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

2 Ingmar R. Staude^{1,2}, Henrique M. Pereira^{1,2,3}, Gergana Daskalova⁴, Markus Bernhardt-Römermann⁵, Martin Diekmann⁶,
3 Harald Pauli^{7,8}, Hans Van Calster⁹, Mark Vellend¹⁰, Anne D Bjorkman^{11,12}, Jörg Brunet¹³, Pieter De Frenne¹⁴, Radim Hédli^{15,16},
4 Ute Jandt^{1,2}, Jonathan Lenoir¹⁷, Isla H. Myers-Smith⁴, Kris Verheyen¹⁴, Sonja Wipf^{18,19}, Monika Wulf²⁰, Christopher Andrews²¹,
5 Peter Barančok²², Elena Barni²³, José-Luis Benito-Alonso²⁴, Jonathan Bennie²⁵, Imre Berki²⁶, Volker Blüml²⁷, Markéta
6 Chudomelová¹⁵, Guillaume Decocq¹⁷, Jan Dick²¹, Thomas Dirnböck²⁸, Tomasz Durak²⁹, Ove Eriksson³⁰, Brigitta Erschbamer³¹,
7 Bente Jessen Graae³², Thilo Heinken³³, Fride Høistad Schei³⁴, Bogdan Jaroszewicz³⁵, Martin Kopecký^{36,37}, Thomas
8 Kudernatsch³⁸, Martin Macek³⁶, Marek Malicki^{39,40}, František Máliš^{41,42}, Ottar Michelsen⁴³, Tobias Naaf⁴⁴, Thomas A. Nagel⁴⁵,
9 Adrian C. Newton⁴⁶, Lena Nicklas³¹, Ludovica Oddi²³, Adrienne Ortmann-Ajkai⁴⁷, Andrej Palaj²², Alessandro Petraglia⁴⁸, Petr
10 Petřík⁴⁹, Remigiusz Pielech^{50,51}, Francesco Porro⁵², Mihai Pușcaș^{53,54}, Kamila Reczyńska³⁹, Christian Rixen¹⁸, Wolfgang
11 Schmidt⁵⁵, Tibor Standovár⁵⁶, Klaus Steinbauer⁸, Krzysztof Świerkosz⁵⁷, Balázs Teleki^{58,59}, Jean-Paul Theurillat^{60,61}, Pavel Dan
12 Turtureanu⁵³, Tudor-Mihai Ursu⁶², Thomas Vanneste¹⁴, Philippine Vergeer⁶³, Ondřej Vild³⁶, Luis Villar⁶⁴, Pascal Vittoz⁶⁵,
13 Manuela Winkler^{7,8}, Lander Baeten¹⁴

14

15

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

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

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

20 4. School of GeoSciences, University of Edinburgh, Edinburgh, Scotland, UK

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

22 6. Institut für Ökologie, Universität Bremen, Bremen, Germany

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

24 8. GLORIA Coordination, Department of Integrative Biology and Biodiversity Research at the University of Natural Resources and Life Sciences,
25 Vienna (BOKU), Vienna, Austria

26 9. Research Institute for Nature and Forest, Brussels, Belgium

27 10. Département de biologie, Université de Sherbrooke, Québec, Canada

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

29 12. Gothenburg Global Biodiversity Centre, 40530 Gothenburg, Sweden

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

31 14. Forest & Nature Lab, Ghent University, Gontrode, Belgium

32 15. Institute of Botany, Czech Academy of Sciences, Brno, Czech Republic

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

34 17. UR "Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN, UMR7058 CNRS), Université de Picardie Jules Verne, 1 rue des Louvels, F-
35 80000 Amiens, France

36 18. WSL Institute for Snow and Avalanche Research SLF, Flüelastrasse 11, Davos, Switzerland

37 19. Swiss National Park, 7530 Zernez, Switzerland

38 20. Leibniz Centre for Agricultural Landscape Research (ZALF), Research Area 2, Müncheberg, Germany

39 21. UK Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB, UK

40 22. Institute of Landscape Ecology, Slovak Academy of Sciences, Štefánikova 3, 814 99 Bratislava, Slovakia

41 23. Department of Life Sciences and Systems Biology, University of Turin, Italy

42 24. GLORIA-Aragon Coordination, Jolube Consultor Botánico y Editor, Jaca, Huesca, Spain

43 25. Centre for Geography and Environmental Science, Exeter University, Penryn Campus, Penryn, Cornwall TR10 9FE, UK

44 26. Faculty of Forestry, University of Sopron, Sopron, Hungary

45 27. BMS-Umweltplanung, Osnabrück, Germany

46 28. Environment Agency Austria, Spittelauer Lände 5, 1090 Vienna, Austria

- 47 29. Laboratory of Plant Physiology and Ecology, University of Rzeszów, Rejtana 16c, PL-35-959 Rzeszów, Poland
- 48 30. Department of Ecology, Environment and Plant Sciences, Stockholm University, Sweden
- 49 31. Department of Botany, University of Innsbruck, Sternwartestr. 15, 6020 Innsbruck, Austria
- 50 32. Department of Biology, NTNU, Høgskoleringen 5, 7091 Trondheim, Norway
- 51 33. University of Potsdam, Institute of Biochemistry and Biology, Maulbeerallee 3, 14469 Potsdam, Germany
- 52 34. Norwegian Institute of Bioeconomy Research, Thormøhlensgate 55, 5006 Bergen, Norway.
- 53 35. Białowieża Geobotanical Station, Faculty of Biology, University of Warsaw, Sportowa 19, 17-230 Białowieża, Poland
- 54 36. Institute of Botany of the Czech Academy of Sciences, Zámek 1, CZ-252 43, Průhonice, Czech Republic
- 55 37. Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, CZ-165 21, Praha 6 – Suchbát, Czech
- 56 Republic
- 57 38. Bavarian State Institute of Forestry Hans-Carl-von-Carlowitz-Platz 1 85354 Freising (Deutschland - Germany)
- 58 39. Department of Botany, Faculty of Biological Sciences, University of Wrocław, Kanonia 6/8, PL-50-328 Wrocław, Poland
- 59 40. Department of Pharmaceutical Biology and Biotechnology, Wrocław Medical University, Poland
- 60 41. Faculty of Forestry, Technical University in Zvolen, Zvolen, Slovakia
- 61 42. National Forest Centre, Zvolen, Slovakia
- 62 43. Department of Industrial Economics and Technology Management, Norwegian University of Science and Technology (NTNU), 7491
- 63 Trondheim, Norway
- 64 44. Leibniz Centre for Agricultural Landscape Research (ZALF), Muencheberg, Germany
- 65 45. Department of forestry and renewable forest resources, Biotechnical Faculty, University of Ljubljana, Večna pot 83, Ljubljana 1000,
- 66 Slovenia
- 67 46. Department of Life and Environmental Sciences, Bournemouth University, Poole, Dorset, UK BH21 5BB
- 68 47. Institute of Biology, University of Pécs, Hungary
- 69 48. Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parco Area delle Scienze 11/A, 43124,
- 70 Parma, Italy
- 71 49. Czech Academy of Sciences, Institute of Botany, Zámek 1, CZ-25243 Průhonice
- 72 50. Department of Forest Biodiversity, University of Agriculture, al. 29 Listopada 46, 31-425 Kraków, Poland
- 73 51. Foundation for Biodiversity Research, ul. Terenowa 4c/6, 52-231 Wrocław, Poland
- 74 52. University of Pavia, Department of Earth and Environmental Sciences, via Ferrata 1, Pavia, 27100, Italy
- 75 53. A. Borza Botanical Garden, Babeş-Bolyai University Cluj-Napoca, Republicii 42, Romania
- 76 54. Center for Systematic Biology, Biodiversity and Bioresources - 3B, Faculty of Biology and Geology, Babeş-Bolyai University Cluj-Napoca,
- 77 Republicii 42, Romania
- 78 55. Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Germany
- 79 56. Department of Plant Systematics, Ecology and Theoretical Biology, Institute of Biology, Loránd Eötvös University, Pázmány s. 1/C, H-1117
- 80 Budapest, Hungary
- 81 57. Museum of Natural History, University of Wrocław, Sienkiewicza 21, PL-50-335 Wrocław, Poland
- 82 58. MTA-DE Lendület Functional and Restoration Ecology Research Group, H-4032 Debrecen Egyetem sqr. 1, Hungary
- 83 59. PTE KPVK Institute for Regional Development 7100 Szekszárd Rákóczi str. 1, Hungary
- 84 60. Fondation J.-M. Aubert, Champex-Lac, Switzerland
- 85 61. Department of Botany and Plant Biology, University of Geneva, Chambésy, Switzerland
- 86 62. Institute of Biological Research Cluj-Napoca, branch of NIRDBS Bucharest, Romania.
- 87 63. Wageningen University, Department of Environmental Sciences, PO Box 47, 6700 AA, Wageningen, the Netherlands
- 88 64. Instituto Pirenaico de Ecología, IPE-CSIC. Avda. de la Victoria, 12. 22700 Jaca, Huesca, Spain
- 89 65. Institute of Earth Surface Dynamics, Faculty of Geosciences and Environment, University of Lausanne, 1015 Lausanne, Switzerland

90

91

92 **Corresponding author:** Ingmar R. Staude

93 **Email:** ingmar.staude@idiv.de

94 **Author Contributions:** IRS, HMP, GD and LB conceived the study, with input from the sREplot working
95 group (MBR, MD, HP, MV, ADB, JB, PDF, RH, UJ, JL, IHM, KV, SW, M. Wulf). IRS performed the analyses,
96 with input from HMP, GD, LB and HVC. IRS, HMP, GD and LB wrote the manuscript, with substantial
97 input from MBR, ADB, MD, IHM, HP, MV, and contributions from JB, HVC, PDF, RH, UJ, JL, KV, SW, M.
98 Wulf, CA, PB, EB, J. Benito-Alonso, J. Bennie, IB, VB, MC, GD, JD, T. Dirnböck, T. Durak, OE, BE, BJG, TH,
99 FHS, BJ, MK, TK, M. Macek, M. Malicki, FM, OM, TN, TAN, ACN, LN, LO, AO, A. Palaj, A. Petraglia, PP,
100 RP, FP, MP, KR, CR, WS, TS, KS, KŚ, BT, JT, PDT, TU, TV, P. Vergeer, P. Vittoz, OV, LV and M. Winkler.
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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 al.*
243 *et 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 m² and 25 m², 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).

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 km² (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. 1.2x10⁶ km²), the species with the smallest AOO were

268 the highly endemic *Draba dolomitica* (c. 11 km²) on summits, *Galium abaujense* (c. 21 km²; endemic to
269 the Carpathians) in forests, and *Pentanema germanicum* (c. 503 km²; 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 (Staude *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.

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

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 (Staudé *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 (β_r for range size (r_i) and β_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 (β_{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 β_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 (β_{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 km²; 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^{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 km² 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 β_{SOR} and β_{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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625

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