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# 1 Directional temporal turnover toward plant species with larger ranges across habitats

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126 **Abstract**

127 Species turnover is ubiquitous. However, it is unknown whether certain types of species are consistently  
128 gained or lost across different habitats. Here, we analyzed the trajectories of 1,827 plant species over  
129 time intervals of up to 78 years at 141 sites across mountain summits, forests, and lowland grasslands  
130 in Europe. We found, albeit with relatively small effect sizes, displacements of smaller- by larger-ranged  
131 species across habitats. Communities shifted in parallel toward more nutrient-demanding species, with  
132 species from nutrient-rich habitats having larger ranges. Because these species are typically strong  
133 competitors, declines of small-ranged species could reflect not only abiotic drivers of global change, but  
134 also biotic pressure from increased competition. The ubiquitous component of turnover based on  
135 species range size we found here may partially reconcile findings of no net loss in local diversity with  
136 global species loss, and link community-scale turnover to macroecological processes such as biotic  
137 homogenization.

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143 **Introduction**

144 During the Anthropocene, the rate of plant extinctions is estimated to be up to 500 times the  
145 background rate, with nearly 600 plant extinctions since Linnaeus *Species Plantarum* in 1758  
146 (Humphreys *et al.* 2019). These extinctions represent 0.2% of existing plant diversity, but typically  
147 plants have longer extinction lag times than other taxa (Cronk 2016), and recent studies estimate that  
148 approximately 40% of existing plant diversity is at risk of global extinction (Lughadha *et al.* 2020). This  
149 global pattern contrasts with long-term studies of changes in local plant diversity, which show no  
150 systematic evidence of decline in local diversity, but variable trends with as many communities  
151 increasing in species richness as decreasing (Dornelas *et al.* 2014; Vellend *et al.* 2017; Blowes *et al.*  
152 2019). While the assertion of no net loss of local diversity remains controversial (Murphy & Romanuk  
153 2014; Newbold *et al.* 2015; Gonzalez *et al.* 2016; Isbell *et al.* 2019), the high variability in the direction  
154 and magnitude of diversity trends at local scales raises questions about how this can be reconciled  
155 with biodiversity loss at the global scale (Dornelas *et al.* 2019). This biodiversity conservation paradox  
156 (Vellend 2017) may be partially resolved by considering directional changes in community composition  
157 (McKinney & Lockwood 1999; Sax & Gaines 2003). Compositional change over time could lead to  
158 biotic homogenization, where widespread local losses of species with small geographic ranges could  
159 scale to global losses while local gains of widely distributed species offset local losses of rare species  
160 (Newbold *et al.* 2018; Staude *et al.* 2020). However, whether such temporal turnover of species is  
161 ubiquitous across habitats or only occurring in specific contexts, remains an open question.

162 There are several possible explanations for a linkage between species turnover and range size. From a  
163 stochastic perspective, range size and mean local abundance are expected to correlate positively

164 across taxa and spatial scales (Gaston & Blackburn 1996; Gaston *et al.* 2000). According to this  
165 relationship, which is considered one of the few general laws in ecology (Pimm *et al.* 2014), species  
166 with small ranges have lower local abundances and are therefore more susceptible to demographic  
167 stochastic effects. However, recent analyses using over 700,000 vegetation plots across Europe along  
168 with curated species range maps, found no evidence of a range size-abundance relationship for plants  
169 in Europe (Sporbert *et al.* 2020), questioning whether for plants any such relationship exists. Another  
170 stochastic process that could lead to greater persistence of species with large ranges is rooted in  
171 meta-community dynamics (Leibold *et al.* 2004). Species with large ranges are expected to have more  
172 source habitats from which to disperse and, via the “rescue effect”, uphold populations in sink  
173 habitats (Hanski 1991). However, it is unclear whether lower recolonization rates alone could lead to  
174 preferential declines in small-ranged species, especially if these are locally abundant (Rabinowitz 1986;  
175 Thompson *et al.* 1998; Sporbert *et al.* 2020). Overall, there is mixed evidence for the hypothesis that  
176 directional turnover in relation to species range size might be driven by stochastic processes alone.

177 From a niche perspective, small-ranged species are hypothesized to have a smaller niche breadth  
178 (Brown 1984) and thus a lower tolerance to anthropogenic global change. For plants, however,  
179 measurement of niche breadth independent of spatial extent is a major challenge and tests of this  
180 hypothesis remain scarce. For example, species climatic niche breadth can be directly related to range  
181 size, simply because larger areas encompass greater environmental variation (Köckemann *et al.* 2009).  
182 Spatial autocorrelation can therefore lead to artefactual correlations, bringing into question the causal  
183 relationship between niche breadth and range size (Moore *et al.* 2018). When using null-models to  
184 account for spatial extent, or estimating niche breadth from species co-occurrence data, there seems  
185 to be less support for the niche-breadth hypothesis (Kambach *et al.* 2019; Vela Diaz *et al.* 2020).

186 Recent analyses suggest that instead of niche breadth, niche position is a much stronger predictor of a  
187 species' geographic range size (Vela Diaz *et al.* 2020). Humans have substantially transformed Earth's  
188 terrestrial surface, creating arable, more productive habitats, which has likely benefitted range  
189 expansions of species associated with nutrient-rich habitats and anthropogenic dispersal (Fristoe *et al.*  
190 2021). Thus, the niche position of species along nutrient gradients may covary positively with range  
191 size, with large-ranged species positioned at the more productive end of the gradient (Sonkoly *et al.*  
192 2017). If global change increases the availability of limiting resources, such as soil nutrients, this could  
193 favor species with larger ranges (Staude *et al.* 2020). Gains of such species could, in addition to direct  
194 abiotic effects, reduce the persistence of small-ranged species via increased competition. Taken  
195 together, preferential declines of small- over large-ranged species may be driven in part not only by  
196 stochastic but also by deterministic processes based on species niche breadth and position.

197 Community assembly and environmental drivers of change vary substantially among habitats. Here,  
198 we study biodiversity change in relation to species range size across three contrasting habitats –

199 mountain summits, deciduous and coniferous forests, and lowland grasslands (Figure 1). Previous  
200 studies have shown that in grasslands eutrophication is decreasing species numbers (Stevens *et al.*  
201 2004; Diekmann *et al.* 2019), with competition for light being an important mechanism for species  
202 exclusion (Hautier *et al.* 2009). On summits, climate warming leads to increasing species numbers  
203 (Pauli *et al.* 2012; Steinbauer *et al.* 2018), with sparse vegetation limiting the importance of  
204 competition despite eutrophication (Rumpf *et al.* 2018). In forests, many plant species are adapted to  
205 low-light conditions, and a range of drivers, including changes in historical forest management  
206 regimes, eutrophication, climate warming and widespread increases in large herbivores, leads to both  
207 increases and decreases in species numbers (De Frenne *et al.* 2013; Bernhardt-Römermann *et al.*  
208 2015; Bernes *et al.* 2018; Staude *et al.* 2020). In terms of compositional change, anthropogenic global  
209 change typically favors nutrient-demanding species in these habitats (summits: Rumpf *et al.* 2018,  
210 forests: Bernhardt-Römermann *et al.* 2015 and grasslands: Diekmann *et al.* 2019), while natural  
211 succession shifts communities away from these species (Odum 1969). Thus, given an association  
212 between range size and species niche position for nutrients, we might expect consistencies among  
213 habitats with respect to turnover in relation to range size. Global change might favor species with  
214 larger ranges, while natural succession could lead to increases in species with smaller ranges.

215 Here, we coalesced vegetation resurveys for 141 sites (totaling 5,221 resurveyed plots) across  
216 summits, forests and grasslands in Europe to quantify species gains and losses, and test whether range  
217 size explains species losses and increases. We account for stochastic demographic effects to test for  
218 the role of species niche. We also test the association between range size and species niche position  
219 for nutrients and whether communities have shifted toward more or less nutrient demanding species  
220 over time. We hypothesized that drivers of change, albeit different, alter ecological selection  
221 processes in favor of widespread species, whilst small-ranged species are lost preferentially. This  
222 hypothesis is based on the following three expectations. First, we expect preferential gains in larger-  
223 ranged species as these can disperse from more source habitats, and may also be dispersed more by  
224 humans (owing to an association with nutrient-rich habitats). Second, as global change drivers make  
225 limiting resources more available, either indirectly due to accelerated nutrient cycling from climate  
226 warming (Salazar *et al.* 2020), or directly due to aerial deposition of nitrogen (Bobbink *et al.* 2010), we  
227 expect that larger-ranged species might also be more likely to increase at sites. Third, we expect that  
228 declines in species with smaller ranges are not due solely to stochastic processes, but also reflect  
229 direct effects of environmental changes on the one hand, and increased competition due to the arrival  
230 of new competitors on the other. Our study tests for a ubiquitous component of species turnover in  
231 relation to species range size, and thus the prediction that directional changes in community  
232 composition could partially resolve the biodiversity conservation paradox.

233

## 234 Materials and Methods

235 **Databases.** We synthesized data from three databases, each of which is a collation of vegetation  
236 resurveys in a specific habitat in Europe. Mountain summits are represented by 52 sites from the  
237 Global Observation Research Initiative in Alpine environments (GLORIA, gloria.ac.at, Pauli *et al.* 2015),  
238 deciduous and coniferous forests understories by 68 sites from the forestREplot database  
239 (forestreplot.ugent.be, Verheyen *et al.* 2016) and lowland grasslands by 21 sites from the GRACE  
240 database (Diekmann *et al.* 2019; Figure 1 and Table S1). At each site, plant communities were  
241 surveyed across multiple permanent or quasi-permanent plots in either natural vegetation (summits)  
242 or semi-natural vegetation (forests and grasslands, semi-natural *sensu* Peterken 1996 and Peeters *et*  
243 *al.* 2014, respectively) at two points in time (baseline survey and resurvey) with the same sampling  
244 effort (i.e., same number and size of plots), and no major changes in land use before and between  
245 surveys (further details available in Pauli *et al.* 2015; Verheyen *et al.* 2016; Diekmann *et al.* 2019). The  
246 median time spans between surveys were 14, 42 and 34 years for summits, forests and grasslands,  
247 respectively (Fig. S1a). In forest and grassland surveys, the median number of plots per site was 43 and  
248 36, and the median size of plots was 400 m<sup>2</sup> and 25 m<sup>2</sup>, respectively (Fig. S2a and b). Summits were  
249 always resurveyed in eight spatial sections that together covered the entire area from the highest  
250 summit point to the contour line 10 m in elevation below this point. The median summit area was 0.25  
251 ha. In forests and grasslands, the median study area was 1,700 ha and 1,000 ha, respectively (Fig. S1b).

252 **Species data.** *Taxonomy.* We accounted for within-and among-study variation in taxonomy by  
253 determining the accepted species name for each species using the Global Biodiversity Information  
254 Facility's (GBIF) backbone taxonomy (gbif.org). Harmonization thus ensured no double-counting of  
255 species owing to synonymy. We included only vascular plants identified to the species level. In total,  
256 our data comprises 1,827 accepted vascular plant species (see Data Table 1 at  
257 [figshare.com/s/b37f6167b13ad5da9e9c](https://figshare.com/s/b37f6167b13ad5da9e9c)).

258 *Range size.* We estimated species range sizes as area of occupancy (AOO) (Gaston & Fuller 2009) using  
259 all available point occurrence records of the species in GBIF (gbif.org; 28 May 2020). After excluding  
260 incomplete, impossible and unlikely coordinates (Chamberlain 2020), there were c. 131 million  
261 geographically referenced records available for the species in our database. Records were aggregated  
262 to a hexagonal grid (ISEA3H) at a spatial grain of 10.7 km<sup>2</sup> (Barnes *et al.* 2017), where the number of  
263 cells that a species occupies on this grid represents its AOO estimate (see Data Table 1 for species  
264 AOO estimates and GBIF urls). Range size is a static variable in our analysis. Although losses and gains  
265 of species result in range expansion and contraction, range size is largely constant on a relative scale  
266 over decadal time periods (Fig. S3). The species with the largest AOO in all three habitats were *Achillea*  
267 *millefolium* and *Trifolium repens* (both with ca. 1.2x10<sup>6</sup> km<sup>2</sup>), the species with the smallest AOO were



268 the highly endemic *Draba dolomitica* (c. 11 km<sup>2</sup>) on summits, *Galium abaujense* (c. 21 km<sup>2</sup>; endemic to  
269 the Carpathians) in forests, and *Pentanema germanicum* (c. 503 km<sup>2</sup>; critically endangered in Germany  
270 and Austria (Fischer *et al.* 2008)) in grasslands (Fig. S4). Owing to sampling biases and data gaps in  
271 GBIF, our AOO estimates are likely to underestimate absolute range sizes of species (Meyer *et al.*  
272 2016). However, for plant species in Europe, GBIF-derived range sizes correlate strongly with expert-  
273 drawn range maps and may therefore provide good relative estimates of range size, whilst being  
274 available for many more species (Staudé *et al.* 2020). Here, we also found strong correlations  
275 between GBIF-derived range sizes and expert-based range sizes from two published databases:  
276 Vangansbeke *et al.* 2021 and Kambach *et al.* 2019 (Fig. S5). It is important to note, however, that  
277 ranges from such databases differ from AOO, in that they measure species extent of occurrence (EOO)  
278 and therefore include areas that are unoccupied by species. Thus, species with disjunct distributions,  
279 e.g., orchid species that occur throughout Europe but only in very fragmented, well-conserved habitat,  
280 can have a small AOO but a large EOO. AOO is therefore a markedly better representation of species  
281 population sizes and differences related to species niche than is EOO, and provides a general measure  
282 of species vulnerabilities to stochastic and directional threatening processes (Gaston & Fuller 2009).

283 *Occupancy.* Measures of plot-level species abundance varied across studies (e.g., frequencies,  
284 percentage cover, and categorical cover-abundance scales) and were often not available if only  
285 species presence/absence was recorded. In order to estimate species abundance in a consistent way,  
286 we estimated species occupancy at the spatial scale of a study. We therefore divided the number of  
287 plots (grasslands, forests) or sections (summits) a species occupied at a given study site by the total  
288 number of plots/sections in that study. This was done separately for the baseline survey and the  
289 resurvey. Occupancy (i.e., the fraction of plots a species occupies at a site) has been shown to  
290 correlate strongly and positively with abundance at local to regional scales, i.e., a species with a high  
291 population size at a site does also occupy more plots at a site (Wright 1991; Gaston *et al.* 2000).

292 *Trajectory.* We evaluated species trajectories (i.e. lost, gained or persisting) at the spatial scale of a  
293 study site. Lost species were present (in at least one plot/section) during the baseline survey and  
294 absent (from all plots/sections) during the resurvey. Gained species were absent during the baseline  
295 survey and present during the resurvey. Persisting species were present during both the baseline  
296 survey and resurvey. Resurveys, even of permanent plots, always miss some species, generating  
297 pseudo-gains and losses that can be inflated for rare species (Verheyen *et al.* 2018; Futschik *et al.*  
298 2020). We account for this bias by adjusting for species baseline abundances, which is strongly  
299 correlated with any such bias (Kopecký & Macek 2015), as explained below. Site-level trajectories are  
300 independent from GBIF-derived range sizes in that site-level gains and losses in our data do not result  
301 in de facto large/small ranges.

302 **Analysis.** The brms package (Bürkner 2017) in R was used for all statistical analyses. R code for all  
303 analyses and visualization is available on figshare at <https://figshare.com/s/b37f6167b13ad5da9e9c>. A  
304 brief overview of all analyses and their rationale are provided in the Supplementary Material. For all  
305 analyses, we use the 95% credible interval to determine statistical clarity (Dushoff *et al.* 2019).

306 *Species gains and losses.* Using species trajectories we quantified the number of lost and gained  
307 species on the spatial scale of a study site (Extended Data Table 2). The highest losses (126 species)  
308 occurred in Hungarian forest-steppe landscapes, the highest gains (102 species) occurred in  
309 acidic/mesic oak woods in the Czech Republic. We assessed the expected ratio between the number  
310 of species gained and the number of species lost for each habitat. We used a Poisson regression  
311 model with a log-link to predict the number of species ( $s_i$ ) with the categorical variable “gained/lost”  
312 ( $g_i$ ) and included a group-level effect for study site ( $\alpha_{study[i]}$ ) to indicate pairs of observations and  
313 test for differences in the number of gained vs. lost species within sites, while accounting for  
314 differences between sites.

$$s_i \sim \text{Poisson}(\lambda_i)$$
$$\log(\lambda_i) = \alpha_{study[i]} + \beta_g * g_i$$

315

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

321 *Probability of loss.* We estimated the effect of species range size on the probability that a species  
322 being present at the baseline survey is lost from a study site by the time of the resurvey. The effect of  
323 range size can be confounded by species baseline occupancy (i.e., the fraction of plots occupied at a  
324 site during the baseline survey) if small-ranged species also tend to have a lower abundance at a study  
325 site. Species with small population sizes are more likely to be lost owing to 1) stochastic demographic  
326 processes and 2) an observer error, where rare species are more likely to be overlooked in resurveys.  
327 Therefore, we tested first for a positive range size – occupancy relationship in our data (see Methods  
328 below). To estimate the effect of range size that is not due to demographic effects, we statistically  
329 controlled for variation in species baseline occupancies by including it as a covariate in our model  
330 (Staute *et al.* 2020). Furthermore, species with small ranges may be disproportionately vulnerable at  
331 low abundances. This could be the case if range size covaries with specific traits, such as, for example,  
332 height, where small plants would be expected to be more vulnerable than tall plants at low occupancy.  
333 To account for this possibility, we also included an interaction effect between range size and  
334 occupancy in our model. Finally, the effect of species occupancy on species loss probability is likely to

335 vary with the number of plots per study site. For example, a species with 10% occupancy in a study of  
336 10 plots, is more likely to be lost than a species with 10% occupancy in a study of 100 plots. We  
337 therefore allowed the effect of occupancy to vary by study site.

338 Our model thus predicts a Bernoulli indicator variable that a given species was lost or persisted ( $e_i$ )  
339 with two fixed effects ( $\beta_r$  for range size ( $r_i$ ) and  $\beta_f$  for occupancy ( $f_i$ ), where both  $r_i$  and  $f_i$  were  
340 log10-transformed and scaled within habitats to have a mean of zero and a standard deviation of one)  
341 and an interaction effect between the two fixed effects ( $\beta_{fr}$ ). We allowed the intercept and the effect  
342 of occupancy to vary by study site ( $\alpha_{study[i]}$  and  $\beta_{f,study[i]}$ , respectively). Since many species occur at  
343 more than one study site and considering each species within a site as independent data points may  
344 lead to pseudoreplication, we also included species as an additional crossed varying effect ( $\gamma_{species[i]}$ ).  
345 We ran this model for each habitat (see Table S2 for model R syntax, sample settings and convergence  
346 diagnostics). The resulting model in mathematical form is:

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

348 As a further means to test whether demographic effects confound estimates of  $\beta_r$ , we ran the same  
349 model but excluded rare species (with site occupancies below 5%) from our data (Table S3). Finally, we  
350 also explored the influence of sampling methods (e.g., plot number, plot size, site area and survey  
351 interval) on the effect of range size on loss probability (methods and results can be found in  
352 Supplementary Materials Table S5). Since we only had data on the species that were newly gained at a  
353 study site but not on all those that tried to colonize, we were not able to directly calculate  
354 probabilities of gain in relation to range size.

355 *Probability of increasing.* We tested whether species with larger ranges were more likely to increase in  
356 occupancy at a site (i.e., the fraction of plots occupied at a site). Since changes in occupancy may  
357 depend on species baseline occupancy (e.g., species with a higher baseline occupancy could be more  
358 likely to increase in occupancy due to a higher propagule pressure), we estimated the effect of species  
359 range size on the probability of increasing, controlling for variation in species baseline occupancies.  
360 For this logistic model, we recoded the difference in occupancy at the resurvey and the baseline  
361 survey ( $d_i$ ) into a binary variable  $h_i$ , with  $h_i = 1$  when occupancy increased ( $d_i > 0$ ) and  $h_i = 0$  when  
362 occupancy decreased ( $d_i \leq 0$ ). We predicted  $h_i$  with range size (log10-transformed), including baseline  
363 occupancy as a covariate. Since baseline occupancy ranges from 0 to 1, species with an occupancy of  
364 1 cannot increase in occupancy. These species were therefore excluded from the model. The model in  
365 math form is:

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

367 , where parameters are defined as in the model for species loss probability. However, we did not  
368 include the interaction effect between occupancy and range size ( $\beta_{fr}$ ) in this model, as a potentially  
369 greater vulnerability of small-ranged species at low occupancy is likely to not be very relevant to  
370 explain increases in occupancy (see Table S3 for model R syntax, sample settings and convergence  
371 diagnostics).

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

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

382 In order to estimate the difference in mean range size between species gained and lost, we calculated  
383 the posterior difference in mean range size between these trajectories in each habitat. Since the  
384 posterior difference between gained and lost species is in the log10-scale, this gives a ratio of range  
385 size of species gained/lost after back-transformation to the original scale (see Table S4 for model R  
386 syntax, sample settings and convergence diagnostics). To test whether these posterior differences are  
387 affected by the grain size at which we estimate AOO ranges, we re-run the above model for range  
388 sizes estimated with a three times larger grain size (i.e., AOO estimated on the hexagonal ISEA3H grid  
389 with a grain size of 32 km<sup>2</sup>; see Methods above) (Fig. S6).

390 *Changes in beta-diversity.* We quantified the temporal change in compositional dissimilarity between  
391 the species pools of grasslands, forests and summits. To quantify the compositional dissimilarity  
392 between habitats we calculated both the incidence-based multiple-site Sørensen dissimilarity index,  
393 and the abundance-based multiple-site Bray Curtis dissimilarity index (Baselga 2010; Baselga & Orme  
394 2012). To calculate the Sørensen index, we aggregated species from all study sites in a given habitat at  
395 the time of the baseline surveys and, separately, the resurveys, resulting in three species pools (i.e.

396 one for each habitat) per time period. To calculate the Bray-Curtis dissimilarity index, we weighted  
397 species by their frequency across study sites in a given habitat at the time of the baseline surveys and,  
398 separately, the resurveys, resulting in three frequency-weighted species pools (i.e. one for each  
399 habitat) per time period. For the baseline and resurvey time, we then calculated the respective  
400 dissimilarity index between the three species pools. A lower dissimilarity index at a given time period  
401 indicates a lower heterogeneity in species composition among the three habitats.

402 *Range size and nutrient demand.* We used Ellenberg's indicator values for nutrient (N-number) to  
403 approximate species niche position for nutrients (Diekmann 2003; Ellenberg & Leuschner 2010;  
404 Bartelheimer & Poschlod 2016). These values describe each species' niche position on a scale from 1  
405 (adapted to unproductive, nutrient-poor soils) to 9 (adapted to fertile soils). We obtained N-numbers  
406 from sci.muni.cz/botany/juice/ELLENB.TXT and harmonized the taxonomy with our data. If an  
407 accepted species had more than one N-number (either due to synonyms or subspecies, e.g.,  
408 *Melampyrum pratense* ssp. *paludosum* has an N-number of 1, while *Melampyrum pratense* has an N-  
409 number of 2), we calculated the average. 1,297 species of the 1,827 species in our data also had N-  
410 numbers (71%). For the species in each habitat, we calculated Pearson's correlation coefficient  
411 between range size (log10-transformed and scaled) and N-number (scaled).

412 *Community weighted mean of species nitrogen niche position.* We tested whether communities shift  
413 towards species with higher nutrient demands over time by quantifying the community weighted  
414 mean N-number (CWM-N) at the time of the baseline survey and resurvey. CWM-N was calculated for  
415 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-  
416 number and site-occupancy of the  $i^{\text{th}}$  species, respectively. We quantified the difference between  
417 resurvey and baseline survey CWM-N, by predicting CWM-N ( $c_i$ ) with survey period ( $p_i$ ), including  
418 study site as a group-level effect ( $\alpha_{study[i]}$ ) to indicate pairs of observations:

$$419 \quad \begin{aligned} c_i &\sim Normal(\mu_i, \sigma) \\ \mu_i &= \alpha_{study[i]} + \beta_p * p_i \end{aligned}$$

420 To gain insight into how much of the change in CWM-N is due to changes in species occupancy or  
421 species composition, we also calculated community unweighted means by simply averaging N-  
422 numbers across species at a study site for both the baseline survey and resurvey, and tested for  
423 changes over time using the same model as above.

424

## 425 Results

426 The change in species numbers at sites over time varied among habitats. On mountain summits, there  
427 were few species losses and species gained outweighed losses by a factor of 2.11 (95% CI [1.85, 2.41]).  
428 In contrast, species gains were lower than losses by a factor of 0.83 (95% CI [0.78, 0.88]) in forest and  
429 0.78 (95% CI [0.69, 0.86]) in grasslands (Figure 2a and b). Consequently, species numbers increased on  
430 summits and decreased in forests and grasslands (Fig. S8).

431 Next, we tested the association of species loss probability with species geographic range size. Given  
432 the possibility that small-ranged species are lost at a site simply because of a smaller local population  
433 size, we assessed the relationship between species range size and baseline occupancy (i.e., the  
434 fraction of plots a species occupied at a site during the baseline survey). We found no relationship for  
435 summits and statistically clear positive slopes for forests and grasslands (Fig. S9). Even after  
436 accounting for baseline occupancy, range size was negatively associated with species loss probability  
437 in all three habitats, although for summits the association was not statistically clear (summits:  $\beta = -$   
438  $0.08$ , 95% CI [-0.34, 0.17]; forests:  $\beta = -0.18$ , 95% CI [-0.27, -0.10]; grasslands:  $\beta = -0.40$ , 95% CI [-0.59,  
439  $-0.20$ ]; Figure 3a; see Table S2). In grasslands, where the association was strongest, species with small  
440 ranges had up to 60% higher probability of loss than those with the largest ranges (Fig. S10a). The  
441 statistically clear effect estimates for forests and grasslands were also robust to excluding locally rare  
442 species (with baseline occupancies below 5%) from the data (Table S2). We then tested whether  
443 occupancy changes of species were related to range size. Accounting for species baseline occupancy;  
444 larger-ranged species increased preferentially in occupancy (summits:  $\beta = 0.14$ , 95% CI [0.04, 0.24];  
445 forests:  $\beta = 0.34$ , 95% CI [0.23, 0.46]; grasslands:  $\beta = 0.29$ , 95% CI [0.15, 0.34]; Figure 3a and Table S2).  
446 In forests, where the effect was strongest, species with the smallest ranges had only a 2% chance of  
447 increasing, while species with the largest ranges had a 25% chance of increasing (Fig. S10b). Across all  
448 sites, range size explained 7% (95% CI [0.05, 0.09]) and 3% (95% CI [0.02, 0.05]) of the variance in the  
449 probability of loss and increasing, respectively.

450 To aid interpretation of how much range sizes differ between species trajectories, we estimated the  
451 mean range sizes of species gained, lost and persisting (Figure 3c and Fig. S11 for raw data  
452 distribution). In all three habitats, species newly gained at a site had, on average, larger ranges than  
453 species lost. On summits, the ratio between range size of gained and lost species was greatest, with  
454 gained species having, on average, a range 1.43 times larger (95% CI [1.10, 1.85]) than lost species  
455 (forests:  $\beta = 1.30$ , 95% CI [1.21, 1.40]; grasslands:  $\beta = 1.29$ , 95% CI [1.17, 1.43]; Figure 3c, d, Fig. S11  
456 and Table S4). The absolute difference in range size was greatest in grasslands, with ranges of species  
457 gained averaging *c.* 81,000 km<sup>2</sup> larger than those lost. Effect estimates of these contrasts were robust  
458 to estimating range size at a larger spatial grain (Fig. S6). Concurrent with displacements of smaller-  
459 larger ranged species, the compositional similarity between habitats increased. At the habitat level,

460 the species pools of summits, forests and grasslands became slightly more similar over time (baseline:  
461  $\beta_{\text{SOR}} = 0.75$ ,  $\beta_{\text{BRAY}} = 0.72$  versus resurvey:  $\beta_{\text{SOR}} = 0.74$ ,  $\beta_{\text{BRAY}} = 0.70$ , where  $\beta_{\text{SOR}}$  and  $\beta_{\text{BRAY}}$  are the multiple-  
462 site Sørensen and Bray Curtis dissimilarity respectively (Baselga 2010); but note that the temporal  
463 change in these indices is mathematically independent from the temporal turnover analyzed above).

464 Finally, we asked whether species niche position for nutrients might be linked to these replacements.  
465 We found, for each habitat, that the species with the highest nutrient demands had the largest ranges,  
466 where the residual variance of this relationship increased towards species with low nutrient-demands,  
467 indicating that species from nutrient-poor habitats can have either large or small ranges (Figure 4a).  
468 The positive correlation between species niche position for nutrients and range size was strongest for  
469 grassland species with a Pearson correlation of  $\rho = 0.43$  (95% CI [0.36, 0.49]) (summits:  $\rho = 0.26$ , 95%  
470 CI [0.17, 0.35]; forests:  $\rho = 0.21$ , 95% CI [0.15, 0.28]). In each habitat, the community weighted mean  
471 of species niche positions for nutrients increased over time, indicating community shifts towards more  
472 nutrient-demanding species. These shifts were statistically clear for each habitat, ranging from  $\Delta =$   
473 0.05 (95% CI [0.012, 0.078]) for summits to  $\Delta = 0.53$  (95% CI [0.30, 0.76]) for grasslands (forests:  $\Delta =$   
474 0.28, 95% CI [0.13, 0.33]; Figure 4b). Comparison of weighted with unweighted means showed that  
475 these shift were primarily due to changes in species composition in forests and grasslands, and due to  
476 changes in species occupancy on summits (Fig. S12).

477

## 478 Discussion

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

491 The success of large-ranged species could be due to previously limiting resources (e.g., nutrients)  
492 becoming more available as a result of global changes. In all three habitats, anthropogenic activities  
493 have led to a greater availability of nutrients. On summits, climate warming has increased nutrient  
494 cycling (Salazar *et al.* 2020), and in forests and grasslands, aerial deposition of nutrients has led to soil  
495 eutrophication (Bobbink *et al.* 2010). A greater availability of limiting resources allows less specialized  
496 species to colonize, where larger-ranged species may be more likely to colonize because they can  
497 disperse from more sites and may be more likely to be dispersed by humans due to an association  
498 with more productive, and therefore, often anthropogenic habitat (Figure 4). Nutrient-demanding,  
499 often large-ranged species may also preferentially persist and increase in occupancy (Figure 3),  
500 because they are likely to benefit more from increased nutrients being able to invest them more  
501 quickly in their growth (Estrada *et al.* 2015; Bartelheimer & Poschlod 2016; Sonkoly *et al.* 2017). The  
502 consequent shift toward more nutrient-demanding species that we observe across habitats (Figure 4)  
503 is in accordance with findings from single-habitat studies that link these shifts to anthropogenic  
504 change drivers (summits: Rumpf *et al.* 2018, forests: Staudé *et al.* 2020 and grasslands: Diekmann *et*  
505 *al.* 2014). Gains in larger-ranged species, therefore, appear consistent with the predicted effects of  
506 human agency, such as increasing the productivity of land.

507 In contrast to large-ranged species, species with small-ranges are generally less nutrient-demanding  
508 (Figure 4) and may therefore have, on average, a more conservative resource strategy (Bartelheimer &  
509 Poschlod 2016). Since a higher prevalence of larger-ranged, typically more resource-acquisitive,  
510 species, is likely to exert increased biotic pressure on extant species, the preferential loss of small-  
511 ranged species could be due to competitive exclusion by faster growing species (i.e. biotic filtering;  
512 Tylianakis *et al.* 2008; Levine *et al.* 2010). Furthermore, small-ranged species might have adaptations  
513 to the stresses specific to their habitat and therefore possibly a lower tolerance to new types of stress,  
514 such as stoichiometric imbalances in resource supply from eutrophication (Kleijn *et al.* 2008). Thus,  
515 the displacement of small-ranged species could also be due to direct effects of environmental change  
516 (i.e. abiotic filtering; Adler *et al.* 2009; Harpole *et al.* 2016). Importantly, we can largely exclude the  
517 potential explanation that a higher loss probability of small-ranged species is due only to stochastic,  
518 demographic effects (Table S2). Even after excluding locally rare species and accounting for species  
519 baseline occupancy (i.e., the fraction of plots occupied at a site during the baseline survey), the  
520 negative association between species loss probability and range size persisted. Thus, preferential loss  
521 of small-ranged species is likely due not only to demographic stochasticity, but also, in part, to aspects  
522 of species niche that confer a higher vulnerability to global change.

523 Despite the congruence across habitats of displacements of smaller-by larger-ranged species, our  
524 results also indicate differences between habitats. On summits, replacements of small- by large-  
525 ranged species were primarily driven by gains in larger-ranged species (Figure 3), with generally few



526 species losses (Figure 2). On summits, colonizations from lower elevational species, which generally  
527 have larger ranges (Fig. S13), have accelerated owing to climate warming over the last three decades  
528 (Steinbauer *et al.* 2018), coinciding with the survey intervals of our study. In spite of these rapid  
529 changes, and in accordance with our study, evidence points to hitherto limited effects of warming on  
530 the persistence of summit species (Steinbauer *et al.* 2018). Extant summit species may persist and  
531 escape changes in abiotic and biotic pressures due to a high variation of micro-habitats (Scherrer &  
532 Körner 2011; Graae *et al.* 2018) and a still sparse or less tall-growing vegetation (Billings & Mooney  
533 1968; Callaway *et al.* 2002). However, far stronger changes in climate are expected in the future  
534 (O'Neill *et al.* 2016), putting summit species increasingly at risk. Taller and more competitive species  
535 are expected to arrive on summits under warming (Steinbauer *et al.* 2018), and because extant  
536 species have nowhere to go to escape competition, they are likely to be displaced (Alexander *et al.*  
537 2015), with studies finding that direct effects of warming are typically exceeded by indirect effects  
538 mediated via novel competitors (Suttle *et al.* 2007; Levine *et al.* 2010; Alexander *et al.* 2015). A major  
539 uncertainty, however, is whether species from lower elevations can colonize and establish everywhere  
540 on summits, or whether microhabitats will allow the continued persistence of summit species.

541 In forests and grasslands, on the other hand, replacements of smaller- by larger-ranged species are  
542 driven both by directional gains and directional losses of species. In these habitats, the vegetation is  
543 typically denser than on summits. The stress gradient hypothesis predicts that as resource availability  
544 increases and vegetation becomes denser, competitive interactions and exclusion become important  
545 (Bertness & Callaway 1994). Primary change drivers in these habitats, such as eutrophication (Stevens  
546 *et al.* 2004; Bobbink *et al.* 2010) or declines in traditional land use (i.e., low-intensity farming with e.g.,  
547 sheep grazing) (Kopecky *et al.* 2013; Diekmann *et al.* 2014), are thus likely to lead, in addition to  
548 abiotic changes, to higher biotic pressure. In grasslands, for example, studies have shown that while  
549 some of the species loss under eutrophication is due to direct abiotic effects from altered niche  
550 dimensions (Harpole *et al.* 2016), much of it is due to increased competition for light (Hautier *et al.*  
551 2009). Furthermore, evidence suggests that directional species loss and trait shifts in grasslands under  
552 eutrophication can be mitigated by herbivory that regulates increased competition (Borer *et al.* 2014;  
553 Kaarlejärvi *et al.* 2017). This may suggest a greater relevance of biotic filtering in denser habitats could  
554 contribute to the more directional loss of small-ranged species in grasslands and forests (Figure 3).  
555 Importantly, we can largely rule out that greater directional loss in these habitats than on summits  
556 simply arises from differences in sampling methods. The number of plots, plot size, site area and time  
557 span between surveys did not change the effect of range size on the probability of loss (see Methods  
558 and Table S5). Our cross-habitat comparison therefore supports a possible role of increased  
559 competition in understanding preferential loss of small-ranged species.

560 Although we argue that the above patterns could be directly or indirectly due to global change, we  
561 emphasize that natural succession is also likely to play a role. In semi-natural habitats, successional  
562 dynamics can linger centuries after disturbance and habitat formation (Lichter 1998; Isbell *et al.* 2019).  
563 This raises the question of the extent to which observed vegetation changes are due to global change  
564 or succession (Phillips 1934). The observed shift toward more nutrient-demanding species over time in  
565 our study, appears to be at odds with what would be expected from succession alone. In secondary  
566 succession, the species that establish earliest are those that disperse well (Clements 1916). Thus, fast-  
567 growing, nutrient-demanding species, that tend to produce smaller, more numerous seeds (Waller  
568 1988; Aarssen & Taylor 1992) and have large ranges (Figure 4a), are characteristic of early rather than  
569 late successional stages (Odum 1969; Harper *et al.* 1970). Our findings are therefore more indicative  
570 of human agency, where it has been shown, for instance, that eutrophication can push systems back  
571 to an early successional stage and promote pioneer species (Odum 1969; Walker & Wardle 2014).  
572 However, a complete characterization of the turnover patterns expected from succession alone is still  
573 lacking to compare the results of global change studies with a natural background (Chang & Turner  
574 2019). Further studies of how global change modifies the direction and rate of successional  
575 trajectories will be essential to understanding current biodiversity change.

576 Together, our findings provide a step forward in understanding the nature of compositional turnover  
577 over time. We observe smaller- by larger-ranged species replacement across plant communities of  
578 contrasting habitats. Our results suggest this ubiquitous component of biodiversity change could be  
579 driven by aspects of species niche. Species from nutrient-rich habitats are large-ranged and, nutrient-  
580 demanding species increased across habitats in parallel with the displacement of smaller- by larger-  
581 ranged species. These findings largely agree with studies on plant invasions, where species with the  
582 greatest establishment success typically originate from anthropogenic, fertile habitats (Kalusová *et al.*  
583 2017), and species that are most likely to be invasive and thus expand their range have an acquisitive  
584 resource strategy (Fristoe *et al.* 2021). We speculate that the increase in nutrient-demanding species  
585 may be partially driving the loss of small-ranged species through increased competition, particularly in  
586 habitats with denser vegetation; consistent with the stress gradient hypothesis (Bertness & Callaway  
587 1994). We emphasize that our findings correspond to vegetation dynamics in semi-natural and natural  
588 habitats and are thus not representative of the full impact of human activity (Gonzalez *et al.* 2016).  
589 Given directional species replacements even in these habitats, this raises the question of whether  
590 habitat protection alone is sufficient for species conservation: active conservation efforts may be  
591 needed to prevent biodiversity deficits (Benayas *et al.* 2009; Isbell *et al.* 2019). Finally, the temporal  
592 turnover in relation to species range size that we observe can link biodiversity change across spatial  
593 scales. On the one hand, it can link to macroecological processes such as biotic homogenization,  
594 where increasing evidence suggests spatially disparate communities are becoming more similar in

595 species composition (Li *et al.* 2020). On the other hand, pervasive small- by large-ranged species  
596 replacement can reconcile findings of no net loss in local diversity (Vellend *et al.* 2013; Dornelas *et al.*  
597 2014) with global species loss (Humphreys *et al.* 2019; Lughadha *et al.* 2020), thus partially resolving  
598 the biodiversity conservation paradox.

599

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