Extinction drives recent thermophilization but does not trigger homogenization in forest understory

Jeremy Borderieux[1, *], Jean-Claude Gégout[1], Josep M. Serra-Diaz[1, 2]

1. Université de Lorraine, AgroParisTech, INRAE, UMR Silva, 54000 Nancy, France
2. Eversource Energy Center and Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, United States of America

Orcid ID:

Jeremy Borderieux : 0000-0003-3993-1067

Jean-Claude Gégout : 0000-0002-5760-9920

Josep M. Serra-Diaz: 0000-0003-1988-1154

Corresponding author: Jeremy Borderieux: jeremy.borderieux@agroparistech.fr

Abstract

The ongoing climate change is triggering plant community thermophilization. Such selection process towards warm-adapted species may also lead to biotic homogenization. The link between those two processes and the community dynamic driving them (colonization and extinction) remain unknow but are critical to understand community response under rapid environmental change.

We used 12,764 pairs of plots to study plant community change in 16 years of rising temperatures in 80 forest ecoregions of France. We computed thermophilization and Δβ-diversity (homogenization) for each ecoregion, and partitioned these changes into extinction and colonization dynamics for cold and warm-adapted species.

Forest understory communities thermophilized on average by 0.12 °C decade^{-1} and up to 0.20 °C decade^{-1} in warm ecoregions. This rate was entirely driven by extinction dynamics. Extinction of cold-adapted species was a driver of homogenization, but it was compensated by the colonization of rare species and the extinction of common species. This results in a lack of apparent trend of homogenization.

An extinction-driven thermophilization is concerning as it reflects the dieback of current species rather than adaptation of understory to climate change. These results suggest that a future loss of biodiversity and a delayed biotic homogenization should be considered.

Keywords

Community ecology, thermophilization, homogenization, β-diversity, climate change, forest, understory.

1. Introduction

The unprecedent speed of the current climate warming is causing major biodiversity shifts and the reshuffling of ecological communities(Lenoir & Svenning, 2015; Svenning & Sandel, 2013). Such reshuffling could lead to a major risk for biodiversity worldwide (Sala et al., 2000) and the services it provides (Reu et al., 2022; Wang et al., 2021). Two major patterns in community composition have been reported as a result of global changes: thermophilization and biotic homogenization. On the one hand, thermophilization of plant communities – the increase in the average temperature affiliation of species in a community over time – is increasing as a result of climate warming (De Frenne et al., 2013; Martin et al., 2019; Richard et al., 2021), albeit at a slower pace than climate e.g. (Bertrand et al., 2011, 2016). In parallel, evidence also suggests that biotic homogenization across plant communities is occurring (Cholewińska et al., 2020; Olden & Rooney, 2006; Staude et al., 2022).This is evidenced by a decrease in β-diversity, a measure that signal an increase of similarity among community of a region. To date, whether these processes occur simultaneously, their linkages, and which community dynamics underlie such shifts is unknown.

Baseline expectations from global warming suggest that warm-adapted species may increasingly substitute cold-adapted species (De Frenne et al., 2013; Gottfried et al., 2012; Svenning & Sandel, 2013), with some degree of individual species adaptation (Franks et al., 2014; Lavergne et al., 2010). At large scale, biogeographic predictions suggest species displacement via range shifts (Lenoir & Svenning, 2015), with lagged dynamics caused by dispersal and colonization constraints of warm-adapted species to colonize climatic suitable area (Boulangeat et al., 2012; Govaert et al., 2021; Ozinga et al., 2009). Thermophilization is thus the product of different rates of colonization and/or extinction (sensu local extirpation) of warm- vs. cold- adapted species in a community. At one extreme, thermophilization may stem from colonization of warm-adapted species without any extinction of cold-adapted species (Fig.1). Conversely, thermophilization may stem from extinction of cold-adapted species only thus implying biotic erosion of communities rather than community adaptation under climate change (Fig.1).

Thermophilization effects on local-scale diversity (α-diversity) are straightforward, extinction could cause a loss of species richness and colonization a gain of species richness (Staude et al., 2022; Steinbauer et al., 2018). This change in diversity is particularly documented in mountains forest and summits, where colonization is facilitated (Steinbauer et al., 2018). Less known is how thermophilization causes a decrease of β-diversity, homogenization hereafter. Indeed, thermophilization can be driven by the increase of an already common ubiquitous

warm-adapted species, and thus reduces β-diversity (Fig.1.b). Conversely, local extinction-driven thermophilization can homogenize communities if the declining cold-adapted species are rare (Fig.1.b). Understanding which community dynamics drive these processes and how thermophilization is linked with biodiversity changes is thus necessary to understand climate-change induced community shifts (Baeten et al., 2012; Tatsumi et al., 2020, 2021).

Here, we unveil the community dynamics (extinction and colonization) responsible for shifts in both thermophilization and β-diversity. We disentangled both β-diversity and thermophilization dynamics based on recent methods to decompose extinction and colonization processes of temporal changes in communities (Tatsumi et al., 2021). We applied our framework to analyze temporal shifts in 12,764 plots (with 745 plant species) of understory forest communities in 80 forest ecoregions France (homogenous areas in environmental conditions, a total of 535,218 km^2), from 2005 to 2021 (IGN, 2013, 2019). We computed the individual contribution of each species to the change in mean thermal optimum (i.e. thermophilization) and in β-diversity (i.e. homogenization) in each ecoregion (Fig1.b). We partitioned those contribution into 4 community processes: extinction and colonization of cold and warm-adapted species, respectively.

With this partitioning we specifically asked: (1) Is there a significant thermophilization of forests, and what community processes drive it? (2) Is there a significant flora homogenization of forests and what community processes drive it? And (3) is mean annual temperature significantly linked to thermophilization and homogenization or their extinction and/or colonization processes? Our initial expectation was that thermophilization is a product of both extinction of cold-adapted species and colonization of warm-adapted species, with faster rates in warmer ecoregions, and that homogenization is pervasive and triggered by abundant warm-adapted species colonization (Merle et al., 2020; Tobias & Monika, 2012; Zwiener et al., 2018).

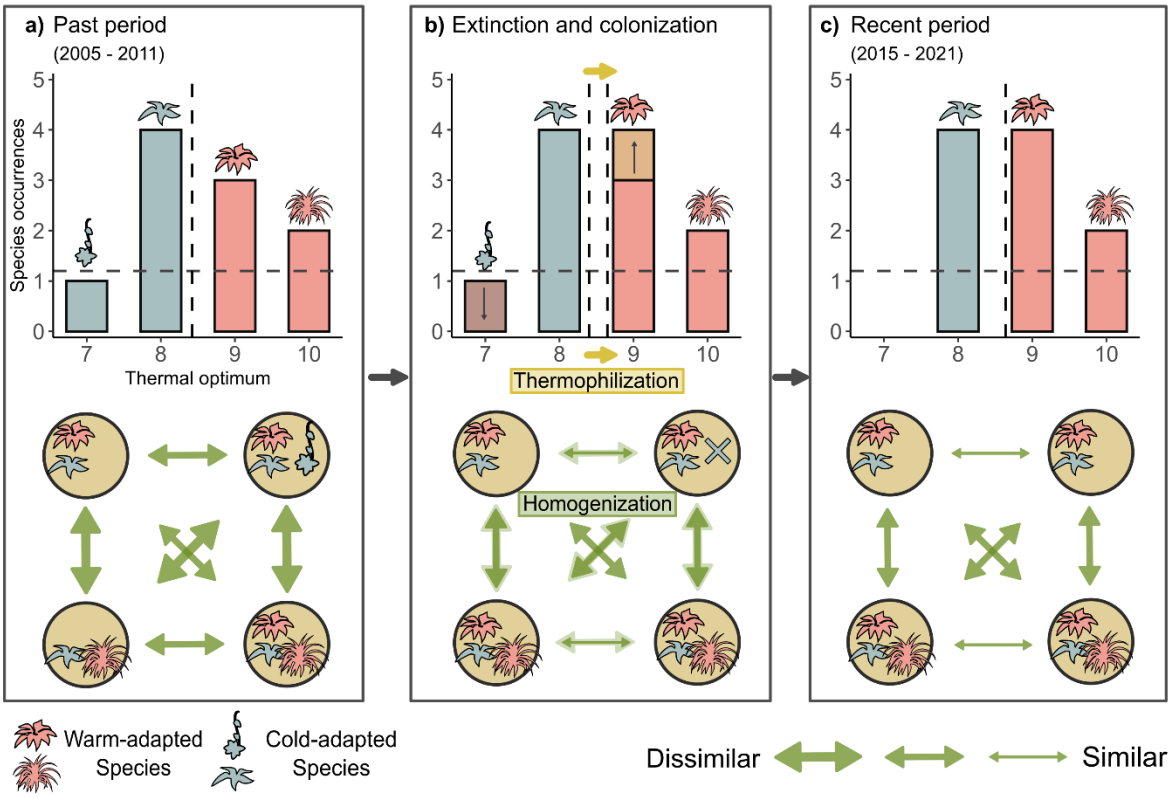


Figure 1: Example of the coupling between thermophilization and homogenization under increasing temperatures (a): An artificial ecoregion comprised of four communities. The ecoregion has two cold and two warm-adapted species depending on whether their thermal optimum is lower or higher than the mean thermal optimum of the ecoregion. The communities are heterogenous as they are all unique. The vertical dotted line represents the mean thermal optimum of the species, the horizontal dotted line represents a threshold differentiating rare from common species (b): An example of thermophilization triggered by the spread of a warm-adapted species and the extinction of one cold-adapted species. The loss of a rare species that made a community unique trigger homogenization, the spread of a common species can also trigger homogenization by increasing similarity with other community (arrow width shrinks). Thermophilization can also heterogenize communities by removing common cold-adapted species or by promoting a rare or absent warm-adapted species (not shown). (c): The resulting ecoregion with a higher mean thermal optimum and more similar communities.

2. Results & Discussion

Climate-driven extinction of species drives thermophilization

The absolute number of occurrences with low thermal optimum decreased within a decade (2005-2011 vs. 2015-2021, Fig.2). As a consequence, 72 out of the 80 ecoregions had a

positive thermophilization rate. The mean thermophilization rate of an ecoregion was 0.012 °C yr^{-1} (s.d. 0.011, Fig.3.a). This rate was entirely driven by extinction (Fig.3.a) – species which occurrences decreased over time. The thermophilization rate we found is consistent with previous studies of temperate forest understory flora change (Bertrand et al., 2011; Dietz et al., 2020; Govaert et al., 2021; Martin et al., 2019; Richard et al., 2021), that reported rates of c.a 0.010 °C yr^{-1}, a value lagging behind the observed warming rate of c.a 0.025°C yr^{-1} in our study region (Dietz et al., 2020). These studies, however, did not provide a quantification of the species turnover driving these rates.

Thermophilization is generally interpreted as the gradual replacement of cold-adapted species by warm-adapted species, which growth and establishment are facilitated by temperature increase (De Frenne et al., 2013). As we measured the extinction contribution to be 0.012 °C yr^{-1} (s.d. 0.009), we only found evidence of a decrease of occurrences as a driver of the thermophilization. This result was confirmed by a null model in which the change of occurrences of a species is independent of its thermal optimum (Fig.3.a, see methods: null models). Extinction of warm-adapted species was significantly lower compared to this expected random rate. The observed colonization effects on thermophilization were not significantly different from those random rates (Fig.3.a). Our interpretation of an extinction-driven thermophilization was robust to different databases used to infer species thermal optima (Table S1, see methods: null models), and to the uncertainty of thermal optima estimation (Rodríguez-Sánchez et al., 2012) (Table S1, see methods: null models). We also rejected the hypothesis of an overall decrease of occurrences (Fig.2) as an explanation for the significance of the extinction component with a rarefaction model (Table S2, see methods: null models).

Extinction has already been identified as a key driver of thermophilization in drylands (Pérez-Navarro et al., 2021), via a selection of the most drought-resistant species at the expense of the colder-adapted species after a drought-pulse event. Our results extend this observation to the European Temperate, Mediterranean and Mountainous forests biomes (Extended table.1) over 16 years of continued warming. The Mediterranean and the warmest lowlands ecoregions displayed the fastest thermophilization rates, as we estimated the increase of the extinction component of 0.003 °C yr^{-1} per rise of degree in MAT (Fig.4.a), up to an extinction component of 0.020 °C yr^{-1} in the southmost ecoregions (Fig.4.a). This higher extinction rate indicates that thermal stress induced by a warmer climate is sufficient to trigger mortality or impair the establishment of cold-adapted individuals. This finding concurs with projections of species climatic suitability, where extinction is expected at the warm edge of a species distribution (Barbet-Massin et al., 2010; Dullinger et al., 2012; Engler et al., 2011).

The thermophilization rates we found do not match the climate warming rates during our study period (on average 0.026 °C yr^{-1}, Dietz et al., 2020), implying a delay between community dynamics and climate change. This discrepancy could be explained by the lack of colonizing warm-adapted species needed to speed up thermophilization. As our analysis is set at the ecoregion level, our results confirm the lack of migration of understory plants over large areas and triggered by climate change (Fig.4.a). This observation is likely a consequence of the limited dispersal capacities of plants (depending on life cycle, seeds traits etc…) that are not fast enough to follow isotherms shifts induced by climate warming in lowlands ecosystems (Lenoir & Svenning, 2015; Loarie et al., 2009; Serra-Diaz et al., 2014). The only ecoregions where the colonization component drives thermophilization significantly (without exceeding a third of thermophilization) are the mountainous ecoregions (Extended Table 1), concurring with other studies (Bertrand et al., 2011; Lenoir et al., 2008). Indeed, the distance to track shifting isotherms is shorter than in lowlands (Rolland, 2003) which facilitates colonization. Other explanatory factors of the lagged rate could stem from local adaptation of plant populations (Franks et al., 2014; Kubisch et al., 2013; Lavergne et al., 2010) and forest microclimate (De Frenne et al., 2019). Indeed, the temperature buffering of forest canopy slows down thermophilization, as it reduces the exposure of cold-adapted species to stress and extreme events (De Frenne et al., 2019; De Lombaerde et al., 2021; Suggitt et al., 2018; Zellweger et al., 2020). Conversely, warm-adapted species are promoted by canopy opening that increases temperature and light availability (De Frenne et al., 2015; Dietz et al., 2020; Gasperini et al., 2021; Zellweger et al., 2020) However, canopy cover did not influence our results as the mean canopy cover of plots did not meaningfully change between the two periods (mean across ecoregions: past period= 75.9%, present period= 78.5%).

Absence of large-scale community homogenization despite extinction of cold-adapted species

We expected the ecoregion to homogenize toward warmer-adapted communities, concurring with the strong signal of extinction-driven thermophilization (Fig.1). However, homogenization was not a significant trend as only 32 out of the 80 ecoregions displayed a negative Δβ-diversity, whereas 48 showed a positive one. The mean Δβ-diversity across ecoregions was 0.33 (s.d. 1.4) and it was not significantly different from 0 (Fig.3.b). The mean β-diversity of an ecoregion in the past period was 12.0 (s.d. 3.5). As a reminder, Whitaker β-diversity (β_w) index reflects the total number of species of the ecoregion when multiplied over the average local (community) richness. The absence of a clear trend in homogenization did not imply a stasis

in community dynamics. We found significant contributions of colonization and extinction of warm- and cold-adapted species (Fig.3.b) to changes in β-diversity, except for the extinction of warm-adapted species. These dynamics displayed opposite directions and cancelled each other out, resulting in an overall weak signal of community homogenization.

Colonization dynamics contributed significantly to heterogenization (mean effect of 1.04 s.d. 0.94, Fig.3.b). This implies that the heterogenizing effect of the colonization of rare or new species surpassed the homogenization (β-diversity decrease) caused by the increase of already widespread species. Surprisingly, this effect was explained by the colonization of cold-adapted species (Fig.3.b, 0.84 s.d. 0.68). As no significant increase of cold-adapted species were detected in the thermophilization analysis, this positive contribution is explained by stochastic colonization of rare or previously absent cold-adapted species (Fig.1). The unpredictability of such events may arise from extreme but exceptional values of some species dispersal distance (Vittoz & Engler, 2007), dormant seeds of the seedbank (Gasperini et al., 2021), but also from the limited number of plots in certain ecoregions. With a low number of plots, γ-diversity (total number of species in the ecoregion) is lower, the species partitioning methods will thus be sensitive to local colonization of rare species that affect the γ-diversity.

Extinction of cold-adapted species, the main driver of community thermophilization (see above), contributed significantly to homogenization (-0.72 s.d. 0.82, Fig.3.b). The magnitude of this contribution is, however, comparable to the colonization effects. This is explained by the decline of rare cold-adapted species strongly contributed to homogenization (-1.95, Extended Fig.2), that was mitigated by simultaneous gains in heterogeneity via the decline of widespread cold-adapted species (1.23, Extended Fig.2). While the widespread cold-adapted species effect on Δβ-diversity was lower, it should not be undermined as it corresponds to species contributing to two third of the thermophilization (Extended Fig.2). Furthermore, the decline of widespread cold-adapted species compensated for the extinction of rare cold-adapted species by reducing local diversity, thus increasing the heterogeneity between plots. This is confirmed by the rarefaction null model we created where the number of total occurrences was kept constant (thus the α-diversity term of the Whitaker β is constant- see methods) displayed a significantly lower Δβ-diversity compared to the original dataset (Δβ-diversity = - 0.32).

Our results likely reflect transient community dynamics where the beginning of an anthropogenic stressor could initially increase β-diversity by reducing the occurrences of widespread species, but is not acute enough to trigger definitive extinction. This first increase in β-diversity could thus be transitory as every species becomes rarer over time, and

eventually become extinct (Socolar et al., 2016). In our case, the contribution of the decline of rare cold-adapted species to homogenization outweighed the positive effect of its colonization counterpart. That is, more rare species declined (with climate change as a driver of this decline) than rare species sporadically colonized. In addition to the thermal stress imposed by climate-change, populations of rare species are isolated from their source population, lack the critical size for maintenance and can be located at the warm edge of its distribution (Leibold & Chase, 2017; Pérez-Navarro et al., 2021).

The differences in homogenization contribution depending on the relative thermal optimum of a species is indicative of the relationship between thermophilization and β-diversity. Thermophilization is a selective process, in our study, we mostly documented a decline of cold-adapted species with antagonistic effect on β-diversity. The correlation of the homogenization components with MAT (Fig.4.b) is significantly positive and consistent with the correlation of thermophilization with MAT (Fig.4.a). This control of climate over the underlying community dynamics confirms that the thermophilization and homogenization rates could increase with climate change.

Implications for forest understory in a warming climate

Thermophilization is often interpreted as an adaptation of communities to warmer conditions or community substitution (De Frenne et al., 2013; Gottfried et al., 2012), but our results show that thermophilization stems from local extinctions of cold-adapted species, with little substitution from warm adapted species. Indeed, our results show the lack of individual resistance of understory plant species to raising temperature, which exceeds the establishment and dispersal capacities of those plants better adapted to warmer climates. This effect jeopardizes the ecosystems services that the herbaceous layer (Landuyt et al., 2019) and its β-diversity provide (Mori et al., 2018; Tobias & Monika, 2012; Wang et al., 2021). While the effects of an extinction-driven thermophilization on local diversity is clear, how it can cause homogenization is not apparent. We documented a lack of a unidirectional trend of community homogenization, but we observed a rarefaction of cold-adapted species that may trigger homogenization in the future.

Our consistent finding of extinction being the driving force behind thermophilization calls for increased needs to assess future biodiversity trends as it is positively correlated with MAT. In other ecosystems, where the spread of warm-adapted species can be faster than in lowland

forest (e.g. mountains), the effects of β-diversity should still be studied and monitored (Staude et al., 2022; Xu et al., 2023).

We demonstrated that the extinction of cold-adapted species occurs independently of their rarity. The decline of rare species is pervasive and hard to detect without dedicated conservation studies, but widespread cold-adapted species could be used to bioindicate early sign of climate induced extinctions. The question of whether increased thermophilization and lack of homogenization are transient and respond to the current flora-climate disequilibrium will need further monitoring, but remain critical under future needs to preserve biodiversity. Explicitly unveiling the community dynamics at play to strengthen our capacity to understand and predict community composition under an accelerating warming rate.

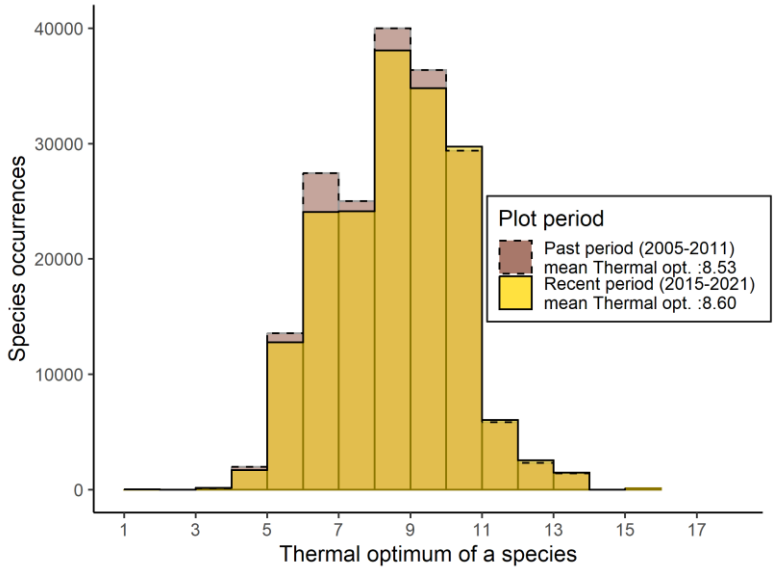


Figure 2: Count of species occurrences in the two periods as function of their thermal optimum. *The dataset is comprised of 12,764 "past" plots (surveyed in 2005-2011) and 12,764 "recent" plots (surveyed in 2015-2021). The thermal optimum of a species is estimated as the mean of the mean annual temperature within a species distribution (Vangansbeke et al., 2021).*

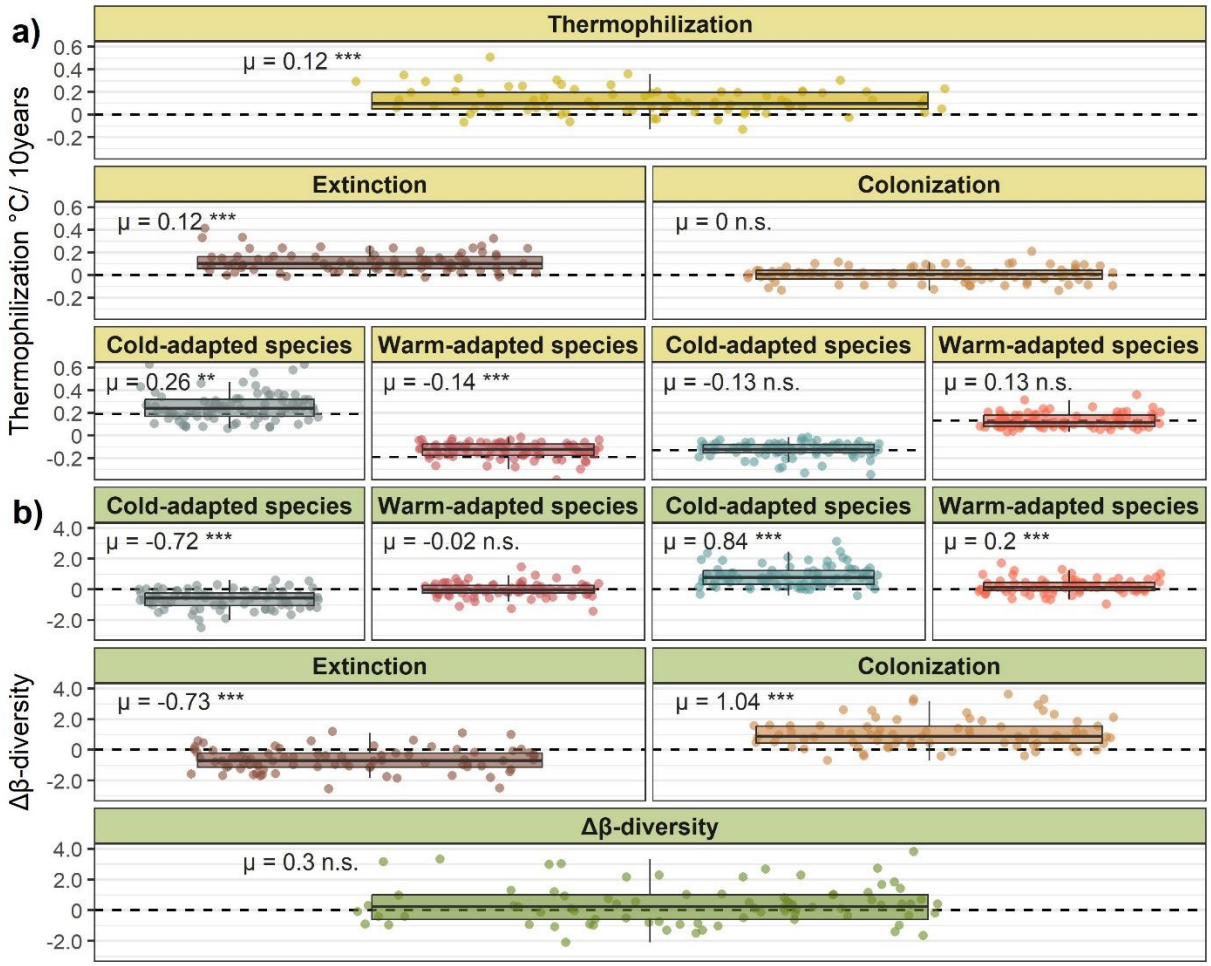


Figure 3: Thermophilization (a) and homogenization (b) partition of the 80 studied ecoregions. *Change in mean thermal optimum (a) of recorded species and β-diversity (b) (respectively thermophilization and Δβ-diversity) of the 80 ecoregions (represented by a point). Those changes are broken-up in two components: colonization and extinction, estimated from the contribution of species with more or with less occurrences in the recent period. Those components are subsequently divided into the contribution of cold or warm-adapted species, defined as the species with a lower or higher thermal optimum than the mean thermal optimum of the ecoregion in the past period. For each component, the mean value is displayed (°C decades^{-1} for thermophilization, no unit for Δβ-diversity). The statistical difference between this value and a null model (for thermophilization) or 0 (for Δβ-diversity) is also displayed, p<0.05 (*), p<0.01 (**), p<0.001 (***). One outlier ecoregion is not displayed in (b), due to a low number of plots it displayed an extinction component of -4.8 and -5.6 respectively.*

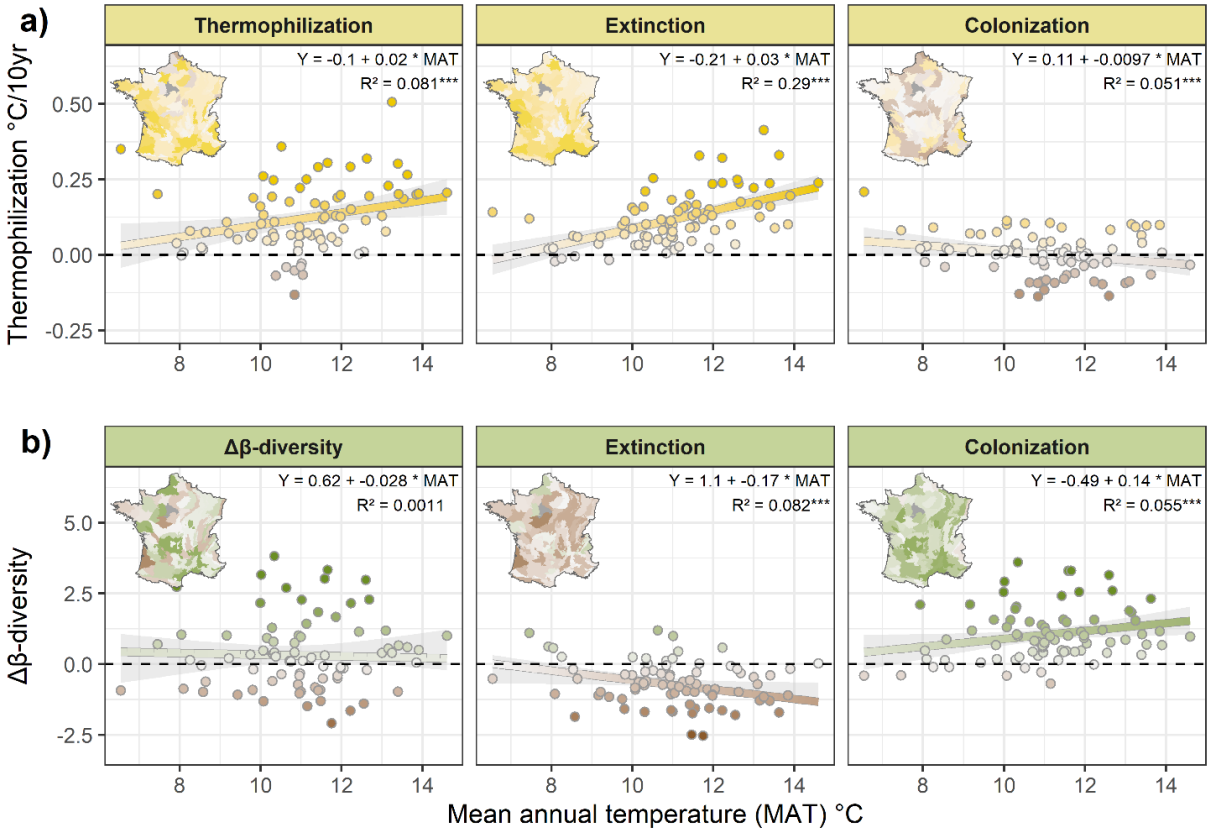


Figure 4: Relationship of thermophilization (a), β-diversity change (b) and their extinction and colonization components with mean annual temperature (MAT). *One point represents one ecoregion, the map of the ecoregion with the associated value is displayed for each component, the color scale of the point and the mapped ecoregion are the same. One outlier ecoregion is not displayed in (b), due to a low number of plots it displayed an extinction component of -4.8 and -5.6 respectively. The summary statistics corresponds to a linear model Value ~ MAT, if the MAT coefficient is significant, *** is displayed next to the R².*

3. Materials and methods

Study region and forest ecoregion

Our study area corresponds to metropolitan France (excluding Corsica island), including the temperate mixed forest biomes, the coniferous mountain biome and the Mediterranean forest biome. The territory has been divided into 86 forest ecoregions (hereafter ecoregions) characterized by similar and unique climatic and soil conditions combination (IGN, 2013). We used those ecoregions to delineate the sampling areas used to study understory flora change

and diversity at a wider scale than the plot scale. As they display distinct climate and soil characteristics, we assume the pool of species to be similar within an ecoregion, but differ from the pools of other ecoregions.

Lowland ecoregions are characterized by mosaics of forest, meadow and croplands, with a climate ranging from oceanic to semi-continental (contemporary climate range at the ecoregion scale: MAT range=9.4 to 13.9 °C, Precipitation range= 300 to 559 mm yr^{-1}). Mountainous and pre-mountainous ecoregions display higher forest cover and continental mountainous climate, with the exception of the oceanic influence over the Pyrenees (MAT range=6.5 to 12.4 °C, Precipitation range= 409 to 815 mm yr^{-1}). The southmost ecoregions encompass the Mediterranean border from Spain into Italy and display the warmer and dryer climate of European France (MAT range=11.6 to 14.6 °C, Precipitation range= 284 to 451 mm yr^{-1}) (IGN, 2013).

Plot selection

We extracted data from the French National Forest Inventory (NFI). We selected the plots from the year 2005 to 2021. The systematic sampling of the NFI is based on 1km-by-1km grid, with one tenth of the grid nodes being surveyed each year. Once the grid is completely surveyed, a new cycle of survey is performed. The plots of the new cycle are thus not a revisit of the previous plots but a new plot performed in a proximity of the node. We extracted from each plots the Mean Annual Temperature from a climate model calibrated with 214 French weather station (MAT) of the 1990-2015 period (Piedallu et al., 2019) and elevation from a 25m resolution digital elevation model.

We took advantage of the spatial representativeness the systematic sampling offers to study vegetation changes by creating a dataset balanced in sampling intensity and along environmental conditions through time. We assigned plots from the 2005 to 2011 campaign to the “past” category and the plots from the 2015-2021 campaign to the “recent” category. Plots between those two time-frames were removed as their geographically close plot from the new cycle was not available yet. We also removed plots identified as deforested at the time of the survey and plots with less than five species with a known thermal optimum.

We then paired “past” and “recent” plots based on several criterion: (1) The distance between the two plots must be less than 2 km, (2) the time interval between plots must be 9 or 10 years, (3) the plots must be in the same ecoregion, (4) the difference of elevation of two plots should be less than 50 m. Criteria (1) allowed us to select plots from two NFI cycles of the same node, and compensate for the coordinates fuzziness of the NFI plots (of ± 500m) due to private property protection laws. Furthermore, out of the initial 83 ecoregions, we removed three ecoregions with low number (N<10) of pairs.

The selection procedure yielded 12,764 pairs of NFI plots separated on average by 9.7 years (Extended Fig.1), distributed in 80 Ecoregions. Ecoregions had a minimum of 15 pairs, a maximum of 1,747. The median value was 104 pairs. In the absence of true remeasurements of past surveys, the selection of geographically close plots to study vegetation changes is the better alternative, but can still misestimate or detect changes where there are none (Chytrý et al., 2014). However, by conducting 80 separate flora change analyses, one per ecoregion, identifying consistent trends across ecoregions, as well as averaging the results limit the risk of misinterpretation.

Floristic database

Among dentrometric, canopy cover and soil measurement, the NFI also includes a floristic survey performed in a 15 m radius circle (area = 709 m²). From this survey, we selected vascular plants identified to the species level, and removed trees, as their presence in the understory can be induced by management and they respond slowly to environmental changes (Lenoir et al., 2008). After homogenization of the taxonomy to the TaxRef V13 standard (Gargominy, 2022), we assigned to each species a thermal optimum from the ClimPlant V1.2 database (Vangansbeke et al., 2021). Those thermal optima have been computed by averaging the mean annual temperature within the species distribution obtained from European atlases. We also extracted two additional thermal optima (one computed in 2005 and one computed in 2019 with updated information and methods) based on Gégout et al. (2005) to test the sensitivity of our results to the source information of thermal optimum estimation.

In our 12,764 plot pairs, we recorded 183,608 species occurrences in the past plots, and 175,617 species occurrences in the recent plots. We identified 745 different species with a known thermal optimum from ClimPlant V1.2. Those occurrences represented 78% of the total number of occurrences recorded in our plot pairs, showing a large taxonomic coverage of the thermal optimum database.

Thermophilization computation and partitioning

To compute thermophilization, we first defined the mean thermal optimum of the recorded species in the “past” and “recent” plots of each ecoregion. To this end, we calculated the weighted mean of the thermal optimum of the species using their occurrence count in the ecoregion, independently of their local abundance. Thermophilization was then obtained by subtracting the “recent” from the” past” occurrence-weighted mean of thermal optimum. As

our plots were not exactly separated by 10 years on average, we corrected the thermophilization rates by the average time difference of the plots to express thermophilization in degree Celsius per year (°C yr^{-1}). This method of computing thermophilization differs from past studies with permanent plots, where change in mean thermal optimum is computed at the plot scale through time. Our approach does not investigate plot scale changes (that were blurred by the semi-permanent nature of our pairs) but allows to study the change of occurrence rates of species at regional scale under homogenous environmental conditions.

We then computed the individual contribution of a species to thermophilization, $contrib_i$, with the following formula:

$$Contrib_i = \frac{(Topt_i - Topt_{ecoreg\ past}) \cdot (occ_{i\ recent} - occ_{i\ past})}{\sum occ_{recent}} \quad (1)$$

Where $Topt_i$ is the thermal optimum of a species *i*, $Topt_{ecoreg\ past}$ the weighted mean thermal optimum of the "past" occurrences, occ_i is the count of plots where the species is recorded in the "past" and "recent" period, and $\Sigma\ occ_{recent}$ is the total number of occurrences of the "recent" period, it allows to scale $contrib_i$ as the two periods will not have an equal number of total occurrences. Species with equal occurrences in the two periods results in a $contrib_i$ of 0, thus they do not contribute any further to the computation.

When summing every $contrib_i$, we obtain the thermophilization value of the given ecoregion. As a result, we can partition the sums of $contrib_i$ into components that can be added to obtain the thermophilization value. To create the extinction and colonization components, we added the $contrib_i$ of species with declining occurrences for extinction ($occ_{i\ recent} - occ_{i\ past} < 0$), and the $contrib_i$ of species with increasing occurrences for colonization ($occ_{i\ recent} - occ_{i\ past} > 0$). We subdivided those two components into the contribution of cold and warm-adapted species to those components. Those subcomponents depend on whether a species is locally cold-adapted ($Topt_i - Topt_{ecoreg\ past} < 0$) or warm-adapted ($Topt_i - Topt_{ecoreg\ past} > 0$) compared to the weighted mean thermal optimum of the ecoregion $Topt_{ecoreg\ past}$.

Consequently, the contribution of the extinction of cold-adapted species will always be positive (contribute to thermophilization) as denoted by Eq. (1), but the extinction component as a whole could either be positive or negative (contribute to slow thermophilization), as it also includes the extinction of warm-adapted species that is negative by design (eq (1)).

Beta-diversity change computation and partitioning

In parallel to the thermophilization analysis, we computed a β-diversity, the Whittaker β_w metric, for the two periods (Whittaker, 1960). the Whittaker β_w is calculated as described in Eq (2):

$$\beta_w = \frac{\gamma}{\alpha} \quad (2)$$

Where γ is the total number of different species recorded in the ecoregion and α is the mean species richness of the plots present in the ecoregion. This metric is more suited to investigate differences between multiple communities than mean of pairwise differences metrics as it accounts for species co-occurrences, and measures heterogeneity by directly assessing the proportionality between local and ecoregion diversity (Baselga, 2010; Socolar et al., 2016; Tatsumi et al., 2021).

We computed β-diversity change (Δβ-diversity) at the ecoregion level by subtracting the β_w of the "recent" plots by the β_w of the "past" plots. We then computed the contribution of each species to this change in β-diversity by adapting the methods and code presented in Tatsumi et al. (2021). This method assigns an extinction and colonization component to each species; however, we added those two components to obtain a unique value of contribution to Δβ-diversity per species. As a consequence, a species can decrease β-diversity (homogenize) by declining if it was already rare, or by colonizing if it is an already widespread species. Conversely, the colonization of a rare species, or an extinction of a widespread species have a positive impact on Δβ-diversity (heterogenize). We summed the contribution to Δβ-diversity following the same procedure described in the previous part. This allowed to obtain the contribution to Δβ-diversity of declining species (extinction) and spreading species (colonization), and whether these species were locally cold or warm-adapted, for a total of 4 components.

As other ecologically relevant processes can lie behind an extinction or a colonization component, e.g. the extinction of a rare species decreases β-diversity whereas the extinction of a common one increases β-diversity, we further split the 4 components into "common" and "rare" species subcomponents. A species is tagged "rare" if its decline reduces β-diversity, its colonization increases it between the two timeframes of our data, and conversely, a species is considered "common" if its decline increases β-diversity and its colonization decreases it (Extended Fig.2).

In order to have a comparable set of species and components than the thermophilization analysis, this analysis was done with the subset of species included in the thermal optimum database ClimPlant V1.2.

We run the thermophilization and the Δβ-diversity analysis and partitioning with the two other thermal optima databases (Gégout et al., 2005) and found similar results and interpretations (Table S3).

Null models and bootstrapping

We created two null models to test whether the change of species occurrences is independent of thermal optimum, and to correct the analysis when the two periods did not have an equal number of occurrences.

To test the independence of species occurrence changes to their respective thermal optimum, we ran 200 iterations of the thermophilization analysis by randomizing the thermal optimum of species drawn from the species pool of each ecoregion. This model (hereafter random thermal optimum model) was used to test its difference with the partitioning result of the original dataset, but the lack of thermophilization in this model demonstrated a link between species occurrences changes and their thermal optima (Table S2).

The total number of occurrences recorded in our dataset decreased between the two periods despite our sample having a balanced number of "past" and "recent" plots. While this decrease could be caused by true ecological factors such as climate change induced extinction, confounding methodological factors could be also be at play. In our dataset, more plots from the "past" period have been surveyed during the vegetation period (53% in the "past" plots vs 49% in the "recent" plot), during this period, species identification is easier and more species will be visible. To account for this potential bias, but also to explore Δβ-diversity in setting without a decrease in mean species richness, we ran both the thermophilization and the β-diversity change analysis by rarefying the occurrences. Specifically, for each ecoregion, we randomly removed occurrences of the period with the most total occurrences to match the total occurrences of the other period. We repeated this resampling and the analysis 200 times, (hereafter the rarefaction null model).

With this stricter methodology thermophilization is still estimated at 0.12 °C yr^{-1} (s.d 0.11), the extinction component at 0.11 °C yr^{-1} (s.d 0.07), and the colonization component at 0.01 °C yr^{-1} (s.d 0.08) (Table S2).

We conducted our main analysis by using the MAT within the distribution of a species as an estimation of its thermal optimum, however the high variability of climate within one distribution induces uncertainties in this estimation (Rodríguez-Sánchez et al., 2012; Vangansbeke et al., 2021). To consider this uncertainty, we ran the analysis 500 times by sampling one climatic grid within the distribution instead provided by Vangansbeke et al., (2021) instead of using the mean. Our results did not change with this method but helped quantify the uncertainties of thermophilization estimation of at the ecoregion scale (Table S2, Rodríguez-Sánchez et al., 2012).

Statistical testing

We tested the significance of the seven components (global value, extinction, colonization, and the four subcomponents created with the relative thermal optimum of the species) for the two metrics (thermophilization and Δβ-diversity) with the Wilcoxon signed rank test (Rey & Neuhäuser, 2011). However, we chose a different reference for the test depending on the metrics and what hypothesis we wanted to investigate. We tested the difference between the thermophilization components and the corresponding components of the random thermal optimum model. We tested the difference between the Δβ-diversity with 0 as our null hypothesis was “no change in β-diversity” and unlike thermophilization, the components were not constrained in their value (e.g. the contribution of colonizing warm-adapted species to thermophilization is strictly positive, 0 is not adequate for testing it, but its contribution to Δβ-diversity can be positive or negative).

For simplicity, we tested every component of Thermophilization and Δβ-diversity only against 0 for the two bootstraps presented in previous section (the random thermal optimum model and the rarefaction null model).

We tested the significance and the magnitude of the correlation between thermophilization, Δβ-diversity and their two components (extinction and colonization) with MAT with the use of linear regressions. The applicability of linear regressions was checked via the normality and homoscedasticity of the residuals and the independence to confounding variables following the recommendation of (Zuur et al., 2010).

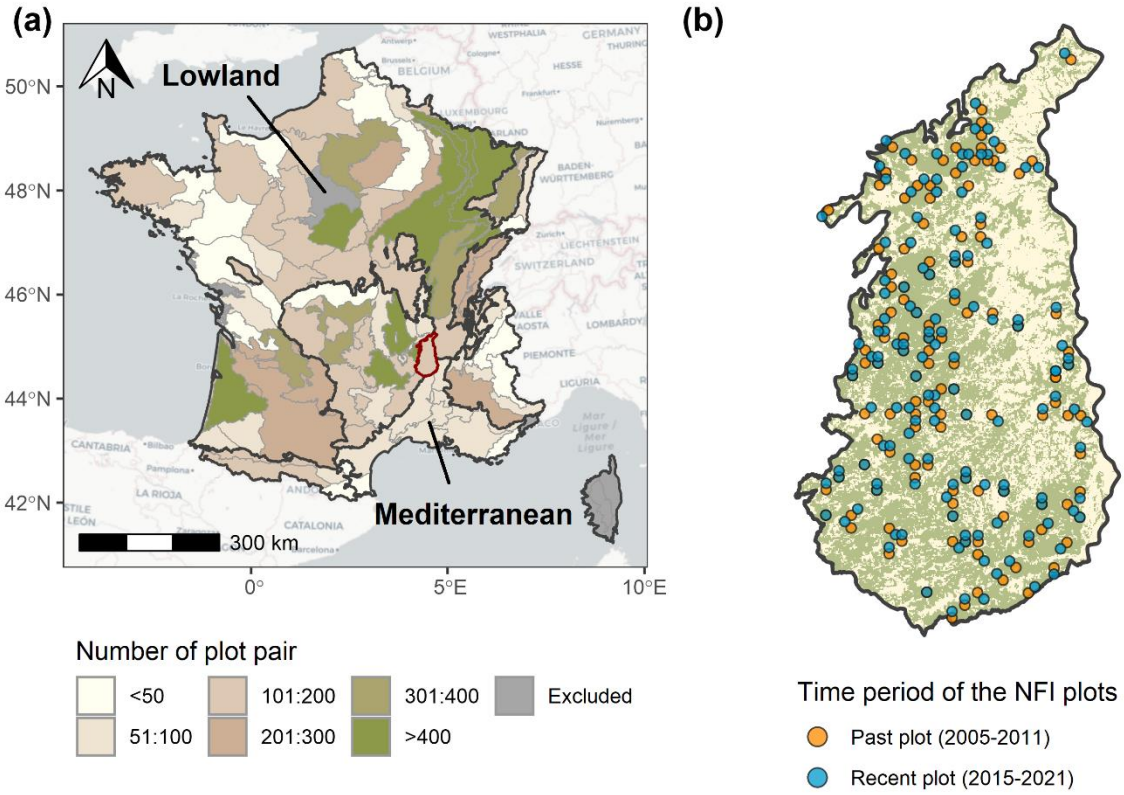
We conducted our analysis in the 4.2.2 R statistical environment (R Core Team, 2019), with ‘data.table’ (Dowle & Srinivasan, 2020), ‘ggplot2’ (Wickham, 2011), ‘sf’ (Pebesma, 2018), ‘ggpubr’ (Kassambara, 2023), ‘foreach’ (Microsoft & Weston, 2022) and the ‘doParallel’ (Corporation & Weston, 2022) packages. We were inspired by the ‘ecopart’ method and adapted the code presented by Tatsumi et al., (2021) for the Δβ-diversity partitioning.

Data availability

French National Forest Inventory data are freely distributed by the French Institute for Geographic and Forest Information (IGN) at https://inventaire-forestier.ign.fr

The dataset and the code used are available from the authors upon request.

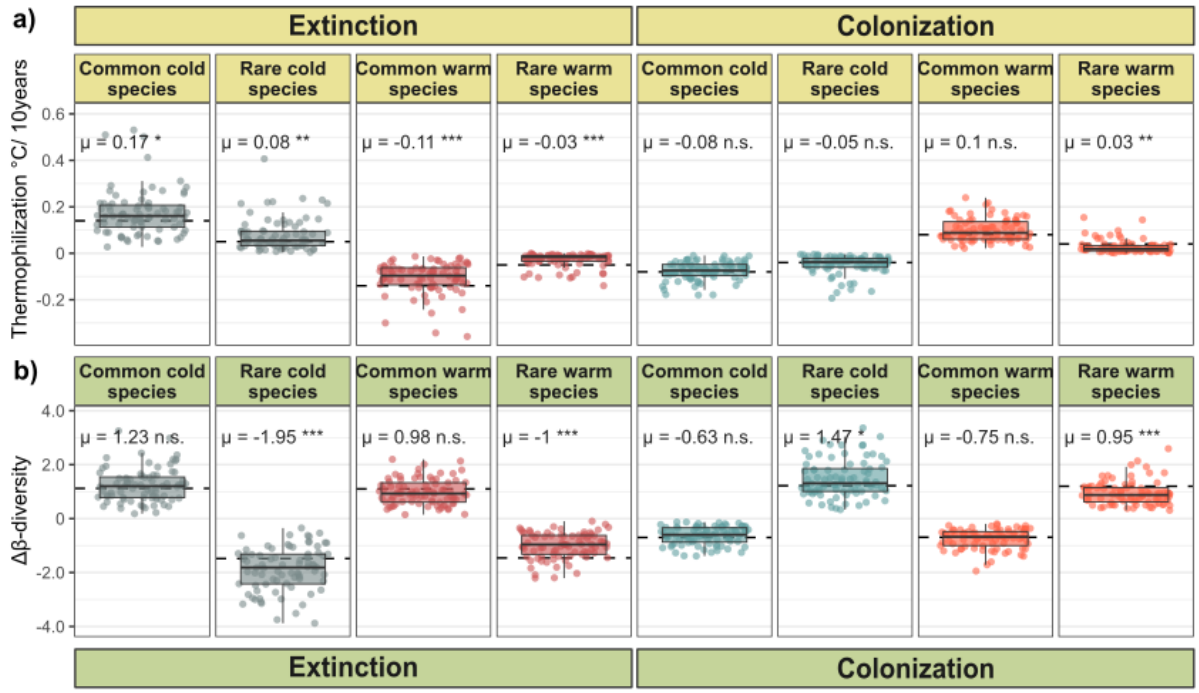
4. Extended Data



Extended Figure 1: *(a) Map of the 86 forest ecoregions of France, with a colored gradient representing the number of plot pairs. Three main biomes (Lowland forests, Mediterranean and Mountain) cluster different ecoregions delineated with bold black lines, the clusters without a label are mountain ecoregions. The zoomed ecoregion in (b) is outlined in red in (a). (b) Example of plot pair sampling design- with the blurred localization of the NFI plots, green represents forested areas.*

Extended Table 1: *Mean of thermophilization (°C decades^{-1}), Δβ-diversity and their components of one ecoregion depending on their cluster. The number of forest ecoregion within one cluster and the sum of plot pairs within that cluster is also displayed.*

Ecoregion cluster	*Thermophilization*	*Extinction*	*Colonization*	*Δβ-diversity*	*Extinction*	*Colonization*	*Ecoregion number*	*Pair number*
Lowland	0,01	0,011	-0,001	-0,171	-0,966	0,795	45	8271
Mountain	0,012	0,01	0,002	0,795	-0,412	1,207	29	4116
Mediterranean	0,027	0,029	-0,002	1,498	-0,56	2,058	6	377



Extended Figure 2: *Subsequent partition of the data presented in Fig.3. The contributions to a) thermophilization (°C decade^{-1}), and b) Δβ-diversity (no unit) are partitioned on the basis of species declining or increasing in occurrences, of their thermal optimum relative to the ecoregion and whether these species are rare (their decline decrease β-diversity) or common (their decline increases β-diversity). One point corresponds to one ecoregion. The mean of each components is displayed. The statistical difference between this value and a null model (species are assigned a random thermal optimum) is also displayed, p<0.05 (*), p<0.01 (**), p<0.001 (***).*

5. Acknowledgements

The authors are grateful to the French institute for geographic and forest information (IGN) for providing the NFI data and a precise description of the forest ecoregions. JB was funded by a joint AgroParisTech and Région Grand- Est grant (grant number 19_GE8_01020p05035) and JMSD was funded by the ANR-JCJC (Agence Nationale de la Recherche, jeunes chercheuses et jeunes chercheurs) SEEDFOR (ANR-21-CE32-0003). JMSD acknowledges the support from NASA for UConn's Ecological Modelling Institute (#80NSSC 22K0883).

6. References

Baeten, L., Vangansbeke, P., Hermy, M., Peterken, G., Vanhuyse, K., & Verheyen, K. (2012). Distinguishing between turnover and nestedness in the quantification of biotic

homogenization. *Biodiversity and Conservation*, *21*(6), 1399–1409. https://doi.org/10.1007/s10531-012-0251-0

Barbet-Massin, M., Thuiller, W., & Jiguet, F. (2010). How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? *Ecography*, *33*(5), 878–886. https://doi.org/10.1111/j.1600-0587.2010.06181.x

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity: Partitioning beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C., & Gégout, J.-C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, *479*(7374), 517–520. https://doi.org/10.1038/nature10548

Bertrand, R., Riofrío-Dillon, G., Lenoir, J., Drapier, J., de Ruffray, P., Gégout, J.-C., & Loreau, M. (2016). Ecological constraints increase the climatic debt in forests. *Nature Communications*, *7*(1), 12643. https://doi.org/10.1038/ncomms12643

Boulangeat, I., Gravel, D., & Thuiller, W. (2012). Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances: The role of dispersal and biotic interactions in explaining species distributions and abundances. *Ecology Letters*, *15*(6), 584–593. https://doi.org/10.1111/j.1461-0248.2012.01772.x

Cholewińska, O., Adamowski, W., & Jaroszewicz, B. (2020). Homogenization of Temperate Mixed Deciduous Forests in Białowieża Forest: Similar Communities Are Becoming More Similar. *Forests*, *11*(5), 545. https://doi.org/10.3390/f11050545

Chytrý, M., Tichý, L., Hennekens, S. M., & Schaminée, J. H. J. (2014). Assessing vegetation change using vegetation-plot databases: A risky business. *Applied Vegetation Science*, *17*(1), 32–41. https://doi.org/10.1111/avsc.12050

Comte, L., Murienne, J., & Grenouillet, G. (2014). Species traits and phylogenetic conservatism of climate-induced range shifts in stream fishes. *Nature Communications*, *5*(1), Article 1. https://doi.org/10.1038/ncomms6053

Corporation, M., & Weston, S. (2022). *doParallel: Foreach Parallel Adaptor for the "parallel" Package*. https://CRAN.R-project.org/package=doParallel

De Frenne, P., Rodriguez-Sanchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Romermann, M., Brown, C. D., Brunet, J., Cornelis, J., Decocq, G. M., Dierschke, H., Eriksson, O., Gilliam, F. S., Hedl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M. A., … Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences*, *110*(46), 18561–18565. https://doi.org/10.1073/pnas.1311190110

De Frenne, P., Rodríguez-Sánchez, F., De Schrijver, A., Coomes, D. A., Hermy, M., Vangansbeke, P., & Verheyen, K. (2015). Light accelerates plant responses to warming. *Nature Plants*, *1*(9), 1–3. https://doi.org/10.1038/nplants.2015.110

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, *3*(5), 744–749. https://doi.org/10.1038/s41559-019-0842-1

De Lombaerde, E., Vangansbeke, P., Lenoir, J., Van Meerbeek, K., Lembrechts, J., Rodríguez-Sánchez, F., Luoto, M., Scheffers, B., Haesen, S., Aalto, J., Christiansen, D. M., De Pauw, K., Depauw, L., Govaert, S., Greiser, C., Hampe, A., Hylander, K.,

Klinges, D., Koelemeijer, I., … De Frenne, P. (2021). Maintaining forest cover to enhance temperature buffering under future climate change. *Science of The Total Environment*, 151338. https://doi.org/10.1016/j.scitotenv.2021.151338

Dietz, L., Collet, C., Dupouey, J.-L., Lacombe, E., Laurent, L., & Gégout, J.-C. (2020). Windstorm-induced canopy openings accelerate temperate forest adaptation to global warming. *Global Ecology and Biogeography*. https://doi.org/10.1111/geb.13177

Dowle, M., & Srinivasan, A. (2020). *data.table: Extension of `data.frame`*. https://CRAN.R-project.org/package=data.table

Dullinger, S., Gattringer, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., Willner, W., Plutzar, C., Leitner, M., Mang, T., Caccianiga, M., Dirnböck, T., Ertl, S., Fischer, A., Lenoir, J., Svenning, J.-C., Psomas, A., Schmatz, D. R., Silc, U., … Hülber, K. (2012). Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature Climate Change*, *2*(8), Article 8. https://doi.org/10.1038/nclimate1514

Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araújo, M. B., Pearman, P. B., Le Lay, G., Piedallu, C., Albert, C. H., Choler, P., Coldea, G., De LAMO, X., Dirnböck, T., Gégout, J.-C., Gómez-García, D., Grytnes, J.-A., Heegaard, E., Høistad, F., … Guisan, A. (2011). 21st century climate change threatens mountain flora unequally across Europe: CLIMATE CHANGE IMPACTS ON MOUNTAIN FLORAE. *Global Change Biology*, *17*(7), 2330–2341. https://doi.org/10.1111/j.1365-2486.2010.02393.x

Franks, S. J., Weber, J. J., & Aitken, S. N. (2014). Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evolutionary Applications*, *7*(1), 123–139. https://doi.org/10.1111/eva.12112

Gargominy, O. (2022). *TAXREF v13.0, référentiel taxonomique pour la France.* [Data set]. UMS PatriNat (OFB-CNRS-MNHN), Paris. https://doi.org/10.15468/VQUEAM

Gasperini, C., Carrari, E., Govaert, S., Meeussen, C., De Pauw, K., Plue, J., Sanczuk, P., Vanneste, T., Vangansbeke, P., Jacopetti, G., De Frenne, P., & Selvi, F. (2021). Edge effects on the realised soil seed bank along microclimatic gradients in temperate European forests. *Science of The Total Environment*, *798*, 149373. https://doi.org/10.1016/j.scitotenv.2021.149373

Gégout, J.-C., Coudun, C., Bailly, G., & Jabiol, B. (2005). EcoPlant: A forest site database linking floristic data with soil and climate variables. *Journal of Vegetation Science*, *16*(2), 257–260. https://doi.org/10.1111/j.1654-1103.2005.tb02363.x

Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, M. R., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., … Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, *2*(2), Article 2. https://doi.org/10.1038/nclimate1329

Govaert, S., Vangansbeke, P., Blondeel, H., Steppe, K., Verheyen, K., & De Frenne, P. (2021). Rapid thermophilization of understorey plant communities in a 9 year-long temperate forest experiment. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.13653

IGN. (2013). *Fiches descriptives des grandes régions écologiques (GRECO) et des sylvoécorégions (SER)*. https://inventaire-forestier.ign.fr/spip.php?article773

IGN. (2019, December 1). Le mémento de l'inventaire forestier. *Institut National de l'Information Géographique et Forestière*. http://www.ign.fr/institut/publications/memento-linventaire-forestier

Kassambara, A. (2023). *ggpubr: "ggplot2" Based Publication Ready Plots*. https://CRAN.R-project.org/package=ggpubr

Kubisch, A., Degen, T., Hovestadt, T., & Poethke, H. J. (2013). Predicting range shifts under global change: The balance between local adaptation and dispersal. *Ecography*, *36*(8), 873–882. https://doi.org/10.1111/j.1600-0587.2012.00062.x

Kuhn, E., & Gégout, J. (2019). Highlighting declines of cold-demanding plant species in lowlands under climate warming. *Ecography*, *42*(1), 36–44. https://doi.org/10.1111/ecog.03469

Landuyt, D., De Lombaerde, E., Perring, M. P., Hertzog, L. R., Ampoorter, E., Maes, S. L., De Frenne, P., Ma, S., Proesmans, W., Blondeel, H., Sercu, B. K., Wang, B., Wasof, S., & Verheyen, K. (2019). The functional role of temperate forest understorey vegetation in a changing world. *Global Change Biology*, *25*(11), 3625–3641. https://doi.org/10.1111/gcb.14756

Lavergne, S., Mouquet, N., Thuiller, W., & Ronce, O. (2010). Biodiversity and Climate Change: Integrating Evolutionary and Ecological Responses of Species and Communities. *Annual Review of Ecology, Evolution, and Systematics*, *41*(1), 321–350. https://doi.org/10.1146/annurev-ecolsys-102209-144628

Leibold, M. A., & Chase, J. M. (2017). *Metacommunity Ecology, Volume 59*. Princeton University Press.

Lenoir, J., Gégout, J. C., Marquet, P. A., Ruffray, P. de, & Brisse, H. (2008). A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century. *Science*, *320*(5884), 1768–1771. https://doi.org/10.1126/science.1156831

Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15–28. https://doi.org/10.1111/ecog.00967

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*(7276), 1052–1055. https://doi.org/10.1038/nature08649

Martin, G., Devictor, V., Motard, E., Machon, N., & Porcher, E. (2019). Short-term climate-induced change in French plant communities. *Biology Letters*, *15*(7), 20190280. https://doi.org/10.1098/rsbl.2019.0280

Merle, H., Garmendia, A., Hernández, H., & Ferriol, M. (2020). Vegetation change over a period of 46 years in a Mediterranean mountain massif (Penyagolosa, Spain). *Applied Vegetation Science*, *23*(4), 495–507. https://doi.org/10.1111/avsc.12507

Microsoft, & Weston, S. (2022). *foreach: Provides Foreach Looping Construct*. https://CRAN.R-project.org/package=foreach

Mori, A. S., Isbell, F., & Seidl, R. (2018). β-Diversity, Community Assembly, and Ecosystem Functioning. *Trends in Ecology & Evolution*, *33*(7), 549–564. https://doi.org/10.1016/j.tree.2018.04.012

Olden, J. D., & Rooney, T. P. (2006). On defining and quantifying biotic homogenization. *Global Ecology and Biogeography*, *15*(2), 113–120. https://doi.org/10.1111/j.1466-822X.2006.00214.x

Ozinga, W. A., Römermann, C., Bekker, R. M., Prinzing, A., Tamis, W. L. M., Schaminée, J. H. J., Hennekens, S. M., Thompson, K., Poschlod, P., Kleyer, M., Bakker, J. P., & van Groenendael, J. M. (2009). Dispersal failure contributes to plant losses in NW

Europe. *Ecology Letters*, *12*(1), 66–74. https://doi.org/10.1111/j.1461-0248.2008.01261.x

Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, *10*(1), 439–446. https://doi.org/10.32614/RJ-2018-009

Pérez-Navarro, M. Á., Serra-Diaz, J. M., Svenning, J., Esteve-Selma, M. Á., Hernández-Bastida, J., & Lloret, F. (2021). Extreme drought reduces climatic disequilibrium in dryland plant communities. *Oikos*. https://doi.org/10.1111/oik.07882

Piedallu, C., Chéret, V., Denux, J. P., Perez, V., Azcona, J. S., Seynave, I., & Gégout, J. C. (2019). Soil and climate differently impact NDVI patterns according to the season and the stand type. *Science of The Total Environment*, *651*, 2874–2885. https://doi.org/10.1016/j.scitotenv.2018.10.052

R Core Team. (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reu, J. C., Catano, C. P., Spasojevic, M. J., & Myers, J. A. (2022). Beta diversity as a driver of forest biomass across spatial scales. *Ecology*, *103*(10). https://doi.org/10.1002/ecy.3774

Rey, D., & Neuhäuser, M. (2011). Wilcoxon-Signed-Rank Test. In M. Lovric (Ed.), *International Encyclopedia of Statistical Science* (pp. 1658–1659). Springer. https://doi.org/10.1007/978-3-642-04898-2_616

Richard, B., Dupouey, J.-L., Corcket, E., Alard, D., Archaux, F., Aubert, M., Boulanger, V., Gillet, F., Langlois, E., Macé, S., Montpied, P., Beaufils, T., Begeot, C., Behr, P., Boissier, J.-M., Camaret, S., Chevalier, R., Decocq, G., Dumas, Y., … Lenoir, J. (2021). The climatic debt is growing in the understorey of temperate forests: Stand characteristics matter. *Global Ecology and Biogeography*, *n/a*(n/a). https://doi.org/10.1111/geb.13312

Rodríguez-Sánchez, F., De Frenne, P., & Hampe, A. (2012). Uncertainty in thermal tolerances and climatic debt. *Nature Climate Change*, *2*(9), 636–637. https://doi.org/10.1038/nclimate1667

Rolland, C. (2003). Spatial and Seasonal Variations of Air Temperature Lapse Rates in Alpine Regions. *Journal of Climate*, *16*(7), 1032–1046. https://doi.org/10.1175/1520-0442(2003)016<1032:SASVOA>2.0.CO;2

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science (New York, N.Y.)*, *287*(5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Serra-Diaz, J. M., Franklin, J., Ninyerola, M., Davis, F. W., Syphard, A. D., Regan, H. M., & Ikegami, M. (2014). Bioclimatic velocity: The pace of species exposure to climate change. *Diversity and Distributions*, *20*(2), 169–180. https://doi.org/10.1111/ddi.12131

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How Should Beta-Diversity Inform Biodiversity Conservation? *Trends in Ecology & Evolution*, *31*(1), 67–80. https://doi.org/10.1016/j.tree.2015.11.005

Staude, I. R., Pereira, H. M., Daskalova, G. N., Bernhardt-Römermann, M., Diekmann, M., Pauli, H., Van Calster, H., Vellend, M., Bjorkman, A. D., Brunet, J., De Frenne, P., Hédl, R., Jandt, U., Lenoir, J., Myers-Smith, I. H., Verheyen, K., Wipf, S., Wulf, M., Andrews, C., … Baeten, L. (2022). Directional turnover towards larger-ranged plants

764 over time and across habitats. *Ecology Letters*, *25*(2), 466–482.
765 https://doi.org/10.1111/ele.13937
766 Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C.,
767 Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A. D., Breiner, F. T., Burg,
768 S., Czortek, P., Dawes, M. A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V.
769 A., … Wipf, S. (2018). Accelerated increase in plant species richness on mountain
770 summits is linked to warming. *Nature*, *556*(7700), Article 7700.
771 https://doi.org/10.1038/s41586-018-0005-6
772 Suggitt, A. J., Wilson, R. J., Isaac, N. J. B., Beale, C. M., Auffret, A. G., August, T., Bennie,
773 J. J., Crick, H. Q. P., Duffield, S., Fox, R., Hopkins, J. J., Macgregor, N. A., Morecroft,
774 M. D., Walker, K. J., & Maclean, I. M. D. (2018). Extinction risk from climate change
775 is reduced by microclimatic buffering. *Nature Climate Change*, *8*(8), Article 8.
776 https://doi.org/10.1038/s41558-018-0231-9
777 Svenning, J.-C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future
778 climate change. *American Journal of Botany*, *100*(7), 1266–1286.
779 https://doi.org/10.3732/ajb.1200469
780 Tatsumi, S., Iritani, R., & Cadotte, M. W. (2021). Temporal changes in spatial variation:
781 Partitioning the extinction and colonisation components of beta diversity. *Ecology*
782 *Letters*. https://doi.org/10.1111/ele.13720
783 Tatsumi, S., Strengbom, J., Čugunovs, M., & Kouki, J. (2020). Partitioning the colonization
784 and extinction components of beta diversity across disturbance gradients. *Ecology*,
785 *101*(12), e03183. https://doi.org/10.1002/ecy.3183
786 Tobias, N., & Monika, W. (2012). Does taxonomic homogenization imply functional
787 homogenization in temperate forest herb layer communities? *Plant Ecology*, *213*(3),
788 431–443. https://doi.org/10.1007/s11258-011-9990-3
789 Vangansbeke, P., Máliš, F., Hédl, R., Chudomelová, M., Vild, O., Wulf, M., Jahn, U., Welk,
790 E., Rodríguez-Sánchez, F., & Frenne, P. D. (2021). ClimPlant: Realized climatic
791 niches of vascular plants in European forest understoreys. *Global Ecology and*
792 *Biogeography*, *30*(6), 1183–1190. https://doi.org/10.1111/geb.13303
793 Vittoz, P., & Engler, R. (2007). Seed dispersal distances: A typology based on dispersal
794 modes and plant traits. *Botanica Helvetica*, *117*(2), 109–124.
795 https://doi.org/10.1007/s00035-007-0797-8
796 Wang, S., Loreau, M., Mazancourt, C., Isbell, F., Beierkuhnlein, C., Connolly, J.,
797 Deutschman, D. H., Doležal, J., Eisenhauer, N., Hector, A., Jentsch, A., Kreyling, J.,
798 Lanta, V., Lepš, J., Polley, H. W., Reich, P. B., Ruijven, J., Schmid, B., Tilman, D., …
799 Craven, D. (2021). Biotic homogenization destabilizes ecosystem functioning by
800 decreasing spatial asynchrony. *Ecology*, *102*(6). https://doi.org/10.1002/ecy.3332
801 Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California.
802 *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563
803 Wickham, H. (2011). Ggplot2. *WIREs Computational Statistics*, *3*(2), 180–185.
804 https://doi.org/10.1002/wics.147
805 Xu, W.-B., Blowes, S. A., Brambilla, V., Chow, C. F. Y., Fontrodona-Eslava, A., Martins, I. S.,
806 McGlinn, D., Moyes, F., Sagouis, A., Shimadzu, H., van Klink, R., Magurran, A. E.,
807 Gotelli, N. J., McGill, B. J., Dornelas, M., & Chase, J. M. (2023). Regional occupancy
808 increases for widespread species but decreases for narrowly distributed species in
809 metacommunity time series. *Nature Communications*, *14*(1), Article 1.
810 https://doi.org/10.1038/s41467-023-37127-2

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., … Coomes, D. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, *368*(6492), 772–775. https://doi.org/10.1126/science.aba6880

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Zwiener, V. P., Lira-Noriega, A., Grady, C. J., Padial, A. A., & Vitule, J. R. S. (2018). Climate change as a driver of biotic homogenization of woody plants in the Atlantic Forest. *Global Ecology and Biogeography*, *27*(3), 298–309. https://doi.org/10.1111/geb.12695