Lilium martagon* and *Epipactis atrorubens* within forests of BW (chapter 3). Thus, both concerning carbon sequestration and species conservation, negative aspects are probably outweighing positive aspects of the increases in forest area found in this thesis.

Loss in nutrient-poor habitats (chapters 2 & 3: heaths and semi-natural grasslands in HH and BW) and their characteristic species (chapter 4: negative Beals trends for species of heaths and semi-natural grasslands in all states; negative Beals trends for species of bogs, transition mires, marshes and fens in SH and BW; negative Beals trends for most characteristic species within heaths and semi-natural grasslands and bogs, transition mires, marshes and fens within their habitats in SH and BW) point to increases in nutrients via atmospheric or direct nutrient input (Janssen et al., 2016). However, for semi-natural grasslands, losses are most likely also caused by the abandonment of extensive management, as indicated by increases in woody vegetation (chapter 3: scrubs, copses and field hedges gaining area from semi-natural grasslands in BW; chapter 4: positive Beals trends for species of scrubs, copses and field hedges within heaths and semi-natural grasslands in SH and BW). Bogs might suffer from combined impacts as well, such as nutrient increases, water drainage, and climate change, which puts multiple pressures on different aspects of habitat quality and on bog species (Isbell et al., 2023; Oliver & Morecroft, 2014).

Fresh water-associated species also showed negative Beals trends (chapter 4: species of standing water, of fresh water vegetation, springs and reeds, and of linear and running surface waters). Even though the recording of species within fresh water habitats can be assumed to be more fluctuating and incomplete and thus less reliable than for other habitat types, the found trends mirror declines derived in a trend synthesis for Germany (Feld et al., 2024). Increases of woody species within fresh water habitat types in SH and BW (chapter 4) indicate that the littoral zones of those habitat types might have become less inundated. Further possible drivers of declines in characteristic fresh water species are changes in the natural form and function of fresh water habitats, climate change, and pollution (Feld et al., 2024; Janssen et al., 2016).

Increases of non-native species that were found in this thesis (chapters 2-4) might also be seen as a driver of native species loss across habitat types (Pyšek et al., 2012; Simberloff et al., 2013). However, this probably concerns only a few invasive species such as *Fallopia japonica* or *Prunus serotina*, since most non-native plant species do not have a large impact on the native flora and are not even established in Germany (Nehring et al., 2013).

While my work focuses on plant species, the drivers mentioned and habitat losses found in this thesis also negatively impact many other trophic taxonomic groups (Isbell et al., 2023). Some groups, such as pollinators, are additionally affected by their dependence on plant species, with then plant declines themselves acting as drivers of further biodiversity decline (Bassi & Staude, 2024; Kehoe et al., 2021; Potts et al., 2010).

A question of scale?

To investigate how species trends on the habitat scale compare to trends on the larger scale, I here roughly (only species with matching taxonomy) compare individual species trends from this thesis with trends on the scale of grid cells in Germany (Eichenberg et al., 2021). The Germany-wide trends were calculated using the Frescalo algorithm on aggregated species occurrences on 5x5km grid cells. They showed only weak or even negative Spearman rank correlations with Beals trends from this thesis (r_s = 0, -0.07, 0.12, 0.25, p = 0.99, 0.04, 0.07, 0.02 for SH, HH, BW, and Across-State trends respectively). Still, the Germany-wide trends were overall relatively similar in their direction to Beals trends, that is increasing species in Eichenberg et al. (2021) also increased across the three states in this thesis, and vice versa, decreasing species in the former also decreased in the latter analysis. This was partly surprising, since one could expect more positive trends on the larger grid cell scale compared to the habitat scale of this thesis, as new species are more likely to be found on larger areas while it takes longer for a species to be lost from a larger area. However, Eichenberg et al. (2021) used a longer time span (1960-2017 vs. 1977-2021 in this thesis), and showed that the strongest declines had already happened in the 1960-1980s. Thus, my analysis was less likely to observe significant trends due to a shorter time period and additionally started with a shifted baseline, with many species already having declined beforehand (Jandt et al., 2022; Marx et al., 2024; Mihoub et al., 2017). In addition, my analysis was biased towards positive trends (chapters 2-4). Thus, one should keep in mind that differences between scales can also be caused by different methods and data biases. Certainly, Germany-wide trends might also be driven by trends in states other than the three investigated in this thesis.

ANALYZING HABITAT MAPPING DATA

While blueprints for deriving biodiversity trends from habitat mapping data already exist in chapters 2-4, table 1 summarizes key steps for such analyses, highlighting common and differing approaches applied. Based on the experience gained during my work, I added methodological recommendations in the same table. For example, concerning habitat change, it became apparent that considering not only the broad but also more detailed habitat type level is important to gain a complete picture of change. To not miss changes in especially habitat types that are usually mapped in habitat complexes, it is then important to use each of such complexes' habitat types, instead of only their main type. For species analysis, it is recommended to apply Beals' index, at least in addition to changes in frequency. Then, only species trends that are significant for both frequency and Beals can be reported. Overall, habitat mapping data holds several limitations for analyses, as mentioned in the previous chapters. Some of these limitations could be reduced by following recommendations for habitat mapping practice (chapter 3), e.g., the bias towards positive trends by mapping also non-protected habitat types. Still, an essential component of analyzing data with such biases is discussing methods with and ratifying trends by local experts and stakeholders from governmental agencies, emphasizing the importance of close collaboration between science and practitioners.

Table 1. Methods and analyses used in chapters 2-4, highlighting common practices and differences. Cases in which methods in chapter 3 or 4 are the same as in chapter 2, are tagged as "Likewise". Cases in which methods/analyses were not conducted are tagged as NA. For chapter 4, some methods only apply to the cleaning of SH data, in which case it is noted ("SH:"). For some cases in which manuscripts differ in their methods, recommendations on the best practice are given ("Rec."). In cases where no recommendation is given, methods have been either the same for all chapters or the best method depends on the data. This table is not a comprehensive description of the methods used in each chapter but rather focuses on the most important steps and steps that differ between the manuscripts. For detailed descriptions see chapters 2-4, especially their appendices. SH: Schleswig-Holstein, HH: Hamburg, BW: Baden-Württemberg.

	Chapter 2 (HH)	**Chapter 3 (BW)**	**Chapter 4 (SH, HH, BW)**	**Rec.**
Clean habitat type data	* Harmonize types across times and campaigns * Exclude types that are not consistently recorded * Merge types to broader levels → 16 broad types, 94 intermediate level types	Likewise → 10 broad types, 68 intermediate level types	Likewise, additionally harmonize types across states → 14 broad types	Use broad & intermediate types for habitat analysis if possible
	Only keep the main type per polygon (>50%)	* For Φ calculation and species trends within types keep only the main type per polygon (>50%) * For habitat type trends keep all types	Only keep main type per polygon (>50%)	Keep all types for habitat analysis
Clean species data	Harmonize and aggregate to agg. level using taxonomic reference list GermanSL 1.4	Harmonize and aggregate to sect. level using taxonomic reference list GermanSL 1.5	Harmonize and aggregate to sect. (few genus) level using taxonomic reference list GermanSL 1.5	Aggregate to sect. level
	Exclude groups sporadically recorded (mosses, lichen, algae), hybrids, cultivated forms → 1322 species	Likewise → 1865 species	Likewise → 2212 species	
Calculate species' preferred habitat types (using Φ)	* Based on all HH polygons * No minimum Φ set	* Based on all BW polygons * Set minimum Φ to assign as preferred habitat type (median of all species' highest Φ value = 0.006)	* Based on all SH, HH, BW polygons * Set minimum Φ to assign as preferred habitat type (median of all species' highest Φ value = 0.0073)	Set minimum Φ
Prepare and intersect polygon data	* Merge polygons of the same site ID * Intersect all polygons in GIS	Likewise	Likewise	
Set time periods	t_1: 1979 – 1994 t_2: 1995 – 2017	t_1: 1989 – 2005 t_2: 2006 – 2021	SH: t_1: 1977 – 2005 t_2: 2007 – 2021	
Clean intersection data	Both polygons overlap min. 5%	Likewise	SH: One of the polygons overlap min. 5%	
	Target polygon remapped/previously mapped by at least 95%	Target polygon remapped/previously mapped by at least 75%	Target polygon remapped/previously mapped by at least 50%	
	Select from overlapping polygons of the same time period	Likewise	SH: NA (no overlapping)	
Calculate habitat type trends	Mean change in area: * Using only main habitat type of each polygon * Weight polygon areas by proportion of this main habitat type	Mean change in area: * Using each habitat type of each polygon * Weight polygon areas by proportion remapped/previously mapped and of each habitat type	NA	Use each habitat type of each polygon
	Additional analysis: * Transitions between habitat types	Additional analysis: * Transitions between habitat types * Extrapolation of habitat type trends 200 years into the future * Difference of the summed areas of all polygons per habitat type t_2 - t_1 (only intersecting polygons)	NA	
Calculate species trends across state	Change metrics: * Frequency * Occupied area (main focus) * Beals	Change metrics: * Frequency (main focus) * Occupied area * Beals (main focus)	Change metrics: * Frequency * Beals (main focus)	Always use Beals, at least in addition

	Beals: Degrees of freedom (default = number of all polygons) are divided by 2 to account for duplicated use in $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$	Beals: Degrees of freedom are set as the actual number of occurrences (incl. accounting for duplicated use)	Beals: Degrees of freedom are set as the actual number of occurrences (incl. accounting for duplicated use), Standardize Beals trends	Set degrees of freedom as the actual number of occurrences
	Report trends that are significant for each metric	Main manuscript: Only report trends for species with $n >= 50$ occurrences and that are significant for Beals and frequency	Report mean trends for species with significant and consistent trends for both approaches $t_1 \rightarrow t_2$ and $t_2 \rightarrow t_1$	If possible, report trends significant for both Beals and frequency
Calculate species trends within habitat types	Change metrics: * Frequency * Beals (main focus)	Likewise	Likewise	
	* For all polygons * Only for those polygons that did not change in their main habitat type from t_1 toward t_2	Likewise	For all polygons	
	NA	Plot species groups (habitat preference) within habitat types	* Plot species groups (habitat preference) within habitat types * Plot species trends within habitat types colored by Φ values	
Test for species groups mean trends	Group species by: * Preferred habitat type (HH) * Red List status (HH, GER) * Native status (HH, GER)	Group species by: * Preferred habitat type (BW) * Red List status (BW) * Native status (GER)	Group species by: * Preferred habitat type (all states) * Red List status (GER) * Native status (GER)	
	Significance tests: *t* tests	Significance tests: *t* tests, confirming results of non-normally distributed groups with Wilcoxon signed rank tests	Significance tests: Wilcoxon signed rank tests	At least confirm with Wilcoxon rank tests
Additional tests	* Test mean time span between t_1 and t_2 for all habitat types vs. their mean difference in area * Compare species frequencies in polygons with species frequencies on a grid cell scale in Hamburg (5 x 5 km, Florkart)	* Mean habitat type trends: test for robustness by excluding outliers outside of the 1st to 99th percentile * Test if mapping seasons shifted over time (t_1 vs. t_2) * Additional species trend analysis with subset of species mentioned in the mapping keys ("key species", 46% of species)	* Accumulation curves of species recorded in polygons	For habitat type trends test for robustness by excluding outliers

THE WAY FORWARD

Further research avenues

The next step to get a more complete picture of biodiversity change in Germany could be to analyze trends using habitat mapping data from other states. Suitable data would be available for Hessen, Bayern, Thüringen, Rheinland-Pfalz, Brandenburg, and Niedersachsen. For other states, which yet have not had a second survey campaign, or that only record endangered or no plant species, the available data is probably not suitable for trend analyses. However, data from states with only one survey but sufficient species recordings could be used for other purposes, such as calculating fidelity of species to habitat types, and thus, derive indicator species for habitat types or using the data as background information for Citizen Science projects. For example, knowledge on the habitat type would help interpret the occurrence of plant species via the app FloraIncognita (Mäder et al., 2021).

Since trends might differ depending on the scale, a possible next step coming forth from my thesis would also be to compare trends of already available plant trends in Germany between the scales of plots (Jandt et al., 2022) vs. habitats (this thesis, preferably including more states) vs. grid cells (Eichenberg et al., 2021). Comparisons between those three scales have not been possible so far, since this thesis is one of the first works to provide species trends on the habitat scale. Trends for individual plant species can be compared relatively easily across studies, as shown by the comparison between the habitat and grid-cell scale earlier in this discussion. However, the number of species available for such comparison might be limited by different species pools and by only few species that show significant trends at different scales (see also chapter 4). Thus, one could also again compare trends of plants grouped by e.g., their preferred habitat type or traits. For comparing habitat with plot data, it might also be possible to compare species trends within habitat types.

Because differences between scales can be caused by different methods and data biases, it is also important to investigate the influence of the data collection method on trend estimates. For this, one could compare data collected via habitat mapping with data coming from floristic mapping, as for example available for BW (Wörz et al., 2024). By calculating trends from both data sources on the grid cell level, bias by collection method could be identified. To however really understand which metrics are working best for which heterogeneous data, simulation studies should be implemented, mimicking different communities, trends, and collection biases (Bowler et al., 2025; Isaac et al., 2014).

While the winners and losers found in this thesis hint at several drivers of change, such surrogates can never tell exactly what drives the observed trends. For this, a driver analysis is needed, which should include especially nutrient availability, hydrological change, climate change, and land use change and should differentiate between habitat types. For example, Steven Loebelt, a bachelor student of mine, found different main drivers of observed changes in area of three habitat types in BW from chapter 3 (wet meadows, swamp forests, and raised bogs; Loebelt, 2023). However, this and other studies are commonly limited to an available set of drivers, especially on the habitat scale (Jaureguiberry et al., 2022; Marx et al., 2024).

Improve biodiversity monitoring

Extending and initiating advanced monitoring programs is essential for analyzing biodiversity change, especially given the incompleteness of current species lists. Such monitoring should offer time series that are able to also test for fluctuations of trends or changes in trend directions or strength over time.

The mapping of habitat types in Germany should be continued via field surveys to get reliable fine-level data on habitat types and to keep data comparable over time. As an additional monitoring concept, remote sensing techniques, such as satellite data, should come into play to get continues data, including also non-protected habitat types (European Environment Agency & Museum national d'Histoire naturelle, 2014; Moersberger et al., 2022). While remote sensing mostly still only can detect habitat types on a broad level, models for classifications into more detailed habitat types are currently developed, e.g., on a European level (Bruelheide, Jandt, et al., 2024; Stenzel & Feilhauer, 2020).

For a systematic monitoring of plant species within different habitat types, the main challenge remains on how to survey complete species communities across large areas with limited funding (Kühl et al., 2020). One suitable solution are permanent vegetation plots of the size of $1m^2$-$200m^2$ within different habitat types (Bruelheide et al., 2022; Pescott et al., 2019). In the Countryside Survey in the UK, for example, vegetation plots are recorded across the country in a representative number of habitat types since 1978 (Wood et al., 2017). While for Germany such monitoring does not exist yet, the implementation of a new plant monitoring program is currently discussed, but needs further development (Bruelheide et al., 2022; Stenzel et al., 2021). It is important that monitoring programs do not concentrate solely on endangered species, since this thesis and other work illustrated that also many other species decline (Jansen et al., 2020). To complete plant occurrences on a grid or maybe even habitat scale, observations from citizen science programs could be used, especially since such records are often biased towards highly populated areas, in contrast to both habitat and floristic mapping (Mora et al., 2024). While remote sensing techniques might assist in the monitoring of species in the future, they are still only capable of monitoring large plant species such as trees (Fassnacht et al., 2024; Richter et al., 2016). Mosses and lichen are hard to identify even in the field and their monitoring is thus even more fragmentary than that of vascular plants (Diekmann et al., 2023). Hence, more funding is needed for identification trainings and systematic monitoring of those species.

To conduct driver analyses, we further need a monitoring of multiple drivers of biodiversity change, with the resulting data publicly available (Jaureguiberry et al., 2022; Marx et al., 2024). Monitoring should also include conservation measures/interventions taken, such as rewetting of sites or agricultural extensification, as to assess the best ways to halt biodiversity decline (Lindenmayer et al., 2022; Marx et al., 2024).

More effort is needed to stop the biodiversity crisis

A crisis is defined as "a time of great danger, difficulty or doubt when problems must be solved or important decisions must be made" (Oxford University Press). Thus, while we do not have the complete picture of biodiversity change yet (and probably never will), we already have sufficient information on the main issues and should implement solutions to counteract. Targets to counteract biodiversity loss were recently set again on a global (CBD, 2022). European (European

Commission, 2022; European Commission & Directorate-General for Environment, 2021), and German scale (BMUV, 2024), after previous goals have rarely been met (Bundesverband Beruflicher Naturschutz e.V., 2020; Secretariat of the Convention on Biological Diversity, 2020). Work on biodiversity change, such as this thesis, and systematic monitoring can help to answer the questions where to put new protections, which habitat types and species need special protection, which are the most important drivers to tackle, and which ways of restoration and protection work.

The documented losses of protected habitats and their characteristic (sometimes endangered) species in this thesis raise concern about the effectiveness of current conservation measures. They call for an expansion of protected areas but also for better enforcement of protection regulations within and outside of protected areas, without easy ways to circumvent (Bruelheide, Wirth, et al., 2024; Hauck et al., 2024; Li et al., 2024).

The loss in wet habitats and their characteristic species that I found, emphasize that drainage of sites and river regulations should be halted and reversed wherever possible, especially since drought events will become more frequent in the future in the face of climate change (Pokhrel et al., 2021; Samaniego et al., 2018). However, more research on how much and in which ways the rewetting of e.g., formerly drained peatland benefits different species groups and carbon storage is needed (Kreyling et al., 2021; Martens et al., 2023).

My thesis also showed losses in nutrient-poor habitats and their characteristic species, pointing to a eutrophication of the landscape, which is largely caused by fertilization of agricultural sites (incl. grassland; Marx et al., 2024). Thus, a lowering of nutrient inputs in agriculture is needed, but such target needs larger subsidies for farmers by e.g., the European Union (Lakner et al., 2024; Pe'er et al., 2022). For semi-natural grasslands, losses are also caused by the abandonment of extensive management (Finck et al., 2017). Here, too, targeted subsidies are needed to keep up extensive grazing, which otherwise only yields low financial gains (Rouet-Leduc et al., 2024).

Overall, studies as this thesis emphasize the need to intensify efforts to halt the biodiversity crisis before we lose even more of our planet's nature.

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Appendices

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Bestätigung des Betreuers der Dissertation von Frau Lina Maria Lüttgert

Hiermit bestätige ich als Betreuer/in der o. g. Dissertation, dass die gemeinsame Arbeit mehrerer Personen an der Arbeit durch den Forschungsgegenstand gerechtfertigt ist.

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Entwurf (Design)	45	0	5	0	0	5	0	0	0	0	45
Umsetzung (Implementation)	85	2	2	1	1	2	1	1	1	2	5
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Publications

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Bruelheide, H., Jansen, F., Jandt, U., Bernhardt-Römermann, M., Bonn, A., Bowler, D., Dengler, J., Eichenberg, D., Grescho, V., Kellner, S., Klenke, R. A., Lütt, S., **Lüttgert, L.**, Sabatini, F. M., & Wesche, K. (2021). A checklist for using Beals' index with incomplete floristic monitoring data. *Diversity and Distributions*, *27*(7), 1328-1333. https://doi.org/10.1111/ddi.13277

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Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „Biodiversity trends for Germany using repeated habitat mapping data“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Lina Maria Lüttgert, Halle (Saale), 06.03.2025