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LETTER

Directional turnover towards larger-ranged plants over time and across habitats

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[Corrections added on 24 December 2021, after first online publication: ORCID has been added to the author Hans Van Calster, affiliation 53 has been added to the author Pavel Dan Turtureanu, and the repeated affiliation "Centre for Systems Biology, Biodiversity, and Bioresources (3B), Babeş-Bolyai University, Cluj-Napoca, Romania" has been deleted and the remaining affiliations have been reordered in this version.]

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Abstract

Species turnover is ubiquitous. However, it remains unknown whether certain types of species are consistently gained or lost across different habitats. Here, we analysed the trajectories of 1827 plant species over time intervals of up to 78 years at 141 sites across mountain summits, forests, and lowland grasslands in Europe. We found, albeit with relatively small effect sizes, displacements of smaller- by larger-ranged species across habitats. Communities shifted in parallel towards more nutrient-demanding species, with species from nutrient-rich habitats having larger ranges. Because these species are typically strong competitors, declines of smaller-ranged species could reflect not only abiotic drivers of global change, but also biotic pressure from increased competition. The ubiquitous component of turnover based on species range size we found here may partially reconcile findings of no net loss in local diversity with global species loss, and link community-scale turnover to macroecological processes such as biotic homogenisation.

KEYWORDS
alpine, biodiversity change, forest, forestREplot, GLORIA, grassland, homogenization, resurvey, winner and loser species

INTRODUCTION

During the Anthropocene, the rate of plant extinctions is estimated to be up to 500 times the background rate, with nearly 600 plant extinctions since Linnaeus *Species Plantarum* in 1758 (Humphreys et al., 2019). These extinctions represent 0.2% of existing plant diversity, but typically plants have longer extinction lag times than other taxa (Cronk, 2016), and recent studies estimate that approximately 40% of existing plant diversity is at risk of global extinction (Lughadha et al., 2020). This global pattern contrasts with long-term studies of changes in local plant diversity, which show no systematic evidence of decline in local diversity, but variable trends with as many communities increasing in species richness as decreasing (Blowes et al., 2019; Daskalova et al., 2020; Dornelas et al., 2014; Vellend et al., 2017). While the assertion of no net loss of local diversity remains controversial (Gonzalez et al., 2016; Isbell et al., 2019; Murphy & Romanuk, 2014; Newbold et al., 2015), the high variability in the direction and magnitude of diversity trends at local scales raises questions about how this can be reconciled with biodiversity loss at the global scale (Dornelas et al., 2019). This biodiversity conservation paradox (Vellend, 2017) may be partially resolved by considering directional changes in community composition (McKinney & Lockwood, 1999; Sax & Gaines, 2003). Compositional change over time could lead to biotic homogenisation, where widespread local losses of species with small geographic ranges could scale to global losses while local gains of widely distributed species offset local losses of rare species (Newbold et al., 2018; Staude et al., 2020). However, whether such temporal turnover of species is ubiquitous across habitats or only occurring in specific contexts, remains an open question.

There are several possible explanations for a linkage between species turnover and range size. From a stochastic perspective, range size and mean local abundance are expected to correlate positively across taxa and spatial scales (Gaston & Blackburn, 1996; Gaston et al., 2000). According to this relationship, which is considered one of the few general laws in ecology (Pimm et al., 2014), species with small ranges have lower local abundances and are therefore more susceptible to demographic stochastic effects. However, recent analyses using over 700,000 vegetation plots across Europe along with curated species range maps, found no evidence of a range size-abundance relationship for plants in Europe (Sporbert et al., 2020), questioning whether for plants any such relationship exists. Another stochastic process that could lead to greater persistence of species with large ranges is rooted in meta-community dynamics (Leibold et al., 2004). Species with large ranges are expected to have more source habitats from which to disperse and, via the 'rescue effect', uphold populations in sink habitats (Hanski, 1991). However, it remains unclear whether lower recolonisation rates

alone could lead to preferential declines in small-ranged species, especially if these are locally abundant (Rabinowitz, 1986; Sporbert et al., 2020; Thompson et al., 1998). Overall, there is mixed evidence for the hypothesis that directional turnover in relation to species range size might be driven by stochastic processes alone.

From a niche perspective, small-ranged species are hypothesised to have a smaller niche breadth (Brown, 1984) and thus a lower tolerance to anthropogenic global change. For plants, however, measurement of niche breadth independent of spatial extent is a major challenge and tests of this hypothesis remain scarce. For example species climatic niche breadth can be directly related to range size, simply because larger areas encompass greater environmental variation (Köckemann et al., 2009). Spatial autocorrelation can therefore lead to artefactual correlations, bringing into question the causal relationship between niche breadth and range size (Moore et al., 2018). When using null-models to account for spatial extent, or estimating niche breadth from species co-occurrence data, there seems to be less support for the niche-breadth hypothesis (Kambach et al., 2019; Vela Diaz et al., 2020). Recent analyses suggest that instead of niche breadth, niche position is a much stronger predictor of a species' geographic range size (Vela Diaz et al., 2020). Humans have substantially transformed Earth's terrestrial surface, creating arable, more productive habitats, which has likely benefitted range expansions of species associated with nutrient-rich habitats and anthropogenic dispersal (Fristoe et al., 2021). Thus, the niche position of species along nutrient gradients may covary positively with range size, with large-ranged species positioned at the more productive end of the gradient (Sonkoly et al., 2017). If global change increases the availability of limiting resources, such as soil nutrients, this could favour species with larger ranges (Staude et al., 2020). Gains of such species could, in addition to direct abiotic effects, reduce the persistence of small-ranged species via increased competition. Taken together, preferential declines of small- over large-ranged species may be driven in part not only by stochastic but also by deterministic processes based on species niche breadth and position.

Community assembly and environmental drivers of change vary substantially among habitats. Here, we study biodiversity change in relation to species range size across three contrasting habitats—mountain summits, deciduous and coniferous forests and lowland grasslands (Figure 1). Previous studies have shown that in grasslands eutrophication is decreasing species numbers (Diekmann et al., 2019; Stevens et al., 2004), with competition for light being an important mechanism for species exclusion (Hautier et al., 2009). On summits, climate warming leads to increasing species numbers (Pauli et al., 2012; Steinbauer et al., 2018), with sparse vegetation limiting the importance of competition despite eutrophication (Rumpf et al., 2018). In forests, many plant species are adapted to low-light conditions, and a range of drivers, including changes in historical forest management regimes, eutrophication, climate warming and widespread increases in large herbivores, leads to both increases and decreases in species numbers (Bernes et al., 2018; Bernhardt-Römermann et al., 2015; De Frenne et al., 2013; Staude et al., 2020). In terms of compositional change, anthropogenic global change typically favours

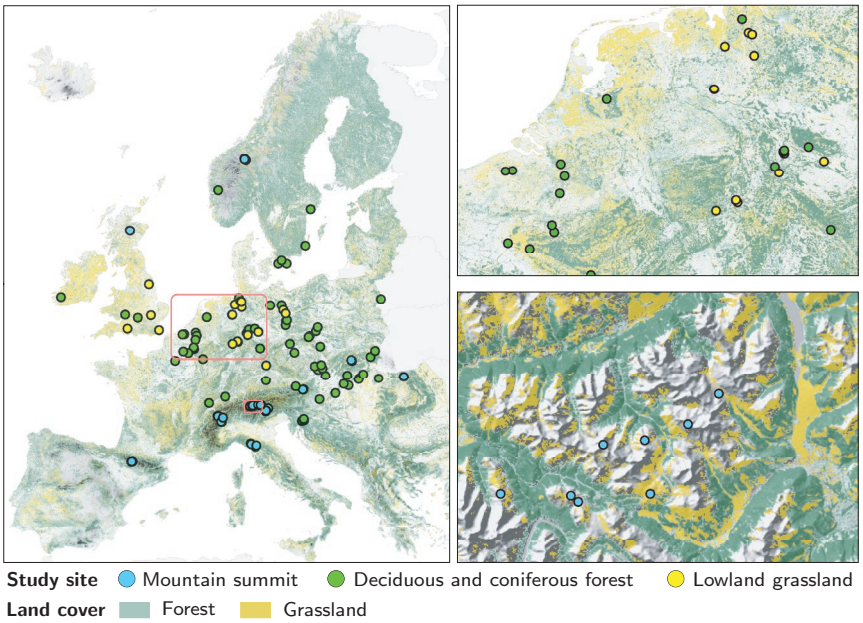

FIGURE 1 Our analysis spans 141 resurvey study sites. Resurveys are from three habitats in Europe: mountain summits = 52 sites (blue), deciduous and coniferous forests = 68 sites (green) and lowland grasslands = 21 sites (yellow). CORINE forest cover (green) and grassland cover (yellow) in Europe are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

nutrient-demanding species in these habitats (summits: Rumpf et al., 2018, forests: Bernhardt-Römermann et al., 2015 and grasslands: Diekmann et al., 2019), while natural succession shifts communities away from these species (Odum, 1969). Thus, given an association between range size and species niche position for nutrients, we might expect consistencies among habitats with respect to turnover in relation to range size. Global change might favour species with larger ranges, while natural succession could lead to increases in species with smaller ranges.

Here, we coalesced vegetation resurveys for 141 sites (totalling 5221 resurveyed plots) across summits, forests and grasslands in Europe to quantify species gains and losses, and test whether range size explains species losses and increases. We account for stochastic demographic effects to test for the role of species niche. We also test the association between range size and species niche position for nutrients and whether communities have shifted towards more or less nutrient demanding species over time. We hypothesised that drivers of change, albeit different, alter ecological selection processes in favour of widespread species, whilst small-ranged species are lost preferentially. This hypothesis is based on the following three expectations. First, we expect preferential gains in larger-ranged species as these can disperse from more source habitats, and may also be dispersed more by humans (owing to an association with nutrient-rich habitats). Second, as global change drivers make limiting resources more available, either indirectly due to accelerated nutrient cycling from climate warming (Salazar et al., 2020), or directly due to aerial deposition of nitrogen (Bobbink et al., 2010), we expect that larger-ranged species might also be more likely to increase at sites. Third, we expect that declines in species with smaller ranges are not due solely to stochastic processes, but also reflect direct effects of environmental changes on the one hand, and increased competition due to the arrival of new competitors on the other. Our study tests for a ubiquitous component of species turnover in relation to species range size, and thus the prediction that directional changes in community composition could partially resolve the biodiversity conservation paradox.

MATERIALS AND METHODS

Databases

We synthesised 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, Pauli et al., 2015), deciduous and coniferous forests understories by 68 sites from the forestREplot database (forestreplot.ugent.be, Verheyen et al., 2016) and lowland grasslands by 21 sites from the GRACE database (Diekmann et al., 2019; 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, semi-natural sensu Peterken, 1996 and Peeters et al., 2014, respectively) at two points in time (baseline survey and resurvey) with the same sampling effort (i.e. same number and size of plots), and no major changes in land use before and between surveys (further details available in Diekmann et al., 2019; Pauli et al., 2015; Verheyen et al., 2016). The median time spans between surveys were 14, 42 and 34 years for summits, forests and grasslands respectively (Figure S1a). In forest and grassland surveys, the median number of plots per site was 43 and 36, and the median size of plots was 400 and 25 m^2 respectively (Figure S2a,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. The median summit area was 0.25 ha. In forests and grasslands, the median study area was 1700 and 1000 ha respectively (Figure S1b).

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). Harmonisation 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 1827 accepted vascular plant species.

Range size

We estimated species range sizes as area of occupancy (AOO) (Gaston & Fuller, 2009) using all available point occurrence records of the species in GBIF (gbif.org; 28 May, 2020). After excluding incomplete, impossible and unlikely coordinates (Chamberlain, 2020), 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 (Barnes et al., 2017), where the number of cells that a species occupies on this grid represents its AOO estimate. Range size is a static variable in our analysis. Although losses and gains of species result in range expansion and contraction, range size is largely constant on a relative scale over decadal time periods (Figure S3). The species with the largest AOO in all three habitats were *Achillea millefolium* and *Trifolium repens* (both with c. 1.2×10^6 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; Fischer et al., 2008) in grasslands (Figure S4). Owing to sampling biases and data gaps in GBIF, our AOO estimates are likely to underestimate absolute range sizes of species (Meyer et al., 2016). However, for plant species in Europe, GBIF-derived range sizes correlate strongly with expert-drawn range maps and may therefore provide good relative estimates of range size, while being available for many more species (Staude et al., 2020). Here, we also found strong correlations between GBIF-derived range sizes and expert-based range sizes from two published databases: Vangansbeke et al. (2021) and Kambach et al. (2019) (Figure S5). It is important to note, however, that ranges from such databases differ from AOO, in that they measure species extent of occurrence (EOO) and therefore include areas that are unoccupied by species. Thus, species with disjunct distributions, for example orchid species that occur throughout Europe but only in very fragmented, well-conserved habitat, can have a small AOO but a large EOO. AOO is therefore a markedly better representation of species population sizes and differences related to species niche than is EOO, and provides a general measure of species vulnerabilities to stochastic and directional threatening processes (Gaston & Fuller, 2009).

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 (i.e. the fraction of plots a species occupies at a site) has been shown to correlate strongly and positively with abundance at local to regional scales, that is a species with a high population size at a site does also occupy more plots at a site (Gaston et al., 2000; Wright, 1991).

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 (Futschik et al., 2020; Verheyen et al., 2018). We account for this bias by adjusting for species baseline abundances, which is strongly correlated with any such bias (Kopecký & Macek, 2015), as explained below. Site-level trajectories are independent from GBIF-derived range sizes in that site-level gains and losses in our data do not result in de facto large/small ranges.

Analysis

The brms package (Bürkner, 2017) in R was used for all statistical analyses. R code for all analyses and visualisation is available on Figshare (doi.org/10.6084/m9.figshare.12514172.v1). A brief overview of all analyses and their rationale is provided in the Supplementary Material. For all analyses, we use the 95% credible interval to determine statistical clarity (Dushoff et al., 2019).

Species gains and losses

Using species trajectories, we quantified the number of lost and gained species on the spatial scale of a study site. 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 the expected ratio between the number of species gained and the number of species lost for each habitat. We used a Poisson regression model with a log-link to predict the number of species (s_i) with the categorical variable 'gained/lost' (g_i) and included a group-level effect for study site ($\alpha_{study[i]}$) to indicate pairs of observations and test for differences in the number of gained versus lost species within sites, while accounting for differences between sites.

$$\begin{aligned} s_i &\sim \text{Poisson}\left(\lambda_i\right) \\ \log(\lambda_i) &= \alpha_{study[i]} + \beta_g * g_i \end{aligned}$$

We then calculated the posterior log-difference between the numbers of gained and lost species, which we back-transformed to a ratio of number of species gained/number of species lost in the original scale. We used the same model as above to calculate the ratio between species richness at the resurvey and baseline survey, with s_i now presenting species richness for each time period.

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 (i.e. the fraction of plots occupied at a site during the baseline

survey) 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—occupancy relationship in our data (see Methods below). 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 (Staude et al., 2020). 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 occupancy. To account for this possibility, we also included 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 allowed 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). Since many species occur at more than one study site and considering each species within a site as independent data points may lead to pseudoreplication, we also included species as an additional crossed varying effect ($\gamma_{species[i]}$). 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:

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

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 (Table S3). Finally, we also explored the influence of sampling methods (e.g. plot number, plot size, site area and survey interval) on the effect of range size on loss probability (methods and results can be found in Table S5). Since we only had data on the species that were newly gained at a study site but not on all those that tried to colonise, we were not able to directly calculate probabilities of gain in relation to range size.

Probability of increasing

We tested whether species with larger ranges were more likely to increase in occupancy at a site (i.e. the fraction of plots occupied at a site). 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 estimated the effect of species range size on the probability of increasing, 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_i) into a binary variable h_i, with $h_i = 1$ when occupancy increased ($d_i > 0$) and $h_i = 0$ when occupancy decreased or remained unchanged ($d_i \leq 0$). 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:

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

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

Mean range size per species trajectory

We estimated species mean range size for each trajectory. Note that the following model does not test the hypothesis that range size explains species trajectories, but intends to provide a summary statistic to aid interpretation of how much gained, lost and persisting species differ in range size (see Figure S11 for histograms and density curves of the raw range size data for lost and gained species). We predicted range size (log10-transformed) with species trajectory (t_i), allowing the intercept to vary by study site ($\alpha_{study[i]}$). We do not include species as a varying effect here, because there is no species-level predictor in this model and thus no problem with pseudoreplication (unlike in the model predicting probability of loss/increasing, where range size is a predictor that varies only at the species level). We ran the model for each habitat:

$$\begin{aligned} r_i &\sim \text{Normal}\left(\mu_i, \sigma\right) \\ \mu_i &= \alpha_{study[i]} + \beta_t * t_i \end{aligned}$$

In order to estimate the difference in mean range size between species gained and lost, we calculated the posterior difference in mean range size between these trajectories 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-transformation to the original scale (see Table S4 for model R syntax, sample settings and convergence diagnostics). To test whether these posterior differences are affected by the grain size at which we estimate AOO ranges, we re-run the above model for range sizes estimated with a three times larger grain size (i.e. AOO estimated on the hexagonal ISEA3H grid with a grain size of 32 km^2; see Section 2 above) (Figure S6).

Changes in beta-diversity

We quantified the temporal change in compositional dissimilarity between the species pools of grasslands, forests and summits. To quantify the compositional dissimilarity between habitats we calculated both the incidence-based multiple-site Sørensen dissimilarity index, and the abundance-based multiple-site Bray–Curtis dissimilarity index (Baselga, 2010; Baselga & Orme, 2012). To calculate the Sørensen index, we aggregated species from all study sites in a given habitat at the time of the baseline surveys and, separately, the resurveys, resulting in three species pools (i.e. one for each habitat) per time period. To calculate the Bray–Curtis dissimilarity index, we weighted species by their frequency across study sites in a given habitat at the time of the baseline surveys and, separately, the resurveys, resulting in three frequency-weighted species pools (i.e. one for each habitat) per time period. For the baseline and resurvey time, we then calculated the respective dissimilarity index between the three species pools. A lower dissimilarity index at a given time period indicates a lower heterogeneity in species composition among the three habitats.

Range size and nutrient demand

We used Ellenberg's indicator values for nutrient (*N*-number) to approximate species niche position for nutrients (Bartelheimer & Poschlod, 2016; Diekmann, 2003; Ellenberg et al., 2001). These values describe each species' niche position on a scale from 1 (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 harmonised 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. A total of 1297 species of the 1827 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 shifted 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. The CWM-N was calculated for each study site and survey period as sums across species: $\sum N_i * f_i / \sum f_i$ 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 (p_i), including study site as a group-level effect ($\alpha_{study[i]}$) to indicate pairs of observations:

$$c_i \sim \text{Normal}\left(\mu_i, \sigma\right)$$
$$\mu_i = \alpha_{study[i]} + \beta_p * p_i$$

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.

RESULTS

Temporal trends in site-level species numbers varied among habitats. On mountain summits, there were few species losses and species gained outweighed losses by a factor of 2.11 (95% CI [1.85, 2.41]). In contrast, species gains were lower than losses by a factor of 0.83 (95% CI [0.78, 0.88]) in forest and 0.78 (95% CI [0.69, 0.86]) in grasslands (Figure 2a,b). Consequently, species numbers increased on summits and decreased in forests and grasslands (Figure S8).

Next, we tested the association of species loss probability with species geographic range size. Given the possibility that small-ranged species are lost at a site simply because of a smaller local population size, we assessed the relationship between species range size and baseline occupancy (i.e. the fraction of plots a species occupied at a site during the baseline survey). We found no relationship for summits and statistically clear positive slopes for forests and grasslands (Figure S9). Even after accounting for baseline occupancy, range size was negatively associated with species loss probability in all three habitats, although for summits the association was not statistically clear (summits: $\beta = -0.08$, 95% CI [−0.34, 0.17]; forests:

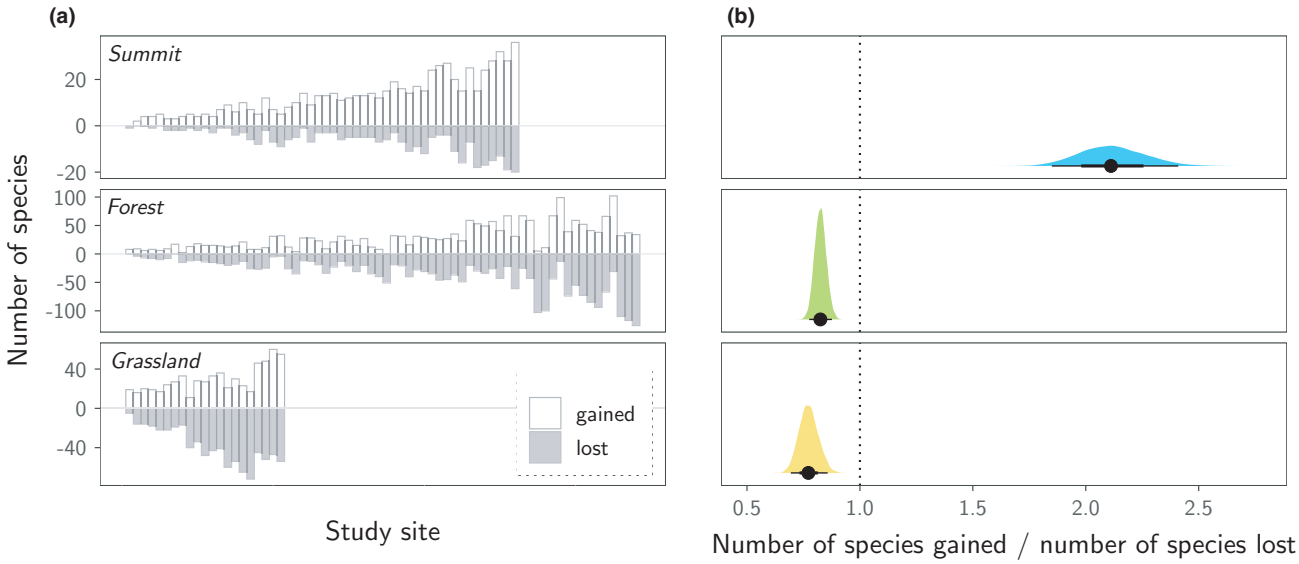

FIGURE 2 Species gains dominate on summits, whilst species losses outweigh species gains in forests and grasslands. (a) Species gains (white) and losses (grey) at each study site (each bar represents a study site, bars are sorted in ascending order by the sum of gained and lost species). (b) Posterior distribution of the ratio between the number of species gained and lost (ratios above 1 present higher species gains than losses, i.e. an increase in species richness). Colours (blue, green, yellow) refer to habitats as in Figure 1. Points represent medians, lines represent the 66% and 95% credible interval

$\beta = -0.18$, 95% CI [−0.27, −0.10]; grasslands: $\beta = -0.40$, 95% CI [−0.59, −0.20]; Figure 3a; see Table S2). In grasslands, where the association was strongest, species with small ranges had up to 60% higher probability of loss than those with the largest ranges (Figure S10a). The statistically clear effect estimates for forests and grasslands were also robust to excluding locally rare species (with baseline occupancies below 5%) from the data (Table S2). We then tested whether occupancy changes of species were related to range size. Accounting for species baseline occupancy; larger-ranged species increased preferentially in occupancy (summits: $\beta = 0.14$, 95% CI [0.04, 0.24]; forests: $\beta = 0.34$, 95% CI [0.23, 0.46]; grasslands: $\beta = 0.29$, 95% CI [0.15, 0.34]; Figure 3b and Table S3). In forests, where the effect was strongest, species with the smallest ranges had only a 2% chance of increasing, while species with the largest ranges had a 25% chance of increasing (Figure S10b). Across all sites, range size explained 7% (95% CI [0.05, 0.09]) and 3% (95% CI [0.02, 0.05]) of the variance in the probability of loss and increasing respectively.

To aid interpretation of how much range sizes differ between species trajectories, we estimated the mean range sizes of species gained, lost and persisting (Figure 3c and Figure S11 for raw data distribution). In all three habitats, species newly gained at a site had, on average, larger ranges than species lost. On summits, the ratio between range size of gained and lost species was greatest, with gained species having, on average, a range 1.43 times larger (95% CI [1.10, 1.85]) than lost species (forests: $\beta = 1.30$, 95% CI [1.21, 1.40]; grasslands: $\beta = 1.29$, 95% CI [1.17, 1.43]; Figure 3c,d, Figure S11 and Table S4). The absolute difference in range size was greatest in grasslands, with ranges of species gained averaging c. 81,000 km^2 larger than those lost. Effect estimates of these contrasts were robust to estimating range size at a larger spatial grain (Figure S6). Concurrent with displacements of smaller- by larger ranged species, the compositional similarity between habitats increased. At the habitat level, the species pools of summits, forests and grasslands became slightly more similar over time (baseline: $\beta_{SOR} = 0.75$, $\beta_{BRAY} = 0.72$ vs. resurvey: $\beta_{SOR} = 0.74$, $\beta_{BRAY} = 0.70$, where β_{SOR} and β_{BRAY} are the multiple-site Sørensen and Bray Curtis dissimilarity respectively (Baselga, 2010); but note that the temporal change in these indices is mathematically independent from the temporal turnover analysed above).

Finally, we asked whether species niche position for nutrients might be linked to these replacements. We found, for each habitat, that the species with the highest nutrient demands had the largest ranges, where the residual variance of this relationship increased towards species with low nutrient demands, indicating that species from nutrient-poor habitats can have either large or small ranges (Figure 4a). The positive correlation between species niche position for nutrients and range size was strongest for grassland species with a Pearson correlation of $\rho = 0.43$ (95% CI [0.36, 0.49]) (summits: $\rho = 0.26$, 95% CI [0.17, 0.35]; forests: $\rho = 0.21$, 95% CI [0.15, 0.28]). In each habitat, the community-weighted mean of species niche positions for nutrients increased over time, indicating community shifts towards more nutrient-demanding species. These shifts were statistically clear for each habitat,

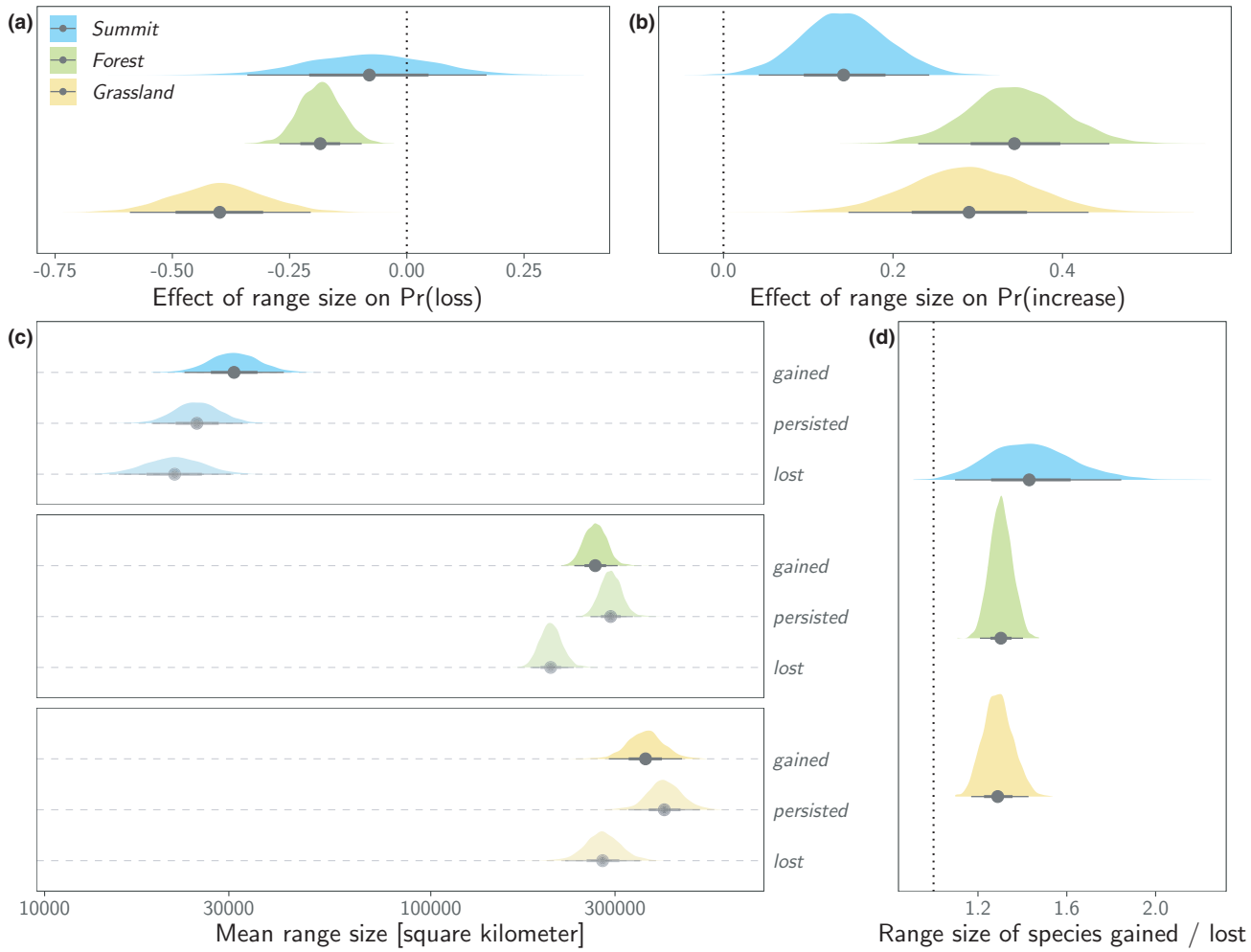

FIGURE 3 Directional temporal turnover in relation to species range size across habitats. Posterior distribution of the effect of range size on (a), the probability (Pr) of a species being lost at a study site and (b), the probability (Pr) of a species increasing in occupancy at a study site, after having accounted for demographic effects (see Section 2). (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 (persisting vs. gained/lost comparison in Table S4). Note that (c) and (d) only provide a summary statistic, and do not test the hypothesis that range size explains species trajectory. Point and lines in (a–d) are the median and its 66% and 95% credible interval. Dotted vertical lines in (a) and (b) represent no effect of range size, and in (d) 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 Tables S2–S4. Mean regression lines for (a) and (b) are presented in Figure S10

ranging from $\Delta = 0.05$ (95% CI [0.01, 0.08]) for summits to $\Delta = 0.53$ (95% CI [0.30, 0.76]) for grasslands (forests: $\Delta = 0.28$, 95% CI [0.13, 0.33]; Figure 4b). Comparison of weighted with unweighted means showed that these shift were primarily due to changes in species composition in forests and grasslands, and due to changes in species occupancy on summits (Figure S12).

DISCUSSION

Our cross-habitat comparison indicates commonalities between contrasting habitats with respect to the nature of biodiversity change based on species geographic range size. Although range size accounted for only a relatively small proportion of the total variation in species trajectory, the direction of the effect was consistent across summits, forests and grasslands. Regardless of whether species numbers increased or decreased over time (Figure 2), plant species with larger ranges gained ground and replaced species with smaller ranges in plant communities across habitats (Figure 3). These replacements coincided with a decrease in compositional dissimilarity of the species pools of the three habitats. Concurrent with increases in larger-ranging species, communities shifted towards more nutrient-demanding species, where species from fertile habitats were large-ranged (Figure 4). This result is consistent with the hypothesis that directional turnover in relation to species range size is not solely due to stochastic and natural processes, but is driven in part by aspects of species niche, likely in response to anthropogenic global change.

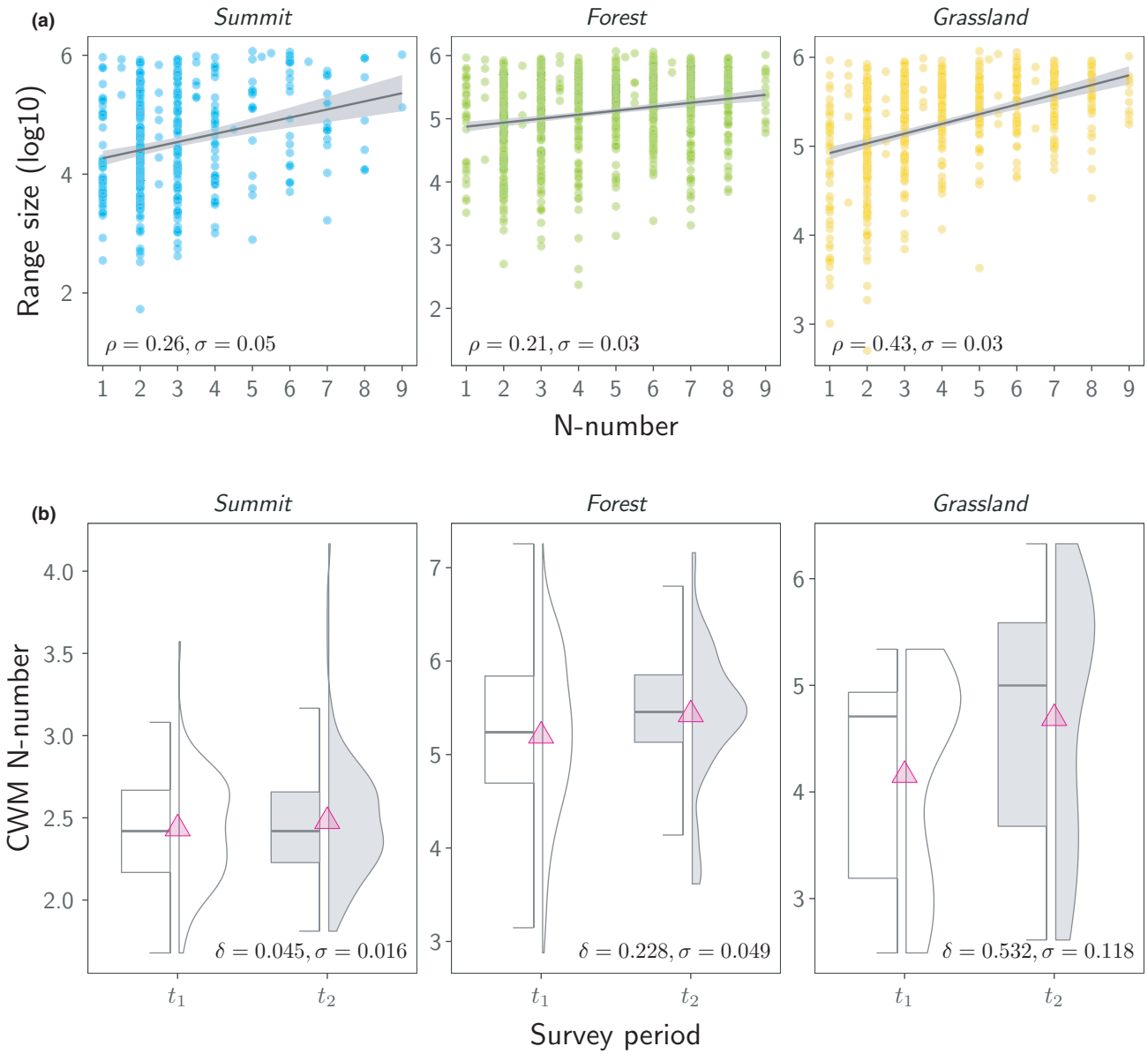

FIGURE 4 Species with high nutrient demands tend to have large ranges and communities shift towards species with higher nutrient demands over time. (a) Relationship between species range size and Ellenberg indicator values for nutrients (*N*-number) across species in each habitat. Line and transparent 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 and σ is the standard deviation of Δ

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. In all three habitats, anthropogenic activities have led to a greater availability of nutrients. On summits, climate warming has increased nutrient cycling (Salazar et al., 2020), and in forests and grasslands, aerial deposition of nutrients has led to soil eutrophication (Bobbink et al., 2010). A greater availability of limiting resources allows less specialised species to colonise, where larger-ranged species may be more likely to colonise because they can disperse from more sites and may be more likely to be dispersed by humans due to an association with more productive, and therefore, often anthropogenic habitats (Figure 4). Nutrient-demanding, often large-ranged species may also preferentially persist and increase in occupancy (Figure 3), because they are likely to benefit more from increased nutrients being able to invest them more quickly in their growth (Bartelheimer & Poschlod, 2016; Estrada et al., 2015; Sonkoly et al., 2017). The consequent shift towards more nutrient-demanding species that we observe across habitats (Figure 4) is in accordance with findings from single-habitat studies that link these shifts to anthropogenic change drivers (summits: Rumpf et al., 2018, forests: Staude et al., 2020 and grasslands: Diekmann et al., 2014). Gains in larger-ranged species,

therefore, appear consistent with the predicted effects of human activities, such as increasing the productivity of land.

In contrast to large-ranged species, species with small-ranges are generally less nutrient-demanding (Figure 4) and may therefore have, on average, a more conservative resource strategy (Bartelheimer & Poschlod, 2016). Since a higher prevalence of larger-ranged, typically more resource-acquisitive, species, is likely to exert increased biotic pressure on extant species, the preferential loss of small-ranged species could be due to competitive exclusion by faster growing species (i.e. biotic filtering; Levine et al., 2010; Tylianakis et al., 2008). Furthermore, small-ranged species might 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 (Kleijn et al., 2008). Thus, the displacement of small-ranged species could also be due to direct effects of environmental change (i.e. abiotic filtering; Adler et al., 2009; Harpole et al., 2016). Importantly, we can largely exclude the potential explanation that a higher loss probability of small-ranged species is due only to stochastic, demographic effects (Table S2). Even after excluding locally rare species and accounting for species baseline occupancy (i.e. the fraction of plots occupied at a site during the baseline survey), the negative association between species loss probability and range size persisted. Thus, preferential loss of small-ranged species is likely due not only to demographic stochasticity but also, in part, to aspects of species niche that confer a higher vulnerability to global change.

Despite the congruence across habitats of displacements of smaller- by larger-ranged species, our results also indicate differences between habitats. On summits, replacements of small- by large-ranged species were primarily driven by gains in larger-ranged species (Figure 3), with generally few species losses (Figure 2). On summits, colonisations from lower elevational species, which generally have larger ranges (Figure S13), have accelerated owing to climate warming over the last three decades (Steinbauer et al., 2018), coinciding with the survey intervals of our study. In spite of these rapid changes, and in accordance with our study, evidence points to hitherto limited effects of warming on the persistence of summit species (Steinbauer et al., 2018). Extant summit species may persist and escape changes in abiotic and biotic pressures due to a high variation in microhabitats (Graae et al., 2018; Scherrer & Körner, 2011) and a still sparse or less tall-growing vegetation (Billings & Mooney, 1968; Callaway et al., 2002). However, far stronger changes in climate are expected in the future (O'Neill et al., 2016), putting summit species increasingly at risk. Taller and more competitive species are expected to arrive on summits under warming (Steinbauer et al., 2018), and because extant species have nowhere to go to escape competition, they are likely to be displaced (Alexander et al., 2015), with studies finding that direct effects of warming are typically exceeded by indirect effects mediated via novel competitors (Alexander et al., 2015; Levine et al., 2010; Suttle et al., 2007). A major uncertainty, however, is whether species from lower elevations can colonise and establish everywhere on summits, or whether microhabitats will allow the continued persistence of summit species.

In forests and grasslands, on the other hand, replacements of smaller- by larger-ranged species are driven both by directional gains and directional losses of species. In these habitats, the vegetation is typically denser than on summits. The stress gradient hypothesis predicts that as resource availability increases and vegetation becomes denser, competitive interactions and exclusion become important (Bertness & Callaway, 1994). Primary change drivers in these habitats, such as eutrophication (Bobbink et al., 2010; Stevens et al., 2004) or declines in traditional land use (i.e. low-intensity farming with e.g. sheep grazing) (Diekmann et al., 2014; Kopecky et al., 2013), are thus likely to lead, in addition to abiotic changes, to higher biotic pressure. In grasslands, for example, studies have shown that while some of the species loss under eutrophication is due to direct abiotic effects from altered niche dimensions (Harpole et al., 2016), much of it is due to increased competition for light (Hautier et al., 2009). Furthermore, evidence suggests that directional species loss and trait shifts in grasslands under eutrophication can be mitigated by herbivory that regulates increased competition (Borer et al., 2014; Kaarlejärvi et al., 2017). This may suggest a greater relevance of biotic filtering in denser habitats could contribute to the more directional loss of small-ranged species in grasslands and forests (Figure 3). Importantly, we can largely rule out that greater directional loss in these habitats than on summits simply arises from differences in sampling methods. 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 Section 2 and Table S5). Our cross-habitat comparison, therefore, supports a possible role of increased competition in understanding preferential loss of smaller-ranged species.

Although we argue that the above patterns could be directly or indirectly due to global change, we emphasise that natural succession is also likely to play a role. In semi-natural habitats, successional dynamics can linger centuries after disturbance and habitat formation (Isbell et al., 2019; Lichter, 1998). This raises the question of the extent to which observed vegetation changes are due to global change or succession (Phillips, 1934). The observed shift towards more nutrient-demanding species over time in our study, appears to be at odds with what would be expected from succession alone. In secondary succession, the species that establish earliest are those that disperse well (Clements, 1916). Thus, fast-growing, nutrient-demanding species, that tend to produce

smaller, more numerous seeds (Aarssen & Taylor, 1992; Waller, 1988) and have large ranges (Figure 4a), are characteristic of early rather than late successional stages (Harper et al., 1970; Odum, 1969). Our findings are therefore more indicative of human agency, where it has been shown, for instance, that eutrophication can push systems back to an early successional stage and promote pioneer species (Odum, 1969; Walker & Wardle, 2014). However, a complete characterisation of the turnover patterns expected from succession alone is still lacking to compare the results of global change studies with a natural baseline (Chang & Turner, 2019). Further studies of how global change modifies the direction and rate of successional trajectories will be essential to understanding current biodiversity change.

Together, our findings provide a step forward in understanding the nature of compositional turnover over time. We observe smaller- by larger-ranged species replacement across plant communities of contrasting habitats. Our results suggest this ubiquitous component of biodiversity change could be driven by aspects of species niche. Species from nutrient-rich habitats are large-ranged and, nutrient-demanding species increased across habitats in parallel with the displacement of smaller- by larger-ranged species. These findings largely agree with studies on plant invasions, where species with the greatest establishment success typically originate from anthropogenic, fertile habitats (Kalusová et al., 2017), and species that are most likely to be invasive and thus expand their range have an acquisitive resource strategy (Fristoe et al., 2021). We speculate that the increase in nutrient-demanding species may be partially driving the loss of small-ranged species through increased competition, particularly in habitats with denser vegetation, consistent with the stress gradient hypothesis (Bertness & Callaway, 1994). We emphasise that our findings correspond to vegetation dynamics in semi-natural and natural habitats and are thus not representative of the full impact of human activities (Gonzalez et al., 2016). Given the directional species replacement even in these habitats, this raises the question of whether habitat protection alone is sufficient for species conservation: active conservation efforts may be needed to prevent biodiversity deficits (Benayas et al., 2009; Isbell et al., 2019). Finally, the temporal turnover in relation to species range size that we observe can help link biodiversity change across spatial scales. On the one hand, it can link to macroecological processes such as biotic homogenisation, where increasing evidence suggests spatially disparate communities are becoming more similar in species composition (Li et al., 2020). On the other hand, pervasive smaller- by larger-ranged species replacement can reconcile findings of no net loss in local diversity (Dornelas et al., 2014; Vellend et al., 2013) with global species loss (Humphreys et al., 2019; Lughadha et al., 2020), thus partially resolving the biodiversity conservation paradox.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

Ingmar R. Staude, Henrique M. Pereira, Gergana N. Daskalova and Lander Baeten conceived the study, with input from the sREplot working group (Markus

Bernhardt-Römermann, Martin Diekmann, Harald Pauli, Mark Vellend, Anne D. Bjorkman, Jörg Brunet, Pieter De Frenne, Radim Hédl, Ute Jandt, Jonathan Lenoir, Isla H. Myers-Smith, Kris Verheyen, Sonja Wipf, Monika Wulf). Ingmar R. Staude performed the analyses, with input from Henrique M. Pereira, Gergana N. Daskalova, Lander Baeten and Hans Van Calster. Ingmar R. Staude, Henrique M. Pereira, Gergana N. Daskalova and Lander Baeten wrote the manuscript, with substantial input from Markus Bernhardt-Römermann, Anne D. Bjorkman, Martin Diekmann, Isla H. Myers-Smith, Harald Pauli, Mark Vellend and contributions from Jörg Brunet, Hans Van Calster, Pieter De Frenne, Radim Hédl, Ute Jandt, Jonathan Lenoir, 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, Adrienne Ortmann-Ajkai, 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, Pascal Vittoz, Ondřej Vild, Luis Villar and Manuela Winkler. Authorship order was determined as follows: (1) core authors; (2) sREplot participants (alphabetical) and other major contributors; (3) authors contributing community composition data and to an advanced version of the manuscript (alphabetical).

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13937.

DATA AVAILABILITY STATEMENT

R Markdown file containing the R code for statistical analyses and data visualisation, and the data supporting the results of this study, are available online on Figshare at https://doi.org/10.6084/m9.figshare.12514172.v1.

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