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Research

Evaluating plant lineage losses and gains in temperate forest understories: a phylogenetic perspective on climate change and nitrogen deposition

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Summary

- Global change has accelerated local species extinctions and colonizations, often resulting in losses and gains of evolutionary lineages with unique features. Do these losses and gains occur randomly across the phylogeny?
- We quantified: temporal changes in plant phylogenetic diversity (PD); and the phylogenetic relatedness (PR) of lost and gained species in 2672 semi-permanent vegetation plots in European temperate forest understories resurveyed over an average period of 40 yr.
- Controlling for differences in species richness, PD increased slightly over time and across plots. Moreover, lost species within plots exhibited a higher degree of PR than gained species. This implies that gained species originated from a more diverse set of evolutionary lineages than lost species. Certain lineages also lost and gained more species than expected by chance, with Ericaceae, Fabaceae, and Orchidaceae experiencing losses and Amaranthaceae, Cyperaceae, and Rosaceae showing gains. Species losses and gains displayed no significant phylogenetic signal in response to changes in macroclimatic conditions and nitrogen deposition.

- As anthropogenic global change intensifies, temperate forest understories experience losses and gains in specific phylogenetic branches and ecological strategies, while the overall mean PD remains relatively stable.

Introduction

Changes in global environmental conditions are increasingly modifying biodiversity and associated ecosystem functions (Haddad *et al.*, 2015; IPBES, 2019). Understanding the processes that underlie spatiotemporal changes in the composition of ecological communities helps us predict the impacts of global change drivers (Purschke *et al.*, 2013; Letten *et al.*, 2014; Chai *et al.*, 2016). Because ongoing environmental changes tend to favor species with particular traits that are suited to the new environmental conditions (Keddy, 1992; Díaz *et al.*, 1998), and because traits partly reflect species' shared evolutionary histories (Losos, 2008), global change drivers can also shift the phylogenetic diversity (PD) and relatedness (PR) of ecological communities (Webb *et al.*, 2002; Gerhold *et al.*, 2015). Understanding how current environmental changes affect various branches of the tree of life thus helps us identify which phylogenetic lineages, reflecting distinct evolutionary histories and functional roles, are most likely to expand or go extinct within local communities.

Temporal shifts in community composition reflect local colonizations, extinctions, and population dynamics (Magurran & Henderson, 2010). The amount of evolutionary history lost and gained following extinction and colonization events depends on the rate of evolution of ecological traits (Cavender-Bares *et al.*, 2004). Because traits related to environmental tolerances are often phylogenetically conserved (Hawkins *et al.*, 2014; De Pauw *et al.*, 2021; Harris *et al.*, 2022a), environmental changes are likely to promote the extinctions of close relatives (Vamosi & Wilson, 2008; Eiserhardt *et al.*, 2015). In such cases, lost species would represent distinct phylogenetically clustered subsets of the habitat species pool and be phylogenetically different from persisting species. Environmental changes and human-mediated biological invasions can also enhance the colonization of species that are phylogenetically and functionally distant from the current residents (Mathakutha *et al.*, 2019). This phenomenon can be intensified by competitive exclusion, which tends to promote the establishment of species displaying functionally dissimilar characteristics compared to the resident species (Valiente-Banuet & Verdú, 2013; Li *et al.*, 2015). For instance, during vegetation succession, late successional plant colonizers represent a broad array of distantly related species with diverse traits (Li *et al.*, 2015). This diversity could stem from environmental alterations that augment the carrying capacity of local habitats, thereby facilitating the establishment of species with distinct functional traits (Valiente-Banuet & Verdú, 2013). Although many studies have measured net changes in the PD of local plant communities over time (e.g. Purschke *et al.*, 2013; Li *et al.*, 2015; Barber *et al.*, 2016), few of these have evaluated whether environmental changes are associated with nonrandom gains and losses of PD. Importantly, none of these studies have evaluated gains and losses in plant community PD at the continental scale.

The understories of temperate forests support a variety of herbaceous plant species (Loidi *et al.*, 2021) that compete for the same resources and are susceptible to various global environmental changes, including climate change, land-use change, habitat fragmentation, biological invasions, and atmospheric nitrogen deposition (Gilliam, 2007). Previous studies at the European scale found few systematic declines in understory plant species richness (Bernhardt-Römermann *et al.*, 2015; Perring *et al.*, 2018), consistent with studies of other terrestrial plant communities (Vellend *et al.*, 2013; Li *et al.*, 2020; Jandt *et al.*, 2022). Nevertheless, temporal turnover in forests is rarely ecologically random (Kopecký *et al.*, 2012). In European forests, light-demanding species that tolerate low nitrogen availability and have small geographic ranges are gradually replaced by shade-tolerant species with higher nutrient requirements and larger ranges (Kopecký *et al.*, 2012; Staude *et al.*, 2020). Therefore, identifying nonrandom losses and gains of specific plant lineages within and across forest understories provides insights into the ecological strategies favored and disadvantaged by recent environmental changes.

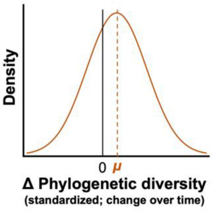
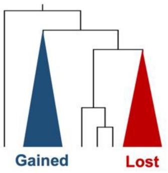
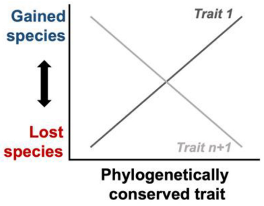
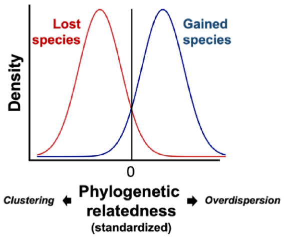
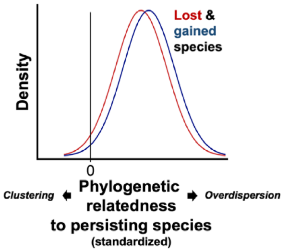
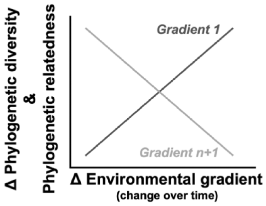
Here, we quantify temporal changes in plot-level PD and PR of lost and gained plant species in the understory of European temperate forests resurveyed after an average period of 40 yr. Additionally, we test how PD and PR respond to changes in macroclimate and atmospheric nitrogen deposition, considering potential confounding factors. We also identify plant lineages that have experienced more species losses and gains than expected by chance. Finally, we explore the relationship between species' tendency to be lost or gained over time and their functional traits. To this end, we test six hypotheses (H1–H6) to understand how species co-existing in specific habitat types respond to recent environmental changes (Table 1).

Materials and Methods

Vegetation surveys

We obtained resurvey data from the forestREplot database v.2.3 (www.forestreplot.ugent.be; Verheyen *et al.*, 2017). This database contains species occurrence and cover data from forest resurveys in permanent or semi-permanent plots in natural or semi-natural temperate forests throughout Europe and North America. Our study focused on European temperate broadleaved deciduous forests (≥ 25% canopy cover of broadleaved trees in the baseline survey) that have been continuously forested since at least 1850 and have remained unaffected by any stand-replacing disturbances between the baseline survey and the last resurvey. Like most forests in Europe, the study sites were largely managed in the past. Plot sizes varied from 25 to 1300 m^2 (mean ± SD: 264 ± 193 m^2). We restricted our analyses to the understory vegetation layer (herbs and woody juveniles).

Table 1 Proposed hypotheses with ecological mechanisms, empirical evidence, and graphical representations.

Hypothesis	Ecological mechanism/Empirical evidence	Graphical representation
(H1) Forest understories in temperate Europe have gained more phylogenetic diversity than expected from random species losses and gains	Lost species are phylogenetically clustered subsets of the habitat species pool (Vamosi & Wilson, 2008; Eiserhardt *et al*., 2015), while gained species include distantly related species with diverse traits (Li *et al*., 2015)	
(H2) Species' losses and gains across communities are not randomly distributed across the phylogeny	Environmental tolerances are often phylogenetically conserved (Cavender-Bares *et al*., 2004; De Pauw *et al*., 2021; Harris *et al*., 2022a)	
(H3) Species' losses and gains across communities are associated with phylogenetically conserved plant traits	Abiotic filters operate on phylogenetically conserved plant traits and their related ecosystem functions (Keddy, 1992; Díaz *et al*., 1998)	
(H4) Lost species are more phylogenetically clustered than gained species within communities	Lost species share conserved traits that make them intrinsically vulnerable to extinction (Vamosi & Wilson, 2008; Eiserhardt *et al*., 2015). Gained species include distantly related species with diverse traits (Li *et al*., 2015)	
(H5) Lost and gained species are phylogenetically distantly related to persisting species	Abiotic filters exclude subsets of closely related species with ecological strategies distinct from those of persisting species (Eiserhardt *et al*., 2015). Environmental changes and competitive exclusion create conditions that enable the establishment of species that are functionally dissimilar and distantly related to those already present in a community (Valiente-Banuet & Verdú, 2013; Li *et al*., 2015)	
(H6) Temporal changes in phylogenetic diversity and the phylogenetic relatedness of lost and gained species within communities are associated with changes in macroclimatic conditions and nitrogen deposition over time	Abiotic filters select for phylogenetically conserved ecological strategies (Keddy, 1992; Gerhold *et al*., 2015)	

We selected 2672 pairs of survey/resurvey plots from 64 datasets representing 14 countries (Supporting Information Notes S1: Fig. S1.1; Table S1.1). We standardized plant species names in the plots according to the World Flora Online taxonomic backbone, using the R package WorldFlora (Kindt, 2020). We restricted this study to angiosperms to prevent inflated overdispersion due to gymnosperms and pteridophytes linked to deep phylogenetic nodes. Baseline surveys occurred between 1933 and 1999 and resurveys between 1987 and 2020. The time interval between surveys ranged from 12 to 72 yr (mean ± SD: 40 ± 13 yr). These plots contained a total of 1152 angiosperm species.

To compare lineage losses and gains in plots with similar baseline and interval times, we restricted analyses related to H1, H2, and H3 to plots resurveyed after 2000 and ≥ 20 yr after the baseline survey ($n = 2443$ pairs of baseline survey and resurvey plots). By adopting this approach, we encompassed a significant period during which major environmental changes occurred in Europe. For example, the European State of the Climate (ESOTC) report for 2022 highlighted that all of the 10 warmest years on record for Europe have taken place since 2000 (European Commission, 2022). These selected plots had baseline surveys between 1935 and 1999 and resurveys between 2001 and 2020. This subset of plots contained 1117 angiosperm species.

Phylogeny

We generated a phylogenetic tree for the 1152 angiosperm species in our dataset with the R package V.PhyloMaker2 (Jin & Qian, 2022). This package uses an improved and expanded version of the mega phylogeny reported by Smith & Brown (2018) as a backbone to construct phylogenies. To complete the phylogeny, we added missing species (*c*. 23% of the total species) and genera (*c*. 4% of the total genera) to the midpoint of their genus or family branch, respectively ('Scenario 3'; Qian & Jin, 2016; Jin & Qian, 2022). A phylogeny created with this approach produces results comparable to a tree fully resolved at the species level if most genera and all families are resolved (Qian & Jin, 2021).

Plant traits

We obtained data on four plant traits known to respond to the biotic or abiotic environment (e.g. climatic conditions or resource availability; Lavorel & Garnier, 2002) and to support a strong phylogenetic signal (Notes S2: Table S2.1). These traits were maximum plant height (H), seed mass (SM), leaf area (LA), and specific leaf area (SLA). These traits are also linked to various ecological functions, including dispersal, establishment, reproduction, and resource acquisition (Westoby, 1998; Díaz *et al*., 2016; Notes S2: Table S2.2). Because our goal was to determine the potential traits and ecological strategies of understory plant species that relate to their tendency to be lost or gained over time, we assumed that the trait values of mature woody plants were indicative of potential, albeit unrealized, traits in juvenile plants. In other words, we regarded these traits as latent qualities that may not necessarily manifest in the surveyed individuals at the time of the study. The four traits were only weakly intercorrelated (|Spearman's| $\rho \leq 0.45$; Notes S3: Table S3.1).

We obtained trait data from the TRY database (www.try-db.org; Kattge *et al*., 2020). We removed trait records that were > 4 standard deviations from the species' mean for each trait to avoid the potential effects of outliers (Bruelheide *et al*., 2018). We averaged intraspecific trait values per species when several trait values occurred for a given trait. Data for individual plant traits (H, SM, LA, or SLA) were available for at least 70% of the species (Notes S3: Table S3.2), but only 34% had data for all four traits.

Missing trait data imputation

We imputed missing trait data with the R package missForest (Stekhoven, 2022). This Random Forest method imputes species trait values using highly accurate phylogenetic information (Penone *et al*., 2014) and fast computation times. We incorporated all phylogenetic eigenvectors (Debastiani *et al*., 2021) derived from the R package pvr (Santos, 2018) as predictor variables in the missForest imputation alongside functional traits.

Explanatory variables

Climate change variables We obtained gridded climatic data from the Climatic Research Unit Time Series (CRU TS; v.4.06) of the University of East Anglia (Harris *et al*., 2022b). The CRU TS data cover the global terrestrial surface from 1901 to 2021 and provide monthly climate data at 0.5° (*c*. 55 km at the equator) resolution. For each year between 1901 and 2021, we obtained data for computing three climatic variables: maximum summer temperature, minimum winter temperature, and annual precipitation. Selecting these variables accounts for the effects of seasonal extremes and broad climatic variation.

For maximum summer temperature, we averaged monthly maximum daily temperatures during June, July, and August. For minimum winter temperature, we averaged monthly daily minimum temperatures during December, January, and February. For annual precipitation, we summed the monthly precipitation over the year. We then computed the long-term mean values for these three variables by averaging the annual data for both the 10 yr before the baseline survey and the 10 yr preceding the resurvey (Bernhardt-Römermann *et al*., 2015). This approach accounts for likely time lags in vegetation dynamics and how plant species adapt to long-term environmental changes (De Frenne *et al*., 2013; Li & Waller, 2017). We then calculated changes in climatic conditions as the difference between the 10-yr average values preceding the baseline survey and the resurvey. We repeated the analyses considering variables capturing the effects of more extreme climatic conditions and obtained similar results (Notes S4: Tables S4.1, S4.2; Figs S4.1, S4.2).

Nitrogen deposition We obtained cumulative dry and wet annual deposition of oxidized nitrogen (hereafter, N) from the EMEP database (https://emep.int/mscw/mscw_moddata.html) at 0.1° (*c*. 11 km) resolution. Annual N deposition was only available for the 1990–2020 period. To obtain annual N deposition for the years before 1990, we used the correction factors for the different decades based on the deposition rates in the year 2000, as described in Duprè *et al*. (2010). To measure cumulative N deposition between surveys, we summed up N deposition data for all years between the baseline survey and the resurvey.

Covariates Because many variables potentially affect species diversity and dynamics, thus confounding our ability to detect particular effects, we included 10 covariates in our models to account for their possible effects on community change (Simkin *et al.*, 2016; Perring *et al.*, 2018). These covariates include plot area; herb-layer species richness and cover from the baseline survey (cf. baseline plant community conditions); baseline climatic conditions (average maximum summer temperature, average minimum winter temperature, and annual precipitation over the 10 yr before the sampling); management (unmanaged vs managed); the temporal change in tree canopy cover to capture changes in microclimate dynamics; current soil pH; and the time (in years) between surveys. We also considered cumulative N deposition estimated between 1901 and the baseline, but this variable was strongly correlated with the time between surveys (Spearman's $\rho = -0.88$), so we discarded it in the final models. We obtained raster data for present-day European soil pH at 15 cm depth (250×250 m resolution) from Poggio *et al.* (2021). We added these covariates to account for potential confounding effects with our main variables of interest: macroclimate change and atmospheric N deposition. We provide details of the covariates, a full rationale for including them in the models, and their inter-correlations in Notes S5: Table S5.1.

Calculation of phylogenetic diversity and phylogenetic relatedness metrics

To measure PD, we calculated Faith's PD, the sum of all phylogenetic branch lengths connecting a set of taxa (Faith, 1992). Faith's PD is a phylogenetic generalization of species richness that captures the evolutionary history of a species assemblage (Chao *et al.*, 2010). We calculated the change in PD over time in the plots as the log-transformed response ratio (RR):

$$\mathrm{RR\_PD} = \frac{\log_e \frac{\mathrm{PD}_{t+\Delta t}}{\mathrm{PD}_t}}{\Delta t}$$

where PD_t is the value for PD at the time of the initial survey, $\mathrm{PD}_{t+\Delta t}$ refers to its value at the time of the resurvey, and Δt is the number of years between surveys.

We calculated two measures of PR within and between species assemblages at terminal phylogenetic levels. First, we calculated the Mean Nearest Taxon Distance (MNTD; Webb *et al.*, 2002) to quantify the degree of PR of lost and gained species in the plots. The MNTD is the mean branch length between each taxon and its phylogenetically nearest neighbor. Second, we used the $\mathrm{D_{nn}}$ metric (Webb *et al.*, 2008) to measure the degree of PR between the lost or gained species and those that persisted in the plots. We calculated $\mathrm{D_{nn}}$ for each plot as the mean branch length between each lost or gained species and its phylogenetically nearest neighbor in the pool of persisting species. We also calculated PR at basal phylogenetic levels (i.e. the mean phylogenetic distance, MPD, and $\mathrm{D_{pw}}$), but we obtained similar results and moved the results of these analyses to Notes S6. A summary table with the PD and PR metrics used in this study and their relationship to the hypotheses is provided in Notes S7: Table S7.1. We calculated the PD and PR metrics using the R package PHYLOMEASURES (Tsirogiannis & Sandel, 2016).

To determine whether RR_PD and PR values for each plot were higher or lower than expected if species were randomly distributed across the phylogeny, we compared the observed empirical values of these metrics to a null distribution derived from 999 random reshufflings of the species across the tips of the phylogenetic tree. These reshufflings included all the species listed within a focal dataset or study site, corresponding to all the species observed across all individual plots surveyed and resurveyed within the focal study site. This allowed us to estimate standardized plot-level effect sizes (SES) for each metric (i.e. RR_PD.ses, MNTD.ses, and $\mathrm{D_{nn}}$.ses) as the difference between the observed empirical value and the mean of the random values divided by the standard deviation of the random values. These SES metrics are thus independent of changes in species richness in the plots. For each plot, positive SES values of RR_PD.ses indicate that more PD was gained than under random expectation, while negative SES values indicate that more PD was lost than under random expectation. Positive SES values of PR metrics indicate that species were more distantly related than under random expectation (phylogenetic overdispersion), while negative SES values indicate that species were more closely related than under random expectation (phylogenetic clustering).

We also calculated the lost and gained PD in each plot as the PD of the set of taxa lost or gained at the site between the resurvey and the baseline survey. However, the standardized effect sizes of these measures (PD.ses) were highly correlated with MNTD.ses (Spearman's $\rho > 0.95$) and discarded from the main text (Notes S8).

Statistical analyses

We used R v.4.2.0 (R Core Team, 2022) for all analyses and set statistical significance at $\alpha = 0.05$.

Has the phylogenetic diversity of forest understories changed over time? (H1) We compared the mean RR_PD and RR_PD.ses across plots to zero using Cohen's *d* (Cohen, 1998) in the R package LSR (Navarro, 2015). Cohen's *d* is a measure of effect size that, unlike the *t*-test statistic, estimates a population parameter and is unaffected by sample size. Effect sizes are considered small *c.* 0.2, medium *c.* 0.5, and large *c.* 0.8 (Cohen, 1998). This approach allowed us to compare the magnitude of the difference between the mean values and zero rather than testing for statistical differences between the mean values and zero.

Were particular plant lineages lost and gained over time across plots? (H2) For each species ($n = 1117$), we calculated its tendency (U) to be lost or gained in the plots as:

$$U = \frac{\sum_{i=1}^{j} S_i}{j}$$

where S is the species' response in plots $i = 1$ to j (1 if the species was gained, 0 if the species persisted, and -1 if the species was lost). A U-value of -1 indicates that the species was lost from all the plots where it occurred at the time of the baseline survey, while a *U*-value of 1 indicates that the species was not present at the time of the baseline survey in any of the plots where it occurred at the time of the resurvey.

We evaluated the phylogenetic signal in *U*-values with Pagel's λ (Pagel, 1999) in the R package PHYTOOLS (Revell, 2012). Values of λ close to zero indicate phylogenetic independence of *U*-values. By contrast, values close to one indicate that *U*-values co-vary directly with their shared evolutionary history. We plotted the *U*-values of each species in the phylogeny to identify lineages with high or low *U*-values. We also calculated for each node in the phylogeny whether the observed mean *U*-value of species descending from that node was higher or lower than expected if species were randomly distributed in the phylogeny. To this end, we reshuffled the tips of the phylogeny 999 times and recalculated the mean *U*-values. Then, we compared the observed mean *U*-value of the node with the distribution of random mean *U*-values to determine a *P*-value based on the quantiles' null distribution. Specifically, we calculated *P*-values as the proportion of random mean *U*-values lower than the observed mean *U*-value. Here, *P*-values below 0.025 or above 0.975 indicated that the observed mean *U*-value was significantly lower or higher, respectively, than expected by chance.

Plot resurveys may inadvertently overlook certain species during the field sampling, potentially leading to the misidentification of pseudo-colonizations and extinctions. These errors can inflate *U*-values of rare species (Verheyen *et al*., 2018). Furthermore, species' absolute *U*-values exhibited a partial negative correlation with their occurrence frequency across plots (Pearson's $r = 0.34$). To mitigate these issues and avoid spurious results associated with random species losses and gains, we recalculated *U*-values considering species present in at least five ($n = 678$ species) and 10 ($n = 534$) plots. This sensitivity analysis allowed us to evaluate the effect of rare species on the results and identify plant lineages that were lost and gained independently from species frequency across plots.

Are *U*-values associated with plant traits? (H3) Species cannot be considered statistically independent in regression models because they are evolutionarily related (Ives & Zhu, 2006). We, therefore, applied phylogenetic generalized least squares (PGLS) regression in the R package CAPER (Orme *et al*., 2018) to test for associations between *U*-values and plant traits (H, SM, LA, and SLA). The PGLS approach allows for flexibility in the underlying evolutionary assumptions and uses generalized least squares to explicitly include the predicted covariance among species into the model's fit. Models using ordinary least squares regressions yielded very similar results and are not presented. We $\log_e$-transformed all traits to improve normality. To test H2 and H3, we repeated these analyses, excluding juvenile trees, to evaluate whether tree recruitment associated with mature traits modified our results.

Does the phylogenetic relatedness of lost and gained species deviate from random expectations? (H4 and H5) We used Cohen's *d* to compare the MNTD.ses and D_{nn}.ses of lost and gained species across plots to zero (Cohen, 1998).

Have environmental changes driven alterations in phylogenetic diversity and relatedness? (H6) We used linear mixed-effect models in the R package NLME (Pinheiro *et al*., 2022) to examine the relationships between plot-level temporal changes in the PD and PR metrics and the set of explanatory variables. We treated the predictor variables of interest (i.e. changes in maximum summer temperature, minimum winter temperature, annual precipitation, and N deposition) and the covariates as fixed effects. In the models predicting temporal changes in PD, we did not use the time between surveys as a covariate because this variable was included in the denominator of the response and focal predictor variables. In all models, we included 'dataset' as a random intercept term to account for variation in residual variances among plots (Zuur *et al*., 2007). To minimize dispersion in model residuals, we $\log_e$-transformed plot area. We standardized and centered all explanatory variables before model fitting to obtain comparable coefficients (Zuur *et al*., 2007). We complemented these analyses with models that separately predicted species' losses and gains within plots (Notes S8). The variance inflation factor (VIF), calculated using the R package USDM (Naimi *et al*., 2014), indicated low multicollinearity among explanatory variables (VIF < 3).

Results

Temporal changes in the phylogenetic diversity of forest understories (H1)

Forest understories experienced a slight decrease in overall PD (Fig. 1a; Cohen's $d = 0.13$). However, after controlling for changes in species richness across plots by randomizing the evolutionary relationships among species, forest understories had a small overall increase in PD (Fig. 1b; Cohen's $d = 0.23$).

Lost and gained lineages across plots (H2) and their association with plant traits (H3)

Species' tendencies to be lost or gained (i.e. their *U*-values) showed a slight but significant phylogenetic signal (Pagel's $\lambda = 0.20$; $P < 0.001$). The *U*-values varied considerably across species (Fig. 2a; Notes S9: Table S9.1) and families (Notes 9: Table S9.2). Roughly 14% of the internal nodes in the phylogeny experienced either more losses (7%) or gains (7%) in descendant species than randomly expected. For example, species from the Apiaceae, Ericaceae, Fabaceae, Orchidaceae, and Orobanchaceae families were more likely to be lost, while species in the Amaranthaceae, Cyperaceae, Rosaceae (subfamily Amygdaloideae), and Urticaceae were more likely to be gained (Fig. 2a; Notes S10: Fig. S10.1). The observed trends among these families remained consistent, regardless of whether all species or only the most common ones were considered (Notes S11: Tables S11.1, S11.2; Figs S11.1, S11.2). Among the tested traits, plant height (H) and SLA were positively and significantly related to species' *U*-values (Fig. 2b). This effect was still significant after removing juvenile trees from the analysis (Notes S12: Fig. S12.1).

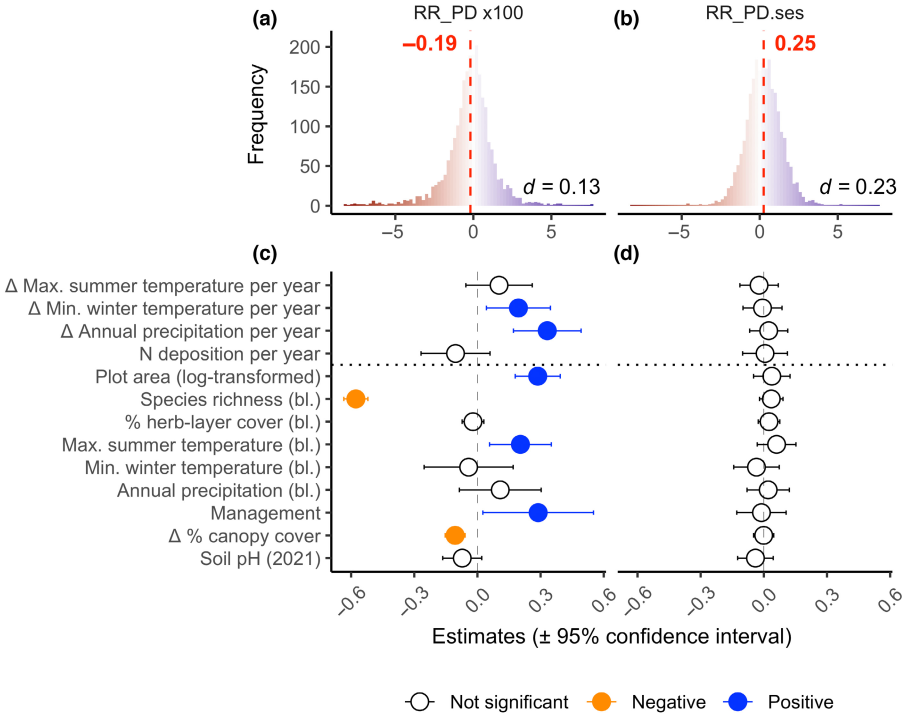


Fig. 1 Temporal changes in phylogenetic diversity (PD) in temperate forest understories and their environmental predictors. (a, b) Histograms of the change in PD between the baseline survey and the resurvey estimated using unstandardized (RR_PD) (a) and standardized (RR_PD.ses) (b) response ratios. The dashed red lines show mean PD values. Cohen's *d* measures the effect size of the difference between the mean and zero. (c, d) Standardized estimated coefficients (±95% confidence intervals) of focal variables and covariates predicting temporal changes in RR_PD (a) and RR_PD.ses (b) from linear mixed-effect models. The dotted horizontal line separates focal predictors (top) from covariates (bottom). bl., baseline; Max., maximum; Min., minimum.

Phylogenetic relatedness of lost and gained species (H4) and between lost or gained species and persisting species (H5)

Both the PR of lost and gained species measured at the tips of the phylogeny (MNTD.ses) and between lost or gained species and persisting species (D_{nn}.ses) were mostly random (Fig. 3a,b). However, lost species were, on average, more phylogenetically clustered (Cohen's $d = 0.31$) than gained species (Cohen's $d = 0.04$). When lost species were phylogenetically clustered (7% of plots), Poaceae were often overrepresented (Notes S13: Figs S13.1, S13.2). By contrast, gained species were, on average, more phylogenetically distantly related to the persisting species (Cohen's $d = 0.20$) than lost species (Cohen's $d = 0.06$). We found almost identical results when we measured PR metrics at basal phylogenetic levels (Notes S6: Fig. S6.1).

Associations between phylogenetic metrics and environmental change variables (H6)

Plots that experienced warmer winters and higher annual precipitation had a significant net increase in PD associated with an increase in species richness (Fig. 1c). When species' losses and gains were analyzed separately, plots that experienced increased precipitation lost less PD and species (Notes S8: Fig. S8.1). By contrast, plots that experienced warmer summers gained more PD and species. However, climate change and N deposition had no effect either on the standardized change in PD (Fig. 1d) or PR metrics for lost (Fig. 3c) and gained (Fig. 3d) species. Among the covariates, baseline species richness had the highest negative effect on the unstandardized change in PD, while management and plot size had the highest positive effects.

Discussion

We measured long-term shifts in plot-level PD and the PR of lost and gained species in the understory of 2672 vegetation plots in temperate forests in 14 European countries. Over periods that averaged 40 yr, species of specific plant lineages (and their associated ecological strategies) persisted or increased while others declined. Within plots, species that colonized or went extinct were phylogenetically random subsets of the forest species pool, suggesting stochastic dynamics. However, lost species within plots exhibited a higher degree of PR than gained species. After accounting for differences in species richness across plots, changes in PD did not respond to climate change or nitrogen deposition, confirming that species are lost or gained randomly throughout the tree of life in response to environmental change.

Temporal changes in phylogenetic diversity and its association with environmental change drivers

We found that forest understories in temperate Europe have mostly experienced slight declines in PD due to a general reduction in species richness. This finding matches reports of few systematic shifts in plot-level plant species richness across continents (Bernhardt-Römermann *et al.*, 2015; Jandt *et al.*, 2022) and globally (Vellend *et al.*, 2013). However, after accounting for differences in species richness among plots, we observed a slightly greater increase in PD than expected by chance (H1). This implies that the newly acquired species come from more diverse evolutionary lineages than the lost species, which were part of more phylogenetically clustered subsets of the habitat species pool. Accordingly, we also found that the lost species within plots were more closely related to each other than the gained species (H4).

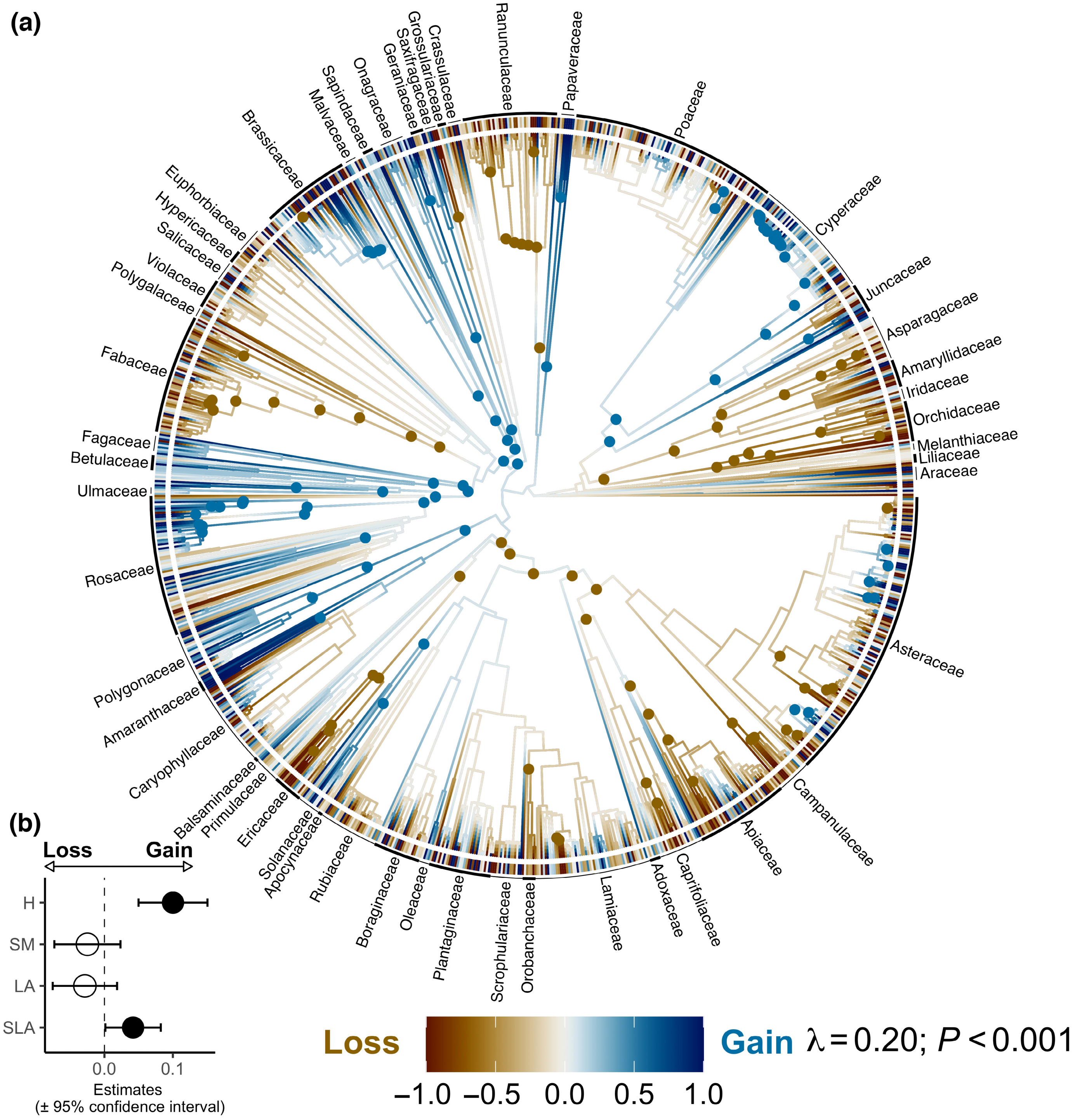


Fig. 2 Species tendency to be lost or gained in temperate forest understories and associated traits. (a) Distribution of U-values of plant species across the phylogeny. Positive (blue) and negative (brown) U-values indicate species and lineages gained or lost over time, respectively. Points in the phylogeny indicate nodes with U-values higher (blue) or lower (brown) than expected if species were randomly distributed across the phylogeny. Only significant nodes with at least three species and the 50 plant families with the largest number of species are shown. The phylogenetic signal of U-values is indicated by Pagel's λ statistic metric. (b) Results from a phylogenetic generalized least squares (PGLS) regression predicting U-values from plant height (H), seed mass (SM), leaf area (LA), and specific leaf area (SLA). Black and empty circles denote significant and nonsignificant effects, respectively. Bars crossing the circles indicate 95% confidence intervals.

These findings suggest that, assuming niche conservatism, species that have been gained possess a broader range of ecological strategies than lost species (see evidence in Notes S14: Fig. S14.1). Nevertheless, this interpretation should be treated cautiously, as evolutionary lability may be a common feature across many ecologically relevant functional traits (Gerhold *et al*., 2015).

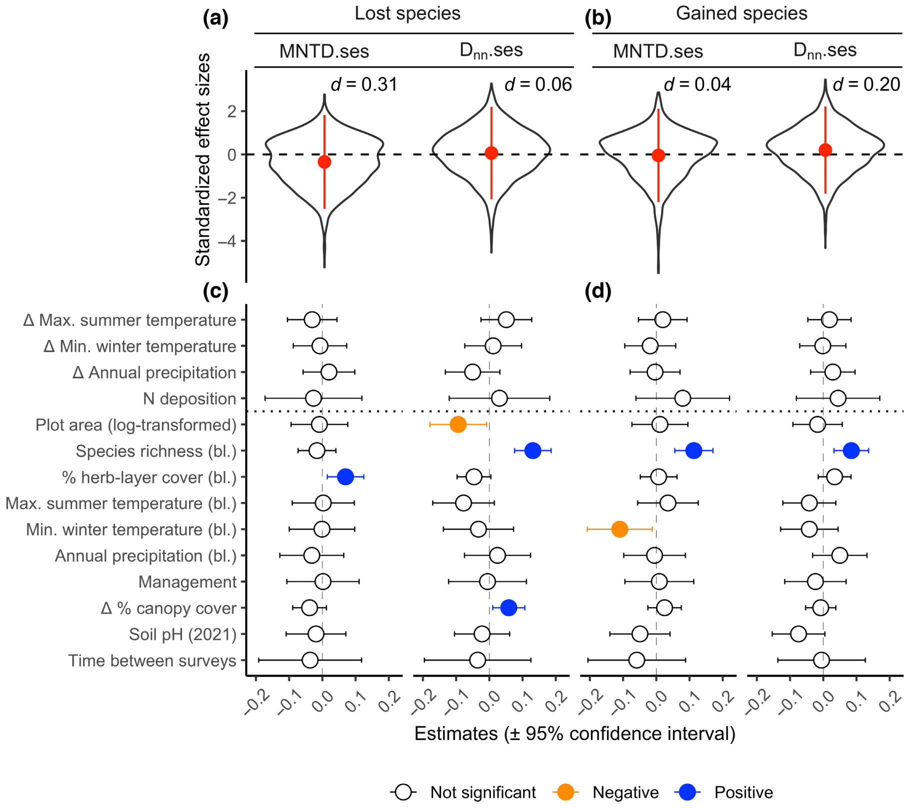


Fig. 3 Phylogenetic relatedness (PR) of lost and gained species, and between lost or gained species and persisting species in temperate forest understories, and their environmental predictors. (a, b), Violin plots showing PR of lost (a) and gained (b) species (MNTD.ses) and between lost or gained species and persisting species (D_{nn}.ses) in forest plots. Positive and negative values indicate phylogenetic overdispersion and clustering, respectively. The dashed horizontal line crossing zero indicates no deviation from the random expectation. Red dots represent median values, and bars indicate the 95% confidence interval. Cohen's *d* measures the effect size of the difference between the mean and zero. (c, d) Standardized estimated coefficients (±95% confidence intervals) of focal variables and covariates predicting PR metrics of lost (a) and gained (b) species from linear mixed-effect models. The dotted horizontal line separates focal predictors (above) from covariates (below). bl., baseline; Max., maximum; Min., minimum.

Forest sites that experienced warmer winters and higher annual precipitation had greater increases in PD and species richness (H6). By contrast, neither changes in summer temperature nor N deposition significantly affected the unstandardized change in PD. Therefore, our findings indicate that diversity changes may increase at forest sites experiencing greater large-scale environmental changes. However, drought-induced losses of plant species can become more common under changing precipitation regimes and varying tree canopy structures (Archaux & Wolters, 2006). At a finer scale, increased canopy cover in forest plots (reducing light availability) promoted greater decreases in unstandardized PD over time. This result can explain, for example, the losses in light-demanding lineages such as Fabaceae and the gains in shade-tolerant woody lineages. Increased shading may also buffer the effects of a hotter and drier macroclimate (De Frenne *et al.*, 2013; Suggitt *et al.*, 2018) by promoting greater thermal stability (Zellweger *et al.*, 2020).

Our findings also suggest that changes in environmental factors do not influence changes in PD in forest understories after accounting for differences in species richness (H6). This implies that losses and gains of specific lineages within local communities and along environmental gradients occur randomly across the phylogeny. Therefore, if species' ecological roles are phylogenetically conserved, then losses and gains of specific functions are independent of recent environmental changes in temperate forests. However, it is possible that filtered traits are not phylogenetically conserved or that their response to abiotic variation is nonlinear and may reach tipping points. Furthermore, other biotic and abiotic covariates not included in our models are also known to affect diversity changes. For example, the interaction between environmental change and forest management practices can favor specific lineages (e.g. clades within Poaceae or Cyperaceae) through soil compaction (Mohieddinne *et al.*, 2022), canopy openness (Pilon *et al.*, 2020), and human-assisted dispersal (Closset-Kopp *et al.*, 2019). In addition, grazing pressure promotes different ecological strategies, particularly along the eutrophication gradient (Segar *et al.*, 2022).

Plant lineage losses and gains across plots

Despite almost no net change in PD, the likelihood of species being lost or gained between surveys across all plots depended on their lineage (H2). For example, species from the Fabaceae family, characterized by strong niche conservatism in their ability to fix atmospheric N, or from the Ericaceae family, which have adapted to survive in acidic and nutrient-deficient soils through ericoid mycorrhiza, were more likely to decline. These species groups are probably being outcompeted by species adapted to using nitrogen supplied by increased atmospheric N deposition (van Strien *et al.*, 2017; Berendse *et al.*, 2021). Accordingly, we found an increase in species with acquisitive leaf economics (i.e. higher SLA) across plots (H3). Additional plant lineages considered of high conservation value, for example, Orchidaceae (CITES, 2019), or with unique ecological functions such as the holo- or hemiparasitic Orobanchaceae, have also experienced consistent declines. These results highlight that regional and global changes in environmental conditions threaten lineages with particular ecological strategies. The ecological strategies of plant families can provide insights into community dynamics and ecosystem functioning that are not immediately apparent when considering individual functional traits alone.

By contrast, in recent decades, nitrophilous weedy Amaranthaceae species, moisture-demanding Cyperaceae species, or woody Rosaceae species have increased across temperate forest understories. These findings parallel positive associations between species' tendency to be lost or gained (their *U*-values) and their potential height and SLA (H3). These associations remained significant even when juvenile trees were removed from the analysis. Increased dominance of taller and nitrogen-demanding species in forest understories has already been documented in Europe (Kopecký *et al.*, 2012; Staude *et al.*, 2020) and may, in part, reflect how environmental changes interact with management legacies that alter soil resources (Perring *et al.*, 2018). Increased recruitment of taller and more acquisitive species could alter forest vegetation dynamics, ultimately reshaping ecosystem function. These results across plots and the phylogenetic signal in species' tendencies to be lost or gained underscore the importance of distinguishing between suppressed and colonizing species when assessing changes in the evolutionary history of ecological communities at the continental scale.

Although plant height and SLA significantly affected species' tendencies to be lost and gained, seed mass and leaf area did not (H3). These results suggest that relating other phylogenetically conserved traits to particular drivers of recent species extinctions and colonizations in temperate forests may be challenging. The overall metric of PD, however, also captures the functional diversity of hard-to-measure or unmeasured traits such as dispersal mode, pollination system, and root traits (e.g. mycorrhizal type and N-fixing symbioses), all known to affect extinction probabilities in other forest types (e.g. Sodhi *et al.*, 2008). The evolutionary history of a species is, therefore, a useful predictor of extinction risk, with greater risks often associated with either more diverse evolutionary branches or more recent speciation (Mace *et al.*, 2003). For both extrinsic (i.e. environmental) and intrinsic (e.g. life-history trait) drivers of extinction, conserving communities with a high PD increases the probability that a broad combination of traits will persist under uncertain future conditions (Owen *et al.*, 2019).

Phylogenetic relatedness of lost and gained species and its association with environmental change drivers

Our results support the hypothesis that locally lost species are more phylogenetically clustered than gained species in forest understories (H4). Nevertheless, PR of locally lost and gained species in these forest understories was generally random. This finding complements previous studies showing nonrandom phylogenetic losses of woody species between glacial–interglacial cycles (Eiserhardt *et al.*, 2015) and nonrandom distributions of global extinction risk among angiosperms (Vamosi & Wilson, 2008). These results also suggest that traits that confer intrinsic susceptibility to extinction or the ability to colonize new environments may not necessarily be shared among closely related species in temperate forests. However, when lost species were phylogenetically clustered (7% of plots), Poaceae were often overrepresented (Notes S13). Poaceae are thought to have originated at tropical forest edges and have since diversified based on their ability to withstand grazing, fire, and drought (Clayton, 1981). Hence, the reported loss of closely related grasses in a small subset of temperate forest understories could be related to a reduction in light availability triggered by canopy closure and rapid expansion of woody species.

The European forest understories that were studied generally exhibited random PR between the lost and gained species and persisting species (H5). Assuming phylogenetic niche conservatism (Losos, 2008), the functional similarity or dissimilarity of the lost and gained species to persisting species did not differ from what would be expected by chance. Notably, the gained species tended to be, on average, more distantly related to the persisting species than were the lost species. Previous studies of vegetation succession have demonstrated that late-stage colonizers comprise species from a wider diversity of lineages with various traits (Li *et al.*, 2015). This pattern may result from environmental modifications that reduce the strength of environmental filtering, increase the carrying capacity of local habitats, and facilitate the colonization of species with distinct functional traits (Valiente-Banuet & Verdú, 2013). Additionally, competition may exclude functionally similar species that occupy similar niches (i.e. competitive exclusion; Li *et al.*, 2015).

We found no evidence that the PR of lost and gained species varied along gradients of environmental change, as initially predicted (H6). The environmental filters imposed by recent macroclimate changes and N deposition may not be strong enough or have operated over sufficient time to exclude ecological strategies that increase intrinsic vulnerability to extinction. Alternatively, these strategies may not be phylogenetically conserved, or stochastic processes could account for many local extinctions.

Our study reveals that despite limited change in mean overall PD in temperate forest understories, substantial differences exist in the loss or gain of phylogenetic lineages in recent decades. Each lineage contains unique evolved features that play distinct ecological roles. We also found that regional shifts in macroclimate only affected changes in PD through changes in species richness. After controlling for differences in species richness within plots, we observed random losses and gains of species throughout the phylogeny across environmental gradients. Moreover, the fact that, within plots, lost species tend to be phylogenetically randomly related implies that close relatives may not share traits that confer intrinsic susceptibility to local extinction. Our results enhance our understanding of how shifts in environmental conditions drive both subtle and profound changes in the phylogenetic and functional structure of forest plant communities.

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Competing interests

None declared.

Author contributions

JPC conceived the study with input from MChytrý, JL, DL, FM-C and JR. LB, MB-R, MChudomelová, DC, GD, PDF, MD, TDirnböck, TDurak, RH, TH, BJ, MK, MM, FM, TN, AO, PP, RP, KR, WS, TS, KŚ, BT, KV, OV, DW and MW contributed community composition data. JPC performed the analyses and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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Data availability

The data and code that support the findings of this study are available in Zenodo via doi: 10.5281/zenodo.8338171.

References

Archaux F, Wolters V. 2006. Impact of summer drought on forest biodiversity: what do we know? *Annals of Forest Science* **63**: 645–652.

Barber N, Jones HP, Duvall MR, Wysocki WP, Hansen MJ, Gibson DJ. 2016. Phylogenetic diversity is maintained despite richness losses over time in restored tallgrass prairie plant communities. *Journal of Applied Ecology* **54**: 137–144.

Berendse F, Geerts R, Elberse WT, Bezemer TM, Goedhart PW, Xue W, Noordijk E, ter Braak CJF, Korevaar H. 2021. A matter of time: recovery of plant species diversity in wild plant communities at declining nitrogen deposition. *Diversity and Distributions* **27**: 1180–1193.

Bernhardt-Römermann M, Baeten L, Craven D, De Frenne P, Hédl R, Lenoir J, Bert D, Brunet J, Chudomelová M, Decocq G *et al.* 2015. Drivers of temporal changes in temperate forest plant diversity vary across spatial scales. *Global Change Biology* **21**: 3726–3737.

Bruelheide H, Dengler J, Purschke O, Lenoir J, Jiménez-Alfaro B, Hennekens SM, Botta-Dukát Z, Chytrý M, Field R, Jansen F *et al.* 2018. Global trait–environment relationships of plant communities. *Nature Ecology & Evolution* **2**: 1906–1917.

Cavender-Bares J, Ackerly DD, Baum DA, Bazzaz FA. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* **163**: 823–843.

Chai Y, Yue M, Liu X, Guo Y, Wang M, Xu J, Zhang C, Chen Y, Zhang L, Zhang R. 2016. Patterns of taxonomic, phylogenetic diversity during a long-term succession of forest on the Loess Plateau, China: insights into assembly process. *Scientific Reports* **6**: 27087.

Chao A, Chiu C-H, Jost L. 2010. Phylogenetic diversity measures based on Hill numbers. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **365**: 3599–3609.

CITES. 2019. *CITES Appendix II.* [WWW document] URL https://cites.org/sites/default/files/eng/app/2019/E-Appendices-2019-11-26.pdf [Accessed 24 November 2022].

Clayton WD. 1981. Evolution and distribution of grasses. *Annals of the Missouri Botanical Garden* **68**: 5–14.

Closset-Kopp D, Hattab T, Decocq G. 2019. Do drivers of forestry vehicles also drive herb layer changes (1970–2015) in a temperate forest with contrasting habitat and management conditions? *Journal of Ecology* **107**: 1439–1456.

Cohen J. 1998. *Statistical power analysis for the behavioral sciences, 2nd edn.* Mahwah, NJ, USA: Erlbaum.

De Frenne P, Rodríguez-Sánchez F, Coomes DA, Baeten L, Verstraeten G, Vellend M, Bernhardt-Römermann M, Brown CD, Brunet J, Cornelis J *et al.* 2013. Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences, USA* **110**: 18561–18565.

De Pauw K, Meeussen C, Govaert S, Sanczuk P, Vanneste T, Bernhardt-Römermann M, Bollmann K, Brunet J, Calders K, Cousins SAO *et al.* 2021. Taxonomic, phylogenetic and functional diversity of understorey plants respond differently to environmental conditions in European forest edges. *Journal of Ecology* **109**: 2629–2648.

Debastiani VJ, Bastazini VAG, Pillar VD. 2021. Using phylogenetic information to impute missing functional trait values in ecological databases. *Ecological Informatics* **63**: 101315.

Díaz S, Cabido M, Casanoves F. 1998. Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science* 9: 113–122.

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC *et al.* 2016. The global spectrum of plant form and function. *Nature* 529: 167–171.

Duprè C, Stevens CJ, Ranke T, Bleeker A, Peppler-Lisbach C, Gowing DJG, Dise NB, Dorland E, Bobbink R, Diekmann M. 2010. Changes in species richness and composition in European acidic grasslands over the past 70 years: the contribution of cumulative atmospheric nitrogen deposition. *Global Change Biology* 16: 344–357.

Eiserhardt WL, Borchsenius F, Plum CM, Ordonez A, Svenning J-C. 2015. Climate-driven extinctions shape the phylogenetic structure of temperate tree floras. *Ecology Letters* 18: 263–272.

European Commission. 2022. *European State of the Climate (ESOTC) 2022.* [WWW document] URL https://climate.copernicus.eu/esotc/2022 [accessed 2 August 2023].

Faith DP. 1992. Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61: 1–10.

Gerhold P, Cahill JF, Winter M, Bartish IV, Prinzing A. 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology* 29: 600–614.

Gilliam FS. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience* 57: 845–858.

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD *et al.* 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1: e1500052.

Harris C, Brummitt N, Cobbold CA, Reeve R. 2022a. Strong phylogenetic signals in global plant bioclimatic envelopes. *Global Ecology and Biogeography* 31: 2191–2203.

Harris IC, Jones PD, Osborn T. 2022b. *CRU TS4.06: Climatic Research Unit (CRU) Time-Series (TS) version 4.06 of high-resolution gridded data of month-by-month variation in climate (Jan. 1901- Dec. 2021).* NERC EDS Centre for Environmental Data Analysis. [WWW document] URL https://catalogue.ceda.ac.uk/uuid/e0b4e1e56c1c4460b796073a31366980 [accessed 17 November 2022].

Hawkins BA, Rueda M, Rangel TF, Field R, Diniz-Filho JAF. 2014. Community phylogenetics at the biogeographical scale: cold tolerance, niche conservatism and the structure of North American forests. *Journal of Biogeography* 41: 23–38.

IPBES. 2019. *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.* Bonn, Germany: IPBES Secretariat.

Ives AR, Zhu J. 2006. Statistics for correlated data: phylogenies, space, and time. *Ecological Applications* 16: 20–32.

Jandt U, Bruelheide H, Jansen F, Bonn A, Grescho V, Klenke RA, Sabatini FM, Bernhardt-Römermann M, Blüml V, Dengler J *et al.* 2022. More losses than gains during one century of plant biodiversity change in Germany. *Nature* 611: 512–518.

Jin Y, Qian H. 2022. V.PhyloMaker2: an updated and enlarged R package that can generate very large phylogenies for vascular plants. *Plant Diversity* 4: 335–339.

Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA, Aakala T, Abedi M *et al.* 2020. TRY plant trait database – enhanced coverage and open access. *Global Change Biology* 26: 119–188.

Keddy PA. 1992. Assembly and response rules –two goals for predictive community ecology. *Journal of Vegetation Science* 3: 157–164.

Kindt R. 2020. WorldFlora: an R package for exact and fuzzy matching of plant names against the World Flora Online taxonomic backbone data. *Applications in Plant Sciences* 8: e11388.

Kopecký M, Hédl R, Szabó P. 2012. Non-random extinctions dominate plant community changes in abandoned coppices. *Journal of Applied Ecology* 50: 79–87.

Lavorel S, Garnier E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.

Letten AD, Keith DA, Tozer MG. 2014. Phylogenetic and functional dissimilarity does not increase during temporal heathland succession. *Proceedings of the Royal Society B* 281: 20142102.

Li D, Olden JD, Lockwood JL, Record S, McKinney ML, Baiser B. 2020. Changes in taxonomic and phylogenetic diversity in the Anthropocene. *Proceedings of the Royal Society B: Biological Sciences* 287: 20200777.

Li D, Waller D. 2017. Fire exclusion and climate change interact to affect long-term changes in the functional composition of plant communities. *Diversity and Distributions* 23: 496–506.

Li SP, Cadotte MW, Meiners SJ, Hua ZS, Jiang L, Shu WS. 2015. Species colonisation, not competitive exclusion, drives community overdispersion over long-term succession. *Ecology Letters* 18: 964–973.

Loidi J, Chytrý M, Jiménez-Alfaro B, Alessi N, Biurrun I, Campos JA, Čarni A, Fernández-Pascual E, Font Castell X, Gholizadeh H *et al.* 2021. Life-form diversity across temperate deciduous forests of Western Eurasia: a different story in the understory. *Journal of Biogeography* 48: 2932–2945.

Losos JB. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* 11: 995–1007.

Mace GM, Gittleman JL, Purvis A. 2003. Preserving the tree of life. *Science* 300: 1707–1709.

Magurran AE, Henderson PA. 2010. Temporal turnover and the maintenance of diversity in ecological communities. *Philosophical Transactions of the Royal Society B* 365: 3611–3620.

Mathakutha R, Steyn C, le Roux PC, Blom IJ, Chown SL, Daru BH, Ripley BS, Louw A, Greve M. 2019. Invasive species differ in key functional traits from native and non-invasive alien plant species. *Journal of Vegetation Science* 30: 994–1006.

Mohieddinne H, Brasseur B, Gallet-Moron E, Lenoir J, Spicher F, Kobaissi A, Horen H. 2022. Assessment of soil compaction and rutting in managed forests through an airborne LiDAR technique. *Land Degradation & Development* 34: 1558–1569.

Naimi B, Hamm N, Groen TA, Skidmore AK, Toxopeus AG. 2014. Where is positional uncertainty a problem for species distribution modelling. *Ecography* 37: 191–203.

Navarro DJ. 2015. *Learning statistics with R: a tutorial for psychology students and other beginners.* Adelaide, SA, Australia: University of Adelaide.

Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2018. *caper: comparative analyses of phylogenetics and evolution in R.* R package v.1.0.1. [WWW document] URL https://CRAN.R-project.org/package=caper [accessed 11 April 2023].

Owen NR, Gumbs R, Gray CL, Faith DP. 2019. Global conservation of phylogenetic diversity captures more than just functional diversity. *Nature Communications* 10: 859.

Pagel M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401: 877–884.

Penone C, Davidson AD, Shoemaker KT, Di Marco M, Rondinini C, Brooks TM, Young BE, Graham CH, Costa GC. 2014. Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution* 5: 961–970.

Perring MP, Bernhardt-Römermann M, Baeten L, Midolo G, Blondeel H, Depauw L, Landuyt D, Maes SL, de Lombaerde E, Carón MM *et al.* 2018. Global environmental change effects on plant community composition trajectories depend upon management legacies. *Global Change Biology* 24: 1722–1740.

Pilon NA, Durigan G, Rickenback J, Pennington RT, Dexter KG, Hoffmann WA, Landuyt D, Maes SL, De Lombaerde E, Carón MM *et al.* 2020. Shade alters savanna grass layer structure and function along a gradient of canopy cover. *Journal of Vegetation Science* 32: e12959.

Pinheiro J, Bates D, R Core Team. 2022. *nlme: linear and nonlinear mixed effects models.* R package v.3.1.157. https://CRAN.R-project.org/package=nlme [accessed 5 April 2023].

Poggio L, de Sousa LM, Batjes NH, Heuvelink GBM, Kempen B, Ribeiro E, Rossiter D. 2021. SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. *The Soil* 7: 217–240.

Purschke O, Schmid BC, Sykes MT, Poschlod P, Michalski SG, Durka W, Kühn I, Winter M, Prentice HC. 2013. Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *Journal of Ecology* 101: 857–866.

Qian H, Jin Y. 2016. An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *Journal of Plant Ecology* 9: 233–239.

Qian H, Jin Y. 2021. Are phylogenies resolved at the genus level appropriate for studies on phylogenetic structure of species assemblages? *Plant Diversity* 4: 255–263.

R Core Team. 2022. *R: a language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical. [WWW document] URL https://www.R-project.org/ [accessed 1 March 2023].

Revell LJ. 2012. PHYTOOLS: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3: 217–223.

Santos T. 2018. *PVR: phylogenetic eigenvectors regression and phylogenetic signal-representation curve.* R Package v.0.3. [WWW document] URL https://CRAN.R-project.org/package=PVR [accessed 1 August 2023].

Segar J, Pereira HM, Baeten L, Bernhardt-Römermann M, De Frenne P, Fernández N, Gilliam FS, Lenoir J, Ortmann-Ajkai A, Verheyen K *et al.* 2022. Divergent roles of herbivory in eutrophying forests. *Nature Communications* 13: 7837.

Simkin SM, Allen EB, Bowman WD, Clark CM, Belnap J, Brooks ML, Cade BS, Collins SL, Geiser LH, Gilliam FS *et al.* 2016. Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. *Proceedings of the National Academy of Sciences, USA* 113: 4086–4091.

Smith SA, Brown JW. 2018. Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany* 105: 302–314.

Sodhi NS, Koh LP, Peh KS-H, Tan HTW, Chazdon RL, Corlett RT, Lee TM, Colwell RK, Brook BW, Sekercioglu CH *et al.* 2008. Correlates of extinction proneness in tropical angiosperms. *Diversity and Distributions* 14: 1–10.

Staude IR, Waller DM, Bernhardt-Römermann M, Bjorkman AD, Brunet J, De Frenne P, Hédl R, Jandt U, Lenoir J, Máliš F *et al.* 2020. Replacements of small- by large-ranged species scale up to diversity loss in Europe's temperate forest biome. *Nature Ecology & Evolution* 4: 802–808.

Stekhoven DJ. 2022. *MISSFOREST: nonparametric missing value imputation using random forest.* R package v.1.5. [WWW document] URL https://cran.r-project.org/web/packages/missForest/ [accessed 1 August 2023].

van Strien AJ, Boomsluiter M, Noordeloos ME, Verweij RJT, Kuyper TW. 2017. Woodland ectomycorrhizal fungi benefit from large-scale reduction in nitrogen deposition in The Netherlands. *Journal of Applied Ecology* 55: 290–298.

Suggitt AJ, Wilson RJ, Isaac NJB, Beale CM, Auffret AG, August T, Bennie JJ, Crick HQP, Duffield S, Fox R *et al.* 2018. Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change* 8: 713–717.

Tsirogiannis C, Sandel B. 2016. PHYLOMEASURES: a package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography* 39: 709–714.

Valiente-Banuet A, Verdú M. 2013. Plant facilitation and phylogenetics. *Annual Review of Ecology, Evolution, and Systematics* 44: 347–366.

Vamosi JC, Wilson JRU. 2008. Nonrandom extinction leads to elevated loss of angiosperm evolutionary history. *Ecology Letters* 11: 1047–1053.

Vellend M, Baeten L, Myers-Smith IH, Elmendorf SC, Beauséjour R, Brown CD, De Frenne P, Verheyen K, Wipf S. 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences, USA* 110: 19456–19459.

Verheyen K, Baž͏ány M, Chećko E, Chudomelová M, Closset-Kopp D, Czortek P, Decocq G, De Frenne P, De Keersmaeker L, Enríquez García C *et al.* 2018. Observer and relocation errors matter in resurveys of historical vegetation plots. *Journal of Vegetation Science* 29: 812–823.

Verheyen K, De Frenne P, Baeten L, Waller DM, Hédl R, Perring MP, Blondeel H, Brunet J, Chudomelová M, Decocq G *et al.* 2017. Combining biodiversity resurveys across regions to advance global change research. *Bioscience* 67: 73–83.

Webb CO, Ackerly DD, Kembel SW. 2008. PHYLOCOM: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 18: 2098–2100.

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 3: 475–505.

Westoby M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 19: 213–227.

Zellweger F, De Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-Römermann M, Baeten L, Hédl R, Berki I, Brunet J *et al.* 2020. Forest microclimate dynamics drive plant responses to warming. *Science* 368: 772–775.

Zuur AF, Leno EN, Smith GM. 2007. *Analysing ecological data.* New York, NY, USA: Springer.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1 Location of forest plots and a list of contributing datasets.

Notes S2 Phylogenetic signal and ecological functions associated with plant traits.

Notes S3 Trait data availability and correlations between traits.

Notes S4 Model results with extreme climate variables.

Notes S5 Rationale for covariate inclusion and correlations between covariates.

Notes S6 Results for metrics of phylogenetic diversity relatedness at basal phylogenetic levels.

Notes S7 Metrics of phylogenetic diversity and relatedness.

Notes S8 Models predicting species' losses and gains separately.

Notes S9 *U*-values of individual understory species.

Notes S10 *U*-values within Rosaceae.

Notes S11 Results excluding rare species.

Notes S12 Results excluding juvenile trees.

Notes S13 Overrepresented lost and gained lineages within clustered plots.

Notes S14 Functional dispersion of lost and gained species.

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