# Persistance ou adaptation de la flore forestière face aux effets conjugués du réchauffement climatique, de la fragmentation des forêts et du microclimat ?Persistence or adaptation of forest flora in the face of the intertwined effects of global warming, forest fragmentation and microclimate?

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# THESE DE DOCTORAT

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*par*

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# Persistence or adaptation of forest flora in the face of the intertwined effects of global warming, forest fragmentation and microclimate?

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**Thèse soutenue à Nancy, le 14 décembre 2023**

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*“If you already know what you are going to write before you start, maybe it is better not to write at all.”*

# Remerciements

La citation qui ouvre ce manuscrit rappelle qu'écrire une thèse est un processus d'apprentissage, l'étudiant affinant ses analyses à mesure qu'il les écrit, dans une danse qui doit éventuellement prendre fin. Se cantonner à cette définition serait d'une tristesse inimaginable car elle omet les personnes qui rendent cette expérience non seulement possible, mais aussi teintée d'une agréable nostalgie avant même le moment fatidique de la soutenance.

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# Foreword

The work presented in this thesis has been carried out in the UMR Silva, Nancy, within the 'Ecosilva' team. This thesis is written in an introduction – articles – discussion format. All methods employed are different and thoroughly explained in their respective chapters. The 3 articles are written in the IMReD format. Chapter 4 was done in collaboration with the ForNaLab of the Ghent University; we collaborated mostly during my two two-week stays in Ghent which were made possible thanks to a PHC Tournesol grant.

Scientific contributions :

## Publications

**Borderieux J**, Gégout J-C, Serra-Diaz J-M (2023). **High landscape-scale forest cover favors cold-adapted plant communities in agriculture–forest mosaics**. *Global Ecology and Biogeography*.

**Borderieux J**, Gégout J-C, Serra-Diaz J-M (2024). **Extinction drives recent thermophilization but does not trigger homogenization of forest understory**. *Nature Ecology and Evolution*.

**Borderieux J**, De lombaerde E, De Pauw K, Sanczuk P, Vangansbeke P, Vanneste T, De Frenne P, Gégout J-C, Serra-Diaz J-M (in prep - version of the 15/03/2024). **Topoclimate buffer floristic diversity from climate in temperate mountain forests.**

## Conferences

**Borderieux J**, Gégout J-C, Serra-Diaz J-M, **Landscape forest cover also buffers plant communities from warming.** *Microclimate Ecology and Biogeography conference 2022*.

**Borderieux J**, Gégout J-C, Serra-Diaz J-M, **What processes lie behind the recent changes of forest vegetation? An insight on thermophilization and ß-diversity**, *SFE2 GFO joint Meeting-International Conference on Ecological Science 2022*.

## Minor contributions not included in this thesis

Kemppinen J, Lembrechts, J-J, Van Meerbeek, K, Carnicer J, Chardon N-I, Kardol P, Lenoir J, Liu D, Maclean I, Pergl J… **Borderieux J** ..., De Frenne P et al. (2024). **Microclimate, an inseparable part of ecology and biogeography** *Global Ecology and Biogeography*

Serra-Diaz, J-M, **Borderieux J**, Maitner B, Boonman C, Park D, Guo W, Callebaut A, Enquist B, Svenning J-S, Merow C (2024) **occTest: an integrated approach for quality control of species occurrence data** *Global Ecology and Biogeography*

Contribution to **SoilTemp: A global database of near-surface temperature**, Lembrechts et al, (2020) *Global Change Biology*

## Science education events

This work is my first opportunity to disseminate and discuss science with the general public. I am a firm believer that every science education event is an occasion to raise public awareness and curiosity for the world we live in. I am grateful for the organization of such events, I wish I could have participated in more of them. I feel like most of the research job is to introduce (and eventually resolve) complexity in even the simplest things. These events are a chance to step back and condense all that complexity into a simpler discourse, which ultimately benefits both ends of the conference panel.

- Nuit Européenne des chercheur.e.s édition 2022 « Plante VS climat, la course du siècle », Université de Lorraine.
- Conférence Lorraine Nature Environnement (2022) « Adaptation des forêts au réchauffement climatique » Metz.

## Open science

I tried my best to follow guidelines and advice to present open and transparent scientific results. To do so, I made available on public repositories every code used to run the analyses, along with the corresponding original dataset, as they originate from public fund. The data of the French National Inventory are already public and free of use, I however created an R package to ease their retrieval and standardize their usage. I plan to increment this package with new functions and standardized workflows suggested by its most active users. My only regret is to have learned too late about the alternate form of scientific publications (such as peer communities, PCI) that offer a compelling response to the current state of private scientific edition. I look forward to submitting a preprint to PCI ecology in the future.

The repositories of the three chapters and the R package can be found at https://github.com/Jeremy-borderieux

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# Chapter 1. Introduction

The word ecology comes from the Greek “oikos”, which translates to “home” or “living place” and defines the study of interactions of organisms with both their biotic and abiotic environment. This concept introduced by Haeckel in 1866 delineated a branch of biological science comprised of older works of botanists and zoologists alike that seek to understand not only their studied organisms and their habitats, but also how the environment shaped their behavior and geographical distribution (Flahault, 1893; Humboldt, 1805; McIntosh, 1985).

Founding works of ecology include – but are not limited to – the geography of plants by Humboldt (1805), the systematic naming introduced by Linnaeus (1758), and the concept of ecosystems described by Tansley (1939). Ecology was still considered a “soft” and descriptive science unable to answer practical problems at that time. Hutchison, “the father of modern ecology” and works that came after his (Hutchinson, 1957; Leibold *et al.*, 2004; Lomolino, 2000) helped ground ecology as a “hard” science with the inclusion of theories, hypothesis testing and mathematics. This would be a fertile soil for both theoretical and applied ecology to form, the former seeks to understand and create theoretical backgrounds used by the latter to describe and study ecosystems empirically.

From the early 1900 to these days, the continuous development of monitoring, experimental and statistical methods led ecology and its subdisciplines to become one major medium by which we understand the interaction between ecosystems and the novel environments human activities create (Thuiller, 2007; Vitousek, 1994). This role took ecology into the public debate and policy-making. Indeed, nature protection was associated with ecology as early as the foundation of the ESA in 1915, hence coining the word ecology in the political term. While advancing theories and knowledge is independent of the context, ecologists now also seek to produce timely research that respond to the challenges society is facing (Marchetti *et al.*, 2023; Schmitz, 2016).

This puts ecologist in a satisfying position where they get to satiate their scientific curiosity while holding true to their ideologies. In concrete terms, during my PhD thesis I got the chance to align different search of meanings; the literal search of meanings that constitutes science and the desire to meaningfully influence society according to my belief of a sustainable world. This holds true under the naïve, but necessary, assumption that a betterment of scientific knowledge will be used to steer the world in a more viable direction. What is certain is that the curiosity sparked by scientific discoveries will outlive the context during this thesis was written.

## 1.1. General Context

### *1.1.1. Global Changes*

The ever-developing human population need for resources and space has led to tremendous changes in the earth system at a global scale (Ellis *et al.*, 2021). These changes are materialized by the transformation of wildlands to cultivated and inhabited spaces, the alteration of the biogeochemical cycles by combustion of fossil fuels and gas emissions through agriculture and the overexploitation of finite resources (IPCC, 2021a; MA, 2005; Nath *et al.*, 2021; Scholes *et al.*, 2018). The results of the increase of greenhouse gas concentration are the rise of air temperature, acidification of oceans, which consequently causes a loss of all kinds of biodiversity.

What sets apart these changes from the previous planetary geological changes is their pace, measured in decades instead of millions of years (Ellis *et al.*, 2021). This comparison with geological cycles has led geologists to consider global changes as a new geological epoch named "Anthropocene" instead of viewing it as a biotic crisis (Waters *et al.*, 2016). While this discussion is not settled, there are multiple evidences of geological footprints of human activities and the crossing of 6 out of the 9 "earth boundaries" (Armstrong McKay *et al.*, 2022; Richardson *et al.*, 2023). Crossing a boundary illustrates the non-linearity of global change impacts, after a crossing, biodiversity and ecosystem functions will be harder, if not impossible to recover (e.g. loss of biodiversity, greenhouse gases, Lenton *et al.*, 2019). Among the drivers of biodiversity loss, global warming attracts most of the media coverage, and along with land use changes, is widely studied for its relevance in understanding past and current biodiversity loss (Ellis *et al.*, 2021; Sala *et al.*, 2012).

### *1.1.2. Global Warming*

The increase of greenhouse gas (GHG) concentration in the atmosphere results in more radiative heat being retained at the surface and thus air temperature rises (Figure 1-1). The global surface temperature of the 2010-2020 period is estimated to be 1.09 °C (c.i. 0.95 to 1.20) higher than the reference period of 1850-1900 (IPCC, 2021a). Lands warmed faster than oceans, with an increase of 1.59 °C (c.i. 1.34 to 1.83), but the rise within lands is not homogenous and already warmer or extremely cold places tend to warm faster. The rise in temperature has been faster in the last 50 years than in any other period on record (IPCC, 2021a). The rise of mean temperature has profound implications for ecologically relevant metrics such as growing degree days, freezing degree days, duration of snow cover, length of the growing season but also implies an increase in frequency and intensity of extreme events that should not be undermined (IPCC, 2021a). For example, drought and heatwaves are more likely to cause tree dieback than a gradual rise in mean temperature. Less is known about the change in precipitation, but its regime is expected to be more variable and extreme, and soil moisture will likely decrease in various areas worldwide like in south and central Europe (IPCC, 2021a). The projected and theorized trends of greenhouse gas emission allow predicting future temperature trends (IPCC, 2021a). Those future

temperature increases for the period 2081-2100 compared to the 1850-1900 reference period are predicted to fall between +1.4 °C to +4.4°C for the lowest and highest GHG emission scenarios, with an intermediate prediction of +2.7°C (IPCC, 2021a).

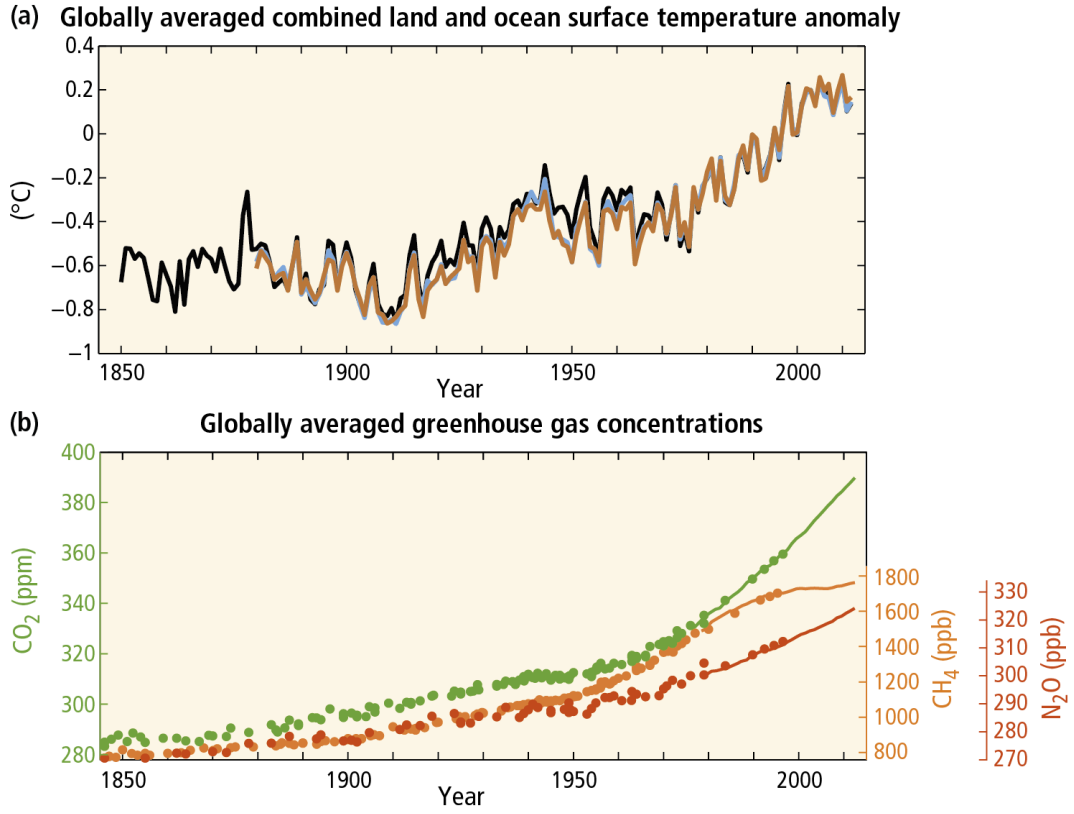


*Figure 1-1: (a) Surface temperature anomaly of land (brown), ocean (blue) combined (black) to a reference period of 1986-2005 (b) Evolution of the three main greenhouse gas concentrations, from (IPCC, 2014).*

### *1.1.3. Land use changes and habitat fragmentation*

Humans have shaped landscapes as early as 12,000 years ago to this day by an increase of land uses where agriculture, pasture, inhabitation, and wildlands coexist (Figure 1-2). This diversification of land use types does not inherently cause biodiversity loss, heterogenous landscapes can offer more diverse habitats and resilience against extreme events (Fischer *et al.*, 2006; Oliver *et al.*, 2015; Stein *et al.*, 2014). What really causes land use change to be one of the main drivers of biodiversity loss is the recent intensification of agriculture and urbanization that comes with biotic homogenization, the use of chemical control and the loss and fragmentation of unique habitats for species (Ellis *et al.*, 2021; Kettle & Koh, 2014; Scholes *et al.*, 2018). Habitat loss increases species extinction risk when the critical surface to sustain a population is not met (Fahrig *et al.*, 2019; Haddad *et al.*, 2015; Watling *et al.*, 2020). Habitat fragmentation (when an even amount of habitat is spread and less connected) can exacerbate this risk by reducing connectivity within populations and limiting the migration capacities of species (Auffret *et al.*, 2017; Dullinger *et al.*, 2015; Honnay *et al.*, 2002). In that regard,

Europe is a telling example of human footprint on landscapes as its intensive usage of land is traced back to 2,000 years, a sharp contrast with continents such as North America whose land has been intensively at the start of the 19th century (Ellis *et al.*, 2021). As a result, European forests (cover around 35% of the territory) are to forest fragmentation due to past logging and the current mosaic of forest and cropland and 70% of landscapes with forests display poorly connected forests, and 40% of the forest surface is located within 100 m of an agricultural area (IES *et al.*, 2013, Figure 1-2-C)

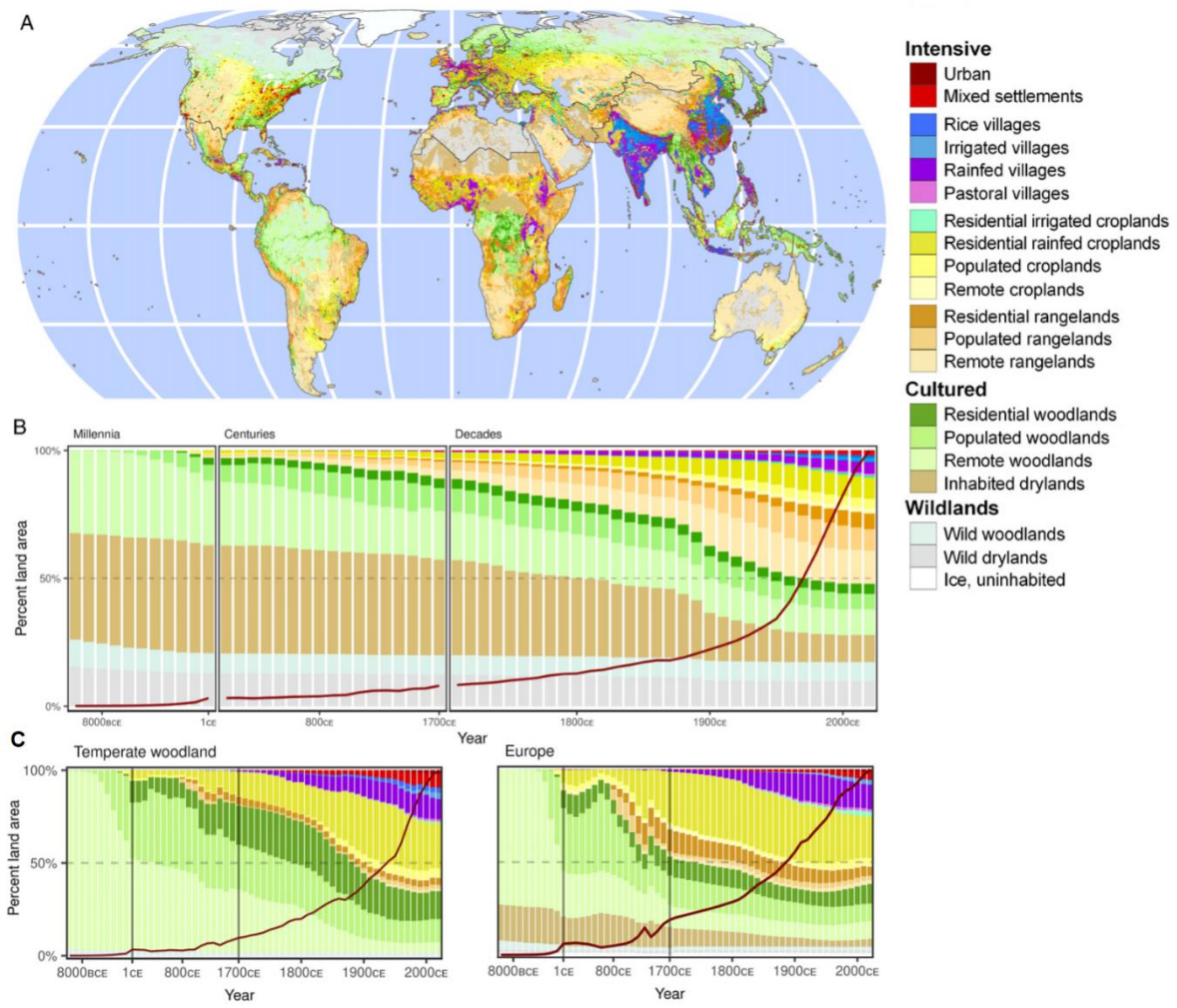


*Figure 1-2: (A): map of anthromes; human created biomes (B): Evolution in anthromes relative areas through time, in accordance with human population change (red line) (C): Evolution of anthromes relative area of the Temperate woodland biome of the European region. Adapted from (Ellis* et al.*, 2021).*

### *1.1.4. Biodiversity Loss*

The consequence of the above-mentioned global changes on biodiversity and ecosystems is first outlined in detail in the Millennium Ecosystem Assessment (MA, 2005). This assessment concluded that human activities unambiguously increased extinction rates of species, by up to three orders of magnitude in the last 100 years (Ceballos *et al.*, 2015;

MA, 2005; Wiens, 2016). This trend did not stop as 16% of species are under extinction threat (Urban, 2015). Specifically for plant species, that risk increases to 39%.

Global extinction of species is not the only way to lose biodiversity, local diversity – the one humans interact with – is also subject to changes without the permanent loss of a species. Local diversity can decrease with local extinctions of species and through the process of biotic homogenization (also known as biotic simplification), where local communities become more similar because of the spread of common species (generally ubiquitous or dependent on human activities) or the loss of rare species (McKinney & Lockwood, 2001, 2001; Olden & Rooney, 2006).

The erosion of biodiversity is a major conservation challenge *per se* but also induces adverse effects on human well-being via the loss of ecosystem services (Brockerhoff *et al.*, 2017; Díaz *et al.*, 2018; Gamfeldt *et al.*, 2013; Gilliam, 2007). Primary productivity, resilience and resistance to extreme events, pollination, water cycle regulation and esthetic qualities are all ecosystem functions and services threatened by the simplification of communities. Consequently, understanding drivers of community changes (Hooper *et al.*, 2005; Socolar *et al.*, 2016; Mori *et al.*, 2018) is of utmost importance. The synthesis of existing knowledge and research gaps to human impacts on communities (and ultimately their diversity) will be developed through the definition of its essential component: species (1.2) and how (abiotic, biotic, geographic) factors influence them (1.3), in a forest understory context.

## 1.2. From the species to the community

### *1.2.1. Species ecological niche and geographical range*

#### *1.2.1.1. The concept of the ecological niche*

The “survival of the fittest” principle proposed by Darwin allowed naturalists to explain species apparitions and extinction and their diversity, as diverse as the habitat Earth offers. This principle, however, failed to explain the coexistence of several organisms in the same habitat, as the less competitive one would eventually go extinct. The niche concepts emerged as an explanatory theory to coexistence, where each species would fill non-overlapping needs (for spaces or resources), reducing interspecific competition. The ecological niche has gone through several definitions, from being a characteristic of the environment to an essential part of species (Pocheville, 2015).

The definition of the niche adopted throughout this manuscript is the one proposed by Hutchinson (1957), where the niche is an intrinsic species characteristic represented by an n-dimensional volume, each dimension represents a resource or environmental condition. This hypervolume is the fundamental niche of a species, it survives (i.e. reproduction and growth rates higher than death rates) within it. However, extrinsic phenomena such as inter-

specific interactions can greatly reduce the fundamental niche to the one we empirically observe in nature, the realized niche (Figure 1-3).

The need for an extrinsic influence to explain the realized niche leaves the Hutchinson definition unsatisfactory, a later proposition by Chase & Leibold, (2003) reconciled the niche definition with a framework where the environment influences the species and the species influences the environment, this newer framework, however, is out of the scope of this thesis.

The estimation of the realized niche relies on statistical methods that creates bell-shaped curves as in Figure 1-3. As a result, a niche optimum can be derived from the curve, where the probability of occurrence is maximized. It is important to note that this statistical property is rarely observed in nature, species population and abundance are evenly spread within the realized niche space (Martínez-Meyer *et al.*, 2013; Matthews & Whittaker, 2015; Soberón *et al.*, 2018; Soberón & Nakamura, 2009). The shape of the estimated niche around the optimum varies too, a specialist species that evolved to fit a specific niche will display a tight niche around its optimum whereas generalist species present wide realized niches with no marked optimum.

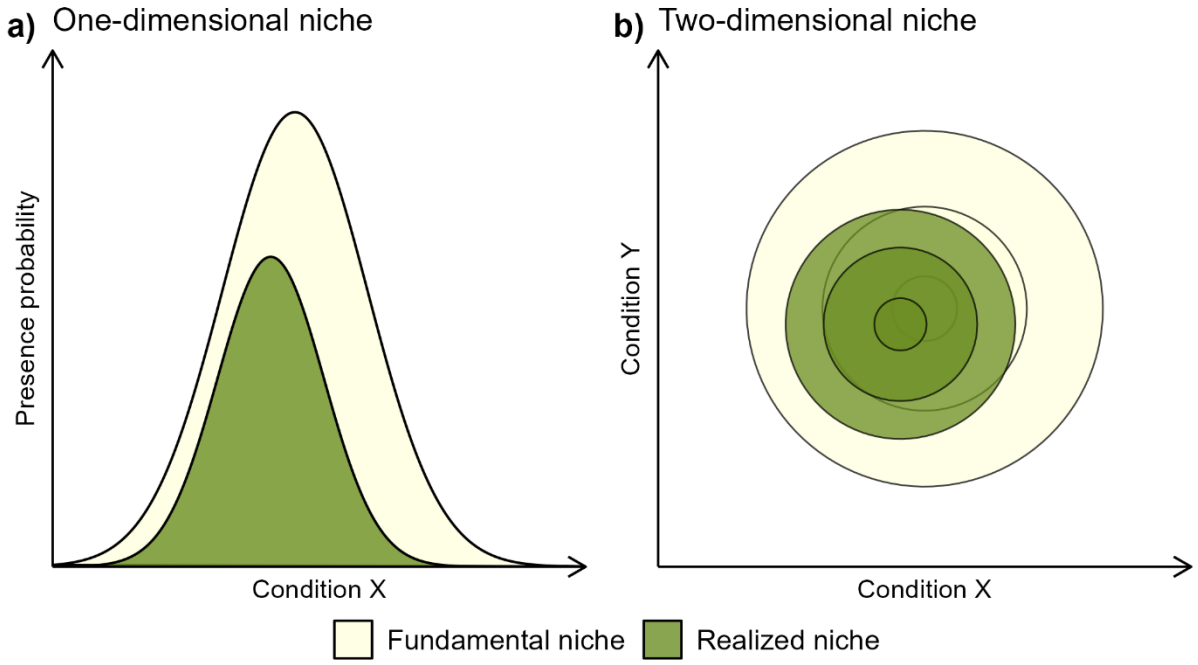


*Figure 1-3: Illustration of a one (a) and two (b) dimensional niche, the y-axis (a) or the concentric circle (b) represents the probability of occurrence of a species (i.e. how much it strives) under one or two theoretical environmental condition. The fundamental and realized niches are differentiated, as biotic interactions determine the realized niche. Facilitation by other species allowing a species to thrive (having a realized niche) outside of its fundamental niche is not shown.*

The estimation of species optima to certain conditions (such as climate, soil pH etc.) leads to the development of bioindication methods, where the niche concept is reversed to estimate environmental properties from biological surveys (Gégout *et al.*, 2005). Niches and

their optima serve as reliable indicators of species affinity to climate (Soberón & Peterson, 2005; Vangansbeke *et al.*, 2021). The thermal niche of the species will be extensively studied throughout this manuscript, thus considering only one of the dimensions proposed by Hutchinson. We will, however, often refer to possible correlations with unmeasured dimensions of the niches, thermal optimum and drought tolerance for example. As an important reminder, the estimation of species optima is only a correlative attempt to obtain physiological tolerances of species. While there is an increasing number of true measurements of species tolerances (e.g. lethal temperature, Lancaster & Humphreys, 2020), these data are still scarcer than optimum, we choose not to rely on them to keep a wider set of studied species, but we will discussion the implications of such measurements.

#### *1.2.1.2. Species Range*

A species range is defined as the geographical space where its individuals and population are found and is conditioned by its ecological niche (Figure 1-4). In other words, it is the delineation of space with the suits of conditions that allows the survival of the species (Soberón & Peterson, 2005). However, the range - mentioned earlier as the realized niche - is also the product of geographic accessibility and biotic interactions. For example, locally adapted competitive species (i.e. close to their optimum) can exert unsustainable competition to species straying far from their optimal, reducing the size of their expected range size (Boulangeat *et al.*, 2012; Sanczuk *et al.*, 2022).

The geographical accessibility criterion poses that range is also a product of species dispersal and historical distribution. Species are ultimately limited in their dispersal capacities; some suitable areas may never or only slowly be colonized. Trees in Europe may have not recovered their full potential range following the last glaciation due to their slow lifecycle and dispersal capacities (Svenning & Skov, 2004). This ongoing slow march toward the North illustrates the difficulty of determining if a species niche reached its expected range, thus at equilibrium with climate. Studies of past and current range of species are in part motivated by the likely disequilibrium that contemporary global warming will inflict on species (Svenning & Sandel, 2013).

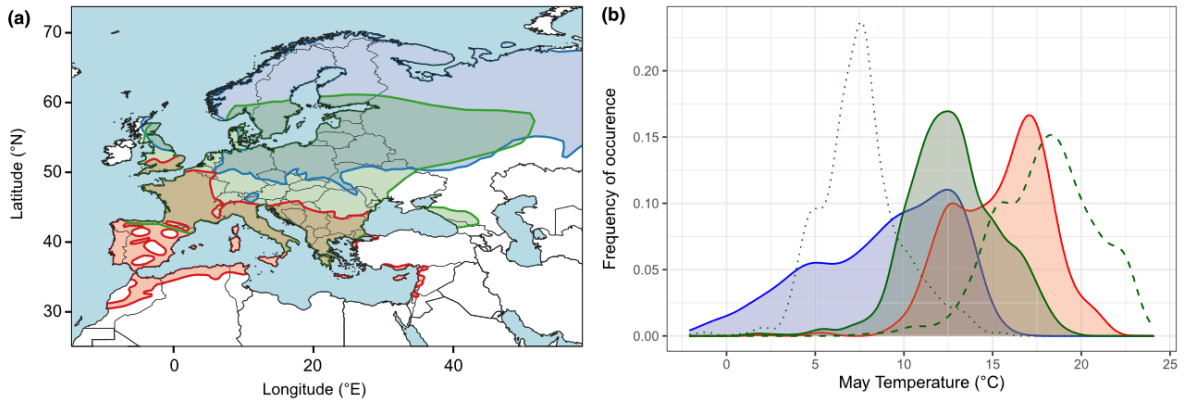


*Figure 1-4: The range (a) and the corresponding realized temperature niche (b) of three species with different climatic adaptations. The three species are Trientalis europaea*

*(blue), Polygonatum multiflorum (green) and Ruscus aculeatus (red). The minimum and maximum May temperature of Polygonatum multiflorum range are also displayed. From (Vangansbeke* et al.*, 2021).*

### *1.2.2. Species shifts under environmental changes*

#### *1.2.2.1. Niche Conservatism*

As species ranges are the result of the equilibrium between the environment and the population dynamics, a change in the environmental conditions should shift species ranges accordingly. For this intuitive reasoning to be observed, however, an assumption should hold true. Species must conserve, at least partly, their niche through time and generations. The history of trade-offs and adaptations species have gone through to fit a given niche is ultimately stored in the genome of a species. The time needed for mutations and gene flows to alter the genome, thus the fundamental niche, far exceeds contemporary changes in climate (including the last glacial maximum that occurred c. 20,000 years ago, Peterson, 2011; Wasof *et al.*, 2015; Wiens *et al.*, 2010). The niche conservatism assumption is also supported by species populations seeking to actively avoid new environmental conditions in order to maintain their actual niche over time (Pyron *et al.*, 2015). The niche conservatism is still under debate as the previously cited studies might have addressed realized niche conservatism, whereas the ongoing environmental changes could instead open unexplored dimensions of the fundamental niche of a species (Pearman *et al.*, 2008; Veloz *et al.*, 2012). The work presented in this thesis follows the assumption of niche conservatism but provides alternate interpretations of how plasticity and local adaptation (that originate from the fundamental niche) could affect the reported results.

#### *1.2.2.2. Environmental changes and species shift*

A shift in environmental conditions will ultimately lead to a disequilibrium between a species range and its niche. Conveniently, environmental change such as climate warming can also be represented spatially via the shift of isotherms in space. Thus, the isotherms delineating a species range are expected to shift; populations of the trailing (or warm) edge of the range are expected to decline whereas previously unoccupied spaces of the leading (or cold) range are expected to be colonized by the species (Lenoir & Svenning, 2015; Svenning & Sandel, 2013). A species range shift is thus a product of those extinction and colonization dynamics, which may be linked to species functional traits (Angert *et al.*, 2011). Species resistance to extinction (persistence in Figure 1-5) dictates whether the trailing edge retracts or not during the shift. A species' ability to migrate dictates how the leading edge is colonized, a species with sufficient colonization rates will have a “march” or “expand” range shift (Figure 1-5), and an intermediate colonization rate leads to leaned or retracted ranges (Figure 1-5). Conversely, species with insufficient colonization rates are the most at risk of extinction (Figure 1-5, Lenoir & Svenning, 2015).

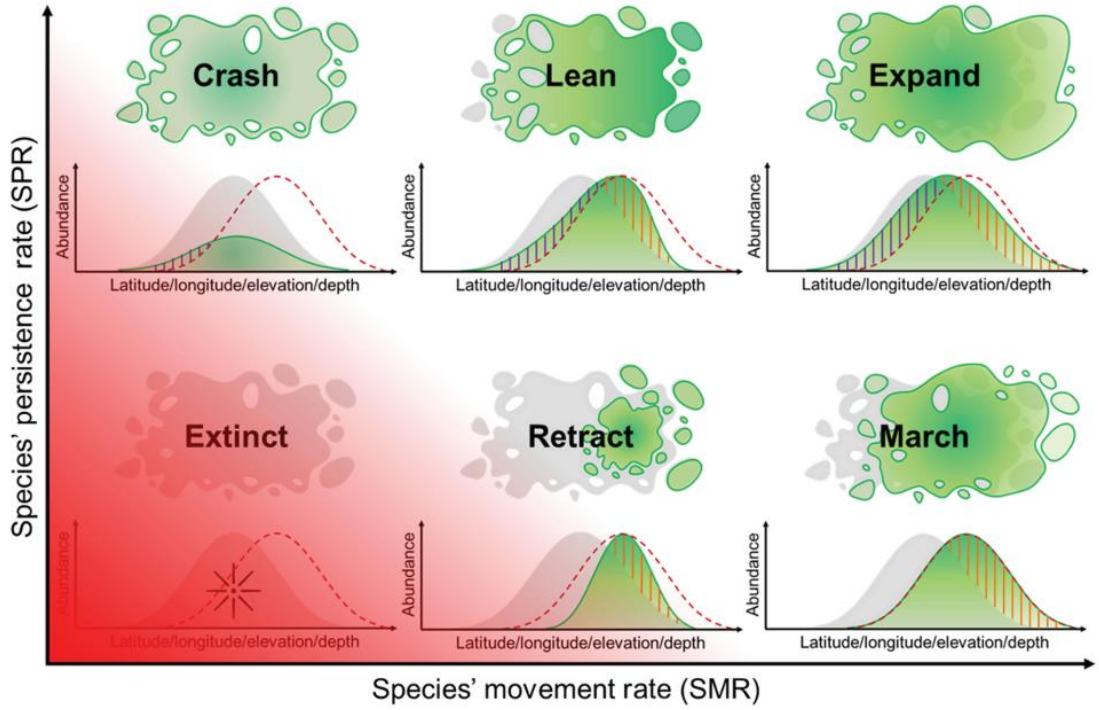


*Figure 1-5: Conceptual illustration of several expected range shifts of species. The expected range shift types are contingent on species abilities to track climate shifts (SMR) and species abilities to resist to the new conditions (SPR). The gray bell curve represents the environmental condition within the species range before the period of change. The dotted red bell curve represents the expected condition within the new species range under a simplistic assumption of a perfectly tracked shift from the species. From (Lenoir & Svenning, 2015).*

Intrinsic species traits are not sufficient to explain range shifts completely, the spatial configuration and velocity of isotherm shifts can greatly vary (Loarie *et al.*, 2009; Serra-Diaz *et al.*, 2014). Range shifts are more likely to be complete where distances needed to track shifting isotherms are low, such as mountain ranges where 100 meters of upward shift corresponds to a 0.6 °C cooling in mean annual temperature (Bertrand *et al.*, 2011; Rolland, 2003).

### *1.2.3. From the Species to the Community*

#### *1.2.3.1. Ecological Communities*

Communities are the assembly of populations of different species in a given place and time made possible by the heterogeneity of niches and habitats. Community ecology is concerned with what biotic and abiotic factors drive the different assemblage of species, their diversity and their functionality (Leibold *et al.*, 2004; Mittelbach & McGill, 2019; Morin, 2009; Vellend, 2010). The process of community assembly is frequently explained through a sequential filtering analogy, with the initial step being the regional filter: the community location should be within a species geographical range or accessible from the range. But every species in range of the community does not get to part of the assemblage as they need

to traverse the abiotic filtering. The local conditions (such as soil pH, moisture, temperature, light availability, etc.) exclude most candidate species in the same fashion their niche dictates their range. Lastly, biotic interactions can filter some species through competition for resources or predation (Kraft *et al.*, 2015).

This metaphor falls short for distinguishing abiotic from biotic interactions when used in empirical studies, and it undermines the importance of stochastic events in shaping the community (Kraft *et al.*, 2015). More broadly, the community is a dynamic constantly reshuffled by both stochastic and deterministic extinction (*sensu* local extinction) and colonization of new species. Communities are indeed interconnected and the upscaled framework of meta-communities, as highlighted in detail in (Leibold & Chase, 2017). One notable example of meta-community structure is the "source-sink" dynamics. A sustainable population can disperse individuals to "sink" sites – sites that cannot sustain local populations without this immigration (Pulliam, 1988). This allows individuals to be found outside of the expected range (i.e. where the populations are self-sustained) and blurs the realized niche calculation (Pulliam, 2000).

#### *1.2.3.2. Community Affinity to Climate*

Among the several ways to summarize a community - mean of functional traits, tolerances, niche optima -, the average thermal optimum is increasingly used. As thermal optimum is computed from the realized niche of a species (Figure 1-4), it is measured in Celsius degree (°C) and allows a comparison with current and change in climate (Bertrand *et al.*, 2011; Vangansbeke *et al.*, 2021). Among the multiple filters of community assembly, the average thermal optimum allows studying the climatic dimension of the environmental filter. Thus, changes in average thermal optimum are likely to be the result of changes in community assembly process induced by climate change.

This metric can also be perceived as a summary of the niche and biogeographic origin of the recorded species. As such, it should be used to bioindicates local temperatures with caution (Marrec *et al.*, 2022). Thermal optimum is a metric that does not consider the width of the species niche and the uncertainties of the mean annual temperature within a species range. Some methods aim to account for the dispersal around the optimum and aggregate species thermal optima at the community level (De Frenne *et al.*, 2013; Rodríguez-Sánchez *et al.*, 2012). Another unforeseen confounding effect of such metrics is the possible correlation between thermal optimum and other environmental conditions. For instance, European plant species that have evolved to thrive in cold climates have also faced conditions involving nutrient-poor soil, often associated with humus generated by conifer needles. Consequently, these cold-adapted species may exhibit a higher degree of adaptation to acidic soils (Ewald, 2003).

### *1.2.4. Thermophilization of Communities*

The colonization and extinction-induced reshuffling of communities can be directional and linked to environmental changes. Climate warming is ought to cause the thermophilization of communities, the increment through time of its average thermal optimum (De Frenne *et al.*, 2013). Thermophilization can be perceived as the community scale observation of the range shifts described earlier (c.f. 1.2.2) as it can be a product of both colonization and local extinction. Evidence of plant communities thermophilization is now widespread and spans different biomes. Slow-responding tree assemblage of North America experiences thermophilization rates of 0.003 °C $yr^{-1}$ (Brice *et al.*, 2019; Rosenblad *et al.*, 2023), whereas the thermophilization of the more dynamic understory communities is consistently estimated at 0.01°c $yr^{-1}$ (De Frenne *et al.*, 2013; Govaert *et al.*, 2021; Richard *et al.*, 2021). The unit of the thermophilization being °C $yr^{-1}$, it is comparable to climate change measurements. As such, analogous to range and isotherms shifts, communities can be considered at equilibrium when their current thermal optimum or thermophilization corresponds to the current climate and its warming rate (Figure 1-6).

Equilibrium is, however, rarely observed in response to the recent rise in temperature, thermophilization rates of 0.01°C $yr^{-1}$ lag behind the rate of climate warming of 0.025°C $yr^{-1}$ (Bertrand *et al.*, 2011; De Frenne *et al.*, 2013; Dietz *et al.*, 2020). This disequilibrium is, however, not uniform in space: due to warmer baseline and increase in climate Mediterranean communities are experiencing higher climatic debt (Bertrand, 2019; Bertrand *et al.*, 2016). Lags in thermophilization are also linked with the velocity of climate change: places warming at faster rates will display larger lags, supporting the idea that species colonization velocity cannot be fastened by climate (Pacheco-Riaño *et al.*, 2023; Serra-Diaz *et al.*, 2014).

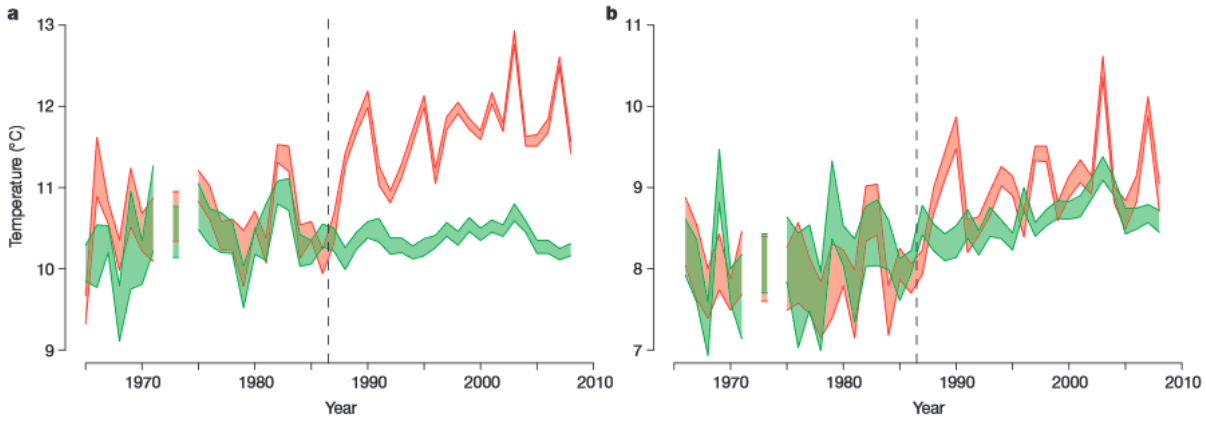


*Figure 1-6: Temperature (red) and community mean optimum (green) reconstructed trends between 1965 and 2008 in lowland (a) and mountain forests (b). The dashed line delineates the contemporary warming, marked differences between the two trends mean a high climatic debt. From (Bertrand* et al.*, 2011).*

### *1.2.5. The blind spot of thermophilization*

#### *1.2.5.1. What are the driving community dynamics?*

The observation of a disequilibrium between communities and climate has also been coined "climatic debt". The term climatic debt implies that communities will have to "repay" to return to equilibrium by either including new warm-adapted species or by the extinction of the now ill-adapted cold climate species (Vaughan & Gotelli, 2021). However, without a clear distinction of which "repayment" process is at play, authors' interpretations of thermophilization (reducing climatic debt) should be considered with caution. Authors often refers to thermophilization as a reshuffling toward communities adapted to warmer climate (Bertrand *et al.*, 2011; De Frenne *et al.*, 2013; Dietz *et al.*, 2020; Pérez-Navarro *et al.*, 2021), but thermophilization as a measure obfuscates which process happened. Thermophilization could also only be the product of cold-adapted species extinctions, as hinted by recent studies documenting species range contraction and local extinctions (Jandt *et al.*, 2022; Kuhn, 2016; Kuhn & Gégout, 2019; Watts *et al.*, 2022; Wiens, 2016). In other words, very different ecological processes are at play: colonization depends especially on a species reproductive cycle, and ability to disperse and establish (that be facilitated by climate changes). Extinction, on the other hand, depends first on the conditions experienced by the individuals and their longevity and ability to tolerate the stress (Comte *et al.*, 2014).

#### *1.2.5.2. Thermophilization reflects adaptation or erosion?*

Adaptation initially refers to the evolutionary process that allows species of all kinds to fit their contemporary environment. This concept can be stretched to the community as the individuals comprising it need to maintain enough functions (growth, flowering, seed dispersal, etc) to survive, leading to a striving community (Figure 1-7). The relationship between plant performance relative to species optimum found by Wei *et al.*, (2024), is yet to be confirmed on a larger set of species, but demonstrates that a species located in its warm edge loses performance, and contributes less to the functioning of its community. Thus, under a niche conservatism assumption, a community is 'adapting' if newly arriving species are adapted to the new conditions, in our case, if they are warm-adapted (Wei *et al.*, 2024). An extinction-driven colonization however reflects a loss of function that ultimately leads to the removal of now ill-adapted species, and an erosion of the community (Landuyt *et al.*, 2019). Our definition of adaptation and erosion is however incomplete: by focusing on the relative position of species' optimum in relation to current and future climate, we ignore evolutionary adaptation and plasticity, and this further constrains the analysis of species whose optimum is available. The potential erosion caused by extinction, rather by adaptation from colonization, of the community further illustrates the need to partition the driving force of thermophilization, as a losses of species will materialize into a loss of local diversity that can be upscaled to a loss of landscape or biome-wide diversity.

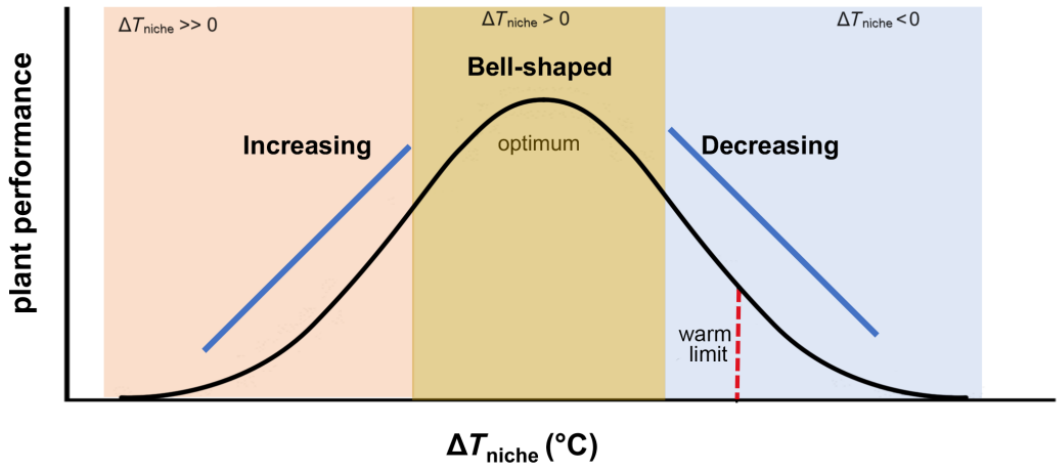


*Figure 1-7: Plant performances (height, growth, flowering, etc.) as a function of the difference between their thermal optima and the actual climate. When ΔTniche >>0, the species is in its cold edge (its performances increase with climate warming), when ΔTniche <0, the species is in its warm edge and its performance decreases. Theorized and measured in a small subset of plants by (Wei* et al.*, 2024)*

#### *1.2.5.3. What is the link between thermophilization and change in diversity?*

Summarizing communities to a mean thermal optimum also blurs the line between thermophilization and diversity metrics. The quantification of colonization-extinction processes leads to straightforward interpretations of change in local diversity (α-diversity) that can be either increased or decreased accordingly. This observation particularly holds true in high mountain ecosystems, where climate warming pushes species and diversity upwards in previously poor or unoccupied sites (Staude *et al.*, 2022; Steinbauer *et al.*, 2018). However, other dimensions of biodiversity could be more evasively affected, the selective process of thermophilization could decrease ß-diversity and ultimately trigger biotic homogenization. The joint increase of warm-adapted species and the extinction of unique cold-adapted species increases the similarity between communities (Tatsumi *et al.*, 2021). Ubiquitous observations of plant community thermophilization call for studies of links to the evolution of local and ß-diversity to put them in the perspective of conservation biology (Socolar *et al.*, 2016).

#### *1.2.5.4. What is the geographical scale of thermophilization?*

Thermophilization is a metric and a process mostly documented at the community level but can be applied to different scales to address different questions. Thermal optima of species is also used as an explanatory factor of range shifts (Duchenne *et al.*, 2021). Thermophilization can be determined separately for protected areas and differing ecoregions (lowland from mountains) and land-use types (Kiebacher *et al.*, 2023; Maciejewski *et al.*, 2020). Upscaling thermophilization from the community scale allows

uncovering different processes. Indeed, dynamics at a landscape scale can detect an absolute decrease or increase of species occurrence as a result of thermophilization, or no change in occurrence if the species is unaffected or tracks the warming climate fast enough. The biosphere has been partitioned into landscapes of different sizes, from biomes to ecoregions to habitats, these landscapes can then be used to upscale the findings of the community-focused thermophilization. For example, French forest classification offers a partitioning of the territory into 85 forest ecoregions, this scale of landscape allows testing the balance of colonizing and locally extinct species and serves as an intermediary scale between communities and Europe-wide ecoregions.

## 1.3. The multiplicity of scale of global change impacts on communities.

### *1.3.1. The meaning of scale in ecology*

The delineation of scale in ecology and biodiversity studies is a long going question because in the absence of general laws governing the upscaling or downscaling of observed patterns, two concerns arise: Global circulation models, macroclimatic predictions and warming projections are all global scale variables that assume homogenous conditions within kilometers to hundreds of kilometers grids. This spatial resolution hinders the accurate prediction of impacts at scales relevant to communities or forest patches, which depend on local processes competition and microclimate (Figure 1-8, Levin, 1992). Conversely, most studies able to capture fine-grained variation through field sampling of communities, microscale climate variables and a refined measurement of biotic and abiotic interactions are inherently limited to small geographical scales. These smaller-scale studies do not cover enough macroscale processes, their findings are thus harder to upscale and to form consensus of observed trends. (Chave, 2013; Levin, 1992).

Some unified theories have proven to be effective at predicting biodiversity and functioning patterns over global scales (neutral theory: Hubbell, 2011), metabolic theory: (Brown *et al.*, 2004) at the expense of simplifying individual species specificity. Another way to leverage the upscaling/downscaling limitation is to study how the intermediary scale factors shape community response to macroclimatic change. This is the approach pursued throughout the studies of the manuscript. We first assess macroclimatic warming impact on communities with the addition of local community dynamics (1.2.5.1), complemented by studies of how landscape forest cover (1.3.5), topoclimate (1.3.3) and microclimate (1.3.4) shape plant communities. This non-trivial list of terms is described in the corresponding parts below and summarized in Figure 1-8.

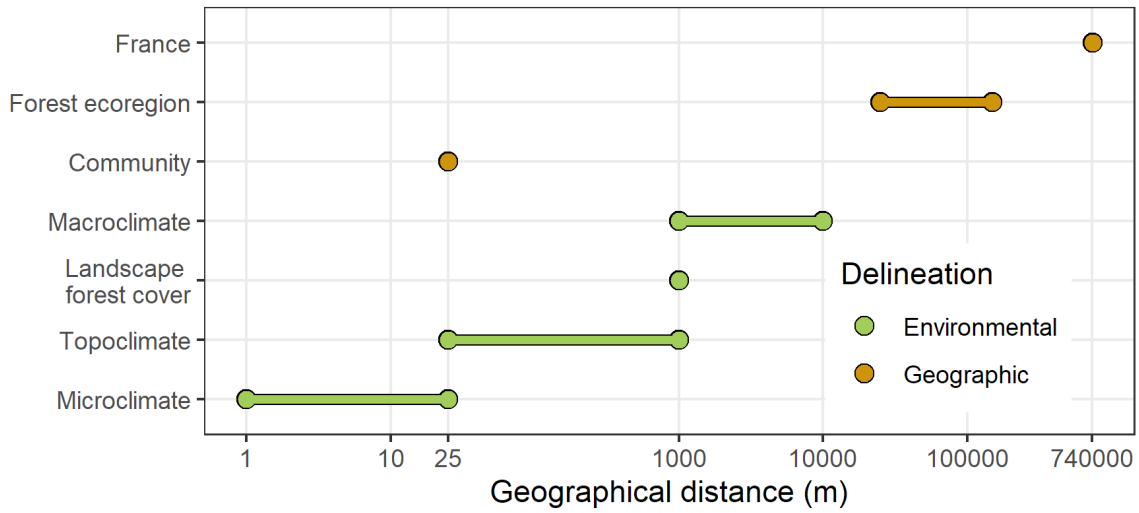


*Figure 1-8: Summary of the resolution of each term used throughout this manuscript. Distance in meters corresponds to the width of a focal pixel when modeling macro, topo and microclimate, it corresponds to the radius of the landscape scale forest cover (in short forest cover) and of the floristic survey (i.e. community). The width of France and the range of widths of the forest ecoregions are also displayed.*

### *1.3.2. Macroclimate affects communities at a large scale.*

One dimension of microclimate is the free-air temperature historically measured and modeled by climatic institutes via a network weather station (measured in open fields, 2 meters from the ground, shaded). The role of macroclimate in shaping species distribution was and still is widely studied (Woodward & Williams, 1987; Pulliam, 2000; Yates *et al.*, 2000). Furthermore, the effect of macroclimatic warming is also increasingly highlighted by the ongoing thermophilization of communities we mentioned above (1.2.4, De Frenne *et al.*, 2013).

Macroclimate is often summarized and modeled as mean temperatures or precipitations. However, the role of extreme events such as heat waves and droughts should not be undermined as their frequency and intensity are also expected to increase (IPCC, 2021a). Observations from population dynamics and tree dieback inform that extinction events shaping communities mostly occur during such events or subsequently arise as a consequence of these (Brice *et al.*, 2019; Pérez-Navarro *et al.*, 2021). Mean annual temperature is the main macroclimatic variable in our work, to both characterize the environment and species thermal niche. There is a positive correlation between mean annual temperature (which the thermal optimum of a species is based on), water limitations and the intensity of extreme events (e.g. drought.). As a consequence, our results can in part be interpreted in the light of extreme events and drought impacts on communities. As an example, it is likely for a relatively cold-adapted to be removed from a community because of a drought event instead of a steady rise in air temperature, whereas a relatively warm-adapted species resisted the drought because of its evolutionary and biogeographical history.

### *1.3.3. Topoclimate mediates macroclimate at an intermediate scale.*

#### *1.3.3.1. Elevation Effect on Climate*

As early as the map drawn in *The Physical Atlas* by Humboldt and Johnston in (1848), topography was brought as an indissociable factor of plant distribution (Figure 1-9). The vertical cooling due to elevation also known as the lapse rate (that can be considered a macro-scale driver) is enough to structure different biomes, from lowland mixed forest to alpine tundra. The elevational gradient was a topical addition to climate warming studies; the same amount of warming can have more impact on cold-constrained ecosystems, and such ecosystems are also expected to warm faster because of several feedback loops (Pepin *et al.*, 2015). As a result, summits and high mountains have already undergone fast thermophilization of communities and gains in species richness some of which now occupy previously unsuitable habitats (Bahn & Körner, 2003; Pauli *et al.*, 2001; Staude *et al.*, 2022; Steinbauer *et al.*, 2018). This upward colonization is greatly facilitated by the short geographical distance needed to track the shift in isotherm (0.6°C per 100 upward, Rolland, 2003). This fast responsiveness also threatens the uppermost flora, which displays high climatic debt as it is impossible for them to shift their distribution higher (Dullinger *et al.*, 2012; Rumpf *et al.*, 2019; Watts *et al.*, 2022).

#### *1.3.3.2. Topography*

Topography, by interacting with solar radiation, cloud formation, air density and movement can significantly alter the local conditions at a constant elevation, at a scale from a kilometer to a tenth of meter (Finocchiaro *et al.*, 2023; Geiger *et al.*, 2009; Lenoir *et al.*, 2013). The slope orientation interacts with the orbit of the sun such as equator-facing slopes display warmer mean and maximum temperatures, creating the difference in strata delineation of mountainous ecosystems already perceived by Humboldt (Figure 1-9, Becker & Geremia, 1984). Aspect also influences snow melting processes and the length of the growing seasons for plants. Such changes in climatic factors are translated on the community compositions: south-facing slopes (in the north hemisphere) consistently display more warm-adapted and Mediterranean flora (Macek *et al.*, 2019; Maclean *et al.*, 2015; Rita *et al.*, 2021). Valley bottoms are also of interest in topoclimate studies for their tendencies to concentrate the denser cold-air and water flows and their overall shader environments. Such moist and cool sites can differ from their immediate surroundings by several degrees (Finocchiaro *et al.*, 2023). For instance, summer temperature can be 1.5°C cooler next to a stream compared to places 50 meters apart. Such cooler conditions can host refugial populations of species located far from their expected range (Dobrowski, 2011; Finocchiaro *et al.*, 2023; Ishiyama *et al.*, 2022). These refugia are created when a species range is displaced by environmental change (see 1.2.2.2, Figure 1-5), but local conditions allow some species to persist outside the displaced range (Ashcroft, 2010; Rull, 2010).

At the time of writing this thesis, species range projections use coarse-grained models (>= 1 kilometer). The variety of the above-mentioned topoclimates can buffer macroclimatic

changes and has elevated thermal heterogeneity as a powerful driver of species persistence and lack of full equilibrium recovery in mountainous regions despite the facilitation of migration mountains present (Kulonen *et al.*, 2018; Lenoir *et al.*, 2013). As this local decoupling originates from topography, it can be perceived as particularly stable in time. This has led to studies of climatic refugia or microrefugia concerned with the determinant and effectiveness of such places to conserve individuals (Ashcroft, 2010). This is of particular interest in extinction-driven thermophilization and range retractions to conserve populations that cannot track – via colonization – the ongoing climate change (Lenoir *et al.*, 2017; Rumpf *et al.*, 2019).

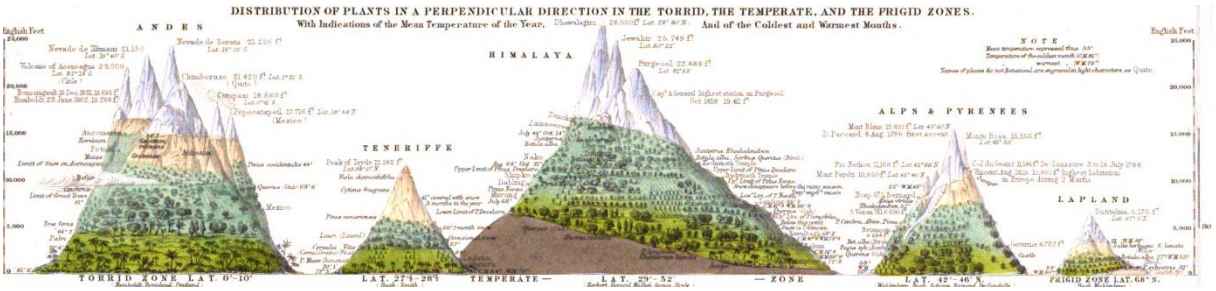


*Figure 1-9: Cross-section maps of vegetation distribution of several mountainous ranges, from (Johnston* et al.*, 1848). The delineation of the vegetation stratification is not horizontal but contingent on the orientation of the massif to the sun exposure.*

### *1.3.4. Microclimate, the true condition experienced by organisms.*

#### *1.3.4.1. Microclimate buffers communities from climate change*

Trees, through light interception, evapotranspiration and wind reduction ultimately alter the conditions understory species experience. Forest microclimate (measured near the ground (15 cm), analogous to the height or basal stem of some plants) can be interpreted as insulation from the regional climate, as canopy buffers climatic extremes. As a result, understories display warmer winter temperatures (on average 1°C warmer), but cooler summer temperatures (on average 4°C cooler) and cooler annual temperatures, and moister air and soil (Figure 1-10 , Chen *et al.*, 1999; De Frenne *et al.*, 2019, 2021). These properties have been identified as an important explanation for the slower thermophilization and range shift observed in understory organisms (De Frenne *et al.*, 2021; Kemppinen *et al.*, 2023).

Initial evidences of slowed thermophilization by canopy were observed by resampling of plots with different degrees of canopy change, thus making only an indirect link with microclimatic change (De Frenne *et al.*, 2013; Richard *et al.*, 2021; Stevens *et al.*, 2015). However, canopy closure also interacts with light availability, and can exclude warmer-adapted species that are also early-successional and adapted to bright understories (De Frenne *et al.*, 2015; Dietz *et al.*, 2020). This is evidenced by faster thermophilization rates for canopy-removed or experimentally lit plots (Dietz *et al.*, 2020; Govaert *et al.*, 2021; Sanczuk *et al.*, 2023). The development of microclimate modeling, through mechanistic

(Maclean *et al.*, 2019) or statistical (Zellweger, Coomes, *et al.*, 2019) approaches allowed to disentangle the true effect of microclimate cooling on communities and the light availability effect (De Frenne *et al.*, 2019; Zellweger *et al.*, 2020).

### *1.3.4.2. Implications and Applications of Microclimate Science*

The microclimate-induced slowing of thermophilization rates highlighted the need to better understand the drivers of such buffering of temperature, through a steep increase of measurements and available methods (Lembrechts *et al.*, 2020, 2021; Zellweger *et al.*, 2020). Canopy-related variables are the first to stand out in the models, an increase of 50% in canopy cover induces a 2°C stronger buffering of maximum summer temperature in temperate forests (Zellweger, Coomes, *et al.*, 2019). Basal area and tree height also contribute in the models, although less consistently, to the buffering effect (Zellweger, Coomes, *et al.*, 2019). The capacity of the canopy to buffer temperature is itself contingent on soil and air moisture because of their control over evapotranspiration, questioning the long-term ability of forest to buffer temperature during the harsher predicted drought (Davis, Dobrowski, *et al.*, 2019; Greiser *et al.*, 2018; von Arx *et al.*, 2013).

The buffering capacity of trees is predicted to increase with climate change as it is more apparent in high mean and extreme temperatures (De Lombaerde *et al.*, 2021). However, logging, disturbances and tree mortality challenge the capacity of forests to be qualified as a thermal refugia in the long term, like the topography-induced ones (Hylander *et al.*, 2022; Stevens *et al.*, 2015). Most of the research cited above focus on lowland forests, and thus the control of topography –*per se* or its interaction with canopy– on microclimate remains to be explored to determine the refugia potential of forested mountains.

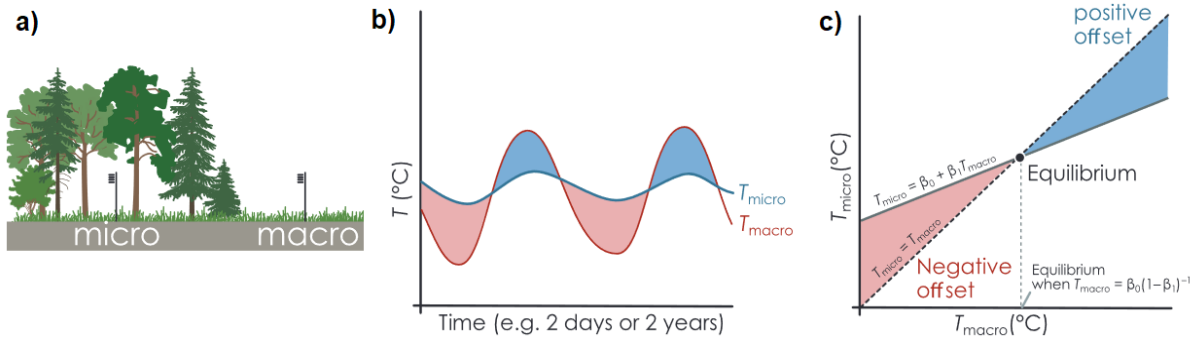


*Figure 1-10: Illustration of macro and microclimate, measured in open air and in forest, respectively (a). Daily or annual fluctuations of temperature are represented in b), climatic extremes are reduced in forest microclimates compared to the macroclimates. The relationship between micro and macro climate is represented in c), the dashed line represents the "no buffering" hypothesis, and the plain line represents the relationship observed in temperate forests. The microclimate is cooler than the macroclimate in periods of warm temperature, and warmer when the open-air temperature is low, from (De Frenne* et al., *2021).*

### *1.3.5. Forest fragmentation interacts with species and microclimate.*

#### *1.3.5.1. Forest fragmentation and biodiversity*

The historical and recent footprint of humans on ecosystems (see 1.1.3) leads to habitat fragmentation (Haddad *et al.*, 2015), which we will often refer to as forest fragmentation as it is the only habitat studied throughout this thesis. The concept of "forest fragmentation" often includes two distinct processes, namely forest loss and forest fragmentation itself, which should be distinguished. Forest loss is a net reduction in forest cover (Figure 1-11.a.b). In contrast, forest fragmentation refers to the restructuring of the same total forest area, resulting in smaller, more isolated fragments that are more exposed to adjacent human land uses (Figure 1-11.c, Fahrig, 2003; Haddad *et al.*, 2015). Forest loss generally leads to forest fragmentation, as a consequence, studying the independent effects of loss and fragmentation *per se* (e.g. independent of forest cover loss) is challenging.

Most of the studies agree on the negative effect forest loss has on the biodiversity of all taxa (Dirzo & Raven, 2003; Hanski, 2011), however theoretical and empirical supports of the effect of fragmentation *per se* diverge (Fahrig, 2017; Haddad *et al.*, 2015). Baseline expectation from metapopulation theory posits that single large habitats are more able to sustain a population by concentrating individuals in the same space and limiting the need for dispersal. This thinking supported the numerous creations of single large and protected conservation areas (Diamond, 1975). Counterintuitively, empirical evidence generally supports an increase in biodiversity with fragmentation *per se*, attributing the ability of several small habitats to cover more heterogenous ecological conditions (Fahrig, 2017; Fahrig *et al.*, 2019).

Aside from the biodiversity patterns, forest fragmentation is also expected to slow the migration and range shift of plant species (Dullinger *et al.*, 2015). The geographical distance between forest patches is sufficient in lowlands to hamper the slowly colonizing plant species and their animal disperser and pollinators (Aguilar *et al.*, 2006; Dullinger *et al.*, 2015; Honnay *et al.*, 2002, 2005). This phenomenon highlights the need for a link between land use and climate change to better predict and cope with the observed lag of thermophilization of understory plants (Auffret & Svenning, 2022; Vanneste *et al.*, 2020).

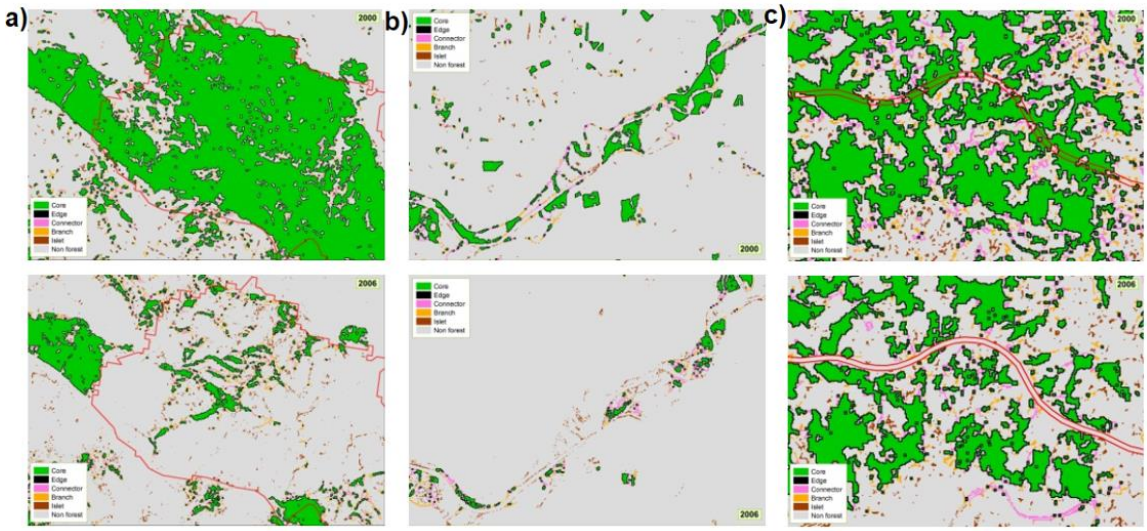


*Figure 1-11: Illustration of forest loss through fire (a), riparian wood clearance (b) and forest fragmentation by highway construction (c), with forest maps from 2000 and 2006, from (IES* et al.*, 2013).*

### *1.3.5.2. Forest fragmentation interacts with soil and legacy.*

The current mosaics of forest fragments –intertwined with pastures and croplands– in Europe are the result of both historical (preindustrial era) and recent logging (Ellis *et al.*, 2021; Vallauri *et al.*, 2012). Consequently, fragments of first successional forest are likely to have richer soil due to past agricultural activities and will therefore display nutrient-demanding communities (Dupouey, Sciama, *et al.*, 2002; Koerner *et al.*, 1997). Even large patches of forest can be influenced by past and current agricultural practices through their edges. Edge effects of several hundreds of meters promote nutrients and light-demanding species that consequently alter the thermal optimum of communities regardless of changes in climatic conditions (Bergès *et al.*, 2013, 2016; Ewald, 2003). The historical inertia of communities also implies that old-growth forests, often the core of large forest patches, may serve as source population refugia for cold-adapted forest specialists, generally are characterized by low dispersal capacities (Brunet *et al.*, 2011, 2021; Dupouey, Sciama, *et al.*, 2002).

### *1.3.5.3. Forest fragmentation interactions with microclimate*

As described in part 1.3.4, forests display significantly lower temperatures than their surrounding agricultural, pastoral or urban matrices (De Frenne *et al.*, 2019). This means that forest fragmentation *per se* has a significant effect on understory microclimate via edge effects, where edges are characterized by warmer temperatures, analogous to the free air that surrounds them (Arroyo-Rodríguez *et al.*, 2017; Meeussen *et al.*, 2021; Tuff *et al.*, 2016). Forest amount, also mentioned as landscape forest cover, could also interact with microclimate by localized cooling of the local climate. During the growing season, the higher

evapotranspiration of trees in a forested area could in turn cool the local climate more than just the immediate effect of the canopy (Bonan, 2008; Hesslerová *et al.*, 2013; Pokorny *et al.*, 2010). The input of the thermal landscape concept to forest fragmentation allows us to test for a potential unexpected effect of forest fragmentation (Arroyo-Rodríguez *et al.*, 2017; Tuff *et al.*, 2016). One could expect highly forested landscapes to thermophilize faster ought to their larger connectivity and species pool. However, the above-described cooling effect of landscape forest cover and historical inertia would, on the other hand, slow down thermophilization. This calls for research to disentangle the relative effects of soil and microclimatic cooling by landscape-scale forest effect on communities' thermal optimum

## 1.4. Aims, research questions and methodology.

### *1.4.1. Aims*

This thesis aims to provide an assessment of the ongoing community thermophilization in French forest ecoregions by unraveling the community dynamics causing it and to strengthen this assessment by studying factors of different scales that interfere with communities' response to climate. Specifically, we aim to disentangle landscape scale (landscape forest cover and topography) control on communities often intertwined with a local factor, canopy cover.

### *1.4.2. Implications*

The multiplicity of processes that control community thermophilization creates scientific and conservation challenges alike. Very different implications can arise from which community dynamics drive thermophilization: a predominance of extinction calls for microrefugia and assisted migration studies, to present new conservation prospects for endangered species. Conversely, a contribution of colonization calls for homogenization and ecological corridor studies as they are processes promoted by species colonization. Abiotic processes at different scales and their interactions also need to be considered in further studies to better understand current and future communities, but also because they imply different management and conservation issues. As an example, forest fragmentation and land-sharing questions depend on regional policymakers whereas individual forest owners and managers can alter immediate cooling by canopy cover via clear-cuts. Lastly, understanding the topography-canopy cover balance in driving community composition allows assessing the stability in time of the refugia these elements can offer, as topography is more stable through time than canopy cover.

### *1.4.3. Research Questions*

The 2 general aims described above can be broken up into three main research questions as follows:

#### *1) How has recent macroclimate warming shaped understory plant communities in French ecoregions?*

To address this question; we quantified recent trends in thermophilization of the French forest ecoregions and identified what community dynamics drove it, as well as identified links with biotic homogenization. To this end, we used an extensive subset of the French National Forest Inventory (NFI) of 28,334 plots and novel partitioning methods to specifically ask:

- What community dynamics drive the recent thermophilization of forest ecoregions?
- Do the recent thermophilization results in forest ecoregions homogenization?

#### *2) How does landscape-scale forest cover mediate community response to climate?*

The underlying aim of this question is to test whether landscape forest cover could influence understory communities, through soil nutrient differences and microclimatic cooling. We used 4,024 NFI plots and a detailed forest cover map to question:

- Does landscape forest cover impact community adaptation to climate in complement to local effects of canopy?
- Can a pure climatic effect, independent of soil properties, of landscape forest cover on communities be detected?

#### *3) How topoclimate and microclimate shape communities?*

We addressed this question with records of understory temperature and community surveys in a Vosges valley with contrasting topography and canopy cover. Thanks to detailed maps, we modeled microclimatic temperatures of the growing season to investigate the following biophysical and community questions:

- Does topography outweigh canopy cover in buffering understory microclimate in mountain ranges?
- To what extent do canopy and topography-induced microclimate shape communities thermal optima and diversity?

### *1.4.4. Manuscript Structure*

We will present in Chapter 2 an assessment of the recent thermophilization of France flora communities, with an emphasis on the dynamics that drive them (question 1). We will also explore its link with a pervasive loss of diversity so-called homogenization. This analysis will provide a recent picture of climate-induced change in plant communities and species

distribution, which we will nuance in further chapters with studies of processes at different scales, in a downscaling fashion (Figure 1-8). The study presented in Chapter 3 aims to link an overlooked aspect of forest fragmentation, landscape forest cover, with community thermal optimum (question 2). Forest fragmentation is often interpreted through the lens of dispersal constraint on plant migration. We aim to go beyond that point by testing how the amount of forest cover in a landscape can cool regional air temperature and favor cold-adapted species. Lastly, we will test the relative effect of canopy cover and topography on understory temperatures, and their subsequent effects on community affinity to climate and richness.

### *1.4.5. Methodology Overview*

The focal point of the three research questions is understory flora communities and their climatic affinity, we used however distinct methods to address each of the questions. We defined the climatic affinity of communities by averaging the individual thermal optimum of the present species, extracted from ClimPlant V1.2 as described in (1.2.3.2, (Vangansbeke *et al.*, 2021).

To address questions (1) and (2), we used National Forest Inventory (NFI) plots from the recent protocol (2005-2021), that have been efficiently documented in (IGN, 2019b; Kuhn, 2016). To be able to compare NFI plots *ceteris paribus*, we used an optimized pairing algorithm to different subsets of the NFI (Chytrý *et al.*, 2014). We created temporal pairs of plots separated by 10 years for question (1) and pairs with contrasting forest cover for question (2). With these pairing, we decomposed the community dynamics behind community thermophilization and homogenization at the ecoregion scale (1) and we tested the difference in community thermal optimum across landscapes (2).

We investigated question (3) by recording growing season understory temperature in a valley of the Vosges massif. We used linear model and variation partitioning to investigate the relative control of canopy cover, aspect and cold-air pooling over temperature. We evaluated their subsequent effect on communities thanks to an independent database of floristic surveys spread across the main ecological gradient of the valley.

We created version-control repositories of code and data following the practices summarized in (Braga *et al.*, 2023), made available at https://github.com/Jeremy-borderieux. Each method will be thoroughly explained, and their limitations discussed in their respective chapter, but we will also present in (Chapter 5: Discussion) general shortcomings and opportunities of the use of NFI data and thermal optimum for the study of communities in a warming world.

# Chapter 2. Extinction drives recent thermophilization but does not trigger homogenization in forest understory.

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## Abstract

The ongoing climate change is triggering plant community thermophilization. This selection process is ought to shift community composition toward species adapted to warmer climates but may also lead to biotic homogenization. The link between thermophilization and homogenization, and the community dynamics that drive them (colonization and extinction) remain unknown but is critical for understanding community responses under rapid environmental change.

We used 14,167 pairs of plots to study shifts in plant community during 10 years of rising temperature, in 80 forest ecoregions of France. We computed community mean thermal optimum (thermophilization) and Δß-diversity (homogenization) for each ecoregion and partitioned these changes into extinction and colonization dynamics of 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 for by the colonization of rare species and the extinction of common species, resulting in the absence of an apparent homogenization trend.

Here we show a dieback of present cold-adapted species rather that an adaptation of communities via the arrivals of warm-adapted species, with mutually cancelling effect on ß-diversity. These results suggest that a future loss of biodiversity and delayed biotic homogenization should be considered.

**NB:** The order of the 'Results and Discussion' and 'Materials and Methods' are reversed for consistency. In the original publication results are found first after the introduction.

Ecoregion summary values are available in appendix Table A1 and the list of species (and their occurrences) used to perform this analysis is available in the appendix Table A2.

Repository: https://github.com/Jeremy-borderieux/Article_thermo_beta_part.git

## 2.1. Introduction

The unprecedented speed of current climate warming is causing major species range shifts and the reshuffling of ecological communities (Franklin *et al.*, 2016; Lenoir & Svenning, 2015; Svenning & Sandel, 2013). This reshuffling could lead to a major risk for biodiversity (Sala *et al.*, 2000) and the services it provides (Reu *et al.*, 2022; Wang *et al.*, 2021). Two major patterns of community composition have been reported as a result of global change, namely thermophilization and biotic homogenization. On the one hand, thermophilization of plant communities – the increase of the average temperature affiliation of species in a community over time – is occurring as a result of climate warming (De Frenne *et al.*, 2013; Martin *et al.*, 2019; Richard *et al.*, 2021), yet at a slower pace than climate change (Bertrand *et al.*, 2011, 2016). On the other hand, evidence also suggests that biotic homogenization across plant communities is taking place (Cholewińska *et al.*, 2020; Olden & Rooney, 2006; Staude *et al.*, 2022). This is shown by a decrease in ß-diversity, which signals an increase of similarity among the communities of a region. To date, we do not know whether these two processes occur simultaneously, what their linkages are, and which community dynamics underlie them.

Baseline expectations from global warming suggest that warm-adapted species may increasingly replace cold-adapted species in communities (De Frenne *et al.*, 2013; Gottfried *et al.*, 2012; Svenning & Sandel, 2013). At large scales, biogeographic theory predicts species range shifts (Lenoir & Svenning, 2015) but lagged dynamics, controlled by the dispersal and establishment capacities of species that may constrain the maximum speed at which , species can colonize suitable climatic areas. (Boulangeat *et al.*, 2012; Govaert *et al.*, 2021; Ozinga *et al.*, 2009). Thus, thermophilization is the product of different rates of colonization and/or extinction (*sensu* local extinction, Leibold et al., 2004) of warm- *vs.* cold-adapted species in a community. At one end, thermophilization may stem from colonization of warm-adapted species without any extinction of cold-adapted species (Figure 2-1). Conversely, thermophilization may exclusively stem from extinction of cold-adapted species, implying biotic erosion of communities rather than colonization of species adapted to warmer climate (Figure 2-1). For instance, extinction-driven thermophilization is expected in Mediterranean communities of Europe, where many temperate species are located at the warm edge of their distribution. As a result, they are subject to extirpation by drought and heat waves, without being replaced by warmer-adapted species as the sea may act as a barrier for colonization (Bertrand et al., 2016; Pérez-Navarro et al., 2021).

Thermophilization is being increasingly detected, but little is known about how it could affect ß-diversity. Both local (α) diversity and ß-diversity are increasing in mountain forests and on summits, where colonization of unoccupied space by new species increases the regional species pool (Bahn & Körner, 2003; Steinbauer *et al.*, 2018). However, lowland forests are showing signs of homogenization (Cholewińska *et al.*, 2020; Naaf & Wulf, 2012; Xu *et al.*, 2023; Zwiener *et al.*, 2018). By selecting species as a function of their thermal

tolerance, thermophilization could decrease ß-diversity. For example, it could promotes already widespread warm-adapted species, increasing redundancy between communities (Figure 2-1, Dietz et al., 2020; Dupouey et al., 2002; Fischer et al., 2002). As species rarity is linked to environmental specialization (Crisfield *et al.*, 2024), thermophilization could also lower ß-diversity by removing specialized cold-adapted species (Figure 2-1.b). This process is not unidirectional: an increase in temperature can also relieve cold constraints on rare specialized warm-adapted species and increase ß-diversity. Finally, thermophilization can induce differentiation between communities by reducing the occurrence of widespread species (without causing definitive removal), as frequently observed at the beginning of an anthropogenic stress (Socolar *et al.*, 2016). These multi-faceted links between climate-change-induced thermophilization and homogenization highlight the need to disentangle the community dynamics at play (Baeten *et al.*, 2012; Gosselin, 2016).

We aimed to unveil the community dynamics (local extinction and colonization) involved in thermophilization and ß-diversity shifts. We disentangled the ß-diversity and thermophilization dynamics based on recent methods to separate the extinction and colonization processes of temporal changes in communities (Tatsumi *et al.*, 2021). We analyzed temporal shifts from 2005 to 2021 in 14,167 pairs of plots ("past" and "recent" plots form spatially proximate (<2 km) pairs of plots) of understory forest communities spanning 756 plant species in 80 forest ecoregions. These ecoregions are homogenous in environmental conditions and cover the French continental area (529,772 $km^2$; 172,080 $km^2$ of forested area). We computed the individual contribution of each species to the changes in mean thermal optima (i.e. thermophilization) and ß-diversity (i.e. homogenization) in each ecoregion (Figure 2-1.b). We partitioned these contributions into 4 community processes: extinction and colonization (decline or gain in occurrences) of cold- and warm-adapted species (relative to the baseline mean thermal 2005-2011 optimum).

In this study we aimed at understanding such community processes by responding to these questions: (1) Is there a recent significant thermophilization of forests, and what community processes drive it? (2) Is there a significant flora homogenization of forests occurring, and what community processes drive it? And (3) is mean annual temperature significantly linked to thermophilization and homogenization and to the extinction and colonization processes? Our initial expectation was that i) thermophilization is a product of both extinction of cold-adapted species and colonization by warm-adapted species, and ii) homogenization is pervasive and triggered by abundant colonization by warm-adapted species and extinction of rare cold-adapted species. We expected faster thermophilization rates in Mediterranean ecoregions because more species could be located at the warm edge of their distribution and prone to local extinctions caused by extreme (drought) events (Pérez-Navarro *et al.*, 2021).

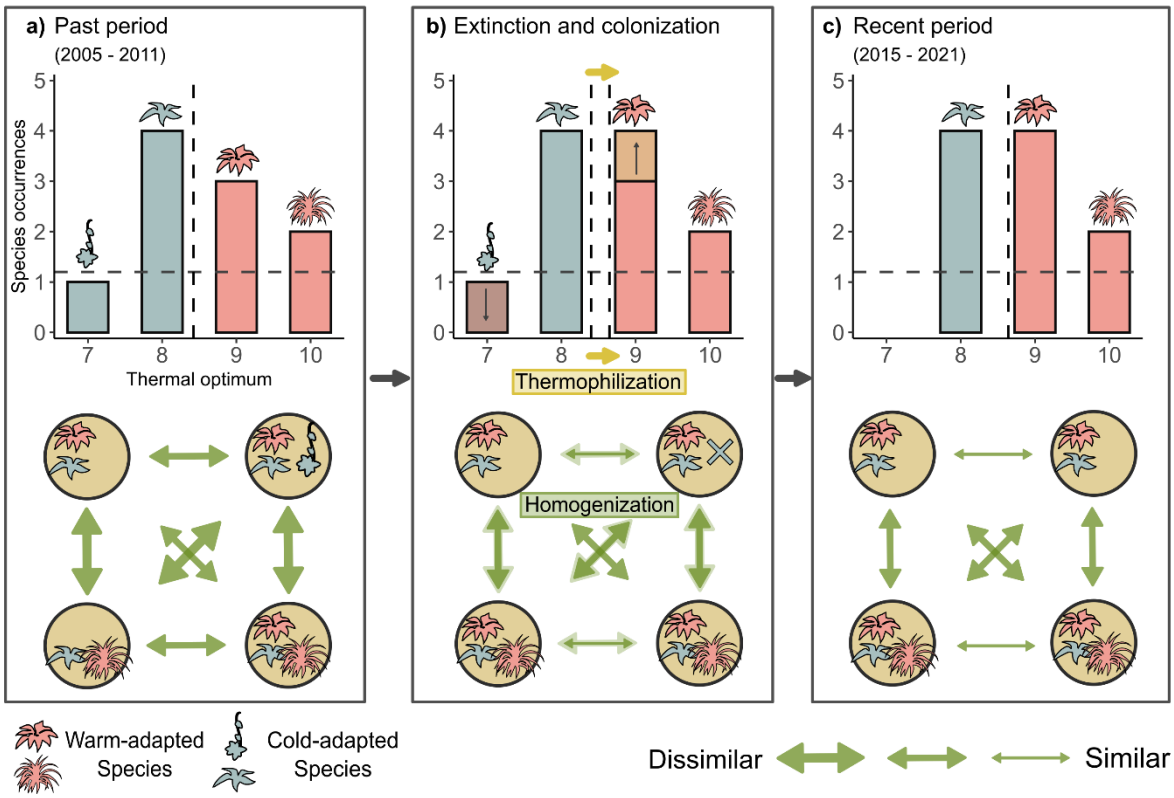


*Figure 2-1: Example of the coupling between thermophilization and homogenization under increasing temperatures*

*(a): Artificial ecoregion composed 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 because they all have unique species composition. The vertical dotted line represents the weighted mean thermal optimum of every species (of the ecoregion); the horizontal dotted line represents the threshold differentiating rare from common species.*

*(b): Example of thermophilization triggered by the spread of a warm-adapted species and the extinction of a cold-adapted species. The loss of a rare species that made the community unique triggers homogenization, and so does the spread of a common species by increasing similarity between communities (the arrow width shrinks). Thermophilization can also heterogenize communities by removing common cold-adapted species or promoting a rare or previously absent warm-adapted species (not shown).*

*(c): The resulting ecoregion with a higher mean thermal optimum and more similar communities.*

## 2.2. Materials and Methods

### *2.2.1. Study region and forest ecoregion*

The study area corresponded to metropolitan France (excluding Corsica island), including the temperate mixed forest biome, the coniferous mountain biome and the Mediterranean forest biome. The territory was divided into 83 forest ecoregions (called "ecoregions" hereafter) characterized by similar and unique combinations of climatic and soil conditions (IGN, 2013). We used these ecoregions to delineate sampling areas and study understory flora changes and diversity at a wider scale than the plot scale. As the ecoregions displayed distinct climate and soil characteristics, we assumed that the pool of species was similar within an ecoregion but differed from the pools of the other ecoregions.

Lowland ecoregions were characterized by mosaics of forest, meadow, and cropland, with a climate ranging from oceanic to semi-continental (mean annual temperature ranges from 9.4 to 13.9 °C at the ecoregion scale and precipitation ranges from 500 to 1,800 mm $yr^{-1}$). Mountainous and pre-mountainous ecoregions displayed a greater forest cover and a continental mountainous climate, except oceanic influence on the Pyrenees (mean annual temperature range 6.5 to 12.4 °C, precipitation range 400 to 2,000 mm $yr^{-1}$). The southernmost ecoregions encompassed the Mediterranean border from Spain to Italy and displayed the warmest and driest climate of European France (mean annual temperature range 11.6 to 14.6 °C, precipitation range 284 to 451 mm $yr^{-1}$) (IGN, 2013).

### *2.2.2. Plot Selection*

We extracted data from the recent protocol of the French National Forest Inventory (NFI), started in 2005. We selected the plots from 2005 to 2021. The systematic sampling of the NFI is based on 1km-by-1km grid, with one tenth of the grid nodes surveyed each year. Once the grid is completely surveyed, a new survey cycle starts, approximately 10 years later. The plots of the new cycle are not a revisit of the previous plots but a new plot proximal to the node. We extracted the mean annual temperature (MAT) of each plot from a climate model calibrated with 214 French weather stations over the 1990-2015 period (Piedallu *et al.*, 2019) and elevation from a 25-m resolution digital elevation model.

We took advantage of the spatial representativeness offered by the systematic sampling to study vegetation changes by creating a dataset balanced in sampling intensity and along environmental conditions over time. We assigned the plots from the 2005-2011 campaign to the "past" category and the plots from the 2015-2021 campaign to the "recent" category. Plots in-between these two timeframes were removed because their nearest plot counterpart from the new cycle (planned for 2022-2024) was not available yet. We also removed the plots identified as deforested at the time of the survey and the plots with less than five species with a known thermal optimum. Our analysis (described below) was performed at the ecoregion scale by pooling all the plots of an ecoregion to reduce the variability that geographically close (but not revisited) plots would have induced.

Then, we paired “past” and “recent” plots based on several criteria: (1) a distance between two plots < 2 km, (2) a time interval of 9, 10 or 11 years between plots, (3) plots located in the same ecoregion, (4) a difference in the elevations of two plots < 50 m. Criterion (1) allowed us to select plots from two NFI cycles belonging to the same node, and compensate for the low precision of the coordinates of the NFI plots (± 500m) due to private property protection laws. Furthermore, we removed three ecoregions with low numbers (N<10) of pairs from the initial 83 ecoregions.

The selection procedure yielded 14,167 pairs of NFI plots separated on average by 9.9 years (Figure 2-2), distributed in 80 ecoregions. The ecoregions had a minimum of 15 pairs and a maximum of 1,892 pairs (median 118). In the absence of true remeasurements of past surveys, the selection of geographically close plots to study vegetation changes was the best alternative, but could misestimate or detect non-existing changes (Chytrý *et al.*, 2014). However, by conducting 80 separate flora change analyses – one *per* ecoregion – we identified consistent trends across ecoregions, and averaging the results limited the risk of misinterpretation. Furthermore, 33 ecoregions had less than 100 plot pairs (Figure 2-2), so that the results from those ecoregions could be interpreted with caution. However, by weighting the means presented in Fig.3 by the number of pairs of each ecoregion, we found no significant difference in our interpretation. Therefore, the number of plot pairs in the ecoregions did not influence the results.

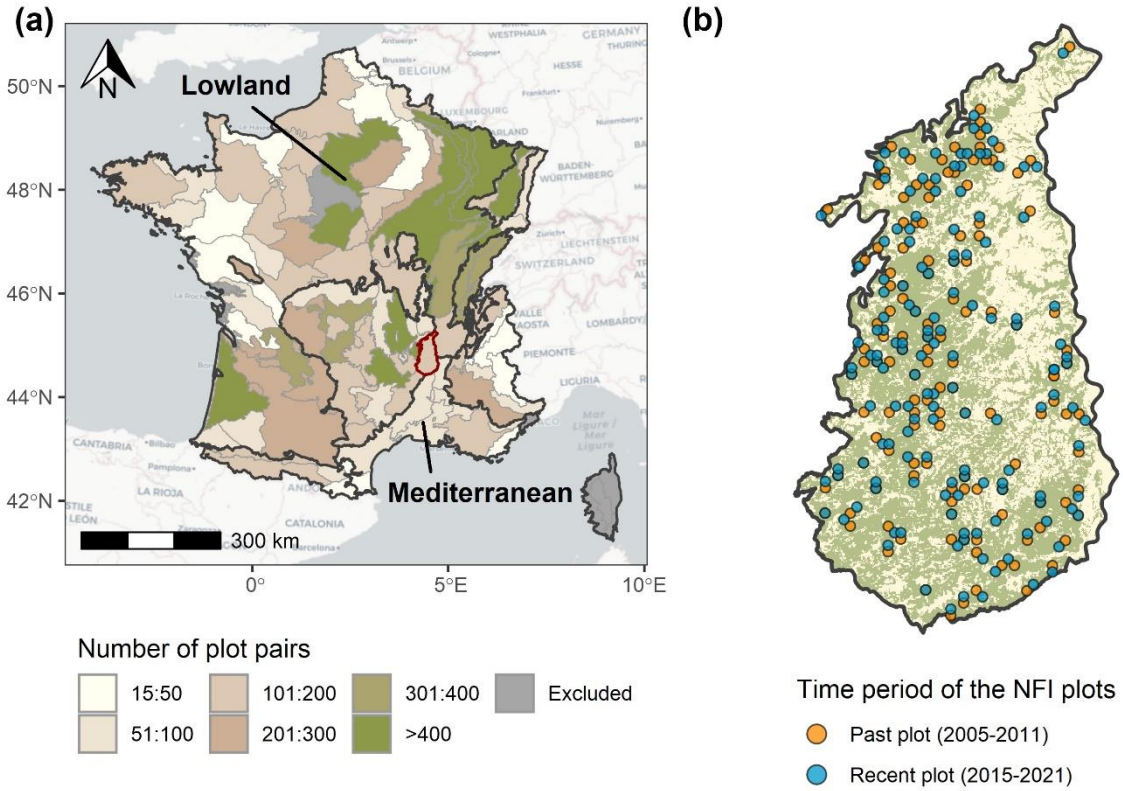


*Figure 2-2 : (a) Map of the 86 forest ecoregions of France, with a colored gradient representing the number of plot pairs. Three main biomes (lowland, Mediterranean, mountain) cluster different ecoregions delineated with bold black lines. The clusters*

*without a label are mountain ecoregions. The zoomed ecoregion in (b) is outlined in red in (a). (b) Example of the plot pair sampling design, with NFI plot localization. Some plots may overlap. Green, forested areas. Basemap credits: (OpenStreetMap contributors, 2017)*

### *2.2.3. Floristic Database*

In addition to the dendrometric, canopy cover and soil measurements, the NFI includes floristic surveys performed in 15-m-radius circles (area = 709 $m^2$). Based on these surveys, we selected vascular plants identified to the species level, and removed trees because their presence in the understory can result from forest 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 a thermal optimum from the ClimPlant V1.2 database (Vangansbeke *et al.*, 2021) to each species. The thermal optima were computed by averaging the mean annual temperature within the species distribution range 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 EcoPlant (Gégout et al. 2005) to test the sensitivity of our results to the source information of thermal optimum estimation. The EcoPlant database compiles French floristic (presence-absence) surveys that allow calibrating an optimal probability of presence along a 1km climatic grid. Ecoplant and ClimPlant are complementary: the ClimPlant database captures the whole climatic gradient of a species distribution range, whereas the EcoPlant database is limited by the French border but is built from detailed surveys and a high-resolution climatic model (Piedallu *et al.*, 2019) that enables an accurate estimation of thermal optima.

We recorded 202,866 species occurrences in the past plots, and 195,692 species occurrences in the recent plots. Out of our initial 1,622 species, we matched 756 species with a known thermal optimum from ClimPlant V1.2. These occurrences represented 78% of the total number of occurrences recorded in our plot pairs, showing a large taxonomic coverage of the thermal optimum database.

### *2.2.4. Computation and partitioning of thermophilization*

To compute thermophilization, we first defined the mean thermal optimum of the species recorded in the “past” and “recent” plots of each ecoregion. To this end, we calculated the weighted mean of the thermal optima of the species using their occurrence count in the ecoregion, independently of their local (plot scale) abundance. Then, thermophilization was obtained by subtracting the “recent” from the “past” occurrence-weighted means of the thermal optima. As our plots were not exactly separated by 10 years, we corrected the thermophilization rates by the average time difference of the plots to express thermophilization in degree Celsius *per* year ($^{\circ}C\ yr^{-1}$). This method of computing thermophilization differs from past studies using permanent plots, where changes in the mean thermal optimum are computed at the plot scale over time. Our approach did not investigate plot-scale changes (that were blurred by the semi-permanent nature of the pairs)

but allowed studying the changes in the occurrence rates of species at the regional scale under homogenous environmental conditions.

We computed the individual contribution of each 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 species $i$, $Topt_{ecoreg\ past}$ the weighted mean thermal optimum of the "past" occurrences, $occ_i$ is the count of plots where the species was recorded in the "past" and "recent" periods, and $\Sigma occ_{recent}$ is the total number of occurrences of the "recent" period. Species with equal occurrences in the two periods resulted in a $contrib_i$ of 0. Therefore, they did not contribute to the computation any further. The rationale behind this formula is that species thermal optima were assumed constant, and the number of "past" and "recent" plots were even, so that we did not expect any change in occurrences. Consequently, only changes in occurrences could alter the mean thermal optimum of an ecoregion. The term ($Topt_i$ - $Topt_{ecoreg\ past}$) represents the extent to which an individual species deviated from the mean optima of the past period of the ecoregion. Thus it measures its relative adaptation to climate relative to every present species. It is then multiplied by ($occ_{i\ recent} - occ_{i\ past}$), the change in occurrences of the individual species, divided by $\Sigma occ_{recent}$ (this allows to scale $contrib_i$ as the two periods will not have an equal number of total occurrences).

The sum of all $contrib_i$ results in the thermophilization value of a given ecoregion (see supplementary equations for a derivation of the equation). As a result, we partitioned the sums of $contrib_i$ into components that could be added to one another 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 these two components into the contributions of cold- and warm-adapted species to these components. The subcomponents depended on whether a species was 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 $Topt_{ecoreg\ past}$.

The equation resulted in an easily interpretable $contrib_i$ term. For example, the contribution of the extinction of cold-adapted species [($occ_{i\ recent} - occ_{i\ past} < 0$) * ($Topt_i$ - $Topt_{ecoreg\ past} < 0$)] was always positive, i.e. it contributed to thermophilization. The contribution of extinction as a whole could either be positive or negative as it includes the extinction of both cold and warm-adapted species (eq (1)).

### *2.2.5. Computation and partitioning of beta-diversity Changes*

In parallel to the thermophilization analysis, we computed ß-diversity using the Whittaker $\beta_w$ metric (Whittaker, 1960) for each period. The Whittaker $\beta_w$ was 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 investigating differences between multiple communities than metrics using the means of pairwise differences because it accounts for species co-occurrences and measures heterogeneity by directly assessing the proportionality between α-diversity and ecoregion diversity (Baselga, 2010; Socolar *et al.*, 2016; Tatsumi *et al.*, 2021). We did not use a metric relying on abundance because abundance is estimated based on a Braun-Blanquet scale in the NFI (Braun-blanquet, 1932) and is less reliable than presence/absence. Using abundance-based metrics can lead to both lower and higher estimates of ß-diversity. Locally abundant ubiquitous species can lead to lower ß-diversity estimates, whereas locally abundant species found in just a few plots lead to higher ß-diversity estimates. Our study mostly documented the decline of cold-adapted species, whose local abundance was most probably low for these local extinctions to happen. Therefore, we did not expect underestimated homogenization following the decline of locally abundant cold-adapted species. However, one caveat is that we cannot draw any conclusion on an increased abundance of warm-adapted species that could cause further homogenization and the removal of cold-adapted individuals.

We tested the assumption that different ecoregions displayed different species pools by comparing the $ß_w$ obtained in one ecoregion with the $ß_w$ obtained from the plots of the neighboring ecoregions. When $ß_w$-diversity included several ecoregions, it increased 2-fold, demonstrating differences in the species pools of the ecoregions.

We computed ß-diversity changes (Δß-diversity) at the ecoregion level by subtracting the $\beta_w$ of the "recent" plots from the $\beta_w$ of the "past" plots. Then, we computed the contribution of each species to this change in ß-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 these two components to obtain a unique value of contribution to Δß-diversity *per* species. For example, a species can decrease ß-diversity (homogenize) by declining if it was already rare, or by colonizing if it was an already widespread species. Conversely, colonization by a rare species or extinction of a widespread species have a positive impact on Δß-diversity (heterogenization). We summed the contributions to Δß-diversity following the same procedure as described in the previous section to obtain the contributions of declining species (extinction) and spreading species (colonization) to Δß-diversity and know whether these species were locally cold- or warm-adapted, for a total of 4 components.

We tagged species as initially “rare” or “common” based on their baseline occupancy. Species occupying less than 10% of the “past” plots of an ecoregion were labeled as initially rare; if they occupied more than 10%, they were labeled as initially common. This simple classification matched the intuitive expectation of Δß-diversity partitioning: extinction of rare species contributes to homogenization, while extinction of common species contributes to differentiation (see Tatsumi et al., 2021 – "Multiple-site variation" – for more information). This classification accounts for species that may be common in one ecoregion but very infrequent or belong to unique communities in another. By design, this definition does not represent a classification of rarity, but rather the commonness of a species occurrences in a given ecoregion during the baseline period.

This common *vs.* rare species classification allowed testing other ecologically relevant processes possibly underlying an extinction or a colonization component. We further split the 4 contributions into “common” and “rare” species subcomponents, for a total of 8 contributions.

More cold-adapted than warm-adapted species were labeled “rare” across the ecoregions. The lower baseline occupancy of rare cold-adapted species, rather than their climate preference, could have been a confounding factor of extinction; that is, rare species might decline more rapidly, creating the pattern reported in the Results section (Figure S4-4). We addressed this confounding factor by rarefying our dataset randomly so that the rare and common cold- and warm-adapted classification would display a balanced number of species and occurrences. Thus, observing the same pattern as the one reported in the main text indicates that increased chances of rare species extinction was not the sole explanation for our results (Table S2-4).

In order to have a comparable set of species and components to the set of the thermophilization analysis, the thermophilization and Δß-diversity partitionings were done with the subset of species included in the thermal optimum database ClimPlant V1.2.

We ran the thermophilization and Δß-diversity analyses and partitionings with the other two thermal optimum databases (Gégout *et al.*, 2005) and found similar results and interpretations (Table S2-4).

### *2.2.6. Null models and bootstrapping*

We created two null models to test whether changes in species occurrences were independent of the thermal optima, and to correct the analysis when the two periods had different numbers of occurrences.

To test the independence of changes in species occurrences relatively to their respective thermal optima, we ran 200 iterations of the above-described thermophilization analysis by randomizing the thermal optimum of species drawn from the species pool of each ecoregion. The 200 iterations of this analysis were averaged to create the null model. This null model (hereafter called random thermal optimum model) was used to test for

differences with the partitioning results of the original dataset. We also tested each component of this model against 0 with a Wilcoxon test. The absence of significant thermophilization in the random thermal optimum model demonstrated a link between changes in species occurrences and their thermal optima (Figure S2-1, Table S2-1).

The total number of occurrences recorded in our dataset decreased between the two periods although our sample had balanced numbers of "past" and "recent" plots. While this decrease may have been caused by true ecological factors such as climate-change-induced extinction, confounding methodological factors may also have been at play. In our dataset, more plots from the "past" period were surveyed during the growing season (53% in the "past" plots *vs.* 49% in the "recent" plot). During this period, species identification is easier, and more species are visible. To account for this potential bias, as well as to investigate Δß-diversity in a scenario where the average species richness remains unchanged, we conducted both the thermophilization and the ß-diversity change analysis by equalizing the occurrence numbers between the historical and recent periods. More specifically, for each ecoregion, we randomly removed occurrences of the period with the greater number of total occurrences to match the total occurrences of the other period. We repeated this resampling and the analysis 200 times, (hereafter called the rarefaction null model). With this stricter methodology, thermophilization was still estimated at 0.012 °C $yr^{-1}$ (s.d. 0.011), the extinction component at 0.010 °C $yr^{-1}$ (s.d. 0.07), and the colonization component at 0.02 °C $yr^{-1}$ (s.d. 0.08). The Δß-diversity value, its extinction and colonization component were -0.31 (s.d. 1.5), -1.0 (s.d. 0.90), and 0.70 (s.d. 1.0), respectively (Table S2-2).

### *2.2.7. Statistical Testing*

We tested the significant difference from 0 (or the mean of the null model) of the mean of the seven components (global value, extinction, colonization, and the four subcomponents created with the relative thermal optima of the species) for the two metrics (thermophilization and Δß-diversity) with the Wilcoxon signed-rank test (Rey & Neuhäuser, 2011). However, we chose a different reference for the test depending on the metrics and which hypothesis we were investigating. We tested the difference between the means of the thermophilization components and the means of the corresponding components of the random thermal optimum model. We tested the differences between the Δß-diversity means with 0 as our null hypothesis ("no change in ß-diversity"). Unlike thermophilization, the components were not constrained in their value (e.g. the contribution of colonizing warm-adapted species to thermophilization was strictly positive, 0 was not adequate for testing it, but its contribution to Δß-diversity could be positive or negative).

For the sake of simplicity, we tested each component of thermophilization and Δß-diversity only against 0 for 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 mean annual temperature using linear regressions. The applicability of linear regressions was checked through normality and homoscedasticity of the residuals and the independence to confounding variables, following the recommendation of Zuur et al. (2010).

We conducted our analyses in R 4.2.2 statistical environment (R Core Team, 2019), with the 'data.table' (Dowle & Srinivasan, 2020), 'ggplot2' (Wickham, 2011), 'sf' (Pebesma, 2018), 'ggpubr' (Kassambara, 2023), 'foreach' (Microsoft & Weston, 2022) 'ggspatial' (Dunnington & Thorne, 2020; OpenStreetMap contributors, 2017), and 'doParallel' (Corporation & Weston, 2022) packages. We were inspired by the 'ecopart' method and adapted the code presented by Tatsumi et al. (2021) for Δβ-diversity partitioning.

## 2.3. Results and Discussion

### *2.3.1. Extinction of species drives thermophilization*

The declines in species occurrences (15,996 lost occurrences) outweighed species expansion (8,822 new occurrences, $n_{plots}$= 14,167 pairs of plots, 2005-2011 *vs*. 2015-2021, Figure 2-3). Extinction was preponderant for the relatively cold-adapted species, and colonization was dominant for the relatively warm-adapted species (Figure 2-3). 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, Figure 2-4.a), entirely driven by extinction (Figure 2-4.a) – local extinction, defined as species with occurrences decreasing over time. Even if occurrences of species were gained (Figure 2-3), colonization did not contribute significantly to thermophilization (Figure 2-4.a) because the gains were lesser in comparison to the losses, and the gained species did not have higher thermal optima than the mean of the ecoregion to contribute to thermophilization. The use of proximate plots instead of resurveyed plots, and the sometime low number of plots within ecoregions resulted in high standard deviations. Our interpretation however, did not vary when weighting our mean values by the number of plots within an ecoregion (see Methods section). The thermophilization rate was consistent with previous studies on flora changes in temperate forest understory (Bertrand *et al.*, 2011; Dietz *et al.*, 2020; Govaert *et al.*, 2021; Martin *et al.*, 2019; Richard *et al.*, 2021), that reported rates of *ca.* 0.010 °C $yr^{-1}$, lower than the observed warming rate of *ca.* 0.026°C $yr^{-1}$ in our study region (Dietz *et al.*, 2020).

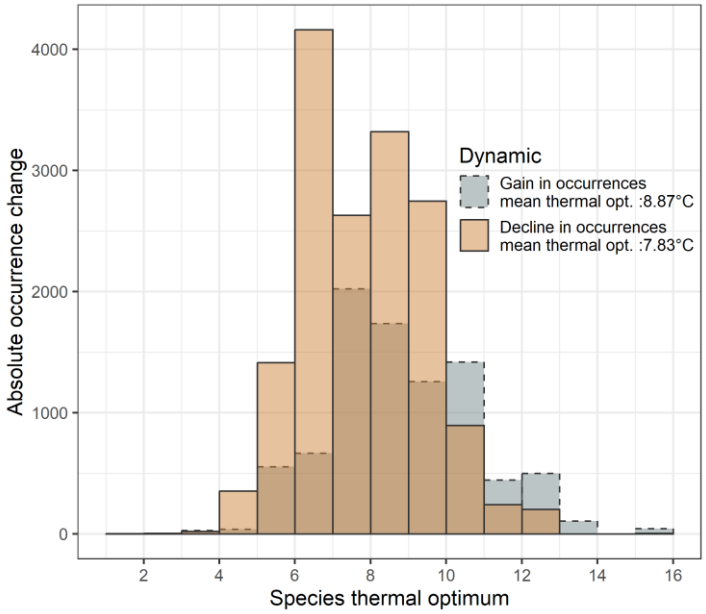


*Figure 2-3: Absolute changes in species occurrences according to their thermal optima. Changes in species occurrences between the 14,167 "past" plots (surveyed in 2005-2011) and 14,167 "recent" plots (surveyed in 2015-2021). The absolute occurrence change was computed by summing every species occurrence change between the "recent" and "past" plots separately for declining (i.e. extinction, less occurrences in "recent" plots) and spreading (i.e. colonization, more occurrences in "recent" plots) species and for each 1 °C thermal optimum class. The weighted (by absolute occurrence changes) means of the species thermal optima are also displayed. The thermal optimum of a species is estimated as the mean of the mean annual temperatures within the distribution range of a species (Vangansbeke et al., 2021).*

Thermophilization is generally interpreted as the gradual replacement of cold-adapted species by warm-adapted species, whose growth and establishment are facilitated by increased temperature (De Frenne *et al.*, 2013). We only found evidence for an extinction dynamic (e.g. decrease in occurrence rates) driving thermophilization, with a contribution of 0.012 °C $yr^{-1}$ (s.d. 0.009), equal to the total observed thermophilization rate. This result was confirmed by a null model in which the change in the occurrences of a species was independent of its thermal optimum. This null model displayed a contribution of extinction to thermophilization not significantly different from 0 (Figure 2-4.a, Figure S2-1, see "Null models" in Methods section). As our study started in 2005, a preexisting disequilibrium between flora and climate may have induced a greater contribution of extinction, induced by the extirpation of already stressed individuals in addition to those that underwent the recent warming from 2005 and onward. Our method does not distinguish these two kinds of extirpations. However, the rates we found remain indicative of the recent effect of warming on communities, as extinction of already stressed species is an integral part of thermophilization (Pérez-Navarro *et al.*, 2021). Conversely, the observed effects of colonization on thermophilization were not significantly different from the random rates of the null model (Figure 2-4.a). Our results and interpretation of extinction-driven

thermophilization were consistent when using a different species thermal optimum database (EcoPlant, Gégout et al., 2005, Table S2-1). We also rejected the hypothesis of overall decreases of occurrences or sampling pressure (Figure 2-3) as explanations for the significance of the contribution of extinction with a rarefaction model – in which the two time frames of an ecoregion have an equal number of total occurrences (Table S2-2, see "Null models" in Methods section).

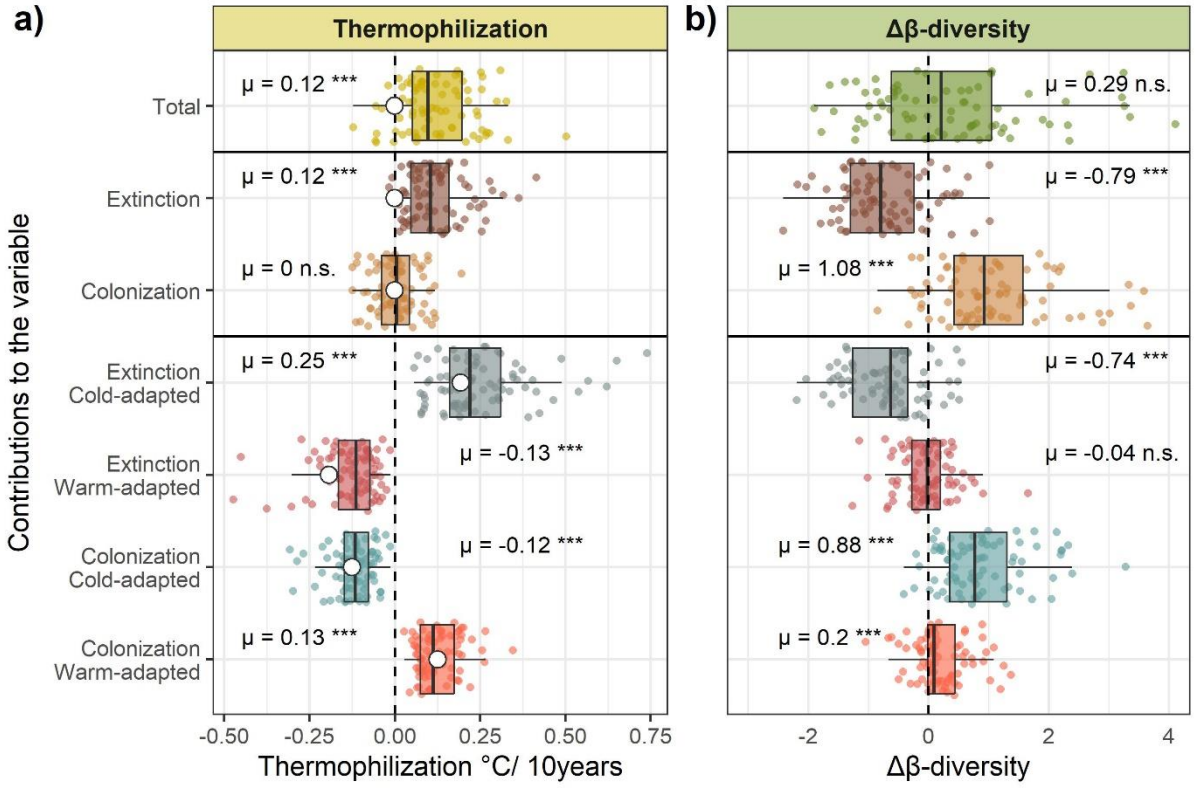


*Figure 2-4: Community dynamics partitioning of thermophilization (a) and homogenization (b). Each dot represents the values of one of the 80 ecoregions (n=80). Changes in the mean thermal optima a) of the recorded species and b) in β-diversity (thermophilization and Δβ-diversity, respectively) in the 80 ecoregions. The changes are broken up in two components – colonization and extinction – estimated from the contributions of species with more/less occurrences in the recent period. These components were subsequently divided into the contributions of relatively cold- or warm-adapted species, defined as 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 decade-1 for thermophilization, no unit for Δβ-diversity). White dots, mean value of the null thermophilization model. The statistical differences between these means and the means of a null model, obtained with a two-sided Wilcoxon test (for thermophilization) or 0 (for Δβ-diversity) are also displayed; p<0.05 (*), p<0.01 (**), p<0.001 (***). Exact P-values are available in Table S1. Boxes, 25th centile, median, and 75th centile; whiskers do not extend further than 1.5 times the interquartile range. One outlier ecoregion is not displayed in b) because a low number of plots yielded a Δβ-diversity value of -5.2.*

Extinction has already been identified as a key driver of thermophilization in drylands (Pérez-Navarro *et al.*, 2021), *via* the 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 forest biomes (Figure S2-2) over 16 years of continued warming. The Mediterranean and the warmest lowland ecoregions experienced the fastest thermophilization rates. We estimated that the contribution of extinction increased by 0.003 °C $yr^{-1}$ *per* degree Celsius rise in mean annual temperature (Figure 2-5.a), and up 0.020 °C $yr^{-1}$ in the southernmost ecoregions (Figure 2-5.a). This higher local extinction rate indicates that thermal stress under warmer climate conditions is sufficient to trigger the mortality of cold-adapted individuals or impair their establishment. This finding concurs with projections of species climatic suitability, which predict extinctions at the warm edge of the range of the species distribution, where their maximum tolerance is expected to be exceeded first (Dullinger *et al.*, 2012; Engler *et al.*, 2011; Kuhn & Gégout, 2019). Our occurrence-based analysis did not account for species abundance or interspecific competition. However, as warm-adapted species could thrive under a warmer climate, their competitive abilities also increase, and this impairs the survival of cold-adapted species (Sanczuk *et al.*, 2022; Staude *et al.*, 2022).

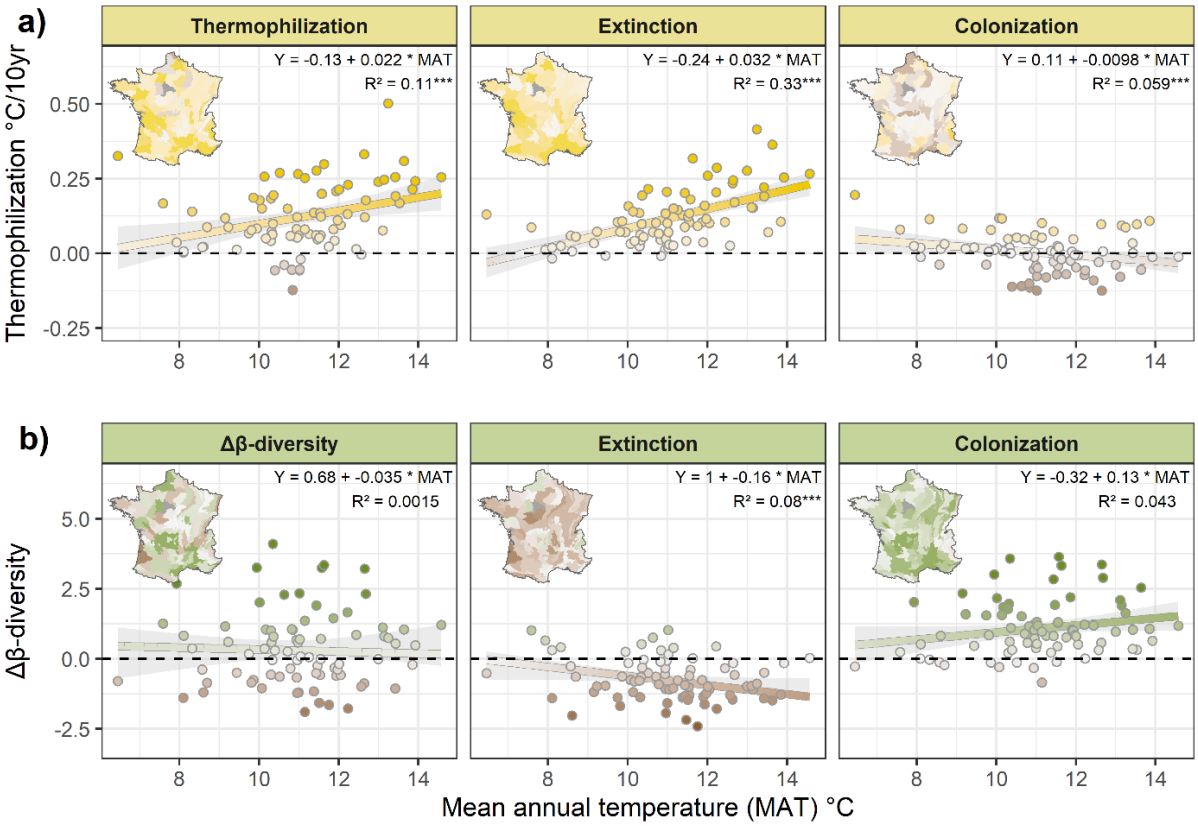


*Figure 2-5: Relationship between i) thermophilization (a), β-diversity changes (b) and their extinction and colonization components, and ii) mean annual temperature (MAT). One point represents one ecoregion, the map of the ecoregion with the associated value is displayed for each component (n=80). The color scale of the points and the mapped ecoregions are the same and refer to the Y axis (thermophilization or Δβ-diversity). The summary statistics corresponds to a linear model value ~ MAT. (***) significant MAT coefficient. One outlier*

*ecoregion is not displayed in (b), because a low number of plots yielded a Δß-diversity value of -5.2. The error band represents the confidence interval of the linear model.*

The thermophilization rates found in the present study do not match the climate warming rates over the study period (0.026 °C $yr^{-1}$ on average, Dietz et al., 2020), implying a delay between climate change and shifts in the community dynamics. This discrepancy could be explained by the absence of colonizing warm-adapted species speeding up thermophilization. As our analysis was at the ecoregion scale, our results (Figure 2-5.a) are in line with the expected colonization debt of understory plants over large homogenous climate areas (Bertrand *et al.*, 2011). The absence of colonization is likely a consequence of climate being only one of the many drivers of plant dispersal and establishment. The increase of the establishment and growth rates of warm-adapted species benefiting from climate change does not compensate for the limited dispersal capacities of plants (depending on their life cycle, seed traits, etc.) that are not fast enough to follow isotherm shifts induced by climate warming in lowland ecosystems (Lenoir & Svenning, 2015; Loarie *et al.*, 2009; Serra-Diaz *et al.*, 2014). The only ecoregions where the contribution of colonization significantly drives thermophilization (yet by no more than a third) are the mountainous ecoregions (Figure S2-2; see also Bertrand et al., 2011; Lenoir et al., 2008), where the distance to track shifting isotherms is shorter than in lowlands (Rolland, 2003) and facilitates colonization. Other explanatory factors could stem from local adaptation of plant populations (Franks *et al.*, 2014; Kubisch *et al.*, 2013; Lavergne *et al.*, 2010) and forest microclimates (De Frenne *et al.*, 2019). Temperature buffering by the forest canopy slows down thermophilization by reducing 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). Denser canopy and forest succession also exclude warm- and light-demanding species, thus slowing down thermophilization (Bergès *et al.*, 2013; Bodin *et al.*, 2013a). Therefore, our results are conservative in the face of increasing forest microclimatic buffering via canopy cover, and the exclusion of warm-adapted species by forest succession. We found a no significant correlation between thermophilization and basal area, and a significant but weak correlation (5.0% $R^2$) between thermophilization and increment canopy cover (Figure S2-4). These results confirm that the thermophilization signal is robust and not dependent on forest maturation.

### *2.3.2. Absence of large-scale community homogenization*

We expected the ecoregion to homogenize toward warmer-adapted communities, in line with the strong signal of extinction-driven thermophilization (Figure 2-1). However, homogenization was not a general trend: only 37 out of the 80 ecoregions displayed a negative Δß-diversity (Whittaker $ß_w$ diversity – see Methods section), whereas 43 showed a positive one. The mean ß-diversities of the ecoregions were 12.8 (s.d. 3.7, n=80) in the past period and 13.1 (s.d. 3.8) in the recent period. The mean Δß-diversity across ecoregions was 0.29 (s.d. 1.4, n=80) and was not significantly different from 0 (Figure 2-4.b). Whitaker ß-

diversity index is a measure of homogeneity as it allows to infer γ-diversity (the number of species of the ecoregion) by multiplying the local diversity (α) by $ß_w$.

The absence of a clear trend in homogenization did not imply a stasis of the community dynamics. We found significant contributions from the colonization of warm- and cold-adapted species relatively to the mean optimum of the ecoregion and from the extinction of cold-adapted species (Figure 2-4.b) to changes in ß-diversity. These dynamics displayed opposite directions and cancelled each other out, resulting in an overall weak signal of community homogenization. The colonization dynamics contributed significantly to heterogenization (mean effect 1.08, s.d. 0.97, Figure 2-4.b). This implies that the heterogenization effect of colonization by rare or new species outweighed the homogenization (ß-diversity decrease) caused by the increase of already widespread species. Surprisingly, this effect was explained by colonization of cold-adapted species (Figure 2-4.b, 0.87, s.d. 0.71). As no significant increase of cold-adapted species was detected in the thermophilization analysis (Figure 2-3), this positive contribution is explained by stochastic colonization by rare or previously absent cold-adapted species. The unpredictability of such events may arise from extreme but exceptional values of the dispersal distance of some species (Vittoz & Engler, 2007), dormant seeds in 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 (the total number of species in the ecoregion) is lower, so that the species partitioning methods are more sensitive to local colonization by rare species that affects γ-diversity.

Extinction of cold-adapted species – the main driver of community thermophilization (see above) – significantly contributed to homogenization (-0.74, s.d. 0.82, Figure 2-4.b). However, the extent of this contribution was comparable to the colonization effect. To better understand the contributions of extinction and colonization, we partitioned them into "rare" and "common" species contributions. Species present in less than 10% of the baseline plots were deemed rare. This further partitioning showed that the decline of rare cold-adapted species strongly contributed to homogenization (-1.73, Figure 2-6) but was mitigated by simultaneous gains in heterogeneity caused by the decline of common cold-adapted species (0.99, Figure 2-6). Although the effect of common cold-adapted species on Δß-diversity was lower, it should not be overlooked because it corresponds to species contributing to two thirds of thermophilization (Figure 2-6). Furthermore, the decline of widespread cold-adapted species offset the extinction of rare cold-adapted species by reducing α-diversity and increasing heterogeneity between plots.

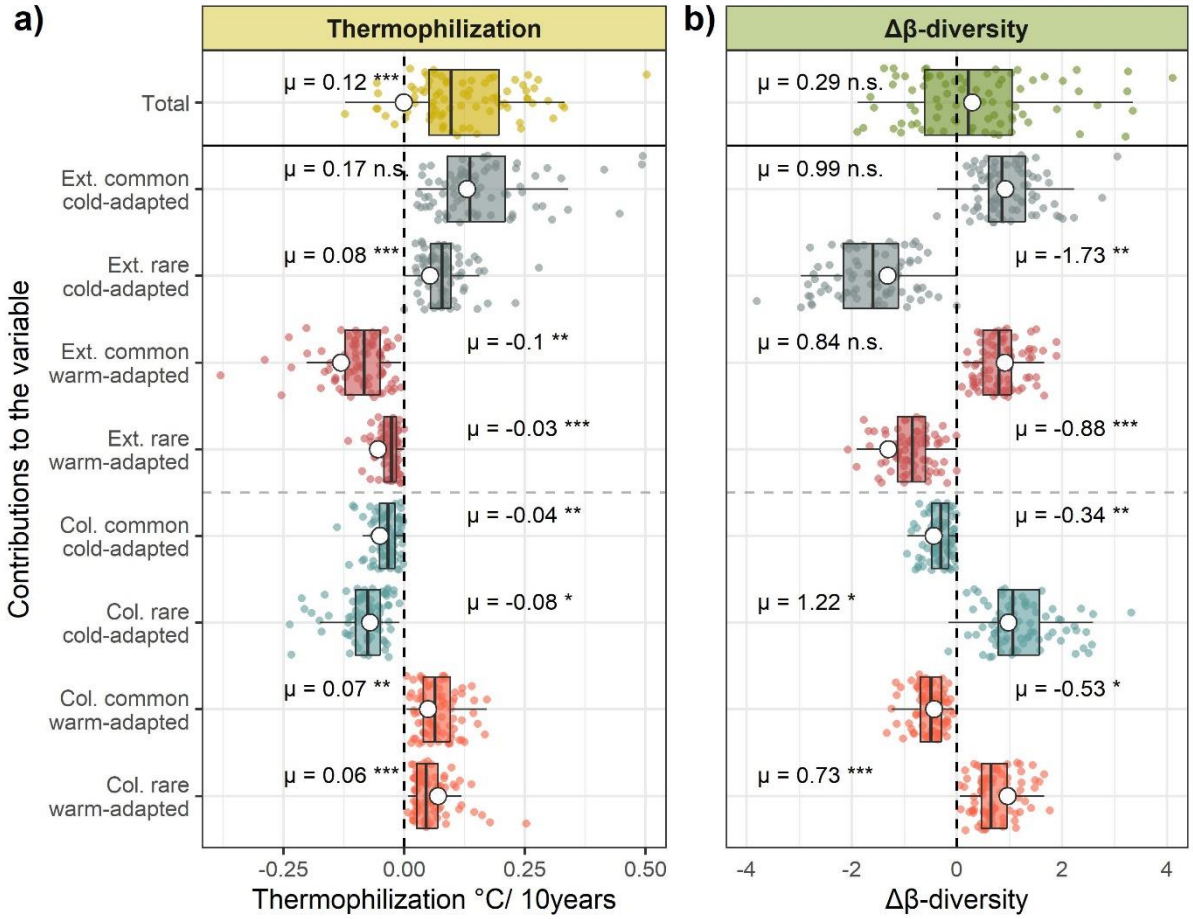


*Figure 2-6: Partitioning of the data presented in Figure 2-4. The contributions to a) thermophilization (°C decade-1), and b) Δβ-diversity (unitless) were partitioned on the basis of species declining or increasing in occurrences, of their thermal optimum relatively to their ecoregion, and whether these species were rare (baseline occurrences <10% of the plots) or common (baseline occurrences >10% of the plots). Each dot represents the values of one of the 80 ecoregions (ntot=80). The dashed gray line delineates the colonization and extinction components. The mean of each component is displayed. White dot; mean value of the thermophilization null model. The statistical difference between the null model value and the original dataset, obtained with a two-sided Wilcoxon test, is also displayed: p<0.05 (*), p<0.01 (**), p<0.001 (***). Exact P-values are available in Table S1. Boxes; 25th centile, median and 75th centile; whiskers, 1.5 times the interquartile range.*

Our results likely reflect transient community dynamics where a new anthropogenic stressor initially increases ß-diversity by reducing the occurrences of widespread species but is not acute enough to trigger definitive species extinction (as opposed to the local extinctions measured here). This first increase in ß-diversity could be temporary: all species would become 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, the number of declining rare species was higher than the number of colonizing rare species. In addition to the thermal stress imposed by climate change, populations of rare species are likely to be isolated from their source population and lack the critical size for population survival

(Leibold & Chase, 2017; Pérez-Navarro *et al.*, 2021). Competition with ubiquitous species could also play a role in the decline of rare species, but only a further analysis with abundance-based surveys and ß-diversity estimates could disentangle the local dynamics driving homogenization. We used a rarefaction null model keeping α-diversity constant to test the sensitivity of ß-diversity estimates to the sampling intensity. This model revealed that a decrease in sampling intensity increased ß-diversity, likely because common species are less sampled. Therefore, our results and the potential observation of homogenization are robust to decreases in occurrences, whether real or resulting from the sampling intensity.

The different contributions to homogenization depending on the relative thermal optima of species are indicative of the relationship between thermophilization and ß-diversity. Thermophilization is a selective process documented in the present study as a decline of cold-adapted species alongside an antagonistic effect on ß-diversity. The homogenization components, e.g. thermophilization, are correlated with the mean annual temperature of each ecoregion (Figure 2-5). The higher sensitivity of ΔB-diversity to extinction in the southernmost Mediterranean ecoregions highlights a faster turnover of communities, which causes risks of homogenization if the decline of rare and common species alike continues.

### *2.3.3. Implications for forest understory in a warming Climate*

Thermophilization is often viewed as the process that leads to communities composed of species adapted to warmer conditions (De Frenne *et al.*, 2013; Gottfried *et al.*, 2012), but our results show that it can also stem from local extinctions of cold-adapted species, with little substitution by warm-adapted species. Our study evidences a lack of persistence of understory plant species concurrent with rising temperature and exceeding the establishment and dispersal capacities of plants better adapted to warmer climates. The discrepancy between communities and climate is often referred to as a climatic debt (Devictor *et al.*, 2012). Our study illustrates that extinction-driven thermophilization is the consequence of the "repayment" of this debt (Jackson & Sax, 2010). These extinctions threaten the ecosystem services that the herbaceous layer and its diversity provide (Landuyt *et al.*, 2019; Mori *et al.*, 2018; Naaf & Wulf, 2012; Wang *et al.*, 2021).

Further research and the use of different methods could add insights to our results. The presence/absence methods used here are indicative of the large-scale changes in species composition, but they do not capture changes in local abundances. The use of abundance-based metrics could reveal ongoing homogenization through the local spread of warm-adapted species despite low new plot colonization or local hotspots by rare species that ultimately decrease the homogenization risk (Tatsumi *et al.*, 2022). Climate-driven reshuffling is not the only potential source of homogenization. Processes like nitrogen deposition, agriculture intensification, and forest succession all introduce and favor certain species and could create redundancy in communities (Danneyrolles *et al.*, 2021; Heinrichs &

Schmidt, 2017; Merle *et al.*, 2020; Staude *et al.*, 2022). These processes could act in synergy with climate change, and need to be further analyzed in future homogenization studies because they can be partly confounded in our results. Our partitioning analysis isolated the effect of the decline of cold-adapted species – a dynamic less impacted than colonization by the aforementioned process and limited the risk of misinterpretation.

Our consistent finding of extinction being the driver of thermophilization calls for increased needs to assess future biodiversity trends. In other ecosystems, where the spread of warm-adapted species can be faster than in forests, the effects of ß-diversity should keep being 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, and partitioning detected opposed dynamics hidden behind a seeming absence of trend. 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 signs of climate-induced extinctions. The question of whether increased thermophilization and the absence of homogenization are transient and respond to the current flora-climate disequilibrium will need further monitoring but remains critical to preserve biodiversity. Explicitly unveiling the community dynamics at play will strengthen our capacity to understand and predict community compositions under an accelerating warming rate.

## 2.4. Supplementary Materials

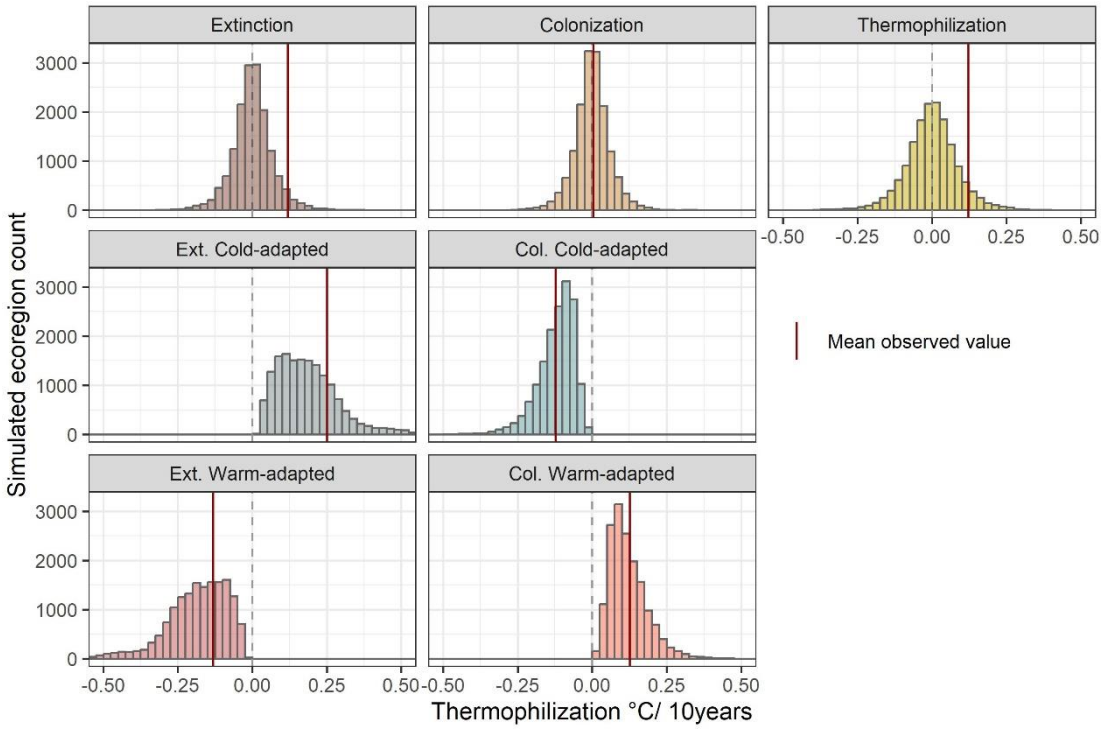


*Figure S2-1: Results of the 200 iterations of the random thermal optimum model (thermal optima randomly assigned to the species). In this figure, the runs are not averaged: the 80 ecoregions randomized 200 times are displayed. The average values of thermophilization, Δβ-diversity and their contribution of the original dataset are displayed.*

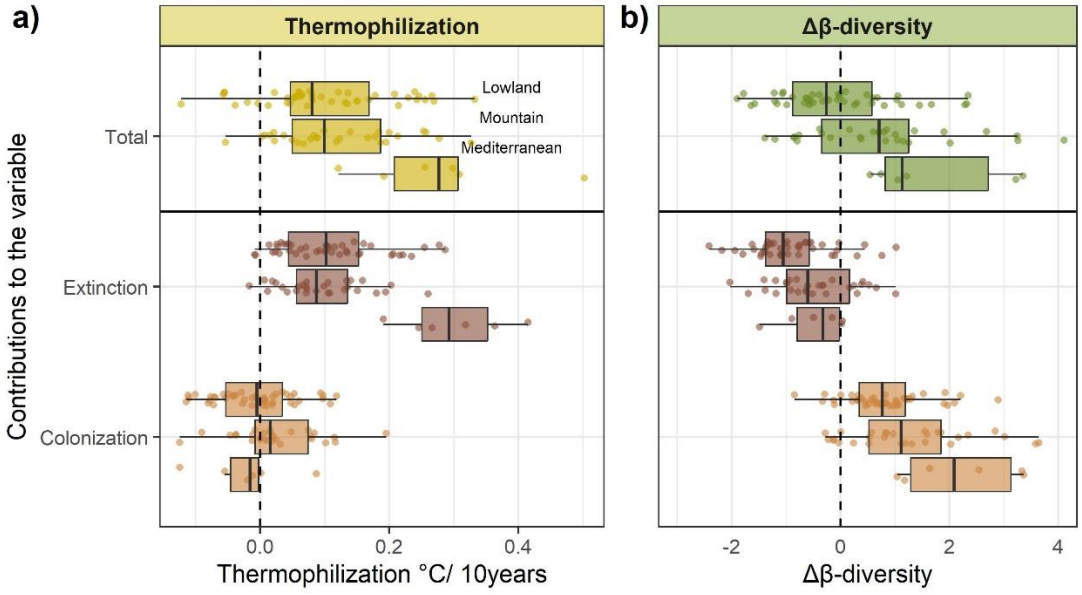


*Figure S2-2: Thermophilization and Δβ-diversity in lowland, mountain and Mediterranean ecoregion clusters (Figure 2-2). Lowland (8,271 pairs, 45 ecoregions), mountain (4,116 pairs, 29 ecoregions), Mediterranean (377 pairs, 6 ecoregions). Each dot represents the values of one of the 80 ecoregions (ntot=80).*

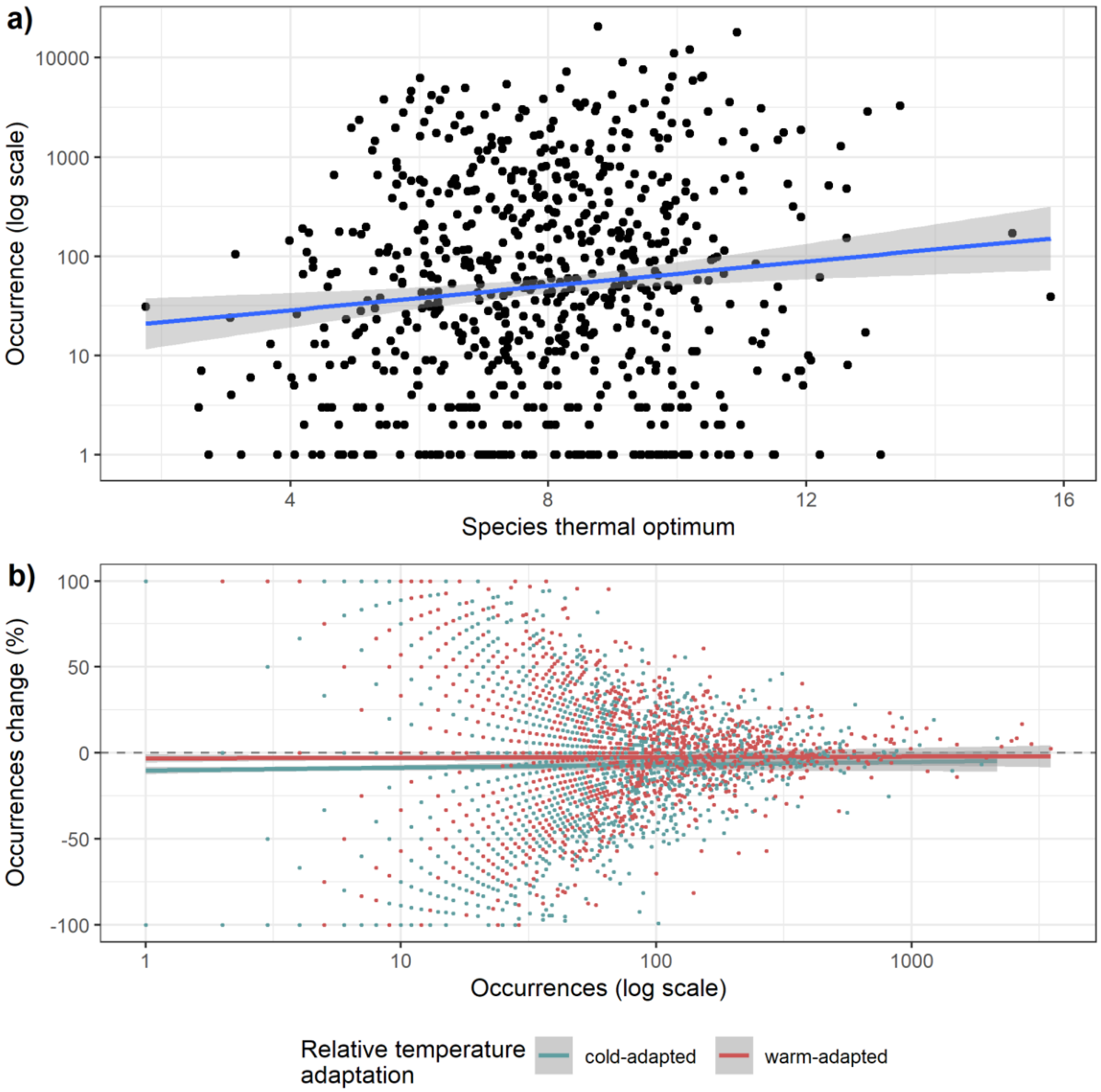


*Figure S2-3: a) Species occurrences (presence in a plot, log scale) in the entire dataset (n= 28,334 plots) in relation to their thermal optimum. The blue line is a fitted linear model log(occurrences) ~ thermal optimum and its uncertainty (error bar, confidence interval). b) Y-axis: Relative change in occurrences in each ecoregion for each species. (0% mean stable occurrences,100% a species whose occurrences are only found in the "recent" period of the ecoregion, - 100% a species that lost every occurrence between the two periods, 50% and -50 an increase or decrease, respectively, of 50% the "past" occurrences). X-axis: total occurrence (log scale). The species and the linear fit Proportion ~ log(occurrences) are separated based on whether they were classified as locally cold or warm-adapted species in the given ecoregion. The error band around the model is the confidence interval of the linear model.*

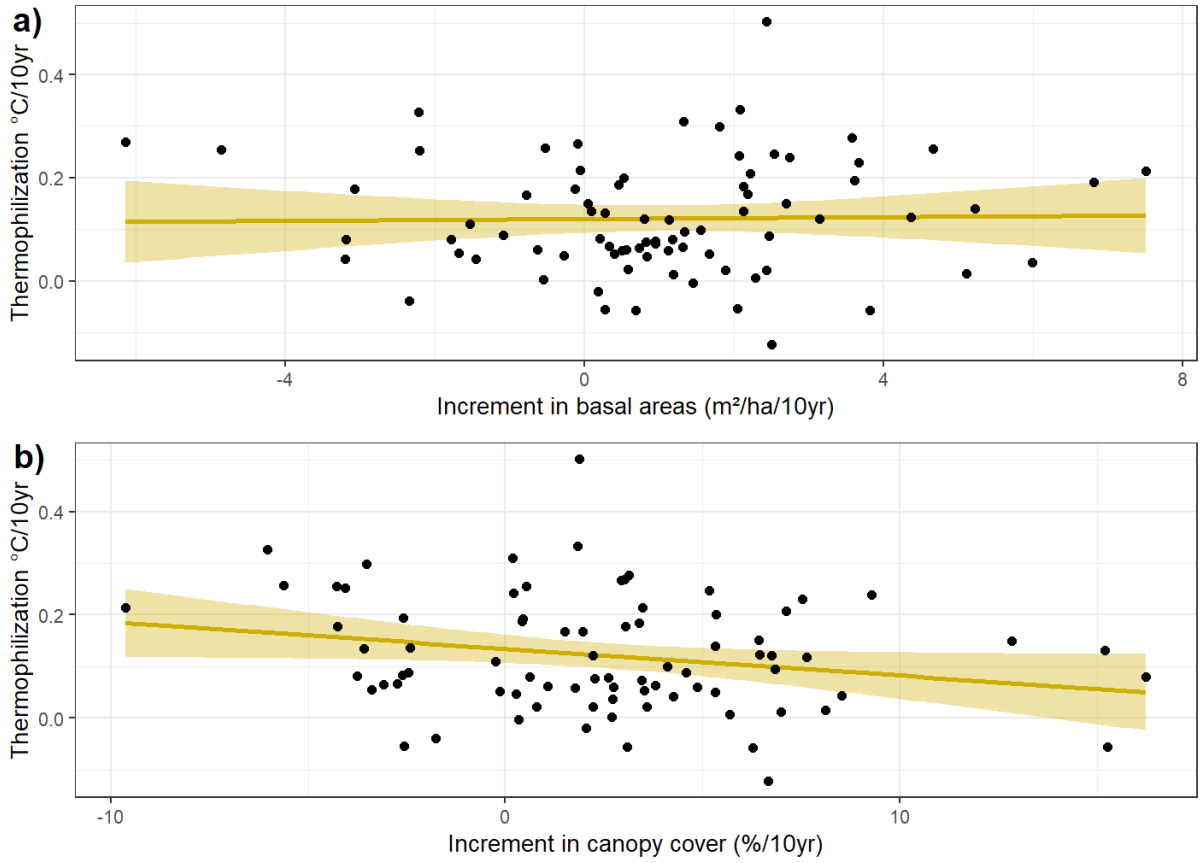


*Figure S2-4: Thermophilization of the 80 ecoregions as a function of the increment of their mean basal area (a) and canopy cover (b). The increments are computed as a difference of the mean value of basal area or canopy cover between the "recent" and the "past" plots, a positive value means an increase. A linear model and its uncertainty is displayed, the $R^2$ of 5.0% of (b) is significantly different from 0. The error band around the model is the confidence interval of the linear model.*

*Table S2-1: Thermophilization (°C/decades$^{-1}$) and ΔB-diversity and their component mean value (Value) and standard deviation (s.d) across 80 forest ecoregions. The value from the original dataset (14,167 pairs of plots) and the randomized thermal optimum null model (see methods) are displayed. The P-value were obtained with a two-sided Wilcoxon one sample test against 0.*

| ***Variable*** | ***Original dataset*** | | | ***Null thermophilization model*** | | |
|---|---|---|---|---|---|---|
| | **Value** | **s.d** | **P-value** | **Value** | **s.d** | **P-value** |
| *Thermophilization* | 0,122 | 0,11 | <0.001 | -4,13e-04 | 0,0054 | 0.583 |
| *Extinction* | 0,118 | 0,089 | <0.001 | -2,05e-04 | 0,0047 | 0.31 |
| *Colonization* | 0,00346 | 0,065 | 0.664 | -2,08e-04 | 0,0037 | 0.522 |
| *Cold-adapted extinction* | 0,25 | 0,14 | <0.001 | 0,185 | 0,096 | <0.001 |
| *Cold-adapted colonization* | -0,132 | 0,087 | <0.001 | -0,186 | 0,096 | <0.001 |
| *Warm-adapted extinction* | -0,123 | 0,061 | <0.001 | -0,122 | 0,055 | <0.001 |
| *Warm-adapted colonization* | 0,126 | 0,061 | <0.001 | 0,121 | 0,055 | <0.001 |
| *ΔB-diversity* | 0,291 | 1,4 | 0.107 | 0,291 | 1,4 | 0.107 |
| *Extinction* | -0,785 | 0,91 | <0.001 | -0,785 | 0,91 | <0.001 |
| *Colonization* | 1,08 | 0,97 | <0.001 | 1,08 | 0,97 | <0.001 |
| *Cold-adapted extinction* | -0,744 | 0,82 | <0.001 | -0,396 | 0,48 | <0.001 |
| *Cold-adapted colonization* | -0,0417 | 0,46 | 0.397 | -0,39 | 0,44 | <0.001 |
| *Warm-adapted extinction* | 0,877 | 0,72 | <0.001 | 0,542 | 0,49 | <0.001 |
| *Warm-adapted colonization* | 0,199 | 0,45 | 0.000159 | 0,534 | 0,49 | <0.001 |

*Table S2-2: Thermophilization (°C/decades$^{-1}$) and ΔB-diversity and their component mean value (Value) and standard deviation (s.d) across 80 forest ecoregions. The value from the original dataset (14,167 pairs of plots) and the randomized original dataset where occurrences are rarefied so that each time period have an equal number of occurrences. The P-value were obtained with a two-sided Wilcoxon one sample test against 0.*

| ***Variable*** | ***Original dataset*** | | | ***Rarefaction null model*** | | |
|---|---|---|---|---|---|---|
| | **Value** | **s.d** | **P-value** | **Value** | **s.d** | **P-value** |
| *Thermophilization* | 0,122 | 0,11 | <0.001 | 0,121 | 0,011 | <0.001 |
| *Extinction* | 0,118 | 0,089 | <0.001 | 0,104 | 0,0071 | <0.001 |
| *Colonization* | 0,00346 | 0,065 | 0.664 | 0,0167 | 0,0072 | 0.049 |
| *Cold-adapted extinction* | 0,25 | 0,14 | <0.001 | 0,205 | 0,0085 | <0.001 |
| *Cold-adapted colonization* | -0,132 | 0,087 | <0.001 | -0,101 | 0,0053 | <0.001 |
| *Warm-adapted extinction* | -0,123 | 0,061 | <0.001 | -0,144 | 0,006 | <0.001 |
| *Warm-adapted colonization* | 0,126 | 0,061 | <0.001 | 0,161 | 0,007 | <0.001 |
| *ΔB-diversity* | 0,291 | 1,4 | 0.107 | -0,314 | 1,5 | 0.0855 |
| *Extinction* | -0,785 | 0,91 | <0.001 | -1,01 | 0,9 | <0.001 |
| *Colonization* | 1,08 | 0,97 | <0.001 | 0,696 | 1 | <0.001 |
| *Cold-adapted extinction* | -0,744 | 0,82 | <0.001 | -0,825 | 0,77 | <0.001 |
| *Cold-adapted colonization* | -0,0417 | 0,46 | 0.397 | -0,185 | 0,4 | 0.000141 |
| *Warm-adapted extinction* | 0,877 | 0,72 | <0.001 | 0,771 | 0,75 | <0.001 |
| *Warm-adapted colonization* | 0,199 | 0,45 | 0.000159 | -0,0752 | 0,55 | 0.253 |

*Table S2-3: Thermophilization (°C/decades$^{-1}$) and ΔB-diversity and their component mean value (Value) and standard deviation (s.d) across 80 forest ecoregions. The analysis was performed with two other thermal optimum value, from the original 2005 and a 2019 analysis of the EcoPlant database(Gégout* et al.*, 2005). The P-value were obtained with a two-sided Wilcoxon one sample test against 0.*

| ***Variable*** | ***EcoPlant Thermal optimum 2005*** | | | ***EcoPlant thermal optimum 2019*** | | |
|---|---|---|---|---|---|---|
| | **Value** | **s.d** | **P-value** | **Value** | **s.d** | **P-value** |
| *Thermophilization* | 0,111 | 0,15 | <0.001 | 0,061 | 0,2 | 0.0038 |
| *Extinction* | 0,0965 | 0,085 | <0.001 | 0,072 | 0,12 | <0.001 |
| *Colonization* | 0,0147 | 0,11 | 0.11 | -0,011 | 0,15 | 0.212 |
| *Cold-adapted extinction* | 0,273 | 0,16 | <0.001 | 0,31 | 0,18 | <0.001 |
| *Cold-adapted colonization* | -0,177 | 0,12 | <0.001 | -0,238 | 0,18 | <0.001 |
| *Warm-adapted extinction* | -0,165 | 0,09 | <0.001 | -0,208 | 0,12 | <0.001 |
| *Warm-adapted colonization* | 0,18 | 0,11 | <0.001 | 0,197 | 0,16 | <0.001 |
| *ΔB-diversity* | 0,0511 | 1,2 | 0.941 | 0,0401 | 1,1 | 0.772 |
| *Extinction* | -0,715 | 0,74 | <0.001 | -0,136 | 0,61 | 0.012 |
| *Colonization* | 0,766 | 0,83 | <0.001 | 0,176 | 0,68 | 0.0422 |
| *Cold-adapted extinction* | -0,628 | 0,68 | <0.001 | -0,307 | 0,49 | <0.001 |
| *Cold-adapted colonization* | -0,0868 | 0,47 | 0.0709 | 0,172 | 0,43 | 0.00206 |
| *Warm-adapted extinction* | 0,578 | 0,55 | <0.001 | 0,24 | 0,48 | <0.001 |
| *Warm-adapted colonization* | 0,188 | 0,48 | 0.00178 | -0,0637 | 0,37 | 0.166 |

*Table S2-4: Thermophilization (°C/decades-1) and ΔB-diversity and their component mean value (Value) and standard deviation (s.d) across 80 forest ecoregions. The value from the original dataset (14,167 pairs of plots) is displayed. The value from subsets of the dataset created by balancing the number of "rare" species within the cold and warm-adapted categories (and to a lesser extend "common") is also displayed.*

| ***Variable*** | ***Original dataset*** | | | ***Even "rare" species null model*** | | |
|---|---|---|---|---|---|---|
| | **Value** | **s.d** | **P-value** | **Value** | **s.d** | **P-value** |
| *Thermophilization* | 0,122 | 0,11 | <0.001 | 0,133 | 0,11 | <0.001 |
| *Extinction* | 0,118 | 0,089 | <0.001 | 0,102 | 0,084 | <0.001 |
| *Colonization* | 0,00346 | 0,065 | 0,664 | 0,0319 | 0,059 | <0.001 |
| *Cold-adapted extinction* | 0,25 | 0,14 | <0.001 | 0,233 | 0,14 | <0.001 |
| *Cold-adapted colonization* | -0,132 | 0,087 | <0.001 | -0,131 | 0,091 | <0.001 |
| *Warm-adapted extinction* | -0,123 | 0,061 | <0.001 | -0,0975 | 0,051 | <0.001 |
| *Warm-adapted colonization* | 0,126 | 0,061 | <0.001 | 0,129 | 0,067 | <0.001 |
| *ΔB-diversity* | 0,291 | 1,4 | 0,107 | 0,391 | 1,2 | 0,0064 |
| *Extinction* | -0,785 | 0,91 | <0.001 | -0,48 | 0,8 | <0.001 |
| *Colonization* | 1,08 | 0,97 | <0.001 | 0,871 | 0,84 | <0.001 |
| *Cold-adapted extinction* | -0,744 | 0,82 | <0.001 | -0,287 | 0,57 | <0.001 |
| *Cold-adapted colonization* | -0,0417 | 0,46 | 0,397 | -0,193 | 0,44 | 0,000175 |
| *Warm-adapted extinction* | 0,877 | 0,72 | <0.001 | 0,544 | 0,48 | <0.001 |
| *Warm-adapted colonization* | 0,199 | 0,45 | 0,000159 | 0,327 | 0,49 | <0.001 |

## Supplementary equations.

We define the weighted thermal optimum of an ecoregion of the past period as follow:

$$Topt_{eco\ past} = \frac{\sum_i topt_i * occ_{i\ past}}{\Sigma occ_{past}} \quad (1)$$

Where $Topt_i$ and $occ_{i\ past}$ are the thermal optimum and occurrences in the "past" period of the species i, respectively.

$\Sigma occ_{past}$ is the sum of past occurrences of every species, can also be written $\Sigma_i occ_{i\ past}$.

We define the weighted thermal optimum of an ecoregion of the recent period as follow:

$$Topt_{eco\ recent} = \frac{\sum_i topt_i * occ_{i\ recent}}{\Sigma occ_{recent}} \quad (2)$$

Where $occ_{i\ recent}$ is the occurrences of the species I in the "recent" period.

Thus, thermophilization is defined as follow:

$$Thermophilization = Topt_{eco\ recent} - Topt_{eco\ past} \quad (3)$$

We defined the species i contribution to thermophilization with the equation:

$$Contrib_i = \frac{(Topt_i - Topt_{eco\ past}) \cdot (occ_{i\ recent} - occ_{i\ past})}{\sum occ_{recent}} \quad (4)$$

And we want to demonstrate that

$$\sum_i contrib_i = Thermophilization \quad (5)$$

We first develop (4)

$$Contrib_i = \frac{Topt_i * occ_{i\ recent} - Topt_{eco\ past} * occ_{i\ recent} + Topt_{eco\ past} * occ_{i\ past} - topt_i * occ_{i\ past}}{\sum occ_{recent}} \quad (6)$$

Then the sum of (6) is written as follow:

$$\sum_i contrib_i = \frac{\sum_i topt_i * occ_{i\ recent} - Topt_{eco\ past} * \sum_i occ_{i\ recent} + Topt_{eco\ past} * \sum_i occ_{i\ past} - \sum_i topt_i * occ_{i\ past}}{\sum occ_{recent}} \quad (7)$$

We can then simply (7) to

$$\sum_i contrib_i = \frac{\sum_i topt_i * occ_{i\ recent}}{\sum occ_{recent}} - \frac{Topt_{eco\ past} * \sum_i occ_{i\ recent}}{\sum occ_{recent}} + \frac{Topt_{eco\ past} * \sum_i occ_{i\ past} - \sum_i topt_i * occ_{i\ past}}{\sum occ_{recent}} \quad (8)$$

We can further simplify (8) to

$$\sum_i contrib_i = Topt_{eco\ recent} - Topt_{eco\ past} + \Phi \quad (9)$$

With:

$$\Phi = \frac{Topt_{eco\ past} * \sum_i occ_{i\ past} - \sum_i topt_i * occ_{i\ past}}{\sum occ_{recent}} \quad (10)$$

We thus need to prove that $\Phi = 0$, however:

$$Topt_{eco\ past} * \sum_i occ_{i\ past} = \sum_i topt_i * occ_{i\ past} \quad (11)$$

Thus:

$$\Phi = \frac{\sum_i topt_i * occ_{i\ past} - \sum_i topt_i * occ_{i\ past}}{\sum occ_{recent}} = 0 \quad (12)$$

Which leads to

$$\sum_i contrib_i = Topt_{eco\ recent} - Topt_{eco\ past} = Thermophilization \quad (13)$$

# Chapter 3. High landscape-scale forest cover favors cold-adapted plant communities in agriculture-forest mosaics.

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## Abstract

The ongoing climate warming is expected to reshuffle understory plant-community composition by increasing the occurrence of warm-adapted species at the expense of cold-adapted species. Previous studies have evidenced a warming Community Thermal Index (CTI) over time. However, data indicate that the local tree canopy can partly explain an observed lag between understory plant CTI and climate warming rates, though landscape-scale forest cover effects have not yet been investigated. Here, we test the hypothesis that the amount of forest cover in the landscape lowers local CTI.

We compared 2,012 pairs of neighboring French forest inventory plots with contrasting percentages of forest cover within a 1-km radius area (landscape forest cover). We computed the difference in the CTI of the understory communities for each pair and tested the contribution of the landscape-scale forest cover, local canopy cover, and soil conditions to the differences in CTI.

Plots located in highly forested areas (>80% in the 1km area) had an average CTI 0.26 °C lower (0.81°C s.d.) than plots in sparsely forested areas (<30% in a 1km area). Fifty percent of this difference was explained by landscape-scale forest cover. Bioindicated soil conditions such as pH and available nutrients, which correlated with cold-adapted species preferences, explained the remaining 50%.

Highly forested landscapes allow colder-adapted species to survive in given macroclimatic conditions. These landscapes meet cold-adapted species soil requirements and may cool the regional climate. Further microclimatic studies are needed to confirm the cooling capacity of landscape-scale forest cover.

**NB:** The term 'Community Temperature Index' used in the publication has been replaced with 'Community Thermal Index' for consistency throughout the thesis.

The list of species (and their characteristics) used in this analysis is available in Table A3.

Repository:

https://github.com/Jeremy-borderieux/Article_Landscape_Forest_Cool_Comm.git

## 3.1. Introduction

Climate change and land-use change are the main drivers of past and current plant diversity. These drivers and their interaction are leading to shifts in species distribution, the extinction of the most vulnerable species, and a reshuffling of existing communities (Franklin *et al.*, 2016; Kuhn & Gégout, 2019; Pecl *et al.*, 2017; Thomas *et al.*, 2004). The flora of the forest understory makes up 80% of forest vascular plant diversity and plays a key role in many ecosystem functions (Landuyt *et al.*, 2019). Likewise, understory flora is being increasingly considered in forest management decisions in the face of climate change (Blondeel *et al.*, 2021; Gilliam, 2007; Landuyt *et al.*, 2019), and in global forest conservation and restoration efforts (Stanturf *et al.*, 2014).

The influence of free-air temperature (the macroclimate) on understory communities is buffered by the cover of local overstory trees (De Lombaerde *et al.*, 2021; Godefroid *et al.*, 2006; Maclean *et al.*, 2015). Tree cover in temperate forests creates an understory microclimate characterized by cooler maximum temperatures and warmer minimum temperatures. Microclimate depends on local stand conditions, but is also driven by broader scale factors. Topography for example is an important factor that can influence temperature through elevation, aspect, cold air pooling, as is macroclimate, which is determined by drivers such as latitude, solar radiation and distance to the coast. The effect of local tree cover on the understory microclimate and species communities is increasingly under study; however, less is known about the effect of landscape-scale forest cover on understory composition.

The forest habitats in central European landscapes have typically undergone intensive logging in the past, which has resulted in the current mosaic of forest patches of different sizes. These patches, where forest understory species may persist under existing tree cover, are embedded in an extensive agricultural matrix (IES, 2013). The influence of landscape-scale forest cover on the regional climate is still under debate and is currently the subject of many studies, since forest cover at the landscape scale involves two processes pulling in opposite directions. On the one hand, temperatures may increase with increasing forest cover because a forest's albedo is lower than other land cover types like grasslands and croplands. This warming effect is most apparent in cooler seasons, when forests do not retain the snow cover and release a latent heat flux at night. On the other hand, forests have a cooling influence during warmer seasons, stemming from their higher evapotranspiration, which directly cools the air and promotes cloud formation (Bonan, 2008; Hesslerová *et al.*, 2013; Pokorny *et al.*, 2010). The growing season is a critical period for both annual and perennial cold-adapted species. One could therefore expect that landscape-scale forest cover could benefit plant species by cooling the hotter and drier (mean and extreme) conditions in spring and summer that could induce the dieback of vulnerable species. In those landscapes, the community could also be comprised of cold-adapted species because they can outcompete the warmer-adapted species located at their cold edge of their

distribution (Sanczuk *et al.*, 2022). Highly forested landscapes could also influence plant-community composition and favor cold-adapted species through other means. For example, large forest patches in central Europe historically grow on low-nutrient soils unsuitable for agriculture, and are less influenced by fertilization from nearby croplands than small forest patches (Bergès *et al.*, 2016). This is relevant as the cold-adapted species in Europe are also adapted to poorer soil conditions (Ewald, 2003). Taken together, these two characteristics increase the potential for highly forested landscapes to conserve cold-adapted species.

In this study, we investigated the role of forest cover in the surrounding landscape on plot-scale (i.e. local) plant-community composition in agricultural-forest mosaics in the temperate biome. We carried out pairwise comparisons of forest plots with contrasted landscape-scale forest cover (1km area) and used community Thermal index (CTI) as a proxy for community adaptation to climate. CTI is calculated as the average thermal optimum of the recorded species of a plot. The thermal optimum of a species is estimated from a species maximum probability of occurrence along the temperature gradient and therefore reflects the climate that the species experiences in its biogeographic area. CTI may be used to compare a species' or a community's tolerance to the warming climate; a large difference between the current climate and a species' optimum can be an early warning sign of local or regional extinctions (Kuhn & Gégout, 2019).

We hypothesized that (1) plant communities surrounded by highly forested areas would have a lower CTI than those located in landscapes with little forest cover; that (2) there would be a pure landscape-forest cover effect, which, (3) together with soil factors, would explain the differences in CTI.

## 3.2. Materials and Methods

### *3.2.1. Overview*

We used floristic surveys from the French National Forest Inventory (NFI) and a 20-meter resolution forest cover map to test the influence of forest cover in the surroundings on local Community Thermal Index (CTI). This CTI aggregated the thermal optima of every species on a given plot, thus reflecting the mean climatic preference of the community. We used pairwise comparisons to reveal differences in the CTI (ΔCTI) of geographically close plots (<5 km from each other) with contrasting landscape-scale forest cover (high vs. low forest cover, calculated within a 1-km-radius area) in a French temperate lowland forest. We then used a linear model to analyze the effect of bioindicated soil conditions, local canopy cover, distance to the forest edge, and difference in landscape-scale forest cover on ΔCTI. We tested the robustness and the relationship between ΔCTI and landscape-scale forest cover by repeating the analysis at different landscape-forest-cover thresholds to separate high vs. low landscape-scale forest cover.

### *3.2.2. Floristic surveys and landscape-scale forest cover.*

We extracted plant-community data from the French National Forest Inventory (NFI). NFI surveys are based on a 1km-by-1km grid sampling scheme. One tenth of the grid nodes (equally-distanced plots) are surveyed each year to ensure spatial and temporal representativeness for French forests. We extracted our study plots from the NFI surveys from 2005 to 2019.

Each NFI plot has a circular nested design where different variables are measured at varying radii from the plot center. The floristic surveys used in our study were performed within a 15-meter-radius circle (area = 709 $m^2$).The taxonomy of the described flora was standardized to the *Euro+ Med PlantBase* taxonomy (Euro + Med, 2006). We removed tree species and the other main woody species from our data, since the presence of trees in the understory is sensitive to management, and because woody species respond more slowly to environmental factors than do herbaceous forest species. We also removed species that had not been identified to the species level.

NFI canopy cover data is estimated at the plot level through visual observation of the light intercepted by the canopy within a 25-meter-radius circle; cover cannot exceed 100%. We extracted the mean annual temperature (hereafter MAT) for each plot from a model calibrated with 214 French weather stations (Piedallu *et al.*, 2019). We extracted elevation from a 25m-resolution digital elevation model produced by the National Geographic Institute (BD_topo).

We obtained the landscape-scale forest cover for each plot by computing the percentage of forest cover in the surrounding 1km-radius area. We selected a 1km radius to capture the immediate surroundings of the plots and to compensate for the fuzziness (± 250 m) of the coordinates the NFI provides to protect private property. This 1km radius is coherent with remote sensing studies that have shown an effect of forest cover on regional climate at a 5km-by-5km scale (Li *et al.*, 2015; Prevedello *et al.*, 2019). Forest cover data were obtained from 'BD_Foret V2', a 20m-resolution forest map (IGN, 2019a). This map was produced through photo interpretation of infrared images and adheres to the definition of a forest established by the Food and Agriculture Organization (FAO), i.e. a surface area exceeding 0.5 ha with more than 10 % tree cover. Lastly, we used the boundaries of the BD_Foret V2 map to compute the distance to the nearest forest edge for a few plots, for which the true coordinates were available (the 2006 to 2011campaign).

### *3.2.3. Calculating Community Thermal Index and soil bioindication*

We calculated CTI as the mean of the thermal optima of all the non-tree vascular plant species occurring in the plot. The species' thermal optima were extracted from the ClimPlant database (Vangansbeke *et al.*, 2021). This database provides thermal optimum estimates based on distribution atlases and the 10km-resolution 1971-2000 climate data of WorldClim v2 (Fick & Hijmans, 2017) at the European scale. The database covers the entire

distribution of the species we recorded, thus providing us with an accurate estimation of their thermal optima. For the 844 different species recorded, we obtained 508 species' thermal optima. On average, a plot hosted 13 (s.d. 7.4) species with a known thermal optimum, representing 78% (s.d. 13%) of the studied species of a plot. Species with no thermal optimum were mostly rare or endemic species.

To go beyond climate, we also selected soil pH and nutrient availability as possible explanatory variables for, differences in CTI between plots with high and low landscape forest cover. This step was critical since evolutionary adaptation may create a correlation between climate and soil preferences for plant species. For instance, cold-adapted species are generally also adapted to acidic soils (Ewald, 2003; Szymura *et al.*, 2014). The litter in cold forests is more likely to have slow biotic activity (low temperature, low nutrients conifer needles), which reduces nutrient cycling and availability (Osman, 2013). By including soil information, we were also to able to isolate the contribution of climate factors to CTI.

We extracted species pH indicator values from the EcoPlant database (Gégout *et al.*, 2005), a phytosociological database linking floristic surveys and soil analyses. We extracted species nitrogen and light requirements, respectively Ellenberg N and L, from Ellenberg et al. (1992), a large survey of expert knowledge on plant ecology. We assigned a pH indicator value and an Ellenberg N and L value to respectively 512, 429 and 453 species, encompassing 92%, 61% and 69% of the total occurrences in our dataset. We then calculated the bioindicated (inferred from the flora) pH, nitrogen availability and light at each plot by averaging the indicator values of the species present without weighting by abundance (Carpenter & Goodenough, 2014). To improve the reliability of our soil bioindication, we maximized the number of species used in our calculations by including all the species possible, even those without a thermal optimum value.

### *3.2.4. Study area, plot selection, and geographical pairing of the plots*

Our study site was located in the French temperate broadleaf and mixed-forest biome where 31% of the land cover is forested (IGN, 2019a). The climate is oceanic to continental (with larger temperature amplitudes) and the MAT ranges from 8 to 11°C (Météo France weather stations; Piedallu et al., 2019). The study area included mountain ranges, but the strict selection procedure described hereafter mainly focused on lowland areas characterized by alternating expanses of croplands, grazing land and deciduous forest patches of different sizes.

We selected NFI plots exclusive to this biome, and refined our selection with two criteria: (1) the plots had to be forested – as opposed to open land or recent clear-cuts, and (2) to ensure the quality of the CTI value, the plots had to host more than five species for which thermal optimum information was available.

The plots with more than 80% of forested area within a 1km radius (251 ha) were classified as “forested” (F) and those with less than 30% (94 ha) were classified as “non-forested” (NF). We selected pairs of “forested” vs. “non-forested” plots based on two constraints: (1) the distance between the plots was <5 km, and (2) the elevation difference was <50 m. These criteria allowed us to minimize the macroclimatic differences between plots. In order to give the same weight to each plot, a given plot was only included in one pair. We used an algorithm to maximize the number of possible pairs respecting the two constraints: we first paired isolated plots, then paired the plots with many neighbors (see the Data Availability section for codes). This process resulted in a larger sample size of paired plots, although the mean distance between the plots of a pair was not minimized.

The final dataset contained 4,024 plots arranged into 2,012 pairs (Figure 3-1.a). The mean distance between two plots in a pair was 3.6 km (see Figure 3-1.b for an example). The maximum and minimum distances between plots were 5km and 1km (NFI grid resolution), respectively. F and NF plots were similar in terms of macroclimatic mean annual air temperature, with a mean average difference of only 0.06 C° across all plots (Table 3-1). The plot-scale basal area and canopy cover differed by 2.1 $m^2$/ha and 0.6%, respectively (Table 3-1). Average pH and mean Ellenberg N values differed between the two landscape classes: they were higher in NF than in F plots by 0.8 and 0.9, respectively (Table 3-1).

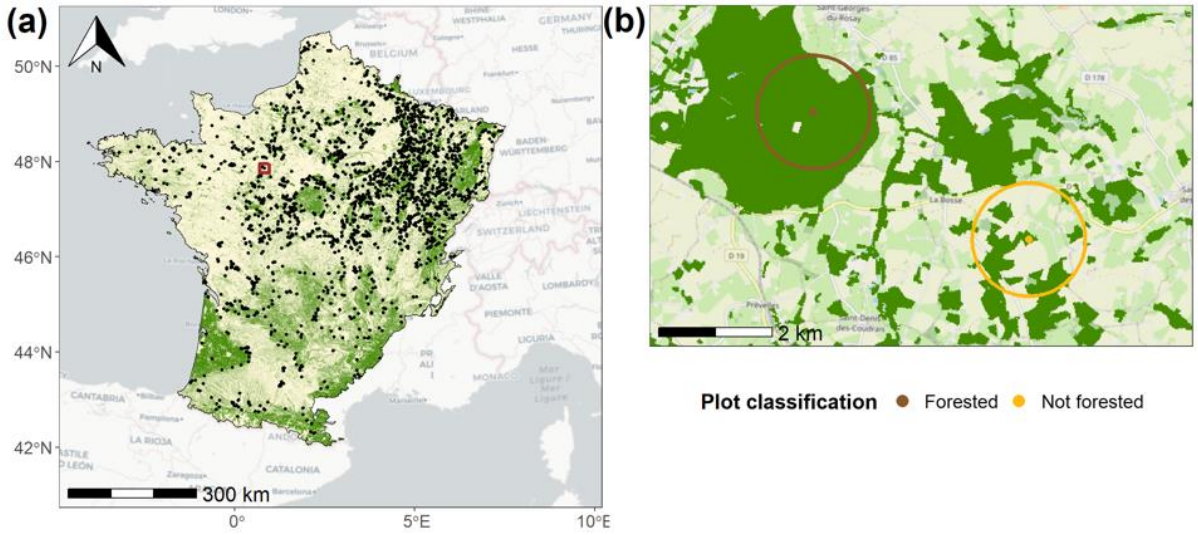


*Figure 3-1:(a) Map of the study area, dots are the centroids of each National Forest Inventory plot pair, background map is a 1km resolution forest cover map of France (IGN, 2019), brown inset indicates the location of the (b) map. (b) Close-up map of a plot pair, dots are the NFI plots, circles are the surrounding area used to compute the percentage of forest cover in the landscape, and dark green is the forest cover at a 20m resolution. Basemaps credits: OpenStreetMap*

*Table 3-1: Environmental characteristics of Forest (F) versus non-forest (NF) plots. Mean of environmental, landscape and stand variables per plot classification ($5^{th}$ and $95^{th}$ quantiles in parentheses). Landscape forest cover is estimated within a 1km radius around the plot.*

| Landscape of the plot | Number of Plots | Mean Annual Temperature (°C) | Elevation (M) | Landscape Forest Cover (Ha) | Landscape Forest Cover (%) | Mean Ellenberg N | Bio indicated Ph | Basal Area ($M^2$/Ha) | Canopy Cover (%) |
|---|---|---|---|---|---|---|---|---|---|
| Non-forested (NF) | 2012 | 11.00 (9.68-12.91) | 252 (61-633) | 62 (19-92) | 19.9 (6.2-29.2) | 5.3 (3.4-6.7) | 6.2 (4.6-7.2) | 24.7 (4.6-49.7) | 78.3 (30-100) |
| Forested (F) | 2012 | 10.94 (9.69-12.81) | 262 (71-639) | 281 (254-312) | 89.4 (80.8-99.4) | 4.4 (2.7-5.9) | 5.4 (4-6.8) | 22.8 (5.2-42.6) | 78.9 (30-100) |

### *3.2.5. Statistical Analyses*

We used a Wilcoxon ranked test to test whether the difference in CTI (hereafter ΔCTI) between the F and the NF plots was significantly different from 0.

To test whether variables other than the difference in landscape-scale forest cover (F vs NF) could explain ΔCTI, we used a linear model with ΔCTI as the dependent variable, and the pairwise differences of the other candidate factors as independent variables. The variables tested were bioindicated pH, mean Ellenberg N and L indices, year of survey, elevation and MAT. A stepwise AIC (Akaike Information Criterion) procedure determined the final model when the addition or the deletion of a variable did not reduce the AIC by more than 2 points (Akaike, 1974).

We also tested for canopy cover and distance to the forest edge, two determinants of understory microclimate (Meeussen *et al.*, 2021). Canopy cover values were only available for 1,940 pairs, and distance to the forest edge for 309 pairs. Consequently, we ran the variable selection procedure on the complete dataset (2,012 pairs) without these two variables. We then fitted the selected model with the addition of the canopy cover or the distance to the edge variable to the appropriate subset of the complete dataset. We thus obtained three models: the model for the complete dataset, the canopy cover model, and the distance-to-forest-edge model. The model formulation is summarized in equation (*1*),

$$\Delta CTI = intercept + \beta_i * \Delta_i + \varepsilon \quad (1)$$

where ΔCTI is the CTI of the F plot minus the CTI of the NF plot for each plot pair; $\Delta_i$ is the subtraction of an explanatory variable i for the same F-NF pair, and ε is the error term of mean 0, following a normal distribution. $ß_i$ is the fitted parameter testing the effect of $\Delta_i$. Any significant difference of a parameter from 0 was assessed with a Wald test. The interest of this formulation is that all the covariables ($\Delta_i$) are differences. If these covariables are set to 0, the intercept represents the effect of a difference in landscape forest cover (F vs NF) *per se*, all other environmental variables considered.

To quantify the effect the predictors had on ΔCTI, we computed effect size by multiplying the fitted parameter $ß_i$ by the mean of $\Delta_i$. For example, a difference $\Delta_i$ can be

strongly correlated with ΔCTI at the pair level, but have no effect on overall ΔCTI because $\Delta_i$ is close to 0.

We checked for residual normality, absence of collinearity among the predictors, homoscedasticity and independence from the other variables not included in the models (Zuur *et al.*, 2010). The above requirements were met for all of the models tested.

We further assessed the robustness of our results by testing different thresholds to separate the F vs. NF classes. Specifically, we ran the above-mentioned analysis (2.d, 2.e) with a varying threshold for F plots. This threshold ranged from [30% – 50%] of forest cover in the 1km radius to [80% - 100%] by increments of 5%. The NF plot classification was kept constant [0% - 30%]. This resulted in a total of eleven assessments of landscape-scale forest effects.

All analyses were performed with the R software v 3.6.1 (R Core Team, 2019) and the 'sf' (Pebesma, 2018), 'raster' (Hijmans, 2020) 'data.table' (Dowle & Srinivasan, 2020), 'ggplot2' (Wickham, 2011) and 'ggspatial' (Dunnington & Thorne, 2020) packages.

## 3.3. Results

The plots in forested landscapes (F) had an average CTI 0.26°C lower than the plots in non-forested landscapes (NF) ($P<0.001$). The difference in CTI between F and NF plots was highly variable (0.81°C s.d.). In 63% of the plot pairs, F plots had a lower CTI (the difference was negative), and for 17% of the pairs this difference was more than -1°C (Figure 3-2). Conversely, for 37% of the plot pairs, the F plots had a higher CTI, and the difference was more than +1C° for 6% of the pairs. Differences in CTI ranged from -3.5°C to +3.0°C (Figure 3-2).

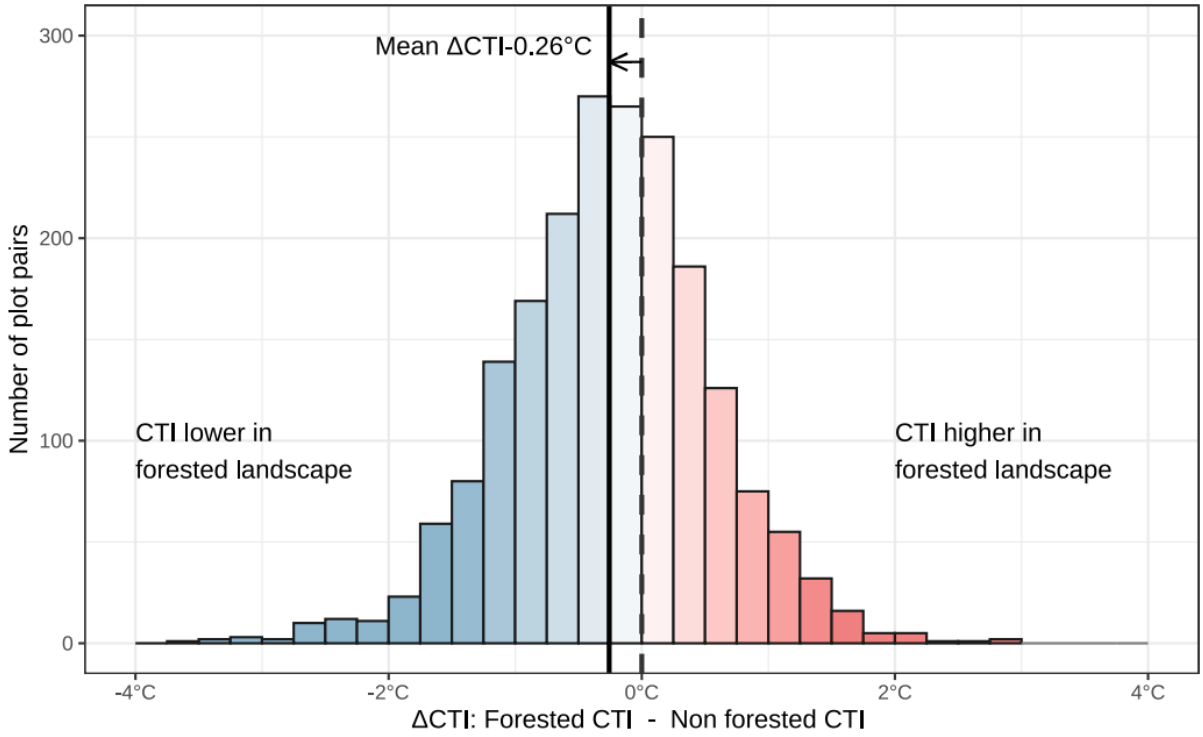


*Figure 3-2: Distribution of the difference in Community Thermal Index (CTI, °C) for all plot pairwise differences (n= 2,012). A negative difference means that the forested plot in the pair displayed a cooler CTI. The solid vertical line represents the mean of this difference, the dashed vertical line indicates no pairwise difference (0 °C).*

We found only minor effects, that is significant but negligible effects, (effect size < 0.03°C) for ΔElevation, ΔMAT, ΔEllenberg L and ΔYear on pairwise differences in CTI (Table 3-2). However, the effects of ΔBioindicated pH and ΔEllenberg N had more importance on ΔCTI: -0.24°C and 0.11°C, respectively (Table 3-2). This greater effect size was caused by the important difference between the F and NF plots for the two soil parameters (Table 3-1). In our subset of species, thermal optimum was positively correlated, with low statistical significance, with the pH indicator value (coefficient: 0.16, P<0.10, Figure S3-1, Table S3-1). Thermal optima and N Ellenberg values were not correlated (P=0.40, Table S3-1).

*Table 3-2: Linear model results relating differences in Community Thermal Index (CTI) to different drivers. Coefficients (Estimate), Standard errors, P-values, effect size of the parameter, and adjusted $R^2$ for the linear model predicting the pairwise difference in CTI. Effect sizes were computed by multiplying an estimate by the mean pairwise difference of the corresponding parameter (except for the intercept).*

| Parameters | Estimate | Std. Error | P-value | Effect size | $R^2$ |
|---|---|---|---|---|---|
| **Intercept** | -0.133 | 0.024 | $<10^{-4}$ | -0.13 | 0.122 |
| **ΔElevation** | 0.00274 | 0.00082 | $<10^{-4}$ | 0.027 | |
| **ΔMAT** | 0.279 | 0.086 | 0.0013 | -0.016 | |
| **ΔEllenberg L** | -0.199 | 0.019 | $<10^{-4}$ | 0.0074 | |
| **ΔBioindicated pH** | 0.318 | 0.025 | $<10^{-4}$ | -0.24 | |
| **ΔEllenberg N** | -0.131 | 0.02 | $<10^{-4}$ | 0.11 | |
| **ΔYear** | 0.00639 | 0.0031 | 0.038 | -0.0093 | |

We found a significant effect of local canopy cover on ΔCTI. This effect however contributed marginally (effect size=0.001°C) to lower CTI in F plots because F and NF plots had on average the same local canopy cover (Table 3-1, Table S3-2). We found no significant effect of distance to forest edge on ΔCTI (P=0.42,Table S3-3).

It should be noted that these two results do not imply that canopy cover or distance to forest edge are unrelated to CTI. Rather, they showed that the balance of those variables created by the pairwise selection successfully reduced their effect size to be negligible. We fitted our linear model with only pairwise differences as a predictor. As a result, setting the differences to 0 meant that the model compared the F and NF categories with all other factors considered to be equal. Thus, the significant intercept we found indicated a decreased in CTI in F plots not explained by any other factors than the difference in landscape classification (NF vs F, Table 3-2). The lower CTI in the F plots was robust to different F-NF classification thresholds (e.g. highly forested landscapes, Figure 3-3) but lower CTIs were especially apparent in landscapes with >70% total forest cover. Effect sizes of the other factors playing a significant role were also robust to changes in NF-F classification thresholds. The decrease in ΔCTI and the contribution of the other factors to it were linear, we did not detect a saturation effect of increasing landscape-scale cover effect.

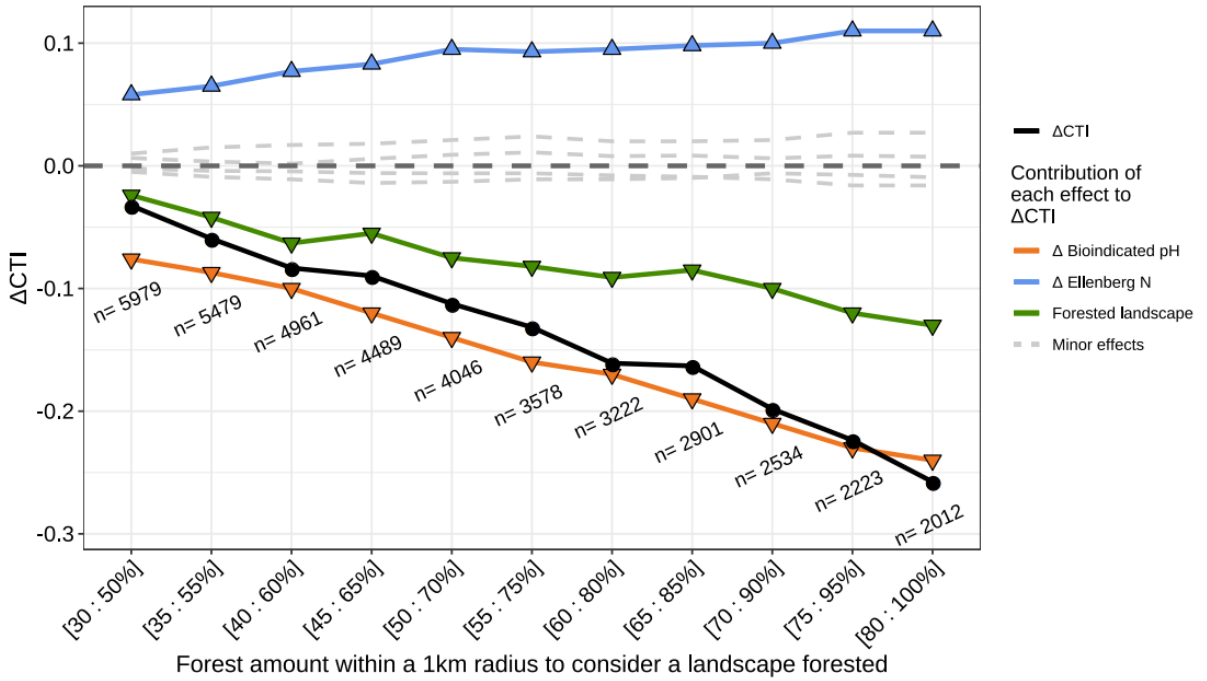


*Figure 3-3: Difference in CTI between a "forested" and a "non-forested" plot (black line) as a function of how much total forest cover surrounds a "forested" plot. A negative value means that the forested plot has a cooler community. Colored lines are the contribution (effect sizes) of the most important drivers of this difference. Effect sizes were computed by multiplying the fitted parameter of a driver to the mean of its difference between "forested" and "non-forested" plots. The number of plot pairs for each analysis is shown. Minor effects are significant predictors but with negligible effect size. Minor effects are: year of the survey, elevation, mean annual temperature and Mean Ellenberg L.*

## 3.4. Discussion

Our results indicate that the CTI of vascular plants in forest understories is 0.26°C lower in forested landscapes than in unforested landscapes. This result can be compared with the recent community thermophilization rates (increasing CTI over time) of ca. 0.1°C per decade found in temperate forest plant communities (Dietz *et al.*, 2020; Martin *et al.*, 2019; Richard *et al.*, 2021), and with recent air-temperature warming rates of ca. 0.26 °C per decade (2002 to 2018) in our study area (Dietz *et al.*, 2020). We found a significant spatial pattern for the CTI of forest understory plants equivalent to three decades of thermophilization, or one decade of macroclimatic warming. By controlling for canopy cover and distance to forest edge, we show that the lower CTI in highly forested landscapes is explained by differences in soil conditions (pH and nutrient content) that favor cold-adapted species. The structure of our sampling allowed us to observe a landscape-scale forest cover cooling on CTI *per se*.

In our study, bioindicated soil characteristics (Ph and nutrient content) drove 50% of the difference in CTI between F and NF plots (0.13°C). In landscapes with less than 30% forest cover, the understory plant communities in our plots were characterized by species requiring nutrient-rich soils and high pH, and by nitrophilous species. These species had

higher thermal optima, thus creating a significant (albeit weak) correlation between soil and climate preference (Figure S3-1, Table S3-1). On average, soil pH and mean N Ellenberg values were respectively 0.8 and 0.9 lower in F plots (Table 3-1). These differences may have affected the CTI, as an increase of 1 in a pH indicator value increases the thermal optimum of a species by 0.16 C° (Table S3-1). Correlations of thermal optimum and soil preferences have been documented before (Ewald, 2003), they may results from adaptation of to poor soils found of cold forests (Osman, 2013).

Landscape forest cover was therefore linked to local soil conditions we observed in the F and NF classes (Table 3-1). In addition, pH and nitrogen are both very sensitive to past agricultural practices. Small forests are more likely to be younger forests growing on past agricultural lands in our study region, as shown by historical maps made in cir. 1750 (Vallauri *et al.*, 2012). The smaller (and generally younger) forests display high nutrient loads because they are located on former agricultural lands, and conversely, the larger forests historically grow on less fertile soils (Bergès *et al.*, 2016). Furthermore, smaller forest patches and forest edges are more affected by horizontal fertilization from nearby fields, and by atmospheric N deposition (Bergès *et al.*, 2016). Agricultural mosaics make up most European forests' immediate surroundings (IES., 2013). Our findings could therefore be applied in most temperate European forests, where the species pool and agriculture mosaics are similar .

The remaining effect of 0.13°C at the intercept of the model represents an effect that none of the other included variables explained, and which can be attributed to the difference in landscape forest cover. The lower CTI in the forested landscapes implies that the species therein have biogeographic origin of cooler climate. Such species can be present due to legacy effects; cold-adapted species are associated with old-growth forests (Bodin *et al.*, 2013b; Dupouey, Sciama, *et al.*, 2002; Ewald, 2003). The remnants of old growth forests in France tend to be large forests that fall into our definition of forested landscapes (Vallauri *et al.*, 2012). Cold-adapted forest species also have limited dispersal capacity (Dupouey, Sciama, *et al.*, 2002). The larger forests in the landscapes with high forest cover could favor species with low dispersal capacity since connectivity is increased in large, closely-knit forest habitats (Saura *et al.*, 2014). We cannot exclude the possibility that parts of our results originate from the temporal dynamic of CTI, that is, thermophilization, as our study is set in a fixed time span and could be a snapshot of different thermophilization rates (Richard *et al.*, 2021).

In our analyses, we controlled for microclimatic effects. We carried out balanced plot pairing and added two well documented determinants of forest microclimate - immediate canopy cover and distance to forest edge - to our sub-models (Chen *et al.*, 1999; De Frenne *et al.*, 2019; Meeussen *et al.*, 2021). The effect of the landscape-scale forest cover remained significant with these controls. This indicates that landscape-scale forest cover may have a cooling effect on regional temperatures, with a subsequent effect on the understory. Forests have higher evapotranspiration than other land cover types such as cropland and grasslands,

thereby lowering the air temperature and promoting cloud formation. The forest cover can cool the regional climate during the growing season (Bonan, 2008; Hesslerová *et al.*, 2013; Pokorny *et al.*, 2010), and this service is critical for the survival of understory plants , especially cold-adapted species, during the hot summer months. Indeed, the conditions in the understory depend on local stand structure, but also on the regional climate (De Frenne *et al.*, 2021).

Our results show a large variability in CTI differences between the F and NF plots (Figure 3-2). Indeed, 37% of the F plots had a higher CTI than the NF plots. This is most likely due to sampling conditions. CTI is sensitive to changes in community composition when the number of occurrences is low. Furthermore, though we selected geographically close plots with contrasting landscape-scale forest cover to balance the environmental and stand variables of the two large classes F and NF for the whole dataset (Table 3-1), some individual pairs no doubt differed in stand conditions (e.g. canopy cover). Such conditions influence the microclimate (De Frenne *et al.*, 2013) and this contributed to the large variability in differences we found in the full sample. Finally, we do not exclude the possible impact of other landscape such as water bodies, urbanized areas, complex edge structures or topographic elements that could significantly influence climate and community dynamics (Meeussen *et al.*, 2021).

Our study relied on plant species indicator values but their use is controversial since indicators can be poorly correlated with actual measurements as they are sometimes derived from expert knowledge (Marrec *et al.*, 2022; Szymura *et al.*, 2014). We strengthened our analysis by including the pH indicator value from Gégout et al., (2005), which was calibrated with soil measurements and a floristic survey database. We maintain that it was useful to include these indicator variables in our study as a proxy for excess fertilization from nearby previous and current agricultural activities. Similarly, we combined Ellenberg L (light) values, when available, and canopy cover data (in one of the sub-model) to better account for canopy density and light conditions.

We used the mean of the recorded understory thermal optima as our response variable. The thermal optima in ClimPlant were computed from distribution maps and grids of macroclimatic temperature (Vangansbeke *et al.*, 2021). These indices are valuable to infer the biogeographic origin of a species. We interpreted cooler CTI within a highly forested landscapes as a regional cooling favoring those species. However, the potential of CTI to infer direct microclimatic temperature is limited (Marrec *et al.*, 2022), future research including microclimatic measurements or analysis of readily available weather station data, will be critical to further elucidating the climatic versus soil effects contributing to the persistence of cold-adapted species observed in our study.

Current climate warming is likely to have particularly harmful effects on cold-adapted species, which may escape regional warming by retracting to climate refugia with locally cooler and more suitable microclimates(Corlett & Westcott, 2013; Hylander *et al.*,

2022; Kuhn & Gégout, 2019). For forest species, these climatic refugia can be topographic (e.g. cold air pooling) (Stark & Fridley, 2022), dense forests (Frey *et al.*, 2016) or even hedgerows in open landscapes (Vanneste *et al.*, 2020). Our study highlights that highly forested landscapes also promote the presence of cold-adapted species, a refugia that is expected to last as the buffering capacity of forest will stay constant or increase with climate change (De Lombaerde *et al.*, 2021). Our results however should not be used to undermine the importance of small forest patches in agriculture mosaics (Valdés *et al.*, 2020). Forests in landscapes with limited forest cover harbor on average warm-adapted species, which are more suited to the warmer climate and are more resilient in the face of disturbances. that could rapidly remove the forest buffering capacity (Christiansen *et al.*, 2021; Hylander *et al.*, 2022). In addition, our results (Figure 3-3) show a linear decrease, without saturation, in CTI with increasing landscape-scale forest cover, as a result, any amount of forest cover in the landscape can have an effect on CTI. This implies that landscape-scale forest cover diversity also matters for understory plant diversity by providing a set of different soil and thermal conditions for a variety of species. Acknowledging such heterogeneity and the potential refugia of large forests is one of the keys to successful forest biodiversity conservation at the landscape scale (Hylander *et al.*, 2022). We acknowledge that part of the difference in CTI could be driven by the colonization of warm-adapted generalist species in edges and low forested landscapes. We chose to emphasize the presence of cold-adapted species in "forested" plots as they are the most threatened by climate change, and are most discussed in recent conservation literature (Hylander *et al.*, 2022). In addition, our regional cooling interpretation complement the current literature on the potential protection forest microclimate offers in the warm edge of the distribution of cold-adapted species (De Frenne *et al.*, 2021; Sanczuk *et al.*, 2022).

Current land use changes will likely drive changes in forest cover and forest distribution (Doelman *et al.*, 2018; Ellis, 2021). We demonstrate that the mean thermal optimum of an understory plant community is sensitive to the amount of forest around it. Large forest masses harbor on average more cold-adapted species, and landscapes with forest patches of contrasting sizes may provide a suite of opportunities for different species. As the climate continues to warm, guaranteeing the availability of both forested and diverse landscapes will be key to ensuring biodiversity protection and ecosystem adaptation and resilience in the near and distant future.

## 3.5. Supplementary Materials

*Table S3-1: Coefficients (Estimate), Standard errors, P-values of the linear model* $Thermal\ optimum \sim pH_{indicator\ value} + N\ Ellenberg$ *. The model was fitted with 243 species recorded in the dataset of 4,024 plots.*

| Parameters | Estimate | Std. Error | P-value |
|---|---|---|---|
| Intercept | 7.11 | 0.594 | $<10^{-4}$ |
| pH indicator value | 0.161 | 0.0826 | 0.0527 |
| N Ellenberg | -0.0460 | 0.0543 | 0.398 |

*Table S3-2: Coefficients (Estimate), Standard errors, P-values, and effect size of the parameter of the canopy cover model fitted with 1,940 pairs. Effect sizes were computed by multiplying an estimate by the mean pairwise differences of the corresponding parameter (except for the intercept).*

| Parameter | Estimate | Std. Error | P-value | Effect size |
|---|---|---|---|---|
| Intercept | -0.131 | 0.024 | $<10^{-4}$ | -0.13 |
| Δ Elevation | 0.00293 | 0.00083 | $<10^{-4}$ | 0.028 |
| Δ Mean annual temperature | 0.281 | 0.087 | 0.0013 | -0.016 |
| Δ Ellenberg L | -0.173 | 0.022 | $<10^{-4}$ | 0.0069 |
| Δ Bioindicated pH | 0.316 | 0.026 | $<10^{-4}$ | -0.24 |
| Δ Ellenberg N | -0.117 | 0.021 | $<10^{-4}$ | 0.094 |
| Δ Year | 0.00555 | 0.0031 | 0.077 | -0.008 |
| Δ Canopy cover | 0.00136 | 0.00063 | 0.032 | 0.00083 |

*Table S3-3: Coefficients (Estimate), Standard errors, P-values, and effect size of the parameter of the distance to the edge model fitted with 309 pairs. Effect sizes were computed by multiplying an estimate by the mean pairwise differences of the corresponding parameter (except for the intercept).*

| Parameter | Estimate | Std. Error | P-value | Effect size |
|---|---|---|---|---|
| Intercept | -0.186 | 0.083 | 0.026 | -0.19 |
| Δ Elevation | 0.00251 | 0.0019 | 0.2 | 0.026 |
| Δ MAT | 0.175 | 0.19 | 0.36 | -0.0063 |
| Δ Ellenberg L | -0.219 | 0.049 | $<10^{-4}$ | -0.0053 |
| Δ Bioindicated pH | 0.342 | 0.065 | $<10^{-4}$ | -0.29 |
| Δ Ellenberg N | -0.192 | 0.052 | $<10^{-4}$ | 0.18 |
| Δ Year | 0.0133 | 0.02 | 0.51 | -0.0032 |
| Δ Distance to the edge | -0.000143 | 0.00017 | 0.41 | -0.046 |

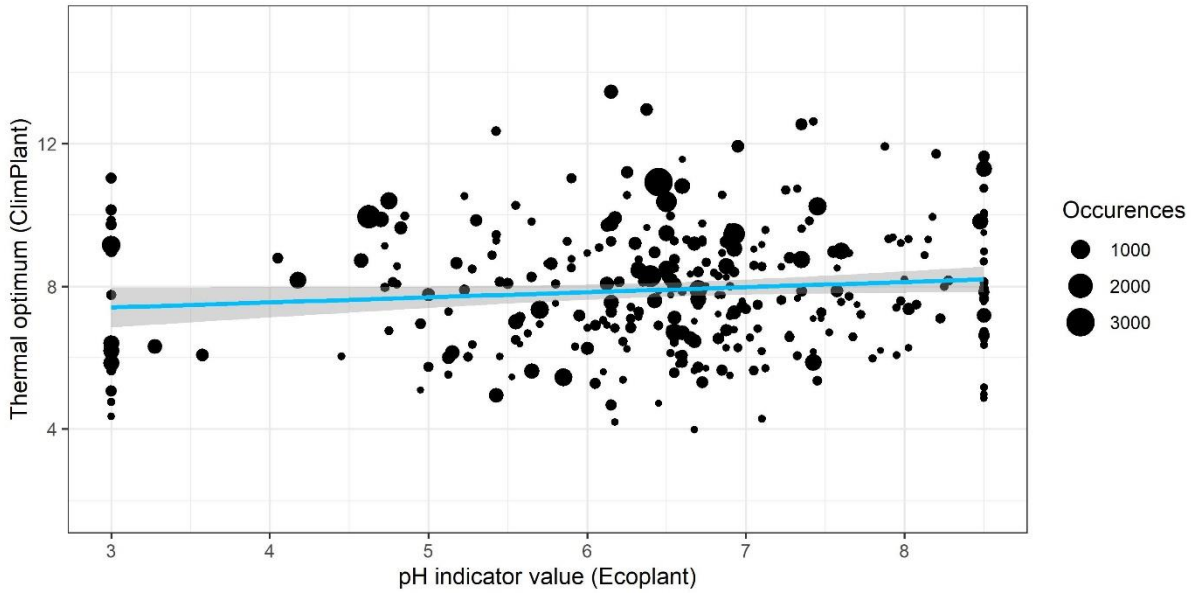


*Figure S3-1: Thermal optimum of a species as a function of its pH indicator value. The occurrence of a species in the dataset (n= 4,024) is represented by the size. The blue line represents a fitted linear model and its error. (coefficient= 0.142, P-value=0.0613).*

# Chapter 4. Topoclimate buffer floristic diversity from climate in temperate mountain forests.

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## Abstract

Microclimates strongly influence the composition and diversity of forest plant communities. Recent studies have highlighted the role of tree canopies in shaping understory thermal conditions at small scale, especially in lowland forests. In mountain forest, however, the influence of the coarser topoclimate created by topography is ought to also influence plants' perceived temperature. Understanding how such factors interactively affect understory temperature is key to identify stable refugia that could shelter cold-adapted forest specialist species under climate change.

Here we report on growing season understory temperatures using 48 loggers in contrasting topographic features of a mid-range mountain valley spanning from 475 m.a.s.l. to 1203 m.a.s.l. in the Vosges Mountains (NE France). We disentangle the relative importance and the effects of topography vs. forest canopy in determining local temperatures. We then evaluate how topography and canopy-induced variation in temperature drive plant community composition and richness in 306 vegetation plots distributed across the studied mountain valley.

Our results show that topography outweighed canopy cover in explaining growing season understory temperatures. The daily mean temperature of the growing season in south-facing ridges was 1.5 °C (CI: ± 0.88 °C) warmer than shaded valley bottoms, while dense canopies cooled temperatures by 0.5 °C (CI: ± 0.48 °C) compared to open canopies. Topoclimate explained community composition as much as elevation and was the only significant predictor of species richness. Cold topoclimates harboured 30% more species than average. This increase in species richness was explained by an increase of cold-adapted species, both forest specialist and generalist species.

*Synthesis*. Our findings highlight a stronger role of topography (compared to canopy cover) on community composition in mountain forests via topoclimatic cooling of north-facing slopes and valley bottoms. The importance of topographic features to explain temperature cooling and diversity underpin their role as present and future microrefugia.

The list of species (and their characteristics) used in this analysis is available in Table A4.

Repository: https://github.com/Jeremy-borderieux/Article_microclim_vosges.git

## 4.1. Introduction

The study of topography influences on vegetation has fascinated ecologists for more than 150 years (Johnston et al., 1848), and has further gained in relevance in the context of the 21st century climate warming (Ashcroft, 2010; IPCC, 2021b; Lenoir *et al.*, 2017). Species distribution and climatic conditions are often modeled at a coarse resolution (typically 1 km or coarser), and thereby fail to capture local variation of climate at fine grains: for instance the topoclimate shaped by topography and the microclimate shaped by forest canopy (Bramer *et al.*, 2018; De Frenne *et al.*, 2021; Kemppinen *et al.*, 2023). Given that these factors can attenuate warm macroclimate temperatures, the study of the relative effects and interactions between topography and forest canopy are key to identify potential areas of climate stability in a warmer future (Ashcroft, 2010; De Frenne *et al.*, 2021; Haesen, Lenoir, *et al.*, 2023).

Variation in aspect can create contrasting topoclimates as slopes oriented to the equator receive more solar radiation. As a result, southwest-facing slopes in northern hemisphere mountains display warmer mean temperatures, longer growing seasons and shorter snow cover durations (Ashcroft *et al.*, 2008; Davis, Synes, *et al.*, 2019; Rita *et al.*, 2021). The physical properties of air also interact with topographic features such as hydrological basins, valley bottoms and sinks, and create local areas of cold and dense air pooling that decouple local conditions from the regional climate (Gudiksen *et al.*, 1992; Pastore *et al.*, 2022). The topoclimate created by these features interacts with the microclimate induced by forest canopies and jointly determines the understory temperature experienced by forest organisms. Canopy shading and evapotranspiration lead to a buffering of summer temperature, warmer winter temperature due to insulation but an overall decrease of temperature throughout the year (De Frenne *et al.*, 2021; Zellweger, Coomes, *et al.*, 2019). This buffering is apparent and well documented in temperate lowland forest, but its relative importance in contrast to elevation and topography is less known, and evidence has not reached consensus (Macek *et al.*, 2019; Vandewiele *et al.*, 2023).

Canopy cover cooling of understory temperature can have important effects on forest communities. This is evidenced by the increases of the average thermal optimum of the species present (a proxy of species' affinity to climate) in forests where canopy was opened (De Frenne *et al.*, 2013; Dietz *et al.*, 2020; Richard *et al.*, 2021) and where warmer understory temperatures are predicted (Zellweger *et al.*, 2020). This sheltering of cold-adapted species by a dense canopy needs to be compared with topography in mountain forests, as topographical refugia are likely to offer long-term buffering of temperature. Topographic refugia also harbor colder-adapted flora and host populations of species outside their expected climatic range (Ellis & Eaton, 2021; Finocchiaro *et al.*, 2023; Macek *et al.*, 2019). Understanding the characteristics of the sheltered species can also bring new insights, an increase of forest generalists for example demonstrates that topoclimate can mimic understory conditions of dense forests.

Here we assessed the effects and relative importance of elevation, topography and canopy cover on *in situ* measured understory temperatures and plant community composition and richness. After accounting for the elevation gradient, we specifically asked: (1) Does topography (aspect and topographic positions) outweigh canopy in explaining understory temperature, (2) does topography and canopy-induced variation in microclimate determine community richness and mean thermal optimum? (3) Are plant characteristics such as habitat preference and climatic affinity related to specific microclimates?

## 4.2. Materials and Methods

### *4.2.1. Study Area*

Our study region (221 $km^2$) is delineated by the basin of the Thur River, located in one of the southmost valleys of the Vosges Mountain range in France (Figure 4-1). The Vosges are characterized by a continental climate with harsh winters and short and stormy summers. Its mean annual temperature ranges from 6 °C to 10°C and precipitation ranges from 800 to 2,000 mm $year^{-1}$(period 1970-2000, Météo France weather stations IGN, 2013). Located at the south-west of the Vosges, the study region is on the warm and dry end of this gradient (IGN, 2013). Forests cover 76% of the Vosges, which transitions from mixed oak stands and monospecific *Picea abies* stands to mixtures of *Picea abies*, *Abies alba* and *Fagus sylvatica* while elevation increases IGN, 2013). The soil of our study region is mostly shallow loam and sand with coarse elements. The most acidic soils are found at higher altitude because of the dominance of needles in the humus and the lower temperature at mountaintops (IGN, 2013; Piqué *et al.*, 1994; Thomas *et al.*, 1999). The topography is highly variable, with an elevation ranging from 400 to 1424 m.a.s.l (but forest occurrence stops past 1250 m.a.s.l) with high topographic heterogeneity (Figure 4-1).

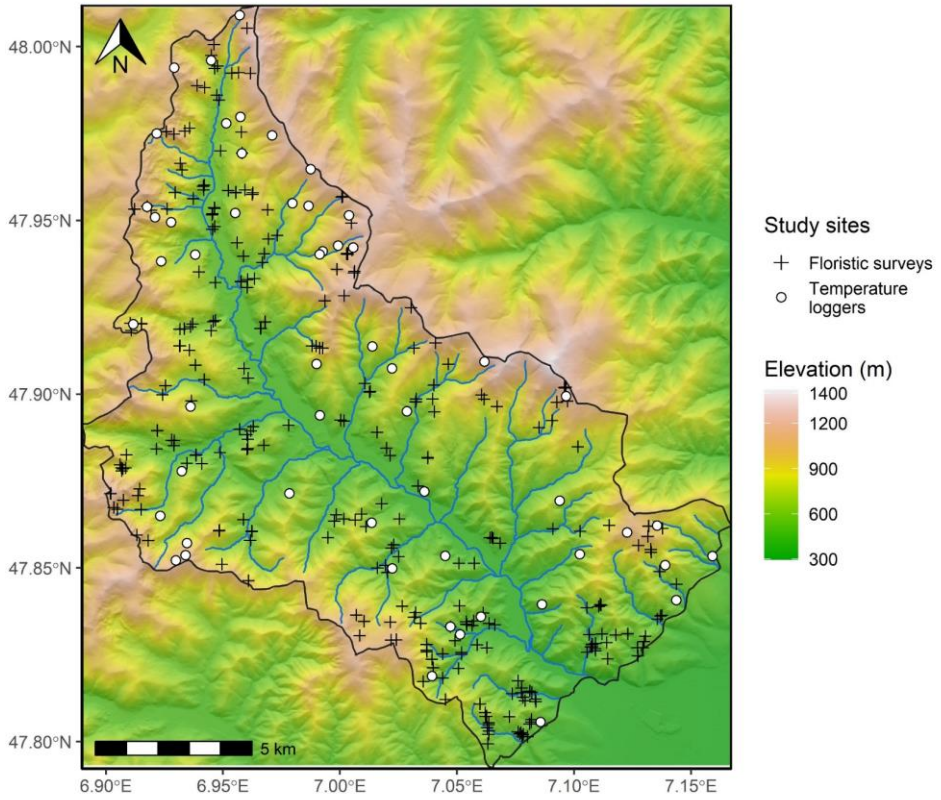


*Figure 4-1: Map of the study area (black outline) with the location of the temperature loggers (white circles) and the vegetation plots (black crosses). The colored scale represents elevation above sea level, in meters, obtained from a 25-m spatial resolution digital elevation model. Hillshade effects have been added to visualize the terrain. The inset shows the Vosges Mountain range (grey) and the location of the studied valley (black point) in western Europe.*

### *4.2.2. Temperature Predictors*

We used 25-meter resolution digital elevation models to extract elevation (m.a.s.l.), slope and aspect and to calculate topographical indices, heat load and topographic position (IGN, 2017). We handled spatial data with the 'raster' and 'sf' package (Hijmans, 2020; Pebesma, 2018), all the later mentioned analyses were carried on with R.4.2.2 (R Core Team, 2019). We used 'ggplot2' and 'ggspatial' packages for data visualization (Dunnington & Thorne, 2020; Wickham, 2011). We computed the heat load index (McCune & Keon, 2002) using the 'spatialEco' R package (Evans & Murphy, 2021). The heat load index ranges from 0 to 1 (least to most incoming solar radiation) contingent on the slope orientation and shading from nearby topographic features. The topographic position index is the relative position of the cell in the shortest trajectory between a ridge and a drainage basin end, ranging from 0 (valley bottom) to 1 (ridge, Piedallu et al., 2023).

We obtained the 'tree cover density' from the 2018 product of the Copernicus monitoring service as proxy for local canopy closure (Copernicus, 2018; Sannier et al., 2023). This product consists of a 10-meter resolution percentage of canopy presence within the pixel (ranging from 0 to 100%) and was successfully used before to model microclimate

buffering by canopy (Haesen et al., 2021). This product was correlated with our field measurements of canopy closure (see below, 2.3 Temperature sampling). We rescaled this product to match the 25-m resolution of our other maps using bilinear interpolation (Hijmans, 2020). We rasterized (25-meter resolution) a 20-meter precision map of French forest to create a mask of the forested area of our study region, in order to limit our analysis and temperature projection to the forest of the region (IGN, 2019a).

### *4.2.3. Temperature Sampling*

We created a stratified sampling scheme to capture forest understory microclimate variability (Lembrechts *et al.*, 2021; Schweiger *et al.*, 2016). We created 8 elevation strata (spanning 20 m intervals) separated by 102 m ranging from [468 - 488] to [1184 - 1204] m a.s.l., aimed to control for the main driver of temperature in the study area, that is the lapse rate (Lembrechts *et al.*, 2021). Inside each of these strata, we defined 8 types of plots: 4 plots of lower and higher than 90% of canopy cover (the median in our study area) with a south or a north-facing slope (defined as lower or higher than 0.75 heat load index). These 4 plots had moderate topographic position indices (between 0.2 and 0.8) and slope (10° < slope < 25°) as not to cofound their effects with the canopy cover and heat load effects. Additionally, we defined 2 plots with contrasting topographic position indices (lower than 0.2 and higher than 0.8) under high canopy cover and moderate slope. We lastly defined 2 plots with contrasting slopes: on flat (slope < 10°) and one steep (slope > 25°) under high canopy cover and moderate topographic position.

Of the initial 64 theoretical plots spanning the 8 strata, only 59 of the defined situations occurred, mostly because we lacked low topographic position indices (valley bottom) in high elevation classes. We randomly selected one pixel for each plot and stratum located in public forests. We repeated this random drawing 10,000 times and kept the set of plots that maximized the mean minimum distance between plots to reduce spatial autocorrelation.

We established the 59 temperature loggers in May 2021 and recorded their location with a GNSS receiver (Trimble TDC600, accuracy= ± 2 m undercover). We placed every logger in public forests because of legal constraints (public forest makes up 80% of the forested area), with no constraints regarding accessibility. We measured canopy closure (0-100% by a visual observation in a 25-meter radius around the logger, this measure was significantly correlated with the remote sensed map of tree density ($R^2$ of the linear relationship = 30.0%). We also estimated canopy cover with a planar picture of the canopy by means of a smartphone placed on top of the logger and the '*Glama*' application (Tichý, 2016). Plots tagged as low canopy cover were placed accordingly by selecting sites with less than 50% canopy closure as computed by '*Glama*'. The visual observation canopy closure measurements (25-meter radius) was significantly correlated with the remote sensed tree density (Figure S4-1), but a weak and non-significant correlation was found with the picture analyzed by '*Glama*' (Figure S4-1).

We recorded air and soil temperatures with TMS-4 loggers (resolution= 0.0625 °C, accuracy= ±0.5 °C) protected with a radiation shield (Wild *et al.*, 2019). The loggers recorded temperature every 15 minutes until August 2022. Here we only used air temperature 15 cm above the soil surface, the most representative of what understory plants experience. We cleaned the time series with the '*myClim*' R package (Man *et al.*, 2023). We calibrated the loggers beforehand for a range of -20 °C to +40 °C by placing them in a freezer and drying oven along with a T-type thermocouple (accuracy= ±0.2 °C). From the recorded period, we focused on the growing season, from 01/04/2023 to 15/08/2023, as it is the most critical period for plant growth. Out of the 59 loggers, 11 were either malfunctioning, stolen, destroyed by animals or displayed erroneous values and were discarded. We checked the capacity of our final sample to cover the variability of our study region following the PCA-based approach of Lembrechts *et al.*, (2021). Our sampling was also able to cover the variability of the valley (except for extreme values of low canopy cover and the unusual valley bottoms of high elevations), the loss of loggers was evenly distributed over plot type, except for the low canopy cover that suffered the most losses (Figure S4-2).

### *4.2.4. Floristic and Species characteristic dataset*

We compiled floristic surveys performed (during the growing season) by students and professors covering soil and climatic transect of the region between 2009 and 2022 (average year= 2015.6). All plots were surveyed for all vascular plant species in the herb layer (smaller than 1 m) and their percentage ground cover was visually estimated. We had 306 floristics surveys in total across the study region. Floristic surveys were performed in 20 x 20 m squares (400 $m^2$) with the GPS position (recorded with built-in tablet GPS; accuracy= ± 10 m) as the center. We used this position to extract elevation, heat load index, topographic position index and canopy cover for every survey. We harmonized taxonomy to the TaxRef V13 standard (Gargominy, 2022). We focused on herbaceous species in the analysis to focus on spontaneous community dynamics (e.g., trees, and to a lesser extent shrub, are mostly the result of the presence of nearby mother trees and forest management).

We used the thermal optimum species' value from ClimPlant V.1.2 (Vangansbeke *et al.*, 2021). These thermal optima are computed from the mean annual temperature within the range of species obtained from Europe-extent distribution atlases. Out of the 348 unique recorded species, 30 were assigned a thermal optimum value, covering 90.0% of the occurrences of the whole floristic dataset. We averaged the thermal optimum of every species (without weighting for abundance) of a given survey to obtain the Community Thermal Index (hereafter CTI), which quantifies the thermal preference of the whole community (Borderieux *et al.*, 2023; Vangansbeke *et al.*, 2021). We calculated species richness of a plot as the number of recorded species whether they had an associated thermal optimum in the database or not. By doing so, we wanted to include less common species that were not included in ClimPlant so that our specific richness is representative of the species pool of our study region. We also assigned a pH optimum value obtained from a

bioindication database to each species (Gégout *et al.*, 2005), and averaged (not weighted by abundance) it to obtain a bioindicated pH per plot.

We used the EuForPlant regional list of forest plant species (Heinken *et al.*, 2022) to assess species habitat affinity. We assigned to each species one of the following affinities: (1.1) species of closed forest (1.2) species which occur in forest edges and openings (2.1) Species which primarily occur in forests but also found in cultural landscapes and forest remnants (2.2) species of open habitats that occurs in forest exclusively through opening and early succession. We excluded species of open vegetation (classified "O") because of their low number of occurrences (42). In total, 274 species were assigned to an affinity class, covering 85.7% of the occurrences.

### *4.2.5. Microclimate Modelling*

We aggregated the 15-minute frequency time series of the recorded temperature of the growing season 2022 to daily mean and maximum temperature. First, we removed values lower than the $5^{th}$ centile of the day and values higher than the $95^{th}$ centile to avoid biasing results due to logger malfunction or a brief burst of sunshine on a logger. We then averaged the mean or maximum daily temperature to obtain one unique value per logger, the mean daily and maximum daily temperature of the growing season.

We used a linear model to predict mean and maximum daily temperature of the growing season with elevation, heat load index, topographic position index and remote sensed canopy density as explanatory variables. We preferred remote-sensed canopy cover over the *in situ* measurements which allowed us to map the temperature models over the entire study area, and thus infer the understory temperature of floristic surveys (mostly without canopy closure records). We also fitted two linear models with the field measured canopy closure (25 m radius observation and planar photography) instead of the remote sensed one in order to test different methods of canopy closure estimations (Table S2, Table S3). The exceed in warming due to radiation can be amplified when canopy cannot intercept light, thus, we tested an interaction between heat load index and canopy closure, and kept it in the final model if found significant (Davis, Synes, *et al.*, 2019).

The mean understory temperature model ($R^2$= 92.2%) allowed us to map the contribution of elevation (i.e., lapse rate), map the topoclimate (heat load index and topographic position) and the microclimate (canopy density) separately to the mean understory temperature (Figure 4-2). We projected the lapse rate by using only the intercept and the elevation parameter. We projected the contribution of topography cooling compared to the warmest situation (heat load index and topographic position index equal to 1) assuming a median canopy cover (90%) and using the two topographic indices. We projected the contribution of canopy cover by multiplying its parameter to the tree density product, this projection is however extrapolated for the 20% of pixels with a canopy closure lower than 79%.

### *4.2.6. Flora Composition Analyses*

The soil of our study region can display very different nutrition status and acidity, which can impact both the richness and composition of a community (Degen et al., 2005; Koerner et al., 1997; Zellweger et al., 2015). In addition, soil pH is also negatively correlated with elevation. To account for soil acidity, we first fitted a linear model to predict species richness and CTI with bioindicated pH as the only predictor. These models had a significant $R^2$ of 32.6% and 21.5%, respectively. We then summed the mean species richness or CTI to the residual of the corresponding bioindicated pH model to obtain the corrected value. The corrected values allow comparison between communities with bioindicated pH considered equal.

We used a linear model to predict the corrected species richness and CTI with the contribution to mean understory temperature of elevation, topoclimate and microclimate as predictors (the unit of every predictor is thus °C). The parameters of these two models (species richness and CTI) are shown in Vegetation plots harbored on average 19 herbaceous species (s.d. 10.7), the mean community thermal index (CTI) was 7.8 (s.d. 0.55). pH was strongly correlated with CTI ($R^2$=28.3%) and species richness ($R^2$=32.6%). More acidic soils had less diverse and cold-adapted communities. We accounted for this relationship by extracting the residual of a linear model predicting CTI or species richness with pH as the sole predictor (see methods). After accounting for soil effects, elevation-induced change in temperature was the main predictor of CTI, but it did not significantly explain species richness (Table 4-2). The microclimate was not a significant predictor in any of the two models (Table 4-2). Topoclimate was the sole significant predictor of species richness, and it significantly explained CTI. The contribution of topoclimatic cooling to the explained variability of CTI (4.64%) was comparable to the explained variability by elevation (4.6%). We centered the latter flora analysis around topoclimate cooling as canopy cooling did not significantly explain the species richness or CTI.

Table 4-2. We discretized our results to better illustrate the control of the significant predictors of the model. We split the 306 surveys into three classes with an equal number of surveys, distributed in “cold”, “intermediate” and “warm” classes. We tested the difference in species richness and CTI between these classes with Wilcoxon rank-sum tests (Rey & Neuhäuser, 2011).

We tested the assumption of normality and homoscedasticity of the residuals of the microclimatic model, the species richness and CTI model following (Zuur & Ieno, 2016), and we tested the significant difference from 0 of the estimated parameters with a Wald test. We partitioned the variance of the predictors of all the models with the ‘*modEvA’* package (Barbosa *et al.*, 2013)

## 4.3. Results

### *4.3.1. Environmental determinant of the understory temperature*

The growing season (GS) temperature of 2022 was above average (mean GS temperature=11.6 °C, mean GS temperature of the period 2005-2020=13.2°C, Markestein whether station (1184 m a.s.l), (Météo France, 2024)), as a result, the mean daily temperature of the understory (15 cm above the soil surface) was 14.6 °C and spanned between 11.9 °C to 17.5 °C for the higher (1203 m a.s.l) and lower (475 m a.s.l) elevation sensors, respectively. The mean daily maximum temperature of the GS was 19.3 °C and reached a maximum of 24.7 °C for the lowest elevation plots. Elevation was the primary driver of mean temperature variability, with a lapse rate estimated at -0.68 °C $100m^{-1}$ (Table 4-1). The heat load index– contingent on aspect and slope – was the second driver of mean temperature, which can vary up to 1°C between low and high radiation slopes (Table 4-1). Topographic position had a lesser control on temperature, the mean temperature was 0.56° C lower in the bottom of a valley compared to ridges (Table 4-1). Lastly, remotely sensed canopy closure cooled understory temperatures. An increase of 20% of total canopy cover resulted in a decrease of 0.57° C (Table 4-1). The lapse rate explained 87.4% of the variability in mean temperature, the topographic factors (heat load and topographic position index) 3.95%, and canopy cover accounted for 0.82%. The $R^2$ of the linear model was 92.2%.

The same predictors except for topographic position were significant in the mean daily maximum temperature model. The heat load index had a higher contribution in the maximum temperature compared to the mean temperature model, daily maxima varied for 3.3°C between low and high heat load indices (Table S4-1).

Canopy cover visually estimated in a 25-meter radius was not significant in predicting mean temperature (Table S4-2). Immediate canopy cover (smartphone photography) above the logger explained significantly mean temperature with an interaction with heat load index, low immediate canopy cover in high radiation slopes displayed warmer mean temperature (Table S4-3).

*Table 4-1: Estimated parameters, their standard error and p-values of the predictors included in models of the daily mean growing season temperature. The range of the predictors in the calibration dataset and their effect size on the temperature (range * estimate) are displayed. The percentage of explained variation per type of predictor is included. P-values were obtained with a Wald test on parameters. Heat load and topographic position have no units, refer to the methods for their calculation.*

| Predictor | Type of predictor | Estimate | Standard error | Range | Effect size (°C) | Explained variation (%) | P-value |
|---|---|---|---|---|---|---|---|
| **Intercept (°C)** | | 21.1 | 1.11 | | | | <10-4 |
| **Elevation (m a.s.l)** | Elevation | -0.00684 | 0.000311 | 475 : 1203 | -4.98 | 87.4 | <10-4 |
| **Heat load index (n.u)** | Topoclimate | 1.53 | 0.333 | 0.335 : 0.951 | 0.945 | 3.95 | <10-4 |
| **Topographic position (n.u)** | Topoclimate | 0.656 | 0.276 | 0.147 : 1 | 0.56 | 3.95 | 0.0220 |
| **Canopy cover (%)** | Microclimate | -0.0272 | 0.0115 | 79.0: 100 | -0.57 | 0.817 | 0.0229 |

Every predictor of the mean temperature model is spatialized and allowed to project it on the forested areas of the study region on a 25m resolution map (Figure 4-2). We also mapped the individual contributions of elevation, topoclimate (heat load index and topographic position summed) and canopy cover (i.e., microclimate) in the study area. We represented topoclimate as a cooling effect compared to a baseline location of a south-facing valley top (heat load index =1, topographic position=1) (Figure 4-2.b). The baseline for canopy cooling of temperature was 0% canopy closure (as pixels displayed the whole 0-100% range), however the range of microclimatic cooling from our model is 79% to 100% (80% of the pixel, Figure 4-2.c). We observe strong effects on understory temperatures caused by steep spatial difference of elevation, topography and fine-grained canopy cover. We also used this map and model to predict the mean understory temperature, and the contribution of the three components above described for further community composition analyses.

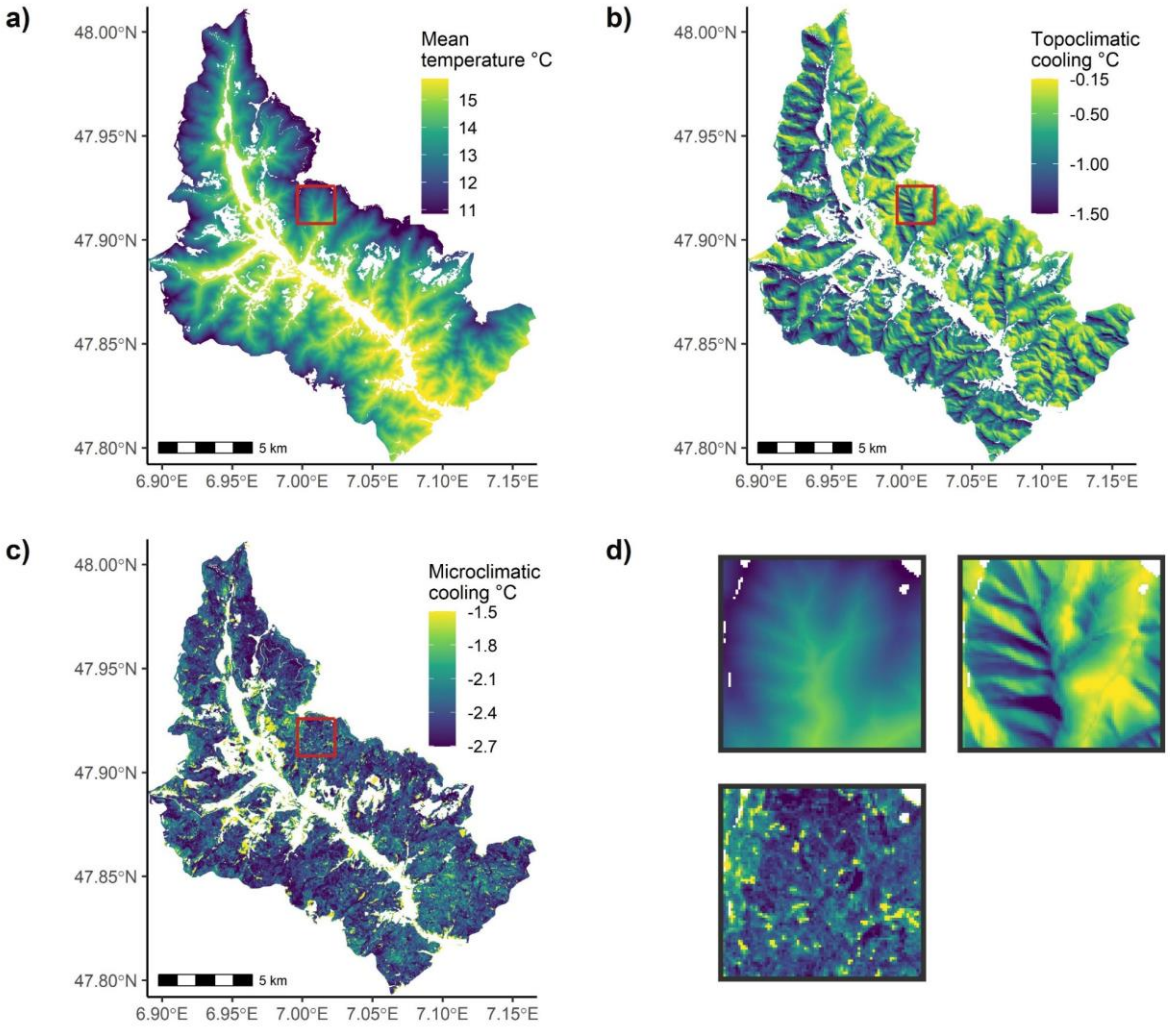


*Figure 4-2: a) Elevation induced change in mean growing season understory temperature of the growing season (lapse of -0.68°C 100 m$^{-1}$), assuming a canopy closure of 90% and no effect from topography. b) mean understory temperature cooling induced by topography (heat load and topographic position, i.e. topography) assuming an average canopy cover (90%), compared to the warmest situation (south-facing ridges). c) mean understory temperature cooling induced by canopy closure (i.e. microclimate) assuming no effect from topography. We restrained the minimal cooling to be -1.5°C, however it some pixels displayed lower values up to 0°C due to low to no canopy closure. d) 2 km per 2 km zoomed inset of the red square of the other panels, their color gradient corresponds to the color scale presented in the other panels a-c, respectively. Blank pixels represent land covers other than forests or forest outside of the study region. Linear model $R^2$: 92.2%.*

### *4.3.2. Determinants of the floristic composition*

Vegetation plots harbored on average 19 herbaceous species (s.d. 10.7), the mean community thermal index (CTI) was 7.8 (s.d. 0.55). pH was strongly correlated with CTI ($R^2$=28.3%) and species richness ($R^2$=32.6%). More acidic soils had less diverse and cold-adapted communities. We accounted for this relationship by extracting the residual of a linear model predicting CTI or species richness with pH as the sole predictor (see methods).

After accounting for soil effects, elevation-induced change in temperature was the main predictor of CTI, but it did not significantly explain species richness (Table 4-2). The microclimate was not a significant predictor in any of the two models (Table 4-2). Topoclimate was the sole significant predictor of species richness, and it significantly explained CTI. The contribution of topoclimatic cooling to the explained variability of CTI (4.64%) was comparable to the explained variability by elevation (4.6%). We centered the latter flora analysis around topoclimate cooling as canopy cooling did not significantly explain the species richness or CTI.

*Table 4-2: Estimated parameters, their standard error and p-values of the predictors of the specific richness and community thermal index (CTI) linear models. The range of the predictors and their effect size on the community predicted variable (range * estimate) are displayed. Both species richness and CTI have previously been corrected for their correlation with soil pH. The P-value is obtained by a Wald test on the parameter.*

| Model | Predictor | Estimate | Standard error | Range | Effect size | P-value | Explained variation (%) | $R^2$ (%) |
|---|---|---|---|---|---|---|---|---|
| **Species richness** | Intercept (°C) | 9.71 | 7.73 | | | 0.21 | | 7.7 |
| | Lapse rate (°C) | 0.324 | 0.329 | 12.6: 18.5 | 1.91 | 0.324 | 0.93 | |
| | Topoclimatic cooling (°C) | -6.91 | 1.54 | -1.55 : -0.13 | -9.78 | <10-4 | 6.76 | |
| | Microclimatic cooling (°C) | 0.682 | 2.35 | -2.72: -1.31 | 0.958 | 0.771 | 0.0184 | |
| **Community thermal index (°C)** | Intercept (°C) | 6.83 | 0.407 | | | <10-4 | | 9.2 |
| | Lapse rate (°C) | 0.076 | 0.0173 | 12.6 : 18.5 | 0.449 | <10-4 | 4.6 | |
| | Topoclimatic cooling (°C) | 0.355 | 0.0805 | -1.55 : -0.13 | 0.503 | <10-4 | 4.64 | |
| | Microclimatic cooling (°C) | -0.00586 | 0.123 | -2.72 : -1.31 | -0.00822 | 0.962 | 0.0063 | |

We divided the 306 floristic surveys into cold, intermediate and warm topoclimatic classes each comprised of 102 surveys based on topography-induced cooling. The cold topoclimatic class displayed 23 species on average, while the two other classes displayed 18.5 species on average (Figure 4-3.a). This difference of approximatively 5 species was significantly different (Figure 4-3.a). The mean CTI of the cold topoclimatic class was 7.7 °C, which is significantly lower by 0.19°C than the CTI of the two other classes (Figure 4-3.b). This discretization of the dataset displayed similar patterns than the one we observed in the continuous analysis of the linear model (Table 4-2, Figure S4-4).

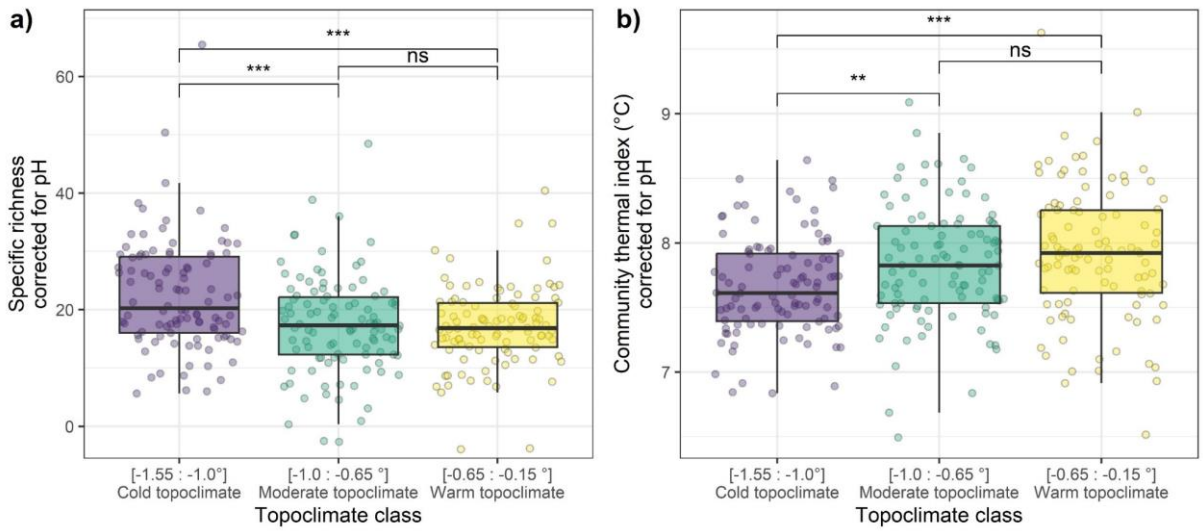


*Figure 4-3: Species richness (a) and community thermal index (b), corrected for bioindicated pH, of 306 floristic surveys evenly spread into three topoclimatic cooling classes. The correction consists of extracting the residuals of a linear model with pH as a sole predictor, this process could thus lead to negative specific richness. The p-value significance of a Wilcoxon test between two classes is displayed as follows: (ns): p>0.05 (*): p<0.05(**): p<0.01 (***): P<0.001.*

The decreases in CTI and the increase in species richness in the cold topoclimatic class were explained by a surplus of relatively cold-adapted species (i.e. with a species thermal optimum of 9 °C or less) (Figure 4-4.a). The plots (n=102) in cold topoclimates displayed in total more than 50 to 100 more occurrences of relatively cold-adapted species per thermal optimum classes (1°C) than the other two categories (Figure 4-4.a). The intermediate topoclimatic class (n=102) also had a higher number of cold-adapted species compared to the warm topoclimatic class (n=102) (Figure 4-4.a). The cold topoclimatic class displayed 300 more forest-specialist species occurrences (Heinken *et al.*, 2022) warmer topoclimates, whereas the occurrences of generalist species increased by 200 in total (Figure 4-4.b). We recorded a total of 246, 242 and 223 species (i.e., species pool) in the cold, intermediate and warm topoclimatic classes, respectively. 58, 41, and 33 species were unique to the cold, intermediate and warm topoclimatic classes, respectively. This mean that there are redundancies of species between communities, as shown in Figure S4-5.

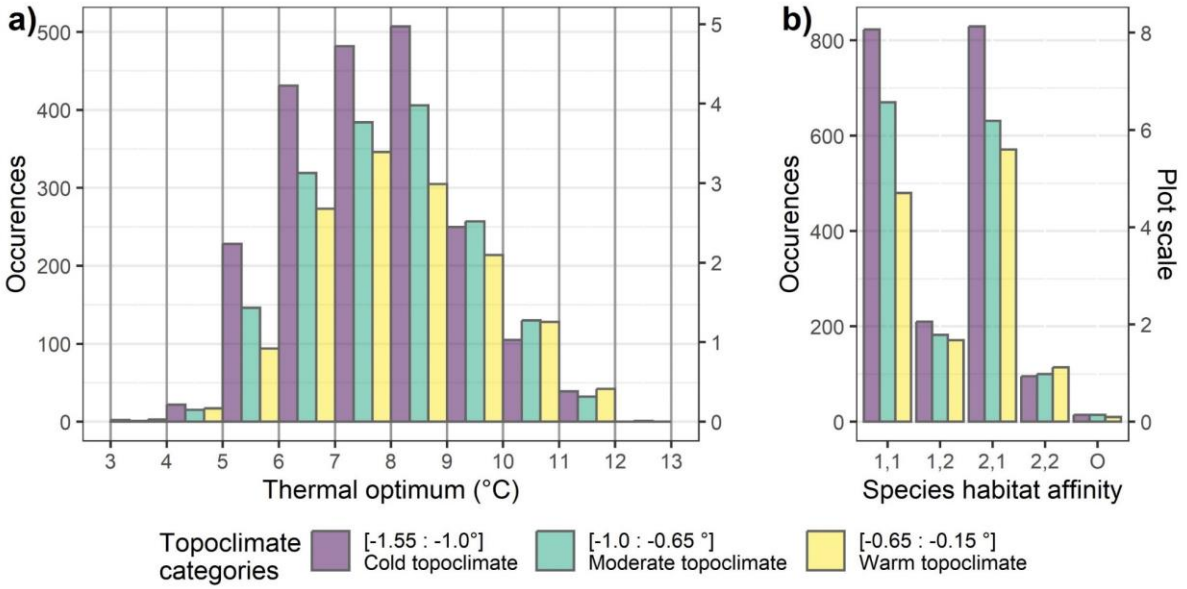


*Figure 4-4: Occurrences of species in the three topoclimatic classes as a function of a) their thermal optimum (°C) and b) their habitat affinity defined by the EuForPlant list as follows: 1,1: closed forest mainly 1,2: forest edges and opening 2,1: forest and open vegetation 2,2: mainly in open vegetation (Heinken* et al.*, 2022) The plot-scale occurrence of species is also shown (e.g., 400 occurrences corresponds to approximately 4 species per plots).*

## 4.4. Discussion

We found that both canopy cover and topographic factors strongly influenced understory temperature during the growing season. We disentangled the elevation gradient from the topoclimatic and microclimatic factors by estimating the lapse separately, which was expectably the main driver of understory temperature (Figure 4-2). After controlling for the lapse and pH, the cooling by topographic factors, namely topoclimate, was the only significant driver of community composition and richness.

The positive correlation found between temperature and heat load can be attributed to the higher radiation an equator-facing slope receives, which increases both the mean and daily maximum temperature of the growing season in closed forests. This contrasts with a previous study which only found an effect of heat load on maximum temperature (Macek *et al.*, 2019). Alongside heat load, we found that topographic position influenced mean temperature so that ridges were warmer and bottoms of valleys were cooler but had no effect on maximum temperature. We attribute this decrease in temperature to cold air pooling that occurs during nighttime, thus influencing mean daily temperature but with a minimal effect during the hottest hour of the day, when air temperature is homogeneously warm (Smith *et al.*, 2010; Vosper & Brown, 2008). The cooling effect of understory temperature by canopy cover was most apparent for maximum temperature but was also significant for mean temperature. These observations concur with studies with comparable sampling (Davis, Synes, *et al.*, 2019; Macek *et al.*, 2019). We showed a strong effect of topoclimatic factors on community composition and richness but no contribution of microclimatic factors. Our microclimatic model allowed us to separately predict the lapse

rate, topoclimatic cooling and canopy cover cooling with mean temperature as a unit. This allows inferring direct links between temperature variation and communities, a necessary step to advance correlative studies.

The lack of correlation between species richness or community composition (climatic affinity) with microclimatic cooling is surprising as a majority of studies conducted in lowland forest concluded that dense canopy cover (or closure) explains both the assembly of communities and their slow temporal response to climate change (De Frenne *et al.*, 2013, 2019; Maclean *et al.*, 2015; Richard *et al.*, 2021; Zellweger *et al.*, 2020). In mountain forests, however, the contribution of canopy cover to understory temperature is still under scrutiny (Davis, Synes, *et al.*, 2019; Macek *et al.*, 2019; Zellweger, Coomes, *et al.*, 2019). We found that topoclimatic factors outweighed canopy closure in explaining understory temperature in our study area (that harbors limited canopy closure variation and high topographic variation), which may explain the absence of a link between canopy cover and communities. This finding adds to the current divergent results from Macek *et al.*, (2019) who found no effect of canopy and Vandewiele *et al.*, (2023) who found a predominance of canopy control on temperature in mountain forests. These apparent contrasting results illustrate the complexity and interactions of factors in mountain forest microclimates, potentially depending on site-specific variations in topography and canopy cover.

Part of the challenge to determine canopy cover controls in mountain forests stems from the myriad of methods that are used to estimate canopy cover, ranging from hemispheric photographs, terrestrial lidar derived metrics to remotely sensed canopy cover estimations (Ma *et al.*, 2017; Zellweger, De Frenne, *et al.*, 2019). We used Copernicus tree density 2018 satellite images to calibrate the microclimatic model and predict its buffering effect onto communities. Remote sensed tree closure density does not account for the vertical profile of trees, which have profound influence on sunlight interception and consequently on understory temperatures (Gril *et al.*, 2023; Zellweger, Coomes, *et al.*, 2019). Remotely sensed canopy cover was significantly but poorly correlated with our field measures (visual estimation and photography), and the year of remote sensing (2018) does not match the average year of a floristic survey (2015.6). These inaccuracies and the missing link of the forest vertical profile could partly explain the lack of a significant relationship between community compositions and cooling induced by canopy cover. We fitted additional understory temperature models with *in situ* measurements of canopy cover to conservatively reject canopy cover as prominent driver of microclimate and consequently community composition. These models showed no correlation between understory temperatures and canopy closure except from the interaction between immediate canopy closure (photography) in equator-facing slopes (Table S4-2, Table S4-3). This demonstrates the need to simultaneously study multiple microclimatic drivers and their interactions in mountain ranges (Davis, Synes, *et al.*, 2019; Greiser *et al.*, 2020).

We found that temperature variation owing to topography was equally important in shaping a community's affinity to climate compared to that of the elevational gradient (Table 4-2,after soil pH has been controlled for). This is understandably a consequence of community assembly dictated in part by the environment. Lower temperature at higher altitudes or in topographically shaded slopes can exert a selection pressure on species not adapted to cold whereas lower elevation and high radiation slopes select species not sensitive to late freezing and adapted to warmer temperature (Figure 4-3). Our prediction of both elevation and topography control on mean temperature are quantified the same unit, Celsius degrees °C, but topography-induced temperature effect on community composition is fourfold compared to that of elevation (Table 4-2). This implies that mean temperature alone cannot drive the difference in community composition, and other biophysical factors correlated with topography-induced temperature should be at play. Maximum temperature could be a better predictor of the crossing of physiological thresholds dictating species selection (Macek *et al.*, 2019; Pérez-Navarro *et al.*, 2021). However, this hypothesis could not be tested with our dataset as mean and maximum understory temperature were highly correlated. Soil moisture and vapor pressure deficit can also explain the important contribution of topography to communities (Davis, Synes, *et al.*, 2019).

Our topographic position metric relies on hydrography, demonstrating that cold air pooling could occur alongside wetter soils and synergistically favor cold-adapted species not tolerant to drought (Bénichou & Le Breton, 1987; Finocchiaro *et al.*, 2023; Raduła *et al.*, 2018). Conversely, ridges and south facing slopes exacerbate the effect of warmer temperature by desiccation, via stronger winds and evaporation, respectively (Davis, Synes, *et al.*, 2019; Piedallu *et al.*, 2023; Rita *et al.*, 2021). These factors altogether and the differences we found in contribution to community composition (Table 4-2) challenge the use of a single microclimate variable (e.g., mean temperature) to predict community patterns and species distribution. Explicitly considering other microscale biophysical factors in a multivariate fashion (Pérez-Navarro *et al.*, 2021), the improvement of mechanistic modeling of microclimate (Maclean, 2020) could improve predictions of present and future community composition.

The cold-adapted communities we observed in cold topoclimates are the result of an increase in relatively cold-adapted species occurrences rather than of a decrease in relatively warm-adapted species (Figure 4-3). This hints that the constraints on community assembly, in our study region, are a result of temperature becoming too warm for cold-adapted species, rather than otherwise. This increase in occurrences explains the higher specific richness in cold topoclimates (Figure 4-3). Canopy cover has been identified as the driver of the diversity of many taxa in lowland forests due to its buffering of microclimate and light interception (Tinya *et al.*, 2021; Zellweger *et al.*, 2015). Its lower contribution to microclimate variation in mountain forests and the limitation in its measurement mentioned earlier may explain why we do not detect this pattern. Further to an understory cooling, colder topoclimates could also increase moisture, thus alleviating competition for water

during summer and allowing more species to co-occur (Raduła *et al.*, 2018; Sanczuk *et al.*, 2022).

How these local cooler and wetter conditions are decoupled from the climate warming trend is of utmost importance as they allow for the persistence of cold-adapted species (Greiser *et al.*, 2020; Lenoir *et al.*, 2017). The thermal heterogeneity topoclimate produced in mountain ranges (Figure 4-2) should also be considered as a driver of landscape-scale diversity (Stein *et al.*, 2014) and a potential source of community adaptation because species of diverging climatic adaptation coexist in a relatively small area (Hylander *et al.*, 2022; Lenoir *et al.*, 2013). More specifically, our results support the "identifying and protecting microrefugia" section highlighted by Hylander *et al.*, (2022), as north-facing slopes and topographic depressions are easily identifiable from maps, and their cooling capacities and cold-adapted communities confirmed by visits in the field. Although we didn't find a significant canopy variation contribution, canopy is essential to create the ultimate understory condition and should be preserved to take advantage of the topoclimate. This could be achieved through selective logging and continuous cover silviculture and the reduction of edge effects thanks to buffer zones around the microrefugia. Conservation targeting cold topoclimates is more robust because of the increase in redundancy and biodiversity those locations provide. Additionally, maintaining a connected forest will foster the benefits of the thermal heterogeneity created by topography (Hylander *et al.*, 2022). Indeed, warm topoclimates will serve as source populations of species adapted to the current climate, and cold topoclimates will maintain cold-adapted populations, resulting in an heterogenous landscape.

In summary, we show that elevation, topography, and to a lesser extent, canopy closure determines growing season understory temperature in the Vosges mountains in France. Besides elevation, the contribution of topoclimate was the main predictor of community composition and diversity. Understory plant communities of cold topoclimates (north facing slopes and valley bottoms) harbored a higher number of generalist and forest specialist cold-adapted species. Our results place topography as a prominent driver of forest temperature and a key factor to consider for protecting forest cold-adapted species in the context of accelerated global warming.

## 4.5. Supplementary Materials

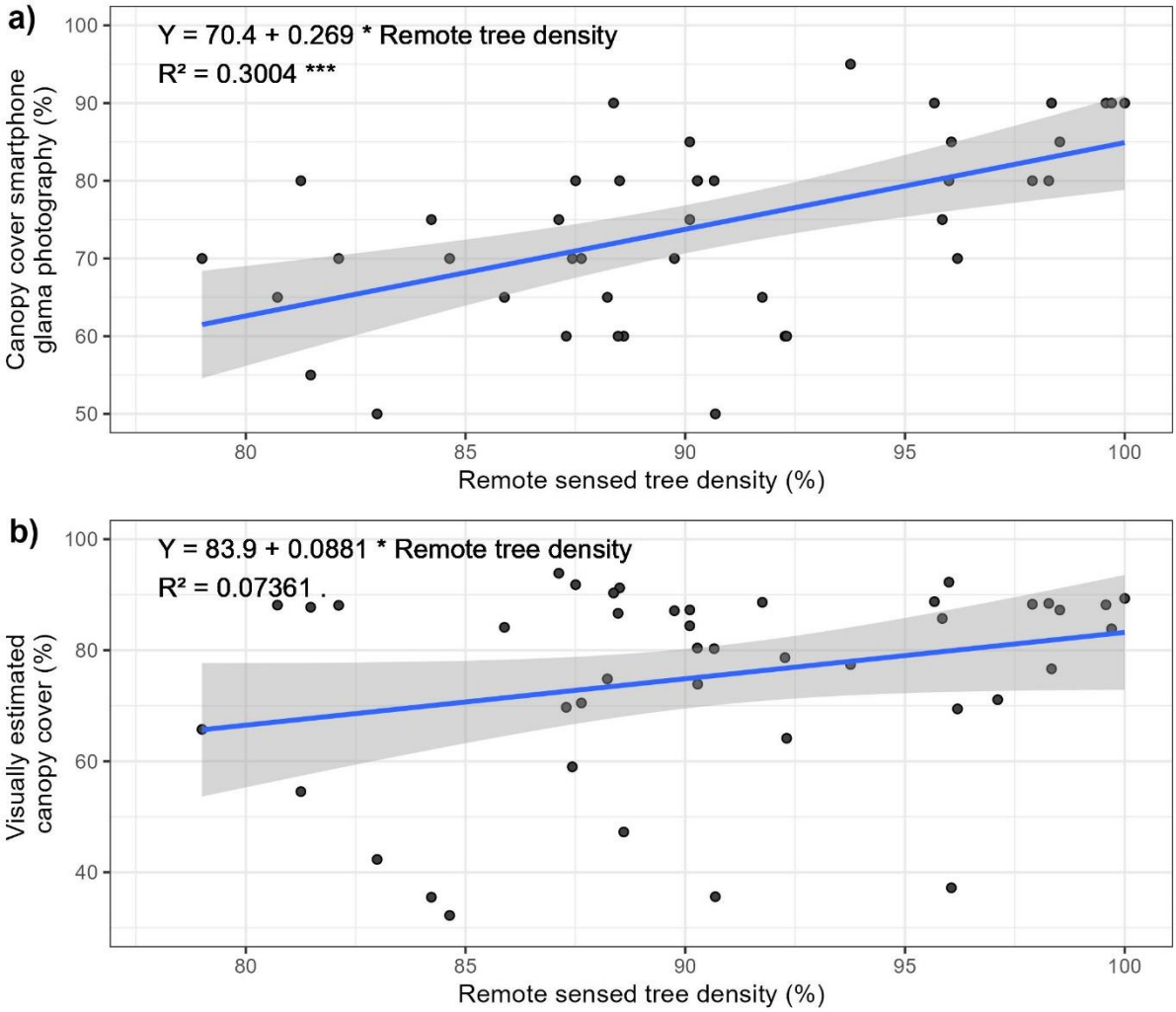


*Figure S4-1: Relationship between Copernicus remote sensed tree density and canopy closure estimated in a 25-meter radius circle (a) and canopy cover estimated by a smartphone photography and segmented by the 'Glama' application (b). The blue line corresponds to a fitted linear model which equation, Person $R^2$ and its statistical significance are displayed (***): P<0.001, (.) P<0.1. The ribbons are the confidence interval of the model.*

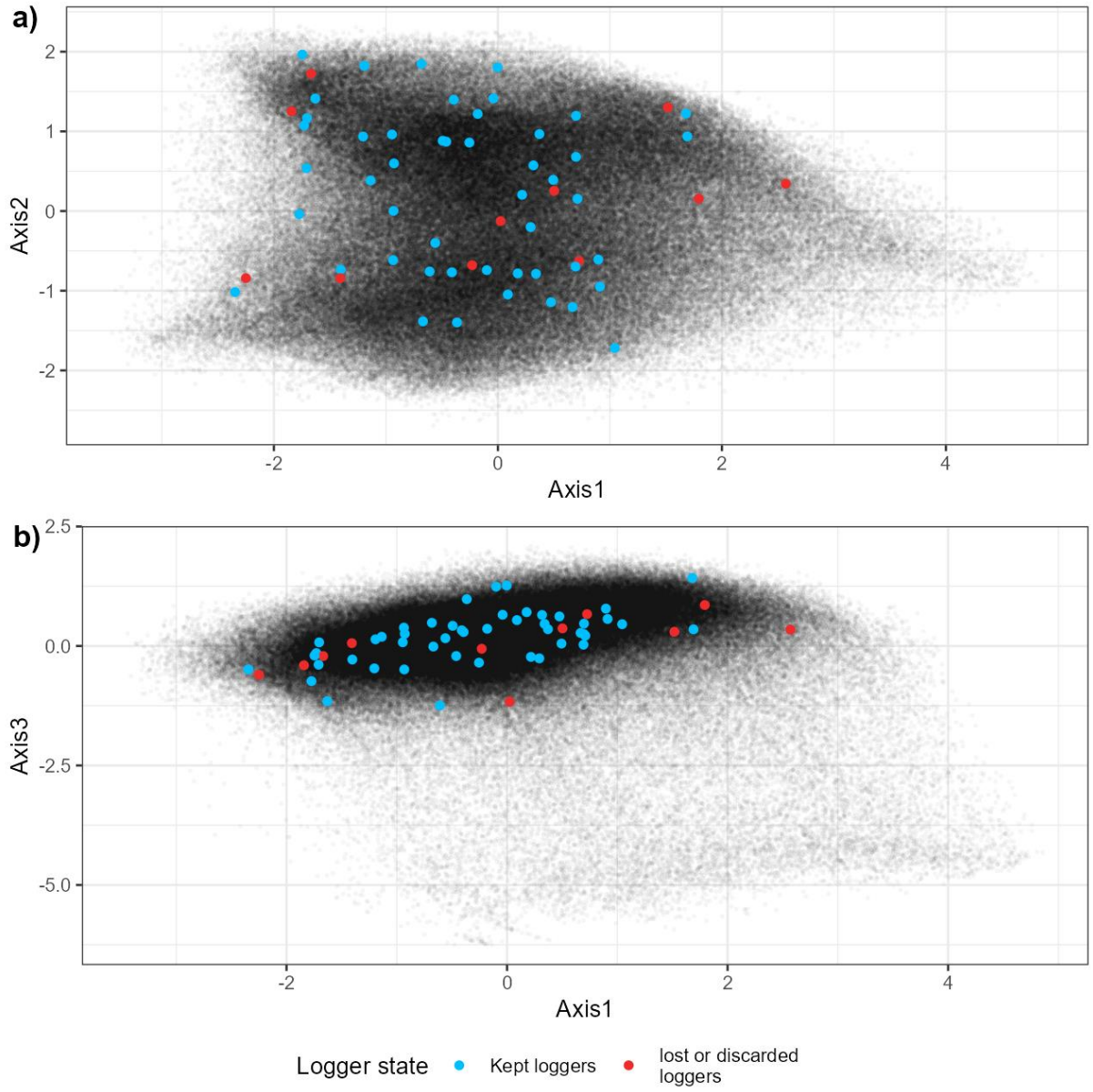


*Figure S4-2: Principal component analysis of the spatial factor ought to influence microclimate. Axis 1 is explained by elevation and topographic position, Axis 2 represents mostly head load index, Axis 3 represents mostly canopy cover. The position in the PCA projection of the initial sampling and the final selection of loggers is shown (Lembrechts* et al., *2021).*

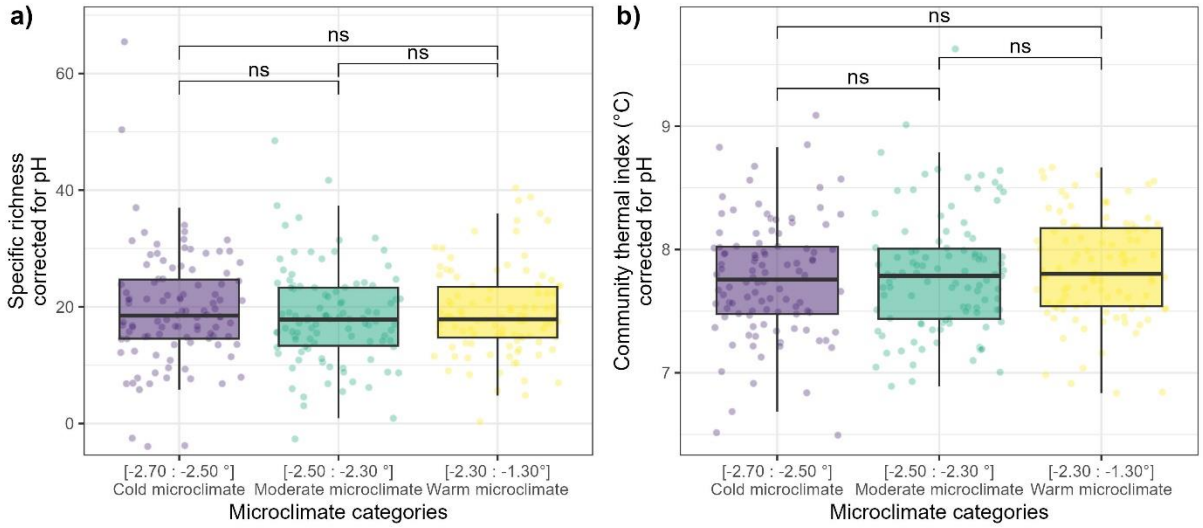


*Figure S4-3: Species richness (a) and community thermal index (b), corrected for bioindicated pH, of 306 floristic surveys evenly spread into three microclimatic cooling classes. The correction consists of extracting the residuals of a linear model with pH as a sole predictor, this process could thus lead to negative specific richness. The p-value significance of a Wilcoxon test between two classes is displayed as follows: (ns): p>0.05.*

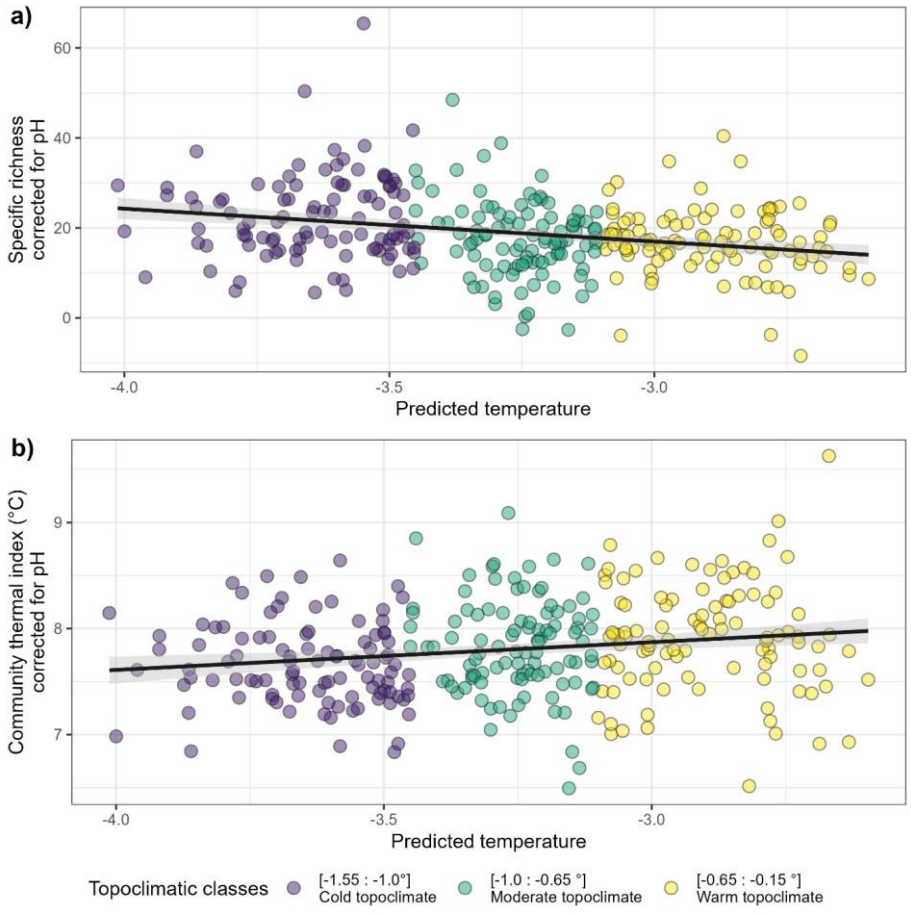


*Figure S4-4 Species richness (a) and community thermal index (b), corrected for bioindicated pH, of 306 floristic surveys evenly spread into three topoclimatic buffering classes, as function of predicted topoclimatic cooling.*

*Table S4-1: Estimated parameters, their standard error and p-values of the predictors included in models of the daily maximum growing season temperature. The range of the predictors in the calibration dataset and their effect size on the temperature (range * estimate) are displayed. The percentage of explained variation per type of predictor is included. P-values were obtained with a Wald test on parameters. Heat load and topographic indices have no units, refer to the methods for their calculation.*

| Predictor | Type of predictor | Estimate | Standard error | Range | Effect size (°C) | Explained variation (%) | P-value |
|---|---|---|---|---|---|---|---|
| **Intercept (°C)** | | 30,6 | 2,45 | | | | <10-4 |
| **Elevation (m a.s.l)** | Elevation | -0,00803 | 0,000685 | 475.69 : 1203.17 | -5,84 | 56,5 | <10-4 |
| **Heat load index (n.u)** | Topoclimate | 5,35 | 0,732 | 0.335 : 0.951 | 3,29 | 21,5 | <10-4 |
| **Topographic index (n.u)** | Topoclimate | 0,333 | 0,607 | 0.147 : 1 | 0,284 | 21,5 | 0.587 |
| **Tree density (%)** | Microclimate | -0,0947 | 0,0253 | 79.004 : 100 | -1,99 | 3,17 | <10-4 |

*Table S4-2: Estimated parameters, their standard error and p-values of the predictors included in models of the field canopy cover daily mean growing season temperature. The range of the predictors in the calibration dataset and their effect size on the temperature (range * estimate) are displayed. The percentage of explained variation per type of predictor is included. P-values were obtained with a Wald test on parameters. The canopy cover was estimated visually in a 25-meter radius circle around the loggers.*

| Predictor | Type of predictor | Estimate | Standard error | Range | Effect size (°C) | P-value |
|---|---|---|---|---|---|---|
| **Intercept (°C)** | | 19,2 | 0,605 | | | <10-4 |
| **Elevation (m a.s.l)** | Elevation | -0,00656 | 0,000333 | 475.69 : 1203.17 | -4,78 | <10-4 |
| **Heat load index (n.u)** | Topoclimate | 1,52 | 0,359 | 0.335 : 0.951 | 0,934 | <10-4 |
| **Topographic index (n.u)** | Topoclimate | -0,00767 | 0,00599 | 0.147 : 1 | -0,00654 | 0.208 |
| **Canopy cover 25 radius (%)** | Microclimate | 0,42 | 0,295 | 50 : 95 | 8,82 | 0.163 |

*Table S4-3: Estimated parameters, their standard error and p-values of the predictors included in models of the immediate canopy cover daily mean growing season temperature. The range of the predictors in the calibration dataset and their effect size on the temperature (range * estimate) are displayed. The percentage of explained variation per type of predictor is included. P-values were obtained with a Wald test on parameters. The canopy cover was estimated visually in a 25-meter radius circle around the loggers. Immediate canopy cover was measured used a hemispherical photography above the logger and a sky segmentation application.*

| Predictor | Type of predictor | Estimate | Standard error | Range | Effect size (°C) | P-value |
|---|---|---|---|---|---|---|
| **Intercept (°C)** | | 16,2 | 0,812 | | | <10-4 |
| **Elevation (m a.s.l)** | Elevation | -0,00672 | 0,000299 | 475.69 : 1203.17 | -4,89 | <10-4 |
| **Heat load index (n.u)** | Topoclimate | 5,47 | 1,22 | 0.335 : 0.951 | | <10-4 |
| **Topographic index (n.u)** | Topoclimate | 0,0346 | 0,0109 | 0.147 : 1 | 0,0295 | 0.00311 |
| **Immediate canopy cover (%)** | Microclimate | 0,481 | 0,256 | 32,2 : 93,9 | | 0.0682 |
| **Topography index X Immediate canopy cover** | Interaction | -0,0547 | 0,0162 | | | 0.00171 |

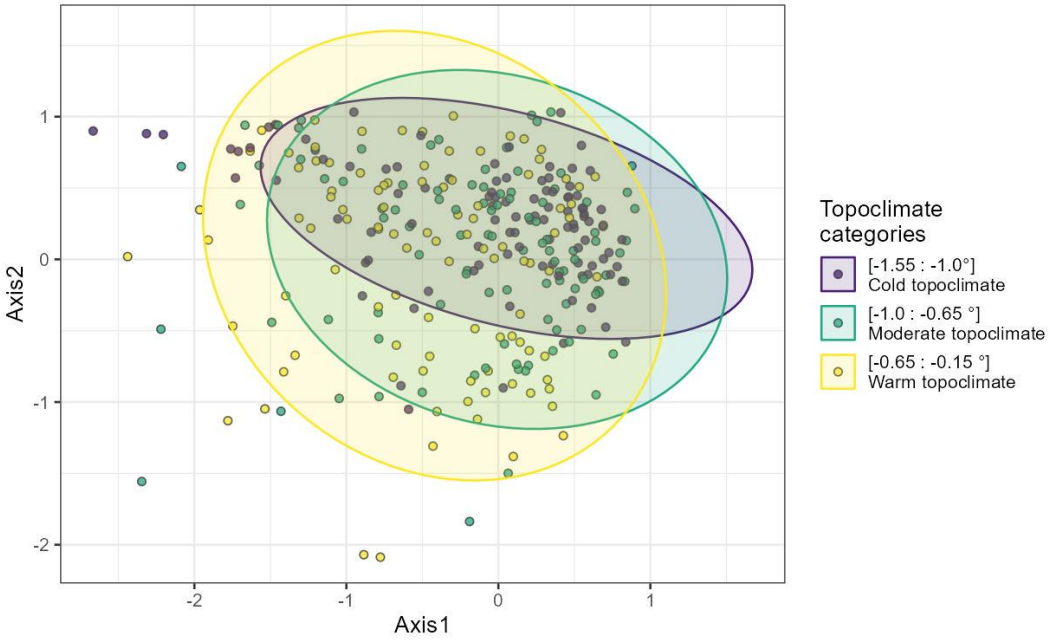


*Figure S4-5: The first two axes of a correspondence analysis of the 306 floristic surveys spread among the three topoclimatic cooling class.*

# Chapter 5. Discussion

## 5.1. Results Synthesis

### *5.1.1. Aims of the thesis summary*

Given the dramatic temperature increase (IPCC, 2021b) and the increase of observed thermophilization phenomena in temperate forests (De Frenne *et al.*, 2013; Govaert *et al.*, 2021; Maciejewski *et al.*, 2020), the aim of this thesis is threefold: (1) Quantify the recent thermophilization in French forests and the community dynamics driving it, as well as its potential impact and local and regional diversity, and investigate potential sources of community persistence (protection from climate change) originating from (2) agricultural-induced mosaic of forest cover and from (3) cooling of understory temperatures by canopy and topography.

To proceed (1), we used a large number of paired National Forest Inventory (NFI) plots (n= 14,167 pairs) separated by 10 years and analyzed shifts in species occurrence at the French ecoregion scale. We computed thermophilization and ß-diversity changes (indicative of homogenization) and partitioned the contribution of colonization and extinction of cold and warm-adapted species to these changes. Our initial hypothesis was that thermophilization results from both warm-adapted species colonization and cold-adapted species local extinctions, and may lead to homogenization triggered by the spread of warm-adapted species.

For question (2), we used a pairing of NFI plots (n=2,012 pairs) to compare *ceteris paribus* communities found in landscapes of varying forest cover. Our initial hypothesis was that forested landscapes harbor colder-adapted communities, due to a combination of different soil properties and microclimatic effects stemming from forest cover and edge effects.

To proceed (3), we measured understory temperatures during the 2022 growing season in one valley of the Vosges Mountains, in order to test how elevation, canopy cover and topography drive understory temperatures and subsequently, communities. We expected cooler temperatures under high canopy and in shaded slopes and valley bottoms. We expected these locations to host more species adapted to cold climates.

### *5.1.2. An extinction-driven thermophilization*

By comparing the NFI plot pairs of the years 2005 to 2021, we found that ecoregions thermophilized on average by 0.012 °C $yr^{-1}$, but this rate could climb to 0.25 °C $yr^{1}$ in Mediterranean ecoregions. The mean rate is comparable to the one established by studies completed in temperate forests (Govaert *et al.*, 2021; Richard *et al.*, 2021; Zellweger *et al.*, 2020). Our results are original in the relatively high number of plots used (the caveat being they are not true revisit plots) and that we pooled our plots at the forest ecoregion scale.

This scale allowed us to jointly study thermophilization and homogenization, and to partition these changes into community dynamics.

We found that a surplus of cold-adapted species extinction (compared to a null model) was the only driving force of thermophilization, our expectation of warm-adapted species colonization was only partly met in mountainous ecoregions. The signal of homogenization was variable among forest ecoregions, but we found no significant trend. The partitioning revealed that an unexpected contribution of rare cold-adapted species colonization, combined with the synchronous extinction of both rare and widespread species prevented homogenization from happening. We found a local loss of diversity as plots displayed on average 0.5 species less, but this loss was very variable among ecoregions. Altogether, these results show that the climate change effects on French forest communities are the consequence of the lack of tolerance of cold-adapted species rather than the promotion of colonization of warm-adapted species, with a visible impact on species richness but not on ß-diversity.

### *5.1.3. Forest cover impacts community's affinity to climate*

With the balanced comparisons of floristic surveys located both in low and high forest cover landscapes, we showed that the thermal optimum has dropped by 0.26 °C in communities of forested landscapes (a figure comparable to the recent 10 years of temperature warming in western Europe). A simple linear model with pairwise differences of bioindicated parameters as predictors allowed us to differentiate the conditions of the plot (soil + light) from a "pure" landscape effect. Indeed, half of the cooling capacity of the forest landscapes was explained by poorer (acidic and low nitrogen content) soil, which favors colder-adapted species, and the remaining half by the "pure" effect that we interpreted as regional and microclimatic cooling of forest cover. We ran this analysis with a varying window to classify plots as "forested"; as a result, we showed that the cooling effect exerted by soil and forest cover increased linearly with the forest cover increase. Forest fragmentation is often interpreted as an impairment regarding forest plants colonization, but our results show that varying degrees of forest cover might also impact communities through biophysical cooling.

### *5.1.4. Microclimate and topography impact community diversity*

Our measurements of microclimate showed that, within a steep valley of the Vosges Mountains, the variation in growing season temperatures was mainly due to topography rather than canopy closure, a proxy of canopy cover (1.5 °C vs. 0.5°C). Once soil pH was accounted for, topography-induced microclimate (namely topoclimate) explained community thermal optimum comparably to elevation, and solely explained species richness. The average thermal optimum of communities was 0.19 °C lower and displayed 5 more species in the most shaded slopes and valley bottoms. This increase in diversity is understandably explained by an increase in cold-adapted species occurrences and an increase in forest specialist and generalist species alike. The low influence of canopy cover

effect on communities highlights that stable topographic features may outweigh canopy cover in explaining the persistence and diversity of communities in mountainous forests.

## 5.2. Limitations and Implications

### *5.2.1. Methodological Limitations*

#### *5.2.1.1. National Forest Inventory dataset*

In chapters 2 and 3, we used subsets of the "recent" protocol of the NFI. This protocol started in 2005 and is planned to continue at the time of writing. This NFI consists in a 10-year cycle sampling of a systematic grid laid over forest territory, and plots surveyed every year are spread evenly all over the territory so that yearly, 5-year or 10-year results can be produced (IGN, 2019b). Using a single database avoids methodological bias introduced by merging different databases, a luxury considering that floristic studies often rely on the aggregation of databases from different studies and periods (Bertrand *et al.*, 2011; Chytrý *et al.*, 2014; Kuhn & Gégout, 2019) or on small sets of controlled plots (Govaert *et al.*, 2021; Richard *et al.*, 2021). The use of that database, however, still falls short for several purposes.

As the starting date of this monitoring is 2005, one caveat of our approach is that our data is already impacted by contemporary climate change, without any "baseline" state - inherently difficult to define- for further comparison. As a result, we cannot disentangle the present dynamic we observe from past dynamics. For example, we cannot exclude a preexisting climatic debt being repaid, on top of the ongoing thermophilization, in explaining the rates reported in Chapter 2. We also cannot test if the difference in community thermal optimum attributed to forest cover in Chapter 3 is a fixed pattern or a result of different rates of thermophilization induced by different forest covers over the forest stand dynamics.

A perfect homogeneity of data should not be assumed when using a unique database, the NFI comprises field teams with operators of variable skills and experience to determine a given taxon. This could lead to some regional differences in naming convention through time (as protocols and operators refine their classification) and space, as teams are spread in given sampling units. Further collaborations with the National Geographic Institute (IGN) in order to obtain operator-related data (which can be anonymized) such as "field team", "time spent", and "sampling unit" and considering it would enhance the quality of initial checks of the floristic surveys.

Due to a combination of time constraints in the field, species identification challenges, and the fact that approximately half of the NFI surveys are performed outside of the growing season, NFIs are not exhaustive. While exhaustivity is less of a problem for the ß-diversity metric we chose (Beck *et al.*, 2013), its influence on the partitioning is yet to be tested (Tatsumi *et al.*, 2021). This is evidenced by the high contributions of rare species to Δß-diversity we observed, the method was very sensitive to species occurring only once

in either the “past” or “recent” period. By summing the contributions, we were able to capture the general trend of species dynamics as a function of rarity, but this raises questions about whether a systemic sampling like the NFI can monitor single and targeted rare species (Bonnet *et al.*, 2015). Local diversity (namely α-diversity) shifts should also be interpreted with caution if the proportion of surveys done outside of the growing season is not stable.

We did not thoroughly review the raw floristic datasets used in the three studies (Table A2,Table A3,Table A4) because of the extensive time and expertise needed to review more than 700 species. While this possibly undermines the quality of our results, the assumption that species are detected/display flawed observations are independent of their thermal optimum (and other characteristics) supports their interpretability. Aside from an expert review of the dataset, further automatic and semi-automatic curation methods can be envisioned for future studies. In addition, to the observer bias described above, readily available species-specific information can be used to control for their absence. The timing of growth and flowering of plants can used conjointly with the date of observation as a new explanatory variable for their absence, taller plants and perennial species are also more likely to be detected, especially outside of the growing season. Species with changing taxonomy or species hard to determine to the species level also need to be controlled for. We checked if discrepancies in assignment through time could explain abrupt changes in occurrences, due to changes in taxonomy knowledge of the field teams. The *Agrostis* and *Rubus* genus were the two instances where changes in occurrences could originate from changes in classification. Without any supplementary file that could be used to homogenize the taxonomy, we ran all the presented analyses without including those species and found no significant differences, they were thus kept in the final datasets.

One last limitation to consider when using the NFI is the imprecision of the coordinates, blurred to comply with private property protection laws. The NFI reports the coordinates of the closest center of the 1 km grid used to prepare the sampling, hence the imprecision can reach 700 m (IGN, 2019b). This imprecision makes studying fine-grained landscape metrics such as distance to the edge and contingency (Hesselbarth *et al.*, 2019) impossible. We used a 1 km radius to assess forest cover around an NFI plot. Extracting climatic data was not affected by this imprecision as our climatic dataset was of similar resolution (1 km). However, such imprecision could hamper the analysis using new higher resolution (25 m) climatic datasets (Haesen *et al.*, 2023a). New methods enabling to reliably query data from the exact coordinates while maintaining coordinates’ secrecy should be implemented to foster the development of NFI spatial analyses (Gessler *et al.*, 2024).Indeed, releasing coordinates should always be done with caution, fully public coordinates could influence forest manager practices (e.g. in fear of not following national guidelines, using open coordinates to conduct restoration actions), hampering the representativeness of permanent (and otherwise) plots (Schadauer *et al.*, 2024).

### *5.2.1.2. Species thermal optimum*

We discussed species individual and community-aggregated thermal optima at length, however, estimating and using these metrics is far from trivial. Our analyses rely mostly on ClimPlant V1.2, a database comprising 1168 species thermal optima (Vangansbeke *et al.*, 2021). This database relies on vegetation atlases and maps that provide historical distributions of plants, from which the mean value of a climatic grid within the distribution can be extracted. This realized climatic niche being a means of the climate, it is mechanistically less variable than the thermal optimum obtained from the maximum probability of occurrence of the species response curve along the temperature gradient. Both the maps and the climatic grid (WorldClim V2, 1970-2000) have a coarse resolution of 10 arcminutes (approximately 12 km in Europe); such low resolution also diminishes the variability of thermal optimum estimation. It is then harder to identify true cold or warm-adapted species. Averaging all the thermal optima of species present in a community further reduces variability via regression toward the mean. All the variability reduction sources of community affinity to climate may lead to underestimation of environmental influence over it.

This loss of variability is offset by a more reliable thermal optimum estimation: we used the thermal optima at the European scale, which means that our result can be interpreted as biogeographical provenance of the recorded species (Araújo & Peterson, 2012). This contrasts with thermal optima computed at the French forest scale (Gégout *et al.*, 2005), which provide more variable and precise optima. These optima, however, do not cover the whole range of one species and are only a subset of the true realized niche, which can lead to incomplete interpretation (Araújo & Peterson, 2012).

Using community thermal optimum as a response variable allows making a causal link (after potential confounding factors are addressed) between community and climate change. Climate change is, however, a complex phenomenon including, but not limited to, water availability decrease, prolonged drought, and higher daily maximum temperature (IPCC, 2021b). In the absence of an estimated niche for these parameters, we based our interpretation on the assumption that they are correlated with mean temperature, leading to a correlation between the different dimensions of one species niche. This reminds us that optima are derived from the presence of a species, they are not a direct measure of plant tolerance and physiology but rather another correlative attempt to estimate them (Araújo & Peterson, 2012; Bennie *et al.*, 2014). The measurements of true physiological limits are still scarce (read 5.3.4 for more details), limiting their use in a full dataset as we did with thermal optima, but can be used to validate such optima. We found a significant correlation between ClimPlant thermal optima and 50% lethal temperature (compiled by Lancaster & Humphreys, (2020)) of $R^2$=30.1% (n=73, $P<10^{-4}$). This correlation shows that thermal optimum measures manage to capture physiological limits, but the large room for improvement shows that they cannot substitute physiological limits measurements.

### *5.2.2. Local extinctions, thermophilization and diversity*

#### *5.2.2.1. An ubiquitous extinction-driven thermophilization*

The study of species' response to climate takes many forms, starting with the fitting of species distribution models that estimate a (realized) niche and are thus able to project the species' suitability with predicted climate change scenarios (Engler *et al.*, 2011; Thuiller *et al.*, 2005, 2009). These models generally predict a poleward and upward shift of species distribution, a shift triggered by an increase in species extinction at the warm edge of the distribution and increased colonization rates (or a decrease in extinction rates) at the cold edge (Cahill *et al.*, 2014; Guyennon *et al.*, 2022; Kunstler *et al.*, 2021). Observations of species range shifts and demography increasingly concur with these predictions, however, except in mountainous regions, observations of extinction outweigh observations of colonization (Kuhn, 2016; Kuhn & Gégout, 2019; Lenoir *et al.*, 2008; Rubenstein *et al.*, 2023). Conversely, thermophilization studies are constrained to the community scale, and how their results tie to the range shift literature is only implied rather than made explicit. Our approach aiming to partition extinction from colonization dynamics of thermophilization is a first step to bridging the gap with the range shift literature, allowing our rates to be interpreted as a local scale observation of range shift dynamics. Species-centered analyses such as co-occurrences species distribution model (Ovaskainen *et al.*, 2017) are a way to validate our observations between community and species centered analysis, as in (Duchenne *et al.*, 2021). This approach will be helpful to identify which optima and traits determine assembly rules of communities (as discussed in 5.3.4) as they can be included as predictors instead of response variables.

The thermophilization rate we estimated to 0.012 °C yr-1, only driven by extinction of the relatively cold-adapted species of the ecoregion, is indicative of range retraction of cold-adapted species. Remarkable in our study is the short time span of data needed to detect this rate (10 years), whereas thermophilization is often detected with multidecadal studies (Bertrand *et al.*, 2011; De Frenne *et al.*, 2013; Richard *et al.*, 2021; Zellweger *et al.*, 2020). This is indicative of the quality and number of the data we used but also hints that thermophilization might be accelerating. The lack or slow rate of thermophilization has been interpreted as temperature buffering of the canopy (Bertrand *et al.*, 2011; De Frenne *et al.*, 2013; Maclean *et al.*, 2015). However, this buffering does not decouple understory temperature entirely from climate change (De Lombaerde *et al.*, 2021), meaning that beyond a given degree of warming, buffering of communities might fall short. This may explain why we observe a thermophilization under closed canopies, unlike what (De Frenne *et al.*, 2013; Zellweger *et al.*, 2020) found. We do not contradict the observations that canopy opening accelerates thermophilization (Dietz *et al.*, 2020), but rather report a background extinction rate under stable canopies.

With the dataset used in Chapter 2, we tested the hypothesis of an acceleration of thermophilization; the results are shown in (Figure 5-1). This exploratory result implies an

acceleration of thermophilization driven by a sharp increase in the extinction rate and a lower increase of the colonization rate. The acceleration of thermophilization is coherent with the rise of mean temperatures in France since 2018 (Ribes *et al.*, 2022). Aside from the insufficient buffering by the canopy described above, other factors should be considered to explain how accelerating thermophilization may occur (Urban, 2015).

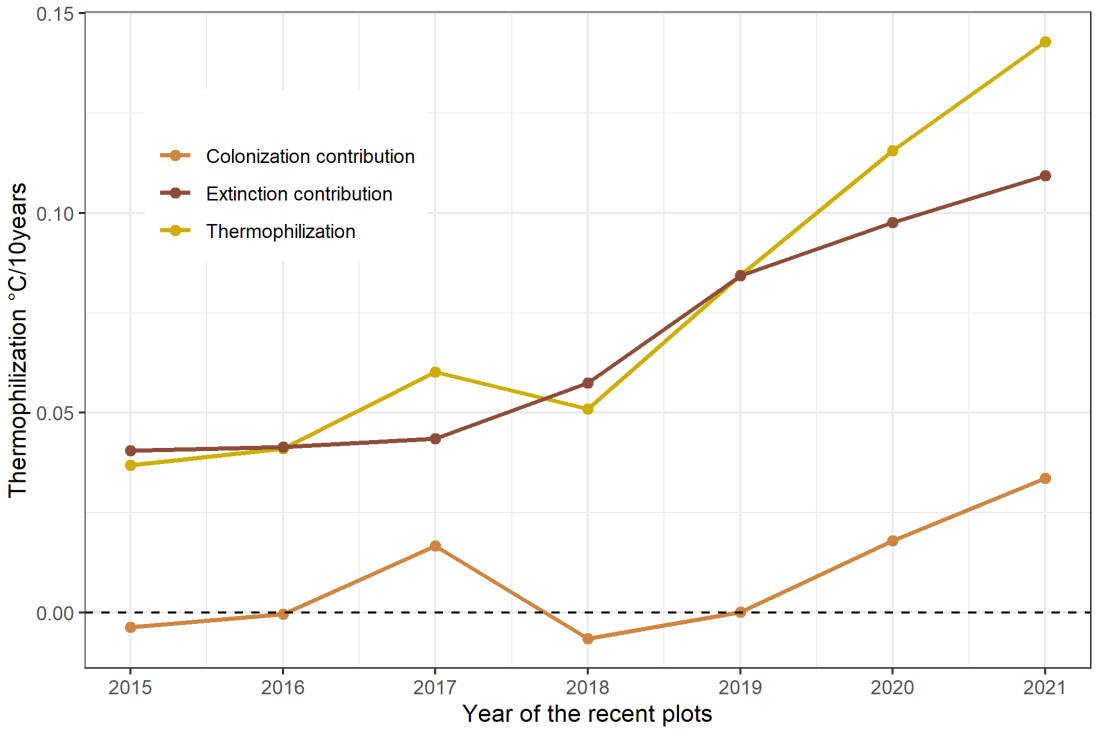


*Figure 5-1: Thermophilization and its extinction and colonization components, computed as in Chapter 2, at the French scale, but with a separate analysis for each year of "recent" plots. Therefore, 2015 reflects the thermophilization analysis of the 2005 and 2015 plots. Conducting one analysis per year reduced drastically the number of plots per forest ecoregions, thus the analysis was only conducted at the France scale (i.e. whole dataset pooled)*

#### *5.2.2.2. Thermophilization: the good, the bad and the diversity*

Thermophilization and climate warming rates are often compared: this comparison coined the terms climatic debt, the lag between flora average thermal optimum and climate temperature (Jackson & Sax, 2010). Thermophilization is often interpreted as an adaptation of communities to the novel climate as it reduces climatic debt (Dietz *et al.*, 2020; Pérez-Navarro *et al.*, 2021; Richard *et al.*, 2021). There is an argument in favor of the gradual reduction of climatic debt by canopy opening (instead of letting climatic debt grow under a high-density canopy, leaving the community exposed to an abrupt shift in microclimatic temperature once the canopy is disturbed, Dietz *et al.*, 2020; Zellweger *et al.*, 2020). However, the absence of evidence of colonization-induced thermophilization (cf. Chapter 2) questions these conclusions. We found that the recent thermophilization denotes an

impoverishment rather than an adaptation of Temperate and Mediterranean plant communities, placing the reduction of the climatic debt as a non-desirable process. In addition to the diversity loss, a loss of functionality from remaining plants can be expected, as plants in the warm edge of their niche lose performances (Wei *et al.*, 2024).

An extinction-driven thermophilization, whether it is accelerating or not, thus begs the question of its impact on community diversity and conservation. Local extinctions reduced local diversity by 0.5 species over the 10 years span of our study, but this rate was not evenly spread throughout all ecoregions. The Alpes, the Massif Central, the Mediterranean and south-west large ecoregions, all displayed local diversity loss rates of ~1 species decades$^{-1}$ (mostly stemming from the relatively cold-adapted species, Figure 5-2). These figures should be interpreted with caution as we calculated them only for species with a known thermal optimum (they are thus conservative, as only 78% of occurrences were involved), thus may be subject to classification change mentioned in the methodological limits (Vellend *et al.*, 2008). But even these conservative estimates of a ~1 species decades$^{-1}$ loss are significant when typical flora communities recorded by the NFI count on average no more than 15 to 30 species, given that time-series are ought to be biased toward a gain of species richness (Kuczynski *et al.*, 2023). Further to the conservation challenge of avoiding definitive extinction of species, local loss of species is likely to alter understory functioning through a loss of complementarity and uniqueness of species function (Landuyt *et al.*, 2019; Liang *et al.*, 2016; Loreau & de Mazancourt, 2013).

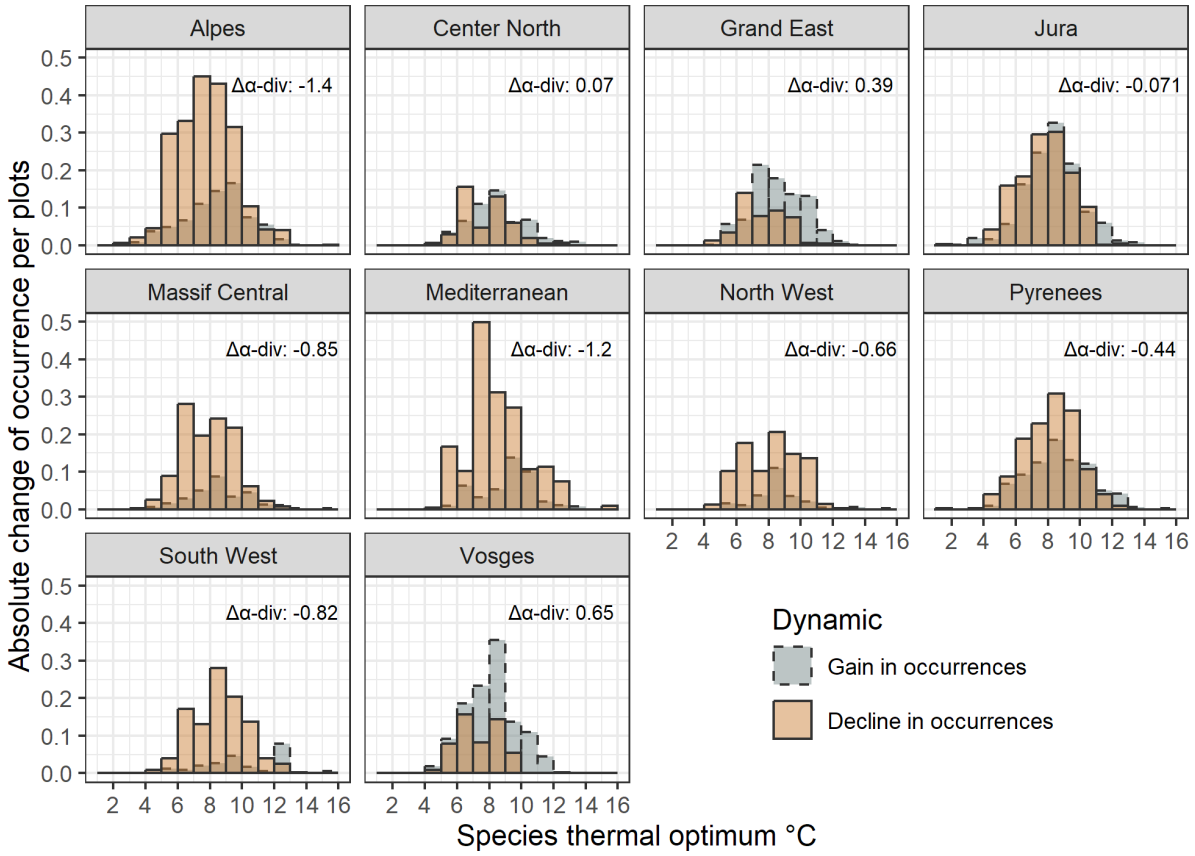

*Figure 5-2: Absolute change of species occurrence per plot as a function of their thermal optimum, distributed in the 10 large forest ecoregions of France. The sum of all the changes of occurrence per plot results in the change of local (a) diversity, hence noted as Δa-diversity.*

While there was an understandable decrease in local diversity, we did not find a significant signal of ecoregion homogenization. Our results thus indicate that the loss of local diversity concerned both common and rare cold-adapted species. This extinction, independent of rarity, could be used to counterintuitively identify communities of high conservation value, usually identified by a set of rare and indicative species. The abundance or decline of the more detectable abundant cold-adapted species allows identifying persistent or exposed communities, respectively.

We used a simple threshold of 10% plots occupancy in an ecoregion to delineate rare from common species of that ecoregion. This threshold met the intuitive expectation of the Δβ-diversity analysis (e.g. a decrease of rare species induces homogenization) and could be used for further NFI occurrence trends monitoring meaningful for conservation. This will be relevant as the absence of communities' homogenization we found might only be a transient state in the response to climate warming. Indeed, β-diversity often increases at the beginning of the anthropic stressor as extinctions diminish common species abundance but are not severe enough to trigger definitive extinctions of the rare and differentiating species (Mori *et al.*, 2018; Socolar *et al.*, 2016). While the ecological causes of rarity are still under scrutiny (Crisfield *et al.*, 2024; Kondratyeva *et al.*, 2019), evidence suggests that rare species, due to their specialization, might be declining at a higher pace than generalist species (Ozinga *et al.*, 2013; Staude *et al.*, 2022; Xu *et al.*, 2023).

An open question is how thermophilization will influence current categorization based on plants. For example, we used in Chapter 2 forest ecoregions in a fixist manner even if their delineation is partly based on climate. Our results show that the ecoregion's flora is not in equilibrium anymore with climate, new delineation based on current and future climate may be needed to represent accurate forest ecoregions. Our Analysis could be redone with these new "shifting" ecoregions, less thermophilization should be detected as species are expected to shift with isotherms (thus with ecoregion delineation, see 1.2.2). In addition, plant communities and their diversity are also relevant to the biodiversity of other taxa they host. Indeed, communities are used either by experts or classification programs to assign a habitat classification (Maciejewski *et al.*, 2022; Teuscher *et al.*, 2013). These habitats are under scrutiny because they are relevant units for conservation and management planning. Thermophilization of habitats is observed in mountains (Maciejewski *et al.*, 2020). However, how extinction-induced thermophilization will affect future classification of habitat is an open question. This selective process could subsequently promotes habitats that will be more redundant, at the expense of habitats associated with cold temperature. Thermophilization could also create novel assemblages, that will need new categorization or new methodologies in order to be considered by contemporary

biodiversity monitoring. The necessity to conserve habitats also highlights the need to identify biophysical factors of community persistence, ideally delineated in space, to contribute to future conservation plans and guidelines.

### *5.2.3. Sources of community persistence exist*

#### *5.2.3.1. Varying spatial and temporal scale of persistence*

We highlighted in the introduction (1.3.1) the difficulty of downscaling macro processes to relevant organism-scale factors, and to upscale fine-grained studies' findings to large territories (Bennie *et al.*, 2014). In the case of forest understory communities, this is demonstrated by the need to study the true microclimatic conditions they experience (Kemppinen *et al.*, 2023). There are increasing efforts and successes to model understory microclimate in relation to field or remotely sensed data (e.g.: Maclean *et al.*, 2019; Zellweger *et al.*, 2019b; Gril *et al.*, 2023; Haesen *et al.*, 2023a) but the methods required may still prove costly in terms of computing and data requirements (e.g. LIDAR). Cost-wise, intermediary scales can thus be very efficient in answering the large questions of community persistence. The fact that microclimatic parameters are relevant for very fine scale organismal processes such as plant physiology (and the challenge that comes with upscaling that process back) and the cost of using such models motivated us to study an intermediary scale of biophysical factors that could explain community compositions. While the links between landscape-scale factors and individuals are more implicit, landscape forest cover and topography data are easy to obtain for every scale and can still have predictive power on community compositions (Bennie *et al.*, 2014).

#### *5.2.3.2. Forest fragmentation impact on community*

Forest fragmentation's role in community response to climate is often viewed through the lens of colonization and dispersal of plants (Aguilar *et al.*, 2006; Dullinger *et al.*, 2015). Our results show that forest fragmentation also influences communities' affinity to climate through differences in soil conditions and the cooling effect of forest cover. The dependence of soil conditions to the bedrock, the historical land use and the subsequent consequences on communities have been studied before (Dupouey *et al.*, 2002b,a; Bergès *et al.*, 2016). The unexpected correlation we found between soil and thermal optima of species enables soil to be a relevant predictor of communities' current and future affinity to climate. Historical land use is dependent on the regional context, but it is likely that the pattern we found - more acid and less fertile soils in high forest covers – can be replicated by agricultural practices in the European forest mosaic (Ellis, 2021; IES *et al.*, 2013). On the other hand, the cooling effect of forest cover we measured here may be more easily generalizable as it stems from the interaction with regional weather and trees (Pokorny *et al.*, 2010). This lines up with the initial expectations that habitat fragmentation alters unevenly temperature within fragments if the different matrices are of different temperatures (Arroyo-Rodríguez *et al.*, 2017; Chen *et al.*, 1999; Tuff *et al.*, 2016). We cannot fully determine what amount of this unexpected cooling originates from regional

cooling of forest cover (Pokorny *et al.*, 2010) or edge-to-interior gradient of temperature (we controlled for it, but with a limited number of plots, Meeussen *et al.*, 2021). As the cooling capacity of forested areas (> 250 ha of forest) may originate from cooling of the regional climate, this could be confirmed by studies compiling wheather stations and using percentage of forest cover as a predictor of temperature. As wheather stations are placed in open fields, this investigation is of interest because it also to test if open vegetation also benefits from the cooling of large forests. The biophysical cooling of forest in a diverse mosaic would thus cool both understory and open species in the same regional climate area. This argument adds up to the body of literature that advocates diverse landscapes as a source of resilience in the face of global changes (Fischer *et al.*, 2006; Stein *et al.*, 2014).

This places large forest patches in the landscape (> 250 ha of forest, in a circle of 300 ha, as with our methods) as important features to favor cold-adapted species in mosaic landscapes. However, the extensive and intensive agriculture of Europe does not allow forests this size, which may lead to an uneven distribution of the forest cooling capacity. To illustrate this, we computed the cooling capacity of every cell of forest of the Copernicus forest cover map (20 meter resolution, Copernicus, 2018) across Europe, when data was available. We obtained the cooling capacity of a cell by multiplying its amount of forest around a 1km radius circle by the decrease in CTI we found in Chapter 3 (- 0.26°C when forest cover increases by 70%, thus a cooling capacity ranging from 0 to 0.37°C for an increase from 0% to 100% forest cover). We summarized this high-resolution map to two values, projected on the 9.25 km resolution map of one land use classification model (e.g. croplands, urban, mosaics of croplands and forests, van Asselen & Verburg, 2012). The two values were the $10^{th}$ and $90^{th}$ centile (i.e. 'minimum' and 'maximum') of the cooling capacity of the forest cells within the land uses cell (Figure 5-3.a). This projection showed a lack of cooling capacity of forest cover over large areas of cropland in the UK, France, and Eastern Europe (Figure 5-3.a). We show that continuous forest systems understandably harbor the higher potential of community cooling, but mosaics of forest and croplands (due to their massifs of diverse sizes) had the highest range of cooling capacity (Figure 5-3.b.c). This means that a variety of forest cover types will lead to communities with various climatic affinity ranges, potentially increasing regional diversity. While there is no substantial evidence of warm-adapted species colonization in lowland forests, diverse landscapes that already host warmer-adapted species could be the first to display thermophilization-induced adaptation because of the proximity of warm-adapted species enabled by the small massifs. This facilitation of colonization could coexist with the large and cold massif that could serve as a population source for the most cold-adapted species of the landscape.

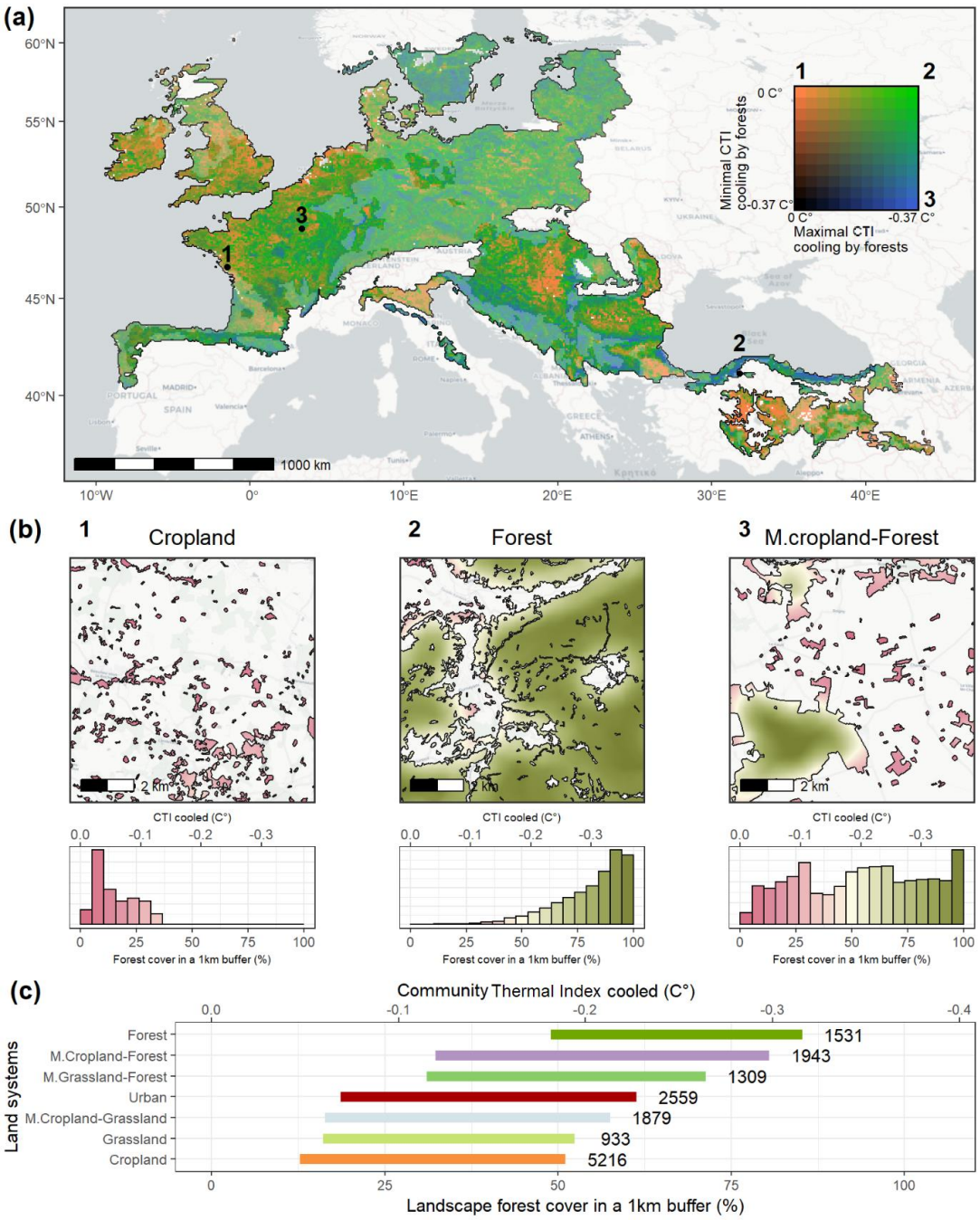


*Figure 5-3: (a): Distribution of the minimum and maximum of the cooling capacity on Community Thermal Index (CTI) by the forest landscape. Minimum and maximum cooling capacity of CTI are defined by the 10th and 90th percentile of the distribution of the cooling capacity of forest cells contained within a land uses cell (resolution: 9.25 km), as shown by the three insets, in (b). Areas where the cooling factor is extrapolated from the initial dataset are shown in lighter areas. (b): Example of three varying land uses cells, a cropland, a forested, and a mosaic of forest and cropland land uses, and their respective distribution of the amount of forest (in a buffer of 1 km radius) around each forested cell, converted to a cooling capacity on CTI. (c): Mean minimum and maximum CTI cooling capacity of land uses cells (within the area without extrapolation) per land uses classification, number of cells are displayed for each classification.*

#### *5.2.3.3. Topographic Cooling Impact on Community*

The study of topography-induced climatic refugia was first mostly concerned with the characterization of the physical processes enabling them, such as the decoupling/buffering of regional temperature by cold air pooling in valleys and by differences in slope aspects (Chen *et al.*, 1999; Dobrowski, 2011; Rull, 2010). Our study is part of the growing body of literature that now seeks to validate the effect of such buffering mechanisms on communities (Bátori *et al.*, 2021; Finocchiaro *et al.*, 2023; Greiser *et al.*, 2020). We cannot test the temporality of the cooling effect we observe on communities because of the lack of vegetation and temperature records series covering longer timespans. Thus, further monitoring and projection of microclimate cooling are needed, especially because the increase of local diversity we found in cold topoclimates (of 5 species) is comparable to the mean extinction of ~1 species decades$^{-1}$. Optimistically, the microclimate induced by topographic features is decoupled from macroscale trends and can conserve durably cold-adapted species. Otherwise, it may only partly buffer trends and slow down thermophilization. In either case, that makes cold refugia relevant targets for conservation planning, which can be first identified from topography maps, and confirmed via measurements and bioindicates of sensitive cold-adapted species (Finocchiaro *et al.*, 2023; Hylander *et al.*, 2022; Pastore *et al.*, 2022). Validation is indeed necessary, as what can make a microrefugia unique is often small-scale topographic features such as rivers and small cliffs, a precise information most digital elevation models lack (Ishiyama *et al.*, 2022; Man *et al.*, 2022).

In our study of topography-induced variation of microclimate and communities, both the loggers and surveys were placed to cover a maximum of variability sources, in a continuous fashion. This approach contrasts with refugia studies which often determine potential microrefugia first and compare them dichotomously with a nearby non-refugium area (Finocchiaro *et al.*, 2023; Greiser *et al.*, 2020). Our approach does not require prior knowledge of targeted refugia but will require setting a threshold and in-situ validation to go from characterizing "cold topoclimate" to a true climatic refugium (Rull, 2010). While cold topoclimates and refugia represent a compelling way to increase the persistence of cold-adapted species, only cold, shade and moisture-adapted communities (and by extension habitats) will be preserved. This means that other sources of persistence should be considered to preserve lowland and mountain communities whose environmental conditions do not match the criteria of the refugia we studied in mountains.

## 5.3. Perspectives

### *5.3.1. A growing dataset of community records*

The increase in quantity and representativeness of resurvey data of baseline situations is key to improve our understanding of community shifts (Verheyen *et al.*, 2017). In that regard, NFI Initiatives integrating understory flora are a powerful tool for further studies and diversity monitoring. The French NFI lacks a true resurvey of plots, but the

systematic nature of the grid sampling makes it so that 10-year cycles are representative of French forests. Every year, approximately 6000 new communities are sampled with a homogenous protocol. Even if yearly-cycle representativeness is less robust (and should be accounted for), they enable year-to-year monitoring of several trends, such as the thermophilization acceleration shown in Figure 5-1. Once the second 10-year cycle is complete, several new types of studies will be made possible. For example, we brought as a limitation the singular time frame of our forest cover study on communities' persistence, but a similar kind of study could be conducted separately for the two cycles, allowing for temporal comparisons of the studied ecological spatial patterns.

The whole NFI or the balanced subset enables a monitoring of local diversity, as brought in (5.2.2). Whether part of the loss of local diversity is due to a diminishing sampling effort over time is up to debate and should be elucidated for robust measurement of diversity loss. However, diversity changes relative to a species thermal optimum (or any other characteristic) may still be assessed because a diminishing sampling effort should affect species independently of their characteristics (e.g. Figure 5-4).

Aggregations of continent-wide ecological datasets are carried out at the species occurrence level, which leaves room for initiatives such as mergings of several countries' NFI to obtain continent scale understory and canopy tree composition (Chirici *et al.*, 2011). This effort requires tremendous homogenization work, a limiting factor that explains why a merged, continent-scale NFI is not available yet (Gschwantner *et al.*, 2022). Furthermore, the majority of European NFIs lack community data. However, our successful study of composition shifts advocates for the start of such surveys. Merges of NFIs are currently constrained to trees (health, growth, etc.), regeneration and habitat typology (Chirici *et al.*, 2011; Kovac *et al.*, 2020). Alternatively, mergings of targeted NFIs could be useful to answer specific questions. For example, finding similarities with the Spanish NFI will allow for a better understanding of the understory dynamics of woody species that could deepen our knowledge of the Mediterranean-temperate forest transition.

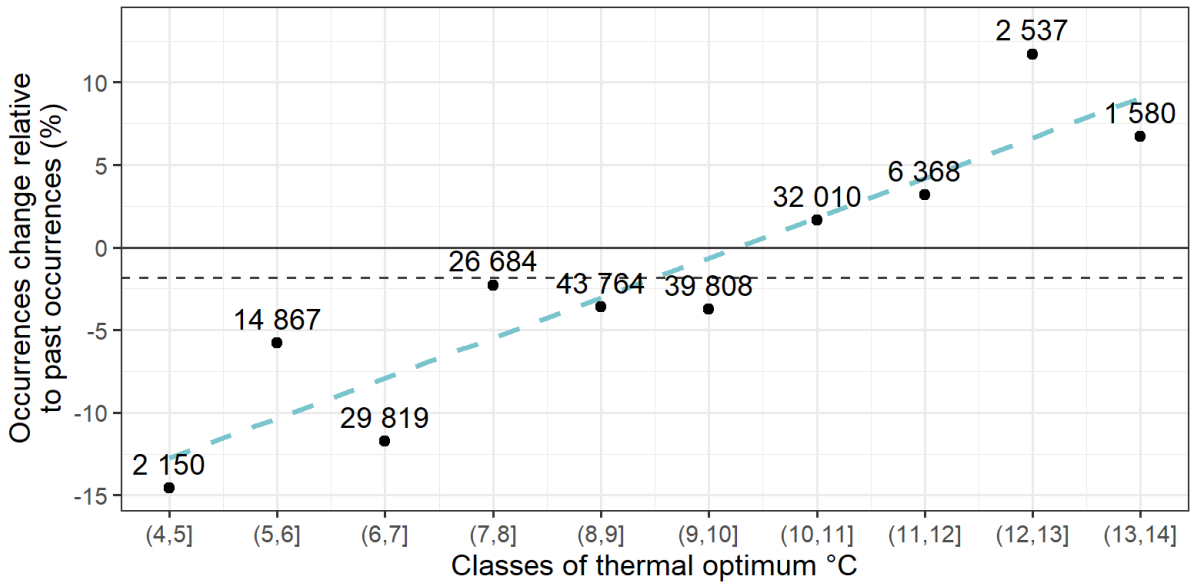


*Figure 5-4: Proportion of occurrence change in 10 years relative to the number of total past occurrences (shown in the labels on top of the points) within a class of species thermal optimum. The gray dotted line represents a theoretical relationship between the two axes under the assumption that a loss in sampling effort alone reduces diversity and is independent of thermal optimum. The blue dotted line represents the actual relationship between the two axes. Species with a thermal optimum lower than 4 ° or higher than 14° were removed because of their low number of occurrences but followed the same trend. Data is from chapter 2 paired dataset.*

### *5.3.2. Opportunities for Space-for-Time substitution studies*

The French NFI (and its subset we built with pairings) are meant to be representative of the spatial resource through time. This highlights the potential of the NFI to both carry out and validate space-for-time substitution studies (SFTS) of community responses to climate change. While SFTS are often employed for projections of species distribution and suitability under future climate, the assumption that the spatial climatic gradient influences communities similarly to the temporal rise of temperature is left unvalidated (Lovell *et al.*, 2023). Spatial (thus climatic) patterns of communities could be first investigated with one cycle of the NFI and validated with newer plots that underwent the recent shift in climatic conditions. To assess the feasibility of this prospect, we must first check if the variability of the mean annual temperature increase (~0.25 °C decades$^{-1}$ in recent years) is sufficient compared to the mean annual temperature gradient in France. The quantification of the true shift in community composition compared to the prediction obtained from a spatial climatic gradient will improve our predictive capabilities.

### *5.3.3. Towards an improvement of niche estimations*

With the increasing availability of microclimatic data, it is now possible to fit species distribution models with much smaller scale data (Haesen, Lenoir, *et al.*, 2023; Lembrechts *et al.*, 2019). It is thus also possible to characterize more precise thermal niches for forest

species (Haesen, Lenoir, *et al.*, 2023). These niches will enable further refugia validation by testing whether a species is in its current range (species within both niche boundaries) or if its presence is contingent on microclimate (the species is within the microclimatic niche but not included in the microclimatic niche).

Another source of improvement of niche estimation is to extend its estimation beyond free air or understory temperature. A first step would be to include soil temperature and moisture (Lembrechts *et al.*, 2020), vapor pressure deficit and other hydric variables (Piedallu *et al.*, 2023). In that regard, the approach taken by (Pérez-Navarro *et al.*, 2021) is promising: by summarizing 12 bioclimatic variables (Fick & Hijmans, 2017) within one species distribution with a principal component analysis, they were able to stay close to the Hutchison hypervolume definition of the niche but with a manageable number of dimensions. It also allowed them to compute multivariate climatic debt, as climate change affected more than just temperature in their study region. This approach is a necessary step to elucidate the ecological questions underlying range shift and community reassembly studies: what process (diffuse heat stresses, heat waves, diffuse water limitation stresses, severe droughts, late frosts, milder springs, etc..) truly eliminates or promotes individuals of a species within a community?

### *5.3.4. Integrating traits and population dynamics into the mix*

The betterment of the use of correlative niche-related approaches (described above) should not undermine the potential for integration of true measurements of species tolerance traits. Through experimental and greenhouse studies, their availability is increasing for both tree, shrub, and herbaceous species. For example, in the flora dataset used in Chapter 2 (Table A2), 38 shrub species, 41 tree species and 56 herbaceous species displayed a determined cold and warm tolerance from (Lancaster & Humphreys, 2020), encompassing 16% of the occurrences (including trees). Cold and freezing tolerance is especially helpful for uncovering the pattern created by late freezing and harsh winter on vegetation. Aside from thermal tolerance, there is also room to explore hydric failure traits (denoting drought tolerance), because as we previously mentioned, drought must be an integral part of the climate change effect on plants (Bartlett *et al.*, 2012; Choat *et al.*, 2012), however, these data are more scarce.

Paradoxically, when it comes to predicting species range shifts and community reshuffling with traits, researchers are often met with poor (albeit significant) predictive power (Angert *et al.*, 2011; Ozinga *et al.*, 2009). The poor predictive power they found is often attributed to the lack of interaction between the traits tested and the environment. In addition to thermal and drought tolerance traits, updated Ellenberg values (Tichý *et al.*, 2023) and dispersal mode and distances are increasingly available (Lososová *et al.*, 2023). These traits can be used to create ambitious multifactorial models with explicit interactions (Decocq *et al.*, 2023). Dispersal traits control on community patterns and reshuffling should be tested interactively with fragmentation metrics to study plant colonization in lowlands.

Traits that induce persistence such as the microclimatic niche should be considered along with canopy opening and south-facing slopes that exacerbate the risk of cold-adapted species local extinction. One interesting modeling prospect when using traits as predictors is the use of Hierarchical Modeling of Species Community (HMSC) that allows to simultaneously fit several species distribution models, using trait and optima as predictors of the assembly of community (Ovaskainen *et al.*, 2017).

One lacking trait for persistence studies is the longevity and detailed life cycle of perennial herbaceous species (Sanczuk *et al.*, 2023). Indeed, we still don't know if refugial populations found in cold topoclimates are viable and reproducing or if they consist of long-lived individuals slowly declining (e.g. Ulrey *et al.*, 2016). The use of phenocams, photography and resurveys of microrefugia will help assess these dynamics and estimate the longevity traits for the species of interest.

### *5.3.5. Interactions and implications for forest management*

Human-induced change in environments has only been studied indirectly throughout this thesis. Canopy cover and landscape forest cover are both susceptible to management, but we did not test any specific management regime. This renders our results unsuitable for a straight handover to forest managers, even though their concerns about understory diversity and forest regeneration are growing (Blondeel *et al.*, 2021).

In our studies, we removed understory regenerating trees from the surveys, as unchecked management practices could confound our results, and because of their slower response to stress, given they are long-lived woody species. However, observations of mismatches of climatic niches between adults and regenerating trees might indicate a change of species in the overstory layer for the coming generation of trees (Bell *et al.*, 2014; Caron *et al.*, 2021; Lenoir *et al.*, 2009). Insights for forest management may be gained if the patterns we report in perennial herbaceous species also apply to juvenile trees. Community reshuffling and response to landscape-scale sources of cooling could be used to bioindicate early signs of the same effect on trees. For example, an extinction-driven thermophilization could indicate a decline in cold and wet-adapted juvenile trees such as *Fagus sylvatica* in lowland forests (Kuhn, 2016; Kuhn & Gegout, 2019). Differences in climatic affinity of juveniles will have different consequences on the diversity of trees depending on the forest patch size (Hertzog *et al.*, 2019), while the better performance of cold-adapted species in cold topoclimate may correlate with better performance of juvenile and adult cold-adapted trees (Bert *et al.*, 2022). As a consequence, our results confirm the need for forestry practice to consider topoclimate beforehand, as the decoupling from local climate could be leveraged to promote the coexistence of cold-adapted stands of *Fagus* and *Abies* and stands adapted to the novel climate in limited geographical extents.

Lastly, our results advocate for maintaining forest cover by reducing clearing or selective logging - especially in the strategic places of high cooling by landscape-scale factors

- to preserve cold-adapted communities and their corresponding habitats. Biodiversity preservation, wood production and public reception are the missions given to the forest manager, but meeting these goals may require facing hard to balance antagonistic forces. This materializes in the increasing demand of forest actors for guidelines and modeling-based decision tools to steer forests in desirable conditions despite an uncertain future (Blades *et al.*, 2016; Blondeel *et al.*, 2021; Wen *et al.*, 2022). This is a reminder that analogous to the climate change discourse, there is a need to summarize all the complexity outlined by researchers into direct and distributable knowledge, empowering the thousands of people collectively shaping future forests in their ability to do so.

# References


Aguilar, R., Ashworth, L., Galetto, L., & Aizen, M. A. (2006). Plant reproductive susceptibility to habitat fragmentation : Review and synthesis through a meta-analysis. *Ecology Letters*, *9*(8), 968-980. https://doi.org/10.1111/j.1461-0248.2006.00927.x

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*(6), 716-723. https://doi.org/10.1109/TAC.1974.1100705

Angert, A. L., Crozier, L. G., Rissler, L. J., Gilman, S. E., Tewksbury, J. J., & Chunco, A. J. (2011). Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, *14*(7), 677-689. https://doi.org/10.1111/j.1461-0248.2011.01620.x

Araújo, M. B., & Peterson, A. T. (2012). Uses and misuses of bioclimatic envelope modeling. *Ecology*, *93*(7), 1527-1539. https://doi.org/10.1890/11-1930.1

Armstrong McKay, D. I., Staal, A., Abrams, J. F., Winkelmann, R., Sakschewski, B., Loriani, S., Fetzer, I., Cornell, S. E., Rockström, J., & Lenton, T. M. (2022). Exceeding 1.5°C global warming could trigger multiple climate tipping points. *Science*, *377*(6611), eabn7950. https://doi.org/10.1126/science.abn7950

Arroyo-Rodríguez, V., Saldaña-Vázquez, R. A., Fahrig, L., & Santos, B. A. (2017). Does forest fragmentation cause an increase in forest temperature? *Ecological Research*, *32*(1), 81-88. https://doi.org/10.1007/s11284-016-1411-6

Ashcroft, M. B. (2010). Identifying refugia from climate change : Identifying refugia from climate change. *Journal of Biogeography*. https://doi.org/10.1111/j.1365-2699.2010.02300.x

Ashcroft, M., Chisholm, L., & French, K. (2008). The effect of exposure on landscape scale soil surface temperatures and species distribution models. *Faculty of Science - Papers (Archive)*, 211-225. https://doi.org/10.1007/s10980-007-9181-8

Auffret, A. G., Rico, Y., Bullock, J. M., Hooftman, D. A. P., Pakeman, R. J., Soons, M. B., Suárez-Esteban, A., Traveset, A., Wagner, H. H., & Cousins, S. A. O. (2017). Plant functional connectivity – integrating landscape structure and effective dispersal. *Journal of Ecology*, *105*(6), 1648-1656. https://doi.org/10.1111/1365-2745.12742

Auffret, A. G., & Svenning, J.-C. (2022). Climate warming has compounded plant responses to habitat conversion in northern Europe. *Nature Communications*, *13*(1), 7818. https://doi.org/10.1038/s41467-022-35516-7

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

Bahn, M., & Körner, Ch. (2003). Recent Increases in Summit Flora Caused by Warming in the Alps. In L. Nagy, G. Grabherr, C. Körner, & D. B. A. Thompson (Éds.), *Alpine Biodiversity in Europe* (p. 437-441). Springer. https://doi.org/10.1007/978-3-642-18967-8_27

Barbosa, A. M., Real, R., Munoz, A. R., & Brown, J. A. (2013). New measures for assessing model equilibrium and prediction mismatch in species distribution models. *Diversity and Distributions*, *19*(10), 1333-1338. https://doi.org/10.1111/ddi.12100

Bartlett, M. K., Scoffoni, C., & Sack, L. (2012). The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes : A global meta-analysis. *Ecology Letters*, *15*(5), 393-405. https://doi.org/10.1111/j.1461-0248.2012.01751.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

Bátori, Z., Erdős, L., Gajdács, M., Barta, K., Tobak, Z., Frei, K., & Tölgyesi, C. (2021). Managing climate change microrefugia for vascular plants in forested karst landscapes. *Forest Ecology and Management*, *496*, 119446. https://doi.org/10.1016/j.foreco.2021.119446

Beck, J., Holloway, J. D., & Schwanghart, W. (2013). Undersampling and the measurement of beta diversity. *Methods in Ecology and Evolution*, *4*(4), 370-382. https://doi.org/10.1111/2041-210x.12023

Becker, M., & Geremia, F. (1984). Indices de climat lumineux selon la pente et l'exposition pour les latitudes de 40 à 50. *Bulletin d'écologie Paris*, *15*(4), 239-252.

Bell, D. M., Bradford, J. B., & Lauenroth, W. K. (2014). Early indicators of change : Divergent climate envelopes between tree life stages imply range shifts in the western United States: Early indications of tree range shift. *Global Ecology and Biogeography*, *23*(2), 168-180. https://doi.org/10.1111/geb.12109

Bénichou, P., & Le Breton, O. (1987). Prise en compte de la topographie pour la cartographie de champs pluviométriques statistiques : La méthode Aurelhy. *Colloques de l'INRA*, *39*(51-69).

Bennie, J., Wilson, R. J., Maclean, I. M. D., & Suggitt, A. J. (2014). Seeing the woods for the trees – when is microclimate important in species distribution models? *Global Change Biology*, *20*(9), 2699-2700. https://doi.org/10.1111/gcb.12525

Bergès, L., Avon, C., Arnaudet, L., Archaux, F., Chauchard, S., & Dupouey, J.-L. (2016). Past landscape explains forest periphery-to-core gradient of understorey plant communities in a reforestation context. *Diversity and Distributions*, *22*(1), 3-16. https://doi.org/10.1111/ddi.12384

Bergès, L., Pellissier, V., Avon, C., Verheyen, K., & Dupouey, J.-L. (2013). Unexpected long-range edge-to-forest interior environmental gradients. *Landscape Ecology*, *28*(3), 439-453. https://doi.org/10.1007/s10980-012-9841-1

Bert, D., Lebourgeois, F., Ouayjan, A., Ducousso, A., Ogée, J., & Hampe, A. (2022). Past and future radial growth and water-use efficiency of Fagus sylvatica and Quercus robur in a long-term climate refugium. *Dendrochronologia*, *72*, 125939. https://doi.org/10.1016/j.dendro.2022.125939

Bertrand, R. (2019). Unequal contributions of species' persistence and migration on plant communities' response to climate warming throughout forests. *Ecography*, *42*(1), 211-213. https://doi.org/10.1111/ecog.03591

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

Blades, J. J., Klos, P. Z., Kemp, K. B., Hall, T. E., Force, J. E., Morgan, P., & Tinkham, W. T. (2016). Forest managers' response to climate change science : Evaluating the constructs of boundary objects and organizations. *Forest Ecology and Management*, *360*, 376-387. https://doi.org/10.1016/j.foreco.2015.07.020

Blondeel, H., Landuyt, D., Vangansbeke, P., De Frenne, P., Verheyen, K., & Perring, M. P. (2021). The need for an understory decision support system for temperate deciduous forest management. *Forest Ecology and Management*, *480*, 118634. https://doi.org/10.1016/j.foreco.2020.118634

Bodin, J., Badeau, V., Bruno, E., Cluzeau, C., Moisselin, J.-M., Walther, G.-R., & Dupouey, J.-L. (2013a). Shifts of forest species along an elevational gradient in Southeast France : Climate change or stand maturation? *Journal of Vegetation Science*, *24*(2), 269-283. https://doi.org/10.1111/j.1654-1103.2012.01456.x

Bodin, J., Badeau, V., Bruno, E., Cluzeau, C., Moisselin, J.-M., Walther, G.-R., & Dupouey, J.-L. (2013b). Shifts of forest species along an elevational gradient in Southeast France : Climate change or stand maturation? *Journal of Vegetation Science*, *24*(2), 269-283. https://doi.org/10.1111/j.1654-1103.2012.01456.x

Bonan, G. B. (2008). Forests and Climate Change : Forcings, Feedbacks, and the Climate Benefits of Forests. *Science*, *320*(5882), 1444-1449. https://doi.org/10.1126/science.1155121

Bonnet, V., Fort, N., Dentant, C., Bonet, R., Salomez, P., & Till-Bottraud, I. (2015). Méthodologie de suivi des espèces végétales rares mise en place par un réseau d'acteurs de la conservation. *Acta Botanica Gallica*, *162*(1), 27-36. https://doi.org/10.1080/12538078.2014.981289

Borderieux, J., Gégout, J.-C., & Serra-Diaz, J. M. (2023). High landscape-scale forest cover favours cold-adapted plant communities in agriculture–forest mosaics. *Global Ecology and Biogeography*, *32*(6), 893-903. https://doi.org/10.1111/geb.13676

Borderieux, J., Gégout, J.-C., & Serra-Diaz, J. M. (2024). Extinction drives recent thermophilization but does not trigger homogenization in forest understorey. *Nature Ecology & Evolution*, 1-10. https://doi.org/10.1038/s41559-024-02362-3

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

Braga, P. H. P., Hébert, K., Hudgins, E. J., Scott, E. R., Edwards, B. P. M., Sánchez Reyes, L. L., Grainger, M. J., Foroughirad, V., Hillemann, F., Binley, A. D., Brookson, C. B., Gaynor, K. M., Shafiei Sabet, S., Güncan, A., Weierbach, H., Gomes, D. G. E., & Crystal-Ornelas, R. (2023). Not just for programmers : How GitHub can accelerate collaborative and reproducible research in ecology and evolution. *Methods in Ecology and Evolution*, *14*(6), 1364-1380. https://doi.org/10.1111/2041-210X.14108

Bramer, I., Anderson, B. J., Bennie, J., Bladon, A. J., De Frenne, P., Hemming, D., Hill, R. A., Kearney, M. R., Körner, C., Korstjens, A. H., Lenoir, J., Maclean, I. M. D., Marsh, C. D., Morecroft, M. D., Ohlemüller, R., Slater, H. D., Suggitt, A. J., Zellweger, F., & Gillingham, P. K. (2018). Chapter Three—Advances in Monitoring and Modelling Climate at Ecologically Relevant Scales. In D. A. Bohan, A. J. Dumbrell, G. Woodward, & M. Jackson (Éds.), *Advances in Ecological Research* (Vol. 58, p. 101-161). Academic Press. https://doi.org/10.1016/bs.aecr.2017.12.005

Braun-blanquet, J. (1932). Plant sociology. The study of plant communities. First ed. *Plant Sociology. The Study of Plant Communities. First Ed.* https://www.cabdirect.org/cabdirect/abstract/19331600801

Brice, M.-H., Cazelles, K., Legendre, P., & Fortin, M.-J. (2019). Disturbances amplify tree community responses to climate change in the temperate–boreal ecotone. *Global Ecology and Biogeography*, *28*(11), 1668-1681. https://doi.org/10.1111/geb.12971

Brockerhoff, E. G., Barbaro, L., Castagneyrol, B., Forrester, D. I., Gardiner, B., González-Olabarria, J. R., Lyver, P. O., Meurisse, N., Oxbrough, A., Taki, H., Thompson, I. D., van der Plas, F., & Jactel, H. (2017). Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and Conservation*, *26*(13), 3005-3035. https://doi.org/10.1007/s10531-017-1453-2

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory of Ecology. *Ecology*, *85*(7), 1771-1789. https://doi.org/10.1890/03-9000

Brunet, J., Hedwall, P.-O., Lindgren, J., & Cousins, S. A. O. (2021). Immigration credit of temperate forest herbs in fragmented landscapes—Implications for restoration of

habitat connectivity. *Journal of Applied Ecology*, *58*(10), 2195-2206. https://doi.org/10.1111/1365-2664.13975

Brunet, J., Valtinat, K., Mayr, M. L., Felton, A., Lindbladh, M., & Bruun, H. H. (2011). Understory succession in post-agricultural oak forests : Habitat fragmentation affects forest specialists and generalists differently. *Forest Ecology and Management*, *262*(9), 1863-1871. https://doi.org/10.1016/j.foreco.2011.08.007

Cahill, A. E., Aiello-Lammens, M. E., Caitlin Fisher-Reid, M., Hua, X., Karanewsky, C. J., Ryu, H. Y., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., & Wiens, J. J. (2014). Causes of warm-edge range limits : Systematic review, proximate factors and implications for climate change. *Journal of Biogeography*, *41*(3), 429-442. https://doi.org/10.1111/jbi.12231

Caron, M. M., Zellweger, F., Verheyen, K., Baeten, L., Hédl, R., Bernhardt-Römermann, M., Berki, I., Brunet, J., Decocq, G., Díaz, S., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Lenoir, J., Macek, M., Malicki, M., Máliš, F., … Frenne, P. D. (2021). Thermal differences between juveniles and adults increased over time in European forest trees. *Journal of Ecology*, *109*(11). https://doi.org/10.1111/1365-2745.13773

Carpenter, W., & Goodenough, A. (2014). How robust are community-based plant bioindicators? Empirical testing of the relationship between Ellenberg values and direct environmental measures in woodland communities. *Community Ecology*, *15*(1), 1-11. https://doi.org/10.1556/comec.15.2014.1.1

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses : Entering the sixth mass extinction. *Science Advances*, *1*(5), e1400253. https://doi.org/10.1126/sciadv.1400253

Chase, J. M., & Leibold, M. A. (2003). *Ecological Niches : Linking Classical and Contemporary Approaches*. University of Chicago Press.

Chave, J. (2013). The problem of pattern and scale in ecology : What have we learned in 20 years? *Ecology Letters*, *16*(s1), 4-16. https://doi.org/10.1111/ele.12048

Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D., Brookshire, B. L., & Franklin, J. F. (1999). Microclimate in Forest Ecosystem and Landscape Ecology : Variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience*, *49*(4). https://doi.org/10.2307/1313612

Chirici, G., Winter, S., & McRoberts, R. E. (2011). *National Forest Inventories : Contributions to Forest Biodiversity Assessments*. Springer Science & Business Media.

Choat, B., Jansen, S., Brodribb, T. J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S. J., Feild, T. S., Gleason, S. M., Hacke, U. G., Jacobsen, A. L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P. J., Nardini, A., Pittermann, J., … Zanne, A. E. (2012). Global convergence in the vulnerability of forests to drought. *Nature*, *491*(7426), 752-755. https://doi.org/10.1038/nature11688

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

Christiansen, D. M., Iversen, L. L., Ehrlén, J., & Hylander, K. (2021). Changes in forest structure drive temperature preferences of boreal understorey plant communities. *Journal of Ecology*, *110*(3). https://doi.org/10.1111/1365-2745.13825

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), 5053. https://doi.org/10.1038/ncomms6053

Copernicus. (2018). *High Resolution Layer Tree Cover Density* [Data set]. https://land.copernicus.eu/en/products/high-resolution-layer-tree-cover-density

Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change? *Trends in Ecology & Evolution*, *28*(8), 482-488. https://doi.org/10.1016/j.tree.2013.04.003

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

Crisfield, V. E., Guillaume Blanchet, F., Raudsepp-Hearne, C., & Gravel, D. (2024). How and why species are rare : Towards an understanding of the ecological causes of rarity. *Ecography*, *2024*(2), e07037. https://doi.org/10.1111/ecog.07037

Danneyrolles, V., Vellend, M., Dupuis, S., Boucher, Y., Laflamme, J., Bergeron, Y., Fortin, G., Leroyer, M., de Römer, A., Terrail, R., & Arseneault, D. (2021). Scale-dependent changes in tree diversity over more than a century in eastern Canada : Landscape diversification and regional homogenization. *Journal of Ecology*, *109*(1), 273-283. https://doi.org/10.1111/1365-2745.13474

Davis, F. W., Synes, N. W., Fricker, G. A., McCullough, I. M., Serra-Diaz, J. M., Franklin, J., & Flint, A. L. (2019). LiDAR-derived topography and forest structure predict fine-scale variation in daily surface temperatures in oak savanna and conifer forest landscapes. *Agricultural and Forest Meteorology*, *269-270*, 192-202. https://doi.org/10.1016/j.agrformet.2019.02.015

Davis, K. T., Dobrowski, S. Z., Holden, Z. A., Higuera, P. E., & Abatzoglou, J. T. (2019). Microclimatic buffering in forests of the future : The role of local water balance. *Ecography*, *42*(1), 1-11. https://doi.org/10.1111/ecog.03836

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D. M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D. H., Koelemeijer, I. A., Lembrechts, J. J., Marrec, R., … Hylander, K. (2021). Forest microclimates and climate change : Importance, drivers and future research agenda. *Global Change Biology*. https://doi.org/10.1111/gcb.15569

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

Decocq, G., Regnault, P., Lenoir, J., Paccaut, F., Di Menza, L., Delvoye, G., Janvresse, E., Closset-Kopp, D., & Goubet, O. (2023). Modelling plant community dynamics in changing forest ecosystems : A review. *Botany Letters*, 1-24. https://doi.org/10.1080/23818107.2023.2231045

Degen, T., Devillez, F., & Jacquemart, A.-L. (2005). Gaps promote plant diversity in beech forests (Luzulo-Fagetum), North Vosges, France. *Annals of Forest Science*, *62*(5), 429-440. https://doi.org/10.1051/forest:2005039

Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D. B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., … Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, *2*(2), 121-124. https://doi.org/10.1038/nclimate1347

Diamond, J. M. (1975). The island dilemma : Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, *7*(2), 129-146. https://doi.org/10.1016/0006-3207(75)90052-X

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R. T., Molnár, Z., Hill, R., Chan, K. M. A., Baste, I. A., Brauman, K. A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P. W., van Oudenhoven, A. P. E., van der Plaat, F., Schröter, M., Lavorel, S., … Shirayama, Y. (2018). Assessing nature's contributions to people. *Science*, *359*(6373), 270-272. https://doi.org/10.1126/science.aap8826

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

Dirzo, R., & Raven, P. H. (2003). Global State of Biodiversity and Loss. *Annual Review of Environment and Resources*, *28*(1), 137-167. https://doi.org/10.1146/annurev.energy.28.050302.105532

Dobrowski, S. Z. (2011). A climatic basis for microrefugia : The influence of terrain on climate. *Global Change Biology*, *17*(2), 1022-1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Doelman, J. C., Stehfest, E., Tabeau, A., Meijl, H. van, Lassaletta, L., Gernaat, D. E. H. J., Neumann-Hermans, K., Harmsen, M., Daioglou, V., Biemans, H., Sluis, S. van der, & Vuuren, D. P. van. (2018). Exploring SSP land-use dynamics using the IMAGE model : Regional and gridded scenarios of land-use change and land-based climate change mitigation. *Global Environmental Change*, *48*, 119-135. https://doi.org/10.1016/j.gloenvcha.2017.11.014

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

Duchenne, F., Martin, G., & Porcher, E. (2021). European plants lagging behind climate change pay a climatic debt in the North, but are favoured in the South. *Ecology Letters*. https://doi.org/10.1111/ele.13730

Dullinger, S., Dendoncker, N., Gattringer, A., Leitner, M., Mang, T., Moser, D., Mücher, C. A., Plutzar, C., Rounsevell, M., Willner, W., Zimmermann, N. E., & Hülber, K. (2015). Modelling the effect of habitat fragmentation on climate-driven migration of European forest understorey plants. *Diversity and Distributions*, *21*(12), 1375-1387. https://doi.org/10.1111/ddi.12370

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), 619-622. https://doi.org/10.1038/nclimate1514

Dunnington, D., & Thorne, B. (2020). ggspatial : Spatial Data Framework for ggplot2. *R package version1*, *1*.

Dupouey, J.-L., Dambrine, E., Laffite, J. D., & Moares, C. (2002). Irreversible Impact of Past Land Use on Forest Soils and Biodiversity. *Ecology*, *83*(11), 2978-2984. https://doi.org/10.1890/0012-9658(2002)083[2978:IIOPLU]2.0.CO;2

Dupouey, J.-L., Sciama, D., Dambrine, E., Rameau, J.-C., & Koerner, W. (2002). La Végétation des forêts anciennes. *Revue Forestière Française*, *6*, 521. https://doi.org/10.4267/2042/4940

Ellenberg, H., Weber, H.-E., Düll, R., Wirth, V., Werner, W., & Paulißen, D. (1992). *Zeigerwerte von Pflanzen in Mitteleuropa* (Vol. 18).

Ellis, C. J., & Eaton, S. (2021). Climate change refugia : Landscape, stand and tree-scale microclimates in epiphyte community composition. *The Lichenologist*, *53*(1), 135-148. https://doi.org/10.1017/S0024282920000523

Ellis, E. (2021). Land Use and Ecological Change : A 12,000-Year History. *Annual Review of Environment and Resources*, *46*(1), 1-33. https://doi.org/10.1146/annurev-environ-012220-010822

Ellis, E., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Díaz, S., Fuller, D. Q., Gill, J. L., Kaplan, J. O., Kingston, N., Locke, H., McMichael, C. N. H., Ranco, D., Rick, T. C., Shaw, M. R., Stephens, L., Svenning, J.-C., & Watson, J. E. M. (2021). People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences*, *118*(17), e2023483118. https://doi.org/10.1073/pnas.2023483118

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: *Global Change Biology*, *17*(7), 2330-2341. https://doi.org/10.1111/j.1365-2486.2010.02393.x

Euro + Med. (2006). *Euro+Med PlantBase—The information resource for Euro-Mediterranean plant diversity. Http:// www.emplantbase.org/home.html*.

Evans, J. S., & Murphy, M. A. (2021). *spatialEco*. https://github.com/jeffreyevans/spatialEco

Ewald, J. (2003). The calcareous riddle : Why are there so many calciphilous species in the Central European flora? *Folia Geobotanica*, *38*(4), 357-366. https://doi.org/10.1007/BF02803244

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 487-515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig, L. (2017). Ecological Responses to Habitat Fragmentation Per Se. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 1-23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fahrig, L., Arroyo-Rodríguez, V., Bennett, J. R., Boucher-Lalonde, V., Cazetta, E., Currie, D. J., Eigenbrod, F., Ford, A. T., Harrison, S. P., Jaeger, J. A. G., Koper, N., Martin, A. E., Martin, J.-L., Metzger, J. P., Morrison, P., Rhodes, J. R., Saunders, D. A., Simberloff, D., Smith, A. C., … Watling, J. I. (2019). Is habitat fragmentation bad for biodiversity? *Biological Conservation*, *230*, 179-186. https://doi.org/10.1016/j.biocon.2018.12.026

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2 : New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302-4315. https://doi.org/10.1002/joc.5086

Finocchiaro, M., Médail, F., Saatkamp, A., Diadema, K., Pavon, D., & Meineri, E. (2023). Bridging the gap between microclimate and microrefugia : A bottom-up approach reveals strong climatic and biological offsets. *Global Change Biology*, *29*(4), 1024-1036. https://doi.org/10.1111/gcb.16526

Fischer, A., Lindner, M., Abs, C., & Lasch, P. (2002). Vegetation dynamics in central european forest ecosystems (near-natural as well as managed) after storm events. *Folia Geobotanica*, *37*(1), 17-32. https://doi.org/10.1007/BF02803188

Fischer, J., Lindenmayer, D. B., & Manning, A. D. (2006). Biodiversity, ecosystem function, and resilience : Ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment*, *4*(2), 80-86. https://doi.org/10.1890/1540-9295(2006)004[0080:BEFART]2.0.CO;2

Flahault, C. (1893). La distribution géographique des végétaux dans un coin du Languedoc. *Imprimerie Ricard Freres, Montpellier, France*.

Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences*, *113*(14), 3725-3734. https://doi.org/10.1073/pnas.1519911113

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

Frey, S. J. K., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016). Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, *2*(4), e1501392. https://doi.org/10.1126/sciadv.1501392

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M. C., Fröberg, M., Stendahl, J., Philipson, C. D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., & Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, *4*(1), 1340. https://doi.org/10.1038/ncomms2328

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

Geiger, R., Aron, R. H., & Todhunter, P. (2009). *The climate near the ground*. Rowman & Littlefield.

Gessler, A., Schaub, M., Bose, A., Trotsiuk, V., Valbuena, R., Chirici, G., & Buchmann, N. (2024). Finding the balance between open access to forest data while safeguarding the integrity of National Forest Inventory-derived information. *New Phytologist*, *242*(2), 344-346. https://doi.org/10.1111/nph.19466

Gilliam, F. S. (2007). The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems. *BioScience*, *57*(10), 845-858. https://doi.org/10.1641/B571007

Godefroid, S., Rucquoij, S., & Koedam, N. (2006). Spatial variability of summer microclimates and plant species response along transects within clearcuts in a beech forest. *Plant Ecology*, *185*(1), 107-121. https://doi.org/10.1007/s11258-005-9088-x

Gosselin, F. (2016). Putting floristic thermophilization in forests into a conservation biology perspective : Beyond mean trait approaches. *Annals of Forest Science*, *73*(2), 215-218. https://doi.org/10.1007/s13595-015-0526-1

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), 111-115. 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*, *109*(6). https://doi.org/10.1111/1365-2745.13653

Greiser, C., Ehrlén, J., Meineri, E., & Hylander, K. (2020). Hiding from the climate : Characterizing microrefugia for boreal forest understory species. *Global Change Biology*, *26*(2), 471–483. https://doi.org/10.1111/gcb.14874

Greiser, C., Meineri, E., Luoto, M., Ehrlén, J., & Hylander, K. (2018). Monthly microclimate models in a managed boreal forest landscape. *Agricultural and Forest Meteorology*, *250-251*, 147–158. https://doi.org/10.1016/j.agrformet.2017.12.252

Gril, E., Laslier, M., Gallet-Moron, E., Durrieu, S., Spicher, F., Le Roux, V., Brasseur, B., Haesen, S., Van Meerbeek, K., Decocq, G., Marrec, R., & Lenoir, J. (2023). Using airborne LiDAR to map forest microclimate temperature buffering or amplification. *Remote Sensing of Environment*, *298*, 113820. https://doi.org/10.1016/j.rse.2023.113820

Gschwantner, T., Alberdi, I., Bauwens, S., Bender, S., Borota, D., Bosela, M., Bouriaud, O., Breidenbach, J., Donis, J., Fischer, C., Gasparini, P., Heffernan, L., Hervé, J.-C., Kolozs, L., Korhonen, K. T., Koutsias, N., Kovácsevics, P., Kučera, M., Kulbokas, G., … Tomter, S. M. (2022). Growing stock monitoring by European National Forest Inventories : Historical origins, current methods and harmonisation. *Forest Ecology and Management*, *505*, 119868. https://doi.org/10.1016/j.foreco.2021.119868

Gudiksen, P. H., Leone, J. M., King, C. W., Ruffieux, D., & Neff, W. D. (1992). Measurements and Modeling of the Effects of Ambient Meteorology on Nocturnal Drainage Flows. *Journal of Applied Meteorology and Climatology*, *31*(9), 1023-1032. https://doi.org/10.1175/1520-0450(1992)031<1023:MAMOTE>2.0.CO;2

Guyennon, A., Reineking, B., Dahlgren, J., Lehtonen, A., Ratcliffe, S., Ruiz-Benito, P., Zavala, M. A., & Kunstler, G. (2022). Colonization and extinction dynamics and their link to the distribution of European trees at the continental scale. *Journal of Biogeography*, *49*(1), 117-129. https://doi.org/10.1111/jbi.14286

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., … Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2), e1500052. https://doi.org/10.1126/sciadv.1500052

Haesen, S., Lembrechts, J. J., De Frenne, P., Lenoir, J., Aalto, J., Ashcroft, M. B., Kopecký, M., Luoto, M., Maclean, I., Nijs, I., Niittynen, P., van den Hoogen, J., Arriga, N., Brůna, J., Buchmann, N., Čiliak, M., Collalti, A., De Lombaerde, E., Descombes, P., … Van Meerbeek, K. (2021). ForestTemp – Sub-canopy microclimate temperatures of European forests. *Global Change Biology*, *27*(23), 6307-6319. https://doi.org/10.1111/gcb.15892

Haesen, S., Lembrechts, J. J., De Frenne, P., Lenoir, J., Aalto, J., Ashcroft, M. B., Kopecký, M., Luoto, M., Maclean, I., Nijs, I., Niittynen, P., van den Hoogen, J., Arriga, N.,

Brůna, J., Buchmann, N., Čiliak, M., Collalti, A., De Lombaerde, E., Descombes, P., … Van Meerbeek, K. (2023). ForestClim—Bioclimatic variables for microclimate temperatures of European forests. *Global Change Biology*, *29*(11), 2886-2892. https://doi.org/10.1111/gcb.16678

Haesen, S., Lenoir, J., Gril, E., Frenne, P. D., Lembrechts, J., Kopecký, M., Macek, M., Man, M., Wild, J., & Meerbeek, K. V. (2023). *Uncovering the hidden niche : Incorporating microclimate temperature into species distribution models*. https://ecoevorxiv.org/repository/view/5364/

Hanski, I. (2011). Habitat Loss, the Dynamics of Biodiversity, and a Perspective on Conservation. *AMBIO*, *40*(3), 248-255. https://doi.org/10.1007/s13280-011-0147-3

Heinken, T., Diekmann, M., Liira, J., Orczewska, A., Schmidt, M., Brunet, J., Chytrý, M., Chabrerie, O., Decocq, G., De Frenne, P., Dřevojan, P., Dzwonko, Z., Ewald, J., Feilberg, J., Graae, B. J., Grytnes, J.-A., Hermy, M., Kriebitzsch, W.-U., Laiviņš, M., … Vanneste, T. (2022). The European Forest Plant Species List (EuForPlant) : Concept and applications. *Journal of Vegetation Science*, *33*(3), e13132. https://doi.org/10.1111/jvs.13132

Heinrichs, S., & Schmidt, W. (2017). Biotic homogenization of herb layer composition between two contrasting beech forest communities on limestone over 50 years. *Applied Vegetation Science*, *20*(2), 271-281. https://doi.org/10.1111/avsc.12255

Hertzog, L. R., Boonyarittichaikij, R., Dekeukeleire, D., de Groote, S. R. E., van Schrojenstein Lantman, I. M., Sercu, B. K., Smith, H. K., de la Peña, E., Vandegehuchte, M. L., Bonte, D., Martel, A., Verheyen, K., Lens, L., & Baeten, L. (2019). Forest fragmentation modulates effects of tree species richness and composition on ecosystem multifunctionality. *Ecology*, *100*(4), e02653. https://doi.org/10.1002/ecy.2653

Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). landscapemetrics : An open-source R tool to calculate landscape metrics. *Ecography*, *42*(10), 1648-1657. https://doi.org/10.1111/ecog.04617

Hesslerová, P., Pokorný, J., Brom, J., & Rejšková – Procházková, A. (2013). Daily dynamics of radiation surface temperature of different land cover types in a temperate cultural landscape : Consequences for the local climate. *Ecological Engineering*, *54*, 145-154. https://doi.org/10.1016/j.ecoleng.2013.01.036

Hijmans, R. J. (2020). *raster : Geographic Data Analysis and Modeling*. https://CRAN.R-project.org/package=raster

Honnay, O., Jacquemyn, H., Bossuyt, B., & Hermy, M. (2005). Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist*, *166*(3), 723-736. https://doi.org/10.1111/j.1469-8137.2005.01352.x

Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B., & Hermy, M. (2002). Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters*, *5*(4), 525-530. https://doi.org/10.1046/j.1461-0248.2002.00346.x

Hooper, D. U., Chapin III, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of Biodiversity on Ecosystem Functioning : A Consensus of Current Knowledge. *Ecological Monographs*, *75*(1), 3-35. https://doi.org/10.1890/04-0922

Hubbell, S. P. (2011). The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32). In *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*. Princeton University Press. https://doi.org/10.1515/9781400837526

Humboldt, A. von. (1805). *Essai sur la géographie des plantes : Accompagne d'un tableau physique des régions équinoxiales, fondé sur des mesures exécutées, depuis le dixième degré la latitude boréale juasqu'au dixième degré de latitude australe,*

*pendant les années 1799, 1800, 1801, 1802 et 1803 par Al. de Humboldt et A. Bonpland*. chez Levrault, Schoell et Cie.

Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*(0), 415‑427. https://doi.org/10.1101/SQB.1957.022.01.039

Hylander, K., Greiser, C., Christiansen, D. M., & Koelemeijer, I. A. (2022). Climate adaptation of biodiversity conservation in managed forest landscapes. *Conservation Biology*, *36*(3), e13847. https://doi.org/10.1111/cobi.13847

IES, Caudullo, G., San Miguel, J., Estreguil, C., & Rigo, D. de. (2013). *Forest landscape in Europe : Pattern, fragmentation and connectivity*. Publications Office of the European Union. https://data.europa.eu/doi/10.2788/77842

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

IGN. (2017). *BD ALTI Le modèle numérique de terrain (MNT) maillé qui décrit le relief du territoire français à moyenne échelle* [Data set]. https://geoservices.ign.fr/documentation/donnees/alti/bdalti

IGN. (2019a). *BD Forêt version 2*. Institut National de l'Information Géographique et Forestière. https://inventaire-forestier.ign.fr/spip.php?article646

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

IPCC. (2014). IPCC Fifth Assessment Report—Synthesis Report. *IPPC Rome, Italy*.

IPCC. (2021a). *Climate Change 2021 : The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change: Vol. In Press*. Cambridge University Press. https://doi.org/10.1017/9781009157896

IPCC. (2021b). Summary for Policymakers. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Éds.), *Climate Change 2021 : The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (p. 3‑32). Cambridge University Press. https://doi.org/10.1017/9781009157896.001

Ishiyama, N., Sueyoshi, M., Jorge, G. M., Iwasaki, K., Negishi, N. J., Koizumi, I., Nagayama, S., Nagasaka, A., Nagasaka, Y., & Nakamura, F. (2022). *The role of geology in creating stream climate-change refugia along climate gradients* (p. 2022.05.02.490355). bioRxiv. https://doi.org/10.1101/2022.05.02.490355

Jackson, S. T., & Sax, D. F. (2010). Balancing biodiversity in a changing environment : Extinction debt, immigration credit and species turnover. *Trends in Ecology & Evolution*, *25*(3), 153‑160. https://doi.org/10.1016/j.tree.2009.10.001

Jandt, U., Bruelheide, H., Jansen, F., Bonn, A., Grescho, V., Klenke, R. A., Sabatini, F. M., Bernhardt-Römermann, M., Blüml, V., Dengler, J., Diekmann, M., Doerfler, I., Döring, U., Dullinger, S., Haider, S., Heinken, T., Horchler, P., Kuhn, G., Lindner, M., … Wulf, M. (2022). More losses than gains during one century of plant biodiversity change in Germany. *Nature*, *611*(7936), 512‑518. https://doi.org/10.1038/s41586-022-05320-w

Johnston, A. K., Brewster, D., & Berghaus, H. K. W. (1848). *The physical atlas : A series of maps & notes illustrating the geographical distribution of natural phenomena* [Map]. William Blackwood & Sons.

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

Kemppinen, J., Lembrechts, J. J., Van Meerbeek, K., Carnicer, J., Chardon, N. I., Kardol, P., Lenoir, J., Liu, D., Maclean, I., Pergl, J., Saccone, P., Senior, R. A., Shen, T., Słowińska, S., Vandvik, V., von Oppen, J., Aalto, J., Ayalew, B., Bates, O., … De Frenne, P. (2023). *Microclimate, an inseparable part of ecology and biogeography*. Zenodo. https://doi.org/10.5281/zenodo.7973314

Kettle, C. J., & Koh, L. P. (2014). *Global Forest Fragmentation*. CABI.

Kiebacher, T., Meier, M., Kipfer, T., & Roth, T. (2023). Thermophilisation of communities differs between land plant lineages, land use types and elevation. *Scientific Reports*, *13*(1), 11395. https://doi.org/10.1038/s41598-023-38195-6

Koerner, W., Dupouey, J. L., Dambrine, E., & Benoit, M. (1997). Influence of Past Land Use on the Vegetation and Soils of Present Day Forest in the Vosges Mountains, France. *Journal of Ecology*, *85*(3), 351-358. https://doi.org/10.2307/2960507

Kondratyeva, A., Grandcolas, P., & Pavoine, S. (2019). Reconciling the concepts and measures of diversity, rarity and originality in ecology and evolution. *Biological Reviews*, *94*(4), 1317-1337. https://doi.org/10.1111/brv.12504

Kovac, M., Gasparini, P., Notarangelo, M., Rizzo, M., Cañellas, I., Fernández-de-Uña, L., & Alberdi, I. (2020). Towards a set of national forest inventory indicators to be used for assessing the conservation status of the habitats directive forest habitat types. *Journal for Nature Conservation*, *53*, 125747. https://doi.org/10.1016/j.jnc.2019.125747

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*(5), 592-599. https://doi.org/10.1111/1365-2435.12345

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

Kuczynski, L., Ontiveros, V. J., & Hillebrand, H. (2023). Biodiversity time series are biased towards increasing species richness in changing environments. *Nature Ecology & Evolution*, 1-8. https://doi.org/10.1038/s41559-023-02078-w

Kuhn, E. (2016). *Expansion and decline of forest plants' species under climate change*. AgroParisTech.

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

Kulonen, A., Imboden, R. A., Rixen, C., Maier, S. B., & Wipf, S. (2018). Enough space in a warmer world? Microhabitat diversity and small-scale distribution of alpine plants on mountain summits. *Diversity and Distributions*, *24*(2), 252-261. https://doi.org/10.1111/ddi.12673

Kunstler, G., Guyennon, A., Ratcliffe, S., Rüger, N., Ruiz-Benito, P., Childs, D. Z., Dahlgren, J., Lehtonen, A., Thuiller, W., Wirth, C., Zavala, M. A., & Salguero-Gomez, R. (2021). Demographic performance of European tree species at their hot and cold climatic edges. *Journal of Ecology*, *109*(2), 1041-1054. https://doi.org/10.1111/1365-2745.13533

Lancaster, L. T., & Humphreys, A. M. (2020). Global variation in the thermal tolerances of plants. *Proceedings of the National Academy of Sciences*, *117*(24), 13580-13587. https://doi.org/10.1073/pnas.1918162117

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.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept : A framework for multi-scale community ecology. *Ecology Letters*, *7*(7), 601-613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lembrechts, J. J., Aalto, J., Ashcroft, M. B., De Frenne, P., Kopecký, M., Lenoir, J., Luoto, M., Maclean, I. M. D., Roupsard, O., Fuentes-Lillo, E., García, R. A., Pellissier, L., Pitteloud, C., Alatalo, J. M., Smith, S. W., Björk, R. G., Muffler, L., Ratier Backes, A., Cesarz, S., … Nijs, I. (2020). SoilTemp : A global database of near-surface temperature. *Global Change Biology*, *26*(11), 6616-6629. https://doi.org/10.1111/gcb.15123

Lembrechts, J. J., Lenoir, J., Scheffers, B., & De Frenne, P. (2021). Designing countrywide and regional microclimate networks. *Global Ecology and Biogeography*. https://doi.org/10.1111/geb.13290

Lembrechts, J. J., Nijs, I., & Lenoir, J. (2019). Incorporating microclimate into species distribution models. *Ecography*, *42*(7), 1267-1279. https://doi.org/10.1111/ecog.03947

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., Gégout, J.-C., Pierrat, J.-C., Bontemps, J.-D., & Dhôte, J.-F. (2009). Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986-2006). *Ecography*, *32*(5), 765-777. https://doi.org/10.1111/j.1600-0587.2009.05791.x

Lenoir, J., Graae, B. J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G., Bergendorff, C., Birks, H. J. B., Bråthen, K. A., Brunet, J., Bruun, H. H., Dahlberg, C. J., Decocq, G., Diekmann, M., Dynesius, M., Ejrnæs, R., Grytnes, J.-A., Hylander, K., Klanderud, K., … Svenning, J.-C. (2013). Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology*, *19*(5), 1470-1481. https://doi.org/10.1111/gcb.12129

Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change : Implications for species redistribution. *Ecography*, *40*(2), 253-266. https://doi.org/10.1111/ecog.02788

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

Lenton, T. M., Rockström, J., Gaffney, O., Rahmstorf, S., Richardson, K., Steffen, W., & Schellnhuber, H. J. (2019). Climate tipping points—Too risky to bet against. *Nature*, *575*(7784), 592-595. https://doi.org/10.1038/d41586-019-03595-0

Levin, S. A. (1992). The Problem of Pattern and Scale in Ecology : The Robert H. MacArthur Award Lecture. *Ecology*, *73*(6), 1943-1967. https://doi.org/10.2307/1941447

Li, Y., Zhao, M., Motesharrei, S., Mu, Q., Kalnay, E., & Li, S. (2015). Local cooling and warming effects of forests based on satellite observations. *Nature Communications*, *6*(1), 6603. https://doi.org/10.1038/ncomms7603

Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A. D., Bozzato, F., Pretzsch, H., de-Miguel, S., Paquette, A., Herault, B.,

Scherer-Lorenzen, M., Barrett, C. B., Glick, H. B., Hengeveld, G. M., Nabuurs, G.-J., Pfautsch, S., … Reich, P. B. (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science*, *354*(6309), aaf8957-aaf8957. https://doi.org/10.1126/science.aaf8957

Linnaeus, C. (1758). Systema naturae, Vol. 1. *Systema naturae, Vol. 1*. https://www.cabdirect.org/cabdirect/abstract/20057000018

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

Lomolino, MarK. V. (2000). A call for a new paradigm of island biogeography. *Global Ecology and Biogeography*, *9*(1), 1-6. https://doi.org/10.1046/j.1365-2699.2000.00185.x

Loreau, M., & de Mazancourt, C. (2013). Biodiversity and ecosystem stability : A synthesis of underlying mechanisms. *Ecology Letters*, *16*, 106-115. https://doi.org/10.1111/ele.12073

Lososová, Z., Axmanová, I., Chytrý, M., Midolo, G., Abdulhak, S., Karger, D. N., Renaud, J., Van Es, J., Vittoz, P., & Thuiller, W. (2023). Seed dispersal distance classes and dispersal modes for the European flora. *Global Ecology and Biogeography*, *32*(9). https://doi.org/10.1111/geb.13712

Lovell, R. S. L., Collins, S., Martin, S. H., Pigot, A. L., & Phillimore, A. B. (2023). Space-for-time substitutions in climate change ecology and evolution. *Biological Reviews*, *98*(6). https://doi.org/10.1111/brv.13004

MA. (2005). *Ecosystems and human well-being* (Millennium Ecosystem Assessment, Vol. 5).

Ma, Q., Su, Y., & Guo, Q. (2017). Comparison of Canopy Cover Estimations From Airborne LiDAR, Aerial Imagery, and Satellite Imagery. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, *10*(9), 4225-4236. https://doi.org/10.1109/JSTARS.2017.2711482

Macek, M., Kopecký, M., & Wild, J. (2019). Maximum air temperature controlled by landscape topography affects plant species composition in temperate forests. *Landscape Ecology*, *34*(11), 2541-2556. https://doi.org/10.1007/s10980-019-00903-x

Maciejewski, L., Kuhn, E., Gégout-Petit, A., & Gégout, J.-C. (2020). Natura 2000 forest habitats : Climatic debt in lowlands and thermophilization in highlands. *Biodiversity and Conservation*, *29*(13), 3689-3701. https://doi.org/10.1007/s10531-020-02044-z

Maciejewski, L., Pinto, P. E., Wurpillot, S., Drapier, J., Cadet, S., Muller, S., Agou, P., Renaux, B., & Gégout, J.-C. (2022). A limited number of species is sufficient to assign a vegetation plot to a forest vegetation unit. *Applied Vegetation Science*, *25*(1), e12650. https://doi.org/10.1111/avsc.12650

Maclean, I. M. D. (2020). Predicting future climate at high spatial and temporal resolution. *Global Change Biology*, *26*(2), 1003-1011. https://doi.org/10.1111/gcb.14876

Maclean, I. M. D., Hopkins, J. J., Bennie, J., Lawson, C. R., & Wilson, R. J. (2015). Microclimates buffer the responses of plant communities to climate change. *Global Ecology and Biogeography*, *24*(11), 1340-1350. https://doi.org/10.1111/geb.12359

Maclean, I. M. D., Mosedale, J. R., & Bennie, J. J. (2019). Microclima : An r package for modelling meso- and microclimate. *Methods in Ecology and Evolution*, *10*(2), 280-290. https://doi.org/10.1111/2041-210X.13093

Man, M., Kalčík, V., Macek, M., Brůna, J., Hederová, L., Wild, J., & Kopecký, M. (2023). myClim : Microclimate data handling and standardised analyses in R. *Methods in Ecology and Evolution*, *14*(9). https://doi.org/10.1111/2041-210X.14192

Man, M., Wild, J., Macek, M., & Kopecký, M. (2022). Can high-resolution topography and forest canopy structure substitute microclimate measurements? Bryophytes say no. *Science of The Total Environment*, *821*, 153377. https://doi.org/10.1016/j.scitotenv.2022.153377

Marchetti, M., Lockwood, J., & Hoopes, M. (2023). *Ecology in a Changing World*. WW Norton & Co.

Marrec, R., Gril, E., Spicher, F., Vital, G., & Lenoir, J. (2022). *Can flora predict forest microclimate?* https://doi.org/10.13140/RG.2.2.29973.40165

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

Martínez-Meyer, E., Díaz-Porras, D., Peterson, A. T., & Yáñez-Arenas, C. (2013). Ecological niche structure and rangewide abundance patterns of species. *Biology Letters*, *9*(1), 20120637. https://doi.org/10.1098/rsbl.2012.0637

Matthews, T. J., & Whittaker, R. J. (2015). REVIEW : On the species abundance distribution in applied ecology and biodiversity management. *Journal of Applied Ecology*, *52*(2), 443-454. https://doi.org/10.1111/1365-2664.12380

McCune, B., & Keon, D. (2002). Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science*, *13*(4), 603-606. https://doi.org/10.1111/j.1654-1103.2002.tb02087.x

McIntosh, R. P. (1985, mai). *The Background of Ecology : Concept and Theory*. Cambridge Core; Cambridge University Press. https://doi.org/10.1017/CBO9780511608537

McKinney, M. L., & Lockwood, J. L. (2001). Biotic Homogenization : A Sequential and Selective Process. In J. L. Lockwood & M. L. McKinney (Éds.), *Biotic Homogenization* (p. 1-17). Springer US. https://doi.org/10.1007/978-1-4615-1261-5_1

Meeussen, C., Govaert, S., Vanneste, T., Bollmann, K., Brunet, J., Calders, K., Cousins, S. A. O., De Pauw, K., Diekmann, M., Gasperini, C., Hedwall, P.-O., Hylander, K., Iacopetti, G., Lenoir, J., Lindmo, S., Orczewska, A., Ponette, Q., Plue, J., Sanczuk, P., … De Frenne, P. (2021). Microclimatic edge-to-interior gradients of European deciduous forests. *Agricultural and Forest Meteorology*. https://doi.org/10.1016/j.agrformet.2021.108699

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

Météo France. (2024). *Meteo.data.gouv.fr*. https://meteo.data.gouv.fr/datasets

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

Mittelbach, G. G., & McGill, B. J. (2019). *Community Ecology*. Oxford University Press.

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

Morin, P. J. (2009). *Community Ecology*. John Wiley & Sons.

Naaf, T., & Wulf, M. (2012). Does taxonomic homogenization imply functional homogenization in temperate forest herb layer communities? *Plant Ecology*, *213*(3), 431-443. https://doi.org/10.1007/s11258-011-9990-3

Nath, S., Shyanti, R. K., & Nath, Y. (2021). 4—Influence of anthropocene climate change on biodiversity loss in different ecosystems. In S. Singh, P. Singh, S. Rangabhashiyam, & K. K. Srivastava (Éds.), *Global Climate Change* (p. 63-78). Elsevier. https://doi.org/10.1016/B978-0-12-822928-6.00001-0

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

Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C. D. L., Petchey, O. L., Proença, V., Raffaelli, D., Suttle, K. B., Mace, G. M., Martín-López, B., Woodcock, B. A., & Bullock, J. M. (2015).

Biodiversity and Resilience of Ecosystem Functions. *Trends in Ecology & Evolution*, *30*(11), 673-684. https://doi.org/10.1016/j.tree.2015.08.009

OpenStreetMap contributors. (2017). *Planet dump retrieved from https://planet.osm.org*.

Osman, K. T. (2013). Forest Soils. In K. T. Osman (Éd.), *Soils : Principles, Properties and Management* (p. 229-251). Springer Netherlands. https://doi.org/10.1007/978-94-007-5663-2_14

Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, *20*(5), 561-576. https://doi.org/10.1111/ele.12757

Ozinga, W. A., Colles, A., Bartish, I. V., Hennion, F., Hennekens, S. M., Pavoine, S., Poschlod, P., Hermant, M., Schaminée, J. H. J., & Prinzing, A. (2013). Specialists leave fewer descendants within a region than generalists : Scarce descendants of specialists. *Global Ecology and Biogeography*, *22*(2), 213-222. https://doi.org/10.1111/j.1466-8238.2012.00792.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

Pacheco-Riaño, L. C., Høistad Schei, F., Flantua, S. G. A., & Grytnes, J.-A. (2023). Lags in the response of plant assemblages to global warming depends on temperature-change velocity. *Global Ecology and Biogeography*, *32*(5), 719-733. https://doi.org/10.1111/geb.13653

Pastore, M. A., Classen, A. T., D'Amato, A. W., Foster, J. R., & Adair, E. C. (2022). Cold-air pools as microrefugia for ecosystem functions in the face of climate change. *Ecology*, *103*(8), e3717. https://doi.org/10.1002/ecy.3717

Pauli, H., Gottfried, M., & Grabherr, G. (2001). High summits of the Alps in a changing climate. In G.-R. Walther, C. A. Burga, & P. J. Edwards (Éds.), *"Fingerprints" of Climate Change : Adapted Behaviour and Shifting Species Ranges* (p. 139-149). Springer US. https://doi.org/10.1007/978-1-4419-8692-4_9

Pearman, P. B., Randin, C. F., Broennimann, O., Vittoz, P., Knaap, W. O. V. D., Engler, R., Lay, G. L., Zimmermann, N. E., & Guisan, A. (2008). Prediction of plant species distributions across six millennia. *Ecology Letters*, *11*(4), 357-369. https://doi.org/10.1111/j.1461-0248.2007.01150.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

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change : Impacts on ecosystems and human well-being. *Science*. https://doi.org/10.1126/science.aai9214

Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M. Z., Liu, X. D., Miller, J. R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M. B., … Mountain Research Initiative EDW Working Group. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, *5*(5), 424-430. https://doi.org/10.1038/nclimate2563

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

Peterson, A. T. (2011). Ecological niche conservatism : A time-structured review of evidence. *Journal of Biogeography*, *38*(5), 817-827. https://doi.org/10.1111/j.1365-2699.2010.02456.x

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

Piedallu, C., Dallery, D., Bresson, C., Legay, M., Gégout, J.-C., & Pierrat, R. (2023). Spatial vulnerability assessment of silver fir and Norway spruce dieback driven by climate warming. *Landscape Ecology*, *38*(2), 341-361. https://doi.org/10.1007/s10980-022-01570-1

Piqué, A., Pluck, P., Schneider, J.-L., & Whitechurch, H. (1994). The Vosges Massif. In J. Chantraine, J. Rolet, D. S. Santallier, A. Piqué, & J. D. Keppie (Éds.), *Pre-Mesozoic Geology in France and Related Areas* (p. 416-425). Springer. https://doi.org/10.1007/978-3-642-84915-2_32

Pocheville, A. (2015). The Ecological Niche : History and Recent Controversies. In T. Heams, P. Huneman, G. Lecointre, & M. Silberstein (Éds.), *Handbook of Evolutionary Thinking in the Sciences* (p. 547-586). Springer Netherlands. https://doi.org/10.1007/978-94-017-9014-7_26

Pokorny, J., Brom, J., Cermak, J., Hesslerova, P., Huryna, H., Nadezhdina, N., & Rejskova, A. (2010). Solar energy dissipation and temperature control by water and plants. *International Journal of Water*, *5*(4), 311-336. https://doi.org/10.1504/IJW.2010.038726

Prevedello, J. A., Winck, G. R., Weber, M. M., Nichols, E., & Sinervo, B. (2019). Impacts of forestation and deforestation on local temperature across the globe. *PLOS ONE*, *14*(3), e0213368. https://doi.org/10.1371/journal.pone.0213368

Pulliam, H. R. (1988). Sources, Sinks, and Population Regulation. *The American Naturalist*, *132*(5), 652-661. https://doi.org/10.1086/284880

Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology Letters*, *3*(4), 349-361. https://doi.org/10.1046/j.1461-0248.2000.00143.x

Pyron, R. A., Costa, G. C., Patten, M. A., & Burbrink, F. T. (2015). Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. *Biological Reviews*, *90*(4), 1248-1262. https://doi.org/10.1111/brv.12154

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

Raduła, M. W., Szymura, T. H., & Szymura, M. (2018). Topographic wetness index explains soil moisture better than bioindication with Ellenberg's indicator values. *Ecological Indicators*, *85*, 172-179. https://doi.org/10.1016/j.ecolind.2017.10.011

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 (Éd.), *International Encyclopedia of Statistical Science* (p. 1658-1659). Springer. https://doi.org/10.1007/978-3-642-04898-2_616

Ribes, A., Boé, J., Qasmi, S., Dubuisson, B., Douville, H., & Terray, L. (2022). An updated assessment of past and future warming over France based on a regional observational constraint. *Earth System Dynamics*, *13*(4), 1397-1415. https://doi.org/10.5194/esd-13-1397-2022

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*, *30*(7). https://doi.org/10.1111/geb.13312

Richardson, K., Steffen, W., Lucht, W., Bendtsen, J., Cornell, S. E., Donges, J. F., Drüke, M., Fetzer, I., Bala, G., von Bloh, W., Feulner, G., Fiedler, S., Gerten, D., Gleeson, T., Hofmann, M., Huiskamp, W., Kummu, M., Mohan, C., Nogués-Bravo, D., … Rockström, J. (2023). Earth beyond six of nine planetary boundaries. *Science Advances*, *9*(37), eadh2458. https://doi.org/10.1126/sciadv.adh2458

Rita, A., Bonanomi, G., Allevato, E., Borghetti, M., Cesarano, G., Mogavero, V., Rossi, S., Saulino, L., Zotti, M., & Saracino, A. (2021). Topography modulates near-ground microclimate in the Mediterranean Fagus sylvatica treeline. *Scientific Reports*, *11*(1), 8122. https://doi.org/10.1038/s41598-021-87661-6

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

Rosenblad, K. C., Baer, K. C., & Ackerly, D. D. (2023). Climate change, tree demography, and thermophilization in western US forests. *Proceedings of the National Academy of Sciences*, *120*(18), e2301754120. https://doi.org/10.1073/pnas.2301754120

Rubenstein, M. A., Weiskopf, S. R., Bertrand, R., Carter, S. L., Comte, L., Eaton, M. J., Johnson, C. G., Lenoir, J., Lynch, A. J., Miller, B. W., Morelli, T. L., Rodriguez, M. A., Terando, A., & Thompson, L. M. (2023). Climate change and the global redistribution of biodiversity : Substantial variation in empirical support for expected range shifts. *Environmental Evidence*, *12*(1), 7. https://doi.org/10.1186/s13750-023-00296-0

Rull, V. (2010). On microrefugia and cryptic refugia. *Journal of Biogeography*, *37*(8), 1623-1625. https://doi.org/10.1111/j.1365-2699.2010.02340.x

Rumpf, S. B., Hülber, K., Wessely, J., Willner, W., Moser, D., Gattringer, A., Klonner, G., Zimmermann, N. E., & Dullinger, S. (2019). Extinction debts and colonization credits of non-forest plants in the European Alps. *Nature Communications*, *10*(1), 4293. https://doi.org/10.1038/s41467-019-12343-x

Sala, A., Woodruff, D. R., & Meinzer, F. C. (2012). Carbon dynamics in trees : Feast or famine? *Tree Physiology*, *32*(6), 764-775. https://doi.org/10.1093/treephys/tpr143

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

Sanczuk, P., De Lombaerde, E., Haesen, S., Van Meerbeek, K., Luoto, M., Van der Veken, B., Van Beek, E., Hermy, M., Verheyen, K., Vangansbeke, P., & De Frenne, P. (2022). Competition mediates understorey species range shifts under climate change. *Journal of Ecology*, *110*(8), 1813-1825. https://doi.org/10.1111/1365-2745.13907

Sanczuk, P., De Pauw, K., De Lombaerde, E., Luoto, M., Meeussen, C., Govaert, S., Vanneste, T., Depauw, L., Brunet, J., Cousins, S. A. O., Gasperini, C., Hedwall, P.-O., Iacopetti, G., Lenoir, J., Plue, J., Selvi, F., Spicher, F., Uria-Diez, J., Verheyen, K., … De Frenne, P. (2023). Microclimate and forest density drive plant population dynamics under climate change. *Nature Climate Change*, 1-8. https://doi.org/10.1038/s41558-023-01744-y

Sannier, C., Gallego, J., Langanke, T., Donezar, U., & Pennec, A. (2023). Tree cover area estimation in europe based on the combination of in situ reference data and the

copernicus high resolution layer on tree cover density. *The International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, *XLVIII-M-1-2023*, 277-284. https://doi.org/10.5194/isprs-archives-XLVIII-M-1-2023-277-2023

Saura, S., Martín-Queller, E., & Hunter, M. L. (2014). Forest landscape change and biodiversity conservation. In J. C. Azevedo, A. H. Perera, & M. A. Pinto (Éds.), *Forest Landscapes and Global Change : Challenges for Research and Management* (p. 167-198). Springer. https://doi.org/10.1007/978-1-4939-0953-7_7

Schadauer, K., Astrup, R., Breidenbach, J., Fridman, J., Gräber, S., Köhl, M., Korhonen, K. T., Johannsen, V. K., Morneau, F., Päivinen, R., & Riedel, T. (2024). Access to exact National Forest Inventory plot locations must be carefully evaluated. *New Phytologist*, *242*(2), 347-350. https://doi.org/10.1111/nph.19564

Schmitz, O. J. (2016). *The New Ecology : Rethinking a Science for the Anthropocene*. Princeton University Press.

Scholes, R., Montanarella, L., Brainich, A., Barger, N., & Brink, B. ten. (2018). *The assessment report on land degradation and restoration : Summary for policymakers*. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES).

Schweiger, A. H., Irl, S. D. H., Steinbauer, M. J., Dengler, J., & Beierkuhnlein, C. (2016). Optimizing sampling approaches along ecological gradients. *Methods in Ecology and Evolution*, *7*(4), 463-471. https://doi.org/10.1111/2041-210X.12495

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

Smith, S. A., Brown, A. R., Vosper, S. B., Murkin, P. A., & Veal, A. T. (2010). Observations and Simulations of Cold Air Pooling in Valleys. *Boundary-Layer Meteorology*, *134*(1), 85-108. https://doi.org/10.1007/s10546-009-9436-9

Soberón, J., & Nakamura, M. (2009). Niches and distributional areas : Concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences*, *106*(supplement_2), 19644-19650. https://doi.org/10.1073/pnas.0901637106

Soberón, J., & Peterson, A. T. (2005). *Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas*. https://doi.org/10.17161/bi.v2i0.4

Soberón, J., Peterson, A. T., & Osorio-Olvera, L. (2018). A comment on "Species are not most abundant in the centre of their geographic range or climatic niche". *Rethinking Ecology*, *3*, 13-18. https://doi.org/10.3897/rethinkingecology.3.24827

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

Stanturf, J. A., Palik, B. J., & Dumroese, R. K. (2014). Contemporary forest restoration : A review emphasizing function. *Forest Ecology and Management*, *331*, 292-323. https://doi.org/10.1016/j.foreco.2014.07.029

Stark, J. R., & Fridley, J. D. (2022). Microclimate-based species distribution models in complex forested terrain indicate widespread cryptic refugia under climate change. *Global Ecology and Biogeography*, *31*(3), 562-575. https://doi.org/10.1111/geb.13447

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 over time and across habitats. *Ecology Letters*, *25*(2), 466-482. https://doi.org/10.1111/ele.13937

Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, *17*(7), 866-880. https://doi.org/10.1111/ele.12277

Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A. D., Breiner, F. T., Burg, S., Czortek, P., Dawes, M. A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V. A., … Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, *556*(7700), 231-234. https://doi.org/10.1038/s41586-018-0005-6

Stevens, J. T., Safford, H. D., Harrison, S., & Latimer, A. M. (2015). Forest disturbance accelerates thermophilization of understory plant communities. *Journal of Ecology*, *103*(5), 1253-1263. https://doi.org/10.1111/1365-2745.12426

Suggitt, A. J., Wilson, R. J., Isaac, N. J. B., Beale, C. M., Auffret, A. G., August, T., Bennie, J. J., Crick, H. Q. P., Duffield, S., Fox, R., Hopkins, J. J., Macgregor, N. A., Morecroft, M. D., Walker, K. J., & Maclean, I. M. D. (2018). Extinction risk from climate change is reduced by microclimatic buffering. *Nature Climate Change*, *8*(8), 713-717. https://doi.org/10.1038/s41558-018-0231-9

Svenning, J.-C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, *100*(7), 1266-1286. https://doi.org/10.3732/ajb.1200469

Svenning, J.-C., & Skov, F. (2004). Limited filling of the potential range in European tree species. *Ecology Letters*, *7*(7), 565-573. https://doi.org/10.1111/j.1461-0248.2004.00614.x

Szymura, T. H., Szymura, M., & Macioł, A. (2014). Bioindication with Ellenberg's indicator values : A comparison with measured parameters in Central European oak forests. *Ecological Indicators*, *46*, 495-503. https://doi.org/10.1016/j.ecolind.2014.07.013

Tansley, A. G. (1939). British Ecology During the Past Quarter-Century : The Plant Community and the Ecosystem. *Journal of Ecology*, *27*(2), 513-530. https://doi.org/10.2307/2256377

Tatsumi, S., Iritani, R., & Cadotte, M. W. (2021). Temporal changes in spatial variation : Partitioning the extinction and colonisation components of beta diversity. *Ecology Letters*. https://doi.org/10.1111/ele.13720

Tatsumi, S., Iritani, R., & Cadotte, M. W. (2022). Partitioning the temporal changes in abundance-based beta diversity into loss and gain components. *Methods in Ecology and Evolution*, *13*(9), 2042-2048. https://doi.org/10.1111/2041-210X.13921

Teuscher, M., Brandl, R., Förster, B., Hothorn, T., Rösner, S., & Müller, J. (2013). Forest inventories are a valuable data source for habitat modelling of forest species : An alternative to remote-sensing data. *Forestry: An International Journal of Forest Research*, *86*(2), 241-253. https://doi.org/10.1093/forestry/cps081

Thomas, A. L., Dambrine, E., King, D., Party, J. P., & Probst, A. (1999). A spatial study of the relationships between streamwater acidity and geology, soils and relief (Vosges, northeastern France). *Journal of Hydrology*, *217*(1), 35-45. https://doi.org/10.1016/S0022-1694(99)00014-1

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*(6970), 145-148. https://doi.org/10.1038/nature02121

Thuiller, W. (2007). Climate change and the ecologist. *Nature*, *448*(7153), 550-552. https://doi.org/10.1038/448550a

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography*, *32*(3), 369-373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences*, *102*(23), 8245-8250. https://doi.org/10.1073/pnas.0409902102

Tichý, L. (2016). Field test of canopy cover estimation by hemispherical photographs taken with a smartphone. *Journal of Vegetation Science*, *27*(2), 427-435. https://doi.org/10.1111/jvs.12350

Tichý, L., Axmanová, I., Dengler, J., Guarino, R., Jansen, F., Midolo, G., Nobis, M. P., Van Meerbeek, K., Aćić, S., Attorre, F., Bergmeier, E., Biurrun, I., Bonari, G., Bruelheide, H., Campos, J. A., Čarni, A., Chiarucci, A., Ćuk, M., Ćušterevska, R., … Chytrý, M. (2023). Ellenberg-type indicator values for European vascular plant species. *Journal of Vegetation Science*, *34*(1), e13168. https://doi.org/10.1111/jvs.13168

Tinya, F., Kovács, B., Bidló, A., Dima, B., Király, I., Kutszegi, G., Lakatos, F., Mag, Z., Márialigeti, S., Nascimbene, J., Samu, F., Siller, I., Szél, G., & Ódor, P. (2021). Environmental drivers of forest biodiversity in temperate mixed forests – A multi-taxon approach. *Science of The Total Environment*, *795*, 148720. https://doi.org/10.1016/j.scitotenv.2021.148720

Tuff, K. T., Tuff, T., & Davies, K. F. (2016). A framework for integrating thermal biology into fragmentation research. *Ecology Letters*, *19*(4), 361-374. https://doi.org/10.1111/ele.12579

Ulrey, C., Quintana-Ascencio, P. F., Kauffman, G., Smith, A. B., & Menges, E. S. (2016). Life at the top : Long-term demography, microclimatic refugia, and responses to climate change for a high-elevation southern Appalachian endemic plant. *Biological Conservation*, *200*, 80-92. https://doi.org/10.1016/j.biocon.2016.05.028

Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, *348*(6234), 571-573. https://doi.org/10.1126/science.aaa4984

Valdés, A., Lenoir, J., De Frenne, P., Andrieu, E., Brunet, J., Chabrerie, O., Cousins, S. A. O., Deconchat, M., De Smedt, P., Diekmann, M., Ehrmann, S., Gallet-Moron, E., Gärtner, S., Giffard, B., Hansen, K., Hermy, M., Kolb, A., Le Roux, V., Liira, J., … Decocq, G. (2020). High ecosystem service delivery potential of small woodlands in agricultural landscapes. *Journal of Applied Ecology*, *57*(1), 4-16. https://doi.org/10.1111/1365-2664.13537

Vallauri, D., Grel, A., Granier, E., & Dupouey, J.-L. (2012). *Les forêts de Cassini. Analyse quantitative et comparaison avec les forêts actuelles* (p. 65 p.) [Technical Report]. WWF. https://hal.archives-ouvertes.fr/hal-01267936

van Asselen, S., & Verburg, P. H. (2012). A Land System representation for global assessments and land-use modeling. *Global Change Biology*, *18*(10), 3125-3148. https://doi.org/10.1111/j.1365-2486.2012.02759.x

Vandewiele, M., Geres, L., Lotz, A., Mandl, L., Richter, T., Seibold, S., Seidl, R., & Senf, C. (2023). Mapping spatial microclimate patterns in mountain forests from LiDAR. *Agricultural and Forest Meteorology*, *341*, 109662. https://doi.org/10.1016/j.agrformet.2023.109662

Vangansbeke, P., Máliš, F., Hédl, R., Chudomelová, M., Vild, O., Wulf, M., Jahn, U., Welk, E., Rodríguez-Sánchez, F., & Frenne, P. D. (2021). ClimPlant : Realized climatic niches of vascular plants in European forest understoreys. *Global Ecology and Biogeography*, *30*(6), 1183-1190. https://doi.org/10.1111/geb.13303

Vanneste, T., Govaert, S., Spicher, F., Brunet, J., Cousins, S. A. O., Decocq, G., Diekmann, M., Graae, B. J., Hedwall, P.-O., Kapás, R. E., Lenoir, J., Liira, J., Lindmo, S., Litza, K., Naaf, T., Orczewska, A., Plue, J., Wulf, M., Verheyen, K., & De Frenne, P. (2020). Contrasting microclimates among hedgerows and woodlands across temperate

Europe. *Agricultural and Forest Meteorology*, *281*, 107818. https://doi.org/10.1016/j.agrformet.2019.107818

Vaughan, I. P., & Gotelli, N. J. (2021). Using Climatic Credits to Pay the Climatic Debt. *Trends in Ecology & Evolution*, *36*(2), 104-112. https://doi.org/10.1016/j.tree.2020.10.002

Vellend, M. (2010). Conceptual Synthesis in Community Ecology. *The Quarterly Review of Biology*, *85*(2), 183-206. https://doi.org/10.1086/652373

Vellend, M., Lilley, P. L., & Starzomski, B. M. (2008). Using subsets of species in biodiversity surveys. *Journal of Applied Ecology*, *45*(1), 161-169. https://doi.org/10.1111/j.1365-2664.2007.01413.x

Veloz, S. D., Williams, J. W., Blois, J. L., He, F., Otto-Bliesner, B., & Liu, Z. (2012). No-analog climates and shifting realized niches during the late quaternary : Implications for 21st-century predictions by species distribution models. *Global Change Biology*, *18*(5), 1698-1713. https://doi.org/10.1111/j.1365-2486.2011.02635.x

Verheyen, K., De Frenne, P., Baeten, L., Waller, D. M., Hédl, R., Perring, M. P., Blondeel, H., Brunet, J., Chudomelová, M., Decocq, G., De Lombaerde, E., Depauw, L., Dirnböck, T., Durak, T., Eriksson, O., Gilliam, F. S., Heinken, T., Heinrichs, S., Hermy, M., … Bernhardt-Römermann, M. (2017). Combining Biodiversity Resurveys across Regions to Advance Global Change Research. *BioScience*, *67*(1), 73-83. https://doi.org/10.1093/biosci/biw150

Vitousek, P. M. (1994). Beyond Global Warming : Ecology and Global Change. *Ecology*, *75*(7), 1861-1876. https://doi.org/10.2307/1941591

Vittoz, P., & Engler, R. (2007). Seed dispersal distances : A typology based on dispersal modes and plant traits. *Botanica Helvetica*, *117*(2), 109-124. https://doi.org/10.1007/s00035-007-0797-8

von Arx, G., Graf Pannatier, E., Thimonier, A., & Rebetez, M. (2013). Microclimate in forests with varying leaf area index and soil moisture : Potential implications for seedling establishment in a changing climate. *Journal of Ecology*, *101*(5), 1201-1213. https://doi.org/10.1111/1365-2745.12121

Vosper, S. B., & Brown, A. R. (2008). Numerical Simulations of Sheltering in Valleys : The Formation of Nighttime Cold-Air Pools. *Boundary-Layer Meteorology*, *127*(3), 429-448. https://doi.org/10.1007/s10546-008-9272-3

Wang, S., Loreau, M., Mazancourt, C., Isbell, F., Beierkuhnlein, C., Connolly, J., Deutschman, D. H., Doležal, J., Eisenhauer, N., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Lepš, J., Polley, H. W., Reich, P. B., Ruijven, J., Schmid, B., Tilman, D., … Craven, D. (2021). Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony. *Ecology*, *102*(6). https://doi.org/10.1002/ecy.3332

Wasof, S., Lenoir, J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G., Bakkestuen, V., Birks, H. J. B., Bråthen, K. A., Broennimann, O., Brunet, J., Bruun, H. H., Dahlberg, C. J., Diekmann, M., Dullinger, S., Dynesius, M., Ejrnæs, R., Gégout, J.-C., Graae, B. J., … Decocq, G. (2015). Disjunct populations of European vascular plant species keep the same climatic niches. *Global Ecology and Biogeography*, *24*(12), 1401-1412. https://doi.org/10.1111/geb.12375

Waters, C. N., Zalasiewicz, J., Summerhayes, C., Barnosky, A. D., Poirier, C., Gałuszka, A., Cearreta, A., Edgeworth, M., Ellis, E. C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J. R., Richter, D. deB., Steffen, W., Syvitski, J., Vidas, D., Wagreich, M., Williams, M., … Wolfe, A. P. (2016). The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science*, *351*(6269), aad2622. https://doi.org/10.1126/science.aad2622

Watling, J. I., Arroyo-Rodríguez, V., Pfeifer, M., Baeten, L., Banks-Leite, C., Cisneros, L. M., Fang, R., Hamel-Leigue, A. C., Lachat, T., Leal, I. R., Lens, L., Possingham, H. P., Raheem, D. C., Ribeiro, D. B., Slade, E. M., Urbina-Cardona, J. N., Wood, E. M., &

Fahrig, L. (2020). Support for the habitat amount hypothesis from a global synthesis of species density studies. *Ecology Letters*, *23*(4), 674-681. https://doi.org/10.1111/ele.13471

Watts, S. H., Mardon, D. K., Mercer, C., Watson, D., Cole, H., Shaw, R. F., & Jump, A. S. (2022). Riding the elevator to extinction : Disjunct arctic-alpine plants of open habitats decline as their more competitive neighbours expand. *Biological Conservation*, *272*, 109620. https://doi.org/10.1016/j.biocon.2022.109620

Wei, L., Sanczuk, P., De Pauw, K., Caron, M. M., Selvi, F., Hedwall, P., Brunet, J., Cousins, S. A. O., Plue, J., Spicher, F., Gasperini, C., Iacopetti, G., Orczewska, A., Uria-Diez, J., Lenoir, J., Vangansbeke, P., & De Frenne, P. (2024). Using warming tolerances to predict understory plant responses to climate change. *Global Change Biology*, *30*(1), e17064. https://doi.org/10.1111/gcb.17064

Wen, B., Blondeel, H., Landuyt, D., & Verheyen, K. (2022). A model-based scenario analysis of the impact of forest management and environmental change on the understorey of temperate forests in Europe. *Forest Ecology and Management*, *522*, 120465. https://doi.org/10.1016/j.foreco.2022.120465

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279-338. https://doi.org/10.2307/1943563

Wickham, H. (2011). Ggplot2. *WIREs Computational Statistics*, *3*(2), 180-185. https://doi.org/10.1002/wics.147

Wiens, J. J. (2016). Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species. *PLOS Biology*, *14*(12), e2001104. https://doi.org/10.1371/journal.pbio.2001104

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Jonathan Davies, T., Grytnes, J.-A., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M., & Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, *13*(10), 1310-1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

Wild, J., Kopecký, M., Macek, M., Šanda, M., Jankovec, J., & Haase, T. (2019). Climate at ecologically relevant scales : A new temperature and soil moisture logger for long-term microclimate measurement. *Agricultural and Forest Meteorology*. https://doi.org/10.1016/j.agrformet.2018.12.018

Woodward, F. I., & Williams, B. G. (1987). Climate and plant distribution at global and local scales. *Vegetatio*, *69*(1), 189-197. https://doi.org/10.1007/BF00038700

Xu, W.-B., Blowes, S. A., Brambilla, V., Chow, C. F. Y., Fontrodona-Eslava, A., Martins, I. S., McGlinn, D., Moyes, F., Sagouis, A., Shimadzu, H., van Klink, R., Magurran, A. E., Gotelli, N. J., McGill, B. J., Dornelas, M., & Chase, J. M. (2023). Regional occupancy increases for widespread species but decreases for narrowly distributed species in metacommunity time series. *Nature Communications*, *14*(1), 1463. https://doi.org/10.1038/s41467-023-37127-2

Yates, D. N., Kittel, T. G. F., & Cannon, R. F. (2000). Comparing the Correlative Holdridge Model to Mechanistic Biogeographical Models for Assessing Vegetation Distribution Response to Climatic Change. *Climatic Change*, *44*(1), 59-87. https://doi.org/10.1023/A:1005495908758

Zellweger, F., Braunisch, V., Morsdorf, F., Baltensweiler, A., Abegg, M., Roth, T., Bugmann, H., & Bollmann, K. (2015). Disentangling the effects of climate, topography, soil and vegetation on stand-scale species richness in temperate forests. *Forest Ecology and Management*, *349*, 36-44. https://doi.org/10.1016/j.foreco.2015.04.008

Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S. L., Wulf, M., Kirby, K. J., Brunet, J., Kopecký, M., Máliš, F., Schmidt, W., Heinrichs, S., den Ouden, J., Jaroszewicz, B., Buyse, G., Spicher, F., Verheyen, K., & De Frenne, P. (2019). Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe.

*Global Ecology and Biogeography*, *28*(12), 1774-1786. https://doi.org/10.1111/geb.12991

Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., & Coomes, D. (2019). Advances in Microclimate Ecology Arising from Remote Sensing. *Trends in Ecology & Evolution*, *34*(4), 327-341. https://doi.org/10.1016/j.tree.2018.12.012

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. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, *7*(6), 636-645. https://doi.org/10.1111/2041-210X.12577

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

# Annexes

## List of appendices:

**Table A1:** Forest ecoregions (NFI Sylvoécoregion code) summary information. Weighted thermal optimum mean (μTopt) of past and recent plots, contribution of extinction and colonization to ΔTopt, Whittaker ß-diversity, mean α-diversity (μα), γ-diversity of past and recent plots, and number of plot (number of pair *2).

**Table A2:** Species names (TaxRef V13), past (2005-2011) and recent (2015-2021) occurrences and thermal optimum (Topt) of the 756 recorded species of the chapter 2 analysis (N plots: 14,167), 434 species (and occurrences identified to the genus level) with more than 10 total occurrences are also displayedTable A3: Chapter 3 List of species

**Table A3:** Species name, occurrences in not forested plots (NF), forested plots (F), thermal optimum from ClimPlant V1.2 (Topt), pH optimum from EcoPlant (pH) and habitat preference classification from the EuForPlant list. Table A4: Chapter 4 List of species

**Table A4:** Species names, their total occurrences (N) in the dataset, broken up in the cold, intermediate and warm topoclimate categories, their thermal optimum (Topt), pH optimum (pH) and the EuForPlant habitat classification (N plots: 306).

The habitat classification presented thorough the annexes (A3, A4) is the one used in the EuForPlant list: (1.1) species of closed forest, (1.2) species which occur in forest edges and openings, (2.1) Species which primarily occur in forests but also found in cultural landscapes and forest remnants, (2.2) species of open habitats that occurs in forest exclusively through opening and early succession, (O) species of open habitat (Heinken *et al.*, 2022).

Table A2 presents species with thermal optimum and without thermal optimum if they had more than 10 occurrences. Table A3 displays only species with thermal optimum. Table A4 displays every recorded species regardless if they had a thermal optimum or not. As species without were sometime removed ClimPlant thermal optimum values and trees were removed, a complete list of species under the names 'list_of_species_full.csv' is available in each chapter's repository: https://github.com/Jeremy-borderieux

## Table A1: Chapter 2 Ecoregion information

*Table A1: Forest ecoregions (NFI Sylvoécoregion code) summary information. Weighted thermal optimum mean (μTopt) of past and recent plots, contribution of extinction and colonization to ΔTopt, Whittaker β-diversity, mean α-diversity (μα), γ-diversity of past and recent plots, and number of plot (number of pair *2).*

| SER code | μTopt past | μTopt recent | ΔTopt Ext | ΔTopt Col | β past | β recent | μα recent | μα recent | γ recent | γ recent | N |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **A11** | 8,72 | 8,86 | 0,13 | 0,01 | 11,66 | 10,5 | 11,66 | 10,47 | 136 | 110 | 312 |
| **A12** | 8,72 | 8,85 | 0,11 | 0,02 | 9,04 | 8,46 | 10,62 | 8,98 | 96 | 76 | 106 |
| **A13** | 8,39 | 8,44 | 0,01 | 0,04 | 10,55 | 11,22 | 9,77 | 8,38 | 103 | 94 | 240 |
| **A21** | 8,79 | 8,83 | 0,04 | 0,01 | 9,54 | 9,22 | 9,64 | 8,57 | 92 | 79 | 112 |
| **A22** | 8,67 | 8,88 | 0,16 | 0,05 | 10,25 | 9,64 | 8,78 | 9,02 | 90 | 87 | 90 |
| **A30** | 9,14 | 9,27 | 0,2 | -0,07 | 6,6 | 8,26 | 14,09 | 10,41 | 93 | 86 | 64 |
| **B10** | 8,54 | 8,51 | 0,07 | -0,11 | 12,88 | 15,17 | 11,18 | 9,76 | 144 | 148 | 324 |
| **B21** | 8,32 | 8,2 | -0,01 | -0,11 | 6,48 | 7,51 | 12,82 | 13,18 | 83 | 99 | 44 |
| **B22** | 8,2 | 8,47 | 0,22 | 0,05 | 7,85 | 7,22 | 10,95 | 10,25 | 86 | 74 | 40 |
| **B23** | 7,84 | 7,98 | 0,03 | 0,12 | 9,58 | 8,53 | 11,06 | 14,77 | 106 | 126 | 130 |
| **B31** | 8,73 | 8,81 | 0,13 | -0,05 | 7,75 | 7,09 | 10,7 | 11,7 | 83 | 83 | 54 |
| **B32** | 8,58 | 8,84 | 0,21 | 0,06 | 13,15 | 13,73 | 10,95 | 8,45 | 144 | 116 | 264 |
| **B33** | 8,74 | 8,68 | 0,02 | -0,08 | 12,48 | 14,83 | 9,93 | 8,9 | 124 | 132 | 270 |
| **B41** | 8,62 | 8,68 | 0,1 | -0,04 | 19,9 | 18,7 | 11,61 | 11,66 | 231 | 218 | 842 |
| **B42** | 8,3 | 8,45 | 0,1 | 0,05 | 14,54 | 14,8 | 13,89 | 14,39 | 202 | 213 | 498 |
| **B43** | 8,4 | 8,34 | 0,05 | -0,1 | 7,79 | 8,85 | 13,34 | 16,72 | 104 | 148 | 58 |
| **B51** | 8,33 | 8,38 | 0,05 | 0,01 | 14,41 | 13,19 | 14,78 | 14,18 | 213 | 187 | 518 |
| **B52** | 8,66 | 8,78 | 0,13 | -0,01 | 13,58 | 13,53 | 11,05 | 11,68 | 150 | 158 | 306 |
| **B53** | 8,77 | 8,75 | 0,03 | -0,05 | 15,3 | 15,39 | 10 | 11,37 | 153 | 175 | 364 |
| **B61** | 8,9 | 8,97 | 0,1 | -0,02 | 14,28 | 15,72 | 9,6 | 9,16 | 137 | 144 | 292 |
| **B62** | 8,97 | 8,99 | 0,09 | -0,07 | 16,95 | 15,31 | 10,8 | 10,58 | 183 | 162 | 422 |
| **B70** | 8,52 | 8,57 | 0,04 | 0 | 20,97 | 20,71 | 9,87 | 10,91 | 207 | 226 | 1184 |
| **B81** | 9,17 | 9,26 | 0,1 | -0,01 | 9,67 | 9,09 | 10,97 | 10,23 | 106 | 93 | 120 |
| **B82** | 9,05 | 9,16 | 0,12 | -0,01 | 13,7 | 13,32 | 11,24 | 11,64 | 154 | 155 | 278 |
| **B91** | 8,87 | 8,93 | 0,1 | -0,04 | 14,87 | 14,86 | 10,29 | 10,97 | 153 | 163 | 362 |
| **B92** | 8,52 | 8,58 | 0,15 | -0,08 | 12,39 | 12,45 | 12,75 | 11,24 | 158 | 140 | 230 |
| **C11** | 7,75 | 7,76 | -0,01 | 0,02 | 12,8 | 12,3 | 9,61 | 10,24 | 123 | 126 | 240 |
| **C12** | 8,11 | 8,15 | 0,02 | 0,02 | 10,4 | 9,83 | 13,46 | 15,16 | 140 | 149 | 204 |
| **C20** | 8,67 | 8,74 | 0,06 | 0,01 | 20,04 | 20,63 | 17,32 | 18,03 | 347 | 372 | 3784 |
| **C30** | 8,18 | 8,24 | 0,04 | 0,02 | 15,8 | 15,76 | 14,49 | 16,56 | 229 | 261 | 942 |
| **C41** | 8,14 | 8,22 | 0,03 | 0,05 | 13 | 11,1 | 12,77 | 15,49 | 166 | 172 | 200 |
| **C42** | 8,07 | 8,02 | 0,06 | -0,11 | 9,2 | 9,5 | 13,15 | 14,32 | 121 | 136 | 106 |
| **C51** | 8,26 | 8,32 | 0,09 | -0,03 | 16,95 | 16,43 | 12,92 | 12,35 | 219 | 203 | 744 |
| **C52** | 8,98 | 9,03 | 0,12 | -0,07 | 15,89 | 14,32 | 15,92 | 14,67 | 253 | 210 | 248 |
| **D11** | 7,73 | 7,85 | 0,03 | 0,08 | 18,71 | 19,86 | 11,23 | 12,79 | 210 | 254 | 832 |
| **D12** | 7,95 | 8 | 0,04 | 0,01 | 15,8 | 16,85 | 10,88 | 11,63 | 172 | 196 | 392 |
| **E10** | 8,51 | 8,69 | 0,14 | 0,05 | 15,95 | 16,96 | 20,62 | 19,22 | 329 | 326 | 650 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **E20** | 7,67 | 7,68 | -0,02 | 0,02 | 12,28 | 10,89 | 32,91 | 33,99 | 404 | 370 | 670 |
| **F11** | 9,4 | 9,63 | 0,29 | -0,06 | 9,12 | 7,34 | 11,84 | 9,27 | 108 | 68 | 90 |
| **F12** | 9,61 | 9,94 | 0,23 | 0,1 | 9,72 | 8,84 | 14,4 | 12,66 | 140 | 112 | 166 |
| **F14** | 9,48 | 9,72 | 0,28 | -0,04 | 8,25 | 8,24 | 12,61 | 11,29 | 104 | 93 | 82 |
| **F15** | 9,27 | 9,45 | 0,17 | 0,01 | 18,25 | 20,56 | 13,54 | 11,82 | 247 | 243 | 744 |
| **F21** | 8,51 | 8,68 | 0,07 | 0,1 | 23,66 | 18,45 | 8,28 | 7,1 | 196 | 131 | 1116 |
| **F22** | 9,24 | 9,45 | 0,11 | 0,11 | 9,25 | 9,04 | 8,86 | 7,08 | 82 | 64 | 222 |
| **F23** | 8,98 | 9,22 | 0,15 | 0,09 | 16,37 | 17,17 | 11,79 | 9,84 | 193 | 169 | 528 |
| **F30** | 9,62 | 9,7 | 0,15 | -0,08 | 18,21 | 19,33 | 12,96 | 12 | 236 | 232 | 600 |
| **F40** | 9,24 | 9,24 | 0,03 | -0,03 | 13,85 | 12,86 | 17,62 | 15,55 | 244 | 200 | 478 |
| **F51** | 9,18 | 9,42 | 0,25 | -0,01 | 9,13 | 9,62 | 17,09 | 13,93 | 156 | 134 | 184 |
| **F52** | 9,27 | 9,52 | 0,22 | 0,03 | 11,07 | 10,01 | 13,46 | 11,39 | 149 | 114 | 178 |
| **G11** | 8,8 | 9 | 0,18 | 0,02 | 14,16 | 17,41 | 13,35 | 10,97 | 189 | 191 | 440 |
| **G12** | 8,83 | 8,78 | 0,07 | -0,12 | 9,69 | 10,39 | 13 | 15,21 | 126 | 158 | 106 |
| **G13** | 8,4 | 8,5 | 0,1 | 0 | 16,19 | 20,3 | 14,2 | 11,53 | 230 | 234 | 758 |
| **G21** | 8,07 | 8,15 | 0,07 | 0,02 | 12,82 | 13,42 | 14,35 | 11,55 | 184 | 155 | 282 |
| **G22** | 7,98 | 8 | 0,01 | 0,02 | 19,76 | 18,55 | 16,2 | 16,01 | 320 | 297 | 960 |
| **G23** | 8,23 | 8,41 | 0,16 | 0,02 | 15,25 | 17,26 | 14,3 | 11,76 | 218 | 203 | 350 |
| **G30** | 7,77 | 7,81 | 0,01 | 0,02 | 11,28 | 13,96 | 23,05 | 20,42 | 260 | 285 | 266 |
| **G41** | 8,53 | 8,73 | 0,19 | 0 | 10,78 | 11,58 | 16,04 | 13,99 | 173 | 162 | 182 |
| **G42** | 8,44 | 8,52 | 0,07 | 0,01 | 12,2 | 15,46 | 15,83 | 12,55 | 193 | 194 | 286 |
| **G50** | 8,87 | 9 | 0,13 | -0,01 | 15,3 | 16,01 | 15,3 | 13,62 | 234 | 218 | 348 |
| **G60** | 8,77 | 9,03 | 0,14 | 0,12 | 11,58 | 11,95 | 15,46 | 12,98 | 179 | 155 | 166 |
| **G70** | 8,75 | 9,03 | 0,2 | 0,07 | 14,58 | 16,48 | 11,38 | 10,62 | 166 | 175 | 224 |
| **G80** | 8,79 | 9,04 | 0,15 | 0,1 | 13,76 | 15,12 | 13,3 | 10,98 | 183 | 166 | 214 |
| **G90** | 8,54 | 8,6 | 0,07 | -0,01 | 11,16 | 10,82 | 16,39 | 18,11 | 183 | 196 | 178 |
| **H10** | 7,79 | 7,8 | 0,02 | -0,01 | 11,38 | 12,21 | 32,07 | 25,79 | 365 | 315 | 234 |
| **H21** | 7,62 | 7,76 | 0,02 | 0,12 | 9,46 | 9,83 | 27,7 | 24,1 | 262 | 237 | 80 |
| **H22** | 7,66 | 7,83 | 0,09 | 0,08 | 7,79 | 9,04 | 31,2 | 22,56 | 243 | 204 | 50 |
| **H30** | 8,92 | 8,99 | 0,1 | -0,04 | 19,19 | 19,36 | 12,87 | 12,24 | 247 | 237 | 420 |
| **H41** | 8,43 | 8,45 | 0,06 | -0,04 | 15,43 | 15,05 | 14,9 | 13,75 | 230 | 207 | 122 |
| **H42** | 7,65 | 7,98 | 0,13 | 0,2 | 9,79 | 8,99 | 14,2 | 14,12 | 139 | 127 | 50 |
| **I11** | 9,23 | 9,24 | 0,11 | -0,09 | 12,26 | 13,11 | 16,23 | 15,1 | 199 | 198 | 264 |
| **I12** | 8,54 | 8,73 | 0,11 | 0,08 | 13,31 | 12,55 | 18,26 | 17,53 | 243 | 220 | 148 |
| **I13** | 9,34 | 9,56 | 0,26 | -0,05 | 7,89 | 7,71 | 15,97 | 13,37 | 126 | 103 | 60 |
| **I21** | 8,5 | 8,58 | 0,07 | 0,01 | 15,54 | 14,69 | 17,89 | 17,5 | 278 | 257 | 342 |
| **I22** | 8,07 | 8,16 | 0,06 | 0,03 | 10,86 | 10 | 21,19 | 20,1 | 230 | 201 | 96 |
| **J10** | 9,89 | 10,2 | 0,36 | -0,05 | 11,65 | 12,7 | 11,42 | 8,98 | 133 | 114 | 190 |
| **J21** | 8,97 | 9,16 | 0,19 | 0 | 8,18 | 8,72 | 13,81 | 9,86 | 113 | 86 | 42 |
| **J22** | 9,69 | 9,81 | 0,25 | -0,12 | 10,09 | 13,3 | 13,08 | 11,58 | 132 | 154 | 146 |
| **J23** | 9,19 | 9,69 | 0,42 | 0,09 | 12,08 | 12,82 | 10,02 | 7,8 | 121 | 100 | 202 |
| **J30** | 9,48 | 9,73 | 0,27 | -0,01 | 5,28 | 6,49 | 8,33 | 6,93 | 44 | 45 | 30 |
| **J40** | 9,07 | 9,37 | 0,32 | -0,02 | 11,5 | 14,85 | 12,44 | 9,09 | 143 | 135 | 174 |

## Table A2: Chapter 2 List of species

*Table A2: Species names (TaxRef V13), past (2005-2011) and recent (2015-2021) occurrences and thermal optimum (Topt) of the 756 recorded species of the chapter 2 analysis (N plots: 14,167), 434 species (and occurrences identified to the genus level) with more than 10 total occurrences are also displayed.*

| Species name | Past | Recent | Topt |
|---|---|---|---|
| *Achillea macrophylla* | 0 | 1 | 4,34 |
| *Achillea millefolium* | 266 | 272 | 5,64 |
| *Achnatherum calamagrostis* | 78 | 72 | / |
| *Aconitum anthora* | 1 | 0 | 6,92 |
| *Aconitum lycoctonum* | 17 | 14 | 1,75 |
| *Aconitum napellus* | 8 | 11 | / |
| *Actaea spicata* | 53 | 57 | 5,5 |
| *Adenostyles alliariae* | 83 | 79 | 7,53 |
| *Adenostyles alpina* | 6 | 8 | 7,54 |
| *Adoxa moschatellina* | 69 | 67 | 6,42 |
| *Aegopodium podagraria* | 33 | 59 | 6,71 |
| *Aesculus hippocastanum* | 9 | 26 | / |
| *Aethusa cynapium* | 29 | 13 | 8,04 |
| *Agrimonia eupatoria* | 156 | 172 | 8,68 |
| *Agrimonia procera* | 8 | 2 | / |
| *Agrostis* | 168 | 310 | / |
| *Agrostis canina* | 200 | 141 | 6,16 |
| *Agrostis capillaris* | 1154 | 465 | 6,01 |
| *Agrostis castellana* | 0 | 11 | / |
| *Agrostis curtisii* | 96 | 64 | / |
| *Agrostis stolonifera* | 260 | 122 | 7,09 |
| *Ailanthus altissima* | 4 | 7 | / |
| *Ajuga genevensis* | 6 | 8 | 8,21 |
| *Ajuga pyramidalis* | 1 | 4 | 5,97 |
| *Ajuga reptans* | 1170 | 1138 | 8,07 |
| *Alchemilla* | 6 | 5 | / |
| *Alchemilla acutiloba* | 113 | 54 | 5,1 |
| *Alchemilla alpina* | 20 | 10 | 6,31 |
| *Alchemilla glaucescens* | 0 | 1 | 6,32 |
| *Alchemilla hoppeana* | 12 | 17 | / |
| *Alchemilla xanthochlora* | 0 | 51 | 9,24 |
| *Alleniella complanata* | 0 | 13 | / |
| *Alliaria petiolata* | 217 | 442 | 8,41 |
| *Allium* | 29 | 28 | / |
| *Allium schoenoprasum* | 3 | 12 | / |
| *Allium ursinum* | 58 | 54 | 8,97 |
| *Allium vineale* | 2 | 3 | 10,28 |
| *Alopecurus pratensis* | 0 | 3 | 6,45 |
| *Alyssum alyssoides* | 13 | 3 | 9,83 |
| *Amaranthus retroflexus* | 1 | 0 | 9,01 |
| *Amelanchier ovalis* | 403 | 384 | / |
| *Anacamptis pyramidalis* | 8 | 8 | 10,81 |
| *Andromeda polifolia* | 1 | 0 | 3,24 |
| *Anemone hepatica* | 308 | 299 | 6,56 |
| *Anemone nemorosa* | 1355 | 1131 | 7,55 |
| *Anemone ranunculoides* | 39 | 13 | 6,94 |
| *Anemone sylvestris* | 22 | 89 | 5,82 |
| *Angelica* | 10 | 10 | / |
| *Angelica razulii* | 8 | 7 | / |
| *Angelica sylvestris* | 285 | 288 | 5,87 |
| *Anisantha sterilis* | 3 | 0 | 9,82 |
| *Anomodon viticulosus* | 0 | 14 | / |
| *Antennaria dioica* | 0 | 1 | 4,47 |
| *Anthericum liliago* | 8 | 8 | 9,51 |
| *Anthericum ramosum* | 8 | 6 | 8,02 |
| *Anthoxanthum odoratum* | 242 | 187 | 6,02 |
| *Anthriscus caucalis* | 1 | 0 | 10,42 |
| *Anthriscus sylvestris* | 38 | 47 | 6,13 |
| *Anthyllis montana* | 12 | 14 | / |
| *Anthyllis vulneraria* | 46 | 23 | 8 |
| *Apera spica-venti* | 1 | 0 | 6,26 |
| *Aphyllanthes monspeliensis* | 266 | 220 | / |
| *Aposeris foetida* | 2 | 3 | 8,01 |
| *Aquilegia* | 8 | 5 | / |
| *Aquilegia vulgaris* | 132 | 137 | 7,72 |
| *Arabidopsis arenosa* | 1 | 2 | 6,65 |
| *Arabis* | 20 | 22 | / |
| *Arabis alpina* | 8 | 3 | 8,11 |
| *Arabis hirsuta* | 63 | 22 | 7,1 |
| *Arctium* | 5 | 27 | / |
| *Arctium lappa* | 1 | 8 | 7,94 |
| *Arctium nemorosum* | 59 | 83 | 8,64 |
| *Arctostaphylos uva-ursi* | 41 | 25 | 4,19 |

| | | | |
|---|---|---|---|
| *Arenaria montana* | 60 | 66 | / |
| *Argentina anserina* | 2 | 0 | 6,8 |
| *Argyrolobium zanonii* | 48 | 61 | / |
| *Aristolochia pistolochia* | 9 | 5 | / |
| *Arnica montana* | 7 | 7 | / |
| *Arrhenatherum elatius* | 43 | 63 | 9,21 |
| *Artemisia absinthium* | 0 | 1 | 7,42 |
| *Artemisia campestris* | 2 | 0 | 7,53 |
| *Artemisia vulgaris* | 3 | 25 | 7,07 |
| *Arum* | 109 | 115 | / |
| *Arum italicum* | 284 | 348 | / |
| *Arum maculatum* | 1212 | 1144 | 9,06 |
| *Aruncus dioicus* | 28 | 19 | 8,35 |
| *Asarum europaeum* | 261 | 257 | 6,58 |
| *Asparagus* | 17 | 7 | / |
| *Asparagus acutifolius* | 139 | 156 | / |
| *Asparagus officinalis* | 7 | 2 | 7,38 |
| *Asparagus tenuifolius* | 2 | 8 | / |
| *Asperula cynanchica* | 24 | 10 | / |
| *Asphodelus* | 5 | 9 | / |
| *Asphodelus albus* | 164 | 167 | / |
| *Asphodelus cerasiferus* | 10 | 6 | / |
| *Asplenium* | 14 | 8 | / |
| *Asplenium adiantum-nigrum* | 316 | 240 | 9,76 |
| *Asplenium ceterach* | 39 | 41 | / |
| *Asplenium onopteris* | 0 | 44 | / |
| *Asplenium ruta-muraria* | 6 | 15 | 9,52 |
| *Asplenium scolopendrium* | 151 | 177 | 9,83 |
| *Asplenium septentrionale* | 5 | 6 | 7,31 |
| *Asplenium trichomanes* | 339 | 334 | 9,34 |
| *Asplenium viride* | 41 | 46 | 6,77 |
| *Astragalus* | 60 | 50 | / |
| *Astragalus danicus* | 1 | 0 | 4,07 |
| *Astragalus glycyphyllos* | 13 | 5 | 7,61 |
| *Astragalus monspessulanus* | 76 | 53 | / |
| *Astragalus sempervirens* | 4 | 1 | 8 |
| *Astrantia major* | 23 | 16 | 8,2 |
| *Athyrium filix-femina* | 1637 | 1342 | 6,15 |
| *Atocion rupestre* | 4 | 7 | / |
| *Atrichum undulatum* | 2584 | 2821 | / |
| *Atropa belladonna* | 54 | 35 | / |
| *Avena* | 11 | 8 | / |
| *Avenella flexuosa* | 3270 | 2969 | 6,01 |
| *Avenula pubescens* | 1 | 0 | 7,04 |
| *Barbarea vulgaris* | 1 | 3 | 7,16 |
| *Bartsia alpina* | 1 | 0 | 2,73 |
| *Bazzania trilobata* | 20 | 45 | / |
| *Bellidiastrum michelii* | 14 | 17 | 7,22 |
| *Bellis* | 7 | 4 | / |
| *Bellis perennis* | 25 | 26 | 9,86 |
| *Berberis aquifolium* | 6 | 20 | / |
| *Berberis vulgaris* | 85 | 93 | 8,7 |
| *Betonica officinalis* | 623 | 493 | 7,89 |
| *Biscutella laevigata* | 11 | 2 | / |
| *Bistorta officinalis* | 38 | 33 | 5,29 |
| *Bistorta vivipara* | 6 | 1 | 2,62 |
| *Bituminaria bituminosa* | 107 | 134 | / |
| *Blackstonia perfoliata* | 14 | 40 | / |
| *Blechnum spicant* | 457 | 494 | 8,79 |
| *Blitum bonus-henricus* | 2 | 1 | 9,4 |
| *Bothriochloa ischaemum* | 1 | 0 | 10,64 |
| *Brachypodium* | 27 | 55 | / |
| *Brachypodium phoenicoides* | 33 | 80 | / |
| *Brachypodium pinnatum* | 1798 | 1350 | 7,19 |
| *Brachypodium retusum* | 106 | 82 | / |
| *Brachypodium rupestre* | 0 | 32 | / |
| *Brachypodium sylvaticum* | 3608 | 4009 | 9,47 |
| *Brachythecium rutabulum* | 42 | 26 | / |
| *Briza media* | 53 | 36 | 8,2 |
| *Briza minor* | 8 | 6 | / |
| *Bromopsis benekenii* | 109 | 147 | 7,29 |
| *Bromopsis erecta* | 234 | 239 | 9,5 |
| *Bromopsis ramosa* | 99 | 78 | 9,81 |
| *Bromus* | 42 | 46 | / |
| *Bromus arvensis* | 0 | 2 | 7,97 |
| *Bromus hordeaceus* | 0 | 1 | 9,43 |
| *Bromus racemosus* | 11 | 1 | 9,83 |
| *Bryonia* | 5 | 12 | / |
| *Bryonia dioica* | 39 | 22 | / |
| *Buddleja* | 4 | 11 | / |
| *Buddleja davidii* | 3 | 13 | / |
| *Buddleja japonica* | 1 | 10 | / |
| *Buglossoides purpurocaerulea* | 30 | 54 | 11,22 |
| *Buphthalmum salicifolium* | 5 | 3 | 7,49 |
| *Bupleurum falcatum* | 17 | 28 | 9,95 |
| *Bupleurum rigidum* | 23 | 13 | / |
| *Buxus sempervirens* | 722 | 713 | 10,71 |
| *Calamagrostis* | 10 | 16 | / |
| *Calamagrostis arundinacea* | 24 | 12 | 5,2 |

| | | | |
|---|---|---|---|
| *Calamagrostis canescens* | 1 | 0 | 5,28 |
| *Calamagrostis epigejos* | 108 | 88 | 7,98 |
| *Calamagrostis varia* | 42 | 60 | 9,18 |
| *Calamagrostis villosa* | 0 | 1 | 6,65 |
| *Calla palustris* | 0 | 2 | 4,75 |
| *Calluna vulgaris* | 2010 | 1756 | 6,32 |
| *Caltha palustris* | 52 | 56 | 5,38 |
| *Campanula* | 49 | 46 | / |
| *Campanula cervicaria* | 2 | 0 | 5,65 |
| *Campanula cochleariifolia* | 2 | 5 | 5,6 |
| *Campanula glomerata* | 11 | 7 | 6,86 |
| *Campanula latifolia* | 2 | 2 | 6,36 |
| *Campanula patula* | 16 | 10 | 5,79 |
| *Campanula persicifolia* | 50 | 45 | 6,41 |
| *Campanula rapunculoides* | 6 | 6 | 7,07 |
| *Campanula rapunculus* | 6 | 1 | 11,89 |
| *Campanula rhomboidalis* | 35 | 34 | 4,72 |
| *Campanula rotundifolia* | 91 | 83 | 4,97 |
| *Campanula scheuchzeri* | 30 | 13 | 6,9 |
| *Campanula trachelium* | 143 | 126 | 8,59 |
| *Campylopus introflexus* | 0 | 54 | / |
| *Cardamine* | 96 | 158 | / |
| *Cardamine amara* | 13 | 54 | 6,07 |
| *Cardamine bulbifera* | 1 | 0 | 8,63 |
| *Cardamine flexuosa* | 160 | 121 | 9,26 |
| *Cardamine heptaphylla* | 187 | 203 | 8,38 |
| *Cardamine hirsuta* | 6 | 8 | 11,17 |
| *Cardamine impatiens* | 60 | 63 | 7,87 |
| *Cardamine pentaphyllos* | 51 | 38 | 7,02 |
| *Cardamine pratensis* | 381 | 275 | 4,68 |
| *Carduus defloratus* | 2 | 21 | 5,33 |
| *Carex* | 762 | 692 | / |
| *Carex acutiformis* | 100 | 145 | 7,65 |
| *Carex alba* | 132 | 144 | 8,09 |
| *Carex arenaria* | 64 | 32 | 8,57 |
| *Carex brizoides* | 126 | 148 | 8,12 |
| *Carex canescens* | 2 | 1 | 5,04 |
| *Carex caryophyllea* | 10 | 6 | 8,27 |
| *Carex demissa* | 0 | 1 | 7,64 |
| *Carex diandra* | 0 | 1 | 5,7 |
| *Carex digitata* | 737 | 709 | 5,31 |
| *Carex disticha* | 2 | 1 | 7,77 |
| *Carex divulsa* | 8 | 3 | 10,24 |
| *Carex echinata* | 2 | 6 | 6,39 |
| *Carex elongata* | 25 | 18 | 6,04 |
| *Carex flacca* | 3030 | 2887 | 10,25 |
| *Carex flava* | 0 | 1 | 7,15 |
| *Carex halleriana* | 306 | 365 | / |
| *Carex hirta* | 19 | 39 | 7,77 |
| *Carex humilis* | 171 | 88 | 8,88 |
| *Carex laevigata* | 4 | 6 | / |
| *Carex lepidocarpa* | 12 | 4 | 8,66 |
| *Carex leporina* | 10 | 6 | 6,67 |
| *Carex montana* | 356 | 361 | 7,61 |
| *Carex muricata* | 116 | 127 | 7,45 |
| *Carex ornithopoda* | 22 | 37 | 6,28 |
| *Carex pallescens* | 110 | 41 | 6,38 |
| *Carex panicea* | 7 | 6 | 7,03 |
| *Carex paniculata* | 24 | 26 | 9,03 |
| *Carex pendula* | 524 | 708 | 11,2 |
| *Carex pilosa* | 49 | 41 | 6,94 |
| *Carex pilulifera* | 2479 | 2449 | 8,18 |
| *Carex remota* | 498 | 636 | 8,63 |
| *Carex riparia* | 47 | 49 | 8 |
| *Carex rostrata* | 2 | 5 | 5,45 |
| *Carex spicata* | 0 | 2 | 8,64 |
| *Carex strigosa* | 38 | 91 | / |
| *Carex sylvatica* | 3477 | 3744 | 8,29 |
| *Carex umbrosa* | 139 | 79 | 8,48 |
| *Carex vesicaria* | 1 | 1 | 5,45 |
| *Carex vulpina* | 3 | 1 | 8,81 |
| *Carlina* | 6 | 5 | / |
| *Carlina acanthifolia* | 36 | 22 | 10,31 |
| *Carlina acaulis* | 31 | 22 | 7,72 |
| *Carlina corymbosa* | 44 | 14 | / |
| *Carlina vulgaris* | 114 | 107 | 9,16 |
| *Carum carvi* | 10 | 4 | 5,55 |
| *Catananche* | 2 | 16 | / |
| *Catananche caerulea* | 87 | 53 | / |
| *Centaurea* | 63 | 68 | / |
| *Centaurea jacea* | 9 | 11 | 6,56 |
| *Centaurea nigra* | 120 | 119 | / |
| *Centaurea pectinata* | 31 | 26 | / |
| *Centaurea scabiosa* | 5 | 9 | 7 |
| *Centaurium erythraea* | 14 | 13 | 9,2 |
| *Cephalanthera* | 33 | 57 | / |
| *Cephalanthera damasonium* | 57 | 42 | 9,32 |
| *Cephalanthera longifolia* | 57 | 53 | 9,31 |
| *Cephalanthera rubra* | 38 | 26 | 9,17 |
| *Cephalaria leucantha* | 7 | 10 | / |

| | | | |
|---|---|---|---|
| *Cerastium arvense* | 11 | 8 | 5,96 |
| *Cerastium fontanum* | 2 | 2 | 6,34 |
| *Cerastium glomeratum* | 2 | 1 | 10,17 |
| *Ceratocapnos claviculata* | 60 | 39 | 10,62 |
| *Cervaria rivini* | 28 | 18 | 9,52 |
| *Chaerophyllum* | 22 | 32 | / |
| *Chaerophyllum aureum* | 2 | 12 | / |
| *Chaerophyllum hirsutum* | 23 | 21 | 8,57 |
| *Chaerophyllum temulum* | 4 | 3 | 9,91 |
| *Chaerophyllum villarsii* | 9 | 3 | / |
| *Chelidonium majus* | 38 | 22 | 8,05 |
| *Chenopodium album* | 0 | 1 | 11,49 |
| *Chrysosplenium alternifolium* | 14 | 8 | 5,81 |
| *Chrysosplenium oppositifolium* | 65 | 76 | 9,81 |
| *Circaea* | 2 | 8 | / |
| *Circaea alpina* | 5 | 3 | 5,34 |
| *Circaea lutetiana* | 549 | 676 | 8,4 |
| *Circaea x intermedia* | 16 | 18 | / |
| *Cirriphyllum piliferum* | 24 | 14 | / |
| *Cirsium* | 311 | 363 | / |
| *Cirsium acaulon* | 11 | 8 | 9,07 |
| *Cirsium arvense* | 300 | 335 | 7,43 |
| *Cirsium eriophorum* | 2 | 8 | / |
| *Cirsium erisithales* | 7 | 3 | 7,34 |
| *Cirsium oleraceum* | 168 | 43 | 6,05 |
| *Cirsium palustre* | 177 | 117 | 6,91 |
| *Cirsium vulgare* | 7 | 28 | 7,97 |
| *Cistus albidus* | 56 | 43 | / |
| *Cistus lasianthus* | 76 | 58 | / |
| *Cistus laurifolius* | 3 | 7 | / |
| *Cistus monspeliensis* | 23 | 23 | / |
| *Cistus salviifolius* | 92 | 83 | / |
| *Clematis* | 10 | 15 | / |
| *Clematis flammula* | 93 | 111 | / |
| *Clematis recta* | 5 | 0 | 7,99 |
| *Clematis vitalba* | 1502 | 1567 | 11,3 |
| *Climacium dendroides* | 5 | 10 | / |
| *Clinopodium* | 10 | 28 | / |
| *Clinopodium acinos* | 1 | 2 | 8,31 |
| *Clinopodium grandiflorum* | 38 | 38 | / |
| *Clinopodium nepeta* | 193 | 170 | / |
| *Clinopodium vulgare* | 224 | 226 | 8,93 |
| *Colchicum autumnale* | 0 | 3 | 10,07 |
| *Colchicum multiflorum* | 30 | 28 | / |
| *Comarum palustre* | 3 | 5 | 4,61 |
| *Conium maculatum* | 1 | 0 | 9,96 |
| *Conopodium majus* | 218 | 178 | 10,26 |
| *Convallaria majalis* | 799 | 780 | 7,12 |
| *Convolvulus* | 11 | 19 | / |
| *Convolvulus arvensis* | 2 | 2 | 8,58 |
| *Convolvulus sepium* | 89 | 74 | 8,34 |
| *Coriaria myrtifolia* | 62 | 55 | / |
| *Coris monspeliensis* | 5 | 9 | / |
| *Coronilla* | 16 | 18 | / |
| *Coronilla coronata* | 10 | 11 | 9,26 |
| *Coronilla glauca* | 27 | 7 | / |
| *Coronilla minima* | 76 | 77 | 12,63 |
| *Coronilla varia* | 17 | 15 | 8,96 |
| *Corydalis cava* | 11 | 2 | 8,26 |
| *Corydalis solida* | 6 | 10 | 7,4 |
| *Corynephorus canescens* | 0 | 1 | 9,57 |
| *Cotinus coggygria* | 33 | 34 | 10,72 |
| *Cotoneaster* | 10 | 17 | / |
| *Cotoneaster integerrimus* | 28 | 23 | 7,67 |
| *Cotoneaster tomentosus* | 11 | 13 | / |
| *Crataegus* | 9 | 21 | / |
| *Crataegus germanica* | 226 | 282 | / |
| *Crataegus laevigata* | 1626 | 1406 | 9,31 |
| *Crataegus monogyna* | 5736 | 6277 | 10,19 |
| *Crepis* | 6 | 8 | / |
| *Crepis biennis* | 2 | 0 | 8,11 |
| *Crepis capillaris* | 0 | 2 | 9,81 |
| *Crepis paludosa* | 35 | 18 | 5,73 |
| *Crocus* | 3 | 7 | / |
| *Crocus vernus* | 6 | 4 | / |
| *Cruciata glabra* | 41 | 52 | 9,87 |
| *Cruciata laevipes* | 65 | 51 | 10,1 |
| *Ctenidium molluscum* | 225 | 539 | / |
| *Cyanus montanus* | 29 | 28 | 7,67 |
| *Cyanus segetum* | 0 | 1 | 6,96 |
| *Cyanus triumfettii* | 0 | 1 | 9,75 |
| *Cyclamen purpurascens* | 11 | 7 | 8,49 |
| *Cynoglossum germanicum* | 1 | 2 | 9,44 |
| *Cynoglossum officinale* | 0 | 3 | 7,93 |
| *Cynosurus cristatus* | 5 | 7 | 8,57 |
| *Cypripedium calceolus* | 2 | 0 | 5,77 |
| *Cystopteris fragilis* | 21 | 10 | 6,3 |
| *Cytisophyllum sessilifolium* | 171 | 183 | / |
| *Cytisus* | 4 | 7 | / |

| | | | |
|---|---|---|---|
| *Cytisus oromediterraneus* | 128 | 97 | / |
| *Cytisus scoparius* | 2610 | 2432 | 9,88 |
| *Cytisus spinosus* | 30 | 17 | / |
| *Cytisus villosus* | 3 | 14 | / |
| *Dactylis* | 6 | 5 | / |
| *Dactylis glomerata* | 1728 | 1780 | 8,56 |
| *Dactylorhiza maculata* | 63 | 80 | 6,07 |
| *Dactylorhiza majalis* | 2 | 8 | / |
| *Dactylorhiza sambucina* | 2 | 1 | 9,89 |
| *Danthonia decumbens* | 111 | 104 | 8,06 |
| *Daphne alpina* | 0 | 1 | 11,11 |
| *Daphne gnidium* | 40 | 28 | / |
| *Daphne laureola* | 882 | 984 | 11,92 |
| *Daphne mezereum* | 339 | 316 | 5,35 |
| *Datura stramonium* | 1 | 0 | 9,6 |
| *Daucus carota* | 31 | 171 | 10,3 |
| *Deschampsia cespitosa* | 1946 | 1837 | 5,45 |
| *Dianthus* | 54 | 25 | / |
| *Dianthus armeria* | 3 | 3 | 9,34 |
| *Dianthus carthusianorum* | 5 | 3 | 9,67 |
| *Dianthus deltoides* | 0 | 1 | 6,32 |
| *Dianthus superbus* | 12 | 7 | 5,14 |
| *Dicranella* | 37 | 74 | / |
| *Dicranella heteromalla* | 184 | 45 | / |
| *Dicranum* | 287 | 135 | / |
| *Dicranum majus* | 10 | 6 | / |
| *Dicranum scoparium* | 2300 | 2527 | / |
| *Dictamnus albus* | 1 | 1 | 10,66 |
| *Digitalis* | 7 | 22 | / |
| *Digitalis grandiflora* | 13 | 11 | 7,82 |
| *Digitalis lutea* | 54 | 79 | 9,71 |
| *Digitalis purpurea* | 887 | 893 | 11,04 |
| *Dioscorea communis* | 665 | 625 | 12,54 |
| *Dipsacus fullonum* | 10 | 11 | / |
| *Dipsacus pilosus* | 7 | 11 | 8,52 |
| *Doronicum* | 4 | 7 | / |
| *Doronicum austriacum* | 14 | 11 | 7,23 |
| *Doronicum pardalianches* | 17 | 25 | / |
| *Draba aizoides* | 1 | 1 | 6,98 |
| *Draba muralis* | 0 | 2 | 10,68 |
| *Draba verna* | 1 | 1 | 10,01 |
| *Dryas octopetala* | 3 | 0 | 5,39 |
| *Drymocallis rupestris* | 1 | 0 | 8,69 |
| *Drymochloa sylvatica* | 292 | 297 | 6,01 |
| *Dryopteris* | 1 | 10 | / |
| *Dryopteris affinis* | 226 | 320 | / |
| *Dryopteris carthusiana* | 1727 | 2045 | 5,85 |
| *Dryopteris dilatata* | 970 | 830 | 8,99 |
| *Dryopteris filix-mas* | 2590 | 2820 | 7,35 |
| *Echinops ritro* | 28 | 30 | 7,52 |
| *Echium vulgare* | 11 | 8 | 8,56 |
| *Elymus caninus* | 34 | 30 | 6,18 |
| *Elytrigia repens* | 1 | 0 | 7,28 |
| *Empetrum nigrum* | 1 | 0 | 3,8 |
| *Epilobium* | 63 | 120 | / |
| *Epilobium angustifolium* | 313 | 119 | 6,46 |
| *Epilobium ciliatum* | 1 | 2 | 4,49 |
| *Epilobium duriaei* | 12 | 3 | / |
| *Epilobium hirsutum* | 52 | 64 | 9,32 |
| *Epilobium lanceolatum* | 4 | 4 | 11,69 |
| *Epilobium montanum* | 684 | 461 | 6,91 |
| *Epilobium palustre* | 4 | 4 | 4,85 |
| *Epilobium parviflorum* | 4 | 6 | 9,26 |
| *Epilobium tetragonum* | 0 | 8 | 9,15 |
| *Epipactis* | 63 | 73 | / |
| *Epipactis atrorubens* | 24 | 7 | 6,17 |
| *Epipactis helleborine* | 141 | 116 | 8,56 |
| *Epipactis purpurata* | 26 | 12 | / |
| *Equisetum* | 13 | 25 | / |
| *Equisetum arvense* | 15 | 17 | 6,26 |
| *Equisetum hyemale* | 16 | 7 | 4,86 |
| *Equisetum palustre* | 2 | 0 | 5,39 |
| *Equisetum pratense* | 5 | 3 | 3,8 |
| *Equisetum sylvaticum* | 9 | 10 | 4,52 |
| *Equisetum telmateia* | 59 | 55 | 10,73 |
| *Erica* | 3 | 7 | / |
| *Erica arborea* | 97 | 99 | / |
| *Erica ciliaris* | 105 | 69 | / |
| *Erica cinerea* | 933 | 783 | 10,19 |
| *Erica scoparia* | 855 | 756 | / |
| *Erica tetralix* | 88 | 72 | 9,54 |
| *Erica vagans* | 71 | 36 | / |
| *Erigeron* | 1 | 16 | / |
| *Erigeron annuus* | 3 | 13 | / |
| *Erigeron canadensis* | 100 | 37 | 8,52 |
| *Eriophorum angustifolium* | 1 | 0 | 4,95 |
| *Eriophorum vaginatum* | 1 | 2 | 4,57 |
| *Ervilia sylvatica* | 9 | 29 | 5,39 |
| *Eryngium campestre* | 178 | 137 | 11,8 |
| *Erythronium dens-canis* | 10 | 11 | / |

| | | | |
|---|---|---|---|
| *Euonymus europaeus* | 1548 | 1703 | 8,75 |
| *Euonymus latifolius* | 11 | 21 | / |
| *Eupatorium cannabinum* | 663 | 563 | 8,98 |
| *Euphorbia* | 27 | 51 | / |
| *Euphorbia amygdaloides* | 1741 | 1833 | 10,82 |
| *Euphorbia angulata* | 4 | 1 | 8,91 |
| *Euphorbia characias* | 100 | 102 | / |
| *Euphorbia cyparissias* | 453 | 427 | 8,17 |
| *Euphorbia dulcis* | 197 | 171 | 9,98 |
| *Euphorbia esula* | 2 | 1 | 6,71 |
| *Euphorbia helioscopia* | 1 | 0 | 9,9 |
| *Euphorbia hyberna* | 45 | 30 | / |
| *Euphorbia nicaeensis* | 17 | 17 | / |
| *Euphorbia peplus* | 0 | 2 | 10,42 |
| *Euphorbia serrata* | 4 | 9 | / |
| *Euphorbia spinosa* | 8 | 2 | / |
| *Euphorbia stricta* | 5 | 8 | / |
| *Euphrasia stricta* | 0 | 1 | 7,04 |
| *Eurhynchium* | 176 | 381 | / |
| *Eurhynchium angustirete* | 0 | 12 | / |
| *Eurhynchium striatum* | 1799 | 2877 | / |
| *Exsertotheca crispa* | 40 | 115 | / |
| *Fallopia convolvulus* | 0 | 1 | 7,76 |
| *Fallopia dumetorum* | 0 | 1 | 7,74 |
| *Festuca* | 222 | 315 | / |
| *Festuca eskia* | 7 | 10 | / |
| *Festuca gautieri* | 22 | 7 | / |
| *Festuca glauca* | 15 | 6 | / |
| *Festuca heterophylla* | 871 | 695 | 9,71 |
| *Festuca ovina* | 524 | 258 | 5,66 |
| *Festuca rubra* | 12 | 2 | 6,65 |
| *Ficaria verna* | 632 | 700 | 8,18 |
| *Ficus carica* | 12 | 17 | / |
| *Filago arvensis* | 1 | 0 | 7,24 |
| *Filipendula ulmaria* | 191 | 195 | 5,58 |
| *Filipendula vulgaris* | 53 | 40 | 7,87 |
| *Fissidens* | 26 | 359 | / |
| *Fissidens taxifolius* | 410 | 400 | / |
| *Fourraea alpina* | 10 | 7 | / |
| *Fragaria moschata* | 1 | 0 | 6,98 |
| *Fragaria vesca* | 2554 | 2431 | 6,71 |
| *Fragaria viridis* | 23 | 5 | 7,33 |
| *Frangula alnus* | 2350 | 2407 | 6,4 |
| *Fumana* | 7 | 9 | / |
| *Fumana ericoides* | 31 | 21 | / |
| *Fumana procumbens* | 26 | 18 | / |
| *Fumana thymifolia* | 16 | 3 | / |
| *Fumaria officinalis* | 0 | 1 | 9,34 |
| *Gagea lutea* | 0 | 2 | 6,98 |
| *Galanthus nivalis* | 5 | 6 | 10,3 |
| *Galeopsis* | 2 | 21 | / |
| *Galeopsis ladanum* | 5 | 7 | 6,86 |
| *Galeopsis tetrahit* | 817 | 823 | 7,77 |
| *Galium* | 260 | 323 | / |
| *Galium album* | 15 | 10 | 7,61 |
| *Galium aparine* | 837 | 925 | 9,2 |
| *Galium aristatum* | 3 | 11 | 7,3 |
| *Galium boreale* | 1 | 1 | 4,54 |
| *Galium corrudifolium* | 0 | 31 | / |
| *Galium glaucum* | 5 | 4 | 9,56 |
| *Galium maritimum* | 23 | 35 | / |
| *Galium mollugo* | 820 | 653 | 7,37 |
| *Galium odoratum* | 1401 | 1593 | 7,6 |
| *Galium palustre* | 67 | 48 | 6,31 |
| *Galium pumilum* | 16 | 10 | 8,25 |
| *Galium rotundifolium* | 203 | 237 | 8,63 |
| *Galium saxatile* | 344 | 279 | 9,85 |
| *Galium sylvaticum* | 80 | 69 | 8,14 |
| *Galium uliginosum* | 11 | 6 | 5,06 |
| *Galium verum* | 56 | 46 | 7,56 |
| *Genista anglica* | 21 | 9 | 10,33 |
| *Genista cinerea* | 135 | 150 | / |
| *Genista germanica* | 13 | 8 | 8,57 |
| *Genista hispanica* | 129 | 127 | / |
| *Genista pilosa* | 374 | 283 | 9,62 |
| *Genista sagittalis* | 36 | 28 | 9,71 |
| *Genista scorpius* | 89 | 83 | / |
| *Genista tinctoria* | 15 | 16 | 8,51 |
| *Gentiana* | 6 | 4 | / |
| *Gentiana asclepiadea* | 3 | 1 | 6,8 |
| *Gentiana lutea* | 90 | 82 | 8,98 |
| *Gentiana verna* | 2 | 9 | / |
| *Gentianopsis ciliata* | 3 | 1 | 10,08 |
| *Geranium* | 36 | 58 | / |
| *Geranium lucidum* | 1 | 7 | 12,64 |
| *Geranium molle* | 4 | 4 | 10,82 |
| *Geranium nodosum* | 67 | 75 | / |
| *Geranium pratense* | 6 | 3 | 4,96 |
| *Geranium purpureum* | 0 | 23 | / |
| *Geranium pusillum* | 0 | 1 | 8,53 |

| | | | |
|---|---|---|---|
| *Geranium pyrenaicum* | 0 | 3 | 9,52 |
| *Geranium robertianum* | 1596 | 1611 | 8,49 |
| *Geranium rotundifolium* | 4 | 9 | / |
| *Geranium sanguineum* | 26 | 18 | 8,99 |
| *Geranium sylvaticum* | 77 | 67 | 3,98 |
| *Geum* | 10 | 6 | / |
| *Geum rivale* | 25 | 24 | 4,58 |
| *Geum sylvaticum* | 8 | 5 | / |
| *Geum urbanum* | 1737 | 2108 | 7,92 |
| *Glechoma hederacea* | 814 | 999 | 6,7 |
| *Globularia* | 13 | 12 | / |
| *Globularia bisnagarica* | 1 | 20 | / |
| *Globularia cordifolia* | 27 | 18 | 9,51 |
| *Globularia vulgaris* | 69 | 58 | / |
| *Glyceria* | 17 | 41 | / |
| *Glyceria fluitans* | 7 | 36 | 8,26 |
| *Goodyera repens* | 44 | 46 | 4,35 |
| *Gymnocarpium dryopteris* | 31 | 35 | 4,63 |
| *Gymnocarpium robertianum* | 26 | 26 | 8,09 |
| *Hedera helix* | 8982 | 9119 | 10,93 |
| *Helianthemum* | 113 | 83 | / |
| *Helianthemum apenninum* | 7 | 7 | / |
| *Helianthemum canum* | 6 | 4 | / |
| *Helianthemum nummularium* | 69 | 83 | 9,1 |
| *Helichrysum stoechas* | 49 | 34 | / |
| *Helictochloa bromoides* | 9 | 7 | / |
| *Helictochloa pratensis* | 2 | 0 | 8,63 |
| *Helleborus foetidus* | 863 | 890 | 11,65 |
| *Helleborus niger* | 1 | 0 | 8,13 |
| *Helleborus viridis* | 66 | 65 | / |
| *Heracleum sphondylium* | 317 | 330 | 5,74 |
| *Hieracium* | 224 | 370 | / |
| *Hieracium bifidum* | 11 | 0 | 5,62 |
| *Hieracium juranum* | 13 | 6 | / |
| *Hieracium laevigatum* | 20 | 8 | 5,09 |
| *Hieracium murorum* | 879 | 576 | 7,27 |
| *Hieracium prenanthoides* | 18 | 12 | 5,31 |
| *Hieracium racemosum* | 0 | 1 | 10,79 |
| *Hieracium sabaudum* | 49 | 26 | 9,13 |
| *Hieracium umbellatum* | 18 | 12 | 6,04 |
| *Hieracium vulgatum* | 35 | 77 | / |
| *Hippocrepis comosa* | 95 | 130 | 10,06 |
| *Hippocrepis emerus* | 248 | 229 | 12,63 |
| *Hippophae rhamnoides* | 7 | 5 | / |
| *Holcus* | 7 | 35 | / |
| *Holcus lanatus* | 905 | 637 | 9,85 |
| *Holcus mollis* | 1720 | 1168 | 8,73 |
| *Homogyne alpina* | 26 | 17 | 6,17 |
| *Hordelymus europaeus* | 401 | 437 | 8,27 |
| *Humulus lupulus* | 41 | 52 | 7,21 |
| *Huperzia selago* | 0 | 2 | 4,21 |
| *Hyacinthoides non-scripta* | 272 | 283 | 10,14 |
| *Hydrocotyle vulgaris* | 24 | 12 | 10,27 |
| *Hylocomiadelphus triquetrus* | 2103 | 2526 | / |
| *Hylocomium splendens* | 919 | 1213 | / |
| *Hylotelephium telephium* | 19 | 22 | 7,11 |
| *Hypericum* | 70 | 150 | / |
| *Hypericum androsaemum* | 237 | 239 | / |
| *Hypericum hirsutum* | 310 | 427 | 7,49 |
| *Hypericum humifusum* | 93 | 40 | 9,6 |
| *Hypericum maculatum* | 28 | 27 | 5,73 |
| *Hypericum montanum* | 118 | 72 | 8,75 |
| *Hypericum perfoliatum* | 4 | 10 | / |
| *Hypericum perforatum* | 897 | 800 | 9,25 |
| *Hypericum pulchrum* | 989 | 777 | 9,64 |
| *Hypericum tetrapterum* | 5 | 5 | 9,95 |
| *Hypnum* | 27 | 121 | / |
| *Hypnum cupressiforme* | 180 | 942 | / |
| *Hypnum jutlandicum* | 523 | 121 | / |
| *Hypochaeris* | 4 | 11 | / |
| *Hypochaeris radicata* | 12 | 6 | 10,49 |
| *Impatiens glandulifera* | 17 | 39 | / |
| *Impatiens noli-tangere* | 64 | 51 | 6,68 |
| *Impatiens parviflora* | 1 | 6 | 8,12 |
| *Imperatoria ostruthium* | 21 | 14 | / |
| *Inula conyza* | 12 | 21 | 10,82 |
| *Inula salicina* | 1 | 2 | 6,88 |
| *Iris* | 19 | 25 | / |
| *Iris foetidissima* | 72 | 80 | / |
| *Iris pseudacorus* | 98 | 77 | 9,27 |
| *Isothecium alopecuroides* | 2 | 9 | / |
| *Jacobaea adonidifolia* | 47 | 32 | / |
| *Jacobaea vulgaris* | 123 | 95 | 7,6 |
| *Jasione montana* | 22 | 12 | 8,14 |
| *Jasminum fruticans* | 9 | 17 | / |
| *Juncus* | 1049 | 1004 | / |
| *Juncus acutiflorus* | 4 | 1 | 9,92 |
| *Juncus bufonius* | 24 | 36 | 8,43 |

| | | | |
|---|---|---|---|
| *Juncus bulbosus* | 1 | 1 | 7,52 |
| *Juncus compressus* | 2 | 0 | 7,35 |
| *Juncus conglomeratus* | 372 | 419 | 7,9 |
| *Juncus effusus* | 673 | 684 | 8,65 |
| *Juncus filiformis* | 1 | 0 | 3,8 |
| *Juncus inflexus* | 3 | 1 | 10,66 |
| *Juncus squarrosus* | 1 | 1 | 8,85 |
| *Juncus tenuis* | 16 | 22 | 8,69 |
| *Juniperus communis* | 1422 | 1215 | 6,63 |
| *Juniperus oxycedrus* | 203 | 177 | / |
| *Juniperus phoenicea* | 22 | 25 | / |
| *Kindbergia praelonga* | 115 | 246 | / |
| *Knautia* | 35 | 31 | / |
| *Knautia arvensis* | 11 | 25 | 6,93 |
| *Knautia arvernensis* | 2 | 9 | 9,29 |
| *Knautia dipsacifolia* | 157 | 136 | 7,18 |
| *Koeleria vallesiana* | 12 | 13 | / |
| *Lactuca* | 18 | 13 | / |
| *Lactuca alpina* | 5 | 19 | 3,06 |
| *Lactuca muralis* | 622 | 622 | 8,76 |
| *Lactuca perennis* | 18 | 21 | / |
| *Lactuca serriola* | 3 | 4 | 9,67 |
| *Lamium* | 40 | 62 | / |
| *Lamium album* | 9 | 8 | 6,61 |
| *Lamium amplexicaule* | 1 | 0 | 9,44 |
| *Lamium galeobdolon* | 1748 | 1721 | 8,44 |
| *Lamium maculatum* | 74 | 112 | 8,29 |
| *Lamium purpureum* | 46 | 33 | 8,25 |
| *Lapsana communis* | 183 | 204 | 8,13 |
| *Laser trilobum* | 12 | 8 | / |
| *Laserpitium gallicum* | 29 | 46 | / |
| *Laserpitium latifolium* | 41 | 47 | 8,8 |
| *Laserpitium nestleri* | 4 | 6 | / |
| *Laserpitium siler* | 8 | 8 | / |
| *Lathraea clandestina* | 8 | 9 | / |
| *Lathraea squamaria* | 2 | 5 | 7,53 |
| *Lathyrus* | 61 | 96 | / |
| *Lathyrus aphaca* | 14 | 3 | 12,92 |
| *Lathyrus latifolius* | 0 | 7 | 11,92 |
| *Lathyrus linifolius* | 455 | 243 | 8,85 |
| *Lathyrus niger* | 35 | 17 | 7,89 |
| *Lathyrus pratensis* | 113 | 89 | 6,07 |
| *Lathyrus sylvestris* | 35 | 26 | 12,21 |
| *Lathyrus vernus* | 240 | 211 | 6,28 |
| *Laurus nobilis* | 63 | 107 | 15,2 |
| *Lavandula* | 4 | 37 | / |
| *Lavandula angustifolia* | 201 | 150 | / |
| *Lavandula latifolia* | 51 | 29 | / |
| *Lavandula stoechas* | 22 | 14 | / |
| *Leontodon* | 15 | 7 | / |
| *Leontodon hispidus* | 4 | 7 | 8,01 |
| *Leucanthemum* | 21 | 36 | / |
| *Leucanthemum vulgare* | 114 | 82 | 6,36 |
| *Leucobryum glaucum* | 349 | 428 | / |
| *Leucojum vernum* | 8 | 9 | 8,55 |
| *Libanotis pyrenaica* | 0 | 7 | 5,97 |
| *Ligustrum vulgare* | 3240 | 3278 | 9,93 |
| *Lilium martagon* | 39 | 38 | 6,79 |
| *Linaria* | 12 | 39 | / |
| *Linaria repens* | 225 | 139 | 9,97 |
| *Linaria vulgaris* | 6 | 14 | 6,37 |
| *Linum* | 7 | 11 | / |
| *Linum narbonense* | 6 | 5 | / |
| *Linum suffruticosum* | 22 | 17 | 15,8 |
| *Lipandra polysperma* | 1 | 1 | 8,07 |
| *Lithospermum officinale* | 0 | 3 | 8,35 |
| *Loeskeobryum brevirostre* | 36 | 79 | / |
| *Lolium perenne* | 1 | 1 | 9,42 |
| *Loncomelos pyrenaicus* | 287 | 364 | 10,97 |
| *Lonicera* | 13 | 24 | / |
| *Lonicera alpigena* | 56 | 46 | 7,75 |
| *Lonicera caerulea* | 7 | 14 | / |
| *Lonicera etrusca* | 210 | 246 | / |
| *Lonicera implexa* | 94 | 66 | / |
| *Lonicera nigra* | 280 | 299 | 7,42 |
| *Lonicera periclymenum* | 5620 | 5452 | 9,95 |
| *Lonicera xylosteum* | 2351 | 2235 | 5,87 |
| *Lotus* | 95 | 59 | / |
| *Lotus corniculatus* | 100 | 109 | 9,38 |
| *Lotus dorycnium* | 187 | 186 | / |
| *Lotus hirsutus* | 71 | 39 | / |
| *Lotus pedunculatus* | 48 | 44 | 10,53 |
| *Lunaria rediviva* | 9 | 6 | 8,17 |
| *Luzula* | 187 | 356 | / |
| *Luzula campestris* | 73 | 33 | 9,28 |
| *Luzula forsteri* | 319 | 198 | 12,35 |
| *Luzula luzulina* | 20 | 24 | 8,06 |
| *Luzula luzuloides* | 377 | 298 | 7,76 |
| *Luzula multiflora* | 202 | 119 | 5,75 |
| *Luzula nivea* | 111 | 127 | 8,77 |

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|---|---|---|---|
| *Luzula pilosa* | 1054 | 917 | 4,94 |
| *Luzula sylvatica* | 641 | 586 | 9,72 |
| *Lychnis flos-cuculi* | 11 | 15 | 7,33 |
| *Lycopodium annotinum* | 3 | 2 | 4,06 |
| *Lycopus europaeus* | 67 | 98 | 8,51 |
| *Lysimachia arvensis* | 2 | 11 | 11,3 |
| *Lysimachia nemorum* | 188 | 199 | 9,45 |
| *Lysimachia nummularia* | 103 | 87 | 7,86 |
| *Lysimachia vulgaris* | 39 | 62 | 7,05 |
| *Lythrum salicaria* | 13 | 37 | 7,76 |
| *Maianthemum bifolium* | 98 | 79 | 4,76 |
| *Malus sylvestris* | 440 | 357 | 8,96 |
| *Malva moschata* | 2 | 4 | 9,24 |
| *Malva sylvestris* | 2 | 7 | 12,08 |
| *Matricaria chamomilla* | 0 | 1 | 8,46 |
| *Medicago* | 17 | 11 | / |
| *Medicago lupulina* | 24 | 16 | 8,73 |
| *Melampyrum* | 58 | 72 | / |
| *Melampyrum cristatum* | 7 | 3 | 7 |
| *Melampyrum nemorosum* | 39 | 22 | 6,2 |
| *Melampyrum pratense* | 312 | 214 | 5,65 |
| *Melampyrum sylvaticum* | 47 | 58 | 3,14 |
| *Melica ciliata* | 9 | 9 | 11,03 |
| *Melica nutans* | 93 | 90 | 5,97 |
| *Melica uniflora* | 1071 | 1132 | 9,92 |
| *Melilotus officinalis* | 3 | 1 | 7,48 |
| *Melittis melissophyllum* | 275 | 261 | 11,71 |
| *Mentha* | 7 | 20 | / |
| *Mentha aquatica* | 25 | 32 | 9,32 |
| *Mentha arvensis* | 25 | 19 | 6,29 |
| *Mentha longifolia* | 2 | 5 | 8,72 |
| *Mentha suaveolens* | 12 | 11 | / |
| *Mercurialis perennis* | 804 | 869 | 7,87 |
| *Meum athamanticum* | 10 | 14 | / |
| *Microthlaspi perfoliatum* | 1 | 0 | 11,51 |
| *Milium effusum* | 988 | 981 | 5,63 |
| *Mnium* | 9 | 18 | / |
| *Mnium hornum* | 62 | 123 | / |
| *Moehringia muscosa* | 123 | 97 | / |
| *Moehringia trinervia* | 562 | 602 | 8,08 |
| *Molinia caerulea* | 2186 | 2019 | 6,19 |
| *Moneses uniflora* | 4 | 2 | 4,01 |
| *Monotropa hypopitys* | 8 | 7 | 7,39 |
| *Montia fontana* | 1 | 0 | 6,29 |
| *Muscari* | 9 | 23 | / |
| *Muscari botryoides* | 3 | 0 | 10,72 |
| *Muscari comosum* | 22 | 12 | / |
| *Muscari neglectum* | 9 | 1 | / |
| *Myosotis* | 50 | 76 | / |
| *Myosotis arvensis* | 3 | 6 | 7,22 |
| *Myosotis scorpioides* | 36 | 24 | 6,92 |
| *Myosotis stricta* | 0 | 1 | 6,46 |
| *Myosotis sylvatica* | 114 | 67 | 9,09 |
| *Myosoton aquaticum* | 4 | 1 | 7,59 |
| *Myrrhis odorata* | 9 | 5 | / |
| *Narcissus bulbocodium* | 17 | 0 | / |
| *Narcissus jonquilla* | 21 | 7 | / |
| *Narcissus pseudonarcissus* | 32 | 62 | / |
| *Nardus stricta* | 25 | 10 | 6,29 |
| *Nectaroscilla hyacinthoides* | 4 | 7 | / |
| *Neottia nidus-avis* | 281 | 253 | 8,39 |
| *Neottia ovata* | 105 | 94 | 6,74 |
| *Odontites luteus* | 58 | 42 | / |
| *Odontites vernus* | 0 | 1 | 8,1 |
| *Oloptum miliaceum* | 9 | 3 | / |
| *Omalotheca sylvatica* | 4 | 5 | 6,1 |
| *Ononis* | 19 | 23 | / |
| *Ononis fruticosa* | 14 | 9 | / |
| *Ononis minutissima* | 103 | 81 | / |
| *Ononis natrix* | 14 | 14 | / |
| *Ononis pusilla* | 7 | 10 | / |
| *Ononis spinosa* | 27 | 22 | 9,68 |
| *Orchis* | 49 | 74 | / |
| *Orchis mascula* | 46 | 41 | 9,57 |
| *Orchis purpurea* | 23 | 25 | 10,01 |
| *Oreopteris limbosperma* | 4 | 6 | 8,41 |
| *Oreoselinum nigrum* | 1 | 1 | 7,82 |
| *Origanum vulgare* | 202 | 177 | 7,6 |
| *Ornithogalum umbellatum* | 6 | 11 | 11,37 |
| *Ornithopus perpusillus* | 1 | 0 | 9,82 |
| *Orobanche* | 37 | 26 | / |
| *Orthilia secunda* | 93 | 79 | 4,29 |
| *Osmunda regalis* | 21 | 39 | / |
| *Ostrya carpinifolia* | 5 | 8 | / |
| *Osyris alba* | 79 | 78 | / |
| *Oxalis* | 11 | 30 | / |
| *Oxalis acetosella* | 1129 | 1125 | 6,08 |
| *Oxalis corniculata* | 3 | 2 | 11,96 |
| *Oxalis dillenii* | 1 | 0 | 8,98 |
| *Paliurus spina-christi* | 7 | 6 | / |

| | | | |
|---|---|---|---|
| *Papaver rhoeas* | 1 | 0 | 11,1 |
| *Paris quadrifolia* | 456 | 439 | 5,65 |
| *Parnassia palustris* | 1 | 1 | 6,01 |
| *Persicaria hydropiper* | 6 | 38 | 7,38 |
| *Persicaria lapathifolia* | 2 | 3 | 8,14 |
| *Persicaria maculosa* | 16 | 15 | 8,4 |
| *Petasites* | 9 | 15 | / |
| *Petasites albus* | 36 | 39 | 8,27 |
| *Petasites hybridus* | 3 | 4 | 9,43 |
| *Petasites paradoxus* | 5 | 8 | / |
| *Peucedanum* | 8 | 3 | / |
| *Peucedanum gallicum* | 59 | 35 | / |
| *Phalaris arundinacea* | 49 | 64 | 6,58 |
| *Phegopteris connectilis* | 6 | 10 | 5,02 |
| *Phelipanche purpurea* | 0 | 1 | 10,15 |
| *Phillyrea angustifolia* | 101 | 79 | / |
| *Phillyrea latifolia* | 166 | 158 | / |
| *Phleum* | 16 | 12 | / |
| *Phleum alpinum* | 9 | 4 | 3,69 |
| *Phleum nodosum* | 0 | 2 | 10,99 |
| *Phleum pratense* | 41 | 22 | 7,49 |
| *Phragmites australis* | 86 | 92 | 7,49 |
| *Physalis alkekengi* | 0 | 1 | 10,09 |
| *Phyteuma* | 38 | 18 | / |
| *Phyteuma betonicifolium* | 15 | 2 | / |
| *Phyteuma nigrum* | 30 | 8 | 8,87 |
| *Phyteuma orbiculare* | 13 | 8 | / |
| *Phyteuma spicatum* | 337 | 291 | 8,31 |
| *Phytolacca americana* | 91 | 82 | / |
| *Picris* | 4 | 9 | / |
| *Picris hieracioides* | 5 | 5 | 7,71 |
| *Pilosella officinarum* | 309 | 269 | 7,75 |
| *Pimpinella* | 12 | 11 | / |
| *Pimpinella major* | 23 | 34 | 9,14 |
| *Pimpinella saxifraga* | 53 | 28 | 6,7 |
| *Pinguicula vulgaris* | 0 | 1 | 5,25 |
| *Pistacia lentiscus* | 25 | 22 | / |
| *Pistacia terebinthus* | 94 | 85 | / |
| *Plagiochila asplenioides* | 152 | 88 | / |
| *Plagiochila porelloides* | 0 | 55 | / |
| *Plagiomnium* | 3 | 15 | / |
| *Plagiomnium affine* | 279 | 236 | / |
| *Plagiomnium undulatum* | 924 | 967 | / |
| *Plagiothecium undulatum* | 11 | 32 | / |
| *Plantago* | 99 | 69 | / |
| *Plantago lanceolata* | 165 | 157 | 9,87 |
| *Plantago major* | 68 | 103 | 9,12 |
| *Plantago media* | 41 | 60 | 6,08 |
| *Platanthera* | 9 | 10 | / |
| *Platanthera bifolia* | 32 | 21 | 6,51 |
| *Platanthera chlorantha* | 15 | 9 | 8,51 |
| *Pleurozium schreberi* | 416 | 460 | / |
| *Poa* | 35 | 122 | / |
| *Poa alpina* | 2 | 4 | 3,38 |
| *Poa annua* | 7 | 16 | / |
| *Poa chaixii* | 329 | 309 | 8,12 |
| *Poa nemoralis* | 962 | 773 | 6,26 |
| *Poa palustris* | 0 | 1 | 4,75 |
| *Poa pratensis* | 5 | 4 | 6,2 |
| *Poa trivialis* | 279 | 316 | 8,14 |
| *Polygala* | 16 | 15 | / |
| *Polygala amarella* | 2 | 2 | 4,89 |
| *Polygala calcarea* | 13 | 13 | / |
| *Polygala comosa* | 3 | 0 | 6,86 |
| *Polygala serpyllifolia* | 21 | 6 | 9,73 |
| *Polygala vulgaris* | 55 | 36 | 9,34 |
| *Polygaloides chamaebuxus* | 21 | 34 | 8,18 |
| *Polygonatum* | 2 | 25 | / |
| *Polygonatum multiflorum* | 996 | 946 | 8,04 |
| *Polygonatum odoratum* | 161 | 102 | 6,59 |
| *Polygonatum verticillatum* | 331 | 359 | 6,8 |
| *Polygonum* | 20 | 26 | / |
| *Polygonum aviculare* | 4 | 6 | 7,74 |
| *Polypodium* | 2 | 16 | / |
| *Polypodium cambricum* | 14 | 15 | / |
| *Polypodium interjectum* | 21 | 32 | / |
| *Polypodium vulgare* | 637 | 588 | 7,95 |
| *Polystichum* | 3 | 14 | / |
| *Polystichum aculeatum* | 198 | 259 | 10,57 |
| *Polystichum braunii* | 1 | 0 | 6,09 |
| *Polystichum lonchitis* | 50 | 28 | 7,59 |
| *Polystichum setiferum* | 278 | 283 | / |
| *Polytrichum* | 8 | 12 | / |
| *Polytrichum commune* | 101 | 83 | / |
| *Polytrichum formosum* | 4762 | 4846 | / |
| *Polytrichum juniperinum* | 16 | 23 | / |
| *Polytrichum piliferum* | 0 | 24 | / |
| *Potentilla* | 63 | 73 | / |
| *Potentilla alba* | 2 | 0 | 7,37 |
| *Potentilla crantzii* | 1 | 0 | 4,82 |

| | | | |
|---|---|---|---|
| *Potentilla erecta* | 579 | 372 | 6,95 |
| *Potentilla heptaphylla* | 0 | 1 | 8,77 |
| *Potentilla hirta* | 7 | 6 | / |
| *Potentilla micrantha* | 2 | 2 | 11,41 |
| *Potentilla montana* | 32 | 29 | / |
| *Potentilla recta* | 25 | 10 | 8,66 |
| *Potentilla reptans* | 131 | 116 | 10,11 |
| *Potentilla sterilis* | 1294 | 1336 | 9,76 |
| *Potentilla verna* | 19 | 29 | 9,45 |
| *Poterium sanguisorba* | 320 | 282 | 10,74 |
| *Prenanthes purpurea* | 401 | 410 | 7,96 |
| *Primula* | 152 | 235 | / |
| *Primula elatior* | 573 | 665 | 9,21 |
| *Primula veris* | 281 | 151 | 7,48 |
| *Primula vulgaris* | 75 | 76 | 10,56 |
| *Prunella* | 21 | 41 | / |
| *Prunella grandiflora* | 15 | 3 | / |
| *Prunella laciniata* | 21 | 8 | 11,64 |
| *Prunella vulgaris* | 290 | 429 | 7,29 |
| *Pseudarrhenatherum longifolium* | 526 | 411 | / |
| *Pseudoscleropodium purum* | 2773 | 3074 | / |
| *Pseudoturritis turrita* | 45 | 60 | / |
| *Pteridium aquilinum* | 4557 | 4492 | 9,15 |
| *Ptilium crista-castrensis* | 12 | 10 | / |
| *Puccinellia distans* | 1 | 0 | 6,63 |
| *Pulicaria dysenterica* | 2 | 4 | 11,7 |
| *Pulmonaria* | 58 | 130 | / |
| *Pulmonaria affinis* | 250 | 272 | / |
| *Pulmonaria longifolia* | 269 | 189 | 11,03 |
| *Pulmonaria montana* | 132 | 146 | / |
| *Pulmonaria obscura* | 0 | 18 | 5,7 |
| *Pulmonaria officinalis* | 55 | 5 | 8,31 |
| *Pyracantha coccinea* | 11 | 13 | / |
| *Pyrola* | 3 | 8 | / |
| *Pyrola chlorantha* | 2 | 1 | 5,12 |
| *Pyrola minor* | 5 | 3 | 4,84 |
| *Pyrola rotundifolia* | 6 | 7 | 4,38 |
| *Pyrus* | 4 | 8 | / |
| *Pyrus communis* | 438 | 360 | 9,11 |
| *Pyrus cordata* | 8 | 7 | / |
| *Pyrus spinosa* | 7 | 7 | / |
| *Ranunculus* | 266 | 337 | / |
| *Ranunculus aconitifolius* | 30 | 23 | / |
| *Ranunculus acris* | 38 | 23 | 5,61 |
| *Ranunculus aduncus* | 15 | 36 | / |
| *Ranunculus auricomus* | 267 | 290 | 6,06 |
| *Ranunculus bulbosus* | 138 | 152 | 9,8 |
| *Ranunculus flammula* | 18 | 22 | 7,31 |
| *Ranunculus lanuginosus* | 18 | 19 | 9,2 |
| *Ranunculus monspeliacus* | 1 | 0 | 9,33 |
| *Ranunculus platanifolius* | 64 | 38 | 5,64 |
| *Ranunculus repens* | 420 | 371 | 6,84 |
| *Ranunculus serpens* | 285 | 200 | / |
| *Reynoutria japonica* | 14 | 18 | / |
| *Rhamnus alaternus* | 153 | 165 | / |
| *Rhamnus alpina* | 48 | 47 | 10,57 |
| *Rhamnus cathartica* | 213 | 202 | 7,81 |
| *Rhamnus saxatilis* | 59 | 60 | / |
| *Rhaponticum coniferum* | 24 | 11 | / |
| *Rhinanthus* | 12 | 4 | / |
| *Rhinanthus alectorolophus* | 7 | 6 | / |
| *Rhinanthus minor* | 2 | 1 | 6,62 |
| *Rhizomnium punctatum* | 59 | 80 | / |
| *Rhodobryum roseum* | 22 | 9 | / |
| *Rhododendron ferrugineum* | 24 | 19 | / |
| *Rhododendron hirsutum* | 1 | 0 | 6 |
| *Rhytidiadelphus* | 13 | 23 | / |
| *Rhytidiadelphus loreus* | 373 | 623 | / |
| *Rhytidiadelphus squarrosus* | 136 | 130 | / |
| *Ribes* | 12 | 31 | / |
| *Ribes alpinum* | 936 | 938 | 6,78 |
| *Ribes nigrum* | 3 | 8 | 5,32 |
| *Ribes petraeum* | 20 | 4 | / |
| *Ribes rubrum* | 298 | 286 | 6,54 |
| *Ribes uva-crispa* | 189 | 200 | 7,87 |
| *Rosa* | 155 | 192 | / |
| *Rosa agrestis* | 2 | 8 | / |
| *Rosa arvensis* | 3270 | 3038 | 10,38 |
| *Rosa canina* | 2246 | 1965 | 8,99 |
| *Rosa montana* | 16 | 0 | / |
| *Rosa pendulina* | 175 | 171 | 8,94 |
| *Rosa rubiginosa* | 17 | 6 | 9,27 |
| *Rosa sempervirens* | 47 | 135 | / |
| *Rosa spinosissima* | 50 | 42 | / |
| *Rosmarinus officinalis* | 23 | 32 | / |
| *Rubia peregrina* | 1995 | 2004 | / |
| *Rubus* | 153 | 599 | / |
| *Rubus caesius* | 152 | 337 | 7,83 |
| *Rubus canescens* | 59 | 7 | / |

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|---|---|---|---|
| *Rubus fruticosus* | 10564 | 9937 | 8,77 |
| *Rubus hirtus* | 3 | 0 | 8,77 |
| *Rubus idaeus* | 1516 | 1277 | 5,75 |
| *Rubus saxatilis* | 99 | 91 | 4,19 |
| *Rubus ulmifolius* | 1191 | 1679 | 12,95 |
| *Rumex* | 139 | 223 | / |
| *Rumex acetosa* | 242 | 228 | 6,87 |
| *Rumex acetosella* | 262 | 190 | 6,75 |
| *Rumex arifolius* | 9 | 9 | 8,68 |
| *Rumex conglomeratus* | 0 | 1 | 10,83 |
| *Rumex crispus* | 0 | 1 | 8,42 |
| *Rumex hydrolapathum* | 7 | 5 | 7,37 |
| *Rumex longifolius* | 1 | 3 | 3,08 |
| *Rumex obtusifolius* | 96 | 117 | 8,07 |
| *Rumex sanguineus* | 286 | 345 | 8,8 |
| *Ruscus aculeatus* | 1580 | 1685 | 13,45 |
| *Salvia glutinosa* | 19 | 21 | 9,59 |
| *Salvia pratensis* | 10 | 7 | 8,71 |
| *Sambucus* | 2 | 10 | / |
| *Sambucus ebulus* | 14 | 19 | 11,35 |
| *Sambucus nigra* | 1315 | 1562 | 10,48 |
| *Sambucus racemosa* | 654 | 514 | 7,05 |
| *Sanguisorba* | 16 | 15 | / |
| *Sanguisorba officinalis* | 4 | 6 | 5,77 |
| *Sanicula europaea* | 217 | 274 | 8,51 |
| *Saponaria ocymoides* | 22 | 20 | / |
| *Satureja* | 2 | 11 | / |
| *Satureja montana* | 37 | 31 | / |
| *Saxifraga* | 13 | 9 | / |
| *Saxifraga aizoides* | 1 | 0 | 5,2 |
| *Saxifraga cuneifolia* | 17 | 7 | / |
| *Saxifraga granulata* | 19 | 12 | 9,54 |
| *Saxifraga hirsuta* | 31 | 21 | / |
| *Saxifraga rotundifolia* | 51 | 39 | 9,65 |
| *Scabiosa* | 21 | 11 | / |
| *Scabiosa columbaria* | 64 | 45 | 9,95 |
| *Schedonorus giganteus* | 139 | 151 | 7,37 |
| *Schedonorus pratensis* | 2 | 0 | 6,53 |
| *Scilla bifolia* | 70 | 80 | 9,24 |
| *Scirpus* | 6 | 5 | / |
| *Scirpus sylvaticus* | 8 | 14 | 6,84 |
| *Scorzonera humilis* | 2 | 1 | 7,68 |
| *Scrophularia alpestris* | 15 | 25 | / |
| *Scrophularia auriculata* | 0 | 1 | 13,16 |
| *Scrophularia nodosa* | 467 | 449 | 7,17 |
| *Scrophularia oblongifolia* | 7 | 4 | / |
| *Scutellaria galericulata* | 15 | 11 | 6,24 |
| *Scutellaria minor* | 16 | 6 | / |
| *Sedum* | 186 | 82 | / |
| *Sedum acre* | 27 | 9 | 7,79 |
| *Sedum album* | 6 | 4 | 12,03 |
| *Sedum annuum* | 2 | 0 | 5,49 |
| *Sedum rupestre* | 10 | 47 | 10,49 |
| *Sedum sediforme* | 51 | 88 | / |
| *Sedum sexangulare* | 0 | 1 | 9,33 |
| *Senecio* | 59 | 111 | / |
| *Senecio hercynicus* | 45 | 65 | 4,25 |
| *Senecio inaequidens* | 22 | 44 | / |
| *Senecio ovatus* | 442 | 365 | 8,88 |
| *Senecio sylvaticus* | 0 | 9 | 8,73 |
| *Senecio viscosus* | 3 | 1 | 9,31 |
| *Senecio vulgaris* | 39 | 19 | 8,45 |
| *Serratula tinctoria* | 39 | 32 | 9,65 |
| *Seseli montanum* | 15 | 10 | / |
| *Sesleria* | 5 | 11 | / |
| *Sesleria argentea* | 9 | 12 | / |
| *Sesleria caerulea* | 165 | 140 | 7,4 |
| *Silene* | 93 | 102 | / |
| *Silene dioica* | 285 | 248 | 6,5 |
| *Silene italica* | 16 | 14 | / |
| *Silene latifolia* | 4 | 3 | 6,34 |
| *Silene nutans* | 33 | 47 | 7,09 |
| *Silene vulgaris* | 196 | 102 | 8 |
| *Simethis mattiazzii* | 60 | 35 | / |
| *Sisymbrium officinale* | 0 | 1 | 9,55 |
| *Smilax aspera* | 110 | 112 | / |
| *Solanum dulcamara* | 209 | 204 | 7,93 |
| *Solanum nigrum* | 0 | 11 | 8,21 |
| *Solidago* | 3 | 9 | / |
| *Solidago canadensis* | 12 | 12 | 8,29 |
| *Solidago gigantea* | 11 | 5 | 7,71 |
| *Solidago virgaurea* | 630 | 531 | 5,27 |
| *Sonchus arvensis* | 6 | 1 | 7,07 |
| *Sonchus asper* | 0 | 2 | 9,59 |
| *Sonchus oleraceus* | 1 | 0 | 8,42 |
| *Sparganium erectum* | 0 | 2 | 7,39 |
| *Spartium junceum* | 66 | 68 | / |
| *Sphagnum* | 165 | 192 | / |
| *Sphagnum palustre* | 8 | 3 | / |
| *Stachys* | 14 | 30 | / |

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|---|---|---|---|
| *Stachys alpina* | 29 | 35 | / |
| *Stachys arvensis* | 1 | 0 | 12,21 |
| *Stachys palustris* | 4 | 6 | 6,76 |
| *Stachys recta* | 33 | 34 | 8,68 |
| *Stachys sylvatica* | 722 | 699 | 7,28 |
| *Staehelina dubia* | 104 | 84 | / |
| *Stellaria* | 86 | 31 | / |
| *Stellaria alsine* | 1 | 0 | 7,1 |
| *Stellaria graminea* | 16 | 17 | 6,14 |
| *Stellaria holostea* | 1307 | 1368 | 7,01 |
| *Stellaria media* | 79 | 57 | 7,29 |
| *Stellaria nemorum* | 77 | 46 | 5,52 |
| *Stellaria palustris* | 1 | 0 | 6,18 |
| *Streptopus amplexifolius* | 1 | 1 | 8,09 |
| *Succisa pratensis* | 42 | 31 | 7,14 |
| *Symphytum* | 1 | 11 | / |
| *Symphytum officinale* | 26 | 22 | 7,62 |
| *Symphytum tuberosum* | 23 | 26 | 11,56 |
| *Tanacetum corymbosum* | 13 | 10 | 8,21 |
| *Tanacetum parthenium* | 0 | 1 | 11,12 |
| *Tanacetum vulgare* | 1 | 3 | 5,88 |
| *Taraxacum* | 49 | 95 | / |
| *Taraxacum officinale* | 727 | 653 | / |
| *Teesdalia nudicaulis* | 1 | 1 | 9,7 |
| *Teucrium chamaedrys* | 771 | 716 | 11,56 |
| *Teucrium montanum* | 79 | 62 | 10,15 |
| *Teucrium polium* | 122 | 64 | / |
| *Teucrium scordium* | 26 | 24 | / |
| *Teucrium scorodonia* | 3311 | 3222 | 10,4 |
| *Thalictrum aquilegiifolium* | 14 | 19 | 7,49 |
| *Thalictrum minus* | 3 | 3 | 7,56 |
| *Thamnobryum alopecurum* | 63 | 160 | / |
| *Thelypteris palustris* | 1 | 1 | 7,25 |
| *Thesium alpinum* | 2 | 1 | 8,45 |
| *Thlaspi arvense* | 0 | 1 | 6,64 |
| *Thuidium tamariscinum* | 3568 | 3912 | / |
| *Thymus* | 21 | 12 | / |
| *Thymus praecox* | 0 | 1 | 6,92 |
| *Thymus pulegioides* | 0 | 1 | 8,32 |
| *Thymus serpyllum* | 115 | 81 | 5,17 |
| *Thymus vulgaris* | 296 | 252 | / |
| *Thysselinum palustre* | 2 | 2 | 5,36 |
| *Torilis japonica* | 46 | 61 | 8,78 |
| *Tortella squarrosa* | 0 | 55 | / |
| *Tortella tortuosa* | 37 | 92 | / |

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|---|---|---|---|
| *Tractema lilio-hyacinthus* | 29 | 12 | / |
| *Tractema verna* | 10 | 5 | / |
| *Tragopogon pratensis* | 5 | 3 | 7,91 |
| *Trichophorum cespitosum* | 1 | 0 | 4,99 |
| *Trifolium* | 349 | 350 | / |
| *Trifolium alpestre* | 6 | 8 | 7,36 |
| *Trifolium arvense* | 9 | 9 | 8,35 |
| *Trifolium aureum* | 3 | 0 | 6,49 |
| *Trifolium campestre* | 5 | 2 | 11,24 |
| *Trifolium hybridum* | 0 | 1 | 7,33 |
| *Trifolium medium* | 11 | 17 | 6,28 |
| *Trifolium montanum* | 5 | 3 | 7,13 |
| *Trifolium pratense* | 29 | 17 | 7,72 |
| *Trifolium repens* | 4 | 17 | 7,88 |
| *Trifolium rubens* | 8 | 10 | 9,65 |
| *Tripleurospermum inodorum* | 1 | 2 | 6,2 |
| *Trisetum flavescens* | 1 | 1 | 9,26 |
| *Trollius europaeus* | 13 | 13 | 4,14 |
| *Tuberaria guttata* | 7 | 4 | / |
| *Turritis glabra* | 3 | 2 | 7,25 |
| *Tussilago farfara* | 53 | 64 | 6,76 |
| *Typha latifolia* | 0 | 2 | 8,04 |
| *Ulex europaeus* | 1122 | 1063 | 10,14 |
| *Ulex gallii* | 10 | 7 | / |
| *Ulex minor* | 390 | 211 | / |
| *Ulex parviflorus* | 13 | 18 | / |
| *Umbilicus* | 0 | 10 | / |
| *Umbilicus rupestris* | 21 | 23 | / |
| *Urtica dioica* | 1375 | 1529 | 7,64 |
| *Vaccinium* | 3 | 21 | / |
| *Vaccinium myrtillus* | 1201 | 1155 | 5,07 |
| *Vaccinium oxycoccos* | 3 | 0 | 4,64 |
| *Vaccinium uliginosum* | 4 | 2 | 4,34 |
| *Vaccinium vitis-idaea* | 39 | 38 | 4,35 |
| *Valeriana* | 12 | 44 | / |
| *Valeriana dioica* | 26 | 6 | 8,93 |
| *Valeriana montana* | 45 | 45 | 9,05 |
| *Valeriana officinalis* | 253 | 205 | 6,83 |
| *Valeriana tripteris* | 28 | 14 | 7,99 |
| *Veratrum album* | 42 | 35 | / |
| *Verbascum* | 31 | 45 | / |
| *Verbascum lychnitis* | 1 | 4 | 7,31 |
| *Verbascum nigrum* | 24 | 8 | 7,2 |
| *Verbascum thapsus* | 8 | 13 | 7,33 |
| *Verbena officinalis* | 4 | 9 | / |

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|---|---|---|---|
| *Veronica* | 11 | 39 | / |
| *Veronica alpina* | 0 | 3 | 2,58 |
| *Veronica anagallis-aquatica* | 0 | 1 | 9,69 |
| *Veronica beccabunga* | 9 | 9 | 7,79 |
| *Veronica chamaedrys* | 666 | 549 | 7,29 |
| *Veronica hederifolia* | 0 | 2 | 10,63 |
| *Veronica montana* | 248 | 278 | 9,26 |
| *Veronica officinalis* | 696 | 625 | 7,12 |
| *Veronica persica* | 0 | 1 | 10,18 |
| *Veronica serpyllifolia* | 3 | 0 | 6,78 |
| *Veronica spicata* | 1 | 0 | 6,48 |
| *Veronica sublobata* | 41 | 48 | / |
| *Veronica urticifolia* | 69 | 69 | 7,77 |
| *Viburnum lantana* | 1807 | 1879 | 9,82 |
| *Viburnum opulus* | 699 | 836 | 6,46 |
| *Viburnum tinus* | 102 | 110 | / |
| *Vicia* | 125 | 227 | / |
| *Vicia cracca* | 115 | 98 | 6,81 |
| *Vicia dumetorum* | 13 | 6 | 8,16 |
| *Vicia sativa* | 1 | 2 | 8,46 |
| *Vicia sepium* | 1159 | 930 | 6,55 |
| *Vicia tenuifolia* | 23 | 26 | 9,1 |
| *Vinca* | 7 | 15 | / |
| *Vinca minor* | 221 | 231 | 10,13 |
| *Vincetoxicum* | 5 | 6 | / |
| *Vincetoxicum hirundinaria* | 195 | 168 | 8,15 |
| *Viola* | 804 | 998 | / |
| *Viola alba* | 137 | 110 | 11,92 |
| *Viola biflora* | 6 | 7 | 4,53 |
| *Viola canina* | 10 | 14 | 6,69 |
| *Viola hirta* | 211 | 182 | 7,11 |
| *Viola mirabilis* | 13 | 61 | 5,7 |
| *Viola odorata* | 23 | 14 | 8,98 |
| *Viola palustris* | 21 | 5 | 4,1 |
| *Viola pyrenaica* | 6 | 21 | / |
| *Viola reichenbachiana* | 1916 | 1582 | 9,49 |
| *Viola riviniana* | 520 | 383 | 8,26 |
| *Viola tricolor* | 3 | 2 | 5,99 |
| *Viscum album* | 94 | 159 | 9,85 |
| *Vitis vinifera* | 45 | 47 | / |
| *Wahlenbergia hederacea* | 21 | 2 | / |
| *Xanthoselinum alsaticum* | 2 | 1 | 8,46 |

## Table A3: Chapter 3 List of species

*Table A3: Species name, occurrences in not forested plots (NF), forested plots (F), thermal optimum from ClimPlant V1.2 (Topt), pH optimum from EcoPlant (pH) and habitat preference classification from the EuForPlant list. The whole dataset is comprised of 4,024 plots.*

| Species name | NF plots | F plots | Topt | pH | Habitat |
|---|---|---|---|---|---|
| *Achillea millefolium* | 35 | 21 | 5,64 | 8,5 | 2.2 |
| *Aconitum lycoctonum* | 2 | 0 | 1,75 | / | / |
| *Actaea spicata* | 1 | 3 | 5,5 | 6,9 | 1.1 |
| *Adenostyles alliariae* | 1 | 2 | 7,53 | 6,2 | / |
| *Adonis vernalis* | 1 | 0 | 5,61 | / | 2.2 |
| *Adoxa moschatellina* | 27 | 11 | 6,42 | 6,2 | 1.1 |
| *Aegopodium podagraria* | 8 | 3 | 6,71 | 7,6 | 2.1 |
| *Aethusa cynapium* | 9 | 6 | 8,04 | / | 1.2 |
| *Agrimonia eupatoria* | 42 | 11 | 8,68 | 7,1 | 2.2 |
| *Agrostis canina* | 36 | 27 | 6,16 | 4,6 | 2.2 |
| *Agrostis capillaris* | 102 | 182 | 6,01 | 5,1 | 2.2 |
| *Agrostis stolonifera* | 26 | 40 | 7,09 | 5,9 | 2.2 |
| *Ajuga reptans* | 162 | 202 | 8,07 | 6,1 | 2.1 |
| *Alchemilla xanthochlora* | 1 | 0 | 9,24 | 6,9 | / |
| *Alliaria petiolata* | 97 | 25 | 8,41 | 6,4 | 2.1 |
| *Allium oleraceum* | 1 | 0 | 7,27 | / | 2.2 |
| *Allium ursinum* | 11 | 9 | 8,97 | 8,5 | 1.1 |
| *Allium vineale* | 2 | 0 | 10,28 | / | 2.2 |
| *Alyssum alyssoides* | 0 | 3 | 9,83 | 7,4 | / |
| *Anemone hepatica* | 4 | 16 | 6,56 | 6,9 | / |
| *Anemone nemorosa* | 198 | 280 | 7,55 | 5,9 | 1.1 |
| *Anemone ranunculoides* | 4 | 10 | 6,94 | 6,4 | 1.1 |
| *Anemone sylvestris* | 7 | 6 | 5,82 | / | 2.2 |
| *Angelica sylvestris* | 82 | 46 | 5,87 | 8,5 | 2.1 |
| *Anthericum liliago* | 0 | 1 | 9,51 | 8,5 | 2.1 |
| *Anthericum ramosum* | 1 | 0 | 8,02 | 8,5 | 2.2 |
| *Anthoxanthum odoratum* | 35 | 24 | 6,02 | 5,6 | 2.2 |
| *Anthriscus sylvestris* | 12 | 2 | 6,13 | 6,2 | 2.2 |
| *Aquilegia vulgaris* | 12 | 22 | 7,72 | 6,9 | 1.2 |
| *Arabidopsis arenosa* | 1 | 0 | 6,65 | / | / |
| *Arabis hirsuta* | 0 | 1 | 7,1 | / | 2.2 |
| *Arctium lappa* | 2 | 0 | 7,94 | / | 2.2 |
| *Arctium nemorosum* | 16 | 13 | 8,64 | 6,4 | 1.2 |
| *Arrhenatherum elatius* | 6 | 3 | 9,21 | 6,2 | 2.2 |
| *Artemisia vulgaris* | 4 | 1 | 7,07 | / | 2.2 |
| *Arum maculatum* | 425 | 158 | 9,06 | 6,9 | 1.1 |
| *Aruncus dioicus* | 0 | 2 | 8,35 | 6,5 | / |
| *Asarum europaeum* | 28 | 48 | 6,58 | 7,2 | 1.1 |
| *Asparagus officinalis* | 1 | 0 | 7,38 | / | 2.2 |

| | | | | | |
|---|---|---|---|---|---|
| *Asplenium adiantum-nigrum* | 11 | 7 | 9,76 | 6,6 | 2.1 |
| *Asplenium scolopendrium* | 25 | 11 | 9,83 | 7,3 | 1.1 |
| *Asplenium septentrionale* | 1 | 0 | 7,31 | / | O |
| *Asplenium trichomanes* | 17 | 8 | 9,34 | 7 | 2.1 |
| *Asplenium viride* | 0 | 1 | 6,77 | 6,9 | / |
| *Astragalus glycyphyllos* | 2 | 2 | 7,61 | / | 2.2 |
| *Astrantia major* | 3 | 1 | 8,2 | 6,2 | / |
| *Athyrium filix-femina* | 138 | 280 | 6,15 | 5,4 | 1.1 |
| *Avenella flexuosa* | 165 | 452 | 6,01 | 3 | 2.1 |
| *Bellidiastrum michelii* | 0 | 1 | 7,22 | 6 | / |
| *Bellis perennis* | 5 | 0 | 9,86 | 6,1 | O |
| *Berberis vulgaris* | 13 | 5 | 8,7 | 8,5 | 2.1 |
| *Betonica officinalis* | 67 | 69 | 7,89 | 6 | / |
| *Bistorta officinalis* | 4 | 5 | 5,29 | 6,1 | 2.2 |
| *Blechnum spicant* | 40 | 79 | 8,79 | 3 | 1.1 |
| *Brachypodium pinnatum* | 228 | 167 | 7,19 | 8,5 | 2.2 |
| *Brachypodium sylvaticum* | 743 | 653 | 9,47 | 6,7 | 1.1 |
| *Briza media* | 6 | 0 | 8,2 | 8,5 | O |
| *Bromopsis benekenii* | 20 | 26 | 7,29 | 6,7 | 1.1 |
| *Bromopsis erecta* | 12 | 6 | 9,5 | 8,5 | 2.2 |
| *Bromopsis ramosa* | 8 | 14 | 9,81 | / | 1.2 |
| *Buglossoides purpurocaerulea* | 8 | 7 | 11,22 | 7,4 | / |
| *Bupleurum falcatum* | 4 | 5 | 9,95 | 8,5 | 2.2 |
| *Buxus sempervirens* | 28 | 20 | 10,71 | 8,5 | 2.1 |
| *Calamagrostis arundinacea* | 4 | 4 | 5,2 | 4,4 | 2.1 |
| *Calamagrostis epigejos* | 9 | 33 | 7,98 | 4,5 | 2.1 |
| *Calluna vulgaris* | 55 | 339 | 6,32 | 3 | 2.1 |
| *Caltha palustris* | 5 | 5 | 5,38 | 6,1 | 2.1 |
| *Campanula glomerata* | 1 | 1 | 6,86 | 8,5 | 2.2 |
| *Campanula patula* | 2 | 0 | 5,79 | / | / |
| *Campanula persicifolia* | 0 | 5 | 6,41 | / | 1.2 |
| *Campanula rapunculoides* | 0 | 1 | 7,07 | / | 2.2 |
| *Campanula rhomboidalis* | 2 | 0 | 4,72 | 6 | / |
| *Campanula rotundifolia* | 5 | 0 | 4,97 | 8,5 | 2.2 |
| *Campanula trachelium* | 13 | 40 | 8,59 | 7 | 1.1 |
| *Cardamine amara* | 6 | 6 | 6,07 | / | 2.1 |
| *Cardamine flexuosa* | 19 | 14 | 9,26 | 5,7 | 1.2 |
| *Cardamine heptaphylla* | 5 | 11 | 8,38 | 6,8 | 1.1 |
| *Cardamine impatiens* | 2 | 1 | 7,87 | 6,5 | 1.2 |
| *Cardamine pentaphyllos* | 0 | 1 | 7,02 | 6,9 | / |
| *Cardamine pratensis* | 50 | 88 | 4,68 | 6,1 | 2.2 |
| *Carduus defloratus* | 1 | 0 | 5,33 | 7,4 | / |
| *Carex acutiformis* | 51 | 27 | 7,65 | 8,5 | 2.1 |
| *Carex alba* | 5 | 23 | 8,09 | 8,2 | / |
| *Carex arenaria* | 3 | 6 | 8,57 | 8,5 | O |
| *Carex brizoides* | 18 | 64 | 8,12 | 4,6 | 1.1 |

| | | | | | |
|---|---|---|---|---|---|
| *Carex caryophyllea* | 0 | 2 | 8,27 | / | O |
| *Carex digitata* | 49 | 128 | 5,31 | 6,9 | 1.1 |
| *Carex echinata* | 0 | 1 | 6,39 | 6 | 2.1 |
| *Carex elongata* | 3 | 2 | 6,04 | / | 1.1 |
| *Carex flacca* | 466 | 441 | 10,25 | 7,6 | 2.2 |
| *Carex hirta* | 9 | 4 | 7,77 | / | 2.2 |
| *Carex humilis* | 6 | 4 | 8,88 | 8,5 | 2.1 |
| *Carex leporina* | 0 | 1 | 6,67 | / | 2.2 |
| *Carex montana* | 27 | 41 | 7,61 | / | 1.2 |
| *Carex muricata* | 21 | 25 | 7,45 | / | 2.1 |
| *Carex ornithopoda* | 2 | 2 | 6,28 | 8,5 | 2.2 |
| *Carex pallescens* | 6 | 23 | 6,38 | 4,7 | 2.1 |
| *Carex panicea* | 0 | 3 | 7,03 | 6,7 | 2.2 |
| *Carex paniculata* | 2 | 2 | 9,03 | 5,8 | 2.1 |
| *Carex pendula* | 78 | 145 | 11,2 | / | 1.1 |
| *Carex pilosa* | 2 | 9 | 6,94 | 5,7 | 1.1 |
| *Carex pilulifera* | 162 | 519 | 8,18 | 4,2 | 2.1 |
| *Carex remota* | 99 | 152 | 8,63 | 5,8 | 1.1 |
| *Carex riparia* | 15 | 9 | 8 | 8,5 | 2.2 |
| *Carex sylvatica* | 702 | 763 | 8,29 | 6,2 | 1.1 |
| *Carex umbrosa* | 9 | 30 | 8,48 | 5 | 1.1 |
| *Carex vesicaria* | 0 | 1 | 5,45 | 5,4 | 2.2 |
| *Carlina acaulis* | 1 | 1 | 7,72 | 8,5 | O |
| *Carlina vulgaris* | 1 | 1 | 9,16 | 8,5 | O |
| *Carum carvi* | 1 | 0 | 5,55 | / | / |
| *Centaurea jacea* | 3 | 0 | 6,56 | 7 | 2.2 |
| *Centaurium erythraea* | 1 | 0 | 9,2 | / | 2.2 |
| *Cephalanthera damasonium* | 11 | 8 | 9,32 | 7,5 | 1.1 |
| *Cephalanthera longifolia* | 2 | 2 | 9,31 | 8,5 | 2.1 |
| *Cephalanthera rubra* | 1 | 1 | 9,17 | 8,5 | 1.1 |
| *Cerastium arvense* | 3 | 1 | 5,96 | 7,2 | / |
| *Ceratocapnos claviculata* | 0 | 1 | 10,62 | / | 2.2 |
| *Cervaria rivini* | 9 | 5 | 9,52 | 7,4 | / |
| *Chaerophyllum hirsutum* | 2 | 1 | 8,57 | 6,1 | 2.1 |
| *Chaerophyllum temulum* | 0 | 1 | 9,91 | / | 1.2 |
| *Chelidonium majus* | 11 | 3 | 8,05 | / | 2.2 |
| *Chrysosplenium alternifolium* | 0 | 3 | 5,81 | 8,5 | 1.1 |
| *Chrysosplenium oppositifolium* | 8 | 6 | 9,81 | 5,3 | 1.1 |
| *Circaea lutetiana* | 138 | 120 | 8,4 | 6,1 | 1.1 |
| *Cirsium arvense* | 103 | 59 | 7,43 | 8,5 | 2.2 |
| *Cirsium erisithales* | 1 | 0 | 7,34 | / | / |
| *Cirsium oleraceum* | 24 | 17 | 6,05 | 7,7 | 2.1 |
| *Cirsium palustre* | 40 | 21 | 6,91 | 6 | 2.2 |
| *Cirsium vulgare* | 3 | 1 | 7,97 | / | 2.2 |
| *Clematis vitalba* | 374 | 185 | 11,3 | 8,5 | 2.1 |
| *Clinopodium acinos* | 0 | 1 | 8,31 | / | / |

| | | | | | |
|---|---|---|---|---|---|
| *Clinopodium vulgare* | 17 | 3 | 8,93 | 8,5 | 2.2 |
| *Comarum palustre* | 1 | 0 | 4,61 | / | 2.2 |
| *Conopodium majus* | 18 | 13 | 10,26 | 5,3 | 2.1 |
| *Convallaria majalis* | 89 | 258 | 7,12 | 8,5 | 1.1 |
| *Convolvulus sepium* | 46 | 5 | 8,34 | 7,5 | / |
| *Coronilla coronata* | 4 | 2 | 9,26 | / | / |
| *Coronilla varia* | 1 | 3 | 8,96 | / | / |
| *Corydalis cava* | 1 | 1 | 8,26 | 6,7 | 1.1 |
| *Corydalis solida* | 2 | 0 | 7,4 | / | 1.1 |
| *Cotoneaster integerrimus* | 2 | 0 | 7,67 | 7,3 | 2.1 |
| *Crepis paludosa* | 4 | 2 | 5,73 | 6,1 | 2.1 |
| *Cruciata glabra* | 3 | 3 | 9,87 | / | 2.2 |
| *Cruciata laevipes* | 10 | 1 | 10,1 | / | 2.2 |
| *Cyanus montanus* | 3 | 0 | 7,67 | 6,5 | O |
| *Cyclamen purpurascens* | 0 | 1 | 8,49 | / | 1.1 |
| *Cynosurus cristatus* | 2 | 0 | 8,57 | 5,8 | / |
| *Cystopteris fragilis* | 1 | 0 | 6,3 | / | 2.1 |
| *Cytisus scoparius* | 211 | 336 | 9,88 | 4,6 | 2.2 |
| *Dactylis glomerata* | 389 | 178 | 8,56 | 6,8 | 2.2 |
| *Dactylorhiza maculata* | 6 | 3 | 6,07 | 6,6 | 2.1 |
| *Danthonia decumbens* | 5 | 29 | 8,06 | 4,8 | 2.2 |
| *Daphne laureola* | 123 | 105 | 11,92 | 6,7 | 1.1 |
| *Daphne mezereum* | 30 | 39 | 5,35 | 7,5 | 1.1 |
| *Datura stramonium* | 0 | 1 | 9,6 | / | / |
| *Daucus carota* | 22 | 7 | 10,3 | 8,5 | 2.2 |
| *Deschampsia cespitosa* | 261 | 568 | 5,45 | 5,6 | 2.1 |
| *Dianthus carthusianorum* | 1 | 1 | 9,67 | / | 2.2 |
| *Dianthus superbus* | 2 | 1 | 5,14 | / | / |
| *Digitalis grandiflora* | 1 | 0 | 7,82 | / | / |
| *Digitalis lutea* | 5 | 6 | 9,71 | / | 2.2 |
| *Digitalis purpurea* | 50 | 79 | 11,04 | 3 | 1.2 |
| *Dioscorea communis* | 144 | 37 | 12,54 | 8,1 | 1.2 |
| *Dipsacus pilosus* | 1 | 2 | 8,52 | / | 1.2 |
| *Doronicum austriacum* | 0 | 4 | 7,23 | 4,9 | / |
| *Drymochloa sylvatica* | 4 | 24 | 6,01 | 3 | 1.1 |
| *Dryopteris carthusiana* | 173 | 390 | 5,85 | 3 | 1.1 |
| *Dryopteris dilatata* | 94 | 118 | 8,99 | 3 | 1.1 |
| *Dryopteris filix-mas* | 412 | 451 | 7,35 | 5,9 | 1.1 |
| *Elymus caninus* | 12 | 4 | 6,18 | 7 | 1.1 |
| *Elytrigia repens* | 1 | 0 | 7,28 | / | 2.2 |
| *Epilobium angustifolium* | 24 | 30 | 6,46 | / | 1.2 |
| *Epilobium hirsutum* | 16 | 8 | 9,32 | 7,1 | 2.2 |
| *Epilobium montanum* | 59 | 50 | 6,91 | 6,2 | 2.1 |
| *Epilobium palustre* | 1 | 0 | 4,85 | / | 2.2 |
| *Epipactis atrorubens* | 2 | 0 | 6,17 | 8,5 | 2.1 |
| *Epipactis helleborine* | 25 | 21 | 8,56 | 7,1 | 1.1 |

| | | | | | |
|---|---|---|---|---|---|
| *Equisetum arvense* | 6 | 0 | 6,26 | 8,5 | 2.2 |
| *Equisetum hyemale* | 3 | 3 | 4,86 | 8,5 | 1.1 |
| *Equisetum sylvaticum* | 1 | 1 | 4,52 | / | 1.1 |
| *Equisetum telmateia* | 14 | 0 | 10,73 | 7,7 | 2.1 |
| *Erigeron canadensis* | 4 | 4 | 8,52 | / | 2.2 |
| *Ervilia sylvatica* | 4 | 4 | 5,39 | / | / |
| *Eryngium campestre* | 9 | 2 | 11,8 | 8,5 | / |
| *Euonymus europaeus* | 584 | 163 | 8,75 | 7,7 | / |
| *Eupatorium cannabinum* | 83 | 141 | 8,98 | 8,5 | 2.2 |
| *Euphorbia amygdaloides* | 166 | 346 | 10,82 | 6,4 | 1.1 |
| *Euphorbia angulata* | 0 | 2 | 8,91 | / | 1.1 |
| *Euphorbia cyparissias* | 36 | 44 | 8,17 | 8,5 | 2.2 |
| *Euphorbia dulcis* | 15 | 22 | 9,98 | 6,5 | 1.1 |
| *Euphorbia helioscopia* | 1 | 1 | 9,9 | / | / |
| *Festuca heterophylla* | 93 | 174 | 9,71 | 5,3 | 1.1 |
| *Festuca ovina* | 13 | 18 | 5,66 | 8,5 | 2.2 |
| *Festuca rubra* | 1 | 0 | 6,65 | 6,1 | 2.2 |
| *Ficaria verna* | 237 | 106 | 8,18 | 6,3 | 2.1 |
| *Filipendula ulmaria* | 78 | 14 | 5,58 | 6,4 | 2.2 |
| *Filipendula vulgaris* | 6 | 2 | 7,87 | / | 2.2 |
| *Fragaria vesca* | 383 | 370 | 6,71 | 6,3 | 2.1 |
| *Fragaria viridis* | 1 | 2 | 7,33 | / | 2.2 |
| *Frangula alnus* | 172 | 398 | 6,4 | 4 | 2.1 |
| *Galanthus nivalis* | 3 | 0 | 10,3 | / | 2.1 |
| *Galeopsis tetrahit* | 153 | 110 | 7,77 | 4,6 | 2.1 |
| *Galium album* | 4 | 3 | 7,61 | / | / |
| *Galium aparine* | 299 | 60 | 9,2 | 8,5 | 2.1 |
| *Galium mollugo* | 133 | 67 | 7,37 | 8,5 | 2.2 |
| *Galium odoratum* | 192 | 264 | 7,6 | 6,4 | 1.1 |
| *Galium palustre* | 8 | 11 | 6,31 | 5,7 | 2.1 |
| *Galium pumilum* | 1 | 2 | 8,25 | 6,3 | 2.2 |
| *Galium rotundifolium* | 12 | 7 | 8,63 | 5,4 | / |
| *Galium saxatile* | 25 | 15 | 9,85 | 3 | 2.1 |
| *Galium sylvaticum* | 15 | 13 | 8,14 | 6,2 | / |
| *Galium uliginosum* | 2 | 2 | 5,06 | / | 2.2 |
| *Galium verum* | 8 | 6 | 7,56 | 7,2 | 2.2 |
| *Genista germanica* | 1 | 1 | 8,57 | / | 2.2 |
| *Genista pilosa* | 10 | 16 | 9,62 | 8,5 | 2.2 |
| *Genista sagittalis* | 4 | 3 | 9,71 | / | 2.2 |
| *Genista tinctoria* | 6 | 4 | 8,51 | 8,5 | 2.2 |
| *Gentianopsis ciliata* | 1 | 0 | 10,08 | / | / |
| *Geranium lucidum* | 0 | 1 | 12,64 | / | 1.2 |
| *Geranium robertianum* | 389 | 141 | 8,49 | 6,2 | 2.1 |
| *Geranium sanguineum* | 7 | 2 | 8,99 | 8,5 | 2.1 |
| *Geranium sylvaticum* | 2 | 3 | 3,98 | 6,3 | 2.1 |
| *Geum rivale* | 4 | 3 | 4,58 | 6,1 | 2.1 |

| | | | | | |
|---|---|---|---|---|---|
| *Geum urbanum* | 646 | 237 | 7,92 | 6,5 | 2.1 |
| *Glechoma hederacea* | 284 | 126 | 6,7 | 6,3 | 2.1 |
| *Glyceria fluitans* | 6 | 4 | 8,26 | / | 2.2 |
| *Goodyera repens* | 1 | 3 | 4,35 | / | 1.1 |
| *Gymnocarpium dryopteris* | 1 | 2 | 4,63 | / | 1.1 |
| *Gymnocarpium robertianum* | 1 | 0 | 8,09 | 7,3 | 2.1 |
| *Hedera helix* | 1620 | 1381 | 10,93 | 6,2 | 2.1 |
| *Helianthemum nummularium* | 11 | 5 | 9,1 | 7,8 | 2.2 |
| *Helleborus foetidus* | 96 | 75 | 11,65 | 7,6 | 1.2 |
| *Helleborus niger* | 1 | 0 | 8,13 | / | 1.1 |
| *Heracleum sphondylium* | 91 | 36 | 5,74 | 6,6 | 2.1 |
| *Hieracium laevigatum* | 1 | 2 | 5,09 | / | 2.1 |
| *Hieracium murorum* | 37 | 33 | 7,27 | 6,6 | 2.1 |
| *Hieracium sabaudum* | 4 | 2 | 9,13 | / | 2.1 |
| *Hieracium umbellatum* | 4 | 6 | 6,04 | 4,6 | 2.1 |
| *Hippocrepis comosa* | 6 | 4 | 10,06 | 8,5 | O |
| *Hippocrepis emerus* | 10 | 12 | 12,63 | 8,5 | 2.1 |
| *Holcus lanatus* | 122 | 94 | 9,85 | 5,6 | 2.2 |
| *Holcus mollis* | 183 | 218 | 8,73 | 4,5 | 2.1 |
| *Hordelymus europaeus* | 29 | 56 | 8,27 | 6,4 | 1.1 |
| *Humulus lupulus* | 37 | 1 | 7,21 | 8,5 | 1.2 |
| *Hyacinthoides non-scripta* | 76 | 55 | 10,14 | 3,9 | 1.1 |
| *Hydrocotyle vulgaris* | 1 | 0 | 10,27 | / | 2.2 |
| *Hylotelephium telephium* | 2 | 4 | 7,11 | / | 2.2 |
| *Hypericum hirsutum* | 54 | 87 | 7,49 | 6,5 | 2.1 |
| *Hypericum humifusum* | 3 | 16 | 9,6 | / | 2.2 |
| *Hypericum maculatum* | 1 | 1 | 5,73 | 5,5 | 2.2 |
| *Hypericum montanum* | 10 | 8 | 8,75 | 8,5 | 1.2 |
| *Hypericum perforatum* | 101 | 136 | 9,25 | 6,4 | 2.2 |
| *Hypericum pulchrum* | 48 | 216 | 9,64 | 4,5 | 2.1 |
| *Hypericum tetrapterum* | 0 | 1 | 9,95 | / | 2.2 |
| *Hypochaeris radicata* | 2 | 0 | 10,49 | / | 2.2 |
| *Impatiens noli-tangere* | 8 | 7 | 6,68 | 5,1 | 1.1 |
| *Impatiens parviflora* | 0 | 1 | 8,12 | / | 1.1 |
| *Inula conyza* | 1 | 2 | 10,82 | / | / |
| *Inula salicina* | 0 | 1 | 6,88 | / | 2.2 |
| *Iris pseudacorus* | 31 | 8 | 9,27 | 5,8 | 2.1 |
| *Jacobaea vulgaris* | 11 | 8 | 7,6 | 7,3 | 2.2 |
| *Jasione montana* | 2 | 0 | 8,14 | 5,1 | O |
| *Juncus conglomeratus* | 33 | 79 | 7,9 | 5 | 2.2 |
| *Juncus effusus* | 72 | 134 | 8,65 | 5,4 | 2.2 |
| *Juncus tenuis* | 2 | 3 | 8,69 | / | 2.2 |
| *Juniperus communis* | 101 | 64 | 6,63 | 8,5 | 2.2 |
| *Knautia arvensis* | 0 | 1 | 6,93 | 6,1 | 2.2 |
| *Knautia arvernensis* | 2 | 0 | 9,29 | / | / |
| *Knautia dipsacifolia* | 12 | 11 | 7,18 | 6,4 | / |

| | | | | | |
|---|---|---|---|---|---|
| *Lactuca muralis* | 63 | 45 | 8,76 | 6,5 | 2.1 |
| *Lamium album* | 2 | 2 | 6,61 | / | 2.2 |
| *Lamium galeobdolon* | 237 | 375 | 8,44 | 6,3 | / |
| *Lamium maculatum* | 14 | 10 | 8,29 | 7,7 | 2.1 |
| *Lamium purpureum* | 10 | 5 | 8,25 | / | / |
| *Lapsana communis* | 49 | 34 | 8,13 | 6,1 | 2.1 |
| *Laserpitium latifolium* | 8 | 5 | 8,8 | 7,4 | 2.1 |
| *Lathraea squamaria* | 1 | 0 | 7,53 | 8,3 | 1.1 |
| *Lathyrus linifolius* | 27 | 53 | 8,85 | / | 2.1 |
| *Lathyrus niger* | 4 | 2 | 7,89 | / | 1.2 |
| *Lathyrus pratensis* | 7 | 2 | 6,07 | 7,1 | 2.2 |
| *Lathyrus sylvestris* | 3 | 5 | 12,21 | / | 2.1 |
| *Lathyrus vernus* | 10 | 23 | 6,28 | 6,8 | / |
| *Laurus nobilis* | 13 | 1 | 15,2 | / | 2.2 |
| *Leontodon hispidus* | 1 | 0 | 8,01 | 5,8 | O |
| *Leucanthemum vulgare* | 6 | 3 | 6,36 | 8,5 | 2.2 |
| *Leucojum vernum* | 5 | 2 | 8,55 | 7,5 | 2.1 |
| *Lilium martagon* | 1 | 4 | 6,79 | 6,9 | 1.1 |
| *Linaria repens* | 16 | 17 | 9,97 | 4,7 | 2.2 |
| *Linaria vulgaris* | 4 | 0 | 6,37 | / | 2.2 |
| *Lonicera alpigena* | 2 | 5 | 7,75 | 6,8 | / |
| *Lonicera nigra* | 5 | 19 | 7,42 | 6,3 | / |
| *Lonicera periclymenum* | 723 | 1039 | 9,95 | 4,5 | 2.1 |
| *Lonicera xylosteum* | 441 | 239 | 5,87 | 7,2 | 2.1 |
| *Lotus corniculatus* | 8 | 5 | 9,38 | 8,5 | 2.2 |
| *Lotus pedunculatus* | 4 | 7 | 10,53 | 5,2 | 2.2 |
| *Luzula campestris* | 4 | 5 | 9,28 | 5,2 | 2.2 |
| *Luzula forsteri* | 19 | 37 | 12,35 | 5,5 | 1.1 |
| *Luzula luzuloides* | 18 | 62 | 7,76 | 3 | 1.1 |
| *Luzula multiflora* | 15 | 59 | 5,75 | 4,9 | 2.1 |
| *Luzula nivea* | 5 | 7 | 8,77 | 5,4 | / |
| *Luzula pilosa* | 91 | 309 | 4,94 | 5,4 | 1.1 |
| *Luzula sylvatica* | 25 | 120 | 9,72 | 3 | 1.1 |
| *Lychnis flos-cuculi* | 4 | 1 | 7,33 | / | / |
| *Lycopus europaeus* | 24 | 8 | 8,51 | 5,7 | 2.2 |
| *Lysimachia nemorum* | 14 | 32 | 9,45 | 5,8 | 1.1 |
| *Lysimachia nummularia* | 21 | 17 | 7,86 | 6,1 | 2.1 |
| *Lysimachia vulgaris* | 9 | 7 | 7,05 | 6 | 2.1 |
| *Lythrum salicaria* | 9 | 2 | 7,76 | 8,5 | 2.1 |
| *Maianthemum bifolium* | 3 | 11 | 4,76 | 3 | 1.1 |
| *Malus sylvestris* | 124 | 66 | 8,96 | 8,5 | 1.1 |
| *Malva sylvestris* | 2 | 0 | 12,08 | / | / |
| *Medicago lupulina* | 0 | 1 | 8,73 | 8,5 | O |
| *Melampyrum nemorosum* | 0 | 1 | 6,2 | / | / |
| *Melampyrum pratense* | 19 | 63 | 5,65 | 3 | 1.2 |
| *Melampyrum sylvaticum* | 1 | 3 | 3,14 | / | / |

| | | | | | |
|---|---|---|---|---|---|
| *Melica nutans* | 8 | 9 | 5,97 | 7,5 | 1.1 |
| *Melica uniflora* | 128 | 219 | 9,92 | 6,2 | 1.1 |
| *Melittis melissophyllum* | 18 | 38 | 11,71 | 7,5 | 1.2 |
| *Mentha aquatica* | 10 | 5 | 9,32 | 7,5 | 2.2 |
| *Mentha arvensis* | 2 | 4 | 6,29 | / | 2.2 |
| *Mentha longifolia* | 1 | 0 | 8,72 | / | O |
| *Mercurialis perennis* | 129 | 97 | 7,87 | 7,2 | 1.1 |
| *Milium effusum* | 207 | 277 | 5,63 | 5,5 | 1.1 |
| *Moehringia trinervia* | 85 | 46 | 8,08 | 5 | 1.1 |
| *Molinia caerulea* | 111 | 457 | 6,19 | 3 | 2.1 |
| *Moneses uniflora* | 1 | 0 | 4,01 | / | / |
| *Myosotis scorpioides* | 3 | 2 | 6,92 | 6 | 2.1 |
| *Myosotis sylvatica* | 12 | 12 | 9,09 | 5,5 | 1.2 |
| *Myosoton aquaticum* | 2 | 1 | 7,59 | / | 2.2 |
| *Nardus stricta* | 6 | 1 | 6,29 | 6,1 | O |
| *Neottia nidus-avis* | 47 | 45 | 8,39 | 6,8 | 1.1 |
| *Neottia ovata* | 37 | 11 | 6,74 | 8,5 | 1.1 |
| *Omalotheca sylvatica* | 0 | 1 | 6,1 | / | / |
| *Orchis mascula* | 14 | 5 | 9,57 | 7 | 2.1 |
| *Orchis purpurea* | 8 | 2 | 10,01 | 8,5 | 2.1 |
| *Origanum vulgare* | 23 | 25 | 7,6 | 8,5 | 2.2 |
| *Ornithogalum umbellatum* | 3 | 1 | 11,37 | / | 2.2 |
| *Orthilia secunda* | 3 | 5 | 4,29 | 6,8 | / |
| *Oxalis acetosella* | 55 | 183 | 6,08 | 3 | 1.1 |
| *Paris quadrifolia* | 70 | 62 | 5,65 | 6,7 | 1.1 |
| *Persicaria hydropiper* | 4 | 1 | 7,38 | 6,3 | 2.2 |
| *Persicaria lapathifolia* | 1 | 1 | 8,14 | / | / |
| *Persicaria maculosa* | 3 | 7 | 8,4 | / | / |
| *Petasites albus* | 1 | 4 | 8,27 | 6,7 | / |
| *Petasites hybridus* | 1 | 0 | 9,43 | / | 2.1 |
| *Phalaris arundinacea* | 32 | 3 | 6,58 | 8,5 | / |
| *Phegopteris connectilis* | 0 | 1 | 5,02 | 4,6 | 1.1 |
| *Phleum alpinum* | 0 | 1 | 3,69 | 5,6 | / |
| *Phragmites australis* | 50 | 12 | 7,49 | 7,7 | 2.2 |
| *Phyteuma nigrum* | 3 | 9 | 8,87 | 8,2 | 1.1 |
| *Phyteuma spicatum* | 25 | 39 | 8,31 | 6,5 | 1.1 |
| *Picris hieracioides* | 0 | 1 | 7,71 | / | O |
| *Pilosella officinarum* | 30 | 20 | 7,75 | 8,5 | 2.2 |
| *Pimpinella major* | 5 | 5 | 9,14 | 8,4 | O |
| *Pimpinella saxifraga* | 4 | 1 | 6,7 | 8,5 | 2.2 |
| *Plantago lanceolata* | 38 | 15 | 9,87 | 6,2 | 2.2 |
| *Plantago major* | 16 | 15 | 9,12 | / | 2.2 |
| *Plantago media* | 10 | 3 | 6,08 | 8,5 | 2.2 |
| *Platanthera bifolia* | 9 | 2 | 6,51 | 8,5 | 2.1 |
| *Platanthera chlorantha* | 0 | 2 | 8,51 | 7,4 | 2.1 |
| *Poa chaixii* | 37 | 56 | 8,12 | 5,2 | 1.1 |

| | | | | | |
|---|---|---|---|---|---|
| *Poa nemoralis* | 154 | 117 | 6,26 | 5,4 | 1.1 |
| *Poa pratensis* | 0 | 1 | 6,2 | 6,25 | 2.2 |
| *Poa trivialis* | 55 | 55 | 8,14 | / | 2.1 |
| *Polygala vulgaris* | 1 | 2 | 9,34 | 8,1 | 2.2 |
| *Polygonatum multiflorum* | 261 | 172 | 8,04 | 6,3 | 1.1 |
| *Polygonatum odoratum* | 16 | 20 | 6,59 | 8,5 | 2.1 |
| *Polygonatum verticillatum* | 16 | 30 | 6,8 | 6,4 | 1.1 |
| *Polygonum aviculare* | 0 | 1 | 7,74 | / | / |
| *Polypodium vulgare* | 41 | 26 | 7,95 | 6,8 | 2.1 |
| *Polystichum aculeatum* | 18 | 12 | 10,57 | 6,9 | 1.1 |
| *Polystichum lonchitis* | 0 | 2 | 7,59 | 6,6 | / |
| *Potentilla erecta* | 41 | 73 | 6,95 | 4,9 | 2.2 |
| *Potentilla micrantha* | 1 | 0 | 11,41 | / | / |
| *Potentilla recta* | 3 | 0 | 8,66 | 7,1 | / |
| *Potentilla reptans* | 14 | 13 | 10,11 | 7,1 | 2.2 |
| *Potentilla sterilis* | 169 | 274 | 9,76 | 6,1 | 1.2 |
| *Potentilla verna* | 2 | 1 | 9,45 | 8,5 | / |
| *Poterium sanguisorba* | 21 | 13 | 10,74 | 8,5 | / |
| *Prenanthes purpurea* | 5 | 28 | 7,96 | 3 | / |
| *Primula elatior* | 135 | 120 | 9,21 | 6,2 | 1.1 |
| *Primula veris* | 44 | 29 | 7,48 | 7 | 2.1 |
| *Primula vulgaris* | 14 | 0 | 10,56 | 6,1 | / |
| *Prunella vulgaris* | 44 | 47 | 7,29 | 6,2 | 2.2 |
| *Pteridium aquilinum* | 294 | 657 | 9,15 | 3 | 2.1 |
| *Pulicaria dysenterica* | 1 | 1 | 11,7 | / | / |
| *Pulmonaria longifolia* | 36 | 41 | 11,03 | 5,5 | 1.2 |
| *Pulmonaria obscura* | 1 | 0 | 5,7 | 6,3 | / |
| *Pulmonaria officinalis* | 5 | 5 | 8,31 | 6,9 | 1.1 |
| *Pyrola chlorantha* | 1 | 1 | 5,12 | / | / |
| *Pyrola rotundifolia* | 3 | 0 | 4,38 | / | 1.1 |
| *Pyrus communis* | 136 | 89 | 9,11 | / | 2.1 |
| *Ranunculus acris* | 1 | 2 | 5,61 | 5,7 | 2.2 |
| *Ranunculus auricomus* | 79 | 56 | 6,06 | 6,6 | 1.1 |
| *Ranunculus flammula* | 1 | 4 | 7,31 | 5,9 | 2.2 |
| *Ranunculus lanuginosus* | 0 | 1 | 9,2 | / | / |
| *Ranunculus platanifolius* | 2 | 3 | 5,64 | 6,6 | / |
| *Ranunculus repens* | 75 | 62 | 6,84 | 6 | 2.1 |
| *Rhamnus alpina* | 1 | 4 | 10,57 | 8,5 | / |
| *Rhamnus cathartica* | 46 | 13 | 7,81 | 8,5 | 2.1 |
| *Ribes alpinum* | 118 | 105 | 6,78 | 6,7 | 1.2 |
| *Ribes nigrum* | 1 | 0 | 5,32 | / | 1.1 |
| *Ribes rubrum* | 117 | 34 | 6,54 | 8 | 1.1 |
| *Ribes uva-crispa* | 109 | 12 | 7,87 | 7,3 | 2.1 |
| *Rosa arvensis* | 703 | 522 | 10,38 | 6,4 | 1.2 |
| *Rosa canina* | 503 | 174 | 8,99 | 8,5 | 2.1 |
| *Rosa pendulina* | 3 | 5 | 8,94 | 6,7 | / |

| | | | | | |
|---|---|---|---|---|---|
| *Rubus caesius* | 102 | 40 | 7,83 | 8,5 | 2.1 |
| *Rubus idaeus* | 138 | 178 | 5,75 | 3 | 1.2 |
| *Rubus saxatilis* | 3 | 4 | 4,19 | 6,9 | 1.2 |
| *Rubus ulmifolius* | 152 | 93 | 12,95 | 5,9 | / |
| *Rumex acetosa* | 56 | 10 | 6,87 | 5,9 | 2.2 |
| *Rumex acetosella* | 18 | 21 | 6,75 | 4,7 | 2.2 |
| *Rumex arifolius* | 1 | 0 | 8,68 | / | / |
| *Rumex crispus* | 1 | 0 | 8,42 | / | / |
| *Rumex hydrolapathum* | 3 | 0 | 7,37 | / | 2.2 |
| *Rumex obtusifolius* | 33 | 19 | 8,07 | 5,7 | 2.2 |
| *Rumex sanguineus* | 90 | 73 | 8,8 | / | 1.1 |
| *Ruscus aculeatus* | 205 | 176 | 13,45 | 6 | 1.1 |
| *Sambucus ebulus* | 1 | 2 | 11,35 | / | 2.2 |
| *Sanicula europaea* | 28 | 17 | 8,51 | 6,3 | 1.1 |
| *Saxifraga granulata* | 1 | 2 | 9,54 | / | 2.2 |
| *Saxifraga rotundifolia* | 2 | 1 | 9,65 | 6,7 | / |
| *Schedonorus arundinaceus* | 1 | 0 | 9,24 | / | / |
| *Schedonorus giganteus* | 32 | 40 | 7,37 | 8,5 | 1.1 |
| *Scilla bifolia* | 8 | 15 | 9,24 | 6,8 | 1.1 |
| *Scirpus sylvaticus* | 4 | 4 | 6,84 | 5,7 | 2.1 |
| *Scrophularia nodosa* | 65 | 117 | 7,17 | 5,7 | 1.1 |
| *Scutellaria galericulata* | 2 | 2 | 6,24 | 6,3 | 2.1 |
| *Sedum acre* | 0 | 1 | 7,79 | 7,5 | 2.2 |
| *Sedum rupestre* | 2 | 3 | 10,49 | 7,3 | 2.1 |
| *Sedum sexangulare* | 1 | 0 | 9,33 | / | O |
| *Senecio hercynicus* | 2 | 4 | 4,25 | / | / |
| *Senecio ovatus* | 25 | 27 | 8,88 | 4,8 | 1.2 |
| *Senecio sylvaticus* | 2 | 0 | 8,73 | / | 1.2 |
| *Senecio viscosus* | 0 | 1 | 9,31 | / | 2.2 |
| *Senecio vulgaris* | 4 | 1 | 8,45 | / | 2.2 |
| *Serratula tinctoria* | 8 | 13 | 9,65 | 5,5 | 2.1 |
| *Sesleria caerulea* | 12 | 9 | 7,4 | 7,6 | 2.2 |
| *Silene dioica* | 43 | 22 | 6,5 | 5,95 | 2.1 |
| *Silene latifolia* | 1 | 0 | 6,34 | / | 2.2 |
| *Silene nutans* | 0 | 1 | 7,09 | 8,5 | 2.1 |
| *Silene vulgaris* | 18 | 6 | 8 | 5,9 | 2.1 |
| *Solanum dulcamara* | 62 | 32 | 7,93 | 8,5 | 2.1 |
| *Solanum nigrum* | 0 | 1 | 8,21 | / | / |
| *Solidago gigantea* | 3 | 3 | 7,71 | 8,3 | 2.2 |
| *Solidago virgaurea* | 69 | 64 | 5,27 | 6,9 | 2.1 |
| *Sonchus arvensis* | 1 | 0 | 7,07 | / | / |
| *Sonchus asper* | 1 | 2 | 9,59 | / | / |
| *Stachys palustris* | 4 | 0 | 6,76 | / | 2.2 |
| *Stachys recta* | 2 | 1 | 8,68 | 8,5 | 2.2 |
| *Stachys sylvatica* | 179 | 145 | 7,28 | 8,5 | 1.2 |
| *Stellaria graminea* | 3 | 0 | 6,14 | / | 2.2 |

| | | | | | |
|---|---|---|---|---|---|
| *Stellaria holostea* | 259 | 211 | 7,01 | 5,3 | 2.1 |
| *Stellaria media* | 19 | 7 | 7,29 | / | 2.2 |
| *Stellaria nemorum* | 8 | 6 | 5,52 | 3,9 | 1.1 |
| *Succisa pratensis* | 1 | 5 | 7,14 | 5,8 | 2.2 |
| *Symphytum officinale* | 14 | 4 | 7,62 | 8,5 | 2.2 |
| *Symphytum tuberosum* | 3 | 0 | 11,56 | 6,3 | 2.1 |
| *Tanacetum vulgare* | 1 | 0 | 5,88 | / | / |
| *Teucrium chamaedrys* | 25 | 18 | 11,56 | 8,5 | 2.2 |
| *Teucrium scorodonia* | 212 | 524 | 10,4 | 4,5 | 2.1 |
| *Thalictrum aquilegiifolium* | 0 | 1 | 7,49 | 7 | / |
| *Thalictrum minus* | 1 | 0 | 7,56 | 8,4 | 2.1 |
| *Thymus serpyllum* | 5 | 3 | 5,17 | / | 2.2 |
| *Torilis japonica* | 15 | 3 | 8,78 | 6,3 | 1.2 |
| *Tragopogon pratensis* | 1 | 0 | 7,91 | 7,5 | / |
| *Trifolium arvense* | 3 | 0 | 8,35 | / | / |
| *Trifolium campestre* | 2 | 0 | 11,24 | / | / |
| *Trifolium medium* | 4 | 2 | 6,28 | 6,9 | 2.1 |
| *Trifolium pratense* | 5 | 1 | 7,72 | 6,3 | 2.2 |
| *Trifolium repens* | 3 | 0 | 7,88 | 5,6 | 2.2 |
| *Trifolium rubens* | 0 | 4 | 9,65 | / | 1.2 |
| *Turritis glabra* | 2 | 0 | 7,25 | / | / |
| *Tussilago farfara* | 5 | 3 | 6,76 | / | 2.2 |
| *Urtica dioica* | 454 | 127 | 7,64 | 6,1 | 2.1 |
| *Vaccinium myrtillus* | 37 | 110 | 5,07 | 3 | 2.1 |
| *Vaccinium uliginosum* | 1 | 0 | 4,34 | 3 | 2.1 |
| *Vaccinium vitis-idaea* | 1 | 3 | 4,35 | 3 | 2.1 |
| *Valeriana dioica* | 3 | 4 | 8,93 | 6 | 2.1 |
| *Valeriana montana* | 1 | 2 | 9,05 | 7,2 | / |
| *Valeriana officinalis* | 45 | 18 | 6,83 | 6,2 | 2.1 |
| *Valeriana tripteris* | 1 | 1 | 7,99 | / | / |
| *Verbascum nigrum* | 1 | 2 | 7,2 | / | 2.2 |
| *Veronica beccabunga* | 1 | 1 | 7,79 | / | 2.2 |
| *Veronica chamaedrys* | 93 | 65 | 7,29 | 6 | 2.1 |
| *Veronica montana* | 46 | 54 | 9,26 | 5,9 | 1.1 |
| *Veronica officinalis* | 44 | 95 | 7,12 | 5,8 | 2.1 |
| *Veronica urticifolia* | 0 | 3 | 7,77 | 6,3 | / |
| *Viburnum lantana* | 381 | 184 | 9,82 | 8,5 | 2.1 |
| *Viburnum opulus* | 204 | 140 | 6,46 | 7,7 | 2.1 |
| *Vicia cracca* | 15 | 8 | 6,81 | 7 | 2.2 |
| *Vicia dumetorum* | 0 | 1 | 8,16 | / | / |
| *Vicia sepium* | 156 | 197 | 6,55 | 6,5 | 2.1 |
| *Vicia tenuifolia* | 12 | 4 | 9,1 | 8,5 | 2.2 |
| *Vinca minor* | 47 | 49 | 10,13 | 8,5 | 1.1 |
| *Vincetoxicum hirundinaria* | 12 | 14 | 8,15 | 8,5 | 2.1 |
| *Viola alba* | 17 | 5 | 11,92 | 7,7 | 1.2 |
| *Viola canina* | 1 | 2 | 6,69 | 5,3 | 2.2 |

| | | | | | |
|---|---|---|---|---|---|
| *Viola hirta* | 43 | 31 | 7,11 | 8,5 | 2.1 |
| *Viola mirabilis* | 12 | 5 | 5,7 | 7,5 | / |
| *Viola odorata* | 6 | 5 | 8,98 | 8,4 | 2.1 |
| *Viola palustris* | 1 | 2 | 4,1 | / | 2.1 |
| *Viola reichenbachiana* | 249 | 333 | 9,49 | 6,3 | 1.1 |
| *Viola riviniana* | 46 | 49 | 8,26 | 5,3 | 1.1 |
| *Viola tricolor* | 1 | 0 | 5,99 | / | / |
| *Viscum album* | 14 | 4 | 9,85 | 8,5 | 2.1 |
| *Xanthoselinum alsaticum* | 0 | 1 | 8,46 | / | / |

## Table A4: Chapter 4 List of species

*Table A4: Species names, their total occurrences (N) in the dataset, broken up in the cold, intermediate and warm topoclimate categories, their thermal optimum (Topt), pH optimum (pH) and the EuForPlant habitat classification (N plots: 306). Only species with a thermal optimum were used for community composition analysis.*

| Species name | N | Cold | Inter | Warm | Topt | pH | Habitat |
|---|---|---|---|---|---|---|---|
| *Achillea millefolium* | 1 | 0 | 1 | 0 | 5,64 | 8,5 | 2.2 |
| *Achillea nobilis* | 3 | 2 | 0 | 1 | 8,54 | / | O |
| *Actaea spicata* | 1 | 1 | 0 | 0 | 5,5 | 6,9 | 1.1 |
| *Adenostyles alliariae* | 10 | 3 | 2 | 5 | 7,53 | 6,2 | 2.1 |
| *Adoxa moschatellina* | 14 | 7 | 6 | 1 | 6,42 | 6,2 | 1.1 |
| *Aegopodium podagraria* | 2 | 2 | 0 | 0 | 6,71 | 7,6 | 2.1 |
| *Agrostis canina* | 1 | 0 | 0 | 1 | 6,16 | 4,6 | 2.2 |
| *Agrostis capillaris* | 21 | 8 | 4 | 9 | 6,01 | 5,1 | 2.2 |
| *Agrostis stolonifera* | 1 | 1 | 0 | 0 | 7,09 | 5,9 | 2.2 |
| *Ailanthus altissima* | 1 | 0 | 1 | 0 | / | / | / |
| *Ajuga reptans* | 27 | 10 | 11 | 6 | 8,07 | 6,1 | 2.1 |
| *Alchemilla monticola* | 1 | 0 | 1 | 0 | 5,61 | / | / |
| *Alchemilla xanthochlora* | 1 | 1 | 0 | 0 | 9,24 | 6,9 | / |
| *Alliaria petiolata* | 51 | 15 | 22 | 14 | 8,41 | 6,4 | 2.2 |
| *Allium ursinum* | 10 | 5 | 4 | 1 | 8,97 | 8,5 | 1.1 |
| *Alopecurus pratensis* | 1 | 1 | 0 | 0 | 6,45 | / | O |
| *Anemone hepatica* | 3 | 0 | 2 | 1 | 6,56 | 6,9 | 1.1 |
| *Anemone nemorosa* | 95 | 38 | 26 | 31 | 7,55 | 5,9 | 2.1 |
| *Anemone ranunculoides* | 1 | 0 | 1 | 0 | 6,94 | 6,4 | 1.1 |
| *Angelica sylvestris* | 21 | 14 | 5 | 2 | 5,87 | 8,5 | 2.1 |
| *Anthericum liliago* | 1 | 0 | 0 | 1 | 9,51 | 8,5 | 2.1 |
| *Anthoxanthum odoratum* | 3 | 0 | 1 | 2 | 6,02 | 5,6 | 2.2 |
| *Anthriscus sylvestris* | 9 | 6 | 2 | 1 | 6,13 | 6,2 | 2.2 |
| *Aquilegia vulgaris* | 3 | 1 | 2 | 0 | 7,72 | 6,9 | 2.1 |
| *Arabidopsis arenosa* | 4 | 1 | 2 | 1 | 6,65 | / | / |
| *Arabidopsis thaliana* | 1 | 0 | 0 | 1 | 8,05 | / | / |
| *Arrhenatherum elatius* | 1 | 0 | 0 | 1 | 9,21 | 6,2 | 2.2 |
| *Arum maculatum* | 33 | 14 | 16 | 3 | 9,06 | 6,9 | 1.1 |
| *Aruncus dioicus* | 4 | 3 | 1 | 0 | 8,35 | 6,5 | 2.1 |
| *Asperula tinctoria* | 1 | 0 | 0 | 1 | 5,38 | / | 2.2 |
| *Asplenium adiantum-nigrum* | 4 | 2 | 1 | 1 | 9,76 | 6,6 | 2.1 |
| *Asplenium trichomanes* | 3 | 1 | 1 | 1 | 9,34 | 7 | 2.1 |
| *Asplenium viride* | 1 | 1 | 0 | 0 | 6,77 | 6,9 | 2.1 |
| *Athyrium filix-femina* | 90 | 45 | 29 | 16 | 6,15 | 5,4 | 2.1 |
| *Atocion rupestre* | 1 | 0 | 1 | 0 | / | / | / |
| *Atrichum undulatum* | 56 | 20 | 17 | 19 | / | 5 | / |
| *Atropa belladonna* | 1 | 0 | 1 | 0 | / | 6,4 | / |
| *Avenella flexuosa* | 108 | 33 | 32 | 43 | 6,01 | 3 | 2.1 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Avenula pubescens* | 1 | 0 | 0 | 1 | 7,04 | / | O |
| *Bazzania trilobata* | 1 | 1 | 0 | 0 | / | 3 | / |
| *Betonica officinalis* | 4 | 1 | 2 | 1 | 7,89 | 6 | 2.2 |
| *Bistorta officinalis* | 4 | 1 | 2 | 1 | 5,29 | 6,1 | 2.2 |
| *Blechnum spicant* | 4 | 3 | 1 | 0 | 8,79 | 3 | 1.1 |
| *Brachypodium sylvaticum* | 33 | 11 | 9 | 13 | 9,47 | 6,7 | 1.1 |
| *Brachythecium rutabulum* | 1 | 1 | 0 | 0 | / | 5,5 | / |
| *Bromopsis benekenii* | 1 | 0 | 1 | 0 | 7,29 | 6,7 | 1.1 |
| *Bromopsis erecta* | 1 | 1 | 0 | 0 | 9,5 | 8,5 | O |
| *Bromopsis ramosa* | 1 | 0 | 0 | 1 | 9,81 | / | 1.2 |
| *Calluna vulgaris* | 5 | 0 | 2 | 3 | 6,32 | 3 | 2.1 |
| *Caltha palustris* | 12 | 9 | 3 | 0 | 5,38 | 6,1 | 2.1 |
| *Campanula persicifolia* | 2 | 0 | 0 | 2 | 6,41 | / | 1.2 |
| *Campanula rapunculus* | 2 | 0 | 0 | 2 | 11,89 | / | 2.2 |
| *Campanula rotundifolia* | 12 | 2 | 5 | 5 | 4,97 | 8,5 | 2.1 |
| *Campanula trachelium* | 4 | 0 | 0 | 4 | 8,59 | 7 | 2.1 |
| *Capsella bursa-pastoris* | 1 | 0 | 1 | 0 | 7,22 | / | / |
| *Cardamine amara* | 2 | 1 | 1 | 0 | 6,07 | / | 2.1 |
| *Cardamine flexuosa* | 31 | 19 | 12 | 0 | 9,26 | 5,7 | 1.2 |
| *Cardamine heptaphylla* | 7 | 2 | 4 | 1 | 8,38 | 6,8 | 1.1 |
| *Cardamine impatiens* | 21 | 13 | 6 | 2 | 7,87 | 6,5 | 2.1 |
| *Cardamine pentaphyllos* | 2 | 0 | 2 | 0 | 7,02 | 6,9 | 1.1 |
| *Cardamine pratensis* | 29 | 14 | 7 | 8 | 4,68 | 6,1 | 2.1 |
| *Carex canescens* | 3 | 1 | 1 | 1 | 5,04 | / | 2.1 |
| *Carex digitata* | 1 | 1 | 0 | 0 | 5,31 | 6,9 | 1.1 |
| *Carex divulsa* | 1 | 0 | 1 | 0 | 10,24 | / | 2.2 |
| *Carex echinata* | 1 | 0 | 0 | 1 | 6,39 | 6 | 2.1 |
| *Carex flacca* | 2 | 2 | 0 | 0 | 10,25 | 7,6 | 2.2 |
| *Carex montana* | 5 | 0 | 2 | 3 | 7,61 | / | 1.2 |
| *Carex ornithopoda* | 1 | 1 | 0 | 0 | 6,28 | 8,5 | 2.2 |
| *Carex pallescens* | 1 | 0 | 0 | 1 | 6,38 | 4,7 | 2.2 |
| *Carex panicea* | 1 | 1 | 0 | 0 | 7,03 | 6,7 | 2.2 |
| *Carex pendula* | 4 | 2 | 2 | 0 | 11,2 | / | 1.1 |
| *Carex pilulifera* | 3 | 0 | 2 | 1 | 8,18 | 4,2 | 2.1 |
| *Carex remota* | 11 | 8 | 3 | 0 | 8,63 | 5,8 | 1.1 |
| *Carex sylvatica* | 40 | 25 | 10 | 5 | 8,29 | 6,2 | 2.1 |
| *Carex vesicaria* | 1 | 1 | 0 | 0 | 5,45 | 5,4 | O |
| *Cephalanthera longifolia* | 4 | 0 | 4 | 0 | 9,31 | 8,5 | 1.1 |
| *Chaerophyllum hirsutum* | 9 | 5 | 4 | 0 | 8,57 | 6,1 | 2.2 |
| *Chaerophyllum temulum* | 2 | 0 | 1 | 1 | 9,91 | / | 1.2 |
| *Chelidonium majus* | 2 | 1 | 1 | 0 | 8,05 | / | 2.2 |
| *Chrysosplenium alternifolium* | 12 | 7 | 5 | 0 | 5,81 | 8,5 | 2.1 |
| *Chrysosplenium oppositifolium* | 15 | 7 | 6 | 2 | 9,81 | 5,3 | 1.1 |
| *Circaea alpina* | 4 | 3 | 1 | 0 | 5,34 | / | 1.1 |

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|---|---|---|---|---|---|---|---|
| *Circaea lutetiana* | 38 | 20 | 11 | 7 | 8,4 | 6,1 | 1.1 |
| *Cirsium oleraceum* | 1 | 1 | 0 | 0 | 6,05 | 7,7 | 2.1 |
| *Cirsium palustre* | 3 | 3 | 0 | 0 | 6,91 | 6 | 2.2 |
| *Cirsium vulgare* | 1 | 1 | 0 | 0 | 7,97 | / | 2.2 |
| *Clinopodium vulgare* | 1 | 1 | 0 | 0 | 8,93 | 8,5 | 2.1 |
| *Colchicum autumnale* | 3 | 0 | 1 | 2 | 10,07 | 7,5 | O |
| *Conium maculatum* | 1 | 1 | 0 | 0 | 9,96 | / | / |
| *Convallaria majalis* | 8 | 4 | 3 | 1 | 7,12 | 8,5 | 2.1 |
| *Convolvulus sepium* | 2 | 0 | 0 | 2 | 8,34 | 7,5 | 2.2 |
| *Corydalis cava* | 1 | 0 | 1 | 0 | 8,26 | 6,7 | 1.1 |
| *Corydalis solida* | 1 | 1 | 0 | 0 | 7,4 | / | 1.1 |
| *Crataegus laevigata* | 11 | 5 | 2 | 4 | 9,31 | 6,3 | / |
| *Crataegus monogyna* | 30 | 6 | 14 | 10 | 10,19 | 8,1 | / |
| *Crepis paludosa* | 4 | 4 | 0 | 0 | 5,73 | 6,1 | 2.1 |
| *Cruciata laevipes* | 1 | 1 | 0 | 0 | 10,1 | / | 2.2 |
| *Cynoglossum germanicum* | 3 | 0 | 2 | 1 | 9,44 | / | 1.2 |
| *Cytisus scoparius* | 36 | 4 | 10 | 22 | 9,88 | 4,6 | 2.2 |
| *Dactylis glomerata* | 10 | 4 | 3 | 3 | 8,56 | 6,8 | 2.2 |
| *Dactylorhiza maculata* | 2 | 1 | 1 | 0 | 6,07 | 6,6 | 2.1 |
| *Daphne mezereum* | 2 | 1 | 0 | 1 | 5,35 | 7,5 | 1.1 |
| *Deschampsia cespitosa* | 12 | 5 | 5 | 2 | 5,45 | 5,6 | 2.1 |
| *Dianthus deltoides* | 1 | 0 | 0 | 1 | 6,32 | / | O |
| *Dicranella heteromalla* | 3 | 1 | 2 | 0 | / | 3 | / |
| *Dicranum majus* | 1 | 1 | 0 | 0 | / | 3 | / |
| *Dicranum scoparium* | 85 | 29 | 23 | 33 | / | 3 | / |
| *Digitalis lutea* | 3 | 0 | 1 | 2 | 9,71 | / | O |
| *Digitalis purpurea* | 68 | 24 | 16 | 28 | 11,04 | 3 | 1.2 |
| *Doronicum pardalianches* | 2 | 0 | 2 | 0 | / | / | / |
| *Drymochloa sylvatica* | 173 | 69 | 59 | 45 | 6,01 | 3 | 1.1 |
| *Dryopteris affinis* | 2 | 0 | 2 | 0 | / | 5,6 | / |
| *Dryopteris carthusiana* | 55 | 26 | 20 | 9 | 5,85 | 3 | 1.1 |
| *Dryopteris dilatata* | 62 | 33 | 18 | 11 | 8,99 | 3 | 1.1 |
| *Dryopteris filix-mas* | 153 | 60 | 51 | 42 | 7,35 | 5,9 | 1.1 |
| *Epilobium angustifolium* | 1 | 0 | 0 | 1 | 6,46 | / | 1.2 |
| *Epilobium hirsutum* | 2 | 1 | 0 | 1 | 9,32 | 7,1 | 2.2 |
| *Epilobium montanum* | 30 | 19 | 7 | 4 | 6,91 | 6,2 | 2.1 |
| *Epilobium parviflorum* | 1 | 1 | 0 | 0 | 9,26 | / | 2.2 |
| *Equisetum arvense* | 1 | 1 | 0 | 0 | 6,26 | 8,5 | 2.1 |
| *Equisetum sylvaticum* | 1 | 0 | 0 | 1 | 4,52 | / | 2.1 |
| *Equisetum telmateia* | 1 | 1 | 0 | 0 | 10,73 | 7,7 | 2.1 |
| *Ervilia hirsuta* | 2 | 0 | 1 | 1 | 7,97 | / | / |
| *Eryngium campestre* | 1 | 1 | 0 | 0 | 11,8 | 8,5 | / |
| *Euonymus europaeus* | 24 | 6 | 8 | 10 | 8,75 | 7,7 | / |
| *Eupatorium cannabinum* | 2 | 1 | 0 | 1 | 8,98 | 8,5 | 2.2 |
| *Euphorbia amygdaloides* | 51 | 15 | 21 | 15 | 10,82 | 6,4 | 1.1 |

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|---|---|---|---|---|---|---|---|
| *Euphorbia cyparissias* | 5 | 1 | 1 | 3 | 8,17 | 8,5 | 2.1 |
| *Eurhynchium striatum* | 30 | 11 | 9 | 10 | / | 6 | / |
| *Fallopia dumetorum* | 2 | 0 | 1 | 1 | 7,74 | / | 2.2 |
| *Festuca heterophylla* | 9 | 1 | 3 | 5 | 9,71 | 5,3 | 2.1 |
| *Festuca ovina* | 3 | 0 | 2 | 1 | 5,66 | 8,5 | 2.2 |
| *Festuca rubra* | 2 | 1 | 1 | 0 | 6,65 | 6,1 | 2.2 |
| *Ficaria verna* | 47 | 22 | 17 | 8 | 8,18 | 6,3 | 2.1 |
| *Filipendula ulmaria* | 18 | 13 | 4 | 1 | 5,58 | 6,4 | 2.2 |
| *Fissidens dubius* | 1 | 0 | 1 | 0 | / | / | / |
| *Fissidens taxifolius* | 1 | 1 | 0 | 0 | / | 6 | / |
| *Fragaria vesca* | 54 | 19 | 15 | 20 | 6,71 | 6,3 | 2.1 |
| *Galeopsis segetum* | 1 | 1 | 0 | 0 | / | / | / |
| *Galeopsis tetrahit* | 63 | 23 | 18 | 22 | 7,77 | 4,6 | 2.1 |
| *Galium aparine* | 88 | 28 | 35 | 25 | 9,2 | 8,5 | 2.1 |
| *Galium mollugo* | 8 | 2 | 2 | 4 | 7,37 | 8,5 | 2.2 |
| *Galium odoratum* | 128 | 50 | 46 | 32 | 7,6 | 6,4 | 1.1 |
| *Galium palustre* | 1 | 0 | 1 | 0 | 6,31 | 5,7 | 2.1 |
| *Galium rotundifolium* | 10 | 3 | 5 | 2 | 8,63 | 5,4 | 1.1 |
| *Galium saxatile* | 19 | 6 | 6 | 7 | 9,85 | 3 | 2.1 |
| *Galium sylvaticum* | 8 | 1 | 4 | 3 | 8,14 | 6,2 | 1.2 |
| *Galium uliginosum* | 1 | 0 | 0 | 1 | 5,06 | / | 2.2 |
| *Galium verum* | 1 | 0 | 1 | 0 | 7,56 | 7,2 | O |
| *Genista pilosa* | 9 | 0 | 5 | 4 | 9,62 | 8,5 | 2.2 |
| *Genista sagittalis* | 3 | 0 | 1 | 2 | 9,71 | / | 2.2 |
| *Gentiana lutea* | 1 | 0 | 0 | 1 | 8,98 | 8,5 | 2.2 |
| *Geranium robertianum* | 111 | 49 | 38 | 24 | 8,49 | 6,2 | 2.1 |
| *Geranium sylvaticum* | 1 | 1 | 0 | 0 | 3,98 | 6,3 | 2.1 |
| *Geum urbanum* | 44 | 21 | 16 | 7 | 7,92 | 6,5 | 2.1 |
| *Glechoma hederacea* | 47 | 27 | 16 | 4 | 6,7 | 6,3 | 2.1 |
| *Glyceria maxima* | 1 | 1 | 0 | 0 | 7,36 | / | 2.2 |
| *Gymnocarpium dryopteris* | 2 | 0 | 1 | 1 | 4,63 | / | 1.1 |
| *Hedera helix* | 112 | 36 | 40 | 36 | 10,93 | 6,2 | 1.2 |
| *Helleborus foetidus* | 31 | 10 | 13 | 8 | 11,65 | 7,6 | 1.2 |
| *Heracleum sphondylium* | 20 | 9 | 5 | 6 | 5,74 | 6,6 | 2.1 |
| *Hieracium lachenalii* | 1 | 0 | 1 | 0 | 6,18 | 7,5 | 2.1 |
| *Hieracium laevigatum* | 1 | 0 | 1 | 0 | 5,09 | / | 2.1 |
| *Hieracium murorum* | 59 | 13 | 18 | 28 | 7,27 | 6,6 | 2.1 |
| *Hieracium sabaudum* | 1 | 0 | 0 | 1 | 9,13 | / | 2.1 |
| *Holcus lanatus* | 2 | 0 | 2 | 0 | 9,85 | 5,6 | O |
| *Holcus mollis* | 14 | 3 | 5 | 6 | 8,73 | 4,5 | 2.1 |
| *Hordelymus europaeus* | 4 | 2 | 1 | 1 | 8,27 | 6,4 | 1.1 |
| *Humulus lupulus* | 1 | 0 | 1 | 0 | 7,21 | 8,5 | 1.2 |
| *Hylocomiadelphus triquetrus* | 11 | 6 | 2 | 3 | / | 6,6 | / |
| *Hylocomium splendens* | 15 | 9 | 3 | 3 | / | 6,4 | / |
| *Hylotelephium telephium* | 2 | 0 | 1 | 1 | 7,11 | / | 2.2 |

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|---|---|---|---|---|---|---|---|
| *Hypericum hirsutum* | 3 | 2 | 1 | 0 | 7,49 | 6,5 | 2.1 |
| *Hypericum montanum* | 2 | 1 | 0 | 1 | 8,75 | 8,5 | 1.2 |
| *Hypericum perforatum* | 21 | 3 | 8 | 10 | 9,25 | 6,4 | 2.2 |
| *Hypericum pulchrum* | 2 | 0 | 2 | 0 | 9,64 | 4,5 | 1.1 |
| *Hypnum cupressiforme* | 33 | 8 | 7 | 18 | / | 3 | / |
| *Hypnum jutlandicum* | 1 | 0 | 1 | 0 | / | 3,9 | / |
| *Impatiens glandulifera* | 3 | 1 | 2 | 0 | / | 8,5 | / |
| *Impatiens noli-tangere* | 69 | 35 | 24 | 10 | 6,68 | 5,1 | 1.1 |
| *Impatiens parviflora* | 2 | 0 | 2 | 0 | 8,12 | / | 1.1 |
| *Iris pseudacorus* | 1 | 1 | 0 | 0 | 9,27 | 5,8 | 2.1 |
| *Jacobaea vulgaris* | 1 | 1 | 0 | 0 | 7,6 | 7,3 | 2.2 |
| *Juncus conglomeratus* | 2 | 1 | 0 | 1 | 7,9 | 5 | 2.2 |
| *Juncus effusus* | 7 | 5 | 1 | 1 | 8,65 | 5,4 | 2.1 |
| *Kindbergia praelonga* | 4 | 4 | 0 | 0 | / | 5,4 | / |
| *Knautia dipsacifolia* | 2 | 0 | 2 | 0 | 7,18 | 6,4 | 2.1 |
| *Lactuca alpina* | 2 | 1 | 0 | 1 | 3,06 | 3 | 2.1 |
| *Lactuca muralis* | 66 | 25 | 25 | 16 | 8,76 | 6,5 | 2.1 |
| *Lactuca virosa* | 1 | 0 | 1 | 0 | / | / | / |
| *Lamium album* | 1 | 0 | 0 | 1 | 6,61 | / | 2.2 |
| *Lamium galeobdolon* | 73 | 36 | 22 | 15 | 8,44 | 6,3 | 1.1 |
| *Lamium purpureum* | 1 | 0 | 1 | 0 | 8,25 | / | / |
| *Lapsana communis* | 13 | 6 | 4 | 3 | 8,13 | 6,1 | 2.1 |
| *Lathraea squamaria* | 1 | 0 | 1 | 0 | 7,53 | 8,3 | 1.1 |
| *Lathyrus linifolius* | 2 | 2 | 0 | 0 | 8,85 | / | 2.1 |
| *Lathyrus linifolius var. montanus* | 15 | 1 | 8 | 6 | / | / | / |
| *Lathyrus niger* | 3 | 0 | 0 | 3 | 7,89 | / | 1.2 |
| *Lathyrus pratensis* | 2 | 0 | 1 | 1 | 6,07 | 7,1 | 2.2 |
| *Leucobryum glaucum* | 2 | 1 | 1 | 0 | / | 3 | / |
| *Leucojum vernum* | 2 | 1 | 0 | 1 | 8,55 | 7,5 | 1.1 |
| *Ligustrum vulgare* | 2 | 0 | 0 | 2 | 9,93 | 8,5 | 2.1 |
| *Lilium martagon* | 1 | 1 | 0 | 0 | 6,79 | 6,9 | 2.1 |
| *Linaria vulgaris* | 1 | 0 | 0 | 1 | 6,37 | / | 2.2 |
| *Lonicera periclymenum* | 35 | 7 | 10 | 18 | 9,95 | 4,5 | 1.2 |
| *Lonicera xylosteum* | 6 | 0 | 2 | 4 | 5,87 | 7,2 | 2.1 |
| *Lotus corniculatus* | 1 | 0 | 0 | 1 | 9,38 | 8,5 | 2.2 |
| *Lunaria rediviva* | 36 | 22 | 12 | 2 | 8,17 | 8,5 | 1.1 |
| *Luzula campestris* | 1 | 0 | 1 | 0 | 9,28 | 5,2 | 2.2 |
| *Luzula forsteri* | 1 | 0 | 1 | 0 | 12,35 | 5,5 | 1.1 |
| *Luzula luzuloides* | 112 | 34 | 31 | 47 | 7,76 | 3 | 1.1 |
| *Luzula pilosa* | 7 | 5 | 1 | 1 | 4,94 | 5,4 | 1.1 |
| *Luzula sylvatica* | 51 | 23 | 18 | 10 | 9,72 | 3 | 2.1 |
| *Lychnis flos-cuculi* | 1 | 0 | 0 | 1 | 7,33 | / | 2.2 |
| *Lysimachia nemorum* | 19 | 12 | 4 | 3 | 9,45 | 5,8 | 1.1 |
| *Lysimachia nummularia* | 3 | 3 | 0 | 0 | 7,86 | 6,1 | 2.1 |

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|---|---|---|---|---|---|---|---|
| *Lysimachia vulgaris* | 1 | 1 | 0 | 0 | 7,05 | 6 | 2.1 |
| *Lythrum salicaria* | 1 | 1 | 0 | 0 | 7,76 | 8,5 | 2.1 |
| *Maianthemum bifolium* | 1 | 0 | 1 | 0 | 4,76 | 3 | 1.1 |
| *Malus sylvestris* | 7 | 1 | 2 | 4 | 8,96 | 8,5 | 1.1 |
| *Melampyrum pratense* | 9 | 3 | 4 | 2 | 5,65 | 3 | 1.2 |
| *Melampyrum sylvaticum* | 3 | 0 | 1 | 2 | 3,14 | / | 1.2 |
| *Melica nutans* | 1 | 0 | 1 | 0 | 5,97 | 7,5 | 2.1 |
| *Melica uniflora* | 64 | 22 | 26 | 16 | 9,92 | 6,2 | 1.1 |
| *Melittis melissophyllum* | 4 | 0 | 1 | 3 | 11,71 | 7,5 | 1.2 |
| *Mentha aquatica* | 1 | 1 | 0 | 0 | 9,32 | 7,5 | 2.2 |
| *Mercurialis perennis* | 63 | 29 | 26 | 8 | 7,87 | 7,2 | 1.1 |
| *Milium effusum* | 57 | 24 | 19 | 14 | 5,63 | 5,5 | 1.1 |
| *Mnium hornum* | 2 | 1 | 1 | 0 | / | 3,5 | / |
| *Moehringia trinervia* | 52 | 18 | 15 | 19 | 8,08 | 5 | 2.1 |
| *Molinia caerulea* | 1 | 0 | 0 | 1 | 6,19 | 3 | 2.1 |
| *Myosotis scorpioides* | 1 | 1 | 0 | 0 | 6,92 | 6 | 2.1 |
| *Myosotis sylvatica* | 4 | 2 | 1 | 1 | 9,09 | 5,5 | 1.2 |
| *Myosoton aquaticum* | 2 | 1 | 1 | 0 | 7,59 | / | 2.2 |
| *Narcissus pseudonarcissus* | 1 | 1 | 0 | 0 | / | / | / |
| *Nasturtium officinale* | 3 | 2 | 1 | 0 | / | / | / |
| *Neottia nidus-avis* | 1 | 1 | 0 | 0 | 8,39 | 6,8 | 1.1 |
| *Orchis mascula* | 6 | 2 | 2 | 2 | 9,57 | 7 | 2.1 |
| *Oreoselinum nigrum* | 1 | 0 | 0 | 1 | 7,82 | / | 2.1 |
| *Oxalis acetosella* | 129 | 60 | 41 | 28 | 6,08 | 3 | 1.1 |
| *Paris quadrifolia* | 29 | 16 | 8 | 5 | 5,65 | 6,7 | 1.1 |
| *Petasites albus* | 4 | 2 | 1 | 1 | 8,27 | 6,7 | 2.1 |
| *Petasites hybridus* | 2 | 1 | 0 | 1 | 9,43 | / | 2.1 |
| *Phalaris arundinacea* | 1 | 1 | 0 | 0 | 6,58 | 8,5 | 2.1 |
| *Phyteuma nigrum* | 5 | 2 | 2 | 1 | 8,87 | 8,2 | 1.1 |
| *Phyteuma spicatum* | 21 | 12 | 6 | 3 | 8,31 | 6,5 | 1.2 |
| *Pilosella officinarum* | 1 | 0 | 1 | 0 | 7,75 | 8,5 | 2.2 |
| *Pimpinella major* | 4 | 0 | 3 | 1 | 9,14 | 8,4 | 2.2 |
| *Plagiochila asplenioides* | 3 | 3 | 0 | 0 | / | 6,5 | / |
| *Plagiomnium affine* | 13 | 8 | 3 | 2 | / | 5,5 | / |
| *Plagiomnium undulatum* | 29 | 14 | 10 | 5 | / | 6,2 | / |
| *Plagiothecium undulatum* | 5 | 3 | 0 | 2 | / | 3 | / |
| *Platanthera bifolia* | 1 | 0 | 0 | 1 | 6,51 | 8,5 | 2.1 |
| *Pleurozium schreberi* | 13 | 4 | 3 | 6 | / | 3 | / |
| *Poa annua* | 2 | 2 | 0 | 0 | / | / | / |
| *Poa chaixii* | 18 | 2 | 2 | 14 | 8,12 | 5,2 | 2.2 |
| *Poa nemoralis* | 48 | 14 | 13 | 21 | 6,26 | 5,4 | 1.1 |
| *Poa pratensis* | 1 | 0 | 1 | 0 | 6,2 | 6,25 | 2.2 |
| *Poa trivialis* | 13 | 6 | 5 | 2 | 8,14 | / | 2.1 |
| *Polygonatum multiflorum* | 60 | 14 | 24 | 22 | 8,04 | 6,3 | 1.1 |
| *Polygonatum odoratum* | 5 | 0 | 2 | 3 | 6,59 | 8,5 | 2.1 |

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|---|---|---|---|---|---|---|---|
| *Polygonatum verticillatum* | 61 | 25 | 19 | 17 | 6,8 | 6,4 | 2.1 |
| *Polypodium vulgare* | 18 | 8 | 4 | 6 | 7,95 | 6,8 | 2.1 |
| *Polystichum lonchitis* | 2 | 2 | 0 | 0 | 7,59 | 6,6 | 1.1 |
| *Polystichum setiferum* | 5 | 2 | 2 | 1 | / | 6,3 | / |
| *Polytrichum commune* | 3 | 1 | 0 | 2 | / | 3,4 | / |
| *Polytrichum formosum* | 119 | 43 | 35 | 41 | / | 3 | / |
| *Potentilla erecta* | 2 | 0 | 0 | 2 | 6,95 | 4,9 | 2.1 |
| *Potentilla micrantha* | 1 | 1 | 0 | 0 | 11,41 | / | 2.2 |
| *Potentilla sterilis* | 17 | 7 | 4 | 6 | 9,76 | 6,1 | 2.1 |
| *Prenanthes purpurea* | 77 | 29 | 23 | 25 | 7,96 | 3 | 1.1 |
| *Primula elatior* | 24 | 12 | 7 | 5 | 9,21 | 6,2 | 1.1 |
| *Primula veris* | 14 | 5 | 5 | 4 | 7,48 | 7 | 2.1 |
| *Pseudoscleropodium purum* | 8 | 4 | 1 | 3 | / | 4 | / |
| *Pteridium aquilinum* | 10 | 2 | 4 | 4 | 9,15 | 3 | 2.1 |
| *Pulmonaria montana* | 2 | 0 | 1 | 1 | / | / | / |
| *Pulmonaria obscura* | 22 | 13 | 7 | 2 | 5,7 | 6,3 | / |
| *Ranunculus aconitifolius* | 3 | 3 | 0 | 0 | / | 6 | / |
| *Ranunculus acris* | 5 | 1 | 2 | 2 | 5,61 | 5,7 | 2.2 |
| *Ranunculus bulbosus* | 4 | 1 | 1 | 2 | 9,8 | 8,2 | / |
| *Ranunculus platanifolius* | 2 | 1 | 0 | 1 | 5,64 | 6,6 | 2.1 |
| *Ranunculus repens* | 14 | 8 | 2 | 4 | 6,84 | 6 | 2.1 |
| *Rhizomnium punctatum* | 6 | 5 | 1 | 0 | / | 6,6 | / |
| *Rhodobryum roseum* | 1 | 1 | 0 | 0 | / | / | / |
| *Rhytidiadelphus loreus* | 49 | 25 | 13 | 11 | / | 3 | / |
| *Rhytidiadelphus squarrosus* | 2 | 0 | 2 | 0 | / | / | / |
| *Ribes alpinum* | 5 | 1 | 2 | 2 | 6,78 | 6,7 | 1.2 |
| *Ribes petraeum* | 1 | 1 | 0 | 0 | / | 6,9 | / |
| *Ribes rubrum* | 1 | 0 | 0 | 1 | 6,54 | 8 | 1.1 |
| *Ribes uva-crispa* | 1 | 0 | 1 | 0 | 7,87 | 7,3 | 2.1 |
| *Rosa arvensis* | 27 | 5 | 7 | 15 | 10,38 | 6,4 | 1.2 |
| *Rosa canina* | 4 | 0 | 3 | 1 | 8,99 | 8,5 | 2.1 |
| *Rubus caesius* | 4 | 2 | 1 | 1 | 7,83 | 8,5 | 2.1 |
| *Rubus fruticosus* | 157 | 58 | 56 | 43 | 8,77 | 5,5 | / |
| *Rubus idaeus* | 71 | 35 | 22 | 14 | 5,75 | 3 | 1.2 |
| *Rumex acetosa* | 6 | 1 | 4 | 1 | 6,87 | 5,9 | O |
| *Rumex arifolius* | 7 | 3 | 1 | 3 | 8,68 | / | 2.1 |
| *Rumex obtusifolius* | 13 | 8 | 4 | 1 | 8,07 | 5,7 | O |
| *Rumex sanguineus* | 1 | 1 | 0 | 0 | 8,8 | / | 1.1 |
| *Sambucus nigra* | 47 | 20 | 19 | 8 | 10,48 | 8,5 | 2.1 |
| *Sambucus racemosa* | 17 | 10 | 4 | 3 | 7,05 | 6,2 | 1.2 |
| *Sanicula europaea* | 5 | 2 | 2 | 1 | 8,51 | 6,3 | 1.1 |
| *Schedonorus giganteus* | 7 | 3 | 2 | 2 | 7,37 | 8,5 | 1.1 |
| *Scilla bifolia* | 4 | 0 | 1 | 3 | 9,24 | 6,8 | 2.1 |
| *Scorzoneroides pyrenaica* | 1 | 0 | 0 | 1 | / | 5,3 | / |
| *Scrophularia nodosa* | 16 | 8 | 6 | 2 | 7,17 | 5,7 | 1.1 |

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|---|---|---|---|---|---|---|---|
| *Senecio hercynicus* | 1 | 1 | 0 | 0 | 4,25 | / | / |
| *Senecio ovatus* | 92 | 43 | 29 | 20 | 8,88 | 4,8 | 1.2 |
| *Senecio sylvaticus* | 3 | 0 | 3 | 0 | 8,73 | / | 1.2 |
| *Silene dioica* | 55 | 26 | 17 | 12 | 6,5 | 5,95 | 2.1 |
| *Silene nutans* | 4 | 0 | 1 | 3 | 7,09 | 8,5 | 2.1 |
| *Solidago gigantea* | 1 | 1 | 0 | 0 | 7,71 | 8,3 | 2.2 |
| *Solidago virgaurea* | 14 | 5 | 3 | 6 | 5,27 | 6,9 | 2.1 |
| *Stachys sylvatica* | 37 | 26 | 10 | 1 | 7,28 | 8,5 | 1.1 |
| *Stellaria graminea* | 2 | 0 | 1 | 1 | 6,14 | / | O |
| *Stellaria holostea* | 32 | 9 | 10 | 13 | 7,01 | 5,3 | 1.1 |
| *Stellaria media* | 5 | 2 | 3 | 0 | 7,29 | / | 2.2 |
| *Stellaria nemorum* | 27 | 16 | 9 | 2 | 5,52 | 3,9 | 2.1 |
| *Succisa pratensis* | 1 | 1 | 0 | 0 | 7,14 | 5,8 | 2.2 |
| *Taraxacum officinale* | 3 | 1 | 1 | 1 | / | / | / |
| *Teucrium chamaedrys* | 2 | 1 | 0 | 1 | 11,56 | 8,5 | 2.1 |
| *Teucrium scorodonia* | 79 | 16 | 23 | 40 | 10,4 | 4,5 | 2.1 |
| *Thuidium tamariscinum* | 54 | 25 | 17 | 12 | / | 5,1 | / |
| *Thymus praecox* | 1 | 1 | 0 | 0 | 6,92 | / | / |
| *Thymus serpyllum* | 1 | 0 | 1 | 0 | 5,17 | / | 2.2 |
| *Torilis japonica* | 1 | 1 | 0 | 0 | 8,78 | 6,3 | 1.2 |
| *Trifolium repens* | 2 | 0 | 1 | 1 | 7,88 | 5,6 | 2.2 |
| *Urtica dioica* | 80 | 43 | 22 | 15 | 7,64 | 6,1 | 2.1 |
| *Vaccinium myrtillus* | 42 | 17 | 12 | 13 | 5,07 | 3 | 2.1 |
| *Vaccinium vitis-idaea* | 1 | 0 | 0 | 1 | 4,35 | 3 | 2.1 |
| *Valeriana dioica* | 1 | 1 | 0 | 0 | 8,93 | 6 | 2.1 |
| *Valeriana officinalis* | 6 | 3 | 2 | 1 | 6,83 | 6,2 | 2.2 |
| *Veronica beccabunga* | 4 | 2 | 2 | 0 | 7,79 | / | 2.2 |
| *Veronica chamaedrys* | 33 | 10 | 12 | 11 | 7,29 | 6 | 2.1 |
| *Veronica hederifolia* | 9 | 3 | 4 | 2 | 10,63 | 7,7 | 2.1 |
| *Veronica montana* | 14 | 9 | 5 | 0 | 9,26 | 5,9 | 1.1 |
| *Veronica officinalis* | 41 | 14 | 11 | 16 | 7,12 | 5,8 | 2.1 |
| *Veronica serpyllifolia* | 1 | 0 | 1 | 0 | 6,78 | / | 2.2 |
| *Veronica sublobata* | 2 | 1 | 1 | 0 | / | / | / |
| *Viburnum opulus* | 3 | 2 | 0 | 1 | 6,46 | 7,7 | 2.1 |
| *Vicia dumetorum* | 1 | 0 | 1 | 0 | 8,16 | / | 1.2 |
| *Vicia sativa* | 2 | 0 | 0 | 2 | 8,46 | 8,5 | / |
| *Vicia sepium* | 18 | 5 | 6 | 7 | 6,55 | 6,5 | 2.1 |
| *Vincetoxicum hirundinaria* | 8 | 2 | 3 | 3 | 8,15 | 8,5 | 2.1 |
| *Viola mirabilis* | 4 | 1 | 0 | 3 | 5,7 | 7,5 | 1.1 |
| *Viola reichenbachiana* | 116 | 42 | 43 | 31 | 9,49 | 6,3 | 1.1 |
| *Viola riviniana* | 21 | 7 | 4 | 10 | 8,26 | 5,3 | 1.1 |
| *Xanthoselinum alsaticum* | 1 | 0 | 1 | 0 | 8,46 | / | 2.1 |

# Persistance ou adaptation de la flore forestière face aux effets conjugués du réchauffement climatique, de la fragmentation des forêts et du microclimat ?

**Mots-clés :** Écologie des communautés, Changements globaux, Modélisation, Microclimat, Fragmentation forestière, Diversité.

## Résumé étendu en Français

### Introduction

La menace que fait peser le réchauffement climatique sur la biodiversité végétale souligne l'intérêt d'étudier conjointement les changements récents des communautés végétales et les facteurs qui pourraient les ralentir (IPCC, 2021a; Sala *et al.*, 2000; Wiens, 2016). En effet, les modèles de distributions d'espèces prédisent des changements d'aires de répartition, déclenchés par des évènements d'extinction et de colonisation (Lenoir & Svenning, 2015). La conséquence attendue de ces déplacements à l'échelle de la communauté est le remplacement graduel des espèces de climat froid par des espèces de climat plus chaud, un processus appelé thermophilisation (Bertrand *et al.*, 2011; De Frenne *et al.*, 2013). Cette thermophilisation, souvent perçue comme une adaptation de la flore au nouveau climat peut être affectée par des facteurs biophysiques multiples, agissant souvent à des échelles trop fines pour être captés par les modèles cités précédemment (Dobrowski, 2011; Greiser *et al.*, 2020). Il est donc urgent de quantifier et de questionner si la thermophilisation représente une adaptation des communautés, ainsi que de mesurer comment le microclimat induit par la topographie ainsi que le couvert forestier - paysager et local - offre un moyen de persistance des communautés végétale de sous-bois.

Les aires de distributions passées et futures des espèces dépendent au moins en partie de leur niche écologique, qui est le résultat de l'ensemble des traits acquis lors de l'évolution d'une espèce pour qu'elle puisse s'adapter à un climat précis (Comte *et al.*, 2014; Soberón & Peterson, 2005). Des estimations (imprécises du fait des interactions entre espèces et des contraintes géographiques) de la niche sont possibles grâce aux modèles climatiques et aux atlas de distribution d'espèces (Vangansbeke *et al.*, 2021). C'est au travers de cette niche des températures que nous étudierons l'affinité des communautés et leurs remaniements au regard du changement climatique. Même si le cœur de ce travail se base sur la température, sa corrélation avec d'autres variables climatiques (humidité du sol, fréquence et intensité des sècheresses) rend nos résultats interprétables aussi par ces autres facteurs (également affectés par le réchauffement climatique).

Agréger la niche climatique à l'échelle de la communauté permet d'étudier l'affinité au climat d'un ensemble d'individus occupant le même habitat (De Frenne *et al.*, 2013; Leibold & Chase, 2017). De là, nous pouvons nous poser la question de l'évolution temporelle de cette affinité au climat (la thermophilisation) et identifier quelles espèces disparaissent, au profit de la colonisation de quelles autres. De plus, nous pouvons dresser un lien entre thermophilisation et une perte discrète de la diversité, l'homogénéisation, qui entraine une augmentation de la ressemblance des communautés entre elles (Tatsumi *et al.*, 2021). Nous pouvons également utiliser la composition des communautés pour identifier des conditions

permettant une préservation des espèces de climat froid, notamment grâce à un microclimat frais et protecteur (De Frenne *et al.*, 2021; Pastore *et al.*, 2022). Plus spécifiquement, nous étudierons deux facteurs agissant à l'échelle du paysage – une échelle intermédiaire entre la communauté et le climat à grande échelle – sur le microclimat : la topographie et le couvert forestier. Au vu des futures prédictions de température (IPCC, 2021a) et de déforestation (Doelman *et al.*, 2018), il est important d'identifier des refuges climatiques pour les espèces, d'autant que la stabilité des refuges est variable. La topographie par exemple est beaucoup plus stable qu'un couvert forestier (Finocchiaro *et al.*, 2023; Pastore *et al.*, 2022).

Les trois questionnements abordés au cours de ce travail à l'échelle des forêts Françaises, prenant les communautés végétales de sous-bois comme sujet d'étude, sont les suivantes :

(1) Est-ce que le réchauffement récent de la température (2005-2021) provoque une thermophilisation des communautés végétales des forêts françaises ? Quelle est la nature de cette thermophilisation (extinction vs colonisation) ? Entraine-t-elle une homogénéisation des communautés ?

(2) Le couvert forestier à l'échelle du paysage peut-il avoir un impact sur l'affinité climatique des communautés ? Par quels processus ?

(3) Quels sont les effets relatifs de la topographie et de la canopée sur le microclimat (température sous la canopée) des forêts de montagne ? Le refroidissement induit par la topographie peut-il conserver en plus grand nombre des espèces de climat froid ?

### 1er chapitre : L'extinction explique la thermophilisation des communautés des forêts tempérées, mais ne déclenche pas d'homogénéisation (Borderieux *et al.*, 2024).

L'objectif de ce chapitre est de quantifier conjointement la thermophilisation et l'homogénéisation des communautés végétales, et les dynamiques des communautés qui leur sont sous-jacentes. Il est important de rappeler qu'un taux donné de thermophilisation (quantifié en °C/an) peut être expliqué par des phénomènes écologiques complètement différents. Une prédominance des phénomènes d'extinction montre que les tolérances à la chaleur ou à la sècheresse des espèces de climat froid en place ont été dépassées (Kuhn & Gégout, 2019), indiquant une perte de diversité locale. Les phénomènes de colonisation quant à eux relèvent avant tout de la capacité de nouvelles plantes (d'un climat plus adapté) à atteindre la communauté (Comte *et al.*, 2014; Dullinger *et al.*, 2015). La thermophilisation étant un processus sélectif, il se peut qu'une redondance dans les espèces sélectionnées entraine une homogénéisation des communautés, une perte de diversité qui peut diminuer les services écosystémiques et la résilience du sous-bois (Landuyt *et al.*, 2019; Pastore *et al.*, 2022; Wang *et al.*, 2021). L'homogénéisation peut avoir lieu si des espèces déjà rares disparaissent ou si des espèces déjà fréquentes s'étendent encore plus (Tatsumi *et al.*, 2021). Cette analyse a été réalisée à l'échelle de la sylvoécoregion (IGN, 2013), nous avons aussi testé comment son climat influence le remaniement des communautés.

Nous avons utilisé les placettes de l'Inventaire Forestier National (IFN) français (IGN, 2019b) pour créer des couples temporels de placettes (Fig.1). Nous avons associé chaque

placette de la maille de l'IFN avec une placette réalisées 10 ans plus tard, pour créer un échantillon de 14,167 paires, réparties dans 80 sylvoécoregions. Nous avons partitionné la thermophilisation et le changement de ß-diversité en 4 composantes : extinction et colonisation des espèces de climat chaud et froids.

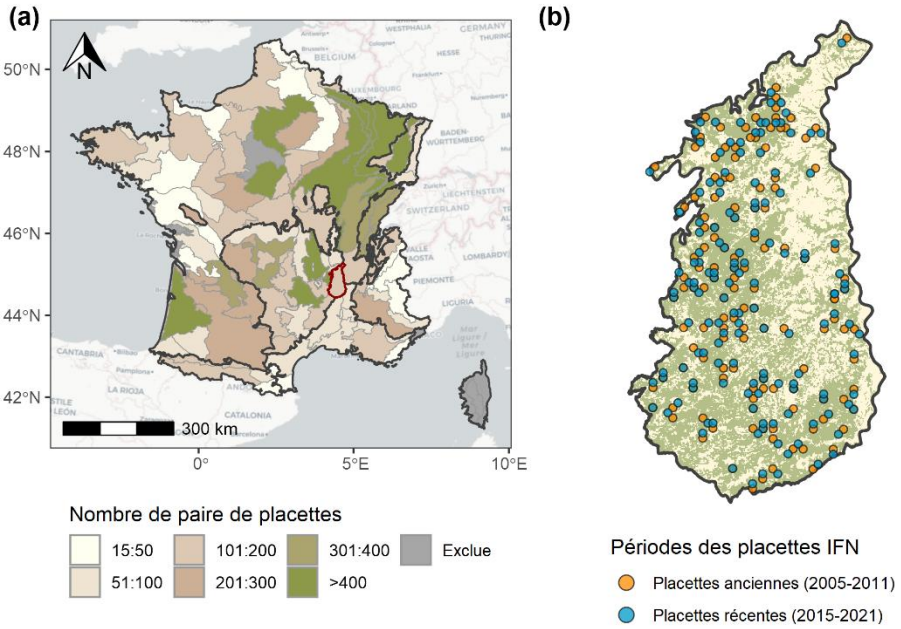


*Fig. 1: Illustration du processus d'appariement des placettes de la sylvoécoregion dessinées en rouge (b), et carte des sylvoécoregions et du nombre de paires qu'elles contiennent (a).*

Nous montrons que l'extinction est la seule dynamique qui provoque la thermophilisation des communautés (estimée à 0.12 C/ 10 ans, Fig.2.a). Ce résultat remet en cause la vision selon laquelle la thermophilisation est une adaptation des communautés. Il s'agirait plutôt d'une altération entrainant des conséquences négatives sur la diversité locale, mais ne provoquant pas d'homogénéisation des sylvoécoregions (Fig.2.b). Nous montrons grâce au partitionnement que les espèces de climat froid en déclin étaient autant rares que fréquentes, provoquant ainsi un changement nul de ß-diversité. Les taux de thermophilisation, et donc d'extinction, sont plus élevés dans les sylvoécoregions méditerranéennes et du sud-ouest, atteignant parfois 0.25°C /10ans.

Ces résultats démontrent que décomposer des métriques aussi simples que la thermophilisation permet de gagner en pouvoir explicatif. Dans les forêts tempérées, l'observation d'une prédominance de l'extinction (liée à une absence de colonisation par des espèces plus adaptées) met en évidence le besoin d'étudier des facteurs biophysiques de persistances des communautés pour mieux évaluer les risques de perte de biodiversité à large échelle et moyen terme.

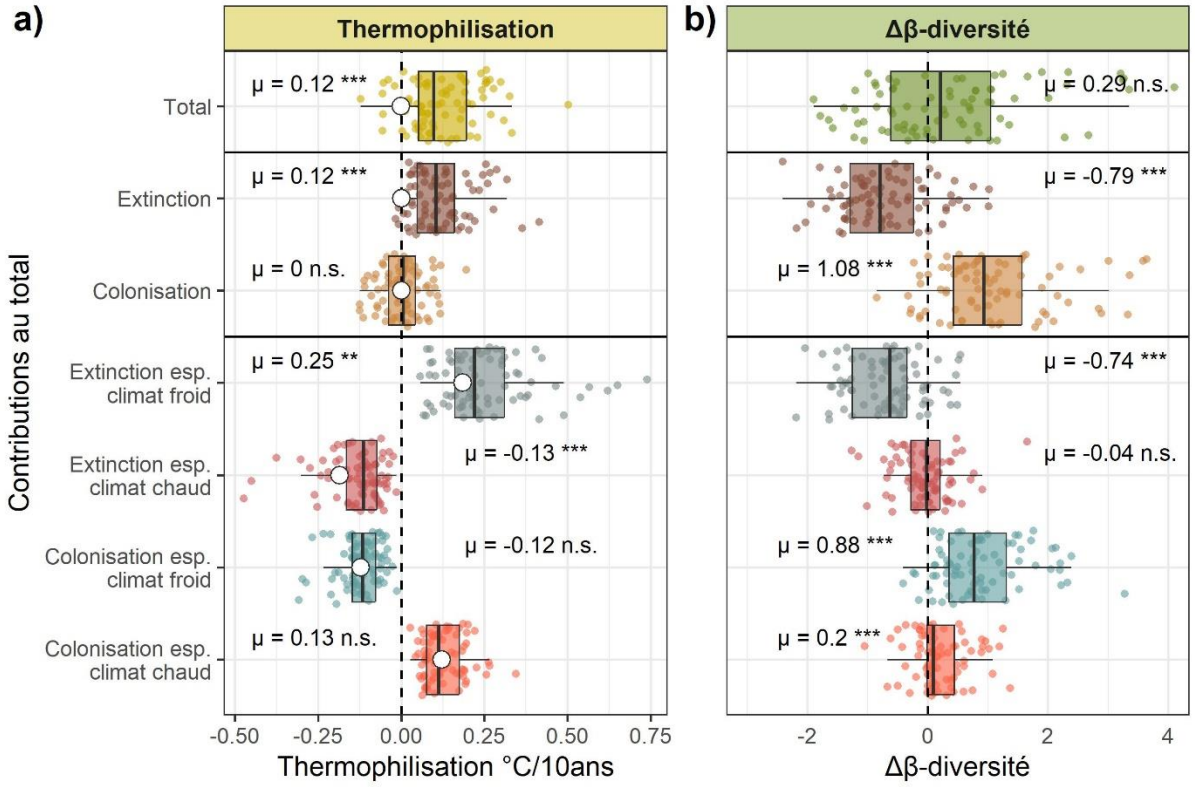


*Fig. 2: Partition de la thermophilisation (a) et de l'homogénéisation (b). Un point représente la valeur d'une sylvoécoregion. Une espèce est classée « extinction » quand elle a perdu en nombre d'occurrences avec le temps, une espèce est classée « climat froid » quand sa niche écologique est plus froide que la niche moyenne des communautés de la sylvoécoregion. Le point blanc représente la valeur d'un modèle nul selon lequel le changement d'occurrence d'une espèce est indépendant de sa niche climatique.*

**2ème chapitre : Le couvert forestier favorise les communautés végétales de climat froid dans les mosaïques agriculture-forêt (Borderieux *et al.*, 2023).**

L'objectif de ce chapitre est de tester comment la couverture forestière peut favoriser les espèces de climat froid, dans le contexte de mosaïques agriculture-forêt caractéristique de l'Europe tempérée (Ellis, 2021). L'hypothèse sous-jacente est qu'en plus du refroidissement local que provoque la canopée (De Frenne *et al.*, 2019; Kemppinen *et al.*, 2023), une couverture forestière importante peut refroidir le climat régional (Bonan, 2008; Hesslerová *et al.*, 2013; Pokorny *et al.*, 2010). La fragmentation actuelle des forêts en massifs inégaux n'est pas indépendante du contexte historique. Les petits massifs forestiers ont plus de chance d'être des forêts jeunes, poussant sur un sol agricole encore riche, alors que les grands et anciens massifs ont perduré car leur sol n'était pas intéressant pour l'agriculture (Bergès *et al.*, 2013, 2016; Dupouey, Sciama, *et al.*, 2002). De ce fait, nous avons testé comment les différences de richesse chimique du sol ont pu influencer l'affinité climatique des communautés. Cela est rendu possible par l'éventuelle corrélation entre la niche climatique et la niche édaphique des espèces. Cette corrélation est probable car les espèces de climat froid ont nécessairement évolué sur des sols plus pauvres du fait du manque d'activité biologique limitée par la contrainte thermique et des humus composés à base d'aiguilles de résineux, Ewald, 2003).

Nous avons utilisé l'IFN pour réaliser un appariement de placettes proches (<5 km) mais situées dans des zones avec des taux de couverture forestière opposés (nombre de paires : 2,012). Nous avons utilisé un modèle linéaire pour étudier distinctement l'effet du sol et un possible effet de la couverture forestière.

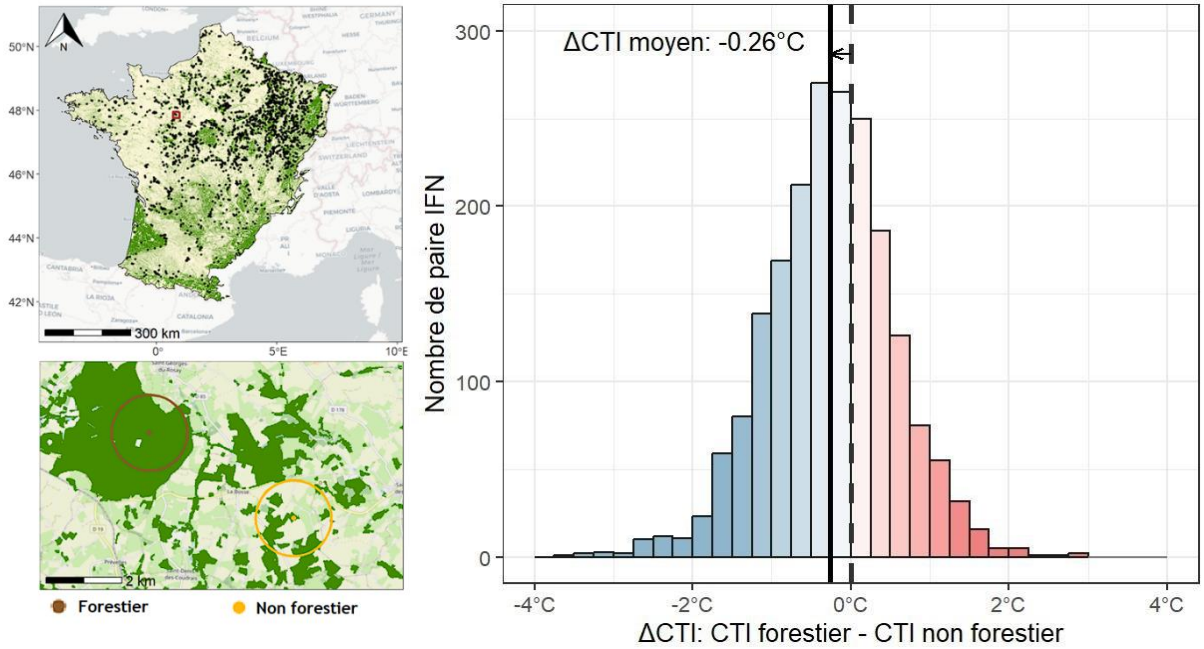


*Fig. 3: Carte des paires de points IFN et illustration du processus d'appariment. Histogramme des différences d'affinité climatique (CTI) entre la placette (communauté) située en zone très forestière et en zone faiblement forestière de la paire. Une différence négative signifie que la placette en milieu très forestier comporte une communauté plus adaptée aux climats froids. La moyenne de différence de CTI est représentée par la ligne pleine verticale.*

Nous avons montré que l'affinité climatique des communautés de paysages très forestiers est en moyenne 0.26°C plus basse (Fig.3). La moitié de cette diminution est expliquée par la différence de conditions du sol : les zones très forestières comportent des sols plus pauvres qui favorisent les espèces de climat froid. L'autre moitié de cette diminution n'est expliquée par aucun des facteurs inclus dans le modèle, ce qui suggère un effet attribuable à la seule différence de couvert forestier entre les placettes. Nous interprétons cet effet comme un refroidissement du climat régional par la couverture forestière.

La fragmentation forestière est traditionnellement interprétée comme un facteur limitant les possibilités de migrations des espèces (Dullinger *et al.*, 2015). Ces résultats placent la fragmentation forestière aussi comme un facteur capable d'altérer le paysage thermique et édaphique des espèces, et montrent que les massifs forestiers favorisent les espèces de climat froid.

**3ème chapitre : Le microclimat induit par la topographie conduit à une forte diversité floristique dans les forêts des montagnes tempérées (Borderieux *et al.*, in prep).**

L'objectif de ce chapitre est de compléter l'étude des facteurs pouvant expliquer la persistance de la composition des communautés floristiques à l'échelle paysagère, dans le contexte des forêts de montagnes cette fois. Nous cherchons à démêler les effets du microclimat provoqué par la canopée et ceux de la topographie (que nous appellerons topoclimat) sur la température du sous-bois forestier. Le microclimat est un résultat de l'ombrage et de l'évapotranspiration qui explique la fraicheur du sous-bois en été (De Frenne *et al.*, 2021). Le topoclimat est quant à lui expliqué par le plus grand ensoleillement des faces exposées au sud (pour une montagne de l'hémisphère nord), et par l'accumulation de l'air froid au fond des vallées. La distinction entre les deux est nécessaire car la canopée peut être brusquement retirée par une perturbation comme une coupe, une attaque de scolyte ou une tempête, alors que le topoclimat, lui, est particulièrement stable dans le temps (Finocchiaro *et al.*, 2023; Pastore *et al.*, 2022). Nous évaluerons donc les effets respectifs du couvert de la canopée et du topoclimat sur l'affinité climatique et la richesse spécifique des communautés.

Nous avons combiné les mesures faites par 48 thermomètres, répartis dans le sous-bois de vallée de la Thur (massif des Vosges) dans différents contextes topographiques et de couverts forestiers pour modéliser la température du sous-bois. Nous avons ensuite utilisé ce modèle pour quantifier les effets de la canopée et du topoclimat sur la composition et la diversité de 306 placettes situées dans la vallée.

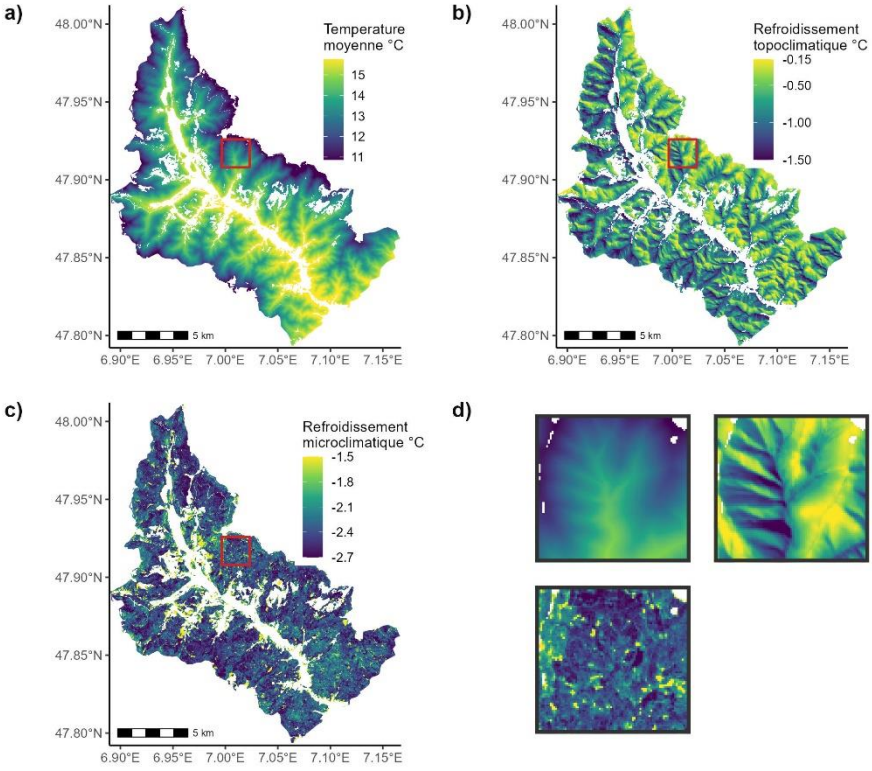


*Fig. 4: Illustration du gradient altitudinal (a), du topoclimat (b) et du microclimat (c) (qui est induit par la canopée). (d) représente un agrandissement d'une partie de la vallée (carré rouge) pour ces trois processus.*

Nous avons montré que le topoclimat (exposition et position dans la vallée) est un facteur plus important que la canopée pour expliquer les températures du sous-bois. Pendant la saison de végétation 2022, la température sous couvert était 1.5°C plus fraiche au fond d'une vallée ombragée comparée à une arrête exposée au sud (Fig.4). Nous montrons aussi que, une fois le gradient altitudinal pris en compte, seul le topoclimat façonne la composition et la diversité des communautés de la région. Les communautés des topoclimats froids comportent en moyenne 5 espèces de plus que celles des autres topoclimats (Fig.5). Cette différence est expliquée par une augmentation du nombre d'espèces de climat froid qui sont aussi bien des espèces forestières spécialistes que généralistes.

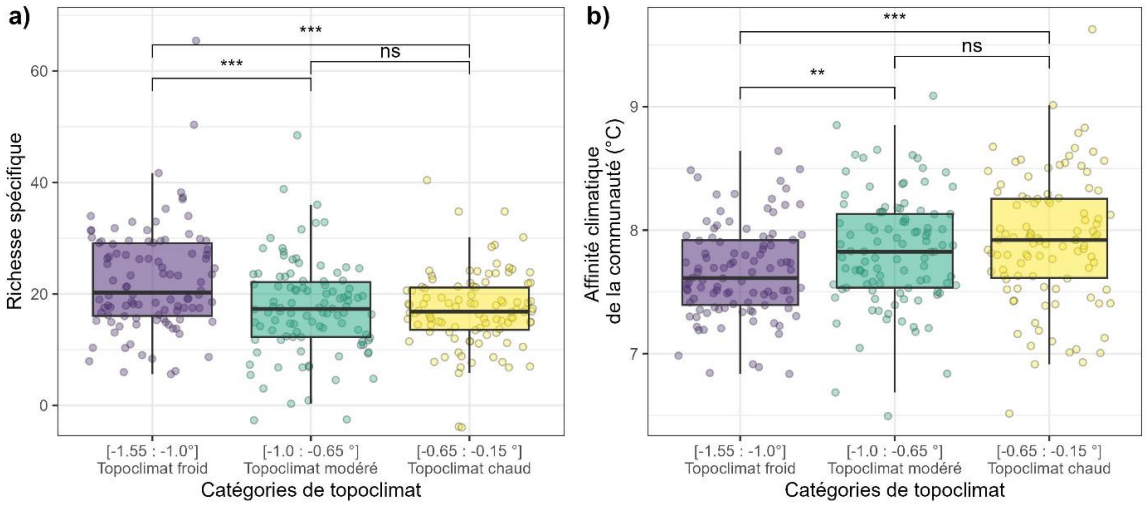


*Fig. 5 : Richesse spécifique (a) et affinité climatique (b) des communautés en fonction des classes 'froid', 'modéré' et 'chaud' de topoclimat, comportant chacune 102 relevés floristiques. Les deux valeurs ont été corrigées par le pH bioindiqué du relevé, les différences significatives (** et ***) sont testées par un test de Wilcoxon.*

Ces résultats démontrent la prévalence de la topographie comme élément structurant des températures et des communautés de montagnes. Cette étude s'ajoute à la littérature s'intéressant aux refuges climatiques, des espaces où les conditions locales peuvent durablement soutenir des espèces pourtant inadaptées au nouveau climat régional (Greiser *et al.*, 2020; Hylander *et al.*, 2022; Pastore *et al.*, 2022). Il est aussi probable que les fonds de vallée soient plus humides grâce aux réseaux hydrographiques, tamponnant d'autant plus la température et permettant aux espèces sensibles aux sècheresses de subsister (Raduła *et al.*, 2018).

## Principales conclusions

Nos résultats ont permis de montrer que la thermophilisation récente de la flore forestière française est due à l'extinction locale d'espèces de climat froid, il ne s'agit donc pas d'une adaptation. Ces extinctions entrainent une baisse de la diversité locale, mais n'ont pas eu d'incidence sur la redondance des communautés. Nous avons identifié deux facteurs de persistances des communautés de climat froid : le couvert forestier du paysage (influencé par la fragmentation des forêts) et les effets de versant nord et de fond de vallée qui favorisent les espèces adaptées au froid et la diversité des communautés qui les accueillent. Ces facteurs seront essentiels pour comprendre et conserver les communautés végétales dans un contexte d'extinctions locales causées par le réchauffement climatique.

**Title: Persistence or adaptation of forest flora in the face of the intertwined effects of global warming, forest fragmentation and microclimate?**

**Keywords:** Community ecology, Global changes, Modeling, Microclimate, Forest fragmentation, Diversity

**Abstract**

Predictions of how forest plant communities and their diversity will respond to the 21st century climate warming are ambiguous. On one hand, warm-adapted species are expected to colonize communities at the expense of locally extinct cold-adapted species, in a process called thermophilization. On the other hand, forest fragmentation and the cooling effects derived from canopy cover and topography on microclimates are thought to prevent such thermophilization. This thesis aims to quantify the processes (extinction vs. colonization) behind the recent trends of community thermophilization (2005-2021) and to identify biophysical factors that can explain local persistence of communities.

We first used French National Forest Inventory (NFI) plots (2005-2021) to create a balanced temporal pairing of plots. We used the 14,167 pairs to study thermophilization and homogenization (increase in similarity between communities) trends in plant communities and partitioned their underlying processes. We found a significant thermophilization trend across French forests, which was solely explained by the regression of cold-adapted species. We found no homogenization because cold-adapted species extinctions occurred independently of their rarity. These results show that thermophilization in lowland temperate forests is a sign of community alteration, rather than adaptation to climate change. This further illustrates the need to identify local refugia for cold-adapted species.

To test how high amount of forest cover could shelter cold-adapted communities, we used the NFI to pair plots in contrasting mosaics of forest and agriculture differing in total forest cover. The 2,012 pairs created allowed to compare communities' affinity to climate of forested and less forested landscapes. We found that forested landscapes harbored colder-adapted communities. This cooling effect was mostly explained by difference of soil conditions, but we also found a unique landscape effect that hints a microclimatic cooling of landscape forest cover. This places forest cover as a landscape-scale driver of community affinity to climate.

Lastly, we conducted measurements of understory temperature in a valley of the Vosges to disentangle the relative effect of canopy and topography on microclimate and communities. By associating a microclimate model (48 loggers) with 306 vegetation plots, we showed that topography (aspect and topographic position) outweighed canopy cover at explaining growing season microclimate. Similarly, the effect of topography –decoupled from elevation– explained community affinity to climate and species richness. Communities displayed richer and colder-adapted communities in north-facing slopes and shaded valley bottoms compared to other topography. These results show that topography, a much more stable microclimatic driver than canopy cover, effectively shelters diverse communities of cold-adapted species in mountain forests.

Our results are aligned with the prediction community reshuffling and diversity decline. This seemingly ubiquitous extinction-driven thermophilization is nuanced by two prominent landscape-scale sources of species persistence, forest cover and topography. Taking advantage of the cooling offered by these two factors will be key for plant community conservation and comprehension.

**Titre : Persistance ou adaptation de la flore forestière face aux effets conjugués du réchauffement climatique, de la fragmentation des forêts et du microclimat ?**

**Mots-clés :** Écologie des communautés, Changements globaux, Modélisation, Microclimat, Fragmentation forestière, Diversité.

**Résumé**

Une contradiction réside dans nos prédictions de l'évolution des communautés forestières végétales face au réchauffement climatique du 21ème siècle. D'un côté, les espèces de climat chaud pourraient coloniser les communautés en remplaçant des espèces de climat froid, un processus appelé thermophilisation. De l'autre, la fragmentation des forêts et la protection qu'offrent les microclimats créés par la canopée et la topographie sont supposées empêcher ce changement. Cette thèse vise à quantifier les processus (extinction vs colonisation) à l'origine des tendances récentes de thermophilisation des communautés (2005 -2021) et à identifier des facteurs biophysiques qui peuvent expliquer la persistance locale de communautés.

Nous avons d'abord utilisé les placettes de l'Inventaire forestier national (IFN) français (2005-2021) pour créer des paires de placettes équilibrées dans le temps. Nous avons utilisé les 14,167 paires pour étudier les tendances de thermophilisation et d'homogénéisation (augmentation de la similarité entre les communautés) des communautés végétales. Nous avons constaté une thermophilisation des communautés forestières françaises, expliquée uniquement par la perte d'espèces de climat froid. Nous n'avons pas détecté d'homogénéisation car les extinctions d'espèces de climat froid se sont produites indépendamment de leurs raretés. Ces résultats montrent que, plutôt qu'être une adaptation, la thermophilisation s'apparente à une altération des communautés. Cela illustre la nécessité d'identifier des refuges locaux pour les espèces de climat froid.

Pour tester si un couvert forestier important peut abriter des communautés adaptées au froid, nous avons utilisé les placettes IFN pour coupler des parcelles avec différents taux de couvert forestier. Les 2,012 paires ainsi créées ont permis de comparer l'affinité climatique des communautés dans des paysages forestiers et moins forestiers. Nous avons montré que les paysages forestiers abritaient des communautés plus adaptées aux climats froids. Ce 'refroidissement' s'explique principalement par des différences de conditions pédologiques, mais nous avons également observé un effet purement lié au paysage qui suggère un refroidissement microclimatique du couvert forestier.

Enfin, nous avons effectué des mesures de la température du sous-bois dans une vallée des Vosges afin de séparer l'effet de la canopée de celui de la topographie sur le microclimat et les communautés. Nous avons montré que la topographie l'emportait sur la canopée pour expliquer le microclimat et la composition des communautés. De plus, les communautés étaient plus riches et comportaient plus d'espèces de climat froid sur les pentes orientées vers le nord et dans les fonds de vallée ombragés que dans le reste de la zone.

Nos résultats confirment le déclin de la diversité prédit et le manque d'adaptation des communautés. Cette thermophilisation due à l'extinction est toutefois à nuancer par deux sources importantes de persistance des espèces : la couverture forestière et la topographie. Tirer parti du refroidissement offert par ces deux facteurs sera essentiel pour la conservation et la compréhension des communautés végétales.

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