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

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Abstract

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

Significance Statement

Vegetation resurveys at intervals of up to 78 years spanning mountain summits, forests and grasslands in Europe, reveal systematic temporal turnover of vascular plant species, despite variable trends in species richness. Large-ranged, nutrient-demanding species are consistently replacing species with small ranges, thus homogenizing vegetation between dominant habitats across Europe. Our cross-continent comparison highlights that such gains of species might increase competition and contribute to directional species loss. Our findings inform predictions of plant community change and prioritization of species conservation during the Anthropocene.

Main text

Introduction

Long-term studies of changes in local plant species richness do not show systematic evidence of decline (1–3). However, local richness changes provide only a limited picture of the extent of ongoing biodiversity change, as they do not capture species turnover and changes in community composition over time (4). While human activities have accelerated species turnover beyond background rates (2, 3), it remains unclear whether the identities of “winner” and “loser” species represent the idiosyncratic local outcomes of drivers of change (e.g., disturbance or climate warming), or whether there are consistent patterns across systems (5). 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 in communities in different habitats.

For plant species, studying temporal turnover in relation to their geographic range size can provide insights on why and how species diversity is changing. On the one hand, the geographic range size of plant species is a key synthetic measure of their ecological profile (6). Range size reflects the ability of species to disperse and colonize (7, 8), as well as their niche breadth (9, 10) and niche position (11–

13), thus capturing multiple factors relating to a species' vulnerability to global environmental changes. On the other hand, range size links temporal with spatial turnover of species, as communities that lose small-ranged while gaining widespread species become more similar over time (14). Therefore, understanding the link between range size and a species' trajectory over time will not only shed light on why certain species "win" or "lose", but also on the consequences of these shifts for the distinctiveness of plant communities, an important component of biodiversity.

Here, we analyze individual trajectories of 1,827 vascular plant species over time in relation to their range size at 141 study sites across three habitats in Europe – mountain summits, deciduous and coniferous forests, and lowland grasslands (Figure 1), using vegetation resurveys spanning intervals of 12 to 78 years. Temporal trends in local species richness and drivers of change are known to vary among these habitats, with climate warming increasing local species richness on summits (15, 16), eutrophication and changes in management reducing richness in grasslands (17, 18), and a combination of these drivers leading to both increases and decreases in richness in forests (13, 19–21). We hypothesize that, regardless of the richness trend in a habitat, smaller-ranged species are consistently replaced by larger-ranged species, as environmental changes (such as increasing temperatures, land-use change and eutrophication) alter ecological selection processes in favor of widespread species; species that are expected to be more resilient, more nutrient-demanding and better dispersed (13, 22). Our study explores whether the temporal turnover of species of vascular plants is systematic, and whether it acts to homogenize vegetation between habitats.

Results and Discussion

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

Across habitats, plant species with larger ranges gained ground. The success of large-ranged species could be due to previously limiting resources (e.g., nutrients) becoming more available as a result of global changes such as eutrophication and warming (23, 24). A greater availability of limiting resources allows less specialized species to colonize, where larger-ranged species may be more likely to colonize simply because they disperse from more sites. Larger-ranged species may also be more likely to persist because they naturally face a larger gradient in environmental conditions and may thus exhibit a greater niche breadth and phenotypic plasticity, making them more resilient to global changes (10, 22, 25). Furthermore, global changes may even favor large-ranged species, as they tend to be species with resource-acquisitive strategies and might therefore benefit more from an increase in resources (12, 13, 22). We found support for this hypothesis in our data; species with larger ranges were associated with higher nutrient demands (Figure 4a) and community weighted means of species niche positions for nutrients indicated community shifts towards more nutrient-demanding species (Figure 4b, see Methods), in accordance with other studies in these habitats (summits: (26), forests: (19) and grasslands: (18)). These findings suggest that a higher prevalence of larger-ranged species, often also more resource-acquisitive species, is likely to exert increased biotic pressure on extant species.

In contrast to large-ranged species, small-ranged species tend to be adapted to lower nutrient availability (Figure 4) and thus are likely to grow more slowly (27), presenting a particular risk of competitive exclusion by faster growing species. The loss of small-ranged species could therefore be a result of the increase in less specialized, more competitive, larger-ranged species (i.e. biotic filtering). Furthermore, small-ranged species tend to have adaptations to the stresses specific to their habitat and therefore possibly a lower tolerance to new types of stress, such as stoichiometric imbalances in resource supply from eutrophication (28). Thus, the decline in small-ranged species could also be due to direct effects of environmental change (i.e. abiotic filtering). Importantly, we can largely exclude the potential explanation that the higher loss probability of small-ranged species is due only to stochastic, demographic effects (Table S2, see Methods). Also, if small-ranged species were simply more prone to demographic fluctuations and therefore had a more variable presence, we would expect comparable range sizes of species lost and gained, which we do not see in the data (Figure 3c and d). Thus, the preferential loss of small-ranged species is likely due not only to demographic stochasticity, but also to aspects of species niche that confer a higher vulnerability to both abiotic and biotic pressures.

Despite the congruence across habitats of small-ranged species being replaced by large-ranged species, our results also indicate differences in the effect of range size on temporal species turnover between habitats. On summits, the effect of range size on species loss probability was weakest and not clearly different from zero (Figure 3a). Moreover, species gained on summits had larger ranges than both persisting and lost species, whereas in forests and grasslands the main distinction was that species lost had smaller ranges than both persisting and gained species (Figure 3c and Table S4). In addition, on summits, species gains dominated and species losses were less important for driving turnover compared with forests and grasslands (Figure 2a and b). These results suggest that the directional turnover on summits in relation to species range size could be mainly due to species differences in dispersal and colonization ability. On summits, warming may allow the colonization of species from lower elevations, which tend to have larger ranges (Fig. S5), while extant species may persist and escape changes in abiotic and biotic filters due to a high variation of micro-habitats (29, 30) and a still sparse or less tall-growing vegetation (31, 32). In forests and grasslands, the vegetation is typically denser than on summits. Environmental changes, such as eutrophication or declines in traditional land use, are thus likely to lead, in addition to abiotic changes, to higher biotic pressure (33, 34). We hypothesize that a greater relevance of biotic filtering in forests and grasslands could contribute to the more directional loss of small-ranged species in these habitats (Figure 3). Although any cross-habitat comparison is limited due to inherent differences between habitats, we can rule out that differences in the relationship of range size and loss probability simply arise from evident differences in sampling methods among study sites. The number of plots, plot size, site area and time span between surveys did not change the effect of range size on the probability of loss (see Methods and Table S5). Our results thus support the potential role of indirect, biotic effects of global change in understanding the preferential loss of small-ranged species.

Altogether, our results suggest that temporal species turnover has a predictable component based on species range size. Regardless of whether site-level trends show increases or decreases in species richness, larger-ranged species replaced smaller-ranged species. This has at least two implications. First, as sites gain species that are already widespread and lose small-ranged species, cumulatively this may lead to shifts from characteristic, often rare vegetation types to more widespread vegetation types – a form of biotic homogenization (14). Indeed, we found that an average pair of study sites became more similar in species composition and, moreover, that the total species pools of the three habitats became more similar over time (Fig. S6a and b). Second, small-ranged species may be doubly at risk of extinction (35), both because of purely geographical reasons, as they by definition occupy fewer sites, and because they can also be more vulnerable to being lost within each site, as we have shown here. While the patterns found in our study suggest that the loss of small-ranged species within sites is partially explained by species niches, it remains a future challenge to disentangle how much of this loss is driven by indirect effects due to altered competitive interactions (i.e. biotic filtering) versus direct effects due to environmental changes (i.e. abiotic filtering) in different habitats. Our study demonstrates that even in seminatural habitats, biodiversity is systematically changing and that this change can be predicted by the geographic range size of species. Thus, our results inform predictions of how plant communities will respond to accelerating global change and the prioritization of conservation efforts towards the species that are more likely to be lost. Insights on the relative importance of biotic versus abiotic filtering will be essential when prioritizing measures to reverse the declines of the most vulnerable species in the Anthropocene.

Materials and 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, (36)), deciduous and coniferous forests understories by 68 sites from the forestREplot database (forestreplot.ugent.be, (37)) and lowland grasslands by 21 sites from the GRACE database (18) (Figure 1 and Table S1). 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 (18, 36, 37)). The median time spans between surveys were 14, 42 and 34 years for summits, forests and grasslands, respectively (Fig. S7a). In forest and grassland surveys, the median number of plots per site was 43 and 36, and the median size of plots was 400 m^2 and 25 m^2, respectively (Fig. S8a 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 at figshare.com/s/b37f6167b13ad5da9e9c).

Range size. We estimated species range sizes as area of occupancy (AOO) (6) using all point occurrence records of the species in GBIF (gbif.org, May 2020; (38)). After excluding incomplete, impossible and unlikely coordinates (e.g., country centroids) (39), 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 km^2 (40), 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. 1.1x10^6 km^2), the species with the smallest AOO were the highly endemic *Draba dolomitica* (*c.* 11 km^2) on summits, *Galium abaujense* (*c.* 21 km^2 ;endemic to the Carpathians) in forests, and *Pentanema germanicum* (*c.* 503 km^2; critically endangered in Germany and Austria (41)) in grasslands (Fig. S9). For plant species in Europe, range sizes calculated from GBIF correlate strongly with expert drawn range maps but are available for many more species (13). 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 (6).

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 (42, 43).

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 (44, 45). We account for this bias by adjusting for species baseline abundances, which is strongly correlated with any such bias (46), as explained below.

Analysis. The brms package (47) 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 (Fig. S1).

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 (Fig. S2). 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 (13). 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 Table S2 for model R syntax, sample settings and convergence diagnostics). The resulting model in mathematical form is:

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

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 (Table S3). 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:

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

, 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 Table S3 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 Table S4 for model R syntax, sample settings and convergence diagnostics).

Range size and nutrient demand. We used Ellenberg's indicator values for nutrient (N-number) to approximate species niche position for nutrients (27, 48, 49). 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, e.g., *Melampyrum pratense* ssp. *paludosum* has an N-number of 1, while *Melampyrum pratense* has an N-number of 2), 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 CMW-N, by predicting CWM-N (c_i) with survey period ($\beta_{survey[i]}$), including study site as a group-level effect ($\alpha_{study[i]}$) to indicate pairs of observations:

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

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 (Fig. S4).

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:

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

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):

$$\begin{aligned} m_i &\sim Normal(\mu_i, \sigma) \\ \mu_i &= \alpha + \beta_l * l_i \end{aligned}$$

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 (Fig. S7 and S8). Moreover, time intervals between surveys varied among habitats, with the shortest intersurvey periods on summits (Table S1). 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 (Fig. S10)):

$$\begin{aligned} e_i &\sim Binomial(1, p_i) \\ logit(p_i) &= \alpha_{study[i]} + \gamma_{species[i]} \\ &+\beta_{f,study[i]} * f_i + \beta_r * r_i + \beta_{fr} * f_i * r_i \\ &+\beta_{nr} * n_i * r_i + \beta_{sr} * s_i * r_i + \beta_{ar} * a_i * r_i + \beta_{tr} * t_i * r_i \end{aligned}$$

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 ($\beta_{survey[i]}$), using the model:

$$\begin{aligned} b_i &\sim Normal(\mu_i, \sigma) \\ \mu_i &= \alpha + \beta_{survey[i]} \end{aligned}$$

Finally, we also quantified the multiple site Sørensen dissimilarity index (50) between the grassland, forest and summit species pool for both survey periods.

Data availability

R code for all analyses and data visualization, and complete species list with species range sizes and GBIF urls (Data Table 1) are available on figshare at https://figshare.com/s/b37f6167b13ad5da9e9c. Species composition data for grasslands is available from published literature compiled in (18); for forest and alpine summits these data are available upon request from forestreplot.ugent.be and gloria.ac.at, respectively.

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Figures

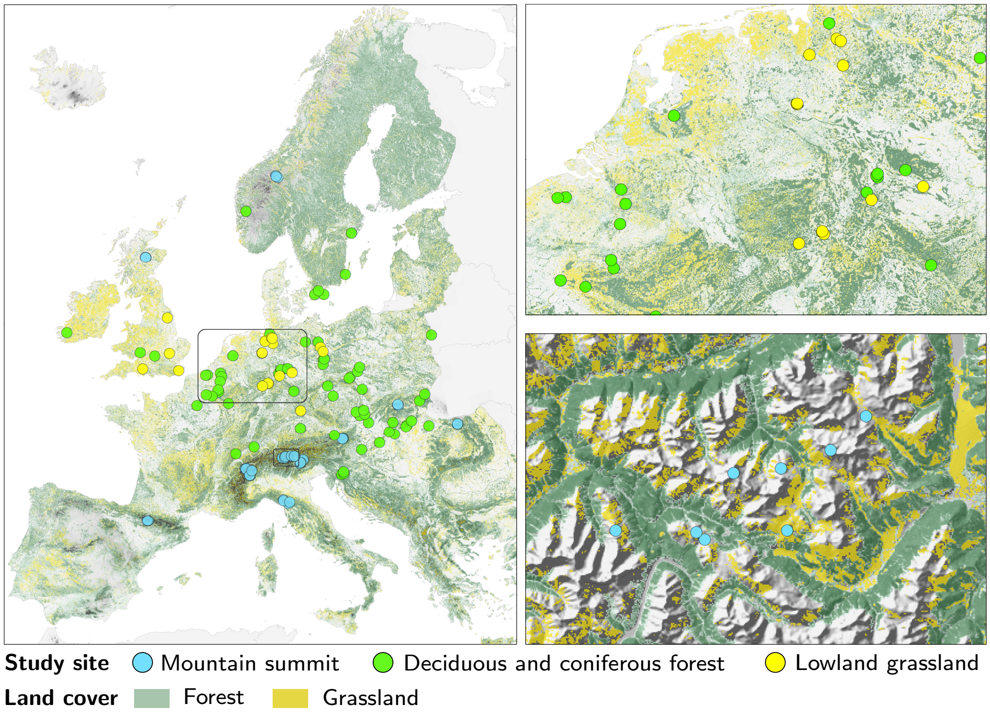

Figure 1. Our analysis spans 141 resurvey study sites. Resurveys are from three habitats in Europe: mountain summits = 52 sites (blue), deciduous and coniferous forests = 68 sites (green), and lowland grasslands = 21 sites (yellow). CORINE forest cover (green) and grassland cover (yellow) in Europe are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

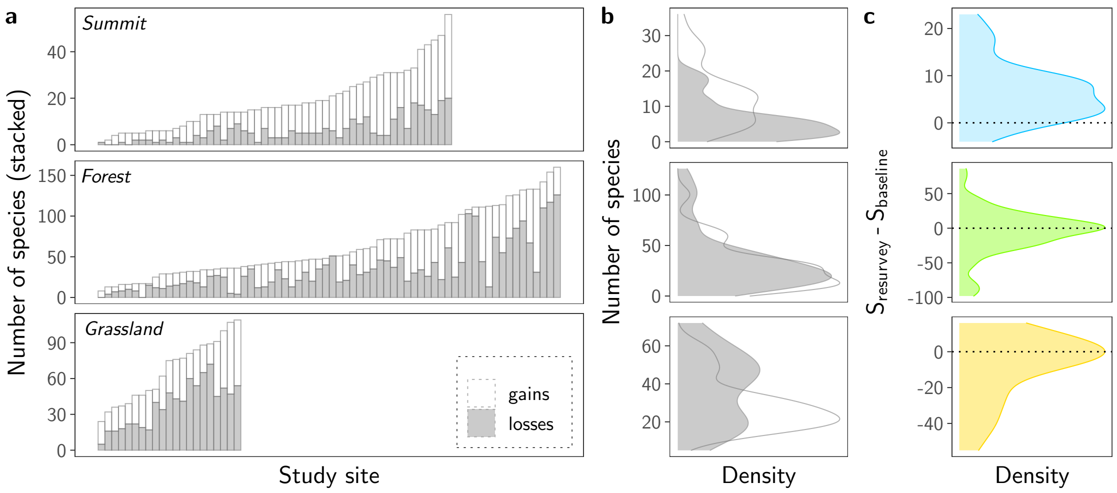

Figure 2. Species losses and gains vary across habitats. **a,** Species gains (white) and losses (grey) at each study site (numbers stacked, each bar represents a study site). **b,** Relative frequency (density) of the number of species lost and gained across sites. **c,** Density across study sites 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.

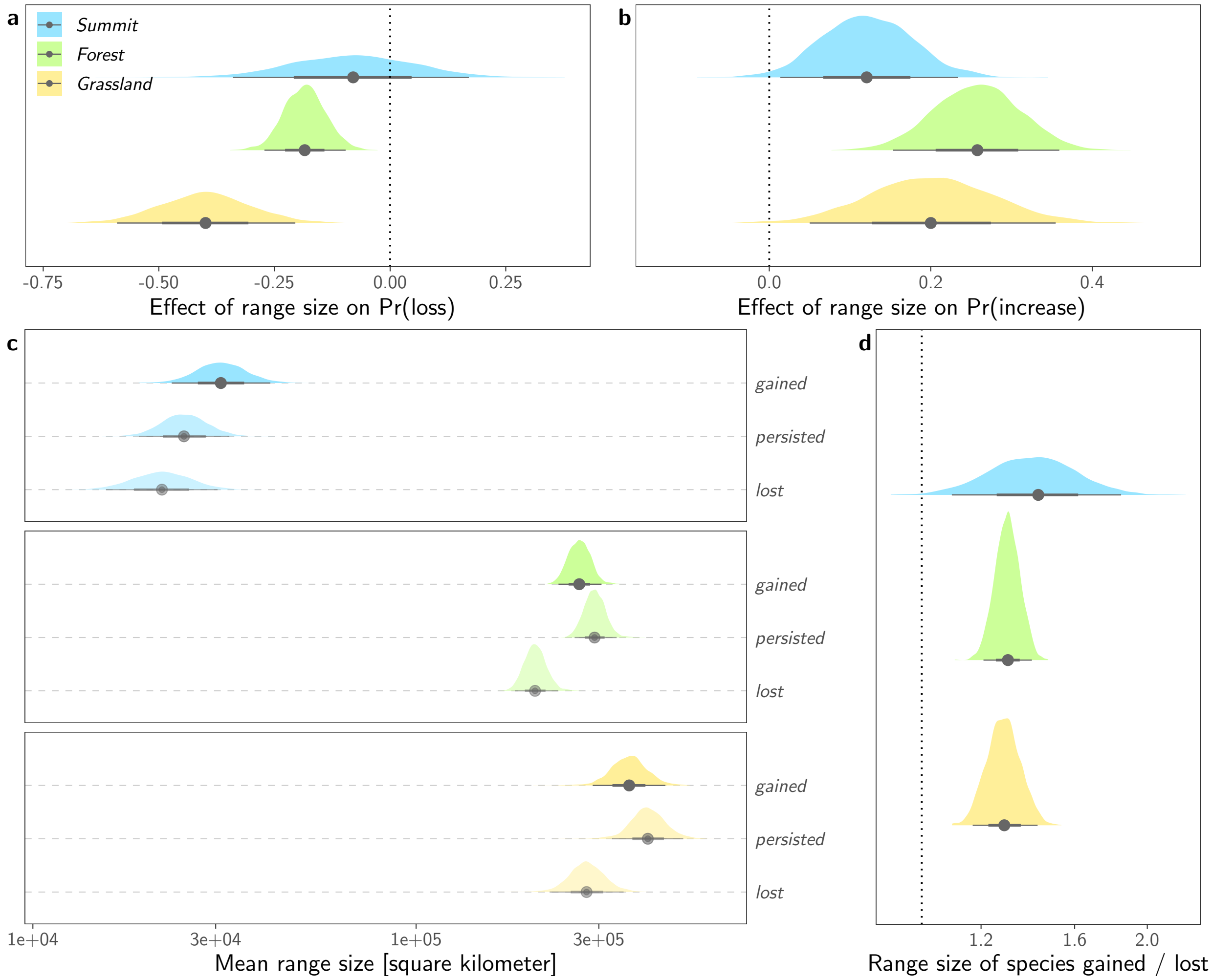

Figure 3. Consistent replacement of small- by large-ranged species across habitats. Posterior distribution of the effect of range size on **a,** the probability (Pr) of a species being lost at a study site and **b,** the probability (Pr) of a persisting species increasing in occupancy at a study site, 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 log10-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.

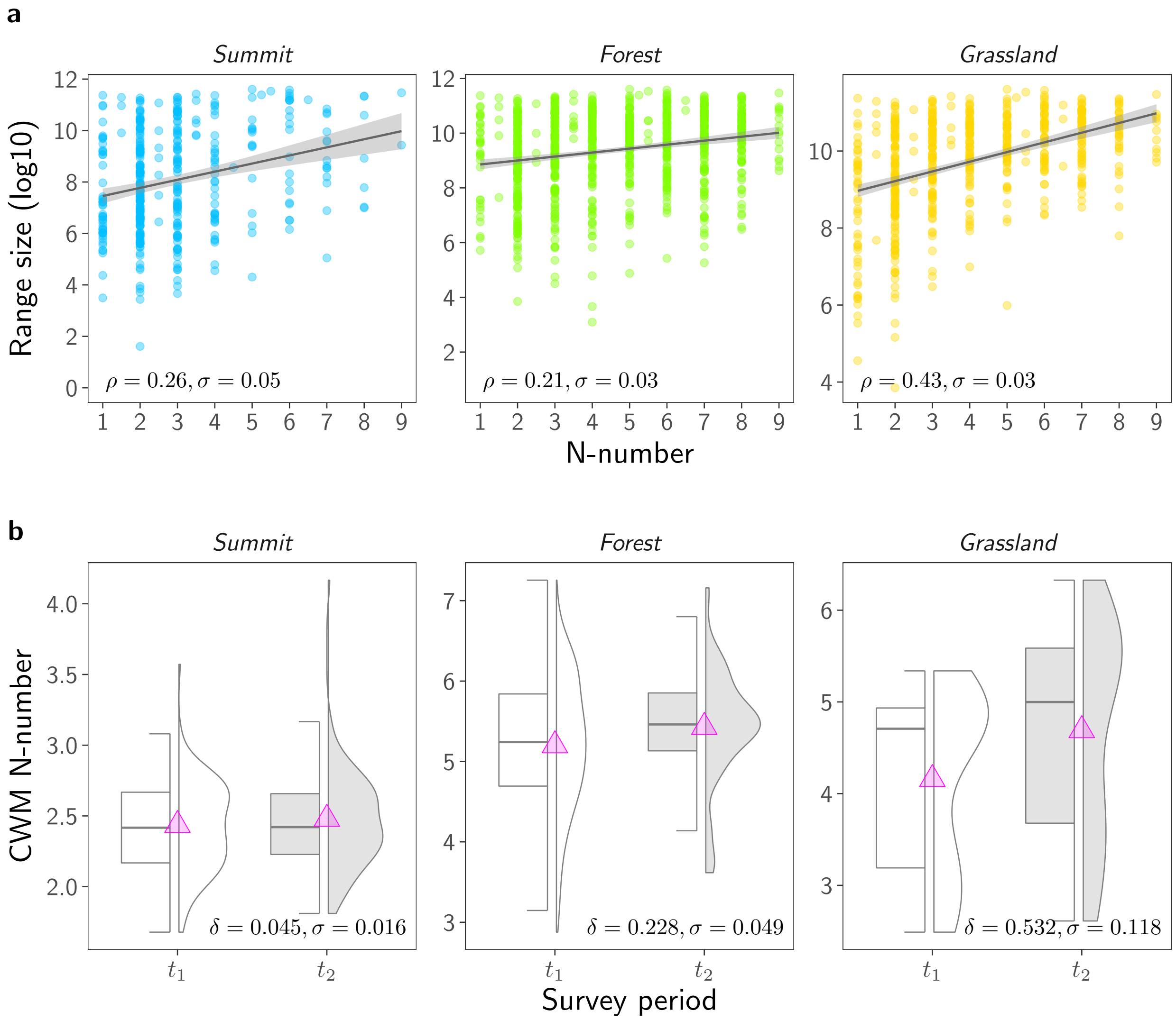

Figure 4. Species with larger ranges tend to have higher nutrient demands and communities shift towards species with higher nutrient demands over time. a, Relationship between species range size and Ellenberg indicator values for nutrients (N-numbers) across species in each habitat. Line and transparent ribbon represent the mean regression line and 95% credible interval, ρ is the estimated correlation coefficient, σ is the standard deviation of ρ. **b,** Boxplot and density plot of the community weighted mean (CWM) niche position for nutrients (N-number) 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.

Supplementary Materials for

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

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Supplementary Figures

Supplementary Tables

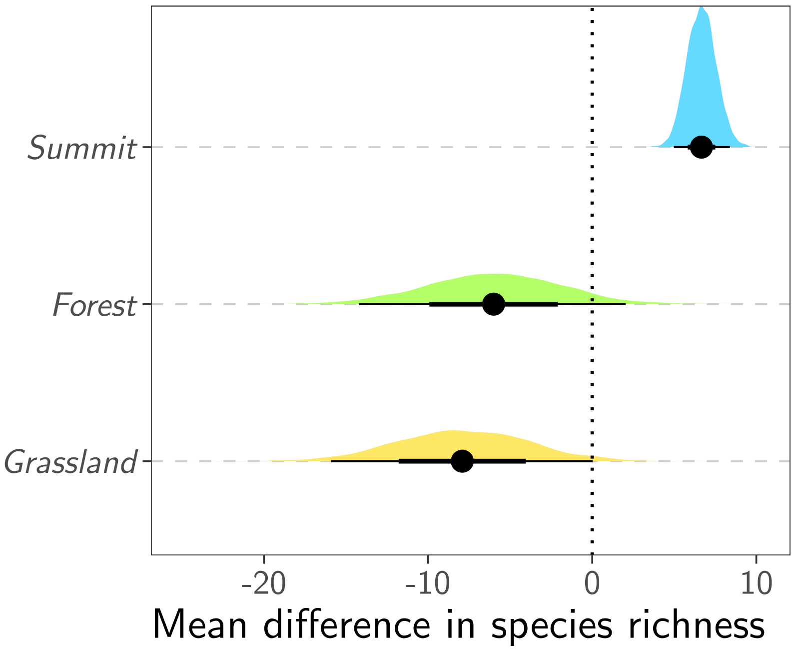

Fig. S1. Temporal trends in species richness vary across habitats. Posterior distribution of the mean difference in species richness at the study-site level between the resurvey and baseline survey. Points represent medians, lines represent the 66% and 95% confidence interval. The mean richness change 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.

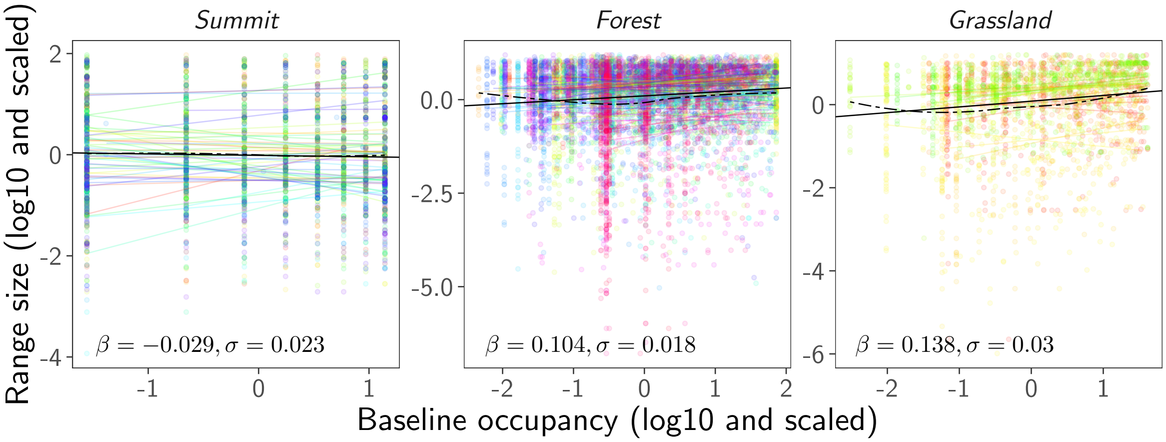

Fig. S2. Relationship between species range size and baseline site-occupancy accounting for the structure of our data. Colors present study sites, transparent dots present species, transparent lines represent the relationship between range size and site occupancy within a single study site, black straight 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.

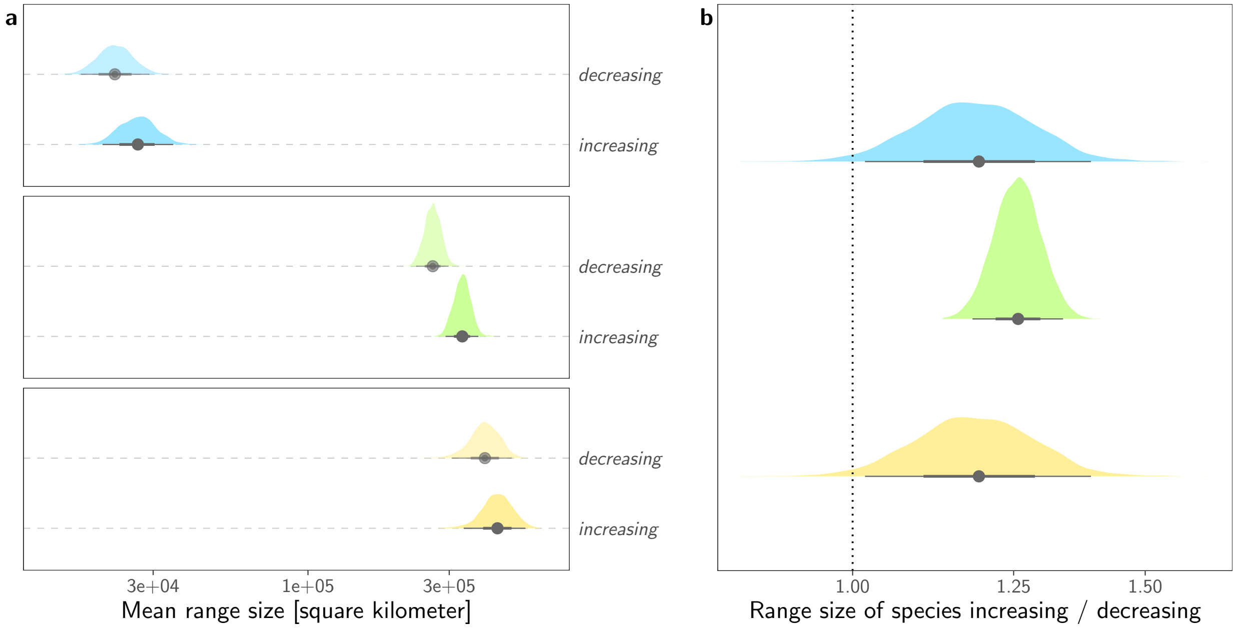

Fig. S3. Persisting species increasing in occupancy have larger ranges on average than species decreasing. a, Posterior distribution of the mean range size of species increasing and decreasing in occupancy at the study site over time. **b,** Comparison between the mean range sizes of species increasing 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.

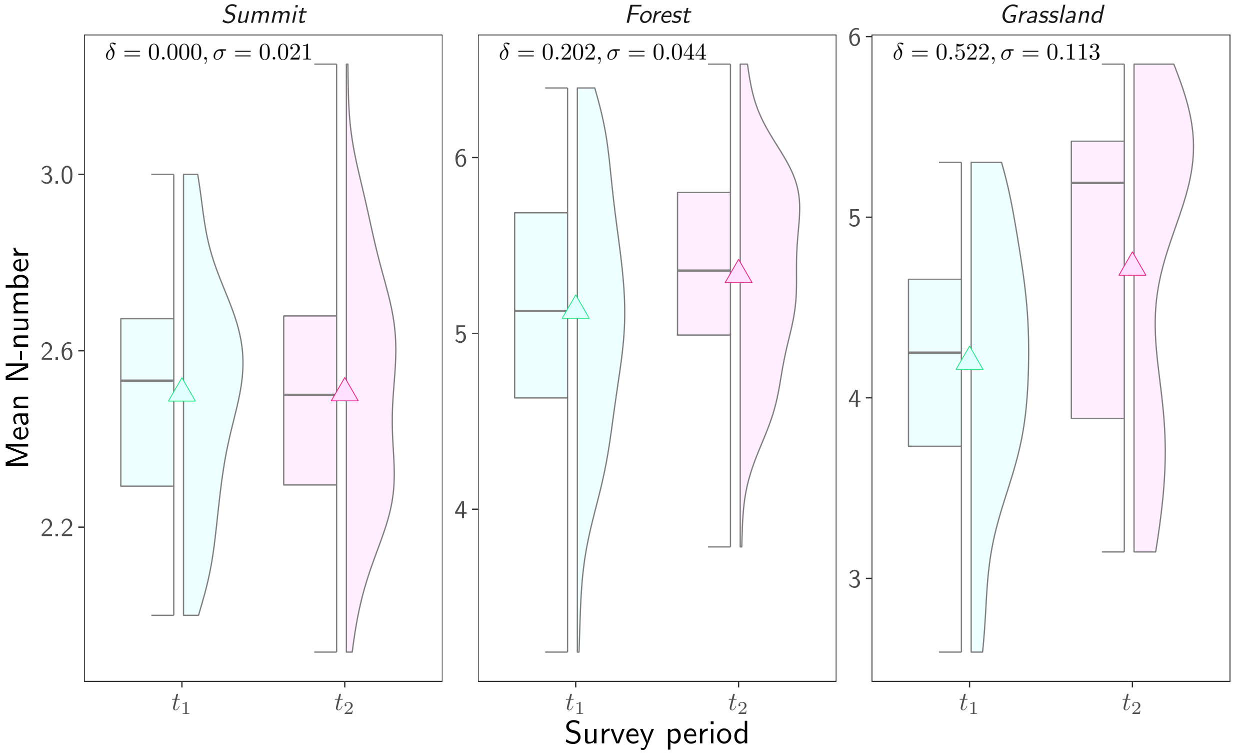

Fig. S4. Temporal change of the mean N-number. Boxplot and density plot of the unweighted mean N-number across species at the baseline survey (t_1) and resurvey (t_2). The comparison of weighted and unweighted means (Figure 4 vs Fig. S4) shows that in forests and grasslands, the shift towards more nutrient-demanding species is largely due to changes in species composition, while on summits the shift is due to changes in species occupancy. δ is the mean (pairwise) difference, σ is the standard deviation of δ.

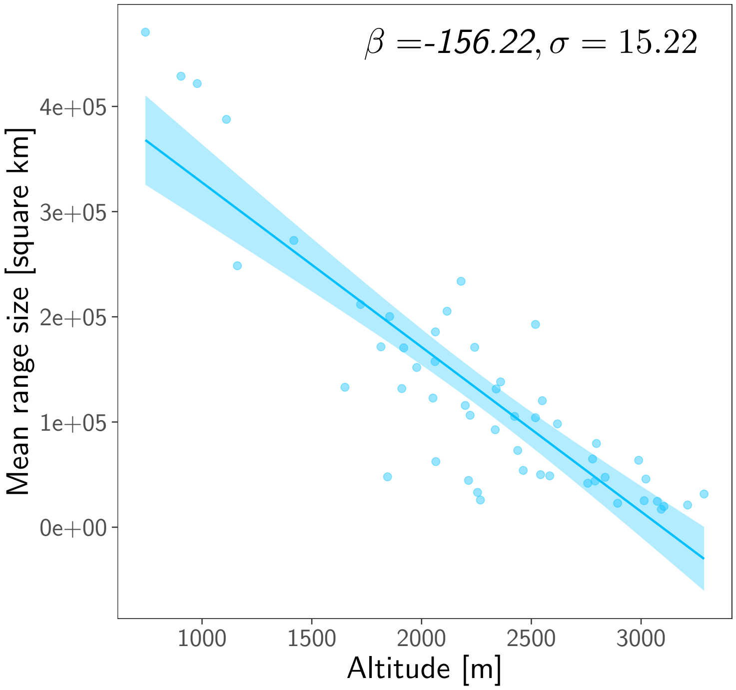

Fig. S5. Species from lower elevations tend to have larger range sizes. Relationship between species' mean range size and elevation. Range size is measured as area of occupancy (AOO; see Methods) and averaged across all species occurring at the baseline survey on a given mountain summit. Elevations of 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.

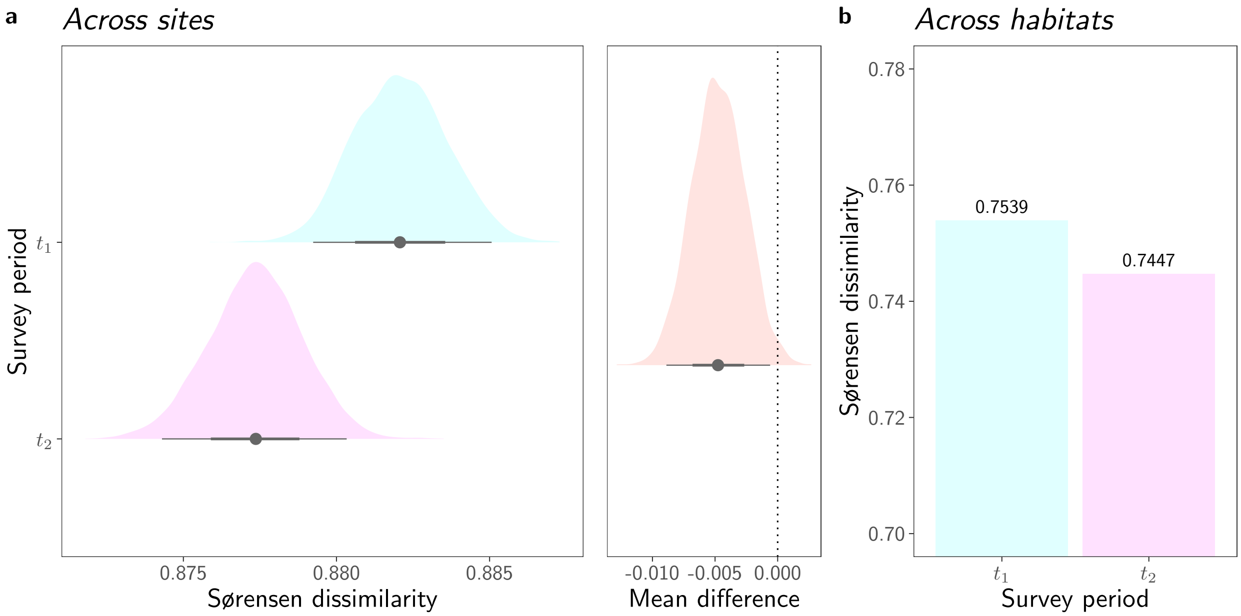

Fig. S6. Loss of beta-diversity over time. **a,** Posterior distribution of the mean beta-diversity of study sites at the baseline survey (t_1) and resurvey (t_2), calculated as Sørensen mean pair-wise dissimilarity between all possible pairs of the 141 sites in our study. **b,** Beta-diversity of the 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.

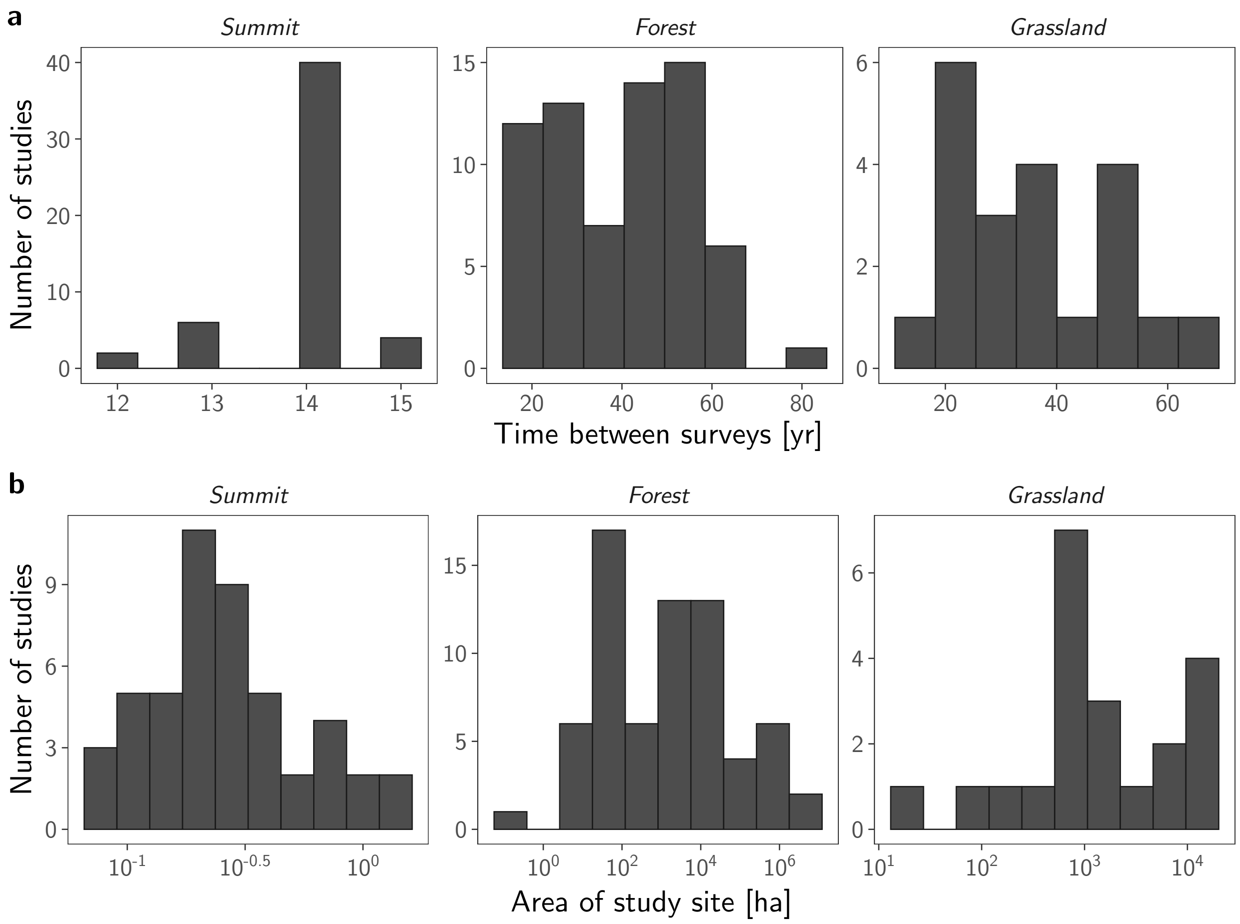

Fig. S7. Histogram of time span between surveys across study sites and site areas. a, Median time spans were 14, 42 and 34 years on mountain summits, forests and grasslands, respectively. **b,** Median site areas were 0.25, 1,700 and 1,000 ha on mountain summits, forests and grasslands, respectively. X-axis in **b** is on the log10-scale.

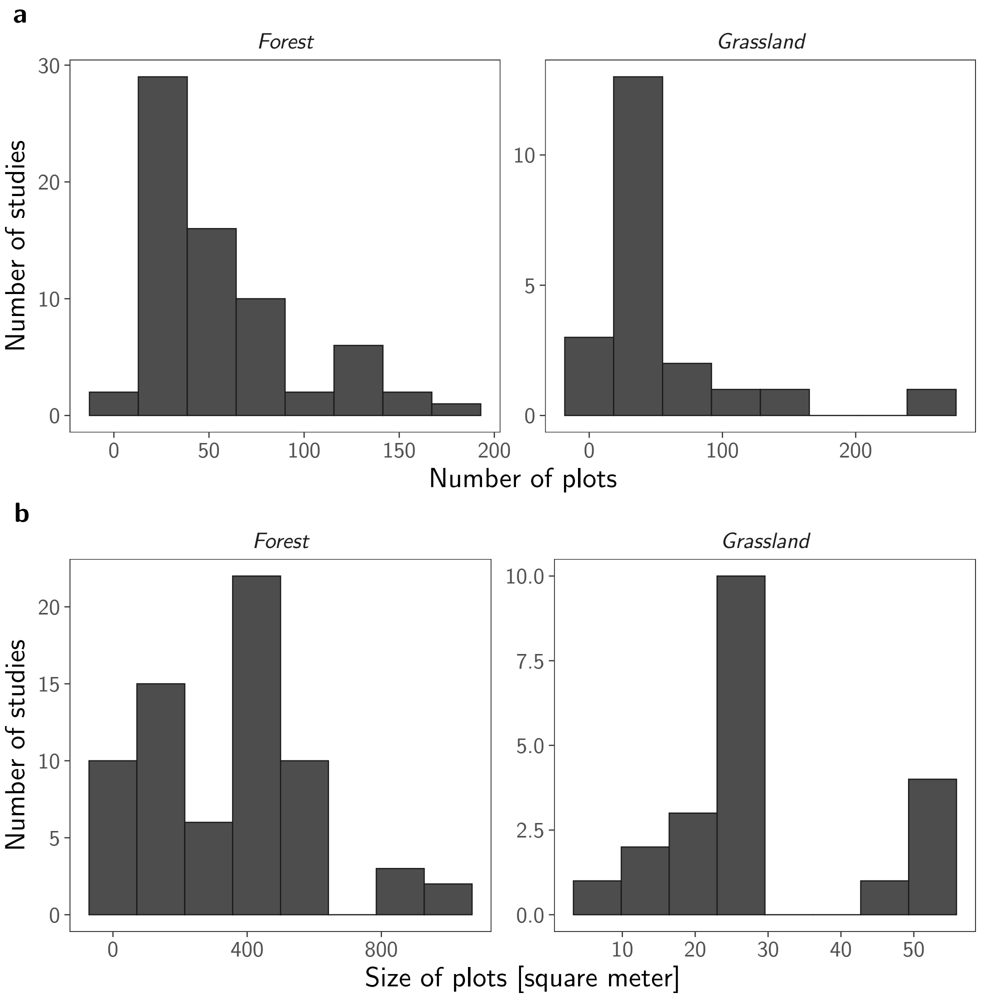

Fig. S8. Histogram of plot number and size. Forest and grasslands studies had a median of 43 and 36 plots with a size of 400 m^2 and 25 m^2, respectively. Studies on mountain summits were always divided into 8 sections that together covered the entire lateral area from the highest summit point to 10 m below this point. In total, our study counts 5,221 plots/sections.

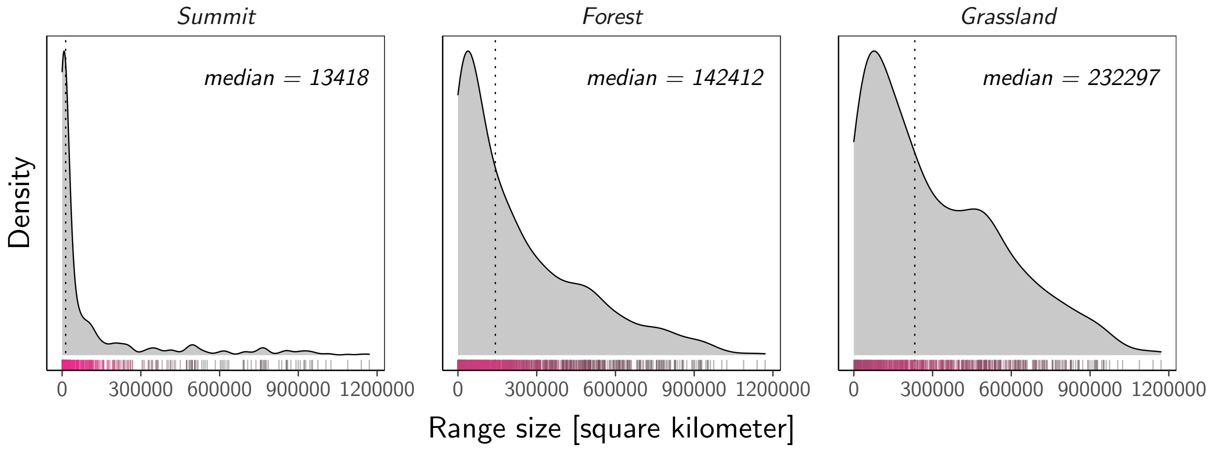

Fig. S9. Range size frequency distribution. Area of occupancy estimates of the species found in a given habitat (summit = 641 species, forest = 1,148 species, grassland = 692 species). Dotted vertical line represents the median range size. Rug at the figure bottom represents the precise range sizes of species and is coloured to match the density of ticks.

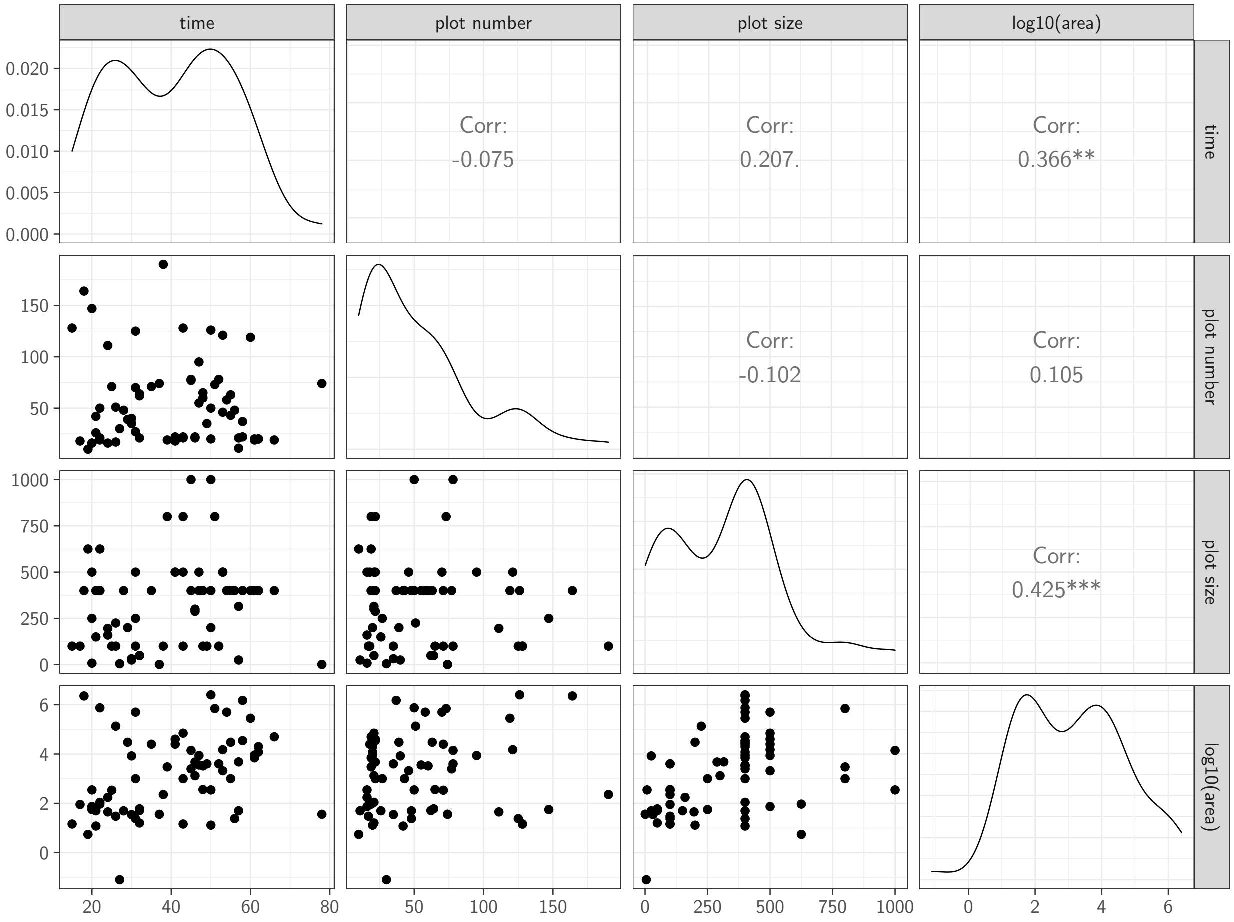

Fig. S10. Correlations between sampling characters of study sites in forests. Sampling characters are time interval between surveys, number of plots per site, size of plots and site area (log10-transformed). Since $\rho < 0.7$ for all correlations, each character was included in the model testing whether 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)
Mountain summits					
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	Ragnaroek, 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 Tatra	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	Vel'ká 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
Deciduous and coniferous forests					
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	Děvín Wood	48.87	16.63	1953	2003
Czech Republic	Hodonínská Dúbrava	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	Őrség	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	Streeseebecken	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: _logit(p) ∼ scale(log10(range)) * scale(log10(occupancy)) + (1 + scale(log10(occupancy)) | site) + (1 | 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
	Range size : occupancy	0.12	0.06	0.01	0.23	1.00	3844	3188
Grassland	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: $log10(range) \sim occtrend + (1 \mid study)$
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
Summit	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
Forest	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
Grassland	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: $logit(p) \sim scale(log10(range)) + scale(log10(occupancy)) + (1 + scale(log10(occupancy)) \mid site) + (1 \mid speciesKey)$
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
Summit	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
Forest	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
Grassland	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: $log10(range) \sim trajectory + (1 \mid study)$
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) ∼scale(log10(range)) * scale(log10(occupancy))*
*+ scale(log10(range)) * scale(log10(area))*
*+ scale(log10(range)) * scale(plot size)*
*+ scale(log10(range)) * scale(plot number)*
*+ scale(log10(range)) * scale(time interval)*
+ (1 + scale(log10(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**