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

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49

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

60

61 Introduction

62 The biological diversity on Earth is changing due to human activities. At the global scale, species are going  
63 extinct at rates that signal a mass extinction<sup>1,2</sup>. Per contra, at local scales whether or not diversity is  
64 declining is controversial. Time-series studies find that sites may gain or lose species with no directional  
65 global trend<sup>3-5</sup>. Space-for-time comparisons find substantial losses in local diversity globally due to human  
66 land use<sup>6</sup>. While spatial comparisons are criticized for neglecting that community dynamics are much

67 slower than the speed of environmental changes<sup>7</sup>, time-series studies are challenged for not being  
68 spatially representative of human land use effects<sup>5,8,9</sup>. Yet even in relatively intact places and independent  
69 from changes in local diversity, species appear to be replacing each other more rapidly than predicted  
70 from only natural changes<sup>4,10</sup>. These local-scale replacements alone could lead to species loss at larger  
71 spatial scales, if species with small geographic ranges are frequently replaced by species with larger  
72 ranges. Tests of this prediction remain, however, sparse.

73 Why should small-ranged species decline relative to those with larger ranges within sites? A greater  
74 tendency of species with small ranges to decline or go locally extinct could reflect lower abundance,  
75 greater ecological specificity (narrower niches), or both. Species with small geographic ranges generally  
76 tend to have smaller local populations<sup>11-13</sup>, and with decreasing population size, vulnerability to  
77 environmental change increases<sup>14</sup>. Species with small range size also tend to be more specialized with  
78 narrower niche breadth<sup>15</sup> and may therefore lack flexibility to cope with anthropogenic changes in their  
79 abiotic and biotic environment. As these changes increase, we might expect niche effects to strengthen  
80 leading to high species replacement.

81 For plants, a primary limiting factor in many natural environments is nitrogen (N)<sup>16</sup>. Humans have  
82 substantially altered the distribution and availability of N over the last century<sup>17</sup>. Chronic high N-  
83 deposition has now saturated many ecological systems, exceeding critical loads<sup>18-21</sup>. Increases in a key  
84 resource like N reorder competitive relationships among plant species within communities, favoring N-  
85 demanding species at sites of high N-deposition across many ecosystems<sup>22-28</sup>. Yet, beyond local-scale  
86 community changes, how these shifts link to biodiversity change across spatial scales remains largely  
87 unexplored.

88 Here, we explore the role of species range size and N-deposition in driving the systematic shifts in species  
89 composition and scale-dependent patterns of diversity changes observed in extensive long-term  
90 vegetation data<sup>27,29,30</sup>. The N-niche of species relates to their range size in that species that use N more

91 efficiently tend to have smaller ranges relative to N-demanding species<sup>31</sup>. This may reflect the ability of N-  
92 demanding species to grow faster<sup>32,33</sup>. Faster-growing species usually have smaller seeds<sup>34</sup> enabling  
93 further dispersal<sup>35</sup>, and more widely dispersed species tend to have wider ranges<sup>36</sup>. Increases in N are thus  
94 hypothesized to favor larger-ranged species that grow faster under more fertile conditions, allowing them  
95 to become superior competitors, reducing the survivorship of N-efficient, small-ranged species. Patterns  
96 of global biodiversity loss and local maintenance of diversity would be consistent with such species  
97 replacements, with a few large-ranged species replacing many small-ranged species in a process termed  
98 biotic homogenization<sup>37</sup>.

99 We compiled a database of 68 resurvey studies of herb-layer communities from semi-natural, temperate  
100 forests spread across Europe (Fig. 1). We use these data to ask: 1. Have small-ranged forest plant species  
101 declined over time? 2. Do any such trends simply reflect their lower abundance (given the range size --  
102 abundance correlation), or does it reflect niche effects that strengthen with N-deposition? 3. Do species  
103 replacements under N-deposition evoke a homogenization pattern with small-scale richness remaining  
104 constant on average while larger-scale richness declines?

105

## 106 Results

107 Plant species that went extinct from a study site had smaller range sizes than species that persisted and  
108 those that colonized. In contrast, persisting and colonizing species had similar range sizes (Fig. 2a and  
109 Supplementary Table 2). If this pattern reflected only lower abundance at the study site, range size should  
110 not add power for predicting extinctions once abundance is controlled for. Here, we estimate abundance  
111 as occupancy across plots within a site<sup>38,39</sup>. Occupancy was a strong predictor of probability of extinction  
112 (slope:  $\beta = -3.63$ , standard deviation:  $\sigma = 0.28$ ). Over an average time interval of 38 years, species of  
113 average occupancy had a 10% chance of going extinct from a study site relative to up to 60% for species of  
114 low occupancy (Fig. 2b and Supplementary Table 3). Range size still had a negative effect on species'

115 extinction probability even after controlling for occupancy ( $\beta = -0.21, \sigma = 0.05$ ). For species of  
116 average occupancy, extinction probabilities declined by more than 50% as range size increased (Fig. 2c  
117 and Supplementary Table 3). The total effect of range size became only slightly stronger when occupancy  
118 was not controlled for ( $\beta = -0.28, \sigma = 0.06$ ), suggesting that only 25 % of the range size effect reflects  
119 occupancy (Supplementary Table 3). As species' range size presents a basic summary of the ecological  
120 characteristics of species (mainly in terms of climatic and edaphic niches<sup>40,41</sup>), the remaining effects of  
121 range size likely reflect aspects of species niches. Higher cumulative N-deposition ( $\Delta N$ , see Methods for  
122 details) between surveys sharply increased probabilities of extinction from a site ( $\beta = 0.37, \sigma = 0.15$ ;  
123 Fig. 3a, Supplementary Table 4), having accounted for confounding variables such as inter-census time  
124 period, study area and latitude (see Methods for all variables). This increase in extinction probability  
125 disproportionately affected small-ranged species, as shown by the negative interaction between range size  
126 and N-deposition ( $\beta = -0.1, \sigma = 0.03$ ). Extinction probability of the species with the smallest range  
127 sizes increased from ~4% to ~27% as N-deposition increased from 45 to 721 kg ha<sup>-1</sup> (with other predictors  
128 at their mean). In contrast, risks of extinction for large-ranged species were much lower and more stable  
129 (Fig. 3b and Supplementary Table 4).

130 These results show that probabilities of extinction increase with N-deposition, mostly due to the loss of  
131 small-ranged species. Has this eroded study-level species richness or have increases in colonization  
132 balanced these extinctions? We found no systematic shifts in species richness within study sites as N-  
133 deposition increased, again accounting for covariates ( $\beta = 0.11, \sigma = 0.15$ ; Fig. 3c, Extended Data 1 and  
134 Supplementary Table 5). This implies that higher levels of N-deposition have facilitated the replacement of  
135 small-ranged species. Colonizing species had larger ranges (Fig. 2a) and included several non-native  
136 species ( $\beta = 0.44, \sigma = 0.16$ ; Fig 3d, Supplementary Table 5). As more N-efficient species went extinct  
137 with higher N-deposition ( $\beta = -0.25, \sigma = 0.12$ ; Fig 3e) and colonizing species generally had higher N-

138 demands (Extended Data 2), community composition has shifted systematically towards more N-  
139 demanding species ( $\beta = 0.28, \sigma = 0.12$ ; Fig. 3e and Supplementary Table 6).

140 Although small-scale diversity has not declined, N-deposition may threaten other forms of diversity. As  
141 small-ranged, N-efficient species are extirpated and replaced by wide-ranging, non-native and N-  
142 demanding species, these forest plant communities have converged in composition. Gilliam<sup>19</sup> predicted  
143 that such declines in beta (and thus gamma) diversity would occur as N-deposition tends to increase the  
144 spatial homogeneity of nutrient availability. Variation in nutrient availability among sites has indeed  
145 declined since the baseline surveys (difference between variances:  $\delta = -0.16, \sigma = 0.08$ ) (Fig. 3f and  
146 Supplementary Table 7, see Methods for estimation of nutrient availability). This homogenization in  
147 nutrient availability appears linked to declines in overall (biome-scale) species richness as gamma-diversity  
148 across these 68 sites declined by 4% (from 1,012 to 972 species).

149

150 Discussion

151 Using large-scale temporal vegetation change datasets, we provide evidence that the geographic range  
152 size of species predicts long-term shifts in forest-floor plant communities. Small-ranged species are  
153 replaced by those with larger ranges and our results suggest this is more due to species niches than  
154 abundances. The loss of small-ranged species amplified under high N-deposition and, consistent with our  
155 expectation that species' range size and N-demand positively correlate, communities shifted towards  
156 species with higher N-demand. Despite the loss of small-ranged species, the number of species within  
157 study sites has not declined in response to increasing N-deposition, suggesting that species losses have  
158 been balanced by species gains. Nevertheless, the floristic distinctiveness of these forests erodes as more  
159 cosmopolitan and non-native species replace a set of more finely-adapted species. These replacements  
160 ran in parallel with the abiotic homogenization resulting from chronic N-deposition and scaled to a loss of  
161 biodiversity in Europe's temperate forests in recent decades.

162 Our study confirms that small population size is a strong predictor of extinction from a site<sup>14,42,43</sup>. Yet this  
163 did not provide much explanation for the greater extinction risk of small-ranged species as would be  
164 expected given a positive range size–abundance relationship. This suggests not all small-ranged plant  
165 species in these forests have small populations. In fact, plants show many exceptions to this relationship.  
166 For example, 87% of small-ranged species from the British Isles are locally common<sup>44</sup>; conversely one of  
167 the largest ranging woody species of the globe, *Juniperus communis*, has small populations in many  
168 regions<sup>45</sup>. Indeed, several plant studies find that range size and abundance do not necessarily covary<sup>45,46</sup>.  
169 This suggests that range size affects species' extinction probability mostly via niche rather than  
170 demographic effects, a conjecture supported by the fact that N-deposition mostly affected small-ranged  
171 (narrow niche) species.

172 Despite declines in small-ranged species, forest sites in our study did not systematically decrease in  
173 species richness. This suggests species losses are offset by species gains. This finding echoes other  
174 resurvey studies that document little directional temporal trend in small-scale species richness despite  
175 increased species turnover<sup>4,10</sup>. But similarly, this finding is likely to not reflect the full impact of intensive  
176 human land use<sup>8,9</sup> as our study sites are confined to semi-natural forests. Given that the effect of range  
177 size reflects species' niches, species turnover accelerated under N-deposition and communities not only  
178 shifted towards larger range size but also towards higher average N-demands. Other studies from forest  
179 ecosystems report the same shifts towards more N-demanding species from eutrophication and similarly  
180 limited effects of N-deposition on forest-floor plant species richness<sup>24,47–49</sup>. This contrasts with open-  
181 canopy ecosystems that, being not primarily light limited, consistently lose species from N-addition  
182 through shading<sup>50,51</sup>. Beyond a threshold, however, N-deposition also reduces plant diversity in forests, as  
183 shown in North America where roughly a quarter of 14,000+ sites showed susceptibility to N-driven  
184 species losses<sup>30</sup>.



185 Although we find no evidence of a directional change in species richness within studies, the total number  
186 of species across studies (gamma diversity) has declined. The observed 4% decline in gamma-diversity  
187 likely underestimates the true species loss in the European temperate forest biome, as studies in our  
188 database are not completely spatially representative of key human pressures in Europe. Resurveys have  
189 been selected to be especially located in large, historically continuously forested (ancient) and semi-  
190 natural forests where no land-use change took place prior to the baseline survey and no large change in  
191 management occurred between the surveys. Change in land use and other disturbances that open up  
192 forest canopies and increase light availability may exacerbate effects of global warming by eliminating the  
193 thermal insulating layer that protects understories from thermophilisation<sup>52,53</sup>. However, changes in light  
194 availability usually occur at the plot-level as opposed to N-deposition that acts at the scale of an entire  
195 study area. Because we evaluated community dynamics at the study-level, we expect that light availability  
196 changes do not confound the N-signal we found.

197 Nitrogen releases to the environment remain high in Europe (<https://www.eea.europa.eu/airs/2018>).  
198 Despite recent declines, these emissions still exceed critical loads for most of Europe's protected  
199 habitats<sup>54</sup>. It is important to learn what long-lasting effects N-deposition may have on Europe's  
200 ecosystems and how reversible these are as emissions decline. In contrast to the rapid recovery of plot-  
201 scale experimental communities, where species are still present in the area and able to colonize once N  
202 additions are ceased<sup>22,55</sup> (but see ref.<sup>56</sup>), the loss of small-ranged species from entire regions is far less  
203 likely to be reversed in the short term. At this point, it is thus unclear whether the declines in N emissions  
204 mandated under the EU National Emission Ceilings Directive (2016/2284/EU) will be feasible or sufficient  
205 to allow the recovery of Europe's plant species and communities.

206

207 Methods

208 Database

209 We compiled a database containing data from 68 understory resurvey studies distributed across the European  
210 temperate deciduous forest biome (see [www.forestreplot.ugent.be](http://www.forestreplot.ugent.be) and ref.<sup>57</sup> for inclusion criteria). These studies  
211 cover 15 European countries, from Norway in the north to Slovenia in the south and from Ireland in the west to  
212 Poland in the east (Fig. 1). All surveys were conducted in historically continuously forested ‘ancient’ and semi-natural  
213 deciduous forest (sensu ref.<sup>58</sup>). These forests did thus not experience historical land-use change prior to the first  
214 (baseline) survey and between the surveys. Furthermore, the forests are mostly managed, but did not experience  
215 stand-replacing disturbances between the baseline survey and the most recent resurvey. In each survey, the  
216 herbaceous understory was recorded in multiple permanent or quasi-permanent plots. Plot size ranged between  
217 1m<sup>2</sup> to 1000m<sup>2</sup> across studies (median: 400 m<sup>2</sup>). Number of plots ranged from 10 to 190 across studies (median: 43  
218 plots, Supplementary Figure 1b). Plots were allocated across areas ranging from 1ha to c. 2.5x10<sup>6</sup> ha (median: 1700  
219 ha, Supplementary Figure 1d). Baseline surveys were carried out between 1933 and 1999. The most recent resurveys  
220 were made between 1969 and 2017 generating time intervals between surveys from 15 to 78 years (median: 42  
221 years, Supplementary Figure 1c). We accounted for changes in taxonomy between surveys by determining the  
222 accepted species name for each species using GBIFs backbone taxonomy ([gbif.org](http://gbif.org)). Harmonization thus ensured no  
223 double-counting species due to synonymy. Our database contains 1,162 species in total.

224 Species level variables

225 Species’ trajectory

226 We determined the trajectory of species at the study level. We classified species present in the baseline survey but  
227 absent in the resurvey as extinct. Those present in both surveys were classified as persisting. Those absent in the  
228 baseline survey but present in the resurvey were classified as colonizing. Resurveys of permanent plots always miss  
229 some species, generating pseudo-colonizations and extinctions that can inflate these estimates for rare species<sup>59,60</sup>.  
230 We did not correct our estimates of colonization and extinction for bias proposed by Beck<sup>59</sup> as we adjust for initial  
231 abundance (occupancy across plots) in our model which is strongly correlated with any such bias<sup>61</sup>. This means our  
232 estimates of the effects of initial abundance on extinction may be slightly inflated.

233 Occupancy

234 For each study, we calculated the initial occupancy of species. This is the number of plots that a species has occupied  
235 in the baseline survey, divided by the total number of plots in that survey. Occupancy approximates abundance  
236 because, empirically and for any biologically relevant point process pattern, they strongly and positively correlate at  
237 local to regional scales<sup>38,39</sup>.

238 Range size

239 Species range sizes were estimated from the species point occurrence records in GBIF (gbif.org, 18 January 2019). In  
240 total, c. 100 million geographically referenced records were available for 1,147 species in our database (1.3 %  
241 missing species) after excluding unlikely and impossible coordinates<sup>63</sup>. Records were aggregated to a hexagonal grid  
242 (ISEA3H) at three spatial grains: 3.6 km<sup>2</sup>, 10.7 km<sup>2</sup> and 32 km<sup>2</sup>. The number of cells any given species occupies on  
243 such grid represents its range size. Range size therefore measures species' area of occupancy (AOO, expressed in  
244 km<sup>2</sup>). Results in the main text are based on range sizes estimated at mid-resolution (10.7 km<sup>2</sup>). At this resolution, the  
245 smallest ranging species was *Poa pannonica* A.Kern. with an estimated AOO of 21.4 km<sup>2</sup>, the species with the largest  
246 range was the annual meadow grass, *Poa annua* L., with an AOO of c. 1.6x10<sup>6</sup> km<sup>2</sup> (Extended Data 3).

247 For our analyses we use AOO and not the extent of occurrence (EOO, which includes also discontinuities in  
248 occupancy) as AOO is a markedly better predictor of mean site abundance and population size<sup>13,64</sup>. While AOO  
249 measured from GBIF point occurrence data is increasingly used in the scientific literature, incomplete spatial  
250 coverage of digital biodiversity data can lead to an underestimation of range sizes<sup>65</sup>. Specifically, Middle and  
251 Northern Asia are some of the most data deficient regions of the world<sup>66</sup>. This may be problematic for European  
252 species that extend into these regions. We therefore tested how well our estimates of AOO match estimates of EOO  
253 for species where range maps from two renowned distribution atlases were available<sup>67,68</sup> (available for 796 species,  
254 31% missing). The distribution ranges were digitized from scanned atlas pages and rasterized on a 20 km x 20 km grid  
255 in the Lambert azimuthal equal-area projection to calculate EOO for all 796 species. Spearman's correlation between  
256 AOO and EOO was high ( $\rho = 0.71$ ) for these species. As an overall positive correlation might obscure a weak  
257 correlation for continental species that extend into data deficient regions, we also tested for range attribution. We  
258 identified 155 species as continental using species indicator values for continentality from ref.<sup>69</sup> (species with values  
259  $\geq 6$  were classified as continental). Excluding those species made the correlation between AOO and EOO only slightly

260 stronger ( $\rho = 0.74$ ; Extended Data 3). We therefore assume that data limitations are a less material problem for our  
261 set of species.

262

263 Study-level variables

264 Nitrogen-deposition

265 We quantified N-deposition using the EMEP database ([https://emep.int/mscw/mscw\\_moddata.html](https://emep.int/mscw/mscw_moddata.html)) with c. 11 km  
266 (0.1°) grid resolution. Here we chose to focus singly on NO<sub>x</sub> deposition for three reasons. 1) Increasing evidence  
267 suggest that the two forms of N-deposition, oxidized (NO<sub>x</sub>) and reduced (NH<sub>y</sub>) N-deposition, have differential,  
268 habitat-specific effects on plant communities<sup>70-72</sup>. Whereas NH<sub>y</sub> is the most important driver for the decline in plant  
269 diversity in grasslands, forest vegetation is found to be most responsive to NO<sub>x</sub><sup>71</sup>. 2) Model estimates of NO<sub>x</sub>  
270 deposition also have a lower degree of uncertainty and bias than estimates of NH<sub>y</sub><sup>73</sup>. Local-scale variability of NH<sub>y</sub>  
271 deposition is considerably higher as most of it is deposited near the source<sup>74</sup>, this variability is likely to be poorly  
272 reflected when studying N-effects over larger regions as done in this study. 3) NO<sub>x</sub> is spatially correlated with NH<sub>y</sub>  
273 deposition in Europe ( $\rho = .69$  in this study) and thus representative for broader N-effects. We quantified the  
274 cumulative wet and dry deposition of oxidized N (hereinafter and in the main text referred to simply as N-deposition)  
275 based on the methods described in ref.<sup>49</sup>. First, we calculated N-deposition between 1900 and the year of the  
276 baseline survey ( $N_{t1}$ ), second we quantified the cumulative N-deposition between 1900 and the resurvey ( $N_{t2}$ ), and  
277 third we calculated the difference,  $N_{t2} - N_{t1}$ , to quantify N-deposition between surveys (inter-census N-deposition or  
278  $\Delta N$ ).  $\Delta N$  ranged from 45 to 721 kg ha<sup>-1</sup> (Supplementary Figure 1). Results in the main text are based on  $\Delta N$ .

279 Change in species numbers

280 Changes in the number of species found in the resurvey versus the baseline survey were quantified as the difference  
281 in size of the recorded species pool for each study (Extended Data 1).

282 Change in non-native species

283 For each study, species were classified as native or non-native. This classification is based on the Global Register of  
284 Introduced and Invasive Species (GRIIS; <http://www.griis.org>). GRIIS lists species that are non-native in a given  
285 country. With these species lists we could flag, for each study, species that are non-native in the country of the  
286 study. To calculate the change in non-native species between surveys, we subtracted the proportion of non-native  
287 species in the total pool of species recorded in the baseline from the proportion of non-native species in the total  
288 pool of species recorded in the resurvey. Thus, we quantify the change in percentage points (Supplementary Figure  
289 3b). Calculation of relative change was not possible because frequently there were no non-native species in the  
290 baseline survey (26% of studies, Supplementary Figure 3a). The mean number of non-native species in the baseline  
291 survey and the resurvey was 5 and 7 (rounded to the next integer), respectively. The mean number of native species  
292 was 110 (baseline survey) and 102 (resurvey).

#### 293 Change in nitrophilous species and nutrient availability

294 We estimated changes in species' N-demands using Ellenberg's indicator values (EIVs). EIVs were developed for  
295 Central Europe and classify species' habitat niches and their peak occurrence along environmental gradients<sup>75</sup>. In  
296 particular, we used EIVs for N or more general productivity<sup>76</sup> that classify species growing on the poorest soils (N-  
297 number = 1) to species growing on the most productive soils with excessive nutrient availability (N-number= 9)  
298 (Extended Data 2). For each study and survey, we averaged N-numbers across species. Because EIVs equally reflect  
299 environmental conditions<sup>47</sup>, these average values approximate both the mean N-demand of a community and the  
300 nutrient availability at each survey. To quantify the change in a community's mean N-demand, we subtracted the  
301 mean N-demand of the baseline community from the mean N-demand of the resurvey community. To better  
302 understand what drives changes in communities mean N-demands, we calculated the average N-demand of extinct  
303 and colonizing species (Extended Data 2) for each study.

304

305 Data analyses

306 The entire statistical analysis and R-code is provided in the supplementary information as an R markdown file. The  
 307 rethinking package<sup>77</sup> was used to compile the following models to Stan Hamiltonian Monte Carlo code. For brevity,  
 308 all models are presented without priors (complete models and R code is available on figshare  
 309 [<https://figshare.com/s/45d71eb77c23c11bc857>]).

310 We first compared range sizes between extinct, persisting and colonizing species, where species' trajectories are  
 311 defined at the study scale. Clearly range size is non-normal distributed and starkly right skewed. Since normality of  
 312 the outcome conditional on the covariates is the central assumption of Gaussian linear models and range size was  
 313 too skewed for Poisson regression, we normalized range size using an order-quantile transformation<sup>78</sup>. We  
 314 predicted range size ( $r_i$ ) with trajectory ( $\beta_{status[i]}$ ) and allowed each coefficient to vary by each study  
 315 ( $\alpha_{study[i],status[i]}$ ). The mathematical form of the resulting model is:

$$316 \quad \begin{aligned} r_i &\sim Normal(\mu_i, \sigma) \\ \mu_i &= \beta_{status[i]} + \alpha_{study[i],status[i]} \end{aligned}$$

317 We calculated pairwise contrasts (e.g.,  $\beta_{colonizing} - \beta_{extinct}$ ) to compare range sizes between species trajectories.

318 Next, we asked can species' extinction probability be predicted by species' occupancy at the time of the baseline  
 319 survey? Here, we only analyzed species present at the baseline survey, omitting colonizing species. The outcome is a  
 320 0/1 (Bernoulli) indicator that a given species persisted or became extinct in a study ( $e_i$ ). As the outcome is binomially  
 321 distributed, we used logistic regression to predict species' extinction probabilities as a function of occupancy. We  
 322 allowed intercepts to vary with study ID ( $\alpha_{study[i]}$ ) and species ( $\gamma_{species[i]}$ ) and the effect of occupancy ( $f_i$ ) to vary by  
 323 study ID ( $\beta_{f,study[i]}$ ). The mathematical form of the model is:

$$324 \quad \begin{aligned} e_i &\sim Binomial(1, p_i) \\ \text{logit}(p_i) &= \bar{\alpha} + \alpha_{study[i]} + \gamma_{species[i]} + \beta_{f,study[i]} * f_i \end{aligned}$$

325 Controlling for the effect of occupancy, we then added the range size predictor to the previous model. We used the  
 326 Widely Applicable Information Criterion (WAIC) to decide whether the model's out of sample predictions improve  
 327 when varying slopes on range size are included<sup>77</sup>. The resulting model is:

328 
$$e_i \sim \text{Binomial}(1, p_i)$$

$$\text{logit}(p_i) = \bar{\alpha} + \alpha_{\text{study}[i]} + \gamma_{\text{species}[i]} + \beta_{f, \text{study}[i]} * f_i + \beta_r * r_i$$

329 where  $\beta_r$  is the effect of range size ( $r_i$ ).

330 We also modelled the effect of range size alone to estimate by how much it decreases occupancy when is part of the  
331 model:

332 
$$e_i \sim \text{Binomial}(1, p_i)$$

$$\text{logit}(p_i) = \bar{\alpha} + \alpha_{\text{study}[i]} + \gamma_{\text{species}[i]} + \beta_r * r_i$$

333 Next, we sought to explain variation in average extinction probability across species between studies. In particular,  
334 we tested the effect of inter-census N-deposition on the outcome. The effect of N-deposition could, however, be  
335 confounded by the time between surveys ( $\Delta t$ ). Cumulative N-deposition is a function of  $\Delta t$ , and  $\Delta t$  itself is likely to  
336 affect average extinction probability. We therefore include  $\Delta t$  in the model.

337 Furthermore, the year of the baseline survey ( $t_1$ ) can influence the outcome. For example, baseline surveys from  
338 later years are likely to be associated to higher cumulative N-deposition than those from earlier years. This might  
339 have already affected community composition to the extent that fewer extinctions occur in communities that were  
340 sampled in later years as these have already lost species. In our data  $t_1$  is strongly and negatively correlated to  $\Delta t$ ;  
341 the earlier the year of the baseline survey, the longer the time between surveys ( $\rho = -0.91$ , Extended Data 4). This  
342 correlation is also reflected in a strong negative correlation between cumulative N-deposition at the year of the  
343 baseline survey and time between surveys ( $\rho = -0.67$ ; Extended Data 4). A directed acyclic graph of presumed  
344 causal links between predictors and response (Extended Data 5) shows that including time between surveys in the  
345 model controls for the confounding effect of year of the baseline survey and importantly, for environmental changes  
346 that preceded this survey, such as the cumulative N-deposition at the year of the baseline survey.

347 In addition to these potential confounding variables, the number of plots, their size and the size of the area in which  
348 surveys were carried out may directly affect the outcome. For instance, a species with occupancy 0.1 occupied 1 or  
349 10 plots in studies of 10 or 100 plots, respectively and demographic fluctuations should be higher in smaller  
350 plots/areas that naturally comprise fewer individuals. As this may clearly affect the average extinction probability  
351 across species, we included these variables in the model. Finally, we also included latitude as a covariate in order to

352 account for latitudinal patterns that might be associated to climate change. Together, this generates the following  
 353 model:

$$\begin{aligned}
 e_i &\sim \text{Binomial}(1, p_i) \\
 \text{logit}(p_i) &= \bar{\alpha} + \alpha_{\text{study}[i]} + \gamma_{\text{species}[i]} \\
 &+ \beta_{f, \text{study}[i]} * f_i + \beta_r * r_i \\
 &+ \beta_n * n_i + \beta_t * t_i + \beta_q * q_i + \beta_s * s_i + \beta_a * a_i + \beta_l * l_i
 \end{aligned}$$

355 where  $\beta_n, \beta_t, \beta_q, \beta_s, \beta_a, \beta_l$  are the effects of inter-census N-deposition ( $n_i$ ), inter-census time period ( $t_i$ ), plot  
 356 number ( $q_i$ ), plot size ( $s_i$ ), site area ( $a_i$ ) and latitude ( $l_i$ ), respectively.

357 We then asked whether any increase in average extinction probability across species due to N-deposition is driven by  
 358 an increasing extinction probability among small-ranged species or simply a generally higher extinction probability  
 359 across all range sizes. For this, we included the interaction effect between N-deposition and range size in the model:

$$\begin{aligned}
 e_i &\sim \text{Binomial}(1, p_i) \\
 \text{logit}(p_i) &= \bar{\alpha} + \alpha_{\text{study}[i]} + \gamma_{\text{species}[i]} \\
 &+ \beta_{f, \text{study}[i]} * f_i + \beta_r * r_i \\
 &+ \beta_n * n_i + \beta_t * t_i + \beta_q * q_i + \beta_s * s_i + \beta_a * a_i + \beta_l * l_i \\
 &+ \beta_{nr} * n_i * r_i
 \end{aligned}$$

361 where  $\beta_{nr}$  is the slope of the interaction between inter-census N-deposition ( $n_i$ ) and range size ( $r_i$ ).

362 Until now, we only analyzed the dynamics of species present at the baseline. To these, we added further models to  
 363 assess effects on colonizing species. We first asked: are changes in species number ( $d_i$ ) explained by N-deposition?  
 364 Again we controlled for inter-census time period, plot number, plot size, site area and latitude, generating the  
 365 following model:

$$\begin{aligned}
 d_i &\sim \text{Normal}(\mu_i, \sigma) \\
 \mu_i &= \alpha + \beta_n * n_i + \beta_t * t_i + \beta_q * q_i + \beta_s * s_i + \beta_a * a_i + \beta_l * l_i
 \end{aligned}$$

367 To visualize the effect of N-deposition, we used a predictor residual plot. In these, the outcome is regressed against  
 368 the variation of N-deposition that is left unexplained by the other predictor variables in the model. Predictor residual  
 369 plots allow us to display the actual data while controlling for all other predictors. Because the unit of observation in



370 this model is the study, we have 68 observations. To display the influence of each data point on posterior  
371 predictions, we scaled point sizes by their Pareto k value<sup>77</sup>. We then predicted the percentage point change in non-  
372 native species using the same predictors as in the previous model, again using a predictor residual plot to display the  
373 results.

374 We also tested whether community composition shifts towards more N-demanding species with higher N-  
375 deposition. For this, we regressed 1) the average N-demand of extinct species ( $m_i$ ) and 2) the change in mean N-  
376 demand of the entire community ( $w_i$ ) against N-deposition:

$$377 \quad \begin{aligned} m_i/w_i &\sim \text{Normal}(\mu_i, \sigma) \\ \mu_i &= \alpha + \beta_n * n_i \end{aligned}$$

378 Finally, we tested whether the variance of nutrient availability across studies was greater in the period of the  
379 resurveys than in the period of the baseline surveys. Here, the model is:

$$380 \quad \begin{aligned} a_{ij} &\sim \text{Normal}(\mu_{ij}, \sigma_{ij}) \\ \mu_{ij} &= \beta_0 + \beta_1 * t_{ij} \\ \sigma_{ij} &= \gamma_0 + \gamma_1 * t_{ij} \end{aligned}$$

381 where  $a_{ij}$  is the availability of N for the  $i$ th study and  $j$ th survey period,  $\beta_0$  and  $\gamma_0$  are the mean and standard  
382 deviation of the baseline survey respectively,  $\beta_1$  and  $\gamma_1$  are the expected difference between mean and standard  
383 deviation of the resurvey and baseline survey respectively, and  $t_{ij}$  is a 0/1 indicator for survey period.

384

385 Author Contributions

386 I.R.S., D.M.W. and L.B. conceived the study, with input from the sREplot working group (M.B.R., A.D.B., J.B., P.D.F.,  
387 R.H., U.J., J.L., F.M., K.V., and M.W.). I.R.S. performed the analyses, with input from D.M.W. and L.B. I.R.S., D.M.W.  
388 and L.B. wrote the manuscript, with input and contributions from M.B.R., A.D.B, J.B., P.D.F., R.H., U.J., J.L., F.M., K.V.,  
389 M.W., H.M.P., P.V., A.O.A., R.M., I.B., M.C., G.D., T. Dirnböck, T. Durak., W.S., T.H., F.H.S., B.J., M.K., M. Macek, M.  
390 Malicki, T.N., T.A.N., P.P., K.R., T.S., K.S., B.T., H.V.C., O.V. Authorship order was determined as follows: (1) core

391 authors; (2) sREplot participants (alphabetical) and other major contributors; (3) authors contributing community  
392 composition data and to an advanced version of the manuscript (alphabetical).

393

394 Data availability

395 Community change and environmental site-level data are available on figshare,  
396 [<https://figshare.com/s/45d71eb77c23c11bc857>]. Species composition data are available from forestreplot.ugent.be  
397 but restrictions apply to the availability of these data, which were used under license for the current study, and so  
398 are not publicly available. Data are however available from the authors upon request and with permission of the  
399 forestREplot consortium.

400

401 Code availability

402 R code for all analyses is available on figshare [<https://figshare.com/s/45d71eb77c23c11bc857>].

403

404 Competing interests

405 The authors declare no competing interests.

406

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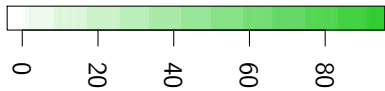
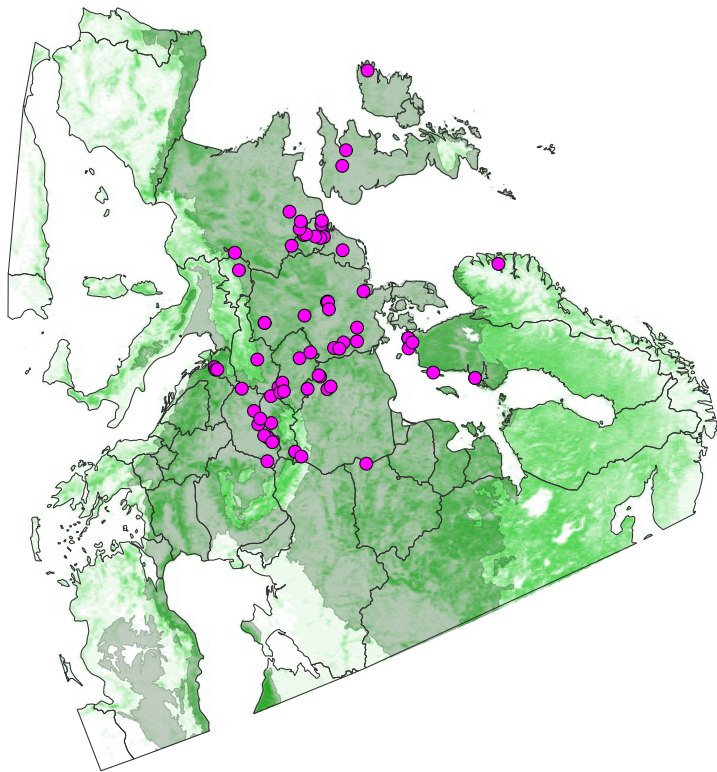
581 Figure legends

582 Figure 1: Map of all 68 resurvey studies included in the forestREplot database, the temperate deciduous  
583 forest biome in Europe (shaded area)<sup>79</sup> and forest cover for the year 2000 (in green)<sup>80</sup>. Light to dark  
584 shades of green represent forest cover ranging from 0 to 100% at a spatial resolution of 30 meters.

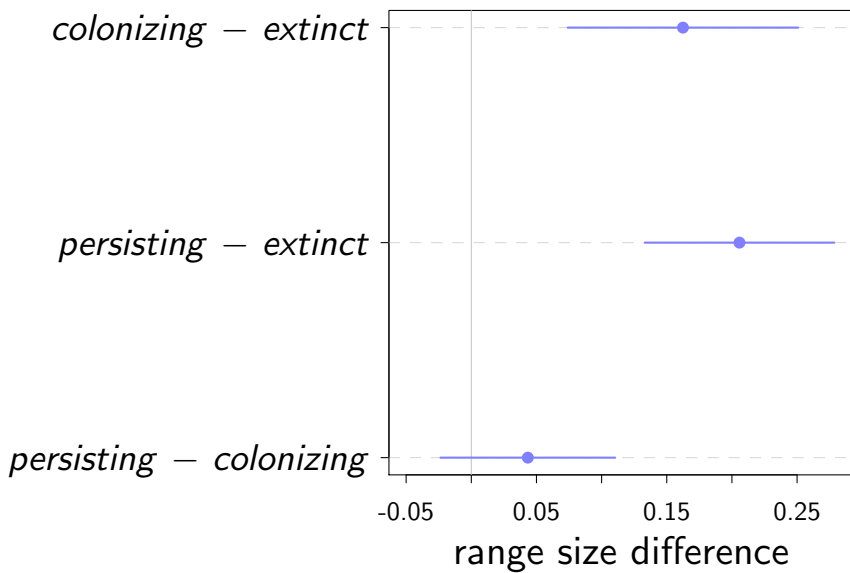
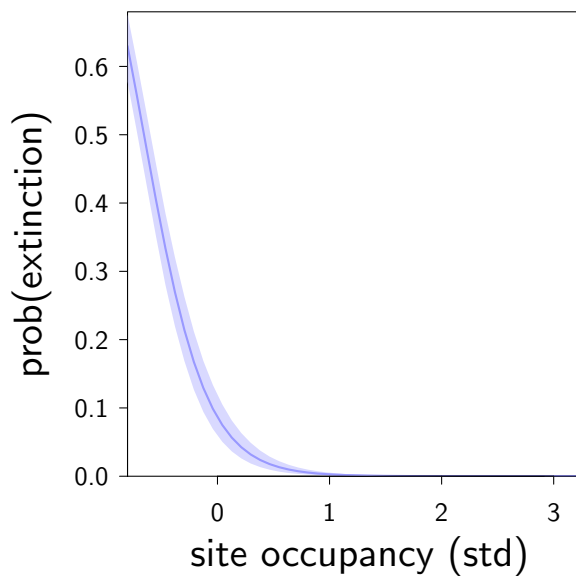
585

586 **Figure 2: Species that go extinct from a study site have smaller ranges than persisting and colonizing ones.**  
587 **Even after controlling for site occupancy, species' range size predicts probability of extinction. a,** Expected  
588 differences in normalized range size between colonizing, persisting and extinct species. **b,** Effect of  
589 species' site occupancy at the time of the baseline survey on probability of extinction, x axis is  
590 standardized, so that zero represents the average site occupancy. **c,** Effect of species' range size on  
591 probability of extinction, after controlling for site occupancy (line shows expectation for site occupancy at  
592 its mean). Line segments in **a** represent  $\pm 2$  standard deviations from the mean. Transparent ribbons in **b**  
593 and **c** represent the 89% credible intervals for model mean predictions. Model parameters are shown in  
594 Supplementary Table 2 and 3.

595  
596 **Figure 3: Small-ranged species drive the increase in average extinction risk from high N-deposition. Although**  
597 **colonizing species sustain species number, composition shifts towards more non-native and N-demanding**  
598 **species. Spatial heterogeneity of nutrient availability decreases over time. a,** Effect of inter-census nitrogen  
599 deposition ( $\Delta N$ ) on average probability of extinction across species. **b,** Triptych plot for the effect of range  
600 size on probability of extinction at different levels of  $\Delta N$ , holding all other predictors at their mean.  $\Delta N$   
601 levels are minimum (left), mean (center), and maximum (right)  $\Delta N$ . **c-d,** Predictor residual response plot of  
602 the relationship between inter-census nitrogen deposition and change in study-level species richness (**c**)  
603 and percentage point change in non-native species (**d**). **e,** Ellenberg indicator values for nitrogen ( $eiv_N$ )  
604 averaged across extinct species and the change in  $eiv_N$  averaged across all species regressed against inter-  
605 census nitrogen deposition. **f,** Violin plot (density curve and boxplot) of nutrient availability (estimated  
606 with community mean  $eiv_N$ ) at the time of the baseline survey ( $t_1$ ) and resurvey ( $t_2$ ). Transparent ribbons  
607 in **a - e** represent the 89% credible intervals for model mean predictions. Point size in **c - e** is scaled by  
608 relative LOOIS Pareto  $k$  values. Larger points are more influential. Model parameters are shown in  
609 Supplementary Table 4, 5, 6 and 7.



Forest cover (%)

**a****b****c**