

Systematic temporal turnover towards species with larger geographic ranges across plant communities

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von Ingmar René Staude, M.Sc.

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Gutachter

1. Professor Henrique Miguel Pereira (iDiv, Martin Luther University Halle - Wittenberg)
2. Professor Helge Bruelheide (iDiv, Martin Luther University Halle - Wittenberg)
3. Professor Brian McGill (University of Maine)

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Summary

In the absence of wholesale conversion of natural habitat to cropland, time series of plant communities show no evidence of consistent and widespread declines in species richness owing to human activities. Instead, time series suggest that human activities have led to widespread increases in temporal species turnover. It is unclear, however, whether this turnover has a systematic and predictable component. In order to gain a general understanding of why and how plant diversity is changing, we need to ask whether similar types of plant species are consistently lost and gained from local communities. In this thesis, I test whether species gains and losses can be explained by species geographic range size. Range size reflects the ability of species to disperse and colonize, their niche breadth and niche position as well as their local abundance, thus capturing multiple factors relating to a species' vulnerability to environmental change. Moreover, range size links temporal with spatial turnover of species, as communities that lose small-ranged while gaining widespread species become more similar over time. Therefore, understanding the link between species range size and the likelihood that species increase or decrease over time can not only help us shed light on why certain species "win" or "lose", but also on the consequences of these shifts for the distinctiveness of plant communities.

Empirical applications to study temporal changes in community composition are, however, constrained by a general paucity of ecological time series. In **Chapter 2**, I therefore reconstruct time series of plant communities by integrating species point-occurrence records from three global data-sharing networks. I combine these data with a global map of reconstructed historical land use to ask whether species with small ranges have declined preferentially in grid cells of a quarter degree due to the loss of natural habitat. I found that the median range size across all species within a grid cell was higher on average after natural habitat was lost. Furthermore, I quantify the probability of persistence of small- and large-ranged species at different levels of habitat loss. I found that species with small ranges had a lower probability of persistence than species with large ranges at already intermediate levels of habitat loss. I conclude that range size may help to explain species trajectories at relatively small spatial scales and therefore hypothesize that temporal turnover within communities could act to increase the similarity between communities when natural habitat is lost. However, the exact reasons for why smaller-ranged species are more likely to be lost remain unclear. Moreover, owing to several limitations of the data used in this study, I was not able to analyze the consequences of directional temporal turnover in relation to species range size on alpha, beta, and gamma diversity.

In **Chapter 3**, I use vegetation resurvey data from 68 forest understory studies spread across Europe's temperate forest biome to validate results of Chapter 2 with better data and understand the reasons and consequences of directional turnover in relation to range size. I therefore ask three main questions: i) Have small-ranged forest plant species declined preferentially over time at study sites? ii) Do any such trends simply reflect stochastic, demographic effects, or do they also reflect niche effects that strengthen with abiotic environmental changes such as atmospheric nitrogen deposition? iii) Do species replacements evoke a homogenization pattern with small-scale richness remaining constant on average while larger-scale richness declines? I found that herb-layer species with

small geographic ranges are being replaced by more widely distributed species, and the results suggest that this is more likely due to species niche position for nutrients than to demographic effects. Nitrogen deposition accelerated both the loss of small-ranged, nutrient-efficient plants and colonization by broadly distributed, nutrient-demanding plants (including non-natives). I found that despite no net change in species richness at the spatial scale of a study site, the cumulative loss of small-ranged species reduced biome-scale (gamma) diversity.

Since Chapter 3 is restricted to forests, it remains unclear whether the identities of "loser" and "winner" species represent idiosyncratic local outcomes of drivers of change (e.g., nitrogen deposition), or whether there are general patterns across systems. In **Chapter 4**, I integrate three resurvey databases from three contrasting habitats in Europe - mountain summits, deciduous and coniferous forest and lowland grasslands - to test for commonalities and differences in the effect of range size on species trajectory between habitats. I found in all three habitats that species with larger ranges replaced species with smaller ranges, regardless of whether the average site-level species richness increased (summits), had no clear trend (forests) or decreased (grasslands). In parallel, plant communities in all three habitats shifted towards more nutrient-demanding species over time, where the data suggests that large-ranged species are more nutrient-demanding. This suggests the loss of species with smaller ranges is likely not only a direct abiotic result of global environmental change, but also of increased biotic pressure (i.e. competition with more resource-acquisitive species) that indirectly results from global change. Since the replacement of small-ranged species acts to homogenize vegetation between unique habitats, a better understanding of the relative importance of abiotic versus biotic effects of global change on systematic turnover is much needed.

Overall, this thesis provides empirical evidence to suggest that temporal species turnover has a systematic and predictable component, based on species range sizes as a key synthetic measure of species ecological differences. Larger-ranged species have consistently replaced smaller-ranged species over time. The results of this thesis suggest this directional turnover is not only due to stochastic, demographic effects but also due to aspects of species niche. Moreover, the patterns documented here suggest losses of small-ranged plant species may not only be due to the direct effects of global environmental changes, but also due to indirect effects from increased competition. Altogether, this thesis provides empirical evidence that small-ranged species can be doubly vulnerable to extinction, both because of purely geographical reasons, as they by definition occupy fewer sites, and also because they can be more vulnerable to being lost at any given site. Finally, this thesis provides supporting evidence for biotic homogenization, the process by which global environmental changes favor larger-ranged plant species, with the consequence that distinct vegetation types become more similar over time.

Chapter 1 - Introduction

A long-standing theory in biodiversity change research is that human activities lead to consistent and widespread declines in local species richness (Gonzalez et al., 2016; Cardinale et al., 2018). The generality of this pattern has been inferred from space-for-time substitution studies, showing that species richness is typically lower in areas perturbed by humans (e.g. McKinney, 2004; Pautasso, 2007; Aronson et al., 2014; Murphy and Romanuk, 2014; Newbold et al., 2015). However, ecological processes occur in time and over the last decade, several studies based on time-series data found contrasting evidence, showing that local diversity is not in fact declining systematically over time (Vellend et al., 2013; Dornelas, Gotelli, McGill, et al., 2014; Blowes et al., 2019). The contrasting results from temporal and space-for-time studies led to the "no net loss debate" (Gonzalez et al., 2016). On the one hand, time series studies have been criticized for not being representative for the geography of human impact and shifted baselines (Gonzalez et al., 2016), creating a strong sampling bias in these analyses. On the other hand, space-for-time studies were criticized for not considering that human changes proceed much faster than the speed at which biological communities respond and that several processes can lead to the same spatial pattern (Damgaard, 2019). Although the "no net loss" debate is still ongoing, it has led to a constructive rethinking of where we sample and monitor biodiversity and how we measure biodiversity change.

The departure from the single-faceted story-line that human activities systematically reduce local species richness stimulated new questions. Among these, whether species richness is a meaningful measure to understand and predict biodiversity change (Santini et al., 2017; Hillebrand et al., 2018). Species richness does not capture changes in community composition, so that even when local species richness is constant, the identities of species may have changed entirely over time. Indeed, biodiversity time-series reveal that the replacement of species occurs in excess of natural rates, despite no net loss in local diversity (Dornelas, Gotelli, McGill, et al., 2014; Blowes et al., 2019). Yet, it is largely unclear whether there is any systematic pattern to this replacement (Dornelas, Gotelli, Shimadzu, et al., 2019). In the case that the identity of loser and winner species is deterministic in that certain ecological profiles of species are favored due to changes in the environment, this could help to better understand the processes underlying biodiversity change and predict its consequences for the global species pool and the functioning and diversity of ecosystems (Pereira, Navarro, and Martins, 2012). However, tests of whether certain types of species are consistently more likely to be lost or gained over time in local communities across habitats remain scarce.

For vascular plant species, studying temporal turnover in relation to their geographic range size can shed light on why certain species "win" or "lose". The range size of plant species is a key synthetic measure of their niche, functional and demographic features (Gaston and Fuller, 2009). Species with larger ranges naturally face a larger gradient in environmental conditions and are therefore expected to have wider niche breadths and a greater capacity to respond to environmental changes (Slatyer, Hirst, and Sexton, 2013; Kambach et al., 2019; Razgour et al., 2019). Moreover, the range size of plant species can be associated with their niche position. Range size is associated with species functional traits and resource strategy (Estrada et al., 2015; Sonkoly et al., 2017), which may affect the probability of losses and gains, as anthropogenic changes favor specific strategies over

others. Finally, range size correlates positively with species abundance. Species with smaller ranges often have smaller local population sizes (Gaston, Blackburn, et al., 2000) and may therefore have a greater vulnerability to being lost due to both stochastic, demographic processes and environmental changes (Schoener and Spiller, 1987).

Studying temporal turnover in relation to species range size can further provide insights into the consequences of biodiversity change beyond the community level. If small-ranged species that act to differentiate vegetation types are consistently replaced by more widespread species, distinct vegetation types may become more uniform – a form of biotic homogenization (McKinney and Lockwood, 1999; Olden and Poff, 2003). In addition, if small-ranged species are more vulnerable to being lost at any given site, this could mean they are at double risk of extinction as they by definition also occupy fewer sites (Pimm et al., 2014). The cumulative replacement of small-ranged species could then relatively quickly translate into extirpation from larger regions (Collen et al., 2016) and thus potentially affect the global species pool. Evidence for such replacement could therefore help to reconcile how local species richness may remain unchanged while global diversity declines (Díaz, Settele, Brondízio, et al., 2019; Dornelas, Gotelli, McGill, et al., 2014). Range size can therefore not only provide insights into the underlying mechanisms of biodiversity change, but also on the consequences of community-level changes for the distinctiveness of vegetation types and the diversity of species at broader spatial scales.

The main objective of this thesis is to test whether species losses and gains in vascular plant communities can be explained by species geographic range size and to gain a better understanding of the processes that lead to any such systematic turnover of species over time. I ask four main questions: i) Are small-ranged plant species more likely to decline at relatively small spatial scales over time (Chapter 2, 3 & 4); ii) To what extent does any such effect of range size on species trajectory reflect niche or stochastic effects (Chapter 3 & 4); iii) Does the common replacement of small- by large-ranged species affect other forms of biodiversity (i.e. gamma and beta diversity) (Chapter 3 & 4), and iv) Do local communities consistently shift towards larger-ranged plant species across contrasting habitats (Chapter 4)? This thesis provides insights into whether temporal turnover in plant communities is predictable and whether any such directional change acts to homogenize vegetation between habitats and reduce species richness at larger geographic scales.

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Chapter 2

Range size predicts the risk of local extinction from habitat loss

by **Ingmar R. Staude**, Laetitia M. Navarro, Henrique M. Pereira. *Global Ecology and Biogeography* (2019).
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Range size predicts the risk of local extinction from habitat loss

Ingmar R. Staude^{1,2} | Laetitia M. Navarro^{1,2} | Henrique M. Pereira^{1,2}

¹German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Leipzig, Germany

²Institute of Biology, Martin-Luther University Halle-Wittenberg, Halle (Saale), Germany

Correspondence

Ingmar R. Staude, German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany.
Email: ingmar.staude@idiv.de

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Abstract

Aim: The geographical range size of species is a strong predictor of vulnerability to global extinction. However, it remains unclear whether range size is also a good predictor of extinction risk at much smaller scales. Here, we reconstruct biodiversity time series to ask whether species with small ranges have declined preferentially with habitat loss at the local scale.

Location: Global.

Time period: 1500–2015.

Major taxa studied: Vascular plants.

Method: We collated 70 million occurrence records of 180,000 species of vascular plants from three biodiversity data-sharing networks. We combined these with data on changes in global land use to find locations (0.25° grid cells) with biodiversity data before and after loss of natural habitat. First, we examined the change in community median range size before and after habitat loss. Second, we quantified the probabilities of local persistence of small- and large-ranged species at different levels of habitat loss.

Results: Community median range size was higher after habitat loss, on average. Species with small ranges had lower probabilities of persistence than species with large ranges at already moderate habitat loss ($\leq 50\%$).

Main conclusions: The loss of natural habitat has a differential effect on the local extinction risk of species with different range sizes. Given that species with small ranges decline preferentially, habitat loss can create a linkage between temporal and spatial species turnover, in that changes within communities decrease compositional differences between communities.

KEYWORDS

biotic homogenization, persistence, range size, spatial species turnover, temporal species turnover

1 | INTRODUCTION

The major driver of the current extinction crisis (Pimm et al., 2014) is, and is also projected to remain for the first half of the 21st century, change in land use (Maxwell, Fuller, Brooks, & Watson,

2016; Pereira et al., 2010; Sala et al., 2000). Yet, vulnerability to extinction from habitat loss is not constant across species. Among the strongest predictors of the threat of extinction in terrestrial species is small geographical range size (Gaston & Fuller, 2009; Manne, Brooks, & Pimm, 1999). In part, this is simply because

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species with small ranges have a lower number of localities at which, upon habitat loss, they either persist or go extinct. But even within a locality, small-ranged species might suffer from a higher extinction risk than widespread ones. One reason for this could be that species with small ranges tend also to have smaller local populations (Brown, 1984; Gaston et al., 2000), and with decreasing population size, the vulnerability to environmental perturbations increases (Christiansen & Fenchel, 2012; Schoener & Spiller, 1987). However, it remains poorly documented whether the threat of local extinction in species experiencing habitat loss can indeed be predicted by range size.

One corollary of an increased local extinction risk for small-ranged species would be that habitat loss creates a linkage between temporal and spatial species turnover, in that spatial turnover is reduced by temporal turnover. This is because previously differentiated local communities would increasingly resemble one another in species composition when habitat loss results in a net loss of exactly the species that drive that very differentiation (McKinney & Lockwood, 1999; Olden & Poff, 2003). Recent analyses of biodiversity time series find that temporal species turnover in local communities is occurring at rates in excess of background levels predicted by null and neutral models (Dornelas et al., 2014; Magurran, Dornelas, Moyes, Gotelli, & McGill, 2015). It is hypothesized that this pattern is driven by biotic homogenization; that is, widespread species replace those with small ranges, and thereby, decrease spatial turnover but maintain local numbers of species (Dornelas et al., 2014). However, the empirical evidence that supports this hypothesis is scarce, all the more so for areas that are representative of habitat loss (Cardinale, Gonzalez, Allington, & Loreau, 2018; Gonzalez et al., 2016).

Moreover, evidence is lacking with regard to the amount of habitat loss that species can tolerate before becoming vulnerable to local extinction. Albeit highly relevant for conservation, we do not know whether thresholds of local habitat loss differ between species with small and large ranges. If small-ranged species are more vulnerable to even moderate habitat loss, the effect of habitat loss on biodiversity might be amplified, simply because most species have small ranges (Gaston, 1996). Although some models predict abrupt species loss when natural habitat availability falls below a threshold of 30% in the landscape (Andr n, 1994), it has recently been documented that initial intrusion in intact landscapes can substantially erode local biodiversity (Betts et al., 2017; Staude et al., 2018). This might be attributable to the local extinction of numerous small-ranged species that are already vulnerable to lower amounts of habitat loss.

Empirical applications to study temporal community changes and species persistence in human modified landscapes on a global scale have been, to date, constrained by a general paucity of representative ecological time series and high-resolution historical land-use data. However, over the last two decades, millions of digital species records have been mobilized via international data-sharing networks, providing spatio-temporal information on species occurrences (Meyer, Weigelt, & Krefl, 2016). Moreover, global change in land use has been reconstructed for the late Holocene and has recently been made available at high temporal and spatial resolution with the

LUH2vh product (<http://luh.umd.edu/data.shtml>; Hurtt et al., 2011). Integrating single point occurrences to the spatio-temporal resolution of such land-use data uncovers new vantage points for ecological research, because community time series data in areas undergoing change in land use can be reconstructed (Johnson et al., 2011).

Here, we use these data sources to compare the frequency distribution of species range sizes in vascular plant communities before and after habitat loss. We test whether this distribution shifts towards larger ranges. Next, we quantify the probability of local persistence of species with small and large ranges along a gradient of habitat loss. We hypothesize that small-ranged species are more vulnerable to local extinction from habitat loss.

2 | METHODS

2.1 | Land-use data

We used historical land-use reconstruction data provided by the Land Use Harmonization v2h product (LUHv2h; <http://luh.umd.edu/data.shtml>; Hurtt et al., 2011). Inputs of LUHv2h include HYDE 3.2 (Klein Goldewijk, Beusen, Dreht, & Vos, 2011), Food and Agriculture Organization (FAO) wood harvest data (FAO, 2008) and Landsat-based forest loss data (Hansen et al., 2013), among others (Hurtt et al., 2011). LUHv2h provides information about the annual states of 12 land-use classes at a 0.25° spatial resolution for the period 850–2015; that is, each grid cell gives a value for the percentage of cover of each of the land-use classes. Land use is divided into two classes of natural vegetation (forests or non-forests) and 10 human land uses (five cropland, two secondary vegetation, two grazing and one urban uses). Here, the natural forest and non-forest classes were aggregated into one natural habitat class. We define habitat loss as the loss of this natural habitat class. Note that the aggregate of the 10 human land uses is complementary to this natural habitat class.

2.2 | Vascular plant data

We downloaded all openly available, georeferenced data on vascular plant occurrences via the Global Biodiversity Information Facility (GBIF; <https://doi.org/10.15468/dl.chiubr>, accessed 6 December 2017), Botanical Information and Ecology Network (BIEN; R package `BIEN`; Maitner et al., 2018) and the Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS; <https://doi.org/10.5519/0066354>; Hudson et al., 2014) databases. We applied geographical filters to exclude impossible, incomplete or unlikely sampling locations (R package `scrubr`; Chamberlain, 2016). Temporal filters confined biodiversity data to the period 1500–2015. Taxonomic filtering and taxon resolution and standardization included iPlant's Taxonomic Name Resolution Service (R package `taxize`; Chamberlain & Sz cs, 2013). We excluded duplicates of species, sampling location and year combination. Joining these data resulted in 73,097,393 unique records for 177,774 vascular plant species (i.e., c. 56% taxonomic coverage of c. 315,000 vascular plant species; theplantlist.org). Missing

species are most likely to be rare, small-ranged species and those endemic to regions with little documentation and data-mobilization effort. We provide R code for data retrieval and cleaning in the Supporting Information (section R code 2.1–2.4).

2.3 | Range sizes

For most species, scarcity of point occurrences at unique locations prevents the construction of meaningful species distribution models (Feeley, 2012; Guisan et al., 2007) or extent-of-occurrence range maps (Gaston & Fuller, 2009). In particular, species with restricted geographical distribution might be underrepresented when confining diversity data to species for which distribution modelling is appropriate. We thus opted for an alternative approximate but transparent approach to estimate range sizes. Initially, we gridded the c. 73 million species records to the spatial resolution of the LUHV2h data, which we had previously re-projected into an equal-area grid (Behrmann projection). Next, we simply counted the number of cells that each species occupied on that grid (Gaston, 1996). Each species thus had one range size estimate that was derived from all its occurrence records to date and measured the species' area of occupancy (Gaston & Fuller, 2009).

Owing to the incomplete spatial coverage of digital biodiversity data, we probably underestimated range size (Isaac & Pocock, 2015). Importantly, underestimation is worse for species that have parts of their ranges in areas with severe data gaps. This uneven spatial coverage is particularly problematic when comparing locations. However, this limitation did not affect our analyses, because we were comparing the temporal change within locations rather than between them.

2.4 | Communities before and after habitat loss

First, we gridded all species occurrence records to the spatial and temporal resolution of the LUHV2h data. This allowed us to identify cells that had species records before ($\geq 80\%$ of natural habitat remaining) and after (0% of natural habitat remaining) habitat loss. Each of these cells therefore gave us an individual set of species for a before and after habitat loss period. Henceforth, we refer to these species sets as communities. We further introduced a lower bound for the number of species in these communities to account for under-documentation. When cells had one community with < 10 species, either before or after habitat loss, we discarded them (see Supporting Information for discussion of thresholds and sensitivity test; Supporting Information Figure S1).

The application of the two rules for inclusion of cells (records before and after habitat loss and ≥ 10 species recorded before and after habitat loss) resulted in an inclusion of one in 1,000 cells. From the c. 90,000 cells, over which the 70 million species occurrence records were distributed, 657 cells had biodiversity data both before and after habitat loss. Of the 657 cells, 89 had ≥ 10 species recorded before and after habitat loss. The final 89 cells cover 11 out of 14 biomes (Figure 1). Their distribution reflects both change in land

use and the spatial bias typical of biodiversity records (e.g., severe gaps across Asia, Northern and Central Africa, Amazonia and Arctic Canada; Meyer et al., 2016) but also that areas of exceptionally high biodiversity might be over-represented (e.g., Atlantic Forest in SE Brazil, the Cape Provinces, Western Australia and California).

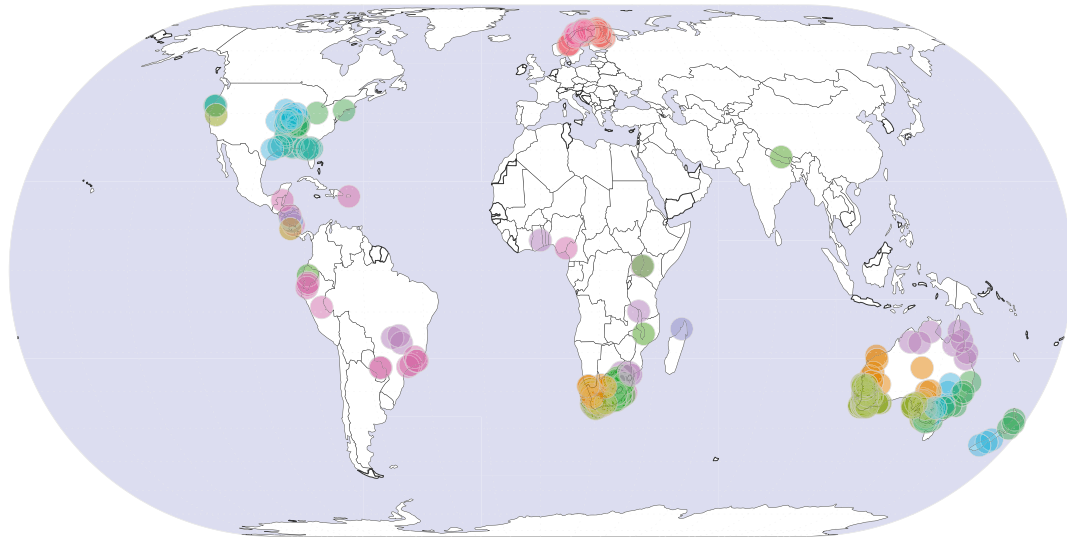
Digital biodiversity data suffer from not only spatial but also temporal bias (Meyer et al., 2016). Typically, the number of species records, and consequently, the number of species, increase progressively in time. In the LUHV2h data, natural habitat can only be lost but not gained with time; more natural habitat generally corresponds to earlier years and little natural habitat to later years. Given that documentation is higher in later years, the number of species is generally higher when little natural habitat remains (i.e., after habitat loss). In our subset of cells, the average time that passed until a cell went from ≥ 80 to 0% natural habitat was 81 years (Supporting Information Figure S2) and the average community richness was 55 and 218 species, respectively.

Nevertheless, because we do not compare the number of species but range size composition before and after habitat loss, we can account for this temporal bias by artificially keeping the number of species constant over time. For each cell, we repeatedly subsampled species from the community with the higher number of species (without replacement), so that the before and after community of a cell had the same number of species (number of sampling repetitions, $n = 100$; Figure 2). For each cell, community and n th subsample, we then calculated a summary statistic that described the composition of species range sizes before and after habitat loss. We calculated median range sizes, because range-size frequency distributions are strongly right skewed. The medians that were obtained from the 100 subsamples of the community with the higher number of species in a cell were averaged. For each cell, we then calculated the log ratio of median range size after and before habitat loss to obtain effect sizes. With a pairwise permutation test (Monte Carlo Fisher–Pitman test) we tested whether the mean of the effect sizes was different from zero.

Finally, we used a simulation approach to test whether our method introduces any bias. We simulated 1,000 before and after habitat loss communities with 50 and 200 species, respectively. For both the before and the after community, species range sizes were simulated from the same log-normal distribution. We followed the protocol above and subsampled the community with more species, in this case always the after community, 100 times. We averaged medians from the subsamples and compared this value with the median range size of the before community. If our method is indeed free of bias, effect sizes obtained from the 1,000 community comparisons should be normally distributed. We provide R code for this simulation in the Supporting Information (section R code 3.1 & 3.2).

2.5 | Probability of persistence along a habitat loss gradient

By gridding species occurrence records to the spatio-temporal resolution of the LUHV2h data, we could link each record to the



- Boreal Forests/Taiga
- Deserts and Xeric Shrublands
- Mangroves
- Mediterranean Forests, Woodlands and Scrub
- Montane Grasslands and Shrublands
- Temperate Broadleaf and Mixed Forests
- Temperate Conifer Forests
- Temperate Grasslands, Savannas and Shrublands
- Tropical and Subtropical Coniferous Forests
- Tropical and Subtropical Dry Broadleaf Forests
- Tropical and Subtropical Grasslands, Savannas and Shrublands
- Tropical and Subtropical Moist Broadleaf Forests
- Tundra

FIGURE 1 Spatial distribution of locations (0.25° cells) with biodiversity data both before (≥80% of natural habitat remaining) and after (0% of natural habitat remaining) habitat loss and with ≥ 10 plant species reported before and after habitat loss. Circles are semi-transparent and coloured according to biomes. Map is in Eckert IV projection [Colour figure can be viewed at wileyonlinelibrary.com]

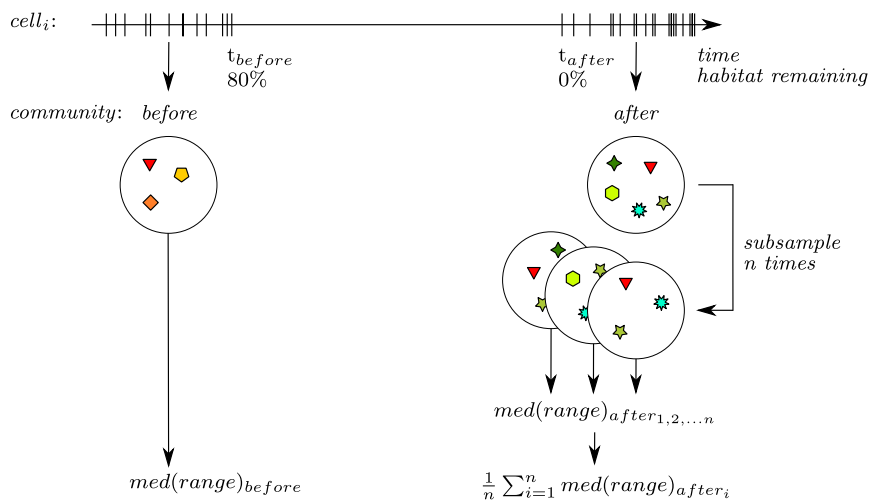


FIGURE 2 Schematic representation of our approach to comparison of species range sizes before and after habitat loss. The scheme focuses on one cell, $cell_i$. Cell_{*i*} has species occurrence records before and after habitat loss. These give an individual set of species for before and after habitat loss. These sets we name communities. Communities had to have ≥ 10 species (not shown for clarity). For each community, we calculate the median (med) range size. Given that digital biodiversity records increase with time, there are typically more species in the after community. We subsample the after community 100 times. Each time, we take as many samples as there are species in the before community and calculate, for that subset, the median range size. These medians are averaged. We compare this value with the median range size from the before community [Colour figure can be viewed at wileyonlinelibrary.com]

amount of natural habitat that remained at the time (year) and location (0.25° grid cell) where it was made. Hence, for each species we could produce a list of habitat values for each cell that it occupied. We could then find, for each species, the amount of habitat that remained at its last record in a given cell (hereafter, minimum

habitat value). The minimum habitat value indicated the amount of habitat loss at the latest time when a species was still reported to be present in a cell. These values were used to calculate persistence curves for small- and large-ranged species experiencing habitat loss.

It was not possible to find minimum habitat values for all species and all cells in our data collation. This was because of insufficient sampling for many species but also because we needed to confine data to cells that had experienced habitat loss. Therefore, we set three rules for the inclusion of species and cells: (a) in each cell, a species had to be sampled at least twice; (b) in each cell, a species had to be recorded before habitat loss ($\geq 80\%$ of natural habitat remaining); and (iii) species had to occur in cells that eventually experienced habitat loss (ultimately 0% natural habitat remaining).

Applying these inclusion rules led again to a drastic reduction of data. From c. 180,000 species, 102,970 met the first rule and were sampled at least twice within one cell. Of those, 53,199 species also met the second rule and were present before habitat loss. Finally, only 2,678 species also met the third rule and occurred in cells that experienced complete loss of natural habitat. Correspondingly, cell numbers reduced from c. 90,000 to c. 43,000 (first rule), to c. 10,000 (second rule) to 365 cells (third rule). The spatial extent of these cells was largely comparable to the previous analysis (Supporting Information Figure S3). For the final subset of species and cells, we found minimum habitat values.

We then used those species' minimum habitat values to calculate probabilities of persistence as follows (for a schematic representation, see Figure 3). Species' minimum habitat values were assigned to one of five 20%-wide intervals of habitat loss. The number of species in each of these intervals was then counted. Finally, these counts were divided by the total number of species. This gave the percentage of species that persisted within a given interval of habitat loss and allowed us to plot a persistence curve. We extend this basic approach conceptually in the following two paragraphs.

Note that a species can have more than one minimum habitat value. Theoretically, a species could have as many minimum habitat

values as cells it occupies. We could simply average these to obtain one value for each species, but this would also return only one persistence curve. Instead, if we sample one minimum habitat value from each species at a time and repeat this many times, we arrive at many persistence curves, one for each sampling repetition. From these, we can still calculate an average persistence curve but also gain information about the variance of this curve. Therefore, we sampled from each species one minimum habitat value at a time, repeated this 100 times, and calculated the mean and standard deviation of the resulting 100 persistence curves.

To arrive at a separate persistence curve for small-ranged species and large-ranged species, we divided the total set of species into two classes as follows. From the range-size frequency distribution of the 2,678 species, we calculated the median range size. Species with range sizes below the median were classified as small-ranged species and species with range sizes above the median as large-ranged species (Supporting Information Figure S4). We then calculated probabilities of persistence for each range size class separately.

The central assumption of our calculation of persistence probability is that a species has become extinct after its last record. Of course, the fact that a species goes unrecorded is not proof that it has become extinct, but a necessary condition for extinction is absence from further samples. We also examined how reasonable this assumption is. We examined the number of years that had passed and the number of occurrence records that had accrued since the last time a species was reported to be present in a cell. If these numbers are low, our assumption is probably unrealistic; that is, a species is not recorded anymore because there was simply no sampling in the meantime. Moreover, low detectability in certain types of plants can make them likely to be present but not recorded in

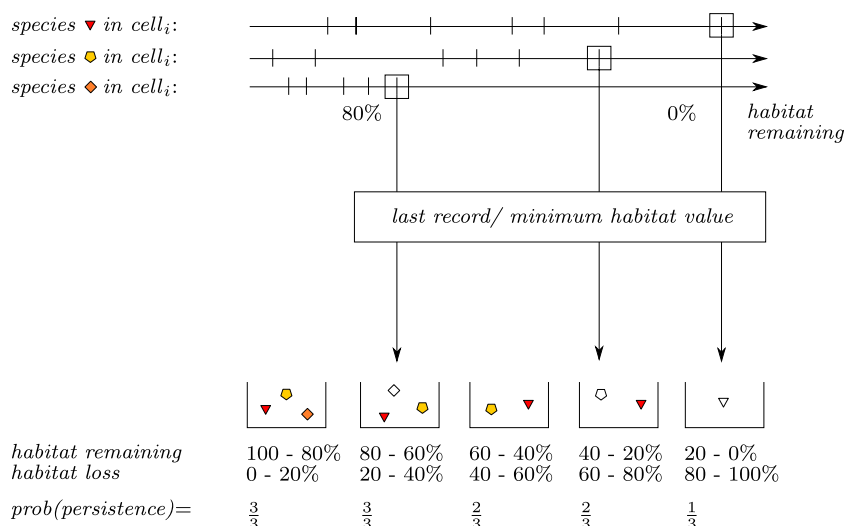


FIGURE 3 Schematic representation of our approach to calculation of persistence curves for species under habitat loss. The scheme focuses on one cell, cell_i. In this cell, the focus is on three species. All of them have been sampled at least twice, occurred before habitat loss, and importantly, cell_i experienced complete habitat loss and was sampled further. For each species, we identified its last record (minimum habitat value). We assigned the species' minimum habitat values to one of five intervals of equal length. Given that species were present before habitat loss, they also occurred in the intervals that preceded those of the last records. Given that species went unrecorded in subsequent intervals, they were absent from those. We calculated the probability of persistence as the number of species in each interval divided by the total number of species [Colour figure can be viewed at wileyonlinelibrary.com]

a census or inventory. In particular, small-ranged species that may be locally less abundant may have a lower probability of being re-sampled. This could bias our results. Therefore, we also examined whether resampling differed between small- and large-ranged species. Assuming that species are resampled at an equal and constant rate, the number of records would always be higher for species that withstood more habitat loss. Hence, we compared the number of records per percentage of habitat loss for small- and large-ranged species.

Finally, we used a simulation approach to test whether our way of calculating persistence probabilities produces any bias. The null hypothesis is that extinction, and consequently, the amount of habitat that remained at the time of extinction is random for both small- and large-ranged species. Thus, we simulated minimum habitat values from a uniform distribution. In particular, we simulated n minimum habitat values for each species, where n is the species' range size (i.e., the number of cells it occupies). We sampled one minimum habitat value from each species, calculated probabilities of persistence as above, repeated this 100 times and compared the average persistence curve of small-ranged species with the average persistence curve of large-ranged species. If our approach is free of bias, the two persistence curves should be largely the same. We provide R code for this simulation in the Supporting Information (section R Code 4.1 & 4.2).

3 | RESULTS

We studied changes in the frequency distribution of the range sizes of vascular plant species in 0.25° grid cells that experienced complete loss of natural habitat. Keeping species richness constant, the distribution of changes was towards higher median range size after habitat loss (pairwise permutation test: $Z = -2.99$, $p < .001$, $r = .22$; Figure 4a). Our approach to control for temporal bias by subsampling

communities to keep numbers of species before and after habitat loss constant did not induce any systematic bias. The distribution of effect sizes was not skewed towards positive log ratios but distributed evenly around zero (Supporting Information Figure S5a). In addition, relaxing our data selection thresholds did not change results (Supporting Information Figure S1).

Next, we studied the role of species range size in predicting vulnerability to local extinction from habitat loss. For this, we investigated the probability of persistence of small- and large-ranged species at different levels of habitat loss. Probabilities of persistence, expressed as the percentage of species of a given range size class that still occurred at, but not above, a given amount of habitat loss, indicated a generally higher vulnerability of small-ranged species to local extinction from habitat loss (Figure 4b). Small-ranged species had a steeper descending persistence curve and, moreover, a lower probability of persistence than widespread ones even at moderate levels (i.e., $\leq 50\%$) of habitat loss.

The absence of a species at higher levels of habitat loss is not proof of extinction. Therefore, we quantified the strength of this assumption. On average, 106 years passed and 806 species records accrued between the last record of a species and the last record of a cell, when species went extinct early (last reported present with $\geq 80\%$ habitat remaining). Species that persisted longer (last reported present between 60 and 80% habitat loss) had, on average, 60 years and 1,591 other species' records between their last record and the last record of a cell (Supporting Information Figure S6). Assessing potential sampling effects, we found that sampling frequencies per percentage of habitat loss were not higher for species with large ranges (Supporting Information Figure S7). Simulation results based on random extinctions of small- and large-ranged species showed that our approach did not produce any systematic bias. The simulated persistence curve of small- and large-ranged species followed the same trajectory (Supporting Information Figure S5b).

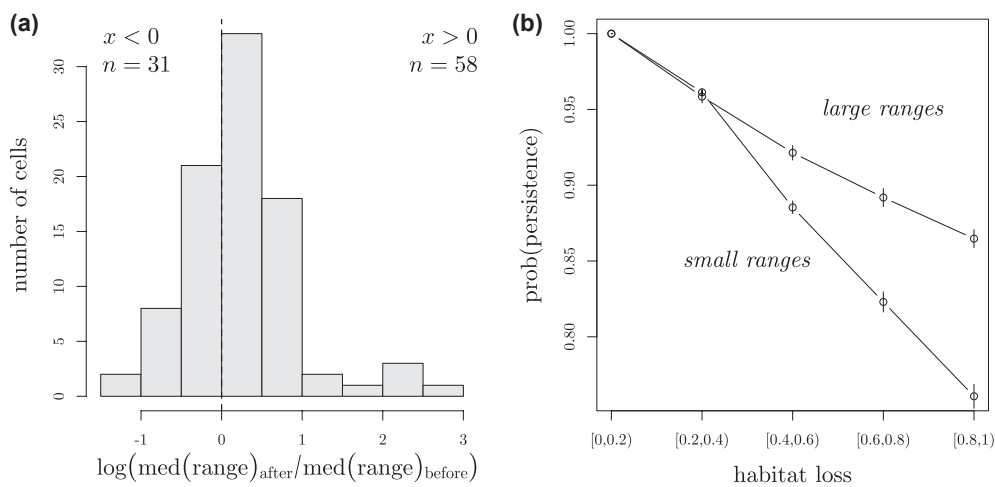


FIGURE 4 (a) Change in median range size of vascular plant communities before and after habitat loss. Positive log ratios indicate that median range size was higher after habitat loss. (b) Relationship between probability of persistence and habitat loss for species with small and large ranges. Small and large ranges include species with ranges from 1 to 63 and from 64 to 5,000 occupied cells, respectively. Error bars represent \pm two standard deviations from the mean

4 | DISCUSSION

Here, we show that habitat loss has a differential effect on the local extinction risk of vascular plant species with different range sizes. We find that the frequency distribution of range sizes in a community changes after habitat loss towards a higher median range size. In addition, we document lower persistence probabilities of small-ranged species at already moderate habitat loss. Together, this suggests that range size can be a predictor of the risk of local extinction from habitat loss. Moreover, our results imply that temporal species turnover under habitat loss can reduce spatial species turnover.

The differential vulnerabilities of species with small and large ranges to local habitat loss might have several explanations; here, we present four. First and most simply, it could follow from the effect of range size on metacommunity dynamics. Species with larger ranges are more likely to retain intact habitats that can act as a source and, via the “rescue effect”, help to uphold local persistence in sites with habitat loss (Hanski, 1991; Leibold et al., 2004). Second, it has been demonstrated for a number of taxa that range size is strongly and positively correlated with local abundance [plants (Gotelli & Simberloff, 1987), birds (Gaston & Blackburn, 1996) and mammals (Brown, 1984)]. Given that the probability of local extinction increases with decreasing population size (Christiansen & Fenchel, 2012; Schoener & Spiller, 1987), species with small ranges could be more vulnerable to habitat loss at any one site. Third, narrow habitat breadth, yet another dimension of rarity that may relate to range size (Brown, 1984), could make species with small ranges more susceptible to anthropogenic change (Rabinowitz, 1986). Fourth, habitat breadth and local abundance may influence the spatial distribution of species (Cornell, 1982). Species with relatively narrow habitat breadth and small population size are often unevenly distributed in aggregations within their range (Condit et al., 2000; Rodríguez, 2002). The more aggregated a species, the less habitat must be lost, on average, to cause local extinction. The individual importance of these potential mechanisms to make species vulnerable to local extinction still needs to be quantified.

Importantly, the higher local extinction risk from habitat loss of species with small ranges might contribute to the explanation of the systematic shifts in species composition and the scale-dependent patterns of diversity change that other studies report with long-term data. Evidence across biomes indicates no net loss in local species richness (Vellend et al., 2013), but loss of species at the continental to global scale (IPBES, 2019). If species with small ranges are preferentially declining at any one site with habitat loss, species with large ranges may also be more likely to colonize successfully, replacing small-ranged species systematically. Given that it is more likely that the entire range of small-ranged species is affected, habitat loss could then produce a homogenization pattern, where small-scale richness is largely unchanged through time, whereas larger-scale richness declines. Although our approach does not allow any inference about local-scale changes in species richness and thus species replacement, we can nevertheless infer homogenization. This is because for biotic

homogenization to occur, it is sufficient that the most localized species are systematically lost (McKinney & Lockwood, 1999; Olden & Poff, 2003) and precisely those, we find, are at higher risk of local extinction from habitat loss. This preferential decline of species with small ranges is consistent with a recent global assessment of the effects of land use on small-ranged and widespread species (Newbold et al., 2018). Those authors used space-for-time substitution to show that disturbed habitats have both reduced abundances of small-ranged species and increased abundances of widespread ones. Here, we used time series data. This allowed us, in addition to studying changes in species' range size composition, to explore how local extinction risk changes with habitat loss. To our knowledge, this is the first time that local extinction curves have been plotted against a habitat loss gradient and shown to differ for species with small and large ranges.

In the case of vascular plants, many species appear to cope well with habitat loss (Figure 4b). Recognition is growing that many species are not entirely constrained to native habitat fragments and persist in agricultural landscapes (Daily, Ehrlich, & Sanchez-Azofeifa, 2001; Mendenhall, Karp, Meyer, Hadly, & Daily, 2014); that is, habitat loss does not create a matrix entirely inhospitable to species, as is commonly assumed in studies that apply the species–area relationship from island biogeography theory to estimate the species loss attributable to change in land use. Countryside biogeography (*sensu* Mendenhall et al. (2014)), instead, considers the affinity of species for human-modified habitats, such as agriculture and forestry (Pereira, Daily, & Roughgarden, 2004), and argues that their qualities are crucial determinants of the conservation of biodiversity (Karp et al., 2012; Prugh, Hodges, Sinclair, & Brashares, 2008). Although we do not quantify the differential importance of anthropogenic habitats on the persistence of species, our results indicate that a large percentage of species can survive loss of natural habitat. Our results therefore highlight that the overextension of island biogeography theory to human-dominated ecosystems might overestimate projections of biodiversity loss driven by change in land use (Mendenhall et al., 2014).

Our approach to combine reconstructed biological time series and land-use data is novel, but also has weaknesses. The land-use harmonization product, although constrained by satellite and census data, is a model-based reconstruction from limited empirical data. It thus has differing accuracy in time and space (Ellis et al., 2013). Nonetheless, it provides the most comprehensive global land-use data available and has been widely applied in the literature. The digital biodiversity data also suffer from biases (Meyer et al., 2016). We accounted for the temporal documentation bias by subsampling communities, and simulations showed that this step did not induce any systematic bias (Supporting Information Figure S5a). We note that different before–after time periods were compared for this analysis (Supporting Information Figure S2). Therefore, cells that lost habitat early on would have had a longer time for extinctions to occur over and also a longer time to accrue opportunistic records. However, comparison of different time periods would not alone lead to higher community median range sizes, on average, after habitat loss.

For the calculation of persistence probabilities, we found no sampling bias towards species with larger ranges in our data subset (Supporting Information Figure S7). This could reflect the ter Steege effect, which describes the fact that botanists tend to avoid collecting large-ranged species that they have already collected in the general vicinity (ter Steege, Haripersaud, Bánki, & Schieving, 2011), but it is more likely that this is because we set strict inclusion rules for species and cells, meaning that our data subset includes rather well-sampled species. But this might also mean that we are neglecting truly rare species (Supporting Information Figure S4), potentially weakening the effect of range size in our analysis. Nonetheless, persistence curves differed between relatively small- and large-ranged species. Importantly, we can exclude the possibility that our approach produced these differences. Under simulated random extinctions, the persistence curves of small- and large-ranged species did not differ (Supporting Information Figure S5b).

In addition, we find that the assumption that a species goes extinct after its last record is justifiable for our data subset, because in general, many other species records were made in the meantime (Supporting Information Figure S6). Finally, we note that locations of this analysis are spatially biased. For example, no cell in Asia or tropical Africa met the inclusion criteria of the before–after comparison. This spatial bias is typical for digital biodiversity data, and only with increasing data-mobilization efforts in these regions will analyses based on such data become truly globally representative. Although we acknowledge that data biases are inherent to our data, we contend that they do not nullify the implications of our results. Given that small-ranged species are at higher risk of local extinction, temporal species turnover is biased towards species with larger ranges in local communities undergoing habitat loss.

Although it is expected that species with smaller ranges will be more vulnerable to global extinction from habitat loss than widespread ones, because the drivers of threat are more likely to affect the entire range of these species (Collen et al., 2016), we emphasize that there is a lack of studies that quantify this expectation at different spatial scales. Here, we find that relatively small-ranged species are more vulnerable to extinction from habitat loss even at a local scale. This will necessarily cause a disproportionate effect of range size on the risk of extinction at broader spatial scales. Understanding and quantifying the mechanisms that determine local extinction risk from anthropogenic change, how these depend on spatial scale and how local extinction risk, in turn, can be used to predict the consequences of range loss will be imperative for the conservation of species.

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DATA AVAILABILITY STATEMENT

Species' point occurrence data are openly available from GBIF (<https://doi.org/10.15468/dl.chiubr>), BIEN (via R package BIEN) and PREDICTS (<https://doi.org/10.5519/0066354>). Global land-use data are openly available from LUH2 (<http://luh.umd.edu/data.shtml>). We provide the R markdown file for data retrieval and cleaning, and all simulations, in the Supporting Information.

ORCID

Ingmar R. Staude  <https://orcid.org/0000-0003-2306-8780>

Laetitia M. Navarro  <https://orcid.org/0000-0003-1099-5147>

Henrique M. Pereira  <https://orcid.org/0000-0003-1043-1675>

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BIOSKETCHES

Ingmar R. Staude is a PhD student working under the supervision of **Henrique M. Pereira** and **Laetitia M. Navarro** in the Biodiversity Conservation group of iDiv. His research focuses on the causes and prediction of species extinction.

SUPPORTING INFORMATION

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

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Chapter 3

Replacements of small- by large-ranged species scale up to diversity loss in Europe's temperate forest biome

by **Ingmar R. Staude**, Donald M. Waller, Markus Bernhardt-Römermann, Anne D. Bjorkman, Jorg Brunet, Pieter De Frenne, Radim Hedl, Ute Jandt, Jonathan Lenoir, František Malíš, Kris Verheyen, Monika Wulf, Henrique M. Pereira, Pieter Vangansbeke, Adrienne Ortmann-Ajkai, Remigiusz Pielech, Imre Berki, Marketa Chudomelova, Guillaume Decocq, Thomas Dirnbock, Tomasz Durak, Thilo Heinken, Bogdan Jaroszewicz, Martin Kopecky, Martin Macek, Marek Malicki, Tobias Naaf, Thomas A. Nagel, Petr Petřík, Kamila Reczyńska, Fride Høistad Schei, Wolfgang Schmidt, Tibor Standovar, Krzysztof Świerkosz, Balázs Teleki, Hans Van Calster, Ondřej Vild & Lander Baeten. *Nature Ecology & Evolution* (2020). 4:802–808.

Abstract: Biodiversity time series reveal global losses and accelerated redistributions of species, but no net loss in local species richness. To better understand how these patterns are linked, we quantify how individual species trajectories scale up to diversity changes using data from 68 vegetation resurvey studies of seminatural forests in Europe. Herb-layer species with small geographic ranges are being replaced by more widely distributed species, and our results suggest that this is due less to species abundances than to species nitrogen niches. Nitrogen deposition accelerates the extinctions of small-ranged, nitrogen-efficient plants and colonization by broadly distributed, nitrogen-demanding plants (including non-natives). Despite no net change in species richness at the spatial scale of a study site, the losses of small-ranged species reduce biome-scale (gamma) diversity. These results provide one mechanism to explain the directional replacement of small-ranged species within sites and thus explain patterns of biodiversity change across spatial scales.

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Chapter 4

Consistent replacement of small- by large-ranged plant species across habitats

by **Ingmar R. Staude**, Henrique M. Pereira, Gergana Daskalova, Markus Bernhardt-Römermann, Martin Diekmann, Harald Pauli, Hans Van Calster, Mark Vellend, Anne D Bjorkman, Jörg Brunet, Pieter De Frenne, Radim Hédli, Ute Jandt, Jonathan Lenoir, Isla H. Myers-Smith, Kris Verheyen, Sonja Wipf, Monika Wulf, Christopher Andrews, Peter Barančok, Elena Barni, José-Luis Benito-Alonso, Jonathan Bennie, Imre Berki, Volker Blüml, Markéta Chudomelová, Guillaume Decocq, Jan Dick, Thomas Dirnböck, Tomasz Durak, Ove Eriksson, Brigitta Erschbamer, Bente Jessen Graae, Thilo Heinken, Fride Høistad Schei, Bogdan Jaroszewicz, Martin Kopecký, Thomas Kudernatsch, Martin Macek, Marek Malicki, František Máliš, Ottar Michelsen, Tobias Naaf, Thomas A. Nagel, Adrian C. Newton, Lena Nicklas, Ludovica Oddi, Andrej Palaj, Alessandro Petraglia, Petr Petřík, Remigiusz Pielech, Francesco Porro, Mihai Puscas, Kamila Reczyńska, Christian Rixen, Wolfgang Schmidt, Tibor Standovár, Klaus Steinbauer, Krzysztof Świerkosz, Balázs Teleki, Jean-Paul Theurillat, Pavel Dan Turtureanu, Tudor-Mihai Ursu, Thomas Vanneste, Philippine Vergeer, Ondřej Vild, Luis Villar, Pascal Vittoz, Manuela Winkler & Lander Baeten.

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1 Consistent replacement of small- by large-ranged plant species across habitats

2

3 *One sentence summary:*

4 Large-ranged, nutrient-demanding species consistently replace species with small ranges and
5 thus homogenize vegetation between habitats, despite variable trends in species richness.

6

7 Ingmar R. Stauder^{1,2}, Henrique M. Pereira^{1,2,3}, Gergana Daskalova⁴, Markus Bernhardt-Römermann⁵, Martin
8 Diekmann⁶, Harald Pauli^{7,8}, Hans Van Calster⁹, Mark Vellend¹⁰, Anne D Bjorkman^{11,12}, Jörg Brunet¹³, Pieter De
9 Frenne¹⁴, Radim Hédli^{15,16}, Ute Jandt^{1,2}, Jonathan Lenoir¹⁷, Isla H. Myers-Smith⁴, Kris Verheyen¹⁴, Sonja Wipf^{18,19},
10 Monika Wulf²⁰, Christopher Andrews²¹, Peter Barančok²², Elena Barni²³, José-Luis Benito-Alonso²⁴, Jonathan
11 Bennie²⁵, Imre Berki²⁶, Volker Blüml²⁷, Markéta Chudomelová¹⁵, Guillaume Decocq¹⁷, Jan Dick²¹, Thomas
12 Dirnböck²⁸, Tomasz Durak²⁹, Ove Eriksson³⁰, Brigitta Erschbamer³¹, Bente Jessen Graae³², Thilo Heinken³³, Fride
13 Høistad Schei³⁴, Bogdan Jaroszewicz³⁵, Martin Kopecký^{36,37}, Thomas Kudernatsch³⁸, Martin Macek³⁶, Marek
14 Malicki^{39,40}, František Máliš^{41,42}, Ottar Michelsen⁴³, Tobias Naaf⁴⁴, Thomas A. Nagel⁴⁵, Adrian C. Newton⁴⁶, Lena
15 Nicklas³¹, Ludovica Oddi²³, Andrej Palaj²², Alessandro Petraglia⁴⁷, Petr Petřík⁴⁸, Remigiusz Pielech^{49,50}, Francesco
16 Porro⁵¹, Mihai Puşcaş^{52,53}, Kamila Reczyńska³⁹, Christian Rixen¹⁸, Wolfgang Schmidt⁵⁴, Tibor Standovár⁵⁵, Klaus
17 Steinbauer⁸, Krzysztof Świerkosz⁵⁶, Balázs Teleki^{57,58}, Jean-Paul Theurillat^{59,60}, Pavel Dan Turtureanu⁵², Tudor-
18 Mihai Ursu⁶¹, Thomas Vanneste¹⁴, Philippine Vergeer⁶², Ondřej Vild³⁶, Luis Villar⁶³, Pascal Vittoz⁶⁴, Manuela
19 Winkler^{7,65}, Lander Baeten¹⁴

20

21 *1. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena Leipzig, Leipzig, Germany*

22 *2. Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany*

23 *3. CIBIO (Research Centre in Biodiversity and Genetic Resources)–InBIO (Research Network in Biodiversity and Evolutionary
24 Biology), Universidade do Porto, 4485-661 Vairão, Portugal*

25 *4. School of GeoSciences, University of Edinburgh, Edinburgh, Scotland, UK*

26 *5. Institute of Ecology and Evolution, Friedrich Schiller University Jena, Jena, Germany*

27 *6. Institut für Ökologie, Universität Bremen, Bremen, Germany*

28 *7. GLORIA Coordination, Institute for Interdisciplinary Mountain Research at the Austrian Academy of Sciences (ÖAW-IGF),
29 Vienna, Austria*

30 *8. GLORIA Coordination, Department of Integrative Biology and Biodiversity Research at the University of Natural Resources
31 and Life Sciences Vienna, Austria*

32 *9. Research Institute for Nature and Forest, Brussels, Belgium*

33 *10. Département de biologie, Université de Sherbrooke, Québec, Canada*

34 *11. Department of Biological and Environmental Sciences, University of Gothenburg, 40530 Gothenburg, Sweden*

35 *12. Gothenburg Global Biodiversity Centre, 40530 Gothenburg, Sweden*

36 *13. Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Box 49, 23053 Alnarp, Sweden*

37 *14. Forest & Nature Lab, Ghent University, Gontrode, Belgium*

38 *15. Institute of Botany, Czech Academy of Sciences, Brno, Czech Republic*

39 *16. Department of Botany, Faculty of Science, Palacký University in Olomouc, Olomouc, Czech Republic*

- 40 17. UR "Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN, UMR7058 CNRS), Université de Picardie Jules Verne, 1
41 rue des Louvels, F-80000 Amiens, France
- 42 18. WSL Institute for Snow and Avalanche Research SLF, Flüelastrasse 11, Davos, Switzerland
- 43 19. Swiss National Park, 7530 Zerne, Switzerland
- 44 20. Leibniz Centre for Agricultural Landscape Research (ZALF), Research Area 2, Müncheberg, Germany
- 45 21. UK Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB, UK
- 46 22. Institute of Landscape Ecology, Slovak Academy of Sciences, Štefánikova 3, 814 99 Bratislava, Slovakia
- 47 23. Department of Life Sciences and Systems Biology, University of Turin, Italy
- 48 24. GLORIA-Aragon Coordination, Jolube Consultor Botánico y Editor, Jaca, Huesca, Spain
- 49 25. Centre for Geography and Environmental Science, Exeter University, Penryn Campus, Penryn, Cornwall TR10 9FE, UK
- 50 26. Faculty of Forestry, University of Sopron, Sopron, Hungary
- 51 27. BMS-Umweltplanung, Osnabrück, Germany
- 52 28. Environment Agency Austria, Spittelauer Lände 5, 1090 Vienna, Austria
- 53 29. Laboratory of Plant Physiology and Ecology, University of Rzeszów, Rejtana 16c, PL-35-959 Rzeszów, Poland
- 54 30. Department of Ecology, Environment and Plant Sciences, Stockholm University, Sweden
- 55 31. Department of Botany, University of Innsbruck, Sternwartestr. 15, 6020 Innsbruck, Austria
- 56 32. Department of Biology, NTNU, Høgskoleringen 5, 7091 Trondheim, Norway
- 57 33. University of Potsdam, Institute of Biochemistry and Biology, Maulbeerallee 3, 14469 Potsdam, Germany
- 58 34. Norwegian Institute of Bioeconomy Research, Thormøhlensgate 55, 5006 Bergen, Norway.
- 59 35. Białowieża Geobotanical Station, Faculty of Biology, University of Warsaw, Sportowa 19, 17-230 Białowieża, Poland
- 60 36. Institute of Botany of the Czech Academy of Sciences, Zámek 1, CZ-252 43, Průhonice, Czech Republic
- 61 37. Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, CZ-165 21, Praha 6 –
62 Suchbátka, Czech Republic
- 63 38. Bavarian State Institute of Forestry Hans-Carl-von-Carlowitz-Platz 1 85354 Freising (Deutschland - Germany)
- 64 39. Department of Botany, Faculty of Biological Sciences, University of Wrocław, Kanonia 6/8, PL-50-328 Wrocław, Poland
- 65 40. Department of Pharmaceutical Biology and Biotechnology, Wrocław Medical University, Poland
- 66 41. Faculty of Forestry, Technical University in Zvolen, Zvolen, Slovakia
- 67 42. National Forest Centre, Zvolen, Slovakia
- 68 43. Department of Industrial Economics and Technology Management, Norwegian University of Science and Technology
69 (NTNU), 7491 Trondheim, Norway
- 70 44. Leibniz Centre for Agricultural Landscape Research (ZALF), Muencheberg, Germany
- 71 45. Department of forestry and renewable forest resources, Biotechnical Faculty, University of Ljubljana, Večna pot 83,
72 Ljubljana 1000, Slovenia
- 73 46. Department of Life and Environmental Sciences, Bournemouth University, Poole, Dorset, UK BH21 5BB
- 74 47. Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parco Area delle Scienze
75 11/A, 43124, Parma, Italy
- 76 48. Czech Academy of Sciences, Institute of Botany, Zámek 1, CZ-25243 Průhonice
- 77 49. Department of Forest Biodiversity, University of Agriculture, al. 29 Listopada 46, 31-425 Kraków, Poland
- 78 50. Foundation for Biodiversity Research, ul. Terenowa 4c/6, 52-231 Wrocław, Poland
- 79 51. University of Pavia, Department of Earth and Environmental Sciences, via Ferrata 1, Pavia, 27100, Italy
- 80 52. A. Borza Botanical Garden, Babeş-Bolyai University Cluj-Napoca, Republicii 42, Romania
- 81 53. Center for Systematic Biology, Biodiversity and Bioresources - 3B, Faculty of Biology and Geology, Babeş-Bolyai University
82 Cluj-Napoca, Republicii 42, Romania

- 83 54. Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Germany
84 55. Department of Plant Systematics, Ecology and Theoretical Biology, Institute of Biology, Loránd Eötvös University, Pázmány
85 s. 1/C, H-1117 Budapest, Hungary
86 56. Museum of Natural History, University of Wrocław, Sienkiewicza 21, PL-50-335 Wrocław. Poland
87 57. MTA-DE Lendület Functional and Restoration Ecology Research Group, H-4032 Debrecen Egyetem sqr. 1, Hungary
88 58. PTE KPVK Institute for Regional Development 7100 Szekszárd Rákóczi str. 1, Hungary
89 59. Fondation J.-M. Aubert, Champex-Lac, Switzerland
90 60. Department of Botany and Plant Biology, University of Geneva, Chambésy, Switzerland
91 61. Institute of Biological Research Cluj-Napoca, branch of NIRDBS Bucharest, Romania.
92 62. Wageningen University, Department of Environmental Sciences, PO Box 47, 6700 AA, Wageningen, the Netherlands
93 63. Instituto Pirenaico de Ecología, IPE-CSIC. Avda. de la Victoria, 12. 22700 Jaca, Huesca, Spain
94 64. Institute of Earth Surface Dynamics, Faculty of Geosciences and Environment, University of Lausanne, 1015 Lausanne,
95 Switzerland
96 65. GLORIA Coordination, Department of Integrative Biology and Biodiversity Research at the University of Natural Resources
97 and Life Sciences, Vienna (BOKU), Vienna, Austria

98

99 Abstract

100 The direction and magnitude of long-term changes in local plant species richness are highly variable
101 among studies, while species turnover is ubiquitous. However, it is unknown whether the nature of
102 species turnover is idiosyncratic or whether certain types of species are consistently gained or lost
103 across different habitats. To address this question, we analyzed the trajectories of 1,827 vascular plant
104 species over time intervals of up to 78 years at 141 sites in three habitats in Europe – mountain
105 summits, forests, and lowland grasslands. Consistent across all habitats, we found that plant species
106 with small geographic ranges tended to be replaced by species with large ranges, despite habitat-
107 specific trends in species richness. Our results point to a predictable component of species turnover,
108 likely explained by aspects of species' niches correlated with geographic range size. Species with larger
109 ranges tend to be associated with nutrient-rich sites and we found community composition shifts
110 towards more nutrient-demanding species in all three habitats. Global changes involving increased
111 resource availability are thus likely to favor large-ranged, nutrient-demanding species, which are
112 typically strong competitors. Declines of small-ranged species could reflect not only abiotic drivers of
113 global change, but also biotic pressure from increased competition. Our study highlights a critical need
114 to better understand the extent to which abiotic or biotic pressures drive systematic species turnover
115 over time.

116

117 Main text

118 Long-term studies of changes in local plant species richness do not show systematic evidence of
119 decline (1–3). However, local richness changes provide only a limited picture of the extent of ongoing
120 biodiversity change, as they do not capture species turnover and changes in community composition

121 over time (4). While human activities have accelerated species turnover beyond background rates (2,
122 3), it remains unclear whether the identities of “loser” and “winner” species represent the
123 idiosyncratic local outcomes of drivers of change (e.g., disturbance or climate warming), or whether
124 there are consistent patterns across systems (5). In order to gain a general understanding of why and
125 how plant diversity is changing, we need to ask whether similar types of plant species are consistently
126 lost and gained in communities in different habitats. Here we focus on the geographic range size of
127 plant species as a key synthetic measure of their ecological profile (6). Range size reflects the ability of
128 species to disperse and colonize (7, 8), as well as their niche breadth (9, 10) and niche position (11–
129 13), thus capturing a species’ vulnerability to global environmental changes. Moreover, range size links
130 temporal with spatial turnover of species, as communities that lose small-ranged while gaining
131 widespread species become more similar over time (14). Therefore, understanding the link between
132 range size and a species’ trajectory over time will not only shed light on why certain species “win” or
133 “lose”, but also on the consequences of these shifts for the distinctiveness of plant communities, an
134 important component of biodiversity.

135

136 Here we analyze individual trajectories of 1,827 vascular plant species over time in relation to their
137 range size at 141 study sites across three habitats in Europe – mountain summits, deciduous and
138 coniferous forests, and lowland grasslands (Fig. 1), using vegetation resurveys spanning intervals of 12
139 to 78 years. Temporal trends in local species richness and drivers of change are known to vary among
140 these habitats, with climate warming increasing local species richness on summits (15, 16),
141 eutrophication and changes in management reducing richness in grasslands (17, 18), and a
142 combination of these drivers leading to both increases and decreases in richness in forests (13, 19–
143 21). In each habitat, we identified all species that were lost, gained or persisted at the study-site level.
144 We then tested whether species gains and losses, and changes in site-occupancy of persisting species
145 at the study site can be explained by range size. We hypothesize that, regardless of the richness trend
146 in a habitat, smaller-ranged species are consistently replaced by larger-ranged species, as
147 environmental changes (such as increasing temperatures, land-use change and eutrophication) alter
148 ecological selection processes in favor of widespread species; species that are expected to be more
149 resilient, more nutrient-demanding and better dispersed (13, 22). Our study explores whether
150 temporal species turnover is predictable, and whether it acts to homogenize vegetation between
151 habitats.

152

153 We found that vascular plant species with larger ranges consistently emerged as winners and those
154 with smaller ranges as losers over time across all three habitats, regardless of trends in species
155 richness. While on mountain summits, species gains were clearly more prominent than species losses,

156 there was substantial species loss in forests and grasslands (Fig. 2a). Losses and gains, however,
157 balanced out in forests, whereas in grasslands losses outweighed gains (Fig. 2b). Thus, the average
158 species richness increased on summits, showed no clear trend in forest and decreased in grasslands
159 (Fig. 2c and fig. S1), in accordance with single-habitat studies from each of these habitats (summits
160 (15, 16), forests (13, 19) and grasslands (17, 18)). Despite variable trends in richness, species turnover
161 was systematic. We tested whether species with smaller ranges have been lost preferentially at a
162 study site. Even after accounting for demographic effects (i.e., due to the likelihood that small-ranged
163 species are lost simply because of a smaller local population size; see Methods), range size was
164 negatively associated with loss probability in all three habitats, although on summits the association
165 was not statistically clear as the 66% credible interval overlapped with zero (Fig. 3a and Table S2).
166 Effect estimates for forests and grasslands were robust to excluding rare species (with site-
167 occupancies below 5% in the baseline survey) from the data (Table S2). We then asked whether
168 changes in site-occupancy of persisting species were related to range size. In all three habitats,
169 persisting species increasing in occupancy had larger ranges on average than species decreasing in
170 occupancy (fig. S3 and Table S3). This relationship persisted after accounting for species baseline
171 occupancy (Fig. 3b, see Methods). Finally, we compared range sizes of species gained to species lost.
172 In all three habitats, species that were newly gained at a study site had, on average, larger ranges than
173 species lost (Fig. 3c, d and Table S4). Together, these findings indicate commonalities between
174 contrasting habitats with respect to the nature of biodiversity change based on species range size.

175 Across habitats, plant species with larger ranges gained ground. The success of large-ranged species
176 could be due to previously limiting resources (e.g., nutrients) becoming more available as a result of
177 global changes such as eutrophication and warming (23, 24). A greater availability of limiting resources
178 allows less specialized species to colonize, where larger-ranged species may be more likely to colonize
179 simply because they disperse from more sites. Larger-ranged species may also be more likely to persist
180 because they naturally face a larger gradient in environmental conditions and may thus exhibit a
181 greater niche breadth and phenotypic plasticity, making them more resilient to global changes (10, 22,
182 25). Furthermore, global changes may even favor large-ranged species, as they tend to be species with
183 resource-acquisitive strategies and might therefore benefit more from an increase in resources (12,
184 13, 22). We found support for this hypothesis in our data; species with larger ranges were associated
185 with higher nutrient demands (fig. S4) and community weighted means of species niche positions for
186 nutrients indicated community shifts towards more nutrient-demanding species (fig. S5, see
187 Methods), in accordance with other studies in these habitats (summits (26), forests (19) and
188 grasslands (18)). These findings suggest that a higher prevalence of larger-ranged species, often also
189 more resource-acquisitive species, is likely to exert increased biotic pressure on extant species.

190 In contrast to large-ranged species, small-ranged species tend to be adapted to lower nutrient
191 availability (fig. S4) and thus are likely to grow more slowly (27), presenting a particular risk of
192 competitive exclusion by faster growing species. The loss of small-ranged species could therefore be a
193 result of the increase in less specialized, more competitive, larger-ranged species (i.e. biotic filtering).
194 Furthermore, small-ranged species tend to have adaptations to the stresses specific to their habitat
195 and therefore possibly a lower tolerance to new types of stress, such as stoichiometric imbalances in
196 resource supply from eutrophication (28). Thus, the decline in small-ranged species could also be due
197 to direct effects of environmental change (i.e. abiotic filtering). Importantly, we can largely exclude the
198 potential explanation that the higher loss probability of small-ranged species is due only to stochastic,
199 demographic effects (Table S2, see Methods). Also, if small-ranged species were simply more prone to
200 demographic fluctuations and therefore had a more variable presence, we would expect comparable
201 range sizes of species lost and gained, which we do not see in the data (Fig. 3c and d). Thus, the
202 preferential loss of small-ranged species is likely due not only to demographic stochasticity, but also to
203 aspects of species niche that confer a higher vulnerability to both abiotic and biotic pressures.

204 Despite the congruence across habitats of small-ranged species being replaced by large-ranged
205 species, our results also indicate differences in the effect of range size on temporal species turnover
206 between habitats. On summits, the effect of range size on species loss probability was weakest and
207 not clearly different from zero (Fig. 3a). Moreover, species gained on summits had larger ranges than
208 both persisting and lost species, whereas in forests and grasslands the main distinction was that
209 species lost had smaller ranges than both persisting and gained species (Fig. 3c and Table S4). In
210 addition, on summits, species gains dominated and species losses were less important for driving
211 turnover compared with forests and grasslands (Fig. 2a and b). These results suggest that the
212 directional turnover on summits in relation to species range size could be mainly due to species
213 differences in dispersal and colonization ability. On summits, warming may allow the colonization of
214 species from lower elevations, which tend to have larger ranges (fig. S6), while extant species may
215 persist and escape changes in abiotic and biotic filters due to a high variation of micro-habitats (29,
216 30) and a still sparse or less tall-growing vegetation (31, 32). In forests and grasslands, the vegetation
217 is typically denser than on summits. Environmental changes, such as eutrophication or declines in
218 traditional land use, are thus likely to lead, in addition to abiotic changes, to higher biotic pressure (33,
219 34). We hypothesize that a greater relevance of biotic filtering in forests and grasslands could
220 contribute to the more directional loss of small-ranged species in these habitats (Fig. 3). Although any
221 cross-habitat comparison is limited due to inherent differences between habitats, we can rule out that
222 differences in the relationship of range size and loss probability simply arise from evident differences
223 in sampling methods among study sites. The number of plots, plot size, site area and time span
224 between surveys did not change the effect of range size on the probability of loss (see Methods and

225 Table S5). Our results thus support the potential role of indirect, biotic effects of global change in
226 understanding the preferential loss of small-ranged species.

227 Altogether, our results suggest that temporal species turnover has a predictable component based on
228 species range size. Regardless of whether site-level trends show increases or decreases in species
229 richness, larger-ranged species replaced smaller-ranged species. This has at least two implications.
230 First, as sites gain species that are already widespread and lose small-ranged species, cumulatively this
231 may lead to shifts from characteristic, often rare vegetation types to more widespread vegetation
232 types – a form of biotic homogenization (14). Indeed, we found that an average pair of study sites
233 became more similar in species composition and, moreover, that the total species pools of the three
234 habitats became more similar over time (fig. S7a and b). Second, small-ranged species may be doubly
235 at risk of extinction (35), both because of purely geographical reasons, as they by definition occupy
236 fewer sites, and because they can also be more vulnerable to being lost within each site, as we have
237 shown here. While the patterns found in our study suggest that the loss of small-ranged species within
238 sites is partially explained by species niches, it remains a future challenge to disentangle how much of
239 this loss is driven by indirect effects due to altered competitive interactions (i.e. biotic filtering) versus
240 direct effects due to environmental changes (i.e. abiotic filtering) in different habitats. Insights on the
241 relative importance of biotic versus abiotic filtering will be essential when prioritizing conservation and
242 restoration measures to reverse the declines of the most vulnerable species in the Anthropocene.

243 [References and Notes](#)

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349

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383 range sizes and GBIF urls (Data Table 1) are available on figshare at figshare.com/s/b37f6167b13ad5da9e9c.
384 Species composition data for grasslands is available from published literature compiled in (18); for forest and
385 alpine summits these data are available upon request and under license from forestreplot.ugent.be and
386 gloria.ac.at, respectively.

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388 Supplementary Materials

389 Materials and Methods

390 Figs. S1 to S11

391 Tables S1 to S4

392 References (36 – 57)

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Figures main text

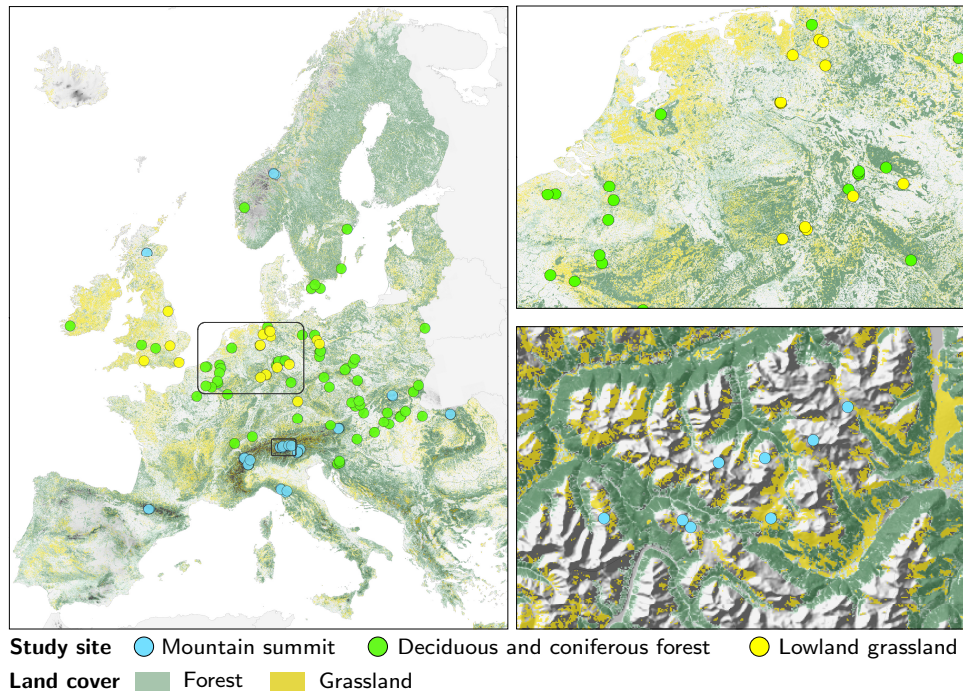


Fig. 1. Our analysis spans 141 resurvey study sites. Resurveys are from three habitats in Europe: mountain summits = 52 sites (blue), deciduous and coniferous forests = 68 sites (green), and lowland grasslands = 21 sites (yellow). CORINE forest cover (green) and grassland cover (yellow) in Europe are displayed along with elevation (dark shades). Insets show details for forests and grasslands (top), and summits (bottom).

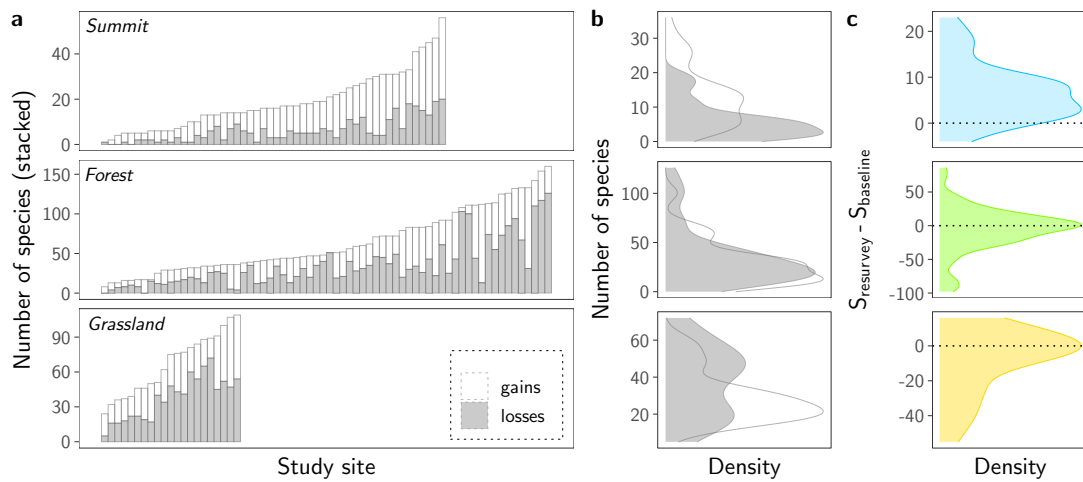


Fig. 2. Species losses and gains vary across habitats. a, Species gains (white) and losses (grey) at each study site (numbers stacked, each bar represents a study site). b, Relative frequency (density) of the number of species lost and gained across sites. c, Density across study sites of the difference in species richness (S) between the baseline survey and resurvey. Dotted horizontal line represents zero change in S . Colours (blue, green, yellow) refer to habitats as in Figure 1. Posterior distribution of the mean difference in S is shown in Supplementary Figure 1.

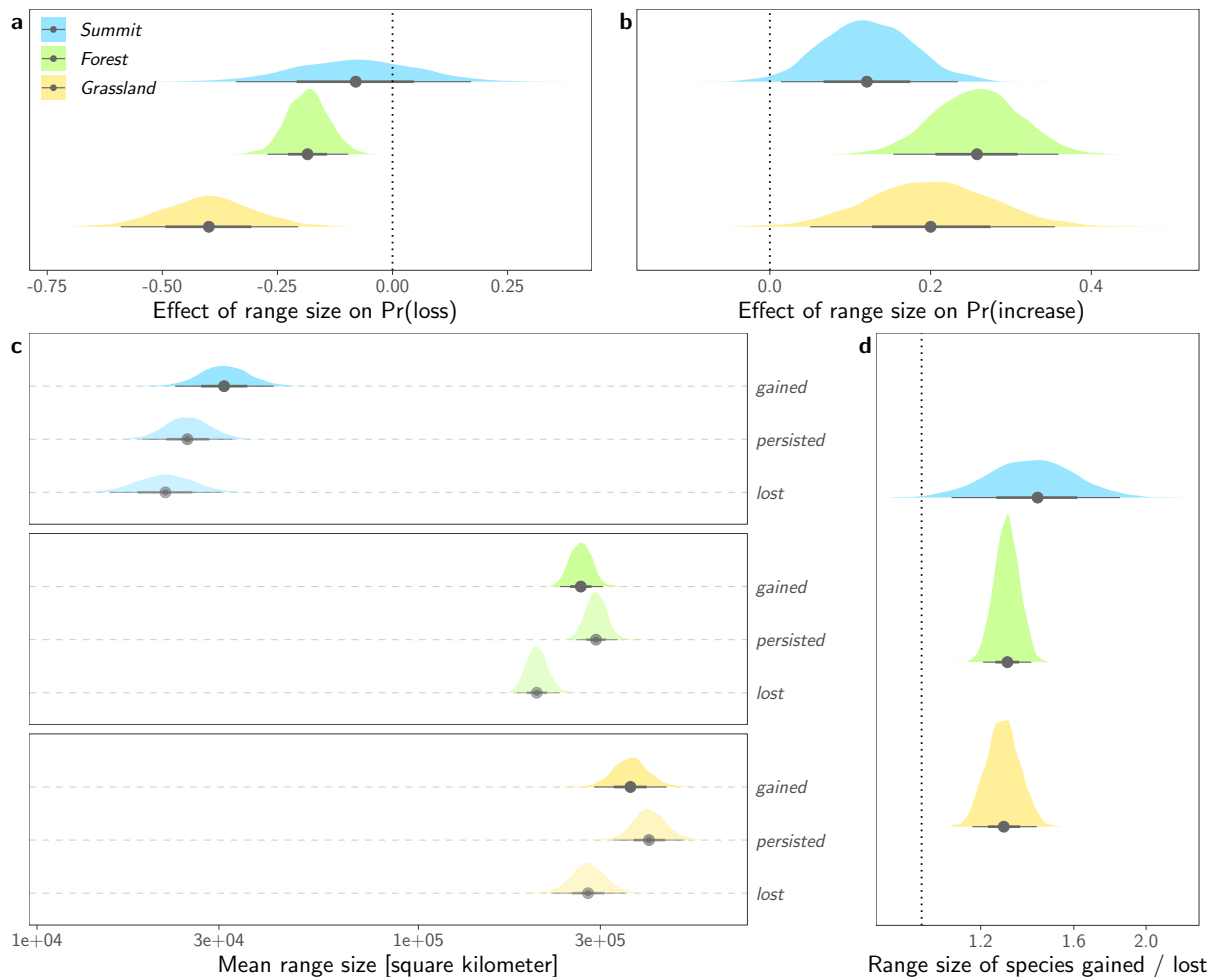


Fig. 3. Consistent replacement of small- by large-ranged species across habitats. Posterior distribution of the effect of range size on **a**, the probability (Pr) of a species being lost at a study site and **b**, the probability (Pr) of a persisting species increasing in occupancy at a study site, after having accounted for demographic effects (see Methods). **c**, Posterior distribution of the mean range size of gained, persisting, and lost species. **d**, Comparison between the mean range sizes of species gained and lost, derived from the posterior distributions in **c** (persisting vs gained/lost comparison in Supplementary Table 4). Point and lines in **a** - **d** are the median and its 66% and 95% credible interval. Dotted vertical line in **d** represents no difference in mean range size. In **a** and **b**, range size was \log_{10} -transformed and scaled to have a mean of zero and a standard deviation of one, effect estimates (x-axis) are in the logit scale. Model summaries and sample sizes for panels **a**-**d** are in Supplementary Table 2-4.

Supplementary Materials for

Consistent replacement of small- by large-ranged plant species across habitats

Ingmar R. Staude*, Henrique M. Pereira, Gergana Daskalova, Markus Bernhardt-Römermann, Martin Diekmann, Harald Pauli, Hans Van Calster, Mark Vellend, Anne D Bjorkman, Jörg Brunet, Pieter De Frenne, Radim Hédli, Ute Jandt, Jonathan Lenoir, Isla H. Myers-Smith, Kris Verheyen, Sonja Wipf, Monika Wulf, Christopher Andrews, Peter Barančok, Elena Barni, José-Luis Benito-Alonso, Jonathan Bennie, Imre Berki, Volker Blüml, Markéta Chudomelová, Guillaume Decocq, Jan Dick, Thomas Dirnböck, Tomasz Durak, Ove Eriksson, Brigitta Erschbamer, Bente Jessen Graae, Thilo Heinken, Fride Høistad Schei, Bogdan Jaroszewicz, Martin Kopecký, Thomas Kudernatsch, Martin Macek, Marek Malicki, František Máliš, Ottar Michelsen, Tobias Naaf, Thomas A. Nagel, Adrian C. Newton, Lena Nicklas, Ludovica Oddi, Andrej Palaj, Alessandro Petraglia, Petr Petřík, Remigiusz Pielech, Francesco Porro, Mihai Puşcaş, Kamila Reczyńska, Christian Rixen, Wolfgang Schmidt, Tibor Standovár, Klaus Steinbauer, Krzysztof Świerkosz, Balázs Teleki, Jean-Paul Theurillat, Pavel Dan Turtureanu, Tudor-Mihai Ursu, Thomas Vanneste, Philippine Vergeer, Ondřej Vild, Luis Villar, Pascal Vittoz, Manuela Winkler, Lander Baeten

*Corresponding author. Email: ingmar.staude@idiv.de

Material and Methods

Supplementary Figures

1. Fig. S1. Temporal trends in species richness vary across habitats.
2. Fig. S2. Relationship between species range size and baseline site-occupancy.
3. Fig. S3. Persisting species increasing in occupancy have larger ranges than species decreasing.
4. Fig. S4. Species with larger ranges tend to have higher nutrient demands.
5. Fig. S5. Communities shift towards species with higher nutrient demands.
6. Fig. S6. Species from lower elevations tend to have larger range sizes.
7. Fig. S7. Loss of beta-diversity over time.
8. Fig. S8. Histogram of time spans between surveys and site area.
9. Fig. S9. Histogram of plot numbers and sizes.
10. Fig. S10. Range size frequency distribution.
11. Fig. S11. Correlations between sampling characters of study sites in forests.

Supplementary Tables

1. Table S1. Study sites.
2. Table S2. Model summary: probability of a species to be lost.
3. Table S3. Model summary: occupancy trends of persisting species.
4. Table S4. Model summary: mean range sizes of gained, lost and persisting species.
5. Table S4. Model summary: interaction effects between sampling methods and range size.

References

Material and Methods

Methods

Databases. We synthesized data from three databases, each of which is a collation of vegetation resurveys in a specific habitat in Europe. Mountain summits are represented by 52 sites from the Global Observation Research Initiative in Alpine environments (GLORIA, gloria.ac.at, (1)), deciduous and coniferous forests understories by 68 sites from the forestREplot database (forestreplot.ugent.be, (2)) and lowland grasslands by 21 sites from the GRACE database (3) (Figure 1 and Supplementary Table 1). At each site, plant communities were surveyed across multiple permanent or quasi-permanent plots in either natural vegetation (summits) or semi-natural vegetation (forests and grasslands) at two points in time (baseline and resurvey, further details available in (1–3)). The median time spans between surveys were 14, 42 and 34 years for summits, forests and grasslands, respectively (Supplementary Figure 8a). In forest and grassland surveys, the median number of plots per site was 43 and 36, and the median size of plots was 400 m² and 25 m², respectively (Supplementary Figure 9a and b). Summits were always resurveyed in eight spatial sections that together covered the entire area from the highest summit point to the contour line 10 m in elevation below this point in a pie slice shape. The median summit area was 0.25 ha. In forests and grasslands, the median study area was 1,700 ha and 1,000 ha, respectively (Figure S8b).

Species data. *Taxonomy.* We accounted for within-and among-study variation in taxonomy by determining the accepted species name for each species using the Global Biodiversity Information Facility's (GBIF) backbone taxonomy (gbif.org). Harmonization thus ensured no double-counting of species owing to synonymy. We included only vascular plants identified to the species level. In total, our data comprises 1,827 accepted vascular plant species (see Data Table 1 on figshare).

Range size. We estimated species range sizes as area of occupancy (AOO) (4) using all point occurrence records of the species in GBIF (gbif.org, May 2020; (5)). After excluding incomplete, impossible and unlikely coordinates (e.g., country centroids) (6), there were c. 131 million geographically referenced records available for the species in our database. Records were aggregated to a hexagonal grid (ISEA3H) at a spatial grain of 10.7 km² (7), where the number of cells that a species occupies on this grid represents its AOO estimate (see Data Table 1 for species AOO estimates and GBIF urls). The species with the largest AOO in all three habitats were *Achillea millefolium* and *Trifolium repens* (both with ca. 1.1x10⁶ km²), the species with the smallest AOO were the highly endemic *Draba dolomitica* (c. 11 km²) on summits, *Galium abaujense* (c. 21 km²; endemic to the Carpathians) in forests, and *Pentanema germanicum* (c. 503 km²; critically endangered in Germany and Austria (8)) in grasslands (Supplementary Figure 10). For plant species in Europe, range sizes calculated from GBIF correlate strongly with expert drawn range maps but are available for many more species (9). However, it is important to note that AOO ranges differ from expert maps, which measure species extent of occurrence

(EOO), in that they do not include areas that are unoccupied by species. Thus, species with disjunct distributions, e.g., orchid species that occur throughout Europe but only in very fragmented, well-conserved habitat, can have a very small AOO but a large EOO. AOO is therefore a markedly better representation of species population sizes and differences related to habitat use and species niche than is EOO, and provides a general measure of species vulnerabilities to stochastic and directional threatening processes (4).

Occupancy. Measures of plot-level species abundance varied across studies (e.g., frequencies, percentage cover, and categorical cover-abundance scales) and were often not available if only species presence/absence was recorded. In order to estimate species abundance in a consistent way, we estimated species occupancy at the spatial scale of a study. We therefore divided the number of plots (grasslands, forests) or sections (summits) a species occupied at a given study site by the total number of plots/sections in that study. This was done separately for the baseline survey and the resurvey. Occupancy has been shown to correlate strongly and positively with abundance at local to regional scales (10, 11).

Trajectory. We evaluated species trajectories (i.e. lost, gained or persisting) at the spatial scale of a study site. Lost species were present (in at least one plot/section) during the baseline survey and absent (from all plots/sections) during the resurvey. Gained species were absent during the baseline survey and present during the resurvey. Persisting species were present during both the baseline survey and resurvey. Resurveys, even of permanent plots, always miss some species, generating pseudo-gains and losses that can be inflated for rare species (12, 13). We account for this bias by adjusting for species baseline abundances, which is strongly correlated with any such bias (14), as explained below.

Analysis. The *brms* package (15) in R was used for all statistical analyses. R code for all analyses and data visualization is available on figshare at <https://figshare.com/s/b37f6167b13ad5da9e9c>.

Species gains and losses. Using species trajectories we quantified the number of lost and gained species on the spatial scale of a study site (Extended Data Table 2). The highest losses (126 species) occurred in Hungarian forest-steppe landscapes, the highest gains (102 species) occurred in acidic/mesic oak woods in the Czech Republic. We assessed changes in species richness (i.e. the change in the total number of species per study site) by calculating the difference, d , between species richness in the resurvey (t_2) and species richness in the baseline survey (t_1). Although species richness at a given time period will be affected by sampling effort, d is not because it is a relative change in species richness with sampling effort being the same for both time periods (baseline surveys vs. resurveys). For each habitat, we modelled d using a Gaussian distribution to compute the posterior distribution of the expected value of d (Supplementary Figure 1).

Probability of loss. We estimated the effect of species range size on the probability that a species being present at the baseline survey is lost from a study site by the time of the resurvey. The effect of range size can

be confounded by species baseline occupancy if small-ranged species also tend to have a lower abundance at a study site. Species with small population sizes are more likely to be lost owing to 1) stochastic demographic processes and 2) an observer error, where rare species are more likely to be overlooked in resurveys. Therefore, we tested first for a positive range size – site occupancy relationship in our data (see Methods below). Range size and occupancy were not related on summits and weakly positively related in forests and grasslands (Supplementary Figure 2). To estimate the effect of range size that is not due to demographic effects, we statistically controlled for variation in species baseline occupancies by including it as a covariate in our model (9). Furthermore, species with small ranges may be disproportionately vulnerable at low abundances. This could be the case if range size covaries with specific traits, such as, for example, height, where small plants would be expected to be more vulnerable than tall plants at low site occupancy. To account for this possible further confounding effect, we also include an interaction effect between range size and occupancy in our model. Finally, the effect of species occupancy on species loss probability is likely to vary with the number of plots per study site. For example, a species with 10% occupancy in a study of 10 plots, is more likely to be lost than a species with 10% occupancy in a study of 100 plots. We therefore allow the effect of occupancy to vary by study site.

Our model thus predicts a Bernoulli indicator variable that a given species was lost or persisted (e_i) with two fixed effects (β_r for range size (r_i) and β_f for occupancy (f_i), where both r_i and f_i were log10-transformed and scaled within habitats to have a mean of zero and a standard deviation of one) and an interaction effect between the two fixed effects (β_{fr}). We allowed the intercept and the effect of occupancy to vary by study site ($\alpha_{study[i]}$ and $\beta_{f,study[i]}$, respectively). Also, we included species as an additional crossed varying effect ($\gamma_{species[i]}$), since many species occur in more than one study site. We ran this model for each habitat (see Supplementary Table 2 for model R syntax, sample settings and convergence diagnostics). The resulting model in mathematical form is:

$$\begin{aligned}
 e_i &\sim \text{Binomial}(1, p_i) \\
 \text{logit}(p_i) &= \alpha_{study[i]} + \gamma_{species[i]} \\
 &\quad + \beta_{f,study[i]} * f_i + \beta_r * r_i + \beta_{fr} * f_i * r_i
 \end{aligned}$$

As a further means to test whether demographic effects confound estimates of β_r , we ran the same model but excluded rare species (with site occupancies below 5%) from our data (Supplementary Table 3). Since we only had data on the species that were newly gained at a study site but not on all those that tried to colonize, we were not able to directly calculate probabilities of gain in relation to range size.

Occupancy trends of persisting species. Here we only evaluate species that have persisted over time, since species lost and gained necessarily decrease and increase in occupancy, respectively. We first tested whether persisting species that increased in occupancy at a study site have on average larger range sizes than persisting species that decreased in occupancy at a study site. We therefore predicted range size (log10-

transformed) with the categorical variable “decrease/increase” ($\beta_{di[i]}$) including a group-level effect for study site ($\alpha_{study[i]}$):

$$\begin{aligned} r_i &\sim Normal(\mu_i, \sigma) \\ \mu_i &= \alpha_{study[i]} + \beta_{di[i]} \end{aligned}$$

Since changes in occupancy may depend on species baseline occupancy (e.g., species with a higher baseline occupancy could be more likely to increase in occupancy due to a higher propagule pressure), we also estimated the effect of species range size on the probability that a persisting species increases in occupancy, controlling for variation in species baseline occupancies. For this logistic model, we recoded the difference in occupancy at the resurvey and the baseline survey (d) into a binary variable with $d > 0$ being “1”, $d \leq 0$ being “0” (h_i) and predicted h_i with range size, including baseline occupancy as a covariate. Since baseline occupancy ranges from 0 to 1, species with an occupancy of 1 cannot increase in occupancy. These species were therefore excluded from the model. The model in math form is:

$$\begin{aligned} h_i &\sim Binomial(1, p_i) \\ \text{logit}(p_i) &= \alpha_{study[i]} + \gamma_{species[i]} \\ &\quad + \beta_{f,study[i]} * f_i + \beta_r * r_i \end{aligned}$$

, where parameters are defined as in the model for species loss probability. However, we did not include the interaction effect between occupancy and range size (β_{fr}) in this model, as a potentially greater vulnerability of small-ranged species at low occupancy is likely to not be very relevant to explain increases in occupancy (see Supplementary Table 3 for model R syntax, sample settings and convergence diagnostics).

Difference in range sizes between trajectories. We calculated species mean range size for each trajectory to test whether species with larger ranges are gained preferentially. We therefore predicted range size (log10-transformed) with species trajectory ($\beta_{traj[i]}$), allowing the intercept to vary by study site ($\alpha_{study[i]}$). We ran this model for each habitat:

$$\begin{aligned} r_i &\sim Normal(\mu_i, \sigma) \\ \mu_i &= \alpha_{study[i]} + \beta_{traj[i]} \end{aligned}$$

In order to test whether range sizes of species gained differ from those being lost, we calculated the posterior difference in mean range size between gained and lost species in each habitat. Since the posterior difference between gained and lost species is in the log10-scale, this gives a ratio of range size of species gained/lost after back-transformed to the original scale (see Supplementary Table 4 for model R syntax, sample settings and convergence diagnostics).

Supplementary analysis. Range size-site occupancy relationship. In each habitat, we predicted species range size with species baseline occupancy at a study site (both variables were log10-transformed and scaled within habitats to have a mean of zero and a standard deviation of one), allowing the intercept and slope to vary by study site:

$$r_i \sim \text{Normal}(\mu_i, \sigma)$$

$$\mu_i = \alpha_{\text{study}[i]} + \beta_{f, \text{study}[i]} * f_i$$

Range size and nutrient demand. We used Ellenberg's indicator values for nutrient (N-number) to approximate species niche position for nutrients (16–18). These values describe each species' niche position on a scale from 1 to 9 (adapted to unproductive, nutrient-poor soils) to 9 (adapted to fertile soils). We obtained N-numbers from sci.muni.cz/botany/juice/ELLENB.TXT and harmonized the taxonomy with our data. If an accepted species had more than one N-number (either due to synonyms or subspecies), we calculated the average. 1,297 species of the 1,827 species in our data also had N-numbers (71%). For the species in each habitat, we calculated Pearson's correlation coefficient between range size (log10-transformed and scaled) and N-number (scaled).

Community weighted mean of species nitrogen niche position. We tested whether communities shift towards species with higher nutrient demands over time by quantifying the community weighted mean N-number (CWM-N) at the time of the baseline survey and resurvey. CWM-N was calculated for each study site and survey period as: $\sum N_i * f_i / \sum f_i$ where N_i and f_i is the N-number and site-occupancy of the i^{th} species, respectively. We quantified the difference between resurvey and baseline survey CWM-N, by predicting CWM-N (c_i) with survey period ($\beta_{\text{survey}[i]}$), including study site as a group-level effect ($\alpha_{\text{study}[i]}$) to indicate pairs of observations:

$$c_i \sim \text{Normal}(\mu_i, \sigma)$$

$$\mu_i = \alpha_{\text{study}[i]} + \beta_{\text{survey}[i]}$$

To gain insight into how much of the change in CWM-N is due to changes in species occupancy or species composition, we also calculated community unweighted means by simply averaging N-numbers across species at a study site for both the baseline survey and resurvey, and tested for changes over time using the same model as above. The comparison of weighted and unweighted means showed that in forests and grasslands, the clear shift towards more nutrient-demanding species was largely due to changes in species composition, while on summits the much weaker shift was due to changes in species occupancy.

Relationship between mean range size and elevation. We tested whether montane species from lower elevations have larger ranges than alpine ones. Therefore, we regressed mean range size (m_i , averaged across species occurring at a summit site at the baseline survey) against summit elevation (l_i):

$$m_i \sim \text{Normal}(\mu_i, \sigma)$$

$$\mu_i = \alpha + \beta_l * l_i$$

Effects of site-characteristics on the effect of range size. While the above model for species loss probability provides estimates for range size-effects within habitats, different sampling methods between habitats make it difficult to compare effect estimates across habitats. Summits are inherently limited in size and were surveyed in always eight sections, while forest and grasslands areas were sampled with differing number of plots of different sizes across differently large study areas (Supplementary Figure 8 and 9). Moreover, time intervals between surveys varied among habitats, with the shortest intersurvey periods on summits (Supplementary Table 1). To better compare effect estimates across habitats, we tested whether the effect of range size, β_r , changed with plot number, plot size, site area (log10-transformed) and survey interval (n_i , s_i , a_i , and t_i , respectively) We tested this in forests, where we had most study sites and sampling varied the most, by including interaction effects between range size and sampling characteristics (there was no strong collinearity between sampling characteristics (Supplementary Figure 10)):

$$e_i \sim \text{Binomial}(1, p_i)$$

$$\text{logit}(p_i) = \alpha_{\text{study}[i]} + \gamma_{\text{species}[i]} + \beta_{f,\text{study}[i]} * f_i + \beta_r * r_i + \beta_{fr} * f_i * r_i + \beta_{nr} * n_i * r_i + \beta_{sr} * s_i * r_i + \beta_{ar} * a_i * r_i + \beta_{tr} * t_i * r_i$$

Changes in beta-diversity. We tested whether an average pair of communities becomes more similar in species composition over time, by calculating the Sørensen dissimilarity index across all possible pairs of the 141 study sites in our data for each survey period (b_i) and estimating the mean difference in beta-diversity between resurvey and baseline survey ($\beta_{\text{survey}[i]}$), using the model:

$$b_i \sim \text{Normal}(\mu_i, \sigma)$$

$$\mu_i = \alpha + \beta_{\text{survey}[i]}$$

Finally, we also quantified the multiple site Sørensen dissimilarity index (19) between the grassland, forest and summit species pool for both survey periods.

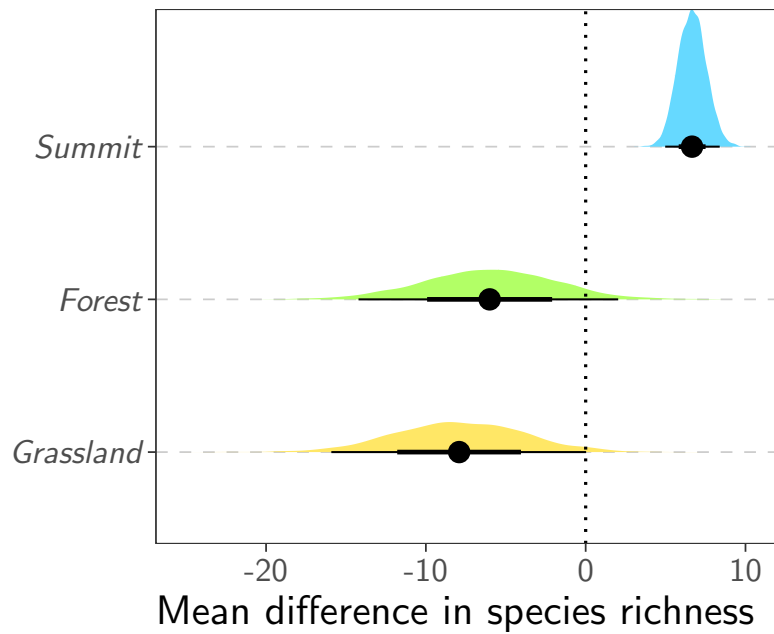


Fig. S1. Temporal trends in species richness vary across habitats. Posterior distribution of the mean difference in species richness at the study-site level between the resurvey and baseline survey. Points represent medians, lines represent the 66% and 95% confidence interval. The mean richness change and its standard deviation is for summits: $\delta = 6.66$, $\sigma = 0.88$; forests: $\delta = -6.04$, $\sigma = 4.15$; and grasslands: $\delta = -7.90$, $\sigma = 3.98$. Dotted vertical line represents zero change in richness.

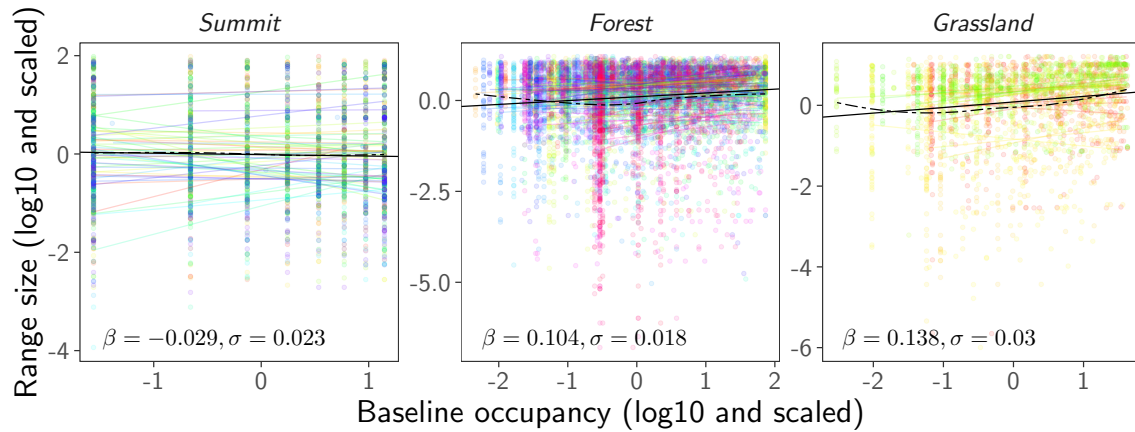


Fig. S2. Relationship between species range size and baseline site-occupancy accounting for the structure of our data. Colors present study sites, transparent dots present species, transparent lines represent the relationship between range size and site occupancy within a single study site, black straight line is the mean regression line across study sites resulting from a linear varying effect model with regression coefficients (slope and intercept) allowed to vary by study site, black dashed line is the mean regression line from a general additive model without varying effects. β is the slope and σ is the standard deviation of β from the linear varying effect model.

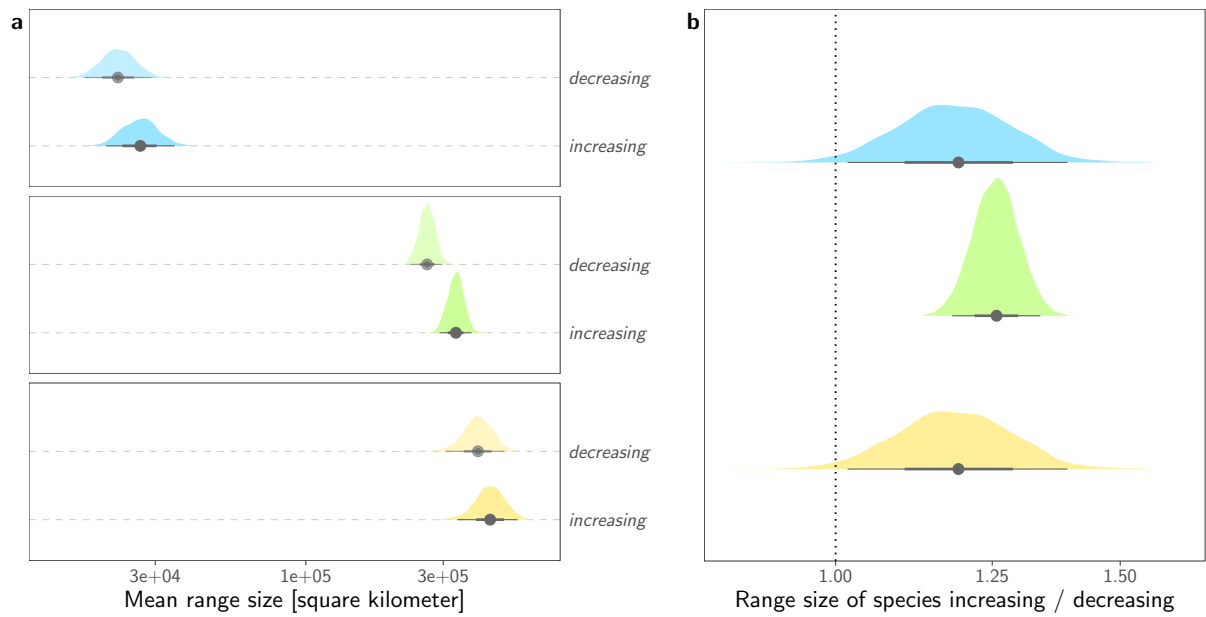


Fig. S3. Persisting species increasing in occupancy have larger ranges on average than species decreasing. **a**, Posterior distribution of the mean range size of species increasing and decreasing in occupancy at the study site over time. **b**, Comparison between the mean range sizes of species increasing and decreasing, derived from the posterior distributions in **a**. Colors refer to habitats as in Figure 1 (blue = summit, green = forest, yellow = grassland). Point and lines are the median and its 66% and 95% credible interval. Dotted vertical line in **b** represents no difference in mean range size. See also Supplementary Table 3.

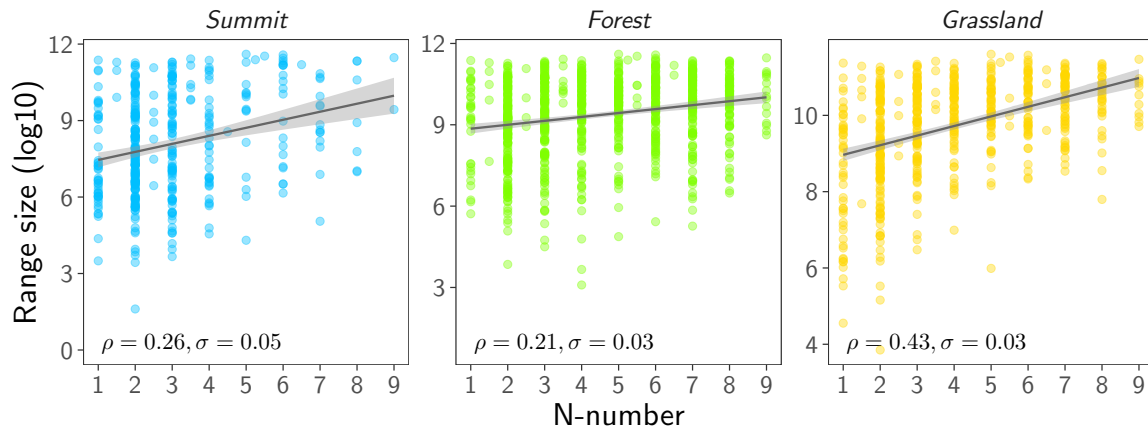


Fig. S4. Species with larger ranges tend to have higher nutrient demands. Relationship between species range size and Ellenberg indicator values for nutrients (N-numbers) across species in each habitat. N-numbers describe a species' niche position for nutrients on a scale from 1 (low nutrient requirements) to 9 (high nutrient affinity). Non-integer N-numbers are mean values of N-numbers from subspecies and synonyms with different N-numbers (e.g. *Melampyrum pratense* ssp. *paludosum* has an N-number of 1, while *Melampyrum pratense* has an N-number of 2). 1,297 species of the 1,827 species in our data also had N-numbers. Line and transparent ribbon represent the mean regression line and 95% credible interval, ρ is the estimated correlation coefficient, σ is the standard deviation of ρ .

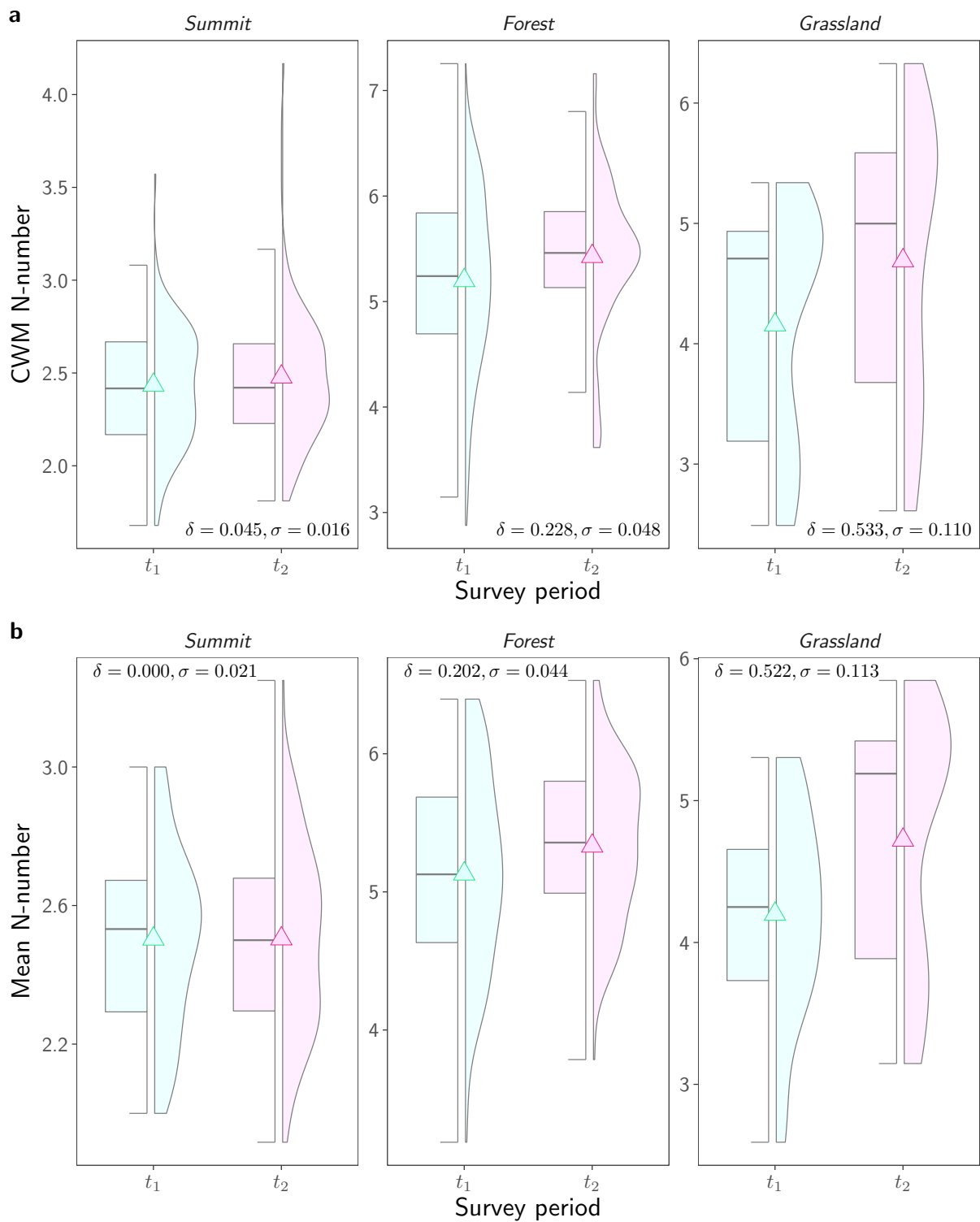


Fig. S5. Communities shift towards species with higher nutrient demands. Boxplot and density plot of **a**, the community weighted mean (CWM) niche position for nutrients (N-number) and **b**, the unweighted mean N-number across species at the baseline survey (t_1) and resurvey (t_2). CWM is weighted by species occupancies at the study site. Triangles represent mean values. δ is the mean (pairwise) difference, σ is the standard deviation of δ .

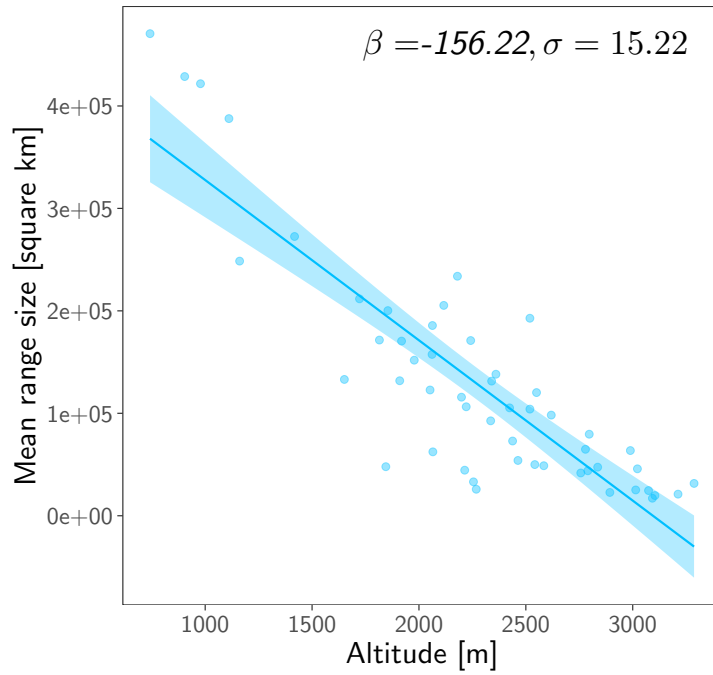


Fig. S6. Species from lower elevations tend to have larger range sizes. Relationship between species' mean range size and elevation. Range size is measured as area of occupancy (AOO; see Methods) and averaged across all species occurring at the baseline survey on a given mountain summit. Elevations of mountain summit sites ranged from 742 to 3,287 m. Line and transparent ribbon present the mean regression line and 95% credible interval, β is the slope, σ is the standard deviation of β .

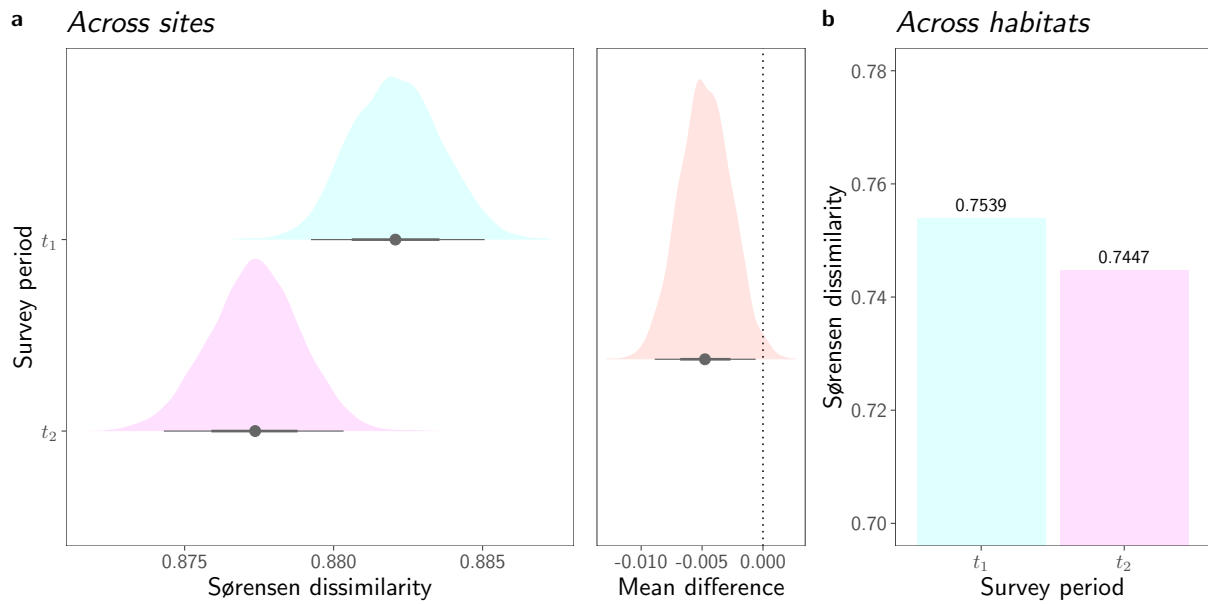


Fig. S7. Loss of beta-diversity over time. **a**, Posterior distribution of the mean beta-diversity of study sites at the baseline survey (t_1) and resurvey (t_2), calculated as Sørensen mean pair-wise dissimilarity between all possible pairs of the 141 sites in our study. **b**, Beta-diversity of the entire species pools of summits, forests and grasslands (calculated as Sørensen multiple-site dissimilarity between habitats) at the baseline survey (t_1) and resurvey (t_2). Point and lines in **a** are the median and its 66% and 95% credible interval. Dotted vertical line in **a** represents zero difference ($t_2 - t_1$) in beta-diversity.

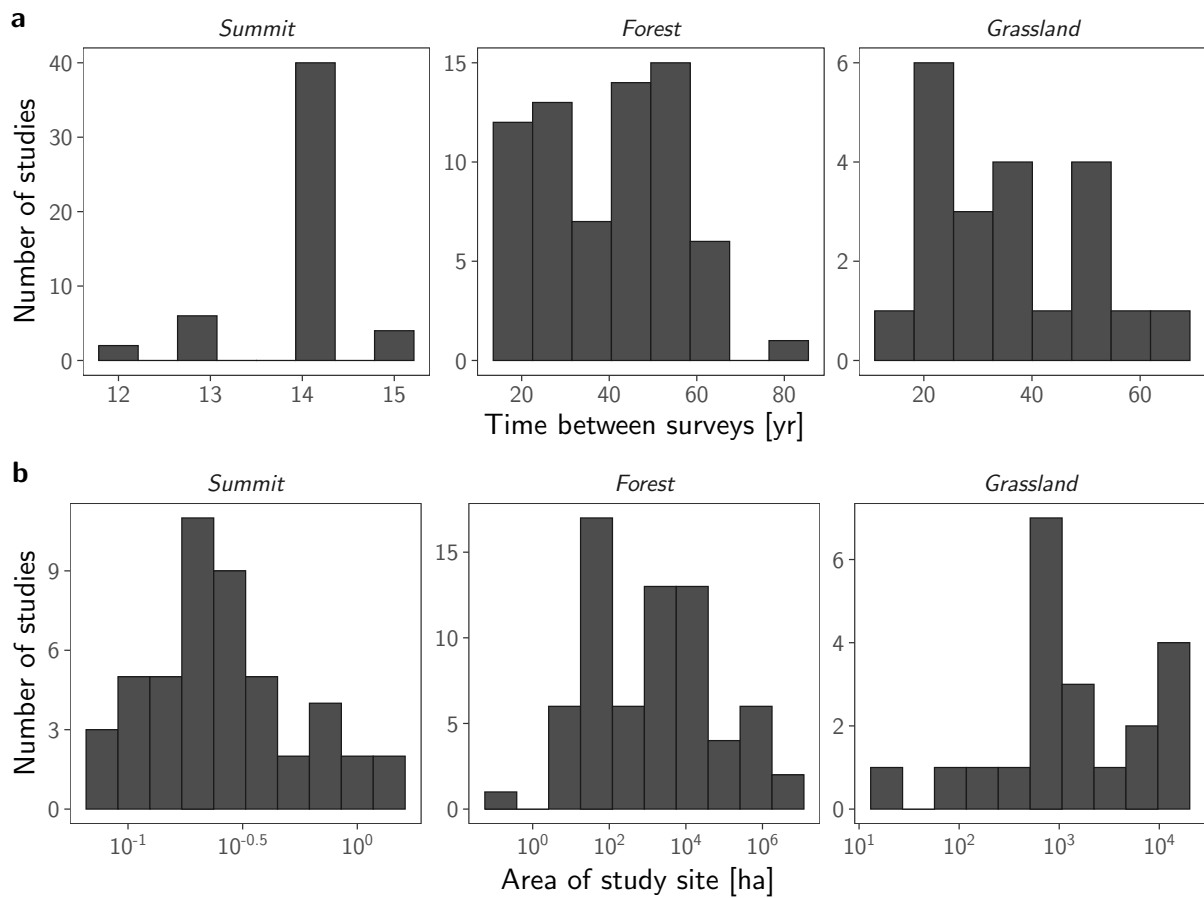


Fig. S8. Histogram of time span between surveys across study sites and site areas. **a**, Median time spans were 14, 42 and 34 years on mountain summits, forests and grasslands, respectively. **b**, Median site areas were 0.25, 1,700 and 1,000 ha on mountain summits, forests and grasslands, respectively. X-axis in **b** is on the log₁₀-scale.

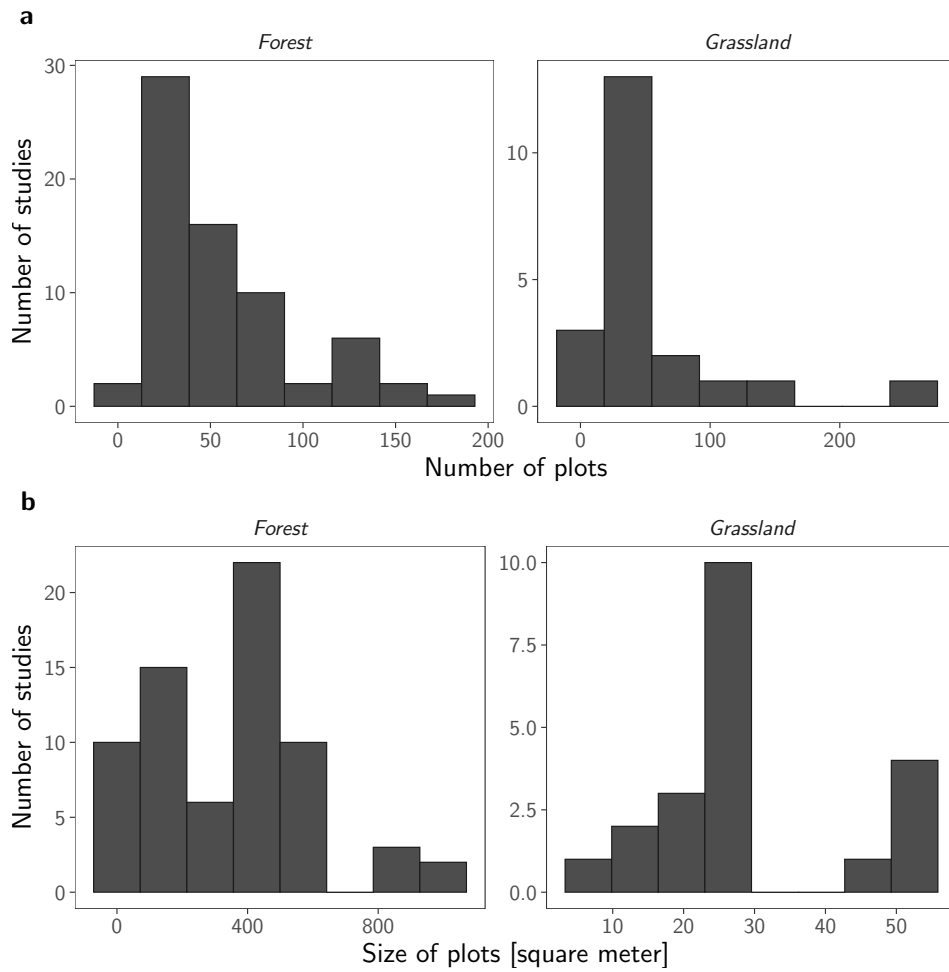


Fig. S9. Histogram of plot number and size. Forest and grasslands studies had a median of 43 and 36 plots with a size of 400 m² and 25 m², respectively. Studies on mountain summits were always divided into 8 sections that together covered the entire lateral area from the highest summit point to 10 m below this point. In total, our study counts 5,221 plots/sections.

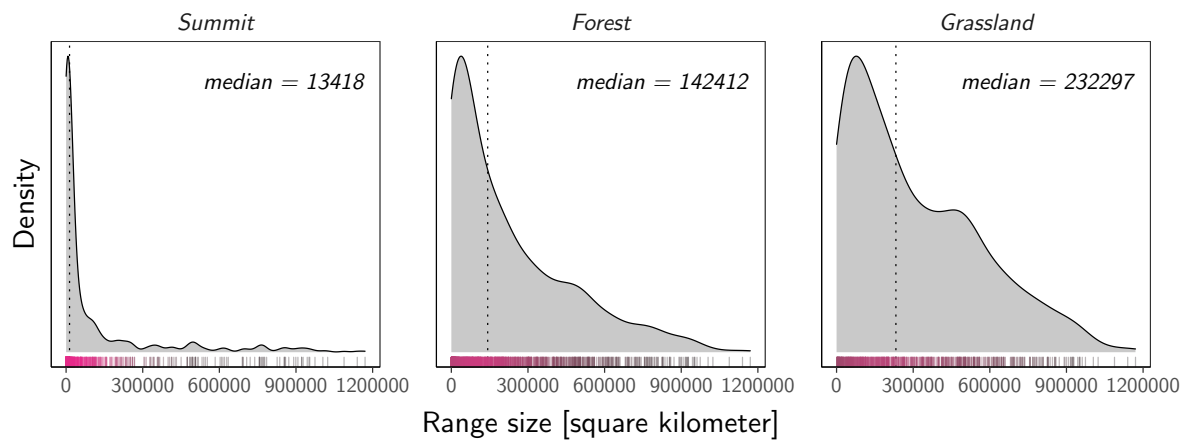


Fig. S10. Range size frequency distribution. Area of occupancy estimates of the species found in a given habitat (summit = 641 species, forest = 1,148 species, grassland = 692 species). Dotted vertical line represents the median range size. Rug at the figure bottom represents the precise range sizes of species and is coloured to match the density of ticks.

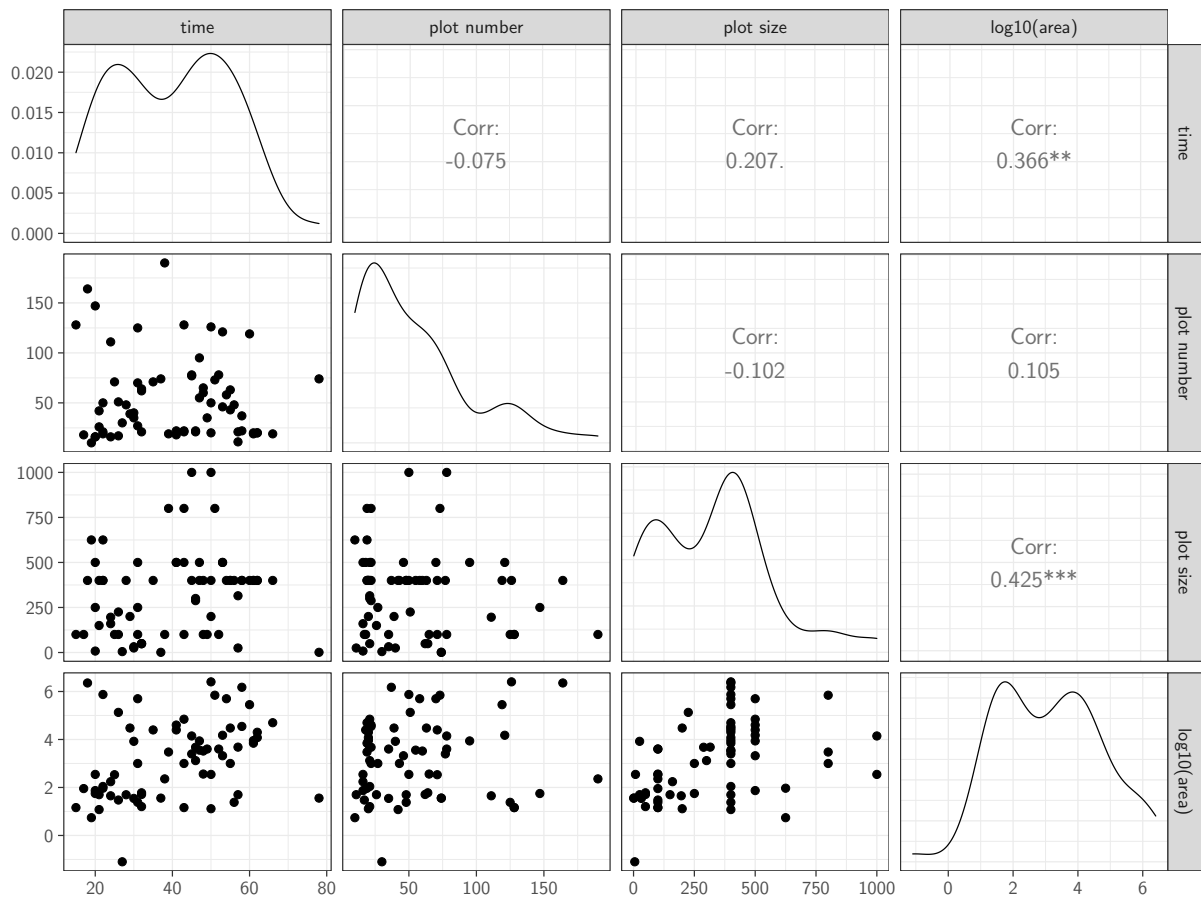


Fig. S11. Correlations between sampling characters of study sites in forests. Sampling characters are time interval between surveys, number of plots per site, size of plots and site area (log10-transformed). Since $\rho < 0.7$ for all correlations, each character was included in the model testing whether the effect of range size depends on sampling method.

Table S1. Country, site name, coordinates, year of the baseline survey and resurvey [when one survey (baseline or resurvey) was carried out over several years, the list shows the earliest baseline survey and the latest resurvey].

| Country | Site | Latitude | Longitude | Baseline (yr) | Resurvey (yr) |
|-------------------------|--|----------|-----------|---------------|---------------|
| <i>Mountain summits</i> | | | | | |
| Austria | G'hacktkogel, NE-Alps / Hochschwab | 47.61 | 15.13 | 2001 | 2015 |
| Austria | Weihbrunnkogel, NE-Alps / Hochschwab | 47.62 | 15.16 | 2001 | 2015 |
| Austria | Zagelkogel-NW-summit, NE-Alps / Hochschwab | 47.61 | 15.12 | 2001 | 2015 |
| Austria | Zinken-NW-summit, NE-Alps / Hochschwab | 47.60 | 15.09 | 2001 | 2015 |
| Great Britain | Camp Cairn, Cairngorms | 57.09 | -3.84 | 2001 | 2015 |
| Great Britain | Creag Mhigeachaidh, Cairngorms | 57.10 | -3.86 | 2001 | 2015 |
| Great Britain | Sgoran Dubh Mor, Cairngorms | 57.08 | -3.81 | 2001 | 2015 |
| Great Britain | Unknown Hillock, Cairngorms | 57.08 | -3.83 | 2001 | 2015 |
| Italy | Alpe di Mommio, Northern Apennines | 44.28 | 10.24 | 2001 | 2015 |
| Italy | Cima di Foce a Giovo, Northern Apennines | 44.12 | 10.61 | 2001 | 2015 |
| Italy | Cima di Pian Cavallaro, Northern Apennines | 44.20 | 10.69 | 2001 | 2015 |
| Italy | Cime Bianche, W-Alps / Mont Avic | 45.92 | 7.70 | 2002 | 2017 |
| Italy | Colle Lago Bianco, W-Alps / Mont Avic | 45.65 | 7.60 | 2002 | 2017 |
| Italy | Da Wöllane, Central Alps / Texelgruppe | 46.73 | 10.96 | 2003 | 2017 |
| Italy | Do Peniola, S-Alps / Dolomites | 46.38 | 11.61 | 2001 | 2015 |
| Italy | Faglmugl, Central Alps / Texelgruppe | 46.74 | 11.16 | 2003 | 2017 |
| Italy | Grasmugl, S-Alps / Dolomites | 46.33 | 11.56 | 2001 | 2015 |
| Italy | Kaserwartl, Central Alps / Texelgruppe | 46.76 | 10.88 | 2003 | 2017 |
| Italy | Lago Balena, W-Alps / Mont Avic | 45.64 | 7.55 | 2002 | 2017 |
| Italy | Monte Casarola, Northern Apennines | 44.33 | 10.21 | 2001 | 2015 |
| Italy | Monte Schutto, S-Alps / Dolomites | 46.52 | 11.81 | 2001 | 2015 |
| Italy | Pra Pelat, W-Alps / Mont Avic | 45.66 | 7.55 | 2002 | 2017 |
| Italy | Ragnarok, S-Alps / Dolomites | 46.38 | 11.59 | 2001 | 2015 |
| Italy | Schafberg, Central Alps / Texelgruppe | 46.74 | 11.11 | 2003 | 2017 |
| Norway | Kolla, S-Scandes / Dovrefjell | 62.29 | 9.49 | 2001 | 2015 |
| Norway | Storkinn, S-Scandes / Dovrefjell | 62.35 | 9.44 | 2001 | 2015 |
| Norway | Vesle Armodshokollen, S-Scandes / Dovrefjell | 62.26 | 9.67 | 2001 | 2015 |
| Norway | Veslekolla, S-Scandes / Dovrefjell | 62.31 | 9.46 | 2001 | 2015 |
| Romania | Buhaiescu, E-Carpathians / Rodnei Mts. | 47.58 | 24.63 | 2001 | 2015 |
| Romania | Golgota, E-Carpathians / Rodnei Mts. | 47.60 | 24.63 | 2001 | 2015 |
| Romania | Gropile, E-Carpathians / Rodnei Mts. | 47.57 | 24.62 | 2001 | 2015 |
| Romania | Rebra, E-Carpathians / Rodnei Mts. | 47.59 | 24.64 | 2001 | 2015 |
| Slovakia | Krátka, W-Carpathians / High Tatras | 49.16 | 20.01 | 2001 | 2015 |

| | | | | | |
|--|---|-------|-------|------|------|
| Slovakia | Krížna, W-Carpathians / High Tatra | 49.18 | 19.95 | 2001 | 2015 |
| Slovakia | Sedielková kopa, W-Carpathians / High Tatra | 49.15 | 20.02 | 2001 | 2015 |
| Slovakia | Veľká kopa, W-Carpathians / High Tatra | 49.20 | 19.97 | 2001 | 2015 |
| Spain | Punta Acuta, Central Pyrenees / Ordesa | 42.64 | -0.06 | 2001 | 2015 |
| Spain | Punta Custodia, Central Pyrenees / Ordesa | 42.65 | 0.03 | 2001 | 2015 |
| Spain | Punta de las Olas, Central Pyrenees / Ordesa | 42.66 | 0.05 | 2001 | 2015 |
| Spain | Punta Tobacor, Central Pyrenees / Ordesa | 42.66 | -0.01 | 2001 | 2015 |
| Switzerland | La Ly, W-Alpes / Alps of Valais-Entremont | 46.03 | 7.25 | 2001 | 2015 |
| Switzerland | Minschuns, Central Alps / Swiss National Park | 46.65 | 10.34 | 2002 | 2015 |
| Switzerland | Mont Brûlé, W-Alpes / Alps of Valais-Entremont | 46.02 | 7.20 | 2001 | 2015 |
| Switzerland | Mot dal Gajer, Central Alps / Swiss National Park | 46.69 | 10.33 | 2002 | 2015 |
| Switzerland | Mot sper Chamana Sesvenna, Central Alps / Swiss National Park | 46.74 | 10.43 | 2003 | 2015 |
| Switzerland | Munt Buffalora, Central Alps / Swiss National Park | 46.64 | 10.24 | 2003 | 2015 |
| Switzerland | Munt Chavagl, Central Alps / Swiss National Park | 46.64 | 10.23 | 2002 | 2015 |
| Switzerland | Piz Foraz, Central Alps / Swiss National Park | 46.69 | 10.28 | 2002 | 2015 |
| Switzerland | Piz Murtèr, Central Alps / Swiss National Park | 46.65 | 10.14 | 2002 | 2015 |
| Switzerland | Piz Plazer, Central Alps / Swiss National Park | 46.71 | 10.39 | 2002 | 2015 |
| Switzerland | Pointe de Boveire, W-Alpes / Alps of Valais-Entremont | 45.99 | 7.24 | 2001 | 2015 |
| Switzerland | Pointe du Parc, W-Alpes / Alps of Valais-Entremont | 46.00 | 7.23 | 2001 | 2015 |
| <i>Deciduous and coniferous forests</i> | | | | | |
| Austria | Zöbelboden | 47.84 | 14.44 | 1993 | 2010 |
| Belgium | Binnen-Vlaanderen | 51.09 | 3.54 | 1977 | 2009 |
| Belgium | Florenne | 50.22 | 4.64 | 1957 | 2005 |
| Belgium | Gaume | 49.62 | 5.56 | 1953 | 2008 |
| Belgium | Herenbossen | 51.07 | 4.79 | 1980 | 2004 |
| Belgium | Meerdaalwoud | 50.80 | 4.71 | 1954 | 2000 |
| Belgium | Tournibus | 50.32 | 4.58 | 1967 | 2005 |
| Belgium | Vorte Bossen | 51.07 | 3.37 | 1977 | 1998 |
| Belgium | Zoerselbos | 51.25 | 4.68 | 1982 | 2008 |
| Czech Republic | České Středohoří | 50.59 | 14.12 | 1965 | 2012 |
| Czech Republic | Děvin Wood | 48.87 | 16.63 | 1953 | 2003 |
| Czech Republic | Hodonínská Důbrava | 48.88 | 17.10 | 1965 | 2012 |
| Czech Republic | Krumlov Wood | 49.05 | 16.38 | 1964 | 2012 |
| Czech Republic | Milíčovský les | 50.02 | 14.53 | 1986 | 2008 |
| Czech Republic | Milovice Wood | 48.82 | 16.70 | 1953 | 2006 |
| Czech Republic | Rychlebské hory Mts. | 50.27 | 17.08 | 1941 | 1999 |
| Czech Republic | Ždánice Wood | 49.10 | 17.03 | 1959 | 2012 |
| France | Andigny | 50.00 | 3.58 | 1957 | 1996 |
| France | Compiègne forest | 49.36 | 2.89 | 1970 | 2015 |

| | | | | | |
|---------------|-------------------------------|-------|-------|------|------|
| France | Hirson | 49.94 | 4.10 | 1956 | 1999 |
| France | Jura | 46.81 | 6.38 | 1989 | 2007 |
| Germany | Brandenburg | 52.06 | 13.86 | 1962 | 2012 |
| Germany | Brandenburg Nord | 53.06 | 13.47 | 1963 | 2014 |
| Germany | Brandenburg Süd | 51.79 | 13.80 | 1960 | 2014 |
| Germany | Echinger Lohe | 48.30 | 11.65 | 1986 | 2003 |
| Germany | Echinger Lohe | 48.30 | 11.65 | 1961 | 2017 |
| Germany | Elbe-Weser | 53.55 | 8.98 | 1986 | 2008 |
| Germany | Göttingen | 51.53 | 10.05 | 1980 | 2001 |
| Germany | Göttingen | 51.33 | 9.82 | 1960 | 2012 |
| Germany | Göttingen | 51.56 | 10.02 | 1960 | 2009 |
| Germany | Göttingen, Hünstollen | 51.58 | 10.05 | 1992 | 2012 |
| Germany | Großer Staufenberg | 51.62 | 10.64 | 1988 | 2016 |
| Germany | Prignitz | 53.08 | 12.28 | 1954 | 2014 |
| Germany | Sonneberg | 50.37 | 11.14 | 1961 | 2016 |
| Germany | Unteres Spreewald-Randgebiet | 52.09 | 13.93 | 1965 | 2010 |
| Great Britain | Lady Park | 51.83 | -2.66 | 1979 | 2009 |
| Great Britain | Wytham Woods | 51.77 | -1.33 | 1974 | 1999 |
| Hungary | Bakony és Gerecse | 47.20 | 18.07 | 1955 | 2016 |
| Hungary | Bükkalja és Dél-Cserehát | 47.91 | 20.40 | 1956 | 2015 |
| Hungary | Gödöllői-dombság | 47.59 | 19.40 | 1955 | 2016 |
| Hungary | Heves | 47.99 | 20.50 | 1989 | 2008 |
| Hungary | Mátra-Bükk-Zemplén | 48.19 | 20.90 | 1955 | 2016 |
| Hungary | Nyírség | 47.77 | 22.27 | 1930 | 1990 |
| Hungary | Órség | 46.92 | 16.57 | 1954 | 2015 |
| Hungary | Visegrádi-hegység | 47.73 | 18.96 | 1953 | 2016 |
| Ireland | County Kerry | 52.02 | -9.50 | 1991 | 2011 |
| Netherlands | Speulderbos | 52.26 | 5.69 | 1957 | 1988 |
| Norway | Hordaland | 60.32 | 6.14 | 1978 | 2009 |
| Poland | Bazaltowa Mt | 51.01 | 16.13 | 1992 | 2014 |
| Poland | Białowieża | 52.70 | 23.87 | 1966 | 2012 |
| Poland | Buki Sudeckie beech forest | 50.94 | 16.03 | 1990 | 2014 |
| Poland | Olszyny Niezgodzkie | 51.51 | 17.03 | 1993 | 2013 |
| Poland | Sanocko-Turczańskie Mountains | 49.54 | 22.37 | 1972 | 2007 |
| Poland | Trzebnickie Hills | 51.26 | 16.82 | 1962 | 2012 |
| Slovakia | Central Slovakia | 48.26 | 19.38 | 1964 | 2007 |
| Slovakia | North-East Slovakia | 49.22 | 21.85 | 1965 | 2006 |
| Slovakia | South-West Slovakia | 48.40 | 17.34 | 1966 | 2007 |
| Slovenia | Pecka | 45.75 | 15.00 | 1983 | 2015 |

| | | | | | |
|---------------------------|----------------------|-------|-------|------|------|
| Slovenia | Rajhenavski Rog | 45.66 | 15.01 | 1983 | 2015 |
| Slovenia | Strmec | 45.62 | 14.82 | 1983 | 2015 |
| Sweden | Dalby | 55.69 | 13.33 | 1935 | 2013 |
| Sweden | Dalby | 55.69 | 13.33 | 1976 | 2013 |
| Sweden | Öland | 56.67 | 16.53 | 1988 | 2014 |
| Sweden | Skåne | 55.88 | 13.72 | 1983 | 2014 |
| Sweden | Stenshuvud | 55.66 | 14.26 | 1988 | 2015 |
| Sweden | Tullgarn | 58.95 | 17.62 | 1971 | 2014 |
| Sweden | Tullgarn | 58.95 | 17.62 | 1999 | 2014 |
| Switzerland | Aargau | 47.25 | 7.83 | 1940 | 1998 |
| Lowland grasslands | | | | | |
| Germany | Fränkischer Jura | 49.29 | 11.71 | 1931 | 1991 |
| Germany | Fränkischer Jura | 49.29 | 11.71 | 1968 | 1991 |
| Germany | Hessen | 50.81 | 8.89 | 1950 | 1990 |
| Germany | Hessen | 50.78 | 8.93 | 1950 | 1990 |
| Germany | Hessen | 50.82 | 8.90 | 1950 | 1990 |
| Germany | Hessen | 51.23 | 9.92 | 1950 | 1991 |
| Germany | Holtumer Moor | 53.00 | 9.30 | 1963 | 2006 |
| Germany | Kyffhäuser Mountains | 51.41 | 11.00 | 1993 | 2012 |
| Germany | Lahn-Dill-Bergland | 50.65 | 8.43 | 1994 | 2010 |
| Germany | Lake Dümmer | 52.49 | 8.32 | 1979 | 2008 |
| Germany | Lake Dümmer | 52.49 | 8.31 | 1987 | 2008 |
| Germany | Lake Dümmer | 52.48 | 8.32 | 1995 | 2016 |
| Germany | Lange Damm Wiesen | 52.52 | 13.85 | 1991 | 2013 |
| Germany | Ostetal | 53.32 | 9.24 | 1952 | 1987 |
| Germany | Ostetal | 53.35 | 9.15 | 1964 | 1993 |
| Germany | Stedinger Land | 53.14 | 8.56 | 1948 | 2015 |
| Germany | Streesebecken | 52.76 | 13.64 | 1992 | 2011 |
| Great Britain | Dorset | 50.98 | -2.19 | 1952 | 2003 |
| Great Britain | East Anglia | 52.04 | -0.04 | 1952 | 2003 |
| Great Britain | Kent | 51.17 | 0.97 | 1952 | 2003 |
| Great Britain | Yorkshire Wolds | 53.97 | -0.71 | 1952 | 2003 |

Table S2. Summary of the model predicting species loss probability with species range size and baseline abundance (Fig. 3a). Model syntax, sampling settings, parameter estimates, their standard deviation (sd) and 95% credible interval (CI). Rhat is the Gelman–Rubin convergence diagnostic, bulk- and tail-ESS are the number of independent samples (i.e. effective sample sizes). Model includes species present at the baseline survey. Also, we ran the model excluding rare species (with a site-occupancy below 5% in the baseline survey) in forest and grassland to test for robustness of the range-size effect within these habitats.

Probability of species being lost at a study site

Formula: $\text{logit}(p) \sim \text{scale}(\text{log10}(\text{range})) * \text{scale}(\text{log10}(\text{occupancy})) + (1 + \text{scale}(\text{log10}(\text{occupancy})) / \text{site}) + (1 / \text{speciesKey})$

Number of observations: 2731 (summit), 7727 (forest), 2402 (grassland)

Number of group levels (species): 575 (summit), 989 (forest), 594 (grassland)

Number of group levels (study): 52 (summit), 68 (forest), 21 (grassland)

Sample settings: 4 chains, each with 2,000 iterations

| Habitat | Parameter | Estimate | sd | l-95% CI | u-95% CI | Rhat | ESS bulk | ESS tail |
|-----------|------------------------|----------|------|----------|----------|------|----------|----------|
| Summit | Intercept | -3.44 | 0.28 | -4.03 | -2.94 | 1.00 | 1963 | 1916 |
| | Range size | -0.08 | 0.13 | -0.34 | 0.17 | 1.00 | 4250 | 3072 |
| | Occupancy | -1.63 | 0.17 | -2.00 | -1.32 | 1.00 | 2225 | 2168 |
| | Range size : occupancy | -0.02 | 0.09 | -0.20 | 0.17 | 1.00 | 4488 | 3163 |
| Forest | Intercept | -1.29 | 0.17 | -1.64 | -0.96 | 1.01 | 578 | 977 |
| | Range size | -0.18 | 0.04 | -0.27 | -0.10 | 1.00 | 4613 | 3426 |
| | Occupancy | -1.65 | 0.08 | -1.81 | -1.49 | 1.00 | 2916 | 3136 |
| | Range size : occupancy | 0.06 | 0.04 | -0.02 | 0.15 | 1.00 | 5990 | 3220 |
| Grassland | Intercept | -1.07 | 0.38 | -1.81 | -0.33 | 1.01 | 465 | 885 |
| | Range size | -0.40 | 0.10 | -0.59 | -0.20 | 1.00 | 2417 | 2796 |
| | Occupancy | -1.80 | 0.17 | -2.15 | -1.47 | 1.00 | 1064 | 2068 |
| | Range size : occupancy | -0.08 | 0.09 | -0.25 | 0.10 | 1.00 | 2769 | 2968 |

Excluding rare species

Number of observations: 5407 (forest), 1684 (grassland)

Number of group levels (species): 834 (forest), 428 (grassland)

Number of group levels (study): 68 (forest), 21 (grassland)

Sample settings: 4 chains, each with 2,000 iterations

| Habitat | Parameter | Estimate | sd | l-95% CI | u-95% CI | Rhat | ESS bulk | ESS tail |
|-----------|------------------------|----------|------|----------|----------|------|----------|----------|
| Forest | Intercept | -2.35 | 0.20 | -2.76 | -1.97 | 1.00 | 691 | 1236 |
| | Range size | -0.16 | 0.06 | -0.28 | -0.04 | 1.00 | 3005 | 3290 |
| | Occupancy | -1.39 | 0.12 | -1.63 | -1.16 | 1.00 | 2115 | 2698 |
| Grassland | Range size : occupancy | 0.12 | 0.06 | 0.01 | 0.23 | 1.00 | 3844 | 3188 |
| | Intercept | -2.23 | 0.47 | -3.19 | -1.34 | 1.00 | 660 | 1296 |
| | Range size | -0.45 | 0.14 | -0.73 | -0.17 | 1.00 | 2795 | 3052 |
| | Occupancy | -1.49 | 0.16 | -1.84 | -1.19 | 1.00 | 1592 | 2359 |
| | Range size : occupancy | -0.16 | 0.12 | -0.39 | 0.08 | 1.00 | 2917 | 2888 |

Table S3. Summaries of models for occupancy trends of persisting species in relation to range size (Supplementary Figure 3 and Fig. 3b Model syntax, sampling settings, parameter estimates, their standard deviation (sd) and 95% credible interval (CI). Rhat is the Gelman–Rubin convergence diagnostic, bulk- and tail-ESS are the number of independent samples (i.e. effective sample sizes). Models only includes persisting species. “ Δ to decreasing” presents the posterior difference in estimated mean range size between increasing and decreasing species. Model on probability of increasing controls for species baseline occupancy, and excludes species with a baseline occupancy of 1 (see Methods).

Persisting increasing vs persisting decreasing: mean range sizes

Formula: $\log_{10}(\text{range}) \sim \text{occtrend} + (1/\text{study})$

Number of observations: 2417 (summit), 5376 (forest), 1612 (grassland)

Number of group levels (study): 52 (summit), 68 (forest), 21 (grassland)

Sample settings: 4 chains, each with 2,000 iterations

| Habitat | Parameter | Estimate | sd | l-95% CI | u-95% CI | Rhat | ESS bulk | ESS tail |
|------------------|--------------------------------------|----------|------|----------|----------|------|----------|----------|
| <i>Summit</i> | Decreasing (Δ to decreasing) | 3.32 | 0.06 | 3.20 | 3.43 | 1.00 | 662 | 1407 |
| | Increasing (Δ to decreasing) | 0.08 | 0.03 | 0.01 | 0.14 | 1.00 | 6139 | 3111 |
| <i>Forest</i> | Decreasing | 4.39 | 0.03 | 4.34 | 4.45 | 1.01 | 345 | 618 |
| | Increasing (Δ to decreasing) | 0.10 | 0.01 | 0.07 | 0.13 | 1.00 | 4990 | 3247 |
| <i>Grassland</i> | Decreasing | 4.57 | 0.05 | 4.46 | 4.66 | 1.01 | 519 | 747 |
| | Increasing (Δ to decreasing) | 0.04 | 0.02 | 0.00 | 0.08 | 1.01 | 3407 | 2449 |

Probability of persisting species increasing in occupancy

Formula: $\text{logit}(p) \sim \text{scale}(\log_{10}(\text{range})) + \text{scale}(\log_{10}(\text{occupancy})) + (1 + \text{scale}(\log_{10}(\text{occupancy})) / \text{site}) + (1 / \text{specieskey})$

Number of observations: 1909 (summit), 5250 (forest), 1600 (grassland)

Number of group levels (species): 511 (summit), 718 (forest), 451 (grassland)

Number of group levels (study): 52 (summit), 68 (forest), 21 (grassland)

Sample settings: 4 chains, each with 2,000 iterations

| Habitat | Parameter | Estimate | sd | l-95% CI | u-95% CI | Rhat | ESS bulk | ESS tail |
|------------------|------------|----------|------|----------|----------|------|----------|----------|
| <i>Summit</i> | Intercept | 0.09 | 0.12 | -0.15 | 0.34 | 1.00 | 1833 | 2139 |
| | Range size | 0.12 | 0.06 | 0.01 | 0.23 | 1.00 | 6277 | 3467 |
| | Occupancy | -0.05 | 0.06 | -0.16 | 0.07 | 1.00 | 4652 | 2900 |
| <i>Forest</i> | Intercept | -0.71 | 0.13 | -0.96 | -0.46 | 1.01 | 476 | 867 |
| | Range size | 0.26 | 0.05 | 0.15 | 0.36 | 1.00 | 1609 | 2275 |
| | Occupancy | -0.56 | 0.07 | -0.69 | -0.43 | 1.00 | 1395 | 2184 |
| <i>Grassland</i> | Intercept | -0.62 | 0.21 | -1.03 | -0.21 | 1.00 | 750 | 1287 |
| | Range size | 0.20 | 0.08 | 0.05 | 0.35 | 1.00 | 3366 | 2931 |
| | Occupancy | -0.92 | 0.14 | -1.20 | -0.64 | 1.00 | 1630 | 2300 |

Table S4. Summary of the model predicting species range size with species trajectory (Fig. 3c and d). Model syntax, sampling settings, parameter estimates, their standard deviation (sd) and 95% credible interval (CI). Rhat is the Gelman–Rubin convergence diagnostic, bulk- and tail-ESS are the number of independent samples (i.e. effective sample sizes). Model includes all 1,827 species in our database. “ Δ to gained” presents the posterior difference in estimated mean range size between lost/persisting and gained species. Contrasts are calculated as differences between the posterior distribution of mean range sizes of trajectories (as opposed to Figure 3c and d, model estimates are here in the log10-scale).

Gained vs lost (vs persisting): mean range sizes

Formula: $\log_{10}(\text{range}) \sim \text{trajectory} + (1/\text{study})$

Number of observations: 3394 (summit), 9749 (forest), 3013 (grassland)

Number of group levels (study): 52 (summit), 68 (forest), 21 (grassland)

Sample settings: 4 chains, each with 2,000 iterations

| Habitat | Parameter | Estimate | sd | l-95% CI | u-95% CI | Rhat | ESS bulk | ESS tail |
|-----------|---------------------------------|----------|------|----------|----------|------|----------|----------|
| Summit | Gained | 4.49 | 0.07 | 4.36 | 4.62 | 1.02 | 474 | 1093 |
| | Lost (Δ to gained) | -0.15 | 0.06 | -0.27 | -0.04 | 1.00 | 4469 | 3068 |
| | Persisted (Δ to gained) | -0.10 | 0.04 | -0.17 | -0.02 | 1.00 | 4070 | 2802 |
| Forest | Gained | 5.43 | 0.03 | 5.37 | 5.48 | 1.01 | 262 | 649 |
| | Lost (Δ to gained) | -0.11 | 0.02 | -0.15 | -0.08 | 1.00 | 2675 | 2703 |
| | Persisted (Δ to gained) | 0.04 | 0.01 | 0.01 | 0.07 | 1.00 | 2767 | 2767 |
| Grassland | Gained | 5.56 | 0.05 | 5.46 | 5.65 | 1.02 | 514 | 677 |
| | Lost (Δ to gained) | -0.11 | 0.02 | -0.15 | -0.07 | 1.00 | 2080 | 2547 |
| | Persisted (Δ to gained) | 0.05 | 0.02 | 0.01 | 0.09 | 1.00 | 2264 | 2474 |

Contrasts

| Habitat | Parameter | Estimate | l-95% CI | u-95% CI |
|-----------|--------------------|----------|----------|----------|
| Summit | Gained - lost | 0.15 | 0.04 | 0.27 |
| | Persisted - lost | 0.06 | -0.04 | 0.16 |
| | Gained - persisted | 0.09 | 0.02 | 0.17 |
| Forest | Gained - lost | 0.12 | 0.08 | 0.15 |
| | Persisted - lost | 0.16 | 0.13 | 0.18 |
| | Gained - persisted | -0.04 | -0.07 | 0.00 |
| Grassland | Gained - lost | 0.11 | 0.07 | 0.15 |
| | Persisted - lost | 0.16 | 0.12 | 0.20 |
| | Gained - persisted | -0.05 | -0.09 | -0.01 |

Table S5. Summary of the model testing for effects of sampling methods on the effect of range size on species loss probability. Model syntax, sampling settings, parameter estimates, their standard deviation (sd) and 95% credible interval (CI). Rhat is the Gelman–Rubin convergence diagnostic, bulk- and tail-ESS are the number of independent samples (i.e. effective sample sizes). Model is on forests, as forest study sites are most numerous and sampling characters (i.e. site areas, plot sizes/numbers and time intervals) varied here the most.

Interaction effect between range size and sampling methods

Formula:

$logit(p) \sim scale(log_{10}(range)) * scale(log_{10}(occupancy))$
 $+ scale(log_{10}(range)) * scale(log_{10}(area))$
 $+ scale(log_{10}(range)) * scale(plot\ size)$
 $+ scale(log_{10}(range)) * scale(plot\ number)$
 $+ scale(log_{10}(range)) * scale(time\ interval)$
 $+ (1 + scale(log_{10}(occupancy)) | site) + (1 | speciesKey)$

Number of observations: 7727

Number of group levels (species): 989

Number of group levels (study): 68

Sample settings: 4 chains, each with 2,000 iterations

| Parameter | Estimate | sd | l-95% CI | u-95% CI | Rhat | ESS bulk | ESS tail |
|----------------------------|----------|------|----------|----------|------|----------|----------|
| Intercept | -1.46 | 0.14 | -1.75 | -1.18 | 1.01 | 946 | 1622 |
| Range size | -0.15 | 0.06 | -0.26 | -0.04 | 1.00 | 2716 | 3063 |
| Occupancy | -1.70 | 0.08 | -1.86 | -1.55 | 1.00 | 2023 | 2762 |
| Area | -0.26 | 0.13 | -0.53 | -0.01 | 1.01 | 897 | 1679 |
| Plot size | -0.06 | 0.12 | -0.30 | 0.18 | 1.00 | 1153 | 2023 |
| Plot number | -0.93 | 0.13 | -1.18 | -0.67 | 1.00 | 921 | 1366 |
| Time interval | 0.18 | 0.12 | -0.06 | 0.42 | 1.00 | 1064 | 1643 |
| Range size : occupancy | 0.06 | 0.05 | -0.04 | 0.16 | 1.00 | 3960 | 3049 |
| Range size : area | -0.05 | 0.06 | -0.16 | 0.06 | 1.00 | 3433 | 3392 |
| Range size : plot size | 0.00 | 0.04 | -0.09 | 0.08 | 1.00 | 7222 | 3096 |
| Range size : plot number | 0.00 | 0.05 | -0.10 | 0.10 | 1.00 | 4436 | 3000 |
| Range size : time interval | -0.07 | 0.05 | -0.16 | 0.03 | 1.00 | 3801 | 2997 |

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Chapter 5 – Synthesis

In this thesis I used temporal data to ask whether individual species trajectories in plant communities can be explained by species geographic range size. The main finding of this thesis is that range size can predict trajectories of vascular plant species across contrasting habitats in Europe, suggesting species temporal turnover in the Anthropocene has a directional and predictable component. Across plant communities, larger-ranged species gained ground and replaced smaller-ranged species over time. The results suggest that alongside demographic effects, aspects of species niche play a role in driving the effect of range size on plant species trajectory. Here I focused on species niche position for nutrients and showed that i) species nutrient-niche is associated positively with range size, ii) the probability of species loss increased disproportionately for small-ranged species under high aerial nitrogen deposition, iii) shifts towards more nutrient-loving species run in parallel with the replacement of smaller- by larger-ranged species, and iv) controlling for demographic effects does not nullify the effect of range size on the loss probability of species. Together, these findings suggest that small-by large-ranged species replacement is partially driven by ecological selection processes.

Human modifications to the environment, such as changes in land use, typically aim at making land more productive (Carpenter et al., 2009; Rockström et al., 2009). These changes are not confined locally but spill over to natural and seminatural systems (J. N. Galloway et al., 2003; Bobbink et al., 2010). Thus, even in natural and seminatural habitats, more resource-acquisitive plants species may be favored (Chapter 3). Since larger-ranged species tend to be more nutrient-loving (Chapter 4), this may explain their success across habitats. Large-ranged species might initially be also more likely to colonize because i) they occupy more sites from where to disperse, ii) nutrient-loving plants have a generally higher resource allocation to reproduction (Bartelheimer and Poschlod, 2016), where a large number of seeds can favor dispersal (Murray et al., 2002; Fenner and Thompson, 2005) and, iii) high-nutrient habitats are often human habitats (e.g. agricultures), where humans may act as a major secondary dispersal agent. Thus, both the colonization and persistence of large-ranged species are likely to be favored by human activities owing to deterministic aspects of species niche. Importantly, the increased prevalence of large-ranged, more resource-acquisitive species, could increase the biotic pressure on extant species and thereby help to explain the preferential loss of small-ranged species.

As larger-ranged, more nutrient-loving species are gained, competition for below-ground resources is likely to shift towards competition for light (Hautier, Niklaus, and Hector, 2009). Extant species may therefore not only experience direct effects from human activities such as an imbalanced stoichiometry of resources (e.g. phosphorous to nitrogen ratio), but also increased competition. Thus, filtering of preferentially small-ranged species, i.e. species that tend to have resource-conservative strategies and grow slower, could be due not only to abiotic but also to biotic pressure. I found that in grasslands, where biotic filtering is presumed to be strong, the range-size effect on the probability of loss was strongest, whereas on summits, where biotic filtering is less important and vegetation cover hitherto much lower, the range-size effect was not clearly different from zero (Chapter 4). This could suggest that biotic filtering may play an important role in explaining the directional turnover in relation to species range

size. Experimental studies in which the number of limiting resources is decreased show that abiotic and biotic effects are both important predictors of species richness change (Harpole et al., 2016). However, the relative importance of abiotic versus biotic filtering for driving directional turnover is in need of further study.

While the exact causes (abiotic versus biotic filtering) of the preferential decline of small-ranged species remain still elusive, this thesis provides evidence for its consequences. Since species with smaller ranges by definition occupy fewer sites and are more likely to be lost within a given site, they are at double risk of going extinct (Pimm et al., 2014). The directional loss of small-ranged species at a given site is therefore likely to have consequences for the diversity of species beyond the community level (Keil et al., 2018). Here I found that the gamma diversity of all forest sites has declined over time (Chapter 3), although site-level diversity remained constant on average. This result sheds light on how local dynamics may change biodiversity across spatial scales. At relatively small spatial scales, gains in larger-ranged species offset losses in smaller-ranged species on average, but the cumulative loss of geographically restricted species can translate to a decrease in species richness at the gamma-scale. In addition, I found that the directional turnover in relation to species range size can link to changes in beta-diversity between habitats. The consistent replacement of small- by large-ranged species acts to homogenize the vegetation between habitats over time (Chapter 4). As this might imply a decline in unique ecosystem functions, understanding and reversing the preferential loss of small-ranged species is of major concern for biodiversity conservation.

Outlook

This thesis highlights an important question, namely to understand the relative importance of abiotic and biotic filtering in explaining the systematic loss of species. One way to test for the importance of biotic pressure is by asking whether herbivory can dampen the effects of global environmental change: Herbivory can modify vegetation changes by downregulating the more frequent and dominant species and by increasing niche space via disturbances. To address this question, we are currently compiling a database in collaboration with the data custodians and park managers of the forestREplot consortium (<https://forestreplot.ugent.be/>). We collate densities of different herbivore species over time in sites with vegetation resurveys. Although the literature on the effects of herbivores in forests remains divided, some previous studies in forestREplot sites have already shown that high herbivore densities can substantially increase species richness (Vild et al., 2017). With this project we want to go beyond analyzing richness trends and ask, which species benefit from increases in herbivory and whether herbivory favors coexistence by preventing species losses from increased competition? Also, we want to quantify at which density of herbivores any such buffering effects become visible. Knowing which herbivore densities are beneficial for plant conservation will be essential for future rewilding and restoration efforts.

On a more personal note. . . While herbivory may be one tool to help the conservation of species in a rewilding or restoration context, it is impossible to introduce large herbivores everywhere. So why not bring the most threatened species to cities and our backyards, where plants can grow in controlled and managed environments and let humans take over the functional role of herbivores. As paradoxical as it sounds, if the most vulnerable species can live in human environments when the biotic effects of faster growing species are controlled for, the conservation of these species could move to the presumed centers of their threat and become an objective of citizen science. Red list plant species could be commercialized, so that people can choose whether to plant an exotic species or a native Red list species (which may eventually even act as an economically viable supplement to payments for maintaining traditional farming practices). Augmenting demographic rates via planting these threatened species

in parks and backyards, may help species with declining population trends to colonize suitable habitat, which is currently impeded due to the rarity of these species. Although not a scientific endeavour, this thesis motivated planting Red list plant species in my backyard. Also, it led me to initiate goodglobe.org, a crowdfunding platform (which is still in development, current mockup version available under <https://lucid-golick-8b9883.netlify.app/>) for science-driven conservation projects that aims to enable everyone to take responsibility for the environment and, guided by science, safeguard biodiversity.

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I thank Thore Engel for being the best friend and flat mate that one can wish for. I thank him for initiating our fourth chapter, a self-built wooden canoe. In times of no material progress (which a Ph.D. is) it was great to see the boat grow from the first wooden blank to its now boat-like character. It was a greatness to go together through this Ph.D. time. And really there would not be enough space here to thank for all.

Finally, I thank my family. I cannot thank them enough for always encouraging me whilst having no expectations.

Appendix A

Supplementary material: Chapter 2

Supplementary information

Range size predicts the risk of local extinction from habitat loss

Figure S1: Sensitivity test of data selection thresholds.

Figure S2: Time interval between and dates of the before and after habitat loss period.

Figure S3: Map of locations meeting criteria of the persistence probability analysis.

Figure S4: Frequency distribution of log transformed range sizes.

Figure S5: Simulations.

Figure S6: Testing the assumption of extinction after last record.

Figure S7: Sampling frequencies per % habitat loss.

R code: available in the online version at <https://doi.org/10.1111/geb.13003>

Justification of thresholds and sensitivity test

Thresholds for data quality are necessarily subjective (Isaac & Pocock, 2015) but we justify our thresholds as follows. We used 0% habitat remaining as threshold for classifying the period after habitat loss because only then we can exclude the possibility that species records were collected in natural habitat remnants. We chose 80% as threshold for the classification of the period before habitat loss because this still gave us a sizeable number of cells. Any higher threshold would prevent meaningful analysis. We required before and after communities to have at least 10 species for the same reason. Telfer, Preston and Rothery (2002) used a threshold of 5 species, this would also increase the number of cells available to our analysis, but we aimed for the most stringent criteria that still returned a sizeable number of cells.

Nonetheless, we tested the sensitivity of our results to chosen thresholds. We repeated the same analysis: first, we required communities to have at least 5 species in both the before

and after habitat loss community (leaving habitat thresholds unchanged); second, we also changed thresholds to $\geq 60\%$ habitat remaining (defining the period before habitat loss) and $\leq 10\%$ habitat remaining (defining the period after habitat loss). Results were consistent (pairwise permutation test: $Z = -4.4$, $p < 0.001$, $r = 0.25$ and $Z = -17.7$, $p < 0.001$, $r = 0.3$ respectively; Figure S1a) and b). As expected, relaxing the thresholds increased the number of available communities (from 89 communities in the main text to 155 and 1,700 communities, respectively).

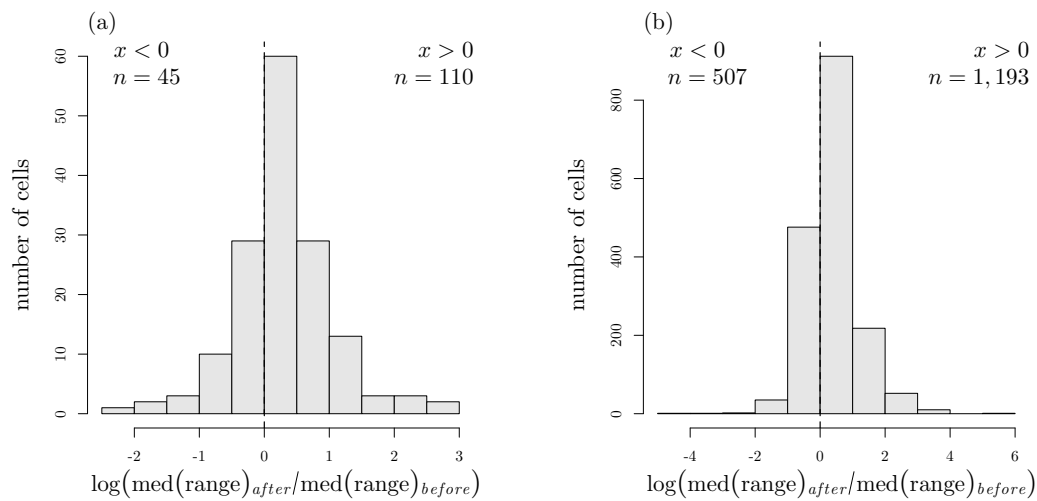


Figure S1: Change in median range size of vascular plant communities (at least 5 species) before and after habitat loss with different data selection thresholds. a) Thresholds of habitat remaining are set to $\geq 80\%$ (defining the before habitat loss period) and 0% (defining the after habitat loss period), and b) thresholds of habitat remaining are set to $\geq 60\%$ (defining the before habitat loss period) and $\leq 10\%$ (defining the after habitat loss period)

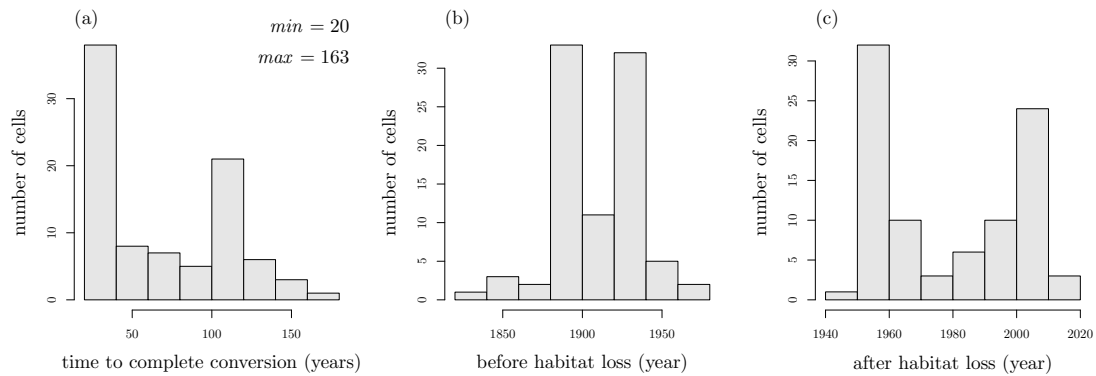


Figure S2: a) Time interval (years) between the last record before habitat loss ($\geq 80\%$ habitat remaining) and the earliest record after habitat loss (0% habitat remaining). The average time that passed between the before and after community was 81 years, the shortest and longest time interval are 20 and 163 years, respectively. b) Date of the last species record in the before habitat loss period. c) Date of the earliest record in the after habitat loss period.

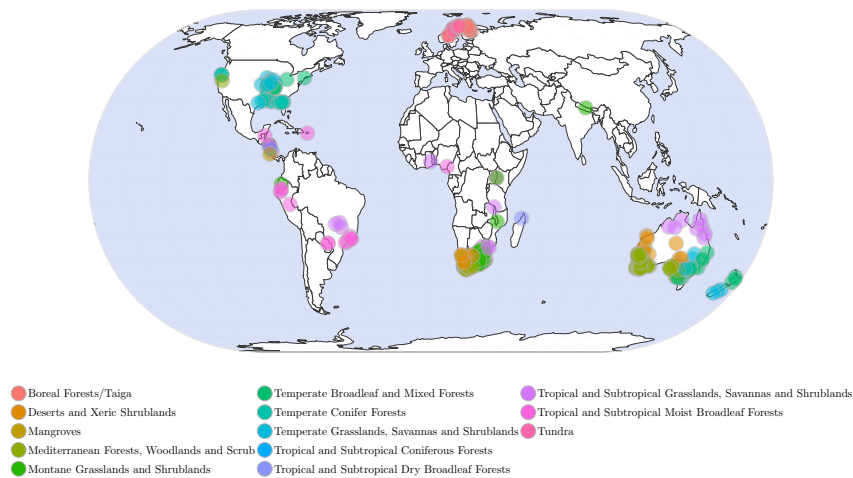


Figure S3: Spatial distribution of 365 locations (quarter degree cells) that experienced complete loss of natural habitat and that harbored species that were sampled at least twice and present before habitat loss. Circles are semitransparent and coloured according to biomes. Map is in Eckert-IV projection.

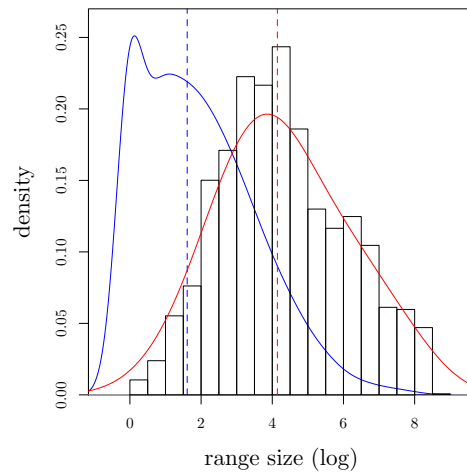


Figure S4: Frequency distribution of log transformed range sizes for 2,678 species (after applying data selection thresholds; red) and 177,774 species (total set; blue). Smooth curves are kernel density estimates. Dashed vertical lines are median range sizes.

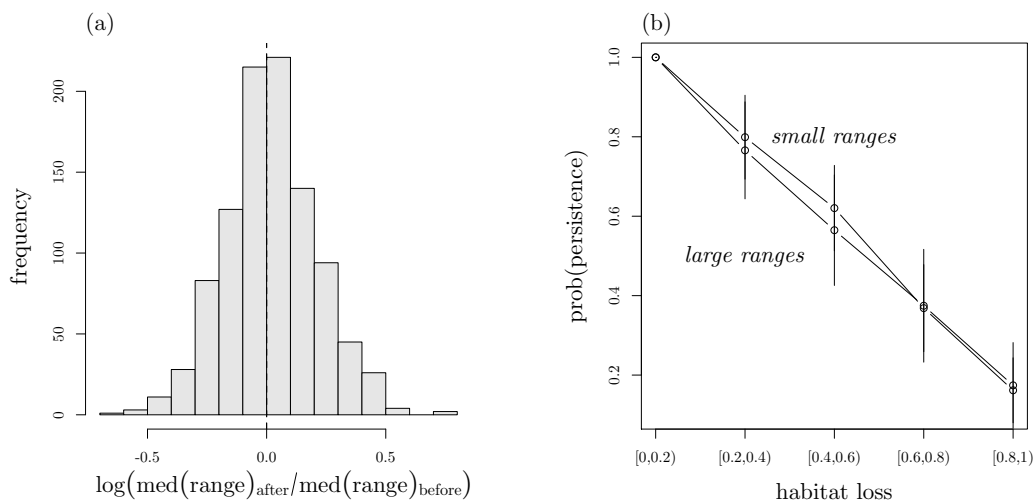


Figure S5: Simulations. a) Distribution of logratios of median species' range size before and median species' range size after habitat loss. Logratios are calculated from 1,000 simulated before and after habitat loss communities. Species range sizes in both communities were simulated from the same log-normal distribution. b) Persistence curve of small- and large-ranged species. Each range size class consists of 50 species. Species' minimum habitat values were simulated from the same uniform distribution for all species.

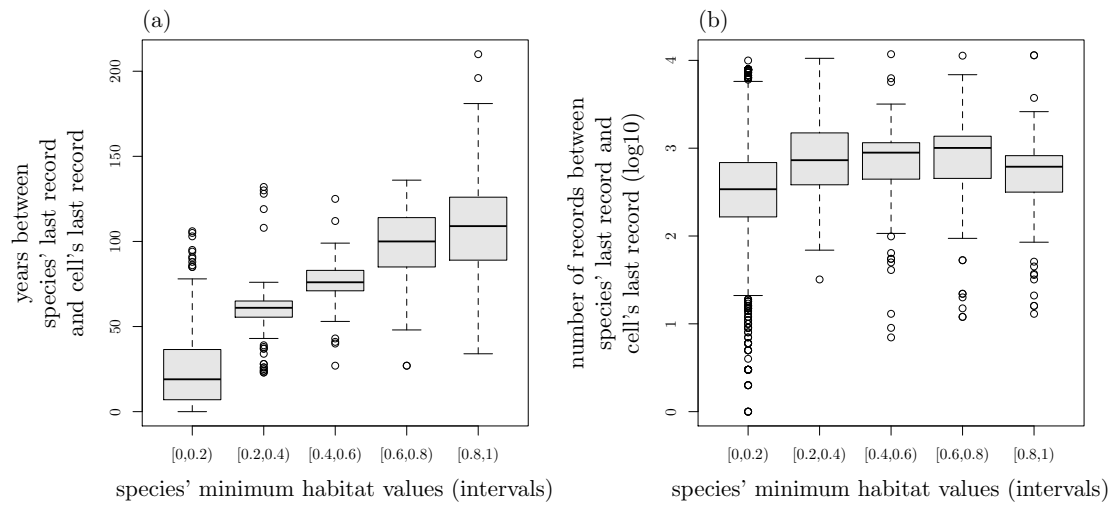


Figure S6: Testing the assumption of extinction after last record. a) Number of years and b) number of records (log10 transformed) between a species' last record in a given cell (minimum habitat value) and the overall last record in that cell. Minimum habitat values are grouped in five 20% wide intervals.

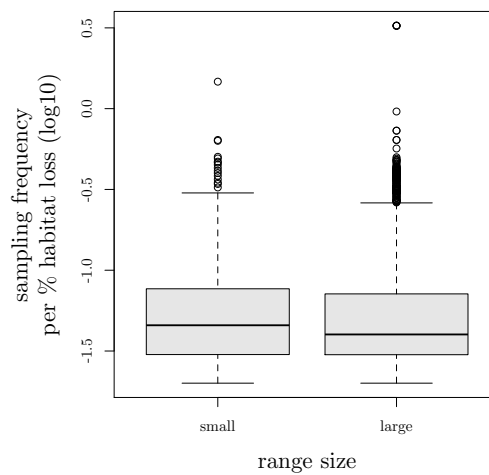


Figure S7: Quartiles and whisker plot of sampling frequencies, calculated as the number of records per percent habitat loss, of small- and large-ranged species. Whiskers extend 1.5 interquartile ranges.

References

- Isaac, N. J. & Pocock, M. J. (2015). Bias and information in biological records. *Biological Journal of the Linnean Society*, *115*(3), 522–531.
- Telfer, M. G., Preston, C. & Rothery, P. (2002). A general method for measuring relative change in range size from biological atlas data. *Biological conservation*, *107*(1), 99–109.

Appendix B

Supplementary material: Chapter 3

Supplementary information

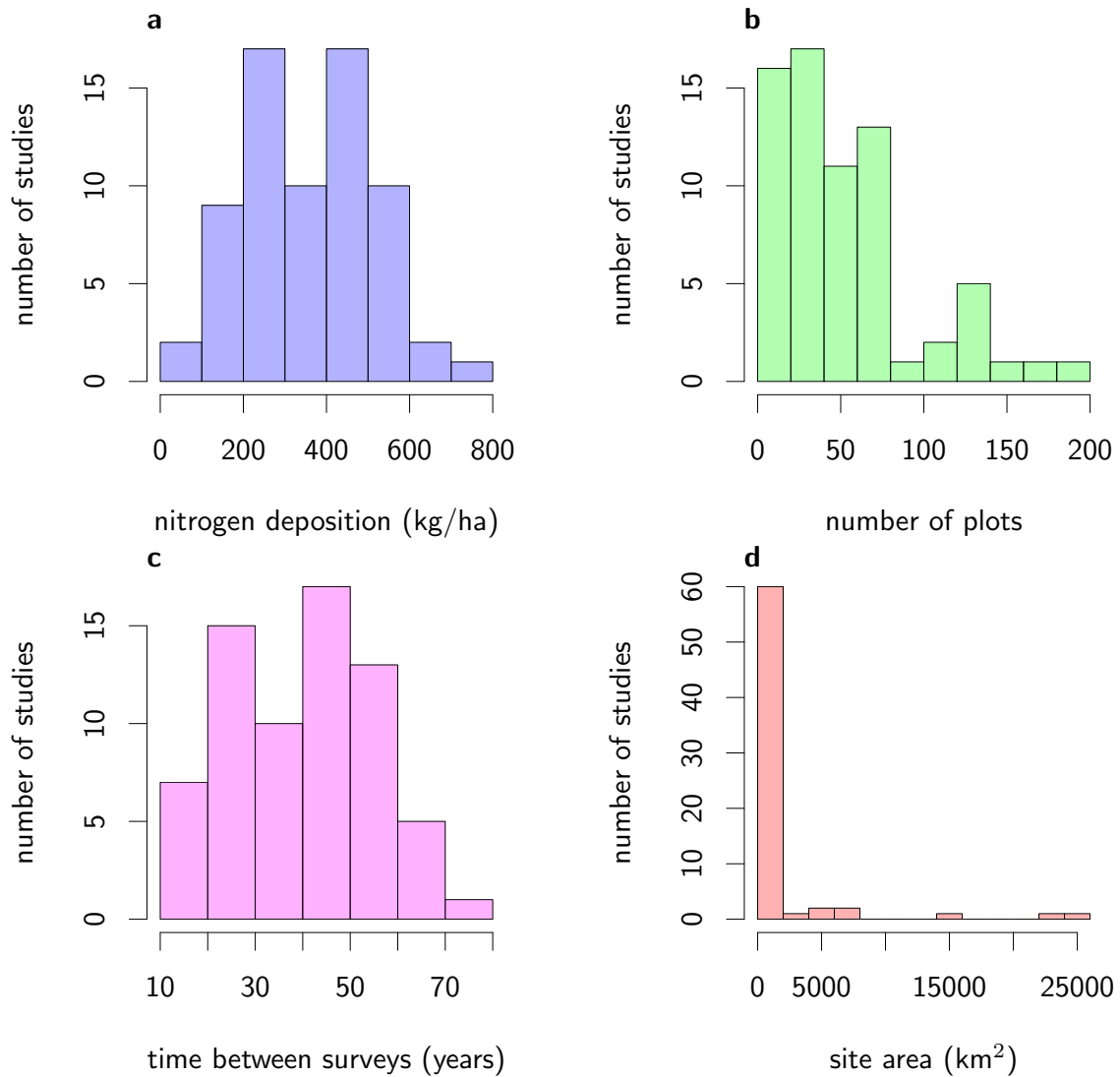
Replacements of small- by large-ranged species scale up to diversity loss in Europe's temperate forest biome

Supplementary Figures

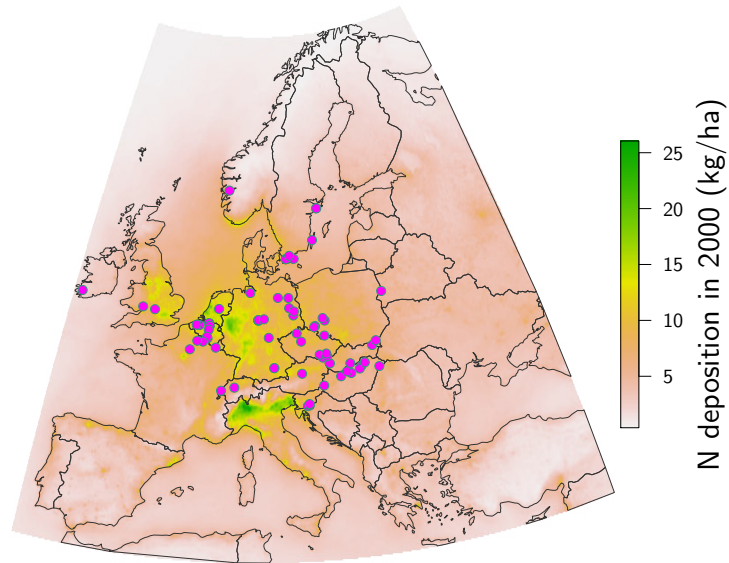
1. Supplementary Figure 1. Study-level predictor variables.
2. Supplementary Figure 2. Map of oxidized nitrogen deposition.
3. Supplementary Figure 3. Change in non-native species.

Supplementary Tables

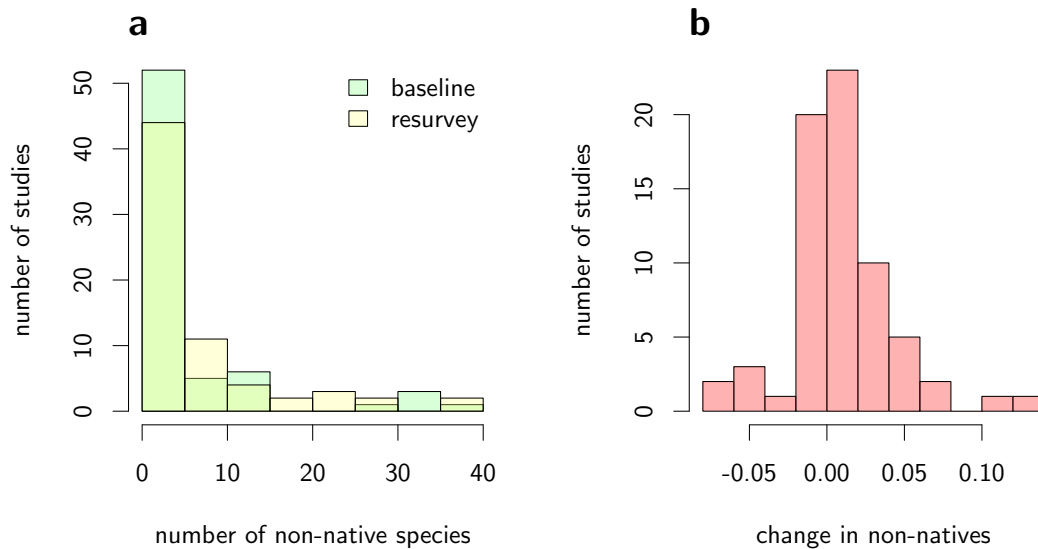
1. Supplementary Table 1. Country, region, coordinates, survey interval, and year of the baseline survey of studies.
2. Supplementary Table 2. Model summary of range size comparison between persisting, colonizing and extinct species.
3. Supplementary Table 3. Model summary for species' extinction probability with i) only species' site occupancy, ii) species' range size and site occupancy, and iii) only species' range size as predictor.
4. Supplementary Table 4. Model summary for species' extinction probability including the interaction between inter-census nitrogen deposition and species' range size as predictor.
5. Supplementary Table 5. Model summary for the change in species number and non-native species with inter-census nitrogen deposition and other contextual variables as predictor of this change.
6. Supplementary Table 6. Model summary for Ellenberg indicator values for N averaged across extinct species and the change in N-numbers averaged across all species regressed against inter-census nitrogen deposition.
7. Supplementary Table 7. Model summary for the change in mean and variance of N-availability across sites over time.



Supplementary Figure 1: Study-level predictor variables. Frequency distributions of **a)** cumulative nitrogen deposition between surveys, **b)** number of plots in a study, **c)** the time period between the baseline survey and the resurvey and **d)** the area of the study site.



Supplementary Figure 2: Map of oxidized nitrogen deposition. Data for dry and wet oxidized N-deposition in the year 2000 from EMEP (c. 11km² resolution) with study locations.



Supplementary Figure 3: Change in non-native species. a) Frequency distribution of the number of non-native species at the time of the baseline survey and resurvey. b) Frequency distribution of the difference in the proportion of non-native species to total richness between the resurvey and baseline survey.

Supplementary Table 1: Country, region, coordinates, survey interval, and year of the baseline survey of studies [when one survey (baseline or resurvey) was carried out over several years, the survey interval represents the time span between the earliest baseline survey and latest resurvey].

| Country | Region | Lat | Long | Interval (years) | Baseline (year) |
|---------|------------------------------|-------|-------|------------------|-----------------|
| A | Zöbelboden | 47.84 | 14.44 | 17 | 1993 |
| B | Gaume | 49.62 | 5.57 | 55 | 1953 |
| B | Binnen-Vlaanderen | 51.07 | 3.69 | 29 | 1980 |
| B | Zoerselbos | 51.25 | 4.68 | 26 | 1982 |
| B | Herenbossen | 51.07 | 4.79 | 24 | 1980 |
| B | Vorte Bossen | 51.07 | 3.37 | 21 | 1977 |
| B | Meerdaalwoud | 50.80 | 4.70 | 46 | 1954 |
| B | Florenne | 50.21 | 4.65 | 48 | 1957 |
| B | Tournibus | 50.32 | 4.58 | 38 | 1967 |
| CH | Switzerland | 46.96 | 7.64 | 58 | 1940 |
| CZ | Děvín Wood | 48.87 | 16.65 | 50 | 1953 |
| CZ | Milovice Wood | 48.83 | 16.69 | 53 | 1953 |
| CZ | Rychlebské hory Mts. | 50.31 | 17.04 | 57 | 1942 |
| CZ | Milíčovský les | 50.02 | 14.54 | 22 | 1986 |
| CZ | České Středohoří | 50.60 | 14.12 | 47 | 1965 |
| CZ | Krumlov Wood | 49.05 | 16.37 | 48 | 1964 |
| CZ | Hodonínská Dúbrava | 48.89 | 17.12 | 47 | 1965 |
| CZ | Ždánice Wood | 49.08 | 17.06 | 53 | 1959 |
| D | Elbe-Weser | 53.41 | 9.12 | 22 | 1986 |
| D | Göttingen, SFB | 51.53 | 10.05 | 21 | 1980 |
| D | Echinger Lohe | 48.30 | 11.65 | 31 | 1986 |
| D | Echinger Lohe | 48.30 | 11.64 | 56 | 1961 |
| D | Göttingen, Carici-Fagetum | 51.56 | 10.01 | 52 | 1960 |
| D | Göttingen, Hordelymo-Fagetum | 51.56 | 10.01 | 49 | 1960 |
| D | Brandenburg | 52.33 | 13.44 | 50 | 1962 |
| D | Sonneberg | 50.36 | 11.13 | 55 | 1961 |
| D | Göttingen, Hünstollen | 51.58 | 10.05 | 20 | 1992 |
| D | Prignitz | 53.06 | 12.23 | 60 | 1954 |
| D | Brandenburg Nord | 53.02 | 13.40 | 51 | 1963 |
| D | Brandenburg Süd | 51.82 | 13.86 | 54 | 1960 |
| D | Unteres Spreewald-Randgebiet | 52.10 | 13.94 | 45 | 1965 |
| D | Großer Staufenberg | 51.63 | 10.64 | 28 | 1988 |
| F | Hirson | 49.97 | 4.18 | 43 | 1956 |
| F | Andigny | 49.99 | 3.58 | 39 | 1957 |
| F | Jura | 46.71 | 6.34 | 18 | 1989 |
| F | Compiègne forest | 49.37 | 2.89 | 45 | 1970 |
| GB | Wytham Woods | 51.77 | -1.33 | 25 | 1974 |
| GB | Lady Park | 51.83 | -2.66 | 30 | 1979 |
| H | Nyírség | 47.77 | 22.27 | 57 | 1933 |
| H | Heves | 47.99 | 20.50 | 19 | 1989 |
| H | Bakony és Gerecse | 47.44 | 18.33 | 61 | 1955 |
| H | Bükkalja és Dél-Cserehát | 47.81 | 20.29 | 62 | 1953 |
| H | Gödöllői-dombság | 47.58 | 19.38 | 66 | 1950 |
| H | Mátra-Bükk-Zemplén | 48.18 | 20.88 | 58 | 1958 |
| H | Órség | 46.93 | 16.56 | 61 | 1954 |

| | | | | | |
|-----|-------------------------------|-------|-------|----|------|
| H | Visegrádi-hegység | 47.73 | 18.97 | 62 | 1953 |
| IRL | County Kerry | 52.01 | -9.56 | 20 | 1991 |
| NL | Speulderbos | 52.25 | 5.69 | 31 | 1957 |
| NO | Hordaland | 60.31 | 6.10 | 30 | 1978 |
| PL | Białowieża | 52.75 | 23.86 | 46 | 1966 |
| PL | Sanocko-Turczańskie Mountains | 49.54 | 22.34 | 35 | 1972 |
| PL | Bazaltowa Mt | 51.01 | 16.13 | 22 | 1992 |
| PL | Buki Sudeckie beech forest | 50.94 | 16.02 | 24 | 1990 |
| PL | Trzebnickie Hills | 51.33 | 17.22 | 50 | 1962 |
| PL | Olszyny Niezgodzkie | 51.51 | 17.03 | 20 | 1993 |
| SE | Dalby | 55.68 | 13.33 | 78 | 1935 |
| SE | Dalby | 55.68 | 13.33 | 37 | 1976 |
| SE | Tullgarn | 58.95 | 17.62 | 43 | 1971 |
| SE | Tullgarn | 58.95 | 17.62 | 15 | 1999 |
| SE | Stenshuvud | 55.66 | 14.26 | 27 | 1988 |
| SE | Skåne | 55.88 | 13.74 | 31 | 1983 |
| SE | Öland | 56.83 | 16.67 | 26 | 1988 |
| SI | Strmec | 45.62 | 14.82 | 32 | 1983 |
| SI | Rajhenavski Rog | 45.66 | 15.01 | 32 | 1983 |
| SI | Pecka | 45.75 | 15.00 | 32 | 1983 |
| SK | Slovakia, South-West | 48.40 | 17.33 | 41 | 1966 |
| SK | Slovakia, Central | 48.25 | 19.40 | 43 | 1964 |
| SK | Slovakia, North-East | 49.26 | 21.88 | 41 | 1965 |

Supplementary Table 2: Model summary of range size comparison between persisting, colonizing and extinct species. Species' trajectory is defined at the study level. Range size was calculated at three spatial grains, the main text focuses on the output of the model using range size calculated at mid-resolution. Range size was normalized using an order-quantile transformation. Displayed are the posterior mean (mean), the standard deviation of the posterior distribution (sd), the 89% credible interval of the mean (5.5% and 94.5% quantiles), the number of independent samples (n eff) and the Gelman-Rubin convergence diagnostic (Rhat). For all models, $n = 9,688$ observations across 68 resurvey studies of 1,147 species.

| Parameter | mean | sd | 5.5% | 94.5% | n eff | Rhat |
|---|-------|------|-------|-------|--------|------|
| Mid-resolution (10.7 km²) | | | | | | |
| Mean range size | | | | | | |
| Colonizing | 0.13 | 0.05 | 0.05 | 0.21 | 113.67 | 1.00 |
| Persisting | 0.09 | 0.04 | 0.01 | 0.15 | 161.63 | 1.00 |
| Extinct | -0.08 | 0.05 | -0.16 | 0.01 | 148.01 | 1.00 |
| Mean difference between groups | | | | | | |
| Persisting – colonizing | 0.04 | 0.03 | -0.01 | 0.10 | NA | NA |
| Persisting – extinct | 0.21 | 0.04 | 0.15 | 0.26 | NA | NA |
| Colonizing – extinct | 0.16 | 0.04 | 0.09 | 0.23 | NA | NA |
| Low-resolution (32 km²) | | | | | | |
| Mean range size | | | | | | |
| Colonizing | 0.13 | 0.05 | 0.05 | 0.20 | 144.96 | 1.01 |
| Persisting | 0.09 | 0.05 | 0.01 | 0.16 | 212.24 | 1.00 |
| Extinct | -0.07 | 0.05 | -0.15 | 0.02 | 209.76 | 1.00 |
| Mean difference between groups | | | | | | |
| Persisting – colonizing | 0.04 | 0.03 | -0.02 | 0.09 | NA | NA |
| Persisting – extinct | 0.20 | 0.04 | 0.14 | 0.25 | NA | NA |
| Colonizing – extinct | 0.16 | 0.05 | 0.08 | 0.23 | NA | NA |
| High-resolution (3.6 km²) | | | | | | |
| Mean range size | | | | | | |
| Colonizing | 0.14 | 0.04 | 0.07 | 0.21 | 71.86 | 1.04 |
| Persisting | 0.09 | 0.05 | 0.01 | 0.16 | 115.63 | 1.02 |
| Extinct | -0.08 | 0.05 | -0.17 | 0.00 | 111.09 | 1.03 |
| Mean difference between groups | | | | | | |
| Persisting – colonizing | 0.05 | 0.03 | 0.00 | 0.11 | NA | NA |
| Persisting – extinct | 0.22 | 0.03 | 0.16 | 0.27 | NA | NA |
| Colonizing – extinct | 0.17 | 0.04 | 0.09 | 0.24 | NA | NA |

Supplementary Table 3: Model summary for species' extinction probability with i) only species' site occupancy, ii) species' range size and site occupancy, and iii) only species' range size as predictor.

Range size was calculated at three spatial grains, the main text focuses on the output of the model using range size calculated at mid-resolution. All parameter estimates are on the log-odds scale. Displayed are the posterior mean (mean), the standard deviation of the posterior distribution (sd), the 89% credible interval of the mean (5.5% and 94.5% quantiles), the number of independent samples (n eff) and the Gelman-Rubin convergence diagnostic (Rhat). For all models, $n = 7,736$ observations across 68 resurvey studies of 1,012 species.

| Parameter | mean | sd | 5.5% | 94.5% | n eff | Rhat |
|---|-------|------|-------|-------|---------|------|
| Site occupancy only | | | | | | |
| Intercept | -2.38 | 0.24 | -2.77 | -2.00 | 619.50 | 1.00 |
| Local occupancy | -3.63 | 0.28 | -4.09 | -3.19 | 490.46 | 1.00 |
| Site occupancy and range size | | | | | | |
| Mid-resolution (10.7 km²) | | | | | | |
| Intercept | -2.42 | 0.25 | -2.82 | -2.04 | 1439.65 | 1.00 |
| Local occupancy | -3.63 | 0.29 | -4.11 | -3.18 | 1085.26 | 1.00 |
| Range size | -0.21 | 0.05 | -0.29 | -0.14 | 1672.13 | 1.00 |
| Low-resolution (32 km²) | | | | | | |
| Intercept | -2.41 | 0.25 | -2.82 | -2.01 | 1891.01 | 1.00 |
| Local occupancy | -3.62 | 0.29 | -4.11 | -3.17 | 1520.66 | 1.00 |
| Range size | -0.21 | 0.05 | -0.28 | -0.13 | 3019.42 | 1.00 |
| High-resolution (3.6 km²) | | | | | | |
| Intercept | -2.42 | 0.25 | -2.82 | -2.02 | 1817.30 | 1.00 |
| Local occupancy | -3.63 | 0.29 | -4.10 | -3.18 | 1377.49 | 1.00 |
| Range size | -0.21 | 0.05 | -0.29 | -0.13 | 2455.92 | 1.00 |
| Range size only | | | | | | |
| Mid-resolution (10.7 km²) | | | | | | |
| Intercept | -0.60 | 0.12 | -0.80 | -0.41 | 536.43 | 1.01 |
| Range size | -0.28 | 0.06 | -0.38 | -0.19 | 1173.73 | 1.00 |
| Low-resolution (32 km²) | | | | | | |
| Intercept | -0.61 | 0.12 | -0.81 | -0.42 | 526.35 | 1.02 |
| Range size | -0.29 | 0.06 | -0.38 | -0.19 | 1458.92 | 1.00 |
| High-resolution (3.6 km²) | | | | | | |
| Intercept | -0.61 | 0.12 | -0.81 | -0.41 | 542.69 | 1.00 |
| Range size | -0.29 | 0.06 | -0.38 | -0.19 | 1247.91 | 1.00 |

Supplementary Table 4: Model summary for species' extinction probability including the interaction between inter-census nitrogen deposition and species' range size as predictor. Range size was calculated at three spatial grains, the main text focuses on the output of the model using range size calculated at mid-resolution. All parameter estimates are on the log-odds scale. Displayed are the posterior mean (mean), the standard deviation of the posterior distribution (sd), the 89% credible interval of the mean (5.5% and 94.5% quantiles), the number of independent samples (n eff) and the Gelman-Rubin convergence diagnostic (Rhat). For all models, $n = 7,736$ observations across 68 resurvey studies of 1,012 species.

| Parameter | mean | sd | 5.5% | 94.5% | n eff | Rhat |
|---|-------|------|-------|-------|---------|------|
| Mid-resolution (10.7 km²) | | | | | | |
| Intercept | -2.48 | 0.23 | -2.86 | -2.12 | 1151.60 | 1 |
| Local occupancy | -3.66 | 0.30 | -4.14 | -3.20 | 994.33 | 1 |
| Range size | -0.21 | 0.05 | -0.29 | -0.13 | 2391.49 | 1 |
| Nitrogen deposition | 0.37 | 0.15 | 0.13 | 0.60 | 1161.29 | 1 |
| Survey interval | -0.16 | 0.15 | -0.39 | 0.08 | 1138.46 | 1 |
| Number of plots | -0.54 | 0.12 | -0.73 | -0.36 | 1430.02 | 1 |
| Size of plots | 0.00 | 0.11 | -0.17 | -0.17 | 1880.32 | 1 |
| Site area | -0.22 | 0.12 | -0.41 | -0.02 | 2366.75 | 1 |
| Latitude | -0.17 | 0.11 | -0.34 | 0.01 | 2460.35 | 1 |
| Range size : nitrogen deposition | -0.10 | 0.03 | -0.15 | -0.04 | 6652.94 | 1 |
| Low-resolution (32 km²) | | | | | | |
| Intercept | -2.48 | 0.22 | -2.85 | -2.13 | 1376.25 | 1 |
| Local occupancy | -3.66 | 0.29 | -4.13 | -3.20 | 1088.06 | 1 |
| Range size | -0.21 | 0.05 | -0.28 | -0.13 | 2763.12 | 1 |
| Nitrogen deposition | 0.36 | 0.15 | 0.13 | 0.59 | 1412.50 | 1 |
| Survey interval | -0.15 | 0.14 | -0.38 | 0.07 | 1387.14 | 1 |
| Number of plots | -0.54 | 0.11 | -0.73 | -0.36 | 1790.99 | 1 |
| Size of plots | 0.00 | 0.11 | -0.16 | -0.17 | 1520.20 | 1 |
| Site area | -0.22 | 0.13 | -0.42 | -0.02 | 2902.16 | 1 |
| Latitude | -0.17 | 0.11 | -0.34 | 0.01 | 2606.14 | 1 |
| Range size : nitrogen deposition | -0.09 | 0.03 | -0.14 | -0.03 | 7873.52 | 1 |
| High-resolution (3.6 km²) | | | | | | |
| Intercept | -2.48 | 0.23 | -2.86 | -2.11 | 1159.04 | 1 |
| Local occupancy | -3.66 | 0.29 | -4.15 | -3.22 | 956.34 | 1 |
| Range size | -0.21 | 0.05 | -0.29 | -0.13 | 2279.24 | 1 |
| Nitrogen deposition | 0.35 | 0.15 | 0.13 | 0.59 | 1329.01 | 1 |
| Survey interval | -0.14 | 0.14 | -0.38 | 0.08 | 1270.44 | 1 |
| Number of plots | -0.55 | 0.11 | -0.73 | -0.37 | 1781.37 | 1 |
| Size of plots | 0.00 | 0.11 | -0.17 | -0.17 | 2180.64 | 1 |
| Site area | -0.22 | 0.12 | -0.41 | -0.03 | 2331.33 | 1 |
| Latitude | -0.17 | 0.11 | -0.34 | 0.02 | 2310.92 | 1 |
| Range size : nitrogen deposition | -0.09 | 0.03 | -0.15 | -0.04 | 5642.08 | 1 |

Supplementary Table 5: Model summary for the change in species number and non-native species with inter-census nitrogen deposition and other contextual variables as predictor of this change. Displayed are the posterior mean (mean), the standard deviation of the posterior distribution (sd), the 89% credible interval of the mean (5.5% and 94.5% quantiles), the number of independent samples (n eff) and the Gelman-Rubin convergence diagnostic (Rhat). For all models, $n = 68$ observations (resurvey studies). Model summaries do not match Fig. 3c-e as these show the outcome regressed against the variation of N deposition that is left unexplained by the other predictor variables.

| Parameter | mean | sd | 5.5% | 94.5% | n eff | Rhat |
|--|-------|------|-------|-------|-------|------|
| Change in species number | | | | | | |
| Intercept | 0.00 | 0.11 | -0.18 | 0.17 | 1931 | 1 |
| Nitrogen deposition | 0.12 | 0.15 | -0.12 | 0.37 | 1353 | 1 |
| Survey interval | -0.43 | 0.15 | -0.67 | -0.18 | 1250 | 1 |
| Number of plots | 0.13 | 0.13 | -0.08 | 0.33 | 1543 | 1 |
| Size of plots | 0.01 | 0.12 | -0.18 | 0.21 | 1827 | 1 |
| Site area | 0.24 | 0.12 | 0.04 | 0.44 | 1623 | 1 |
| Latitude | 0.01 | 0.12 | -0.19 | 0.21 | 1982 | 1 |
| Percentage point change in aliens | | | | | | |
| Intercept | 0.00 | 0.10 | -0.16 | 0.16 | 3915 | 1 |
| Nitrogen deposition | 0.42 | 0.15 | 0.18 | 0.66 | 3058 | 1 |
| Survey interval | -0.05 | 0.15 | -0.29 | 0.19 | 2882 | 1 |
| Number of plots | -0.04 | 0.12 | -0.24 | 0.16 | 3405 | 1 |
| Size of plots | 0.21 | 0.12 | 0.02 | 0.39 | 4218 | 1 |
| Site area | 0.03 | 0.12 | -0.17 | 0.21 | 3742 | 1 |
| Latitude | -0.21 | 0.11 | -0.39 | -0.03 | 3865 | 1 |

Supplementary Table 6: Model summary for Ellenberg indicator values for N averaged across extinct species and the change in N-numbers averaged across all species regressed against inter-census nitrogen deposition. Displayed are the posterior mean (mean), the standard deviation of the posterior distribution (sd), the 89% credible interval of the mean (5.5% and 94.5% quantiles), the number of independent samples (n eff) and the Gelman-Rubin convergence diagnostic (Rhat). For all models, $n = 68$ observations (resurvey studies).

| Parameter | mean | sd | 5.5% | 94.5% | n eff | Rhat |
|--|-------|------|-------|-------|---------|------|
| Ellenberg indicator value for N averaged across extinct species | | | | | | |
| Intercept | 0.00 | 0.12 | -0.19 | 0.20 | 3922.94 | 1 |
| Nitrogen deposition | -0.25 | 0.12 | -0.44 | -0.05 | 3492.03 | 1 |
| Change in community mean N-number | | | | | | |
| Intercept | 0.00 | 0.12 | -0.19 | 0.19 | 3843.73 | 1 |
| Nitrogen deposition | 0.28 | 0.12 | 0.08 | 0.46 | 4032.18 | 1 |

Supplementary Table 7: Model summary for the change in variance of nutrient availability across sites over time. Displayed are the posterior mean (mean), the standard deviation of the posterior distribution (sd), the 89% credible interval of the mean (5.5% and 94.5% quantiles), the number of independent samples (n eff) and the Gelman-Rubin convergence diagnostic (Rhat). For all models, $n = 68$ observations (resurvey studies).

| Parameter | mean | sd | 5.5% | 94.5% | n eff | Rhat |
|---|-------|------|-------|-------|--------|------|
| Mean baseline | 4.93 | 0.17 | 4.65 | 5.21 | 284.85 | 1 |
| Mean resurvey – mean baseline | 0.14 | 0.10 | -0.02 | 0.31 | 290.07 | 1 |
| Sigma baseline | 0.63 | 0.06 | 0.54 | 0.72 | 321.65 | 1 |
| Sigma resurvey | 0.49 | 0.04 | 0.43 | 0.57 | 382.40 | 1 |
| Expected value of the difference between group variances | | | | | | |
| Variance resurvey – variance baseline | -0.16 | 0.08 | -0.29 | -0.03 | NA | NA |

Appendix C

Curriculum vitae

Ingmar René STAUDE – Curriculum Vitae

ADDRESS: Brockhausstr. 47, 04229 Leipzig

EMAIL: staudeingmar@gmail.com

EDUCATION

German Centre for Integrative Biodiversity Research

DPhil in BIODIVERSITY CONSERVATION

Advisor: Henrique Pereira

Germany
2017 - ongoing

Université de Poitiers

Universidade de Coimbra

Universidade Federal do Rio Grande do Sul

International Master of Science in APPLIED ECOLOGY

Advisor: Gerhard Overbeck

magna cum laude; GPA: 4.8/5

France
Portugal
Brazil
2015 - 2017

Universidad San Francisco de Quito

Fieldwork and research

in the Northern Andean páramo, Amazon rainforest and Galapagos islands

Ecuador
Jan - Mar 2016

Freie Universität Berlin

Bachelor of Science in BIOLOGY

Advisor: Thomas Schmülling

magna cum laude; GPA: 1.3/1

Germany
2011 - 2015

University Centre in Svalbard

Fieldwork and research

in the Greenland Sea, Arctic Ocean, Tundra and Polar Desert

Spitzbergen
Jul - Dec 2014

PROFESSIONAL EXPERIENCE

Humbolt Universität zu Berlin

Behavioural Ecology

Research assistant | Advisor: Bernd Ronacher

Germany
Mar - Aug 2015

Charité - Universitätsmedizin Berlin

Neuroimaging

Research experience as undergraduate | Advisor: Chantal Mörsen

Germany
Feb-Jul 2014

Freie Universität Berlin

Applied plant genetics

Research assistant | Advisor: Thomas Schmülling

Germany
Nov 2013 - Mar 2014

LMW2 Partners & Normandy Real Estate

Venture capital and real estate investment

Summer intern | Advisor: Finn Wentworth

New York, USA
Jul - Sep 2013

TEACHING EXPERIENCES: COURSES TA'D

- Nature Conservation** for majors Portugal
2018, 2019
Organized fieldwork and supervised student projects in Peneda-Gerês National Park
Martin-Luther-Universität Halle-Wittenberg
- Spatial Ecology and Modelling** for majors Germany
2018, 2019
Ran coding tutorials
Martin-Luther-Universität Halle-Wittenberg
- Summer School: Ecological Theory and Modelling for the Biodiversity Crisis** Germany
2018
Ran coding tutorials
German Centre for Integrative Biodiversity Research
- Urban Vegetation** for majors Brazil
2017
Ran lecture on nexus of urban infrastructure and biodiversity
Invited by students as plenary speaker at the "Academic Week of Biology UFRGS 2017"
Universidade Federal de Rio Grande do Sul

PUBLICATIONS

- Ingmar R. Staude**, Henrique M. Pereira, ... & Lander Baeten. Consistent replacement of small- by large-ranged plant species across habitats. Submitted to *Science* (2020).
- Ingmar R. Staude**, Gerhard E. Overbeck, ... & Carla S. Fontana. Generalist birds make room for specialists in grassland remnants as land use change intensifies. Accepted in *Frontiers in Ecology and Evolution* (2020).
- Ingmar R. Staude**, Donald M. Waller, ... & Lander Baeten. Replacements of small- by large-ranged species scale up to diversity loss in Europe's temperate forest biome. *Nature Ecology & Evolution* (2020). 4:802–808.
- Ingmar R. Staude**, Laetitia M. Navarro & Henrique M. Pereira. Range size predicts the risk of local extinction from habitat loss. *Global Ecology and Biogeography* (2020). 29.1:16-25.
- Ingmar R. Staude**, Eduardo Vélez-Martin, ... & Gerhard E. Overbeck. Local biodiversity erosion in south Brazilian grasslands under moderate levels of landscape habitat loss. *Journal of Applied Ecology* (2018). 55.3:1241-1251.

MEDIA COVERAGE

- Press Release:** "Plant diversity in European forests is declining", featured in e.g. Spektrum, Deutschlandfunk Nova, Phys.org and Science Bulletin [link](#)
- Press Release:** "Biodiversity erosion in Brazil due to land use change: the case of grasslands", Journal of Applied Ecology Blog, [link](#)

WORKING GROUPS

- Synthesis Centre on Biodiversity and Ecosystem Services** Brazil
2020
GrassSyn
Biodiversity of Brazilian grasslands and savannas: patterns and drivers, ecosystem services, and strategies for conservation and restoration; Participant
- German Centre for Integrative Biodiversity Research** Germany
2018, 2019
sReplot

Upscaling of individual species dynamics to community trends in biodiversity and composition using vegetation change data sets; Participant

PROFESSIONAL SKILLS

Software R, \LaTeX , Markdown, Git, Stan
Languages English, Portuguese (excellent); French (intermediate); German (native)

REFERENCES

Prof. Dr. **Henrique Pereira**, iDiv ☎+49 341 9733137. hpereira@idiv.de
Prof. Dr. **Gerhard E. Overbeck**, UFRGS ☎+55 51 3308 7557. gerhard.overbeck@ufrgs.br

Halle (Saale), den

Ingmar Staude

Appendix D

List of publications

Ingmar R. Staude, Henrique M. Pereira, Gergana Daskalova, Markus Bernhardt-Römermann, Martin Diekmann, Harald Pauli, Hans Van Calster, Mark Vellend, Anne D Bjorkman, Jörg Brunet, Pieter De Frenne, Radim Hédli, Ute Jandt, Jonathan Lenoir, Isla H. Myers-Smith, Kris Verheyen, Sonja Wipf, Monika Wulf, Christopher Andrews, Peter Barančok, Elena Barni, José-Luis Benito-Alonso, Jonathan Bennie, Imre Berki, Volker Blüml, Markéta Chudomelová, Guillaume Decocq, Jan Dick, Thomas Dirnböck, Tomasz Durak, Ove Eriksson, Brigitta Erschbamer, Bente Jessen Graae, Thilo Heinken, Fride Høistad Schei, Bogdan Jaroszewicz, Martin Kopecký, Thomas Kudernatsch, Martin Macek, Marek Malicki, František Máliš, Ottar Michelsen, Tobias Naaf, Thomas A. Nagel, Adrian C. Newton, Lena Nicklas, Ludovica Oddi, Andrej Palaj, Alessandro Petraglia, Petr Petřík, Remigiusz Pielech, Francesco Porro, Mihai Puscas, Kamila Reczyńska, Christian Rixen, Wolfgang Schmidt, Tibor Standovár, Klaus Steinbauer, Krzysztof Świerkosz, Balázs Teleki, Jean-Paul Theurillat, Pavel Dan Turtureanu, Tudor-Mihai Ursu, Thomas Vanneste, Philippine Vergeer, Ondřej Vild, Luis Villar, Pascal Vittoz, Manuela Winkler & Lander Baeten. Consistent replacement of small- by large-ranged plant species across habitats. Submitted to *Science* (2020).

Ingmar R. Staude, Gerhard E. Overbeck, Glayson A. Bencke, Thaiane Weinert da Silva, Anne Mimet, Henrique M. Pereira & Carla S. Fontana. Generalist birds make room for specialists in grassland remnants as land use change intensifies. Accepted in *Frontiers in Ecology and Evolution* (2020).

Ingmar R. Staude, Donald M. Waller, Markus Bernhardt-Römermann, Anne D. Bjorkman, Jorg Brunet, Pieter De Frenne, Radim Hedl, Ute Jandt, Jonathan Lenoir, František Mališ, Kris Verheyen, Monika Wulf, Henrique M. Pereira, Pieter Vangansbeke, Adrienne Ortmann-Ajkai, Remigiusz Pielech, Imre Berki, Marketa Chudomelova, Guillaume Decocq, Thomas Dirnbock, Tomasz Durak, Thilo Heinken, Bogdan Jaroszewicz, Martin Kopecky, Martin Macek, Marek Malicki, Tobias Naaf, Thomas A. Nagel, Petr Petrik, Kamila Reczyńska, Fride Høistad Schei, Wolfgang Schmidt, Tibor Standovar, Krzysztof Świerkosz, Balazs Teleki, Hans Van Calster, Ondřej Vild & Lander Baeten. Replacements of small- by large-ranged species scale up to diversity loss in Europe's temperate forest biome. *Nature Ecology & Evolution* (2020). 4:802–808.

Ingmar R. Staude, Laetitia M. Navarro & Henrique M. Pereira. Range size predicts the risk of local extinction from habitat loss. *Global Ecology and Biogeography* (2019). 29.1:16-25.

Ingmar R. Staude, Eduardo Vélez-Martin, Bianca O. Andrade, Luciana Regina Podgaiski, Ilsi I. Boldrini, Milton Mendonça Jr, Valério D. Pillar & Gerhard E. Overbeck. Local biodiversity erosion in south Brazilian grasslands under moderate levels of landscape habitat loss. *Journal of Applied Ecology* (2018). 55.3: 1241-1251.

Appendix E

Author's contribution

Chapter 2

Ingmar R. Staude, Laetitia M. Navarro & Henrique M. Pereira. Range size predicts the risk of local extinction from habitat loss. *Global Ecology and Biogeography* (2019). 29.1:16-25.

Conception/Statistical analysis: Staude, IR (70%)

Writing: Staude, IR (70%)

Chapter 3

Ingmar R. Staude, Donald M. Waller, . . . & Lander Baeten. Replacements of small- by large-ranged species scale up to diversity loss in Europe's temperate forest biome. *Nature Ecology & Evolution* (2020). 4:802–808.

Conception/Statistical analysis: Staude, IR (80%)

Writing: Staude, IR (60%)

Chapter 4

Ingmar R. Staude, Henrique M. Pereira, . . . & Lander Baeten. Consistent replacement of small- by large-ranged plant species across habitats. Submitted to *Science* (2020).

Conception/Statistical analysis: Staude, IR (80%)

Writing: Staude, IR (60%)

Halle (Saale), den

Ingmar Staude

Appendix F

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel "Systematic temporal turnover towards species with larger geographic ranges across plant communities" bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den

Ingmar Staude