

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

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

31

32 Introduction

33 The biological diversity on Earth is changing due to human activities. At the global scale, species are going
34 extinct at rates that signal a mass extinction^{1,2}. Per contra, at local scales whether or not diversity is
35 declining is controversial. Time-series studies find that sites may gain or lose species with no directional
36 global trend³⁻⁵. Space-for-time comparisons find substantial losses in local diversity globally due to human
37 land use⁶. While spatial comparisons are criticized for neglecting that community dynamics are much
38 slower than the speed of environmental changes⁷, time-series studies are challenged for not being
39 spatially representative of human land use effects^{5,8,9}. Yet even in relatively intact places and independent
40 from changes in local diversity, species appear to be replacing each other more rapidly than predicted
41 from only natural changes^{4,10}. These local-scale replacements alone could lead to species loss at larger
42 spatial scales, if species with small geographic ranges are frequently replaced by species with larger
43 ranges. Tests of this prediction remain, however, sparse.

44 Why should small-ranged species decline relative to those with larger ranges within sites? A greater
45 tendency of species with small ranges to decline or go locally extinct could reflect lower abundance,
46 greater ecological specificity (narrower niches), or both. Species with small geographic ranges generally
47 tend to have smaller local populations¹¹⁻¹³, and with decreasing population size, vulnerability to
48 environmental change increases¹⁴. Species with small range size also tend to be more specialized with
49 narrower niche breadth¹⁵ and may therefore lack flexibility to cope with anthropogenic changes in their
50 abiotic and biotic environment. As these changes increase, we might expect niche effects to strengthen
51 leading to high species replacement.

52 For plants, a primary limiting factor in many natural environments is nitrogen (N)¹⁶. Humans have
53 substantially altered the distribution and availability of N over the last century¹⁷. Chronic high N-
54 deposition has now saturated many ecological systems, exceeding critical loads¹⁸⁻²¹. Increases in a key
55 resource like N reorder competitive relationships among plant species within communities, favoring N-
56 demanding species at sites of high N-deposition across many ecosystems²²⁻²⁸. Yet, beyond local-scale
57 community changes, how these shifts link to biodiversity change across spatial scales remains largely
58 unexplored.

59 Here, we explore the role of species range size and N-deposition in driving the systematic shifts in species
60 composition and scale-dependent patterns of diversity changes observed in extensive long-term
61 vegetation data^{27,29,30}. The N-niche of species relates to their range size in that species that use N more
62 efficiently tend to have smaller ranges relative to N-demanding species³¹. This may reflect the ability of N-
63 demanding species to grow faster^{32,33}. Faster-growing species usually have smaller seeds³⁴ enabling
64 further dispersal³⁵, and more widely dispersed species tend to have wider ranges³⁶. Increases in N are thus
65 hypothesized to favor larger-ranged species that grow faster under more fertile conditions, allowing them
66 to become superior competitors, reducing the survivorship of N-efficient, small-ranged species. Patterns
67 of global biodiversity loss and local maintenance of diversity would be consistent with such species

68 replacements, with a few large-ranged species replacing many small-ranged species in a process termed
69 biotic homogenization³⁷.

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

76

77 Results

78 Plant species that went extinct from a study site had smaller range sizes than species that persisted and
79 those that colonized. In contrast, persisting and colonizing species had similar range sizes (Fig. 2a and
80 Supplementary Table 2). If this pattern reflected only lower abundance at the study site, range size should
81 not add power for predicting extinctions once abundance is controlled for. Here, we estimate abundance
82 as occupancy across plots within a site^{38,39}. Occupancy was a strong predictor of probability of extinction
83 (slope: $\beta = -3.63$, standard deviation: $\sigma = 0.28$). Over an average time interval of 38 years, species of
84 average occupancy had a 10% chance of going extinct from a study site relative to up to 60% for species of
85 low occupancy (Fig. 2b and Supplementary Table 3). Range size still had a negative effect on species'
86 extinction probability even after controlling for occupancy ($\beta = -0.21$, $\sigma = 0.05$). For species of
87 average occupancy, extinction probabilities declined by more than 50% as range size increased (Fig. 2c
88 and Supplementary Table 3). The total effect of range size became only slightly stronger when occupancy
89 was not controlled for ($\beta = -0.28$, $\sigma = 0.06$), suggesting that only 25 % of the range size effect reflects
90 occupancy (Supplementary Table 3). As species' range size presents a basic summary of the ecological
91 characteristics of species (mainly in terms of climatic and edaphic niches^{40,41}), the remaining effects of

92 range size likely reflect aspects of species niches. Higher cumulative N-deposition (ΔN , see Methods for
93 details) between surveys sharply increased probabilities of extinction from a site ($\beta = 0.37, \sigma = 0.15$;
94 Fig. 3a, Supplementary Table 4), having accounted for confounding variables such as inter-census time
95 period, study area and latitude (see Methods for all variables). This increase in extinction probability
96 disproportionately affected small-ranged species, as shown by the negative interaction between range size
97 and N-deposition ($\beta = -0.1, \sigma = 0.03$). Extinction probability of the species with the smallest range
98 sizes increased from ~4% to ~27% as N-deposition increased from 45 to 721 kg ha⁻¹ (with other predictors
99 at their mean). In contrast, risks of extinction for large-ranged species were much lower and more stable
100 (Fig. 3b and Supplementary Table 4).

101 These results show that probabilities of extinction increase with N-deposition, mostly due to the loss of
102 small-ranged species. Has this eroded study-level species richness or have increases in colonization
103 balanced these extinctions? We found no systematic shifts in species richness within study sites as N-
104 deposition increased, again accounting for covariates ($\beta = 0.11, \sigma = 0.15$; Fig. 3c, Extended Data 1 and
105 Supplementary Table 5). This implies that higher levels of N-deposition have facilitated the replacement of
106 small-ranged species. Colonizing species had larger ranges (Fig. 2a) and included several non-native
107 species ($\beta = 0.44, \sigma = 0.16$; Fig 3d, Supplementary Table 5). As more N-efficient species went extinct
108 with higher N-deposition ($\beta = -0.25, \sigma = 0.12$; Fig 3e) and colonizing species generally had higher N-
109 demands (Extended Data 2), community composition has shifted systematically towards more N-
110 demanding species ($\beta = 0.28, \sigma = 0.12$; Fig. 3e and Supplementary Table 6).

111 Although small-scale diversity has not declined, N-deposition may threaten other forms of diversity. As
112 small-ranged, N-efficient species are extirpated and replaced by wide-ranging, non-native and N-
113 demanding species, these forest plant communities have converged in composition. Gilliam¹⁹ predicted
114 that such declines in beta (and thus gamma) diversity would occur as N-deposition tends to increase the
115 spatial homogeneity of nutrient availability. Variation in nutrient availability among sites has indeed

116 declined since the baseline surveys (difference between variances: $\delta = -0.16$, $\sigma = 0.08$) (Fig. 3f and
117 Supplementary Table 7, see Methods for estimation of nutrient availability). This homogenization in
118 nutrient availability appears linked to declines in overall (biome-scale) species richness as gamma-diversity
119 across these 68 sites declined by 4% (from 1,012 to 972 species).

120

121 Discussion

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

133 Our study confirms that small population size is a strong predictor of extinction from a site^{14,42,43}. Yet this
134 did not provide much explanation for the greater extinction risk of small-ranged species as would be
135 expected given a positive range size–abundance relationship. This suggests not all small-ranged plant
136 species in these forests have small populations. In fact, plants show many exceptions to this relationship.
137 For example, 87% of small-ranged species from the British Isles are locally common⁴⁴; conversely one of
138 the largest ranging woody species of the globe, *Juniperus communis*, has small populations in many
139 regions⁴⁵. Indeed, several plant studies find that range size and abundance do not necessarily covary^{45,46}.

140 This suggests that range size affects species' extinction probability mostly via niche rather than
141 demographic effects, a conjecture supported by the fact that N-deposition mostly affected small-ranged
142 (narrow niche) species.

143 Despite declines in small-ranged species, forest sites in our study did not systematically decrease in
144 species richness. This suggests species losses are offset by species gains. This finding echoes other
145 resurvey studies that document little directional temporal trend in small-scale species richness despite
146 increased species turnover^{4,10}. But similarly, this finding is likely to not reflect the full impact of intensive
147 human land use^{8,9} as our study sites are confined to semi-natural forests. Given that the effect of range
148 size reflects species' niches, species turnover accelerated under N-deposition and communities not only
149 shifted towards larger range size but also towards higher average N-demands. Other studies from forest
150 ecosystems report the same shifts towards more N-demanding species from eutrophication and similarly
151 limited effects of N-deposition on forest-floor plant species richness^{24,47-49}. This contrasts with open-
152 canopy ecosystems that, being not primarily light limited, consistently lose species from N-addition
153 through shading^{50,51}. Beyond a threshold, however, N-deposition also reduces plant diversity in forests, as
154 shown in North America where roughly a quarter of 14,000+ sites showed susceptibility to N-driven
155 species losses³⁰.

156 Although we find no evidence of a directional change in species richness within studies, the total number
157 of species across studies (gamma diversity) has declined. The observed 4% decline in gamma-diversity
158 likely underestimates the true species loss in the European temperate forest biome, as studies in our
159 database are not completely spatially representative of key human pressures in Europe. Resurveys have
160 been selected to be especially located in large, historically continuously forested (ancient) and semi-
161 natural forests where no land-use change took place prior to the baseline survey and no large change in
162 management occurred between the surveys. Change in land use and other disturbances that open up
163 forest canopies and increase light availability may exacerbate effects of global warming by eliminating the

164 thermal insulating layer that protects understories from thermophilisation^{52,53}. However, changes in light
165 availability usually occur at the plot-level as opposed to N-deposition that acts at the scale of an entire
166 study area. Because we evaluated community dynamics at the study-level, we expect that light availability
167 changes do not confound the N-signal we found.

168 Nitrogen releases to the environment remain high in Europe (<https://www.eea.europa.eu/airs/2018>).
169 Despite recent declines, these emissions still exceed critical loads for most of Europe's protected
170 habitats⁵⁴. It is important to learn what long-lasting effects N-deposition may have on Europe's
171 ecosystems and how reversible these are as emissions decline. In contrast to the rapid recovery of plot-
172 scale experimental communities, where species are still present in the area and able to colonize once N
173 additions are ceased^{22,55} (but see ref.⁵⁶), the loss of small-ranged species from entire regions is far less
174 likely to be reversed in the short term. At this point, it is thus unclear whether the declines in N emissions
175 mandated under the EU National Emission Ceilings Directive (2016/2284/EU) will be feasible or sufficient
176 to allow the recovery of Europe's plant species and communities.

177

178 Methods

179 Database

180 We compiled a database containing data from 68 understory resurvey studies distributed across the European
181 temperate deciduous forest biome (see www.forestreplot.ugent.be and ref.⁵⁷ for inclusion criteria). These studies
182 cover 15 European countries, from Norway in the north to Slovenia in the south and from Ireland in the west to
183 Poland in the east (Fig. 1). All surveys were conducted in historically continuously forested 'ancient' and semi-natural
184 deciduous forest (sensu ref.⁵⁸). These forests did thus not experience historical land-use change prior to the first
185 (baseline) survey and between the surveys. Furthermore, the forests are mostly managed, but did not experience
186 stand-replacing disturbances between the baseline survey and the most recent resurvey. In each survey, the

187 herbaceous understory was recorded in multiple permanent or quasi-permanent plots. Plot size ranged between
188 1m² to 1000m² across studies (median: 400 m²). Number of plots ranged from 10 to 190 across studies (median: 43
189 plots, Supplementary Figure 1b). Plots were allocated across areas ranging from 1ha to c. 2.5x10⁶ ha (median: 1700
190 ha, Supplementary Figure 1d). Baseline surveys were carried out between 1933 and 1999. The most recent resurveys
191 were made between 1969 and 2017 generating time intervals between surveys from 15 to 78 years (median: 42
192 years, Supplementary Figure 1c). We accounted for changes in taxonomy between surveys by determining the
193 accepted species name for each species using GBIFs backbone taxonomy (gbif.org). Harmonization thus ensured no
194 double-counting species due to synonymy. Our database contains 1,162 species in total.

195 Species level variables

196 Species' trajectory

197 We determined the trajectory of species at the study level. We classified species present in the baseline survey but
198 absent in the resurvey as extinct. Those present in both surveys were classified as persisting. Those absent in the
199 baseline survey but present in the resurvey were classified as colonizing. Resurveys of permanent plots always miss
200 some species, generating pseudo-colonizations and extinctions that can inflate these estimates for rare species^{59,60}.
201 We did not correct our estimates of colonization and extinction for bias proposed by Beck⁵⁹ as we adjust for initial
202 abundance (occupancy across plots) in our model which is strongly correlated with any such bias⁶¹. This means our
203 estimates of the effects of initial abundance on extinction may be slightly inflated.

204 Occupancy

205 For each study, we calculated the initial occupancy of species. This is the number of plots that a species has occupied
206 in the baseline survey, divided by the total number of plots in that survey. Occupancy approximates abundance
207 because, empirically and for any biologically relevant point process pattern, they strongly and positively correlate at
208 local to regional scales^{38,39}.

209 Range size

210 Species range sizes were estimated from the species point occurrence records in GBIF (gbif.org, 18 January 2019). In
211 total, c. 100 million geographically referenced records were available for 1,147 species in our database (1.3 %

212 missing species) after excluding unlikely and impossible coordinates⁶³. Records were aggregated to a hexagonal grid
213 (ISEA3H) at three spatial grains: 3.6 km², 10.7 km² and 32 km². The number of cells any given species occupies on
214 such grid represents its range size. Range size therefore measures species' area of occupancy (AOO, expressed in
215 km²). Results in the main text are based on range sizes estimated at mid-resolution (10.7 km²). At this resolution, the
216 smallest ranging species was *Poa pannonica* A.Kern. with an estimated AOO of 21.4 km², the species with the largest
217 range was the annual meadow grass, *Poa annua* L., with an AOO of c. 1.6x10⁶ km² (Extended Data 3).

218 For our analyses we use AOO and not the extent of occurrence (EOO, which includes also discontinuities in
219 occupancy) as AOO is a markedly better predictor of mean site abundance and population size^{13,64}. While AOO
220 measured from GBIF point occurrence data is increasingly used in the scientific literature, incomplete spatial
221 coverage of digital biodiversity data can lead to an underestimation of range sizes⁶⁵. Specifically, Middle and
222 Northern Asia are some of the most data deficient regions of the world⁶⁶. This may be problematic for European
223 species that extend into these regions. We therefore tested how well our estimates of AOO match estimates of EOO
224 for species where range maps from two renowned distribution atlases were available^{67,68} (available for 796 species,
225 31% missing). The distribution ranges were digitized from scanned atlas pages and rasterized on a 20 km x 20 km grid
226 in the Lambert azimuthal equal-area projection to calculate EOO for all 796 species. Spearman's correlation between
227 AOO and EOO was high ($\rho = 0.71$) for these species. As an overall positive correlation might obscure a weak
228 correlation for continental species that extend into data deficient regions, we also tested for range attribution. We
229 identified 155 species as continental using species indicator values for continentality from ref.⁶⁹ (species with values
230 ≥ 6 were classified as continental). Excluding those species made the correlation between AOO and EOO only slightly
231 stronger ($\rho = 0.74$; Extended Data 3). We therefore assume that data limitations are a less material problem for our
232 set of species.

233

234 Study-level variables

235 Nitrogen-deposition

236 We quantified N-deposition using the EMEP database (https://emep.int/mscw/mscw_moddata.html) with c. 11 km
237 (0.1°) grid resolution. Here we chose to focus singly on NO_x deposition for three reasons. 1) Increasing evidence
238 suggest that the two forms of N-deposition, oxidized (NO_x) and reduced (NH_y) N-deposition, have differential,
239 habitat-specific effects on plant communities^{70–72}. Whereas NH_y is the most important driver for the decline in plant
240 diversity in grasslands, forest vegetation is found to be most responsive to NO_x⁷¹. 2) Model estimates of NO_x
241 deposition also have a lower degree of uncertainty and bias than estimates of NH_y⁷³. Local-scale variability of NH_y
242 deposition is considerably higher as most of it is deposited near the source⁷⁴, this variability is likely to be poorly
243 reflected when studying N-effects over larger regions as done in this study. 3) NO_x is spatially correlated with NH_y
244 deposition in Europe ($\rho = .69$ in this study) and thus representative for broader N-effects. We quantified the
245 cumulative wet and dry deposition of oxidized N (hereinafter and in the main text referred to simply as N-deposition)
246 based on the methods described in ref.⁴⁹. First, we calculated N-deposition between 1900 and the year of the
247 baseline survey (N_{t1}), second we quantified the cumulative N-deposition between 1900 and the resurvey (N_{t2}), and
248 third we calculated the difference, $N_{t2} - N_{t1}$, to quantify N-deposition between surveys (inter-census N-deposition or
249 ΔN). ΔN ranged from 45 to 721 kg ha⁻¹ (Supplementary Figure 1). Results in the main text are based on ΔN . Change in
250 species numbers

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

253 Change in non-native species

254 For each study, species were classified as native or non-native. This classification is based on the Global Register of
255 Introduced and Invasive Species (GRIIS; <http://www.griis.org>). GRIIS lists species that are non-native in a given
256 country. With these species lists we could flag, for each study, species that are non-native in the country of the
257 study. To calculate the change in non-native species between surveys, we subtracted the proportion of non-native
258 species in the total pool of species recorded in the baseline from the proportion of non-native species in the total
259 pool of species recorded in the resurvey. Thus, we quantify the change in percentage points (Supplementary Figure
260 3b). Calculation of relative change was not possible because frequently there were no non-native species in the
261 baseline survey (26% of studies, Supplementary Figure 3a). The mean number of non-native species in the baseline

262 survey and the resurvey was 5 and 7 (rounded to the next integer), respectively. The mean number of native species
263 was 110 (baseline survey) and 102 (resurvey).

264 Change in nitrophilous species and nutrient availability

265 We estimated changes in species' N-demands using Ellenberg's indicator values (EIVs). EIVs were developed for
266 Central Europe and classify species' habitat niches and their peak occurrence along environmental gradients⁷⁵. In
267 particular, we used EIVs for N or more general productivity⁷⁶ that classify species growing on the poorest soils (N-
268 number = 1) to species growing on the most productive soils with excessive nutrient availability (N-number= 9)
269 (Extended Data 2). For each study and survey, we averaged N-numbers across species. Because EIVs equally reflect
270 environmental conditions⁴⁷, these average values approximate both the mean N-demand of a community and the
271 nutrient availability at each survey. To quantify the change in a community's mean N-demand, we subtracted the
272 mean N-demand of the baseline community from the mean N-demand of the resurvey community. To better
273 understand what drives changes in communities mean N-demands, we calculated the average N-demand of extinct
274 and colonizing species (Extended Data 2) for each study.

275

276 Data analyses

277 The entire statistical analysis and R-code is provided in the supplementary information as an R markdown file. The
278 rethinking package⁷⁷ was used to compile the following models to Stan Hamiltonian Monte Carlo code. For brevity,
279 all models are presented without priors (complete models and R code is available on figshare
280 [<https://figshare.com/s/45d71eb77c23c11bc857>]).

281 We first compared range sizes between extinct, persisting and colonizing species, where species' trajectories are
282 defined at the study scale. Clearly range size is non-normal distributed and starkly right skewed. Since normality of
283 the outcome conditional on the covariates is the central assumption of Gaussian linear models and range size was
284 too skewed for Poisson regression, we normalized range size using an order-quantile transformation⁷⁸. We

285 predicted range size (r_i) with trajectory ($\beta_{status[i]}$) and allowed each coefficient to vary by each study

286 ($\alpha_{study[i],status[i]}$). The mathematical form of the resulting model is:

$$\begin{aligned} 287 \quad r_i &\sim Normal(\mu_i, \sigma) \\ \mu_i &= \beta_{status[i]} + \alpha_{study[i],status[i]} \end{aligned}$$

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

289 Next, we asked can species' extinction probability be predicted by species' occupancy at the time of the baseline
290 survey? Here, we only analyzed species present at the baseline survey, omitting colonizing species. The outcome is a
291 0/1 (Bernoulli) indicator that a given species persisted or became extinct in a study (e_i). As the outcome is binomially
292 distributed, we used logistic regression to predict species' extinction probabilities as a function of occupancy. We
293 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
294 study ID ($\beta_{f,study[i]}$). The mathematical form of the model is:

$$\begin{aligned} 295 \quad e_i &\sim Binomial(1, p_i) \\ \text{logit}(p_i) &= \bar{\alpha} + \alpha_{study[i]} + \gamma_{species[i]} + \beta_{f,study[i]} * f_i \end{aligned}$$

296 Controlling for the effect of occupancy, we then added the range size predictor to the previous model. We used the
297 Widely Applicable Information Criterion (WAIC) to decide whether the model's out of sample predictions improve
298 when varying slopes on range size are included⁷⁷. The resulting model is:

$$\begin{aligned} 299 \quad e_i &\sim Binomial(1, p_i) \\ \text{logit}(p_i) &= \bar{\alpha} + \alpha_{study[i]} + \gamma_{species[i]} + \beta_{f,study[i]} * f_i + \beta_r * r_i \end{aligned}$$

300 where β_r is the effect of range size (r_i).

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

$$\begin{aligned} 303 \quad e_i &\sim Binomial(1, p_i) \\ \text{logit}(p_i) &= \bar{\alpha} + \alpha_{study[i]} + \gamma_{species[i]} + \beta_r * r_i \end{aligned}$$

304 Next, we sought to explain variation in average extinction probability across species between studies. In particular,
305 we tested the effect of inter-census N-deposition on the outcome. The effect of N-deposition could, however, be
306 confounded by the time between surveys (Δt). Cumulative N-deposition is a function of Δt , and Δt itself is likely to
307 affect average extinction probability. We therefore include Δt in the model.
308 Furthermore, the year of the baseline survey (t_1) can influence the outcome. For example, baseline surveys from
309 later years are likely to be associated to higher cumulative N-deposition than those from earlier years. This might
310 have already affected community composition to the extent that fewer extinctions occur in communities that were
311 sampled in later years as these have already lost species. In our data t_1 is strongly and negatively correlated to Δt ;
312 the earlier the year of the baseline survey, the longer the time between surveys ($\rho = -0.91$, Extended Data 4). This
313 correlation is also reflected in a strong negative correlation between cumulative N-deposition at the year of the
314 baseline survey and time between surveys ($\rho = -0.67$; Extended Data 4). A directed acyclic graph of presumed
315 causal links between predictors and response (Extended Data 5) shows that including time between surveys in the
316 model controls for the confounding effect of year of the baseline survey and importantly, for environmental changes
317 that preceded this survey, such as the cumulative N-deposition at the year of the baseline survey.
318 In addition to these potential confounding variables, the number of plots, their size and the size of the area in which
319 surveys were carried out may directly affect the outcome. For instance, a species with occupancy 0.1 occupied 1 or
320 10 plots in studies of 10 or 100 plots, respectively and demographic fluctuations should be higher in smaller
321 plots/areas that naturally comprise fewer individuals. As this may clearly affect the average extinction probability
322 across species, we included these variables in the model. Finally, we also included latitude as a covariate in order to
323 account for latitudinal patterns that might be associated to climate change. Together, this generates the following
324 model:

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

325
326 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
327 number (q_i), plot size (s_i), site area (a_i) and latitude (l_i), respectively.

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

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

331

332 where β_{nr} is the slope of the interaction between inter-census N-deposition (n_i) and range size (r_i).

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

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

337

338 To visualize the effect of N-deposition, we used a predictor residual plot. In these, the outcome is regressed against
 339 the variation of N-deposition that is left unexplained by the other predictor variables in the model. Predictor residual
 340 plots allow us to display the actual data while controlling for all other predictors. Because the unit of observation in
 341 this model is the study, we have 68 observations. To display the influence of each data point on posterior
 342 predictions, we scaled point sizes by their Pareto k value⁷⁷. We then predicted the percentage point change in non-
 343 native species using the same predictors as in the previous model, again using a predictor residual plot to display the
 344 results.

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

348
$$m_i/w_i \sim Normal(\mu_i, \sigma)$$
$$\mu_i = \alpha + \beta_n * n_i$$

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

351
$$a_{ij} \sim Normal(\mu_{ij}, \sigma_{ij})$$
$$\mu_{ij} = \beta_0 + \beta_1 * t_{ij}$$
$$\sigma_{ij} = \gamma_0 + \gamma_1 * t_{ij}$$

352 where a_{ij} is the availability of N for the i th study and j th survey period, β_0 and γ_0 are the mean and standard
353 deviation of the baseline survey respectively, β_1 and γ_1 are the expected difference between mean and standard
354 deviation of the resurvey and baseline survey respectively, and t_{ij} is a 0/1 indicator for survey period.

355

356 Author Contributions

357 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.,
358 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.
359 and L.B. wrote the manuscript, with input and contributions from all authors. Authorship order was determined as
360 follows: (1) core authors; (2) sREplot participants (alphabetical) and other major contributors; (3) authors
361 contributing community composition data and to an advanced version of the manuscript (alphabetical).

362

363 Data availability

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

369

370 Code availability

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

372

373 Competing interests

374 The authors declare no competing interests.

375

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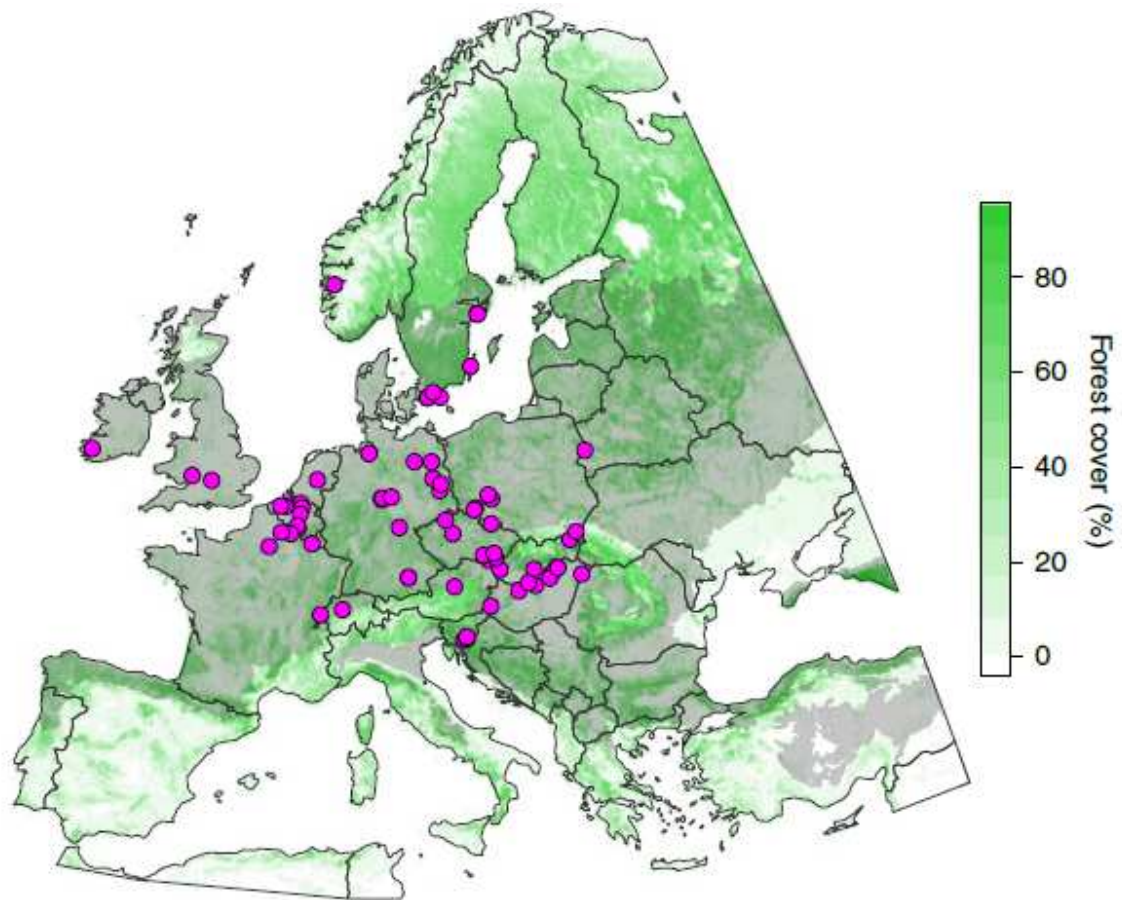
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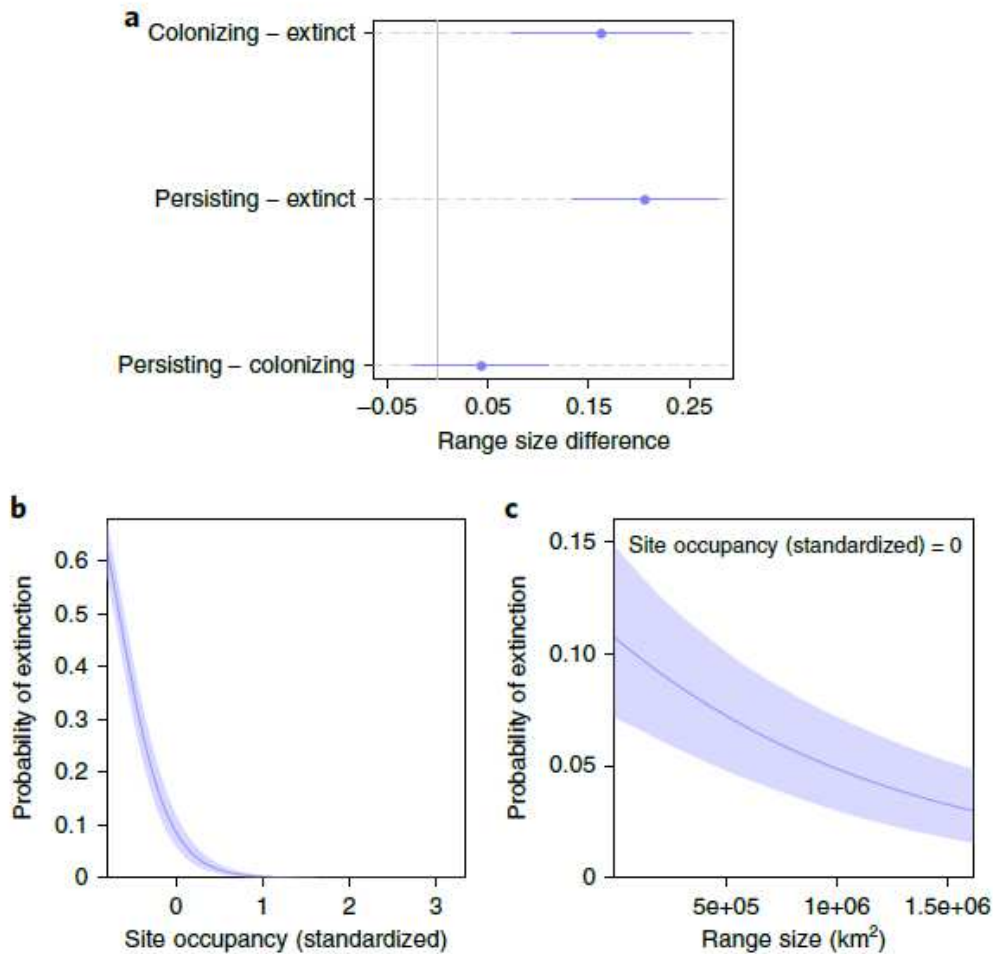
551



552

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

556



557

558 **Figure 2: Species that go extinct from a study site have smaller ranges than persisting and colonizing ones.**

559 **Even after controlling for site occupancy, species' range size predicts probability of extinction. a,** Expected

560 differences in normalized range size between colonizing, persisting and extinct species. **b,** Effect of

561 species' site occupancy at the time of the baseline survey on probability of extinction, x axis is

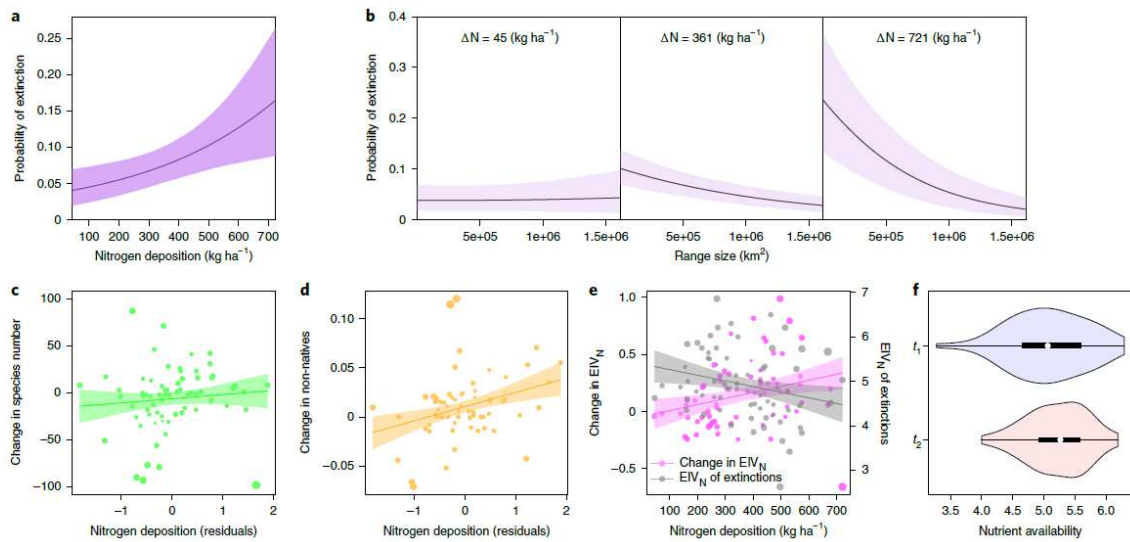
562 standardized, so that zero represents the average site occupancy. **c,** Effect of species' range size on

563 probability of extinction, after controlling for site occupancy (line shows expectation for site occupancy at

564 its mean). Line segments in **a** represent ± 2 standard deviations from the mean. Transparent ribbons in **b**

565 and **c** represent the 89% credible intervals for model mean predictions. Model parameters are shown in

566 Supplementary Table 2 and 3.



567

568 **Figure 3: Small-ranged species drive the increase in average extinction risk from high N-deposition. Although**

569 **colonizing species sustain species number, composition shifts towards more non-native and N-demanding**

570 **species. Spatial heterogeneity of nutrient availability decreases over time. a, Effect of inter-census nitrogen**

571 **deposition (ΔN) on average probability of extinction across species. b, Triptych plot for the effect of range**

572 **size on probability of extinction at different levels of ΔN , holding all other predictors at their mean. ΔN**

573 **levels are minimum (left), mean (center), and maximum (right) ΔN . c-d, Predictor residual response plot of**

574 **the relationship between inter-census nitrogen deposition and change in study-level species richness (c)**

575 **and percentage point change in non-native species (d). e, Ellenberg indicator values for nitrogen (eiv_N)**

576 **averaged across extinct species and the change in eiv_N averaged across all species regressed against inter-**

577 **census nitrogen deposition. f, Violin plot (density curve and boxplot) of nutrient availability (estimated**

578 **with community mean eiv_N) at the time of the baseline survey (t_1) and resurvey (t_2). Transparent ribbons**

579 **in a - e represent the 89% credible intervals for model mean predictions. Point size in c - e is scaled by**

580 **relative LOOIS Pareto k values. Larger points are more influential. Model parameters are shown in**

581 **Supplementary Table 4, 5, 6 and 7.**