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

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

The biological diversity on Earth is changing owing to human activities. At the global scale, species are going extinct at rates that signal a mass extinction[1,2,3]. Per contra, at local scales, whether or not diversity is declining is controversial. Time-series studies find that sites may gain or lose species with no directional global trend[4,6]. Space-for-time comparisons find substantial losses in local diversity globally owing to human land use[7]. While spatial comparisons are criticized for neglecting the fact that community dynamics are much slower than the speed of environmental changes[8], time-series studies are challenged for not being spatially representative of human land-use effects[6,9,10]. Yet even in relatively intact places and independent from changes in local diversity, species seem to be replacing each other more rapidly than predicted from only natural changes[5,11]. These local-scale replacements alone

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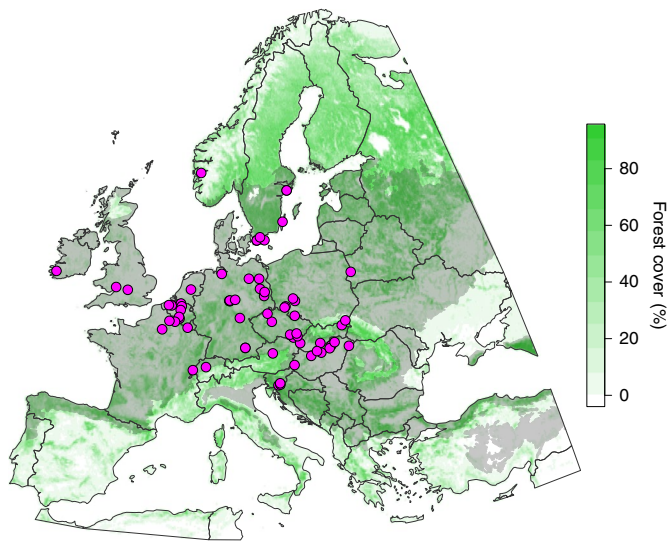
Fig. 1 | Spatial distribution of resurvey studies in Europe. Map of all 68 resurvey studies included in the forestREplot database (purple dots), the temperate deciduous forest biome in Europe (grey shaded area)[79] and forest cover for the year 2000 (in green)[80]. Light to dark shades of green represent forest cover ranging from 0 to 100% at a spatial resolution of 30 m.

Fig. 2 | Species that go extinct from a study site have smaller ranges than persisting and colonizing ones. a, Expected differences in normalized range size between colonizing, persisting and extinct species. The horizontal line segments represent ±2 standard deviations from the mean. The vertical line indicates a difference of zero. **b**, Effect of species' site occupancy at the time of the baseline survey on the probability of extinction. The *x* axis is standardized, so that zero represents the average site occupancy. **c**, Effect of species' range size on the probability of extinction, after controlling for site occupancy (the line shows the expectation for site occupancy at its mean). The shaded areas in **b** and **c** represent the 89% credible intervals for model mean predictions. The model parameters are shown in Supplementary Tables 2 and 3.

could lead to species loss at larger spatial scales, if species with small geographic ranges are frequently replaced by species with larger ranges. However, tests of this prediction remain sparse.

Why should small-ranged species decline relative to those with larger ranges within sites? A greater tendency of species with small ranges to decline or go locally extinct could reflect lower abundance, greater ecological specificity (narrower niches) or both. Species with small geographic ranges generally tend to have smaller local populations[12–14], and with decreasing population size, vulnerability to environmental change increases[15]. Species with small range sizes also tend to be more specialized with narrower niche breadths[16] and may therefore lack the flexibility to cope with anthropogenic changes in their abiotic and biotic environments. As these changes increase, we might expect niche effects to strengthen, leading to high species replacement.

For plants, a primary limiting factor in many natural environments is nitrogen (N) (ref. [17]). Humans have substantially altered the distribution and availability of N over the past century[18]. Chronic high N deposition has now saturated many ecological systems, exceeding critical loads[19–22]. Increases in a key resource like N reorder competitive relationships among plant species within communities, favouring N-demanding species at sites of high N deposition across many ecosystems[23–28]. Yet, beyond local-scale community changes, how these shifts link to biodiversity change across spatial scales remains largely unexplored.

Here, we explore the roles of species' range size and N deposition in driving the systematic shifts in species composition and scale-dependent patterns of diversity changes observed in extensive long-term vegetation data[27,29,30]. The N niche of species relates to their range size in that species that use N more efficiently tend to have smaller ranges than N-demanding species[31]. This may reflect the ability of N-demanding species to grow faster[32,33]. Faster-growing species usually have smaller seeds[34], enabling further dispersal[35], and more widely dispersed species tend to have wider ranges[36]. Increases in N are thus hypothesized to favour larger-ranged species that grow faster under more fertile conditions, allowing them to become superior competitors, reducing the survivorship of N-efficient, small-ranged species. Patterns of global biodiversity
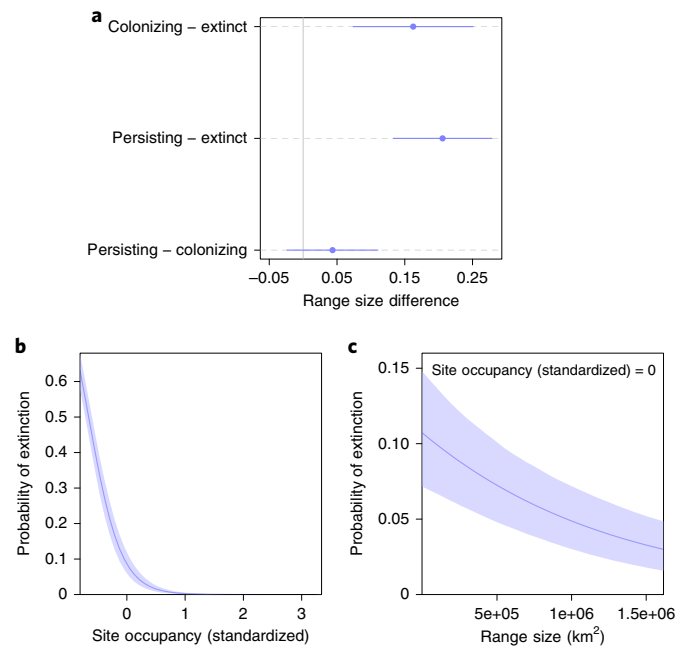
loss and local maintenance of diversity would be consistent with such species replacements, with a few large-ranged species replacing many small-ranged species in a process termed biotic homogenization[37].

We compiled a database of 68 resurvey studies of herb-layer communities from seminatural, temperate forests spread across Europe (Fig. 1 and Supplementary Table 1). We use these data to ask three main questions. (1) Have small-ranged forest plant species declined over time? (2) Do any such trends simply reflect their lower abundance (given the range size–abundance correlation), or do they reflect niche effects that strengthen with N deposition? (3) Do species replacements under N deposition evoke a homogenization pattern with small-scale richness remaining constant on average while larger-scale richness declines?

Results

Plant species that went extinct from a study site had smaller range sizes than species that persisted and those that colonized. In contrast, persisting and colonizing species had similar range sizes (Fig. 2a and Supplementary Table 2). If this pattern reflected only lower abundance at the study site, range size should not add power for predicting extinctions once abundance is controlled for. Here, we estimate abundance as occupancy across plots within a site[38,39]. Occupancy was a strong predictor of the probability of extinction (slope, $\beta = -3.63$; s.d., $\sigma = 0.28$). Over an average time interval of 38 years, species of average occupancy had a 10% chance of going extinct from a study site, whereas species of low occupancy had up to a 60% chance (Fig. 2b and Supplementary Table 3). Range
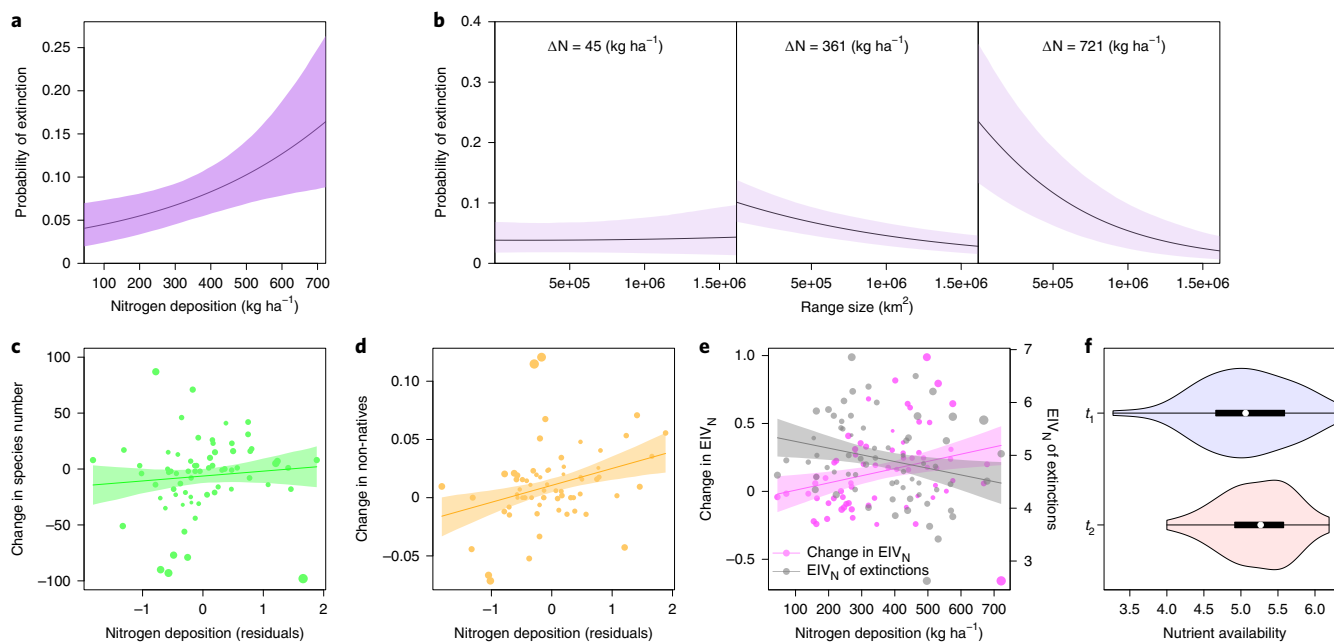
Fig. 3 | Small-ranged species drive the increase in the average extinction risk from high N deposition. a, Effect of intercensus N deposition (ΔN) on the average probability of extinction across species. **b**, Triptych plot for the effect of range size on the probability of extinction at different levels of ΔN, holding all other predictors at their means. ΔN levels are minimum (left), mean (centre) and maximum (right). **c,d**, Predictor residual response plots of the relationship between ΔN and the change in study-level species richness (**c**) and the percentage point change in non-native species (**d**). **e**, Ellenberg's indicator values for N (EIV$_N$) averaged across extinct species and the change in EIV$_N$ averaged across all species regressed against ΔN. **f**, Violin plot (density curve and box plot) of nutrient availability (estimated with community mean EIV$_N$) at the time of the baseline survey (t_1) and resurvey (t_2). The shaded areas in **a**–**e** represent the 89% credible intervals for model mean predictions. The point sizes in **c**–**e** are scaled by relative LOOIS Pareto k values. Larger points are more influential. The model parameters are shown in Supplementary Tables 4–7.

size still had a negative effect on species' extinction probability even after controlling for occupancy ($\beta = -0.21$, $\sigma = 0.05$). For species of average occupancy, extinction probabilities declined by more than 50% as range size increased (Fig. 2c and Supplementary Table 3). The total effect of range size became only slightly stronger when occupancy was not controlled for ($\beta = -0.28$, $\sigma = 0.06$), suggesting that only 25% of the range size effect reflects occupancy (Supplementary Table 3). As species' range size presents a basic summary of the ecological characteristics of species (mainly in terms of climatic and edaphic niches[40,41]), the remaining effects of range size probably reflect aspects of species niches. Higher cumulative N deposition (ΔN, see Methods for the details) between surveys sharply increased probabilities of extinction from a site ($\beta = 0.37$, $\sigma = 0.15$; Fig. 3a and Supplementary Table 4), having accounted for confounding variables such as intercensus time period, study area and latitude (see Methods for all variables). This increase in extinction probability disproportionally affected small-ranged species, as shown by the negative interaction between range size and N deposition ($\beta = -0.1$, $\sigma = 0.03$). The extinction probabilities of the species with the smallest range sizes increased from ~4% to ~27% as N deposition increased from 45 to 721 kg ha^{-1} (with other predictors at their mean). In contrast, the risks of extinction for large-ranged species were much lower and more stable (Fig. 3b and Supplementary Table 4).

These results show that probabilities of extinction increase with N deposition, mostly owing to the loss of small-ranged species. Has this eroded study-level species richness, or have increases in colonization balanced these extinctions? We found no systematic shifts in species richness within study sites as N deposition increased, again accounting for covariates ($\beta = 0.12$, $\sigma = 0.15$; Fig. 3c, Extended Data Fig. 1 and Supplementary Table 5). This implies that higher levels of N deposition have facilitated the

replacement of small-ranged species. Colonizing species had larger ranges (Fig. 2a) and included several non-native species ($\beta = 0.42$, $\sigma = 0.15$; Fig. 3d and Supplementary Table 5). As more N-efficient species went extinct with higher N deposition ($\beta = -0.25$, $\sigma = 0.12$; Fig. 3e) and colonizing species generally had higher N demands (Extended Data Fig. 2), community composition has shifted systematically towards more N-demanding species ($\beta = 0.28$, $\sigma = 0.12$; Fig. 3e and Supplementary Table 6).

Although small-scale diversity has not declined, N deposition may threaten other forms of diversity. As small-ranged, N-efficient species are extirpated and replaced by wide-ranging, non-native and N-demanding species, these forest plant communities have converged in composition. Gilliam[20] predicted that such declines in beta (and thus gamma) diversity would occur as N deposition tends to increase the spatial homogeneity of nutrient availability. The variation in nutrient availability among sites has indeed declined since the baseline surveys (difference between variances, $\delta = -0.16$, $\sigma = 0.08$) (Fig. 3f and Supplementary Table 7; see Methods for the estimation of nutrient availability). This homogenization in nutrient availability seems linked to declines in overall (biome-scale) species richness as gamma diversity across these 68 sites declined by 4% (from 1,012 to 972 species).

Discussion

Using large-scale temporal vegetation change datasets, we provide evidence that the geographic range size of species predicts long-term shifts in forest-floor plant communities. Small-ranged species are replaced by those with larger ranges, and our results suggest that this is due more to species niches than to abundances. The loss of small-ranged species increased under high N deposition, and, consistent with our expectation that species' range sizes and N demands positively correlate, communities shifted towards species with

higher N demands. Despite the loss of small-ranged species, the number of species within study sites has not declined in response to increasing N deposition, suggesting that species losses have been balanced by species gains. Nevertheless, the floristic distinctiveness of these forests erodes as more cosmopolitan and non-native species replace a set of more finely adapted species. These replacements ran in parallel with the abiotic homogenization resulting from chronic N deposition and scaled to a loss of biodiversity in Europe's temperate forests in recent decades.

Our study confirms that small population size is a strong predictor of extinction from a site[15,42,43]. Yet, this did not provide much explanation for the greater extinction risk of small-ranged species as would be expected given a positive range size–abundance relationship. This suggests that not all small-ranged plant species in these forests have small populations. In fact, plants show many exceptions to this relationship. For example, 87% of small-ranged species from the British Isles are locally common[44]; conversely, one of the largest-ranging woody species of the globe, *Juniperus communis*, has small populations in many regions[45]. Indeed, several plant studies find that range size and abundance do not necessarily covary[45,46]. This suggests that range size affects species' extinction probabilities mostly via niche rather than demographic effects, a conjecture supported by the fact that N deposition mostly affected small-ranged (narrow niche) species.

Despite declines in small-ranged species, forest sites in our study did not systematically decrease in species richness. This suggests that species losses are offset by species gains. This finding echoes other resurvey studies that document little directional temporal trend in small-scale species richness despite increased species turnover[5,11]. But similarly, this finding is likely to not reflect the full impact of intensive human land use[9,10], as our study sites are confined to seminatural forests. Given that the effect of range size reflects species niches, species turnover accelerated under N deposition and communities shifted not only towards larger range size but also towards higher average N demands. Other studies from forest ecosystems report the same shifts towards more N-demanding species from eutrophication and similarly limited effects of N deposition on forest-floor plant species richness[47–49]. This contrasts with open-canopy ecosystems that, being not primarily light limited, consistently lose species from N addition through shading[50,51]. Beyond a threshold, however, N deposition also reduces plant diversity in forests, as shown in North America where roughly a quarter of more than 14,000 sites showed susceptibility to N-driven species losses[30].

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

Nitrogen releases to the environment remain high in Europe (https://www.eea.europa.eu/airs/2018). Despite recent declines, these emissions still exceed critical loads for most of Europe's protected habitats[54]. It is important to learn what long-lasting effects N deposition may have on Europe's ecosystems and how

reversible these effects are as emissions decline. In contrast to the rapid recovery of plot-scale experimental communities, where species are still present in the area and able to colonize once N additions are ceased[23,55] (but see ref. [56]), the loss of small-ranged species from entire regions is far less likely to be reversed in the short term. At this point, it is thus unclear whether the declines in N emissions mandated under the European Union National Emission Ceilings Directive (2016/2284/EU) will be feasible or sufficient to allow the recovery of Europe's plant species and communities.

Methods

Database. We compiled a database containing data from 68 understory resurvey studies distributed across the European temperate deciduous forest biome (see www.forestreplot.ugent.be and ref. [57] for the inclusion criteria). These studies cover 15 European countries, from Norway in the north to Slovenia in the south and from Ireland in the west to Poland in the east (Fig. 1 and Supplementary Table 1). All surveys were conducted in historically continuously forested ancient and seminatural deciduous forests (sensu ref. [58]). These forests did not experience historical land-use change before the first (baseline) survey and between the surveys. Furthermore, the forests are mostly managed, but did not experience stand-replacing disturbances between the baseline survey and the most recent resurvey. In each survey, the herbaceous understory was recorded in multiple permanent or quasi-permanent plots. Plot sizes ranged from 1 m² to 1,000 m² across studies (median, 400 m²). The numbers of plots ranged from 10 to 190 across studies (median, 43 plots; Supplementary Fig. 1b). The plots were allocated across areas ranging from 1 ha to ~2.5 × 10⁶ ha (median, 1,700 ha; Supplementary Fig. 1d). The baseline surveys were carried out between 1933 and 1999. The most recent resurveys were made between 1969 and 2017, generating time intervals between surveys from 15 to 78 yr (median, 42 yr; Supplementary Fig. 1c). We accounted for changes in taxonomy between surveys by determining the accepted species name for each species using GBIF's backbone taxonomy (gbif.org). Harmonization thus ensured no double-counting of species owing to synonymy. Our database contains 1,162 species.

Species-level variables. *Species' trajectory.* We determined the trajectories of species at the study level. We classified species present in the baseline survey but absent in the resurvey as extinct. Those present in both surveys were classified as persisting. Those absent in the baseline survey but present in the resurvey were classified as colonizing. Resurveys of permanent plots always miss some species, generating pseudocolonizations and extinctions that can inflate these estimates for rare species[59,60]. We did not correct our estimates of colonization and extinction for bias as proposed by Beck[59], as we adjusted for initial abundance (occupancy across plots) in our model, which is strongly correlated with any such bias[61]. This means that our estimates of the effects of initial abundance on extinction may be slightly inflated.

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

Range size. Species' range sizes were estimated from the species point occurrence records in GBIF (gbif.org, 18 January 2019)[62]. In total, ~100 million geographically referenced records were available for 1,147 species in our database (1.3% missing species) after excluding unlikely and impossible coordinates[63]. The records were aggregated to a hexagonal grid (ISEA3H) at three spatial grains: 3.6 km², 10.7 km² and 32 km². The number of cells that any given species occupies on such grid represents its range size. Range size therefore measures a species' area of occupancy (AOO, expressed in km²). The results in the main text are based on range sizes estimated at mid-resolution (10.7 km²). At this resolution, the smallest-ranging species was *Poa pannonica* A.Kern. with an estimated AOO of 21.4 km², and the species with the largest range was the annual meadow grass, *Poa annua* L., with an AOO of ~1.6 × 10⁶ km² (Extended Data Fig. 3).

For our analyses, we use AOO and not the extent of occurrence (EOO, which includes also discontinuities in occupancy) as AOO is a markedly better predictor of mean site abundance and population size[14,64]. While AOO measured from GBIF point occurrence data is increasingly used in the scientific literature, incomplete spatial coverage of digital biodiversity data can lead to an underestimation of range sizes[65]. Specifically, Middle and Northern Asia are some of the most data-deficient regions of the world[66]. This may be problematic for European species that extend into these regions. We therefore tested how well our estimates of AOO match estimates of EOO for species where range maps from two renowned distribution atlases were available[67,68] (available for 796 species, 31% missing). The distribution ranges were digitized from scanned atlas pages and rasterized on a 20 km × 20 km grid in the Lambert azimuthal equal-area projection to calculate EOO for all 796 species. Spearman's correlation coefficient between AOO and EOO was high ($\rho = 0.71$) for these species. As an overall positive correlation might obscure a

weak correlation for continental species that extend into data-deficient regions, we also tested for range attribution. We identified 155 species as continental using species indicator values for continentality from ref. [69] (species with values ≥6 were classified as continental). Excluding those species made the correlation between AOO and EOO only slightly stronger ($\rho = 0.74$; Extended Data Fig. 3). We therefore assume that data limitations are a less material problem for our set of species.

Study-level variables. *Nitrogen deposition.* We quantified N deposition using the EMEP database (https://emep.int/mscw/mscw_moddata.html) with a grid resolution of ~11 km (0.1°). Here, we chose to focus singly on nitrogen oxide (NO_x) deposition for three reasons. First, increasing evidence suggests that the two forms of N deposition, oxidized (NO_x) and reduced (NH_y), have differential, habitat-specific effects on plant communities[70–72]. Whereas NH_y is the most important driver for the decline in plant diversity in grasslands, forest vegetation is found to be most responsive to NO_x (ref. [71]). Second, model estimates of NO_x deposition also have a lower degree of uncertainty and bias than estimates of NH_y (ref. [73]). The local-scale variability of NH_y deposition is considerably higher, as most of it is deposited near the source[74]; this variability is likely to be poorly reflected when studying N effects over larger regions as done in this study. Third, NO_x is spatially correlated with NH_y deposition in Europe ($\rho = 0.69$ in this study) and is thus representative of broader N effects. We quantified the cumulative wet and dry deposition of oxidized N (hereinafter and in the main text referred to simply as N deposition) on the basis of the methods described in ref. [49]. First, we calculated N deposition between 1900 and the year of the baseline survey (N_{t1}); second, we quantified the cumulative N deposition between 1900 and the resurvey (N_{t2}); and third, we calculated the difference, $N_{t2} - N_{t1}$, to quantify N deposition between surveys (intercensus N deposition or ΔN). The values of ΔN ranged from 45 to 721 kg ha^{-1} (Supplementary Figs. 1a and 2). The results in the main text are based on ΔN.

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

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

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

Data analyses. The entire statistical analysis (including R code) is available as an R markdown file on figshare at https://doi.org/10.6084/m9.figshare.10110713.v1. The rethinking package[77] was used to compile the following models to Stan Hamiltonian Monte Carlo code. For brevity, all models are presented without priors (for complete models see the R markdown file).

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

$$r_i \sim \text{Normal}(\mu_i, \sigma)$$
$$\mu_i = \beta_{\text{status}[i]} + \alpha_{\text{study}[i],\text{status}[i]}$$

We calculated pairwise contrasts (for example, $\beta_{\text{colonizing}} - \beta_{\text{extinct}}$) to compare range sizes between species' trajectories.

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

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

Controlling for the effect of occupancy, we then added the range size predictor to the previous model. We used the widely applicable information criterion (WAIC) to decide whether the model's out-of-sample predictions improve when varying slopes on range size are included[77]. The resulting model is:

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

where β_r is the effect of r_i.

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

$$e_i \sim \text{Binomial}(1, p_i)$$
$$\text{logit}(p_i) = \bar{\alpha} + \alpha_{\text{study}[i]} + \gamma_{\text{species}[i]} + \beta_r r_i$$

Next, we sought to explain the variation in average extinction probability across species between studies. In particular, we tested the effect of intercensus N deposition on the outcome. The effect of N deposition could, however, be confounded by the time between surveys (Δt). Cumulative N deposition is a function of Δt, and Δt itself is likely to affect the average extinction probability. We therefore include Δt in the model.

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

In addition to these potential confounding variables, the number of plots, their sizes and the size of the area in which the surveys were carried out may directly affect the outcome. For instance, a species with an occupancy of 0.1 occupied 1 or 10 plots in studies of 10 or 100 plots, respectively, and demographic fluctuations should be higher in smaller plots or areas that naturally contain fewer individuals. As this may affect the average extinction probability across species, we included these variables in the model. Finally, we also included latitude as a covariate to account for latitudinal patterns that might be associated with climate change. Together, this generates the following model:

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

where β_n, β_t, β_q, β_s, β_a and β_l are the effects of intercensus N deposition (n_i), intercensus time period (t_i), plot number (q_i), plot size (s_i), site area (a_i) and latitude (l_i), respectively.

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

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

where β_{nr} is the slope of the interaction between n_i and r_i.

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

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

To visualize the effect of N deposition, we used a predictor residual plot. In these plots, the outcome is regressed against the variation in N deposition that is left unexplained by the other predictor variables in the model. Predictor residual plots allow us to display the actual data while controlling for all other predictors. Because the unit of observation in this model is the study, we have 68 observations. To display the influence of each data point on the posterior predictions, we scaled point sizes by their Pareto k values[77]. We then predicted the percentage point change in non-native species using the same predictors as in the previous model, again using a predictor residual plot to display the results.

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

$$m_i / w_i \sim \text{Normal}(\mu_i, \sigma)$$
$$\mu_i = \alpha + \beta_n n_i$$

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

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

where a_{ij} is the availability of N for the ith study and jth survey period; β_0 and γ_0 are the mean and standard deviation of the baseline survey, respectively; β_1 and γ_1 are the expected difference between means and standard deviations of the resurvey and baseline survey, respectively; and t_{ij} is a 0/1 indicator for the survey period.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The community change and environmental site-level data are available on figshare at https://figshare.com/s/45d71eb77c23c11bc857. The species composition data are available from forestreplot.ugent.be, but restrictions apply to the availability of these data, which were used under license for the current study and so are not publicly available. These data are, however, available from the authors upon request and with the permission of the forestREplot consortium.

Code availability

The R code for all analyses is available on figshare at https://doi.org/10.6084/m9.figshare.10110713.v1.

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Author contributions

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., 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. 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., M.W., H.M.P., P.V., A.O.-A., R.P., I.B., M.C., G.D., T. Dirnböck, T. Durak, W.S., T.H., F.H.S., B.J., M.K., M. Macek, M. Malicki, T.N., T.A.N., P.P., K.R., T.S., K.Š., B.T., H.V.C. and O.V. The authorship order was determined as follows: (1) core authors, (2) sREplot participants (alphabetical) and other major contributors and (3) authors contributing community composition data and to an advanced version of the manuscript (alphabetical).

Competing interests

The authors declare no competing interests.

Additional information

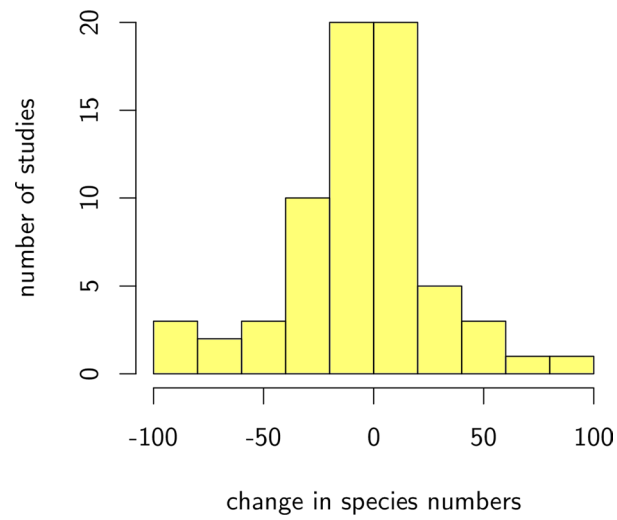**Extended data** is available for this paper at https://doi.org/10.1038/s41559-020-1176-8.

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-020-1176-8.

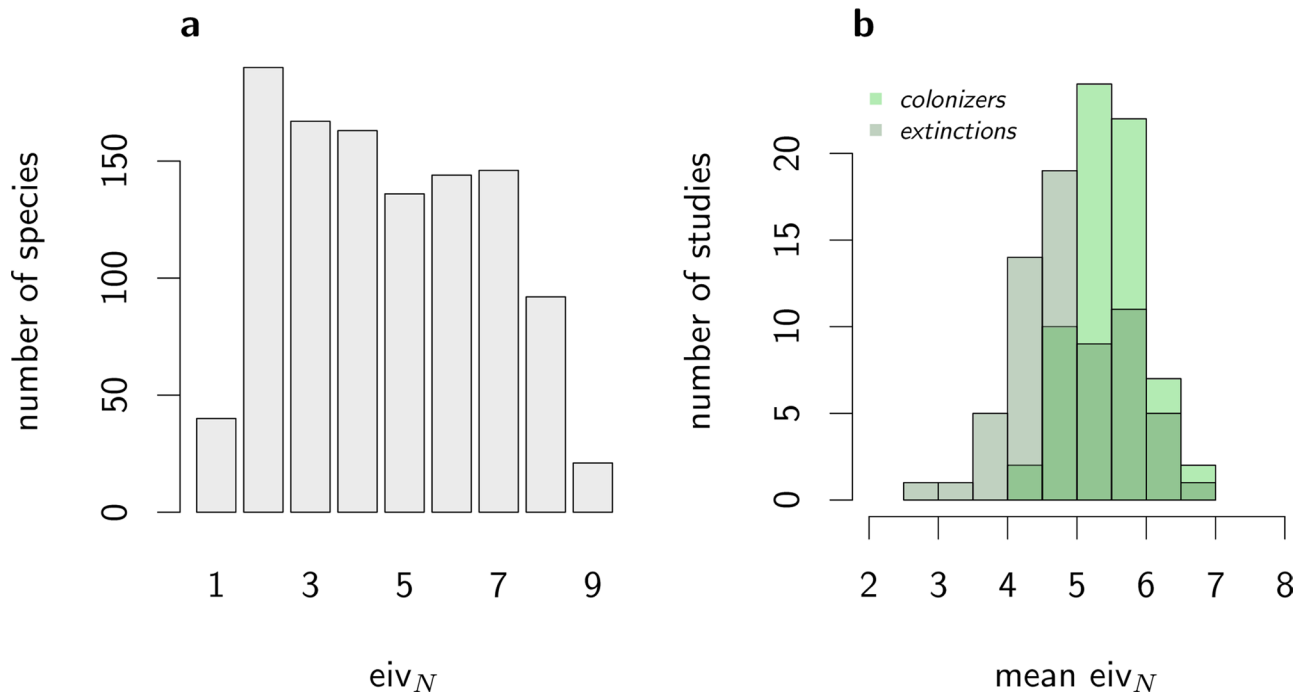**Correspondence and requests for materials** should be addressed to I.R.S.

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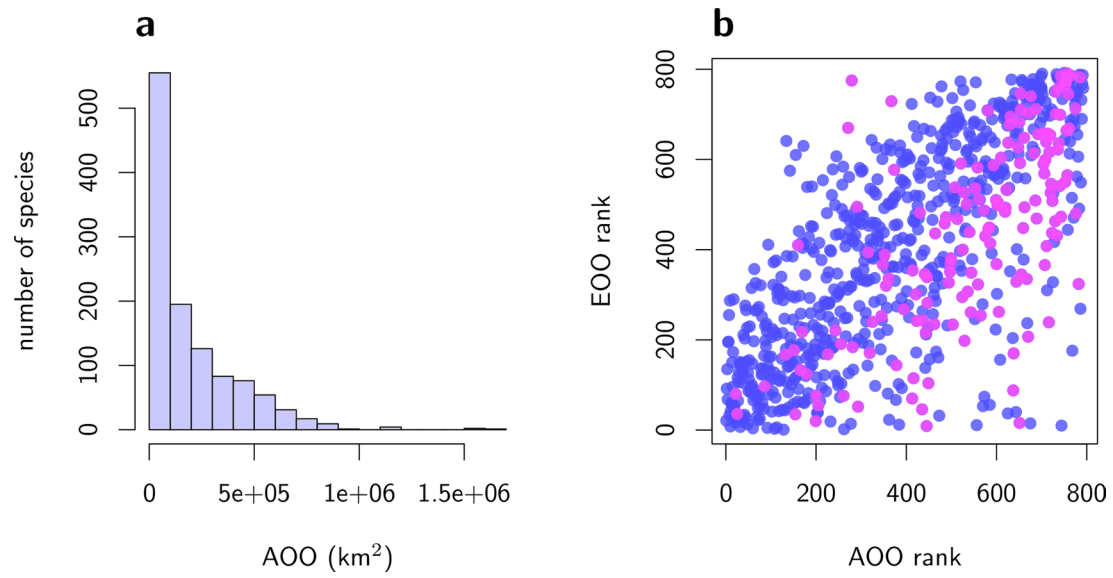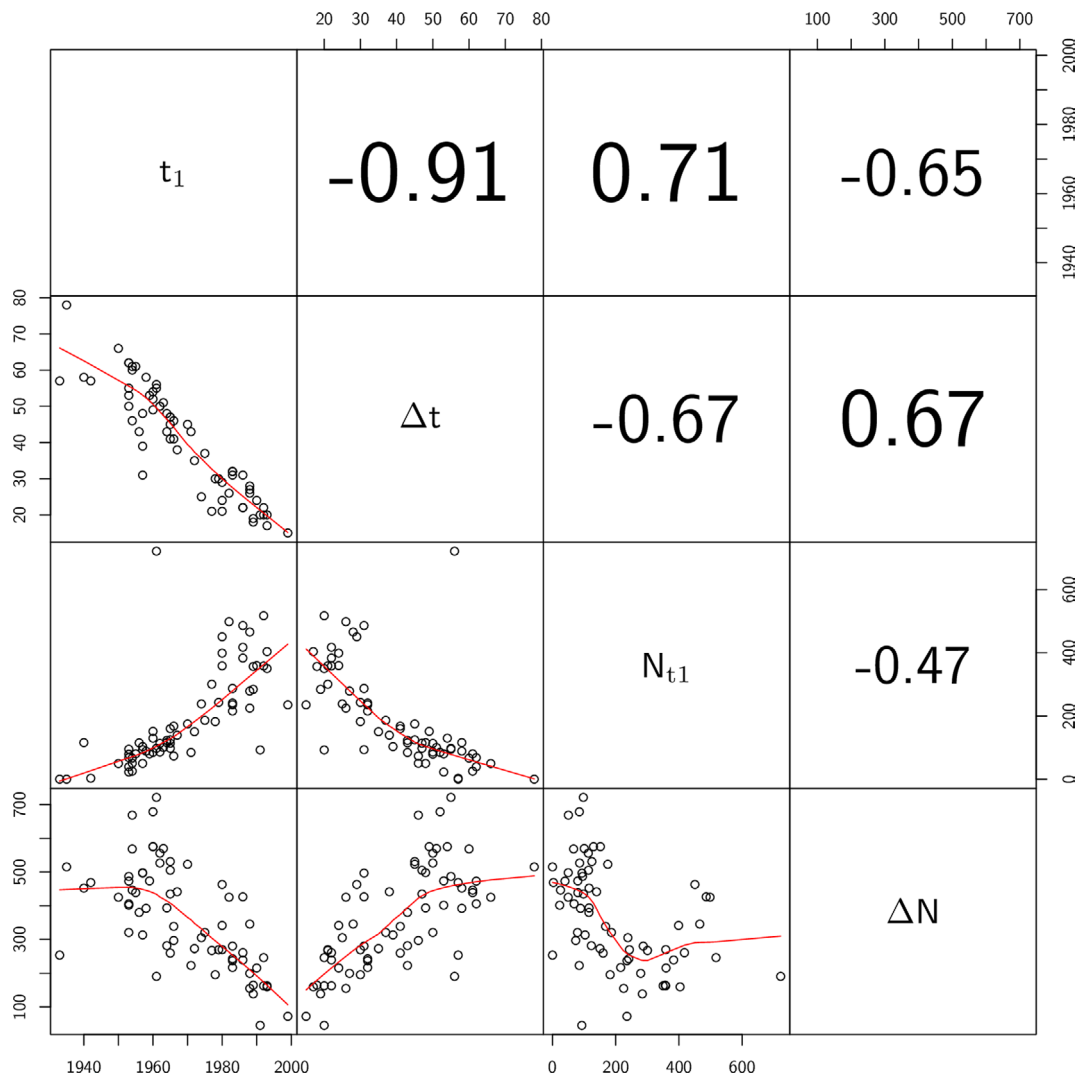
Extended Data Fig. 1 | Change in species numbers. Frequency distribution of the difference in species numbers between the resurvey and baseline survey.
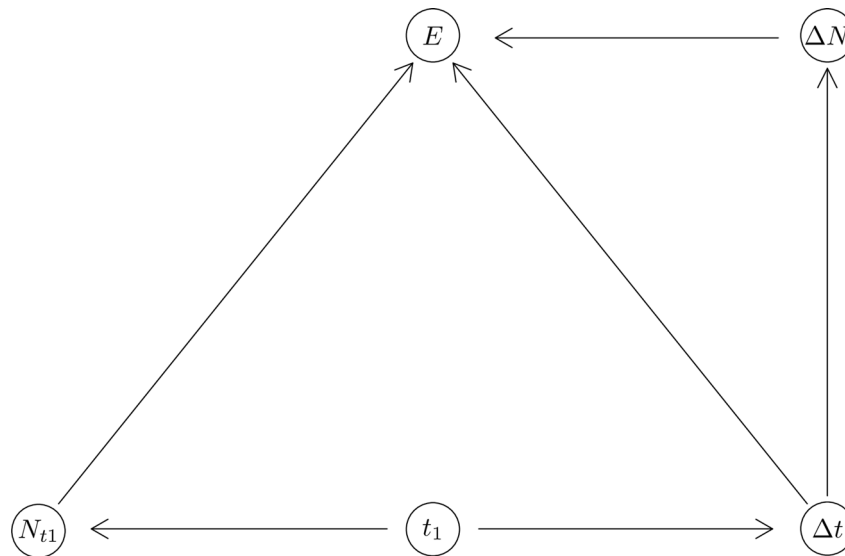
a

b

Extended Data Fig. 2 | Change in nitrophilous species. a, Frequency distribution of Ellenberg indicator values for nitrogen (eiv_N) across species. **b**, Frequency distribution of the mean eiv_N of extinct (dark green) and colonizing (light green) species.

Extended Data Fig. 3 | Range sizes. a, Frequency distribution of range sizes measured as area of occupancy (AOO) from GBIF point occurrence records. **b**, Spearman correlation plot of AOO and extent of occurrence (EOO) range sizes from digitized range maps. Points colored in magenta identify continental species. Correlation coefficient with and without continental species is: $\rho = .71$ and $\rho = .74$, respectively.

Extended Data Fig. 4 | Correlations between predictor variables. the year of the baseline survey (t_1), time between surveys (Δt), cumulative N deposition between 1900 and the year of the baseline survey (N_{t1}) and intercensus cumulative nitrogen deposition (ΔN).

Extended Data Fig. 5 | Directed acyclic graph. Directed acyclic graph of hypothesized causal links between predictor and response variables. Cumulative N deposition at the year of the baseline (N_{t1}), intercensus cumulative N-deposition (ΔN) and time between surveys (Δt) directly influence the outcome (extinction probability, E). Year of the baseline survey (t_1) directly influences Δt and N_{t1}: the earlier the baseline survey, the longer the time between surveys; the earlier the baseline survey, the lower the cumulative N deposition at the year of the baseline survey. To estimate the direct effect of ΔN, it is sufficient to include Δt as a covariate. This closes the backdoor[81] through t_1 ($t_1 \rightarrow N_{t1} \rightarrow E$) and as a result differences in baseline year do not confound the effect of ΔN.

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software or code was used in the collection of community composition data. Data sources of species- and site-level data are provided in the methods.
Data analysis	All Bayesian analyses were done in R (v. 3.6.1) using the rethinking package (McElreath 2016. Statistical Rethinking. CRC Press.; https://github.com/rmcelreath/rethinking/tree/Experimental). Model equations are provided in the methods for all analyses. Model code and description is provided for all analyses in the .html file uploaded on figshare (https://figshare.com/s/45d71eb77c23c11bc857). All graphs are made with R Base.

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

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This study involves 68 resurvey studies of forest-floor plant communities across Europe's temperate forest biome. We analyze how individual species trajectories at the study-scale scale up to diversity changes at the biome scale. We predict trajectories with species geographic range size and changes in community composition in respect to non-native and N-demanding species with cumulative inter-census Nitrogen deposition.
Research sample	The forestREplot database is the largest vegetation resurvey database for Europe's temperate forest biome to date. Studies in the forestREplot database are selected to match the data standards detailed in Verheyen et al .2017. References: Kris Verheyen et al., Combining Biodiversity Resurveys across Regions to Advance Global Change Research, BioScience, Volume 67, Issue 1, January 2017, Pages 73–83, https://doi.org/10.1093/biosci/biw150
Sampling strategy	Sample size was not predetermined but rather a maximum possible based on available resurvey studies.
Data collection	Community composition data were collected by several teams (see authorship contribution statement, teams are part of the forestREplot consortium).
Timing and spatial scale	Baseline surveys were carried out between 1933 and 1999. The most recent resurveys were made between 1969 and 2017 generating time intervals between surveys from 15 to 78 years (mean 38 years). On average 54 plots were allocated across a median area of 1700 ha.
Data exclusions	No data were excluded.
Reproducibility	Our study is not experimental, but the large number of resurvey studies spread across Europe's temperate forest biome ensures good spatial replication.
Randomization	Resurvey sites were selected to be located in semi-natural forests where no change in land use has taken place since the baseline survey. Within sites, plots in the baseline survey were allocated to provide a representative sample of the vegetation (phytosociological approach), corresponding to a stratified random sampling approach. We accounted for site differences by controlling for covariates (inter-census survey interval, plot number, plot size, site area and latitude).
Blinding	As our study is not experimental, blinding was not possible for data aquisition and analysis.

Did the study involve field work?   ☒ Yes   ☐ No

Field work, collection and transport

Field conditions	Climate throughout Europe's temperate forests ranges from temperate oceanic in the west to temperate continental eastward.
Location	Resurvey studies of forest floor plant communities spanned the deciduous temperate forest biome in Europe. Studies cover 15 European countries, from Norway in the north to Slovenia in the south and from Ireland in the west to Poland in the east. All surveys were conducted in ancient, quasi-natural deciduous forest.
Access and import/export	Data collection permits were obtained whenever necessary.
Disturbance	No disturbances were caused by vegetation sampling.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	Antibodies
☒	Eukaryotic cell lines
☒	Palaeontology
☒	Animals and other organisms
☒	Human research participants
☒	Clinical data

Methods

n/a	Involved in the study
☒	ChIP-seq
☒	Flow cytometry
☒	MRI-based neuroimaging