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Transient dynamics of Alpine grasslands linking biodiversity and ecosystem functions in a warming world

Billur Bektaş

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THÈSE

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Dynamique transitoire des prairies alpines - relier la biodiversité et les fonctions des écosystèmes dans un monde qui se réchauffe

Transient dynamics of Alpine grasslands linking biodiversity and ecosystem functions in a warming world

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Invités :



Sevgili anneannem Gönül Özgür,
Doktora tezimi sana ithaf ediyorum.
Biliyorum ki elli sene önce imkân verilseydi
bitki biyoçeşitliliğini korumak adına benden çok önce yola çıkardın.
Senin bitkilere duyduğun aşk, benim tezimin yolunu açtı.
Sana müteşekkirim.

My dear grandma Gönül Özgür,
I dedicate this Ph.D. thesis to you.
I know that five decades ago if you were given the chance you would already be
on the road to protecting plant biodiversity.
Your love of plants paved the way for my manuscript.
I am forever grateful to you.

It is the story that makes the difference. It is the story that hid my humanity from me,
the story the mammoth hunters told about bashing, thrusting, raping, killing, about the Hero.
The wonderful, poisonous story of Botulism. The killer story.

Ursula K. Le Guin, *The Carrier Bag Theory of Fiction*

Listen, there's a man telling a story about the man who holds the world on his shoulders.
Everybody laughs.
Only drunks and children believe that.
No man believes what he does not feel to be true.
I should like to unbelieve myself.
I sleep at night and wake in the morning hoping to be gone.
It never happens.
One knee forward, one knee bent, I bear the world.

Jeanette Winterson, *Weight*

"Even if I had a name I don't remember", it said. "The truth is that I was never called".
The thing that would bring humans and pets closer to their own existence is to forget their name
so that they can hear being called.
To be remembered by a name despite the endless sounds of being called is to be detained.
The weight of human, the fact that he presses the ground so tight with all his strength,
is all because of this.

Deniz Gezgin, *YerKuşAğı*

Table of Contents

Abstract	3
Résumé	4
Introduction	6
1. Revealing the patterns of biodiversity in the midst of a change	6
2. Plants under climate warming and drought	8
2.1. Complexities of biological organizations	8
Box 1: Functional traits as a toolbox for community and functional ecology	12
2.2. Individual and population level responses	15
2.2.2. Acclimation of phenology to warming & drought	16
2.2.3. Acclimation of morpho-physiological functional traits to warming & drought	18
2.3. Species level responses	21
2.3.1 Ignoring intraspecific variability	21
2.3.2 Winner and loser species under climate change	22
2.4. Community scale responses	23
2.4.1. Changes in community assembly processes under warming and drought	23
2.4.2. Changes in community level functional strategies under warming and drought	26
2.5. Changes in ecosystem functioning under warming and drought	27
3. Transient dynamics of plants under warming	31
Box 2: Whole community transplant experiments to study transient dynamics in a in situ laboratory	33
4. Climate warming at a biodiversity hotspot: European Alps	35
5. Main thesis questions and chapter specific questions	36
Chapter 1: Lags in phenological acclimation of mountain grasslands after recent warming	57
Chapter 2: Climate warming losers in alpine grasslands are cold adapted, drought intolerant and less conservative yet smaller than their neighbors	74
Chapter 3: A spatially explicit trait-based approach uncovers changes in assembly processes under warming	100
Chapter 4: Plant functional strategies acclimate quickly to <i>in situ</i> warming but may not provide all their ecosystem functions anymore	136
Discussion	160
1. Direct effects of warming and drought	160
2. Transient dynamics and acclimation lags	162
3. Indirect warming effects via changes of biotic interactions	164
4. Cascades to ecosystem functioning	165
5. Limitations	167
5.1. Methodological limitations	167

5.2. Plant-soil feedbacks	169
5.3. Adaptive plasticity in functional traits	170
6. Perspectives	172
6.1. Methodological limitations: improving the warming experiment & combining warming experiments with observation studies and process-based models	174
6.2. Improving our understanding in plant-soil feedbacks for climate change ecology	175
Conclusion	175
Acknowledgements	180
Appendix	182

Abstract

The plant kingdom not only constitutes nearly 20 % of known terrestrial biodiversity but as primary producers plants are also the scene setters of ecosystems. Therefore, climate warming-driven changes in plants can have repercussions for entire ecosystems. From individuals to species from species to communities and on to ecosystem functioning, acclimation to warming at one scale has cascading effects on the others. However, warming effects at one scale may not result in full acclimation, responses at different scales may not be simultaneous, cascading effects may not be linear, and response dynamics may include feedback between biological scales. Thus, revealing the timing and magnitude of responses to warming at different biological scales is difficult.

Here, I am addressing this challenge with a focus on mountain grassland communities in the French Alps that are biodiversity hotspots and support essential ecosystem services for society. In my first chapter, I focused on changes in the timing of life cycle events and demographic performance at community and species levels. After three years of warming, graminoids were able to complete their acclimation but forbs were less performant in producing flowers: a potential reason why warmed communities were less attractive to diverse pollinators compared to warm-adapted control communities. Even though warmed communities increased their productivity, they still underperformed in comparison to warm-adapted communities. In the second chapter, I identified 13 loser (one of them being extinct) and five winner species after five years of experimental warming. In general, losers were cold-adapted, and drought-intolerant. They also were smaller (and less conservative) than their neighbors. In the third chapter, in order to investigate how warming affects community assembly rules, I developed a new spatially-explicit trait-based community assembly framework. Applying it to the experiment revealed that experimental warming changes the signals and/or the relative importance of abiotic vs. biotic community assembly filters. In the fourth chapter, I focussed on plant above and belowground traits and plant-soil linkages. I found that warmed communities shifted their functional trade-offs towards more conservative and outsourcing strategies, and that these shifts affected ecosystem functions such as productivity, and microbial functioning.

Overall my thesis highlights the variability in the timing and functional forms of climate change responses at different biological scales. Sometimes this desynchronization led to losses of functionality, such as for plant-pollinator interactions or exploitation of plant-mycorrhizal interactions. Although in part fast and strong, many responses to climate warming are not sufficient for full acclimation. This means that the organisms can live under the new climate but are not competitive with better adapted organisms. I conclude that mountain grasslands are in danger of becoming increasingly homogenized, losing the distinctive features of the high and harsh environment at all levels of organisms. This is not so much directly due to warming, but rather to the indirect effects of an altered landscape of biotic interactions.

Résumé

Le règne végétal constitue non seulement près de 20 % de la biodiversité connue de la Terre, mais en tant que producteurs primaires, les plantes sont également les acteurs des écosystèmes. Par conséquent, les changements induits par le réchauffement climatique chez les plantes peuvent affecter des écosystèmes entiers. Des individus aux espèces, des espèces aux communautés, et jusqu'au fonctionnement des écosystèmes, l'acclimatation au réchauffement à une échelle a des effets en cascade sur les autres. Cependant, les effets du réchauffement à une échelle peuvent ne pas entraîner une acclimatation complète, les réponses à différentes échelles peuvent ne pas être simultanées, les effets en cascade peuvent ne pas être linéaires et la dynamique des réponses peut inclure une rétroaction entre les échelles biologiques. Il est donc difficile de révéler le moment et l'ampleur des réponses au réchauffement à différentes échelles biologiques. J'aborde ici ce défi en me concentrant sur les communautés de prairies de montagne dans les Alpes françaises, qui sont des points chauds de la biodiversité et fournissent des services écosystémiques essentiels à la société.

Dans mon premier chapitre, je me suis concentrée sur les changements dans le calendrier des événements du cycle de vie et les performances démographiques au niveau de la communauté et des espèces. Après trois ans de réchauffement, les graminées ont pu achever leur acclimatation mais les plantes herbacées ont moins bien réussi à produire des fleurs : une raison potentielle pour laquelle les communautés réchauffées étaient moins attrayantes pour divers pollinisateurs que les communautés témoins adaptées au réchauffement. Bien que les communautés réchauffées aient augmenté leur productivité, elles sont restées moins performantes que les communautés adaptées à la chaleur. Dans le deuxième chapitre, j'ai

identifié 13 espèces perdantes (dont une a disparu) et cinq espèces gagnantes après cinq ans de réchauffement expérimental. En général, les perdants étaient adaptés au froid et intolérants à la sécheresse. Elles étaient également plus petites (et moins conservatrices) que leurs voisines. Dans le troisième chapitre, pour étudier comment le réchauffement affecte les règles d'assemblage des communautés, j'ai développé un nouveau cadre d'assemblage des communautés basé sur les traits spatialement explicites. L'application de ce cadre à l'expérience a révélé que le réchauffement expérimental modifie les signaux et/ou l'importance relative des filtres d'assemblage des communautés abiotiques et biotiques. Dans le quatrième chapitre, je me suis concentrée sur les caractéristiques des plantes aériennes et souterraines et sur les relations entre les plantes et le sol. J'ai constaté que les communautés réchauffées ont modifié leurs compromis fonctionnels en faveur de stratégies plus conservatrices et d'externalisation, et que ces changements ont affecté les fonctions de l'écosystème telles que la productivité et le fonctionnement microbien.

Dans l'ensemble, ma thèse met en évidence la variabilité de la synchronisation et des formes fonctionnelles des réponses au changement climatique à différentes échelles biologiques. Parfois, cette désynchronisation a conduit à des pertes de fonctionnalité, comme pour les interactions plantes-pollinisateurs ou l'exploitation des interactions plantes-mycorhizes. Bien que partiellement rapides et fortes, de nombreuses réponses au réchauffement climatique ne sont pas suffisantes pour une acclimatation complète. Cela signifie que les organismes peuvent vivre dans un nouveau climat mais ne sont pas compétitifs par rapport aux organismes mieux adaptés. J'en conclus que les prairies de montagne risquent de devenir de plus en plus homogènes, perdant les caractéristiques distinctives de l'environnement élevé et rude à tous les niveaux d'organismes. Ce phénomène n'est pas tant directement dû au réchauffement, mais plutôt aux effets indirects d'un paysage modifié des interactions biotiques.

Introduction

1. Revealing the patterns of biodiversity in the midst of a change

It all starts with a mountain — and “men”’s desire to enveil Nature as Pierre Hadot says. It amazes me that as humanity, we carry with us both an ambition that is hoping to say one day on a summit “*a place higher than all others that men had reached on the backs of the mountains*” and compassion that is trying to understand other life forms’ becoming. This ambition and compassion were somehow hand in hand on a summit in Ecuador in 1802 (Falk et al., 2022). Alexander Humboldt and Aimé Bonpland were climbing Chimborazo and mapping the geography of plants. Were Alexander Humdolt and Aimé Bonpland the first ones ever to ask how the environment shapes where plants happen to be on vast landscapes? They are certainly the ones who helped us to ask this question a thousand more times after them. They were the ones who mapped the geography of plants for the first time along a gradient of climate and soil (von Humboldt, 1807). More precisely, they showed how the air temperature changes with elevation and how the plants’ presence is dependent on that. They even further emphasized how other organisms’ habitats were shaped by the vegetation, long before the first use of the word “ecosystem”. Since then, we have been monitoring biodiversity and ecosystems and trying to theorize the relationship between species and environment.

Only a century later came the first conceptual development on the dependence of species’ distributions on various environmental factors, the *niche*. (Grinnell, 1917) not only precisely drew the borders of the various species’ distributions, he also indicated what is possibly driving their range based on their physiologies or morphologies. He emphasized that it is hard to identify one single factor for all species, yet temperature seems to be common to most. In a way, he was already defining the thermal niche of various species. However, even temperature itself is a complex factor and it was not clear if the summer or winter or annual mean or max temperatures drive species distributions. Grinnell (1917) also mentioned repeatedly the importance of food for species. He opened the door to understanding the role of species interactions in their distribution. Later, Elton (1927) fully established the importance of species interactions, notably food chains, for species’ niches and thus their distributions. From there on, Grinnellian and Eltonian niches were used to define the suitable environmental conditions at large spatial scales and biotic interactions at local spatial scales, respectively (Soberón, 2007). It was (Hutchinson, 1957) who set the definitions clearly as fundamental and realized niche: the

former defining the environmental conditions that are allowed by the species' physiology and the latter what is restricted (thus observed) after species' interactions, for example in the case of competition for the same resources. Pulliam (2000) clarified this followingly: "Some of the confusion over the niche concept can be clarified by keeping in mind that all species not only respond to variation in the environment, but they also all change the environments in which they occur. Thus when two or more species occur together they change both their own and one another's environment. (p. 351)" By the start of the 21st century, we knew that species were not only dependent on their environment but also on each other. Thus, **changes in the niche of one species would mean changes in the others' too**. The complexity in ecological theory was very quickly augmented once we started to take into account both the environment and multispecies interactions.

During the 1900s, while the above-mentioned ecologists were trying to set a framework around the concept of niche, species' niches were already changing. Scientists, especially from northern Europe, started to document range shifts in terrestrial biodiversity due to warmer summers (Parmesan, 2006). However, they were cautious in interpretations as it was not clear if the changes in climate were just stochasticity or a trend. With the first scientific assessment of global climate change, it was declared that Earth's climate was experiencing a human-caused change (IPCC, 1990). Now, we know that human-caused global surface temperature increase from 1850-1900 to 2010-2019 is between 0.8-1.3°C (IPCC, 2022). European land temperatures have increased even faster over the same period by 1.94-1.99°C (*Global and European Temperatures*, n.d.). **Climate warming is additionally tightly linked to increase in ecological drought** — as called by IPCC (2022) to identify abnormal soil moisture deficit that is different from precipitation and streamflow deficits — especially in Western and Central Europe as a result of decreased precipitation yet an increase in evapotranspiration of plants.

As to biodiversity, the consensus came a decade later after the first scientific assessment of climate change: Earth's biodiversity was changing due to human-caused climate warming (Parmesan & Yohe, 2003). Since then, scientists all around the world have been putting a tremendous effort into recording, understanding, and forecasting the effects of climate warming on biodiversity and ecosystems. It is clear now with the (IPBES, 2019) report that current climate warming is threatening worldwide biodiversity and ecosystems. Climate warming is changing the ecosystem structures, species' ranges and their timing of life cycle (i.e. phenology, Box 1) (IPCC, 2022). However, the race between climate warming and ecologists continues:

While the ecologists try to reveal the patterns of biodiversity under warming and drought in order to identify rescue options, climate change is accelerating. Under different scenarios of greenhouse gas emissions, it is projected that by the end of the century the global surface temperature rise compared to 1850-1900 will reach between 1.4-4.4°C (i.e. according to the best estimates of the models (IPCC, 2022)). Despite the unprecedented effort of ecologists, **the projections on biodiversity and ecosystems remain less clear** (Urban et al., 2016, 2021), **partly because we still have knowledge gaps on the processes behind patterns of biodiversity and their drivers.**

2. Plants under climate warming and drought

2.1. Complexities of biological organizations

Plants are at the heart of climate warming's threats. Not only do they make up nearly 20% of the known terrestrial biodiversity in terms of species richness, but they are also the scenesetters of ecosystems as primary producers (Mora et al., 2011). Thus, any changes in the plant kingdom from the timing of plant growth to species extinctions can cascade directly to the ecosystems and threaten the well-being of their functions and dependent species. In fact, plants are organized at different biological scales from individuals to rich communities (Figure 1) and the response of plants to climate warming and drought is thus scale-dependent. This makes revealing the effect of climate warming on plants a complex question in climate change ecology.

Different scales of biological organization of plants may acclimate to climate warming and drought with different timing and magnitude (Figure 1&2). For example, one of the first recorded responses to warming was earlier flowering and tree budburst in multiple studies while only a couple of studies were showing upward/northward range shifts of plants at that time (Parmesan & Yohe, 2003). To some extent, phenology is easier to observe and measure than range shifts, however we also expect that the **first response that individuals give is acclimating their life cycle to the new environmental conditions because metabolic pathways of phenology are already tightly linked to environmental triggers that allow plant survival in variable environments** (Nicotra et al., 2010). Even though advances in the calendar dates of spring events remained the dominant responses under warming, the magnitude of change depends on the period, species and region (Parmesan & Hanley, 2015; Piao et al., 2019). There were also no generalizable patterns of changes in distributions and abundances in rich plant communities and effects were sometimes weak (Parmesan & Hanley, 2015). On one hand, this could be due

to plants that are responding to warming and drought in different directions. For example, some authors show uphill range shifts due to temperature and others show downhill range shifts due to water shortage (Crimmins et al., 2011). On the other hand, at the community level, complex species' interactions are in interplay at the same trophic or multitrophic levels which can buffer or exacerbate the effects of warming on species. **Hence, we first need to disentangle the processes that are in play at each biological scale, second assess separately their responses to warming and drought and third investigate the role of feedbacks through species interactions.**

In order to disentangle the processes at each biological scale and assess how they cascade to each other, we can imagine the following scenario (Figure 1): warming and drought alter individuals' and populations' phenology and morpho-physiological traits (Box 1). If these responses allow acclimation, individuals' and populations' can survive and reproduce, even sometimes increasing their abundances. As much as these processes happen at individual/population level, they are constrained by species level capacities of plasticity. Also a focus at species level can allow us to reduce the complexity in trait and demography measurements. Not only do plants' abiotic conditions change, but they also acquire new neighbors. As interactions between new species are formed, plant communities as a whole are restructured. Persisting viable strategies, for example, selection of warm and drought adapted functional traits, define also the new dominant strategies of the communities. Complete restructuring of communities in return influences the ecosystem functions, such as above-and below-ground productivity and nutrient fluxes (Pugnaire et al., 2019).

Nevertheless, the cascading effects may be more complex than that (Fig. 1). Firstly, they may not be following one after the other as depicted above: Changes in smaller scales may directly affect the largest scale. For example, changes in species' (Ganjurjav et al., 2021) and communities' greening start (Wang et al., 2020) can directly regulate their biomass which alters ecosystem's productivity (Li et al., 2021). Secondly, changes at different scales can feedback each other. For example, growth period mismatches between different grasses and shrubs that had longer growing seasons enhanced the shrub growth and their patchiness where suitable soil conditions lengthen further the shrubs' growth period (Fan et al., 2019).

Complexities within and across scales make predictions of warming effects on biodiversity and ecosystem functioning challenging, especially under future climate warming and even more if

we are not only interested in final states but the temporal dynamics that may already last several decades. Cascading effects and feedback between scales can slow down or speed up the responses of plants to warming. Thus, to understand how warming is altering plant biodiversity, **we need to assess the timing, form, and magnitude of responses to warming and drought at each biological scale.**

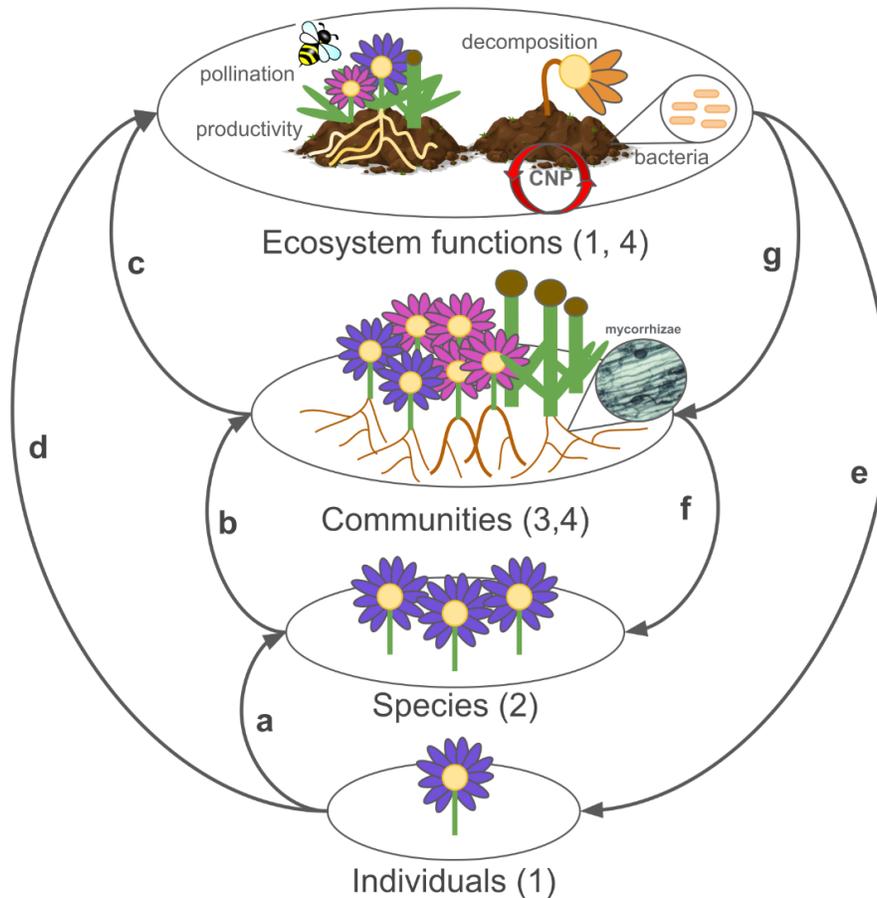


Figure 1: Individuals, species, species-rich communities and ecosystems form different scales of biological organizations in plants. Warming effects can upscale linearly from a smaller to the next larger scale (a-c) or can jump over intermediate scales (d) or can feedback to smaller scales either linearly (g, f) or jumping over intermediate scales (g). Example for these different cascading effects are a) Individuals' phenological plasticity affects individual demographic success and thus species abundances . b) These changing species abundances affect functional community composition. c) Dominant community level functional strategies and keystone species drive ecosystem functions. d) Individuals' phenology directly influences ecosystem functions, e.g. productivity and pollination. e) Multitrophic interactions, notably the

number of pollinators, can give feedback to individuals' phenology. f) Community assembly processes, notably biotic interactions, influences species demographic success. g) Changes in functions affect communities, e.g. more competition on fertile soils. In each chapter of my thesis, I focus on one of these biological organizations (i.e. numbers next to scales indicate the chapters focussing on this level of organization) and how they upscale to each other.

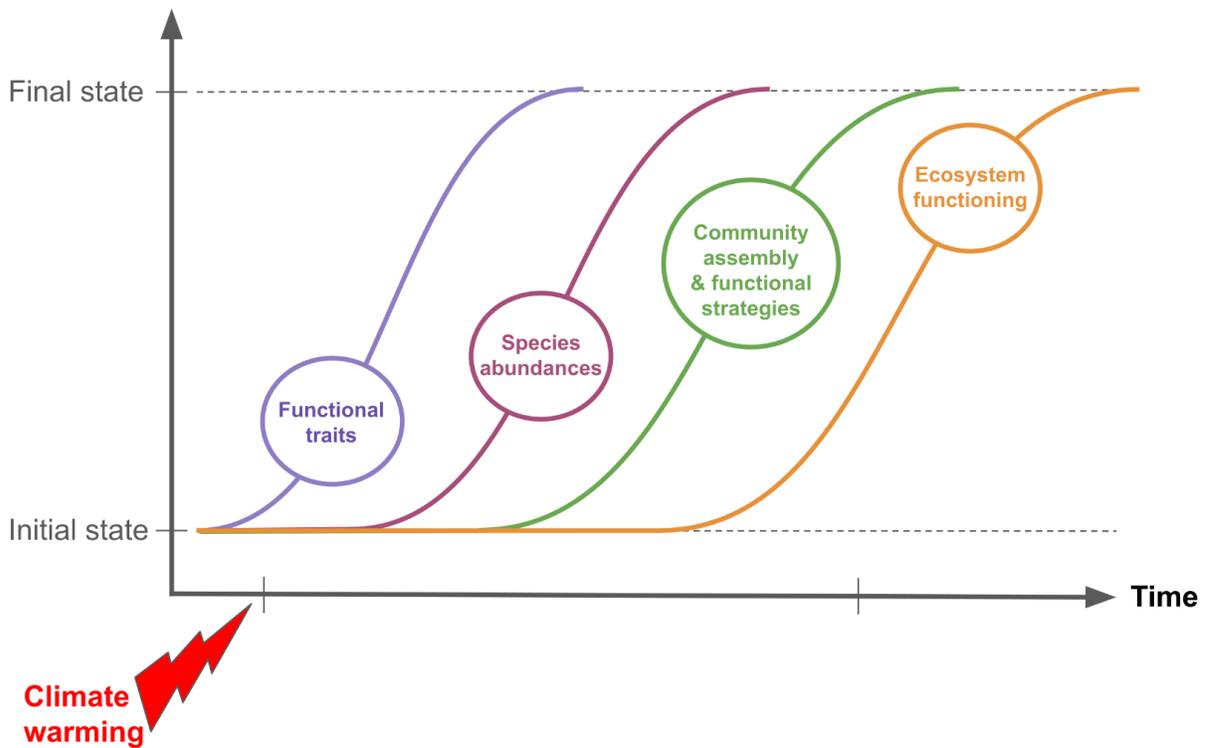


Figure 2: Different scales of biological organization of plants may acclimate to climate warming and drought with different timing due to cascading effects and feedbacks between them (Figure 1). For example, communities at higher biological scales may take longer to react because they are dependent on the responses at lower biological scales. Cascading effects on ecosystem functions would take the longest if cascades would be linear and there would be no direct climate change effects (in reality these two assumptions are improbable to hold).

My aim in the following sections is to i) draw the limits of these scales within the scope of my thesis, ii) explain the processes in play within each scale, iii) provide examples of different measures that we can take in order to understand the drivers at each scale, iv) illustrate how different biological scales upscale and feedback each other and finally, v) review what is know so far about warming effects at the different scales.

Box 1: Functional traits as a toolbox for community and functional ecology

Plant functional traits are morpho-physio-phenological characteristics of species that influence the fitness of an organism via their effects on growth, reproduction and survival (Violle et al., 2007). These traits are usually easy to measure plant above-and below-ground phenology and structures. Functional traits are at the crossroads of community ecology and ecosystem functioning as i) response traits determine species responses to abiotic and biotic conditions and thus co-distribution patterns and ii) effect traits determine the effect of species and communities on ecosystem functioning (Lavorel & Garnier, 2002). Hence, at one hand, we use functional traits to i) understand the responses in the timing and performance of plant growth and reproduction to environmental changes (Chapter 1), ii) the processes behind community assembly through patterns of functional diversity (Chapter 3) (McGill et al., 2006) and iii) functional trade-offs along environmental gradients (Chapter 4). On the other hand, we use them to understand ecosystem responses to changes in abiotic and biotic conditions (Chapter 4).

1. Phenological functional traits

Phenological traits are the measures of the timing and duration of the individuals' plant growth and reproduction. We can have two perspectives of defining the phenological phases of plants: plant growth and life stages. First, we can investigate above-ground plant growth as the greening dynamics: first appearance of leaves (greening), maximum plant growth, start of leaf browning and end of plant growth. In a similar way, we can talk about the phenology of root growth from the start of root growth until the end which can be asynchronous to above-ground plant growth (Schwieger et al., 2019). Having the perspective of the plant growth allows us to measure the greening dynamics at the above-ground easily, especially at community level, for example through Normalized Difference Vegetation Index (NDVI) which is a ratio of the difference between near infrared radiation and visible red and their sum. By tracking the NDVI of communities along a whole growing season, we can construct an area under the NDVI curve, which is a good proxy of photosynthetic activity and thus, above-ground productivity (Myneni & Williams, 1994). Second, we can investigate the plants' life stages as follows: first appearance of leaves (greening), flowers (flowering), and seeds (fruiting) and finally, the dissemination of the

plant above-ground structures. Having a perspective of life stages, especially at species level, can allow us to measure the reproductive dynamics of the plants and even link it to pollination, for example through the flowering stage. For both ways of defining the phenological periods, we can measure both timing (start, peak and end) and duration of phenological events. In addition, we can assess how many individuals happen to be in a phenophase. In my thesis, I measure phenological responses to warming and drought along different stages of plant growth and plant life at community and species level, respectively (Figure 3, blue boxes).

2. Morpho-physiological functional traits

At the above- and below-ground, species and communities show variation in their functional strategies due to functional trade-offs (Bergmann et al., 2020; Díaz et al., 2016; Reich, 2014; Weigelt et al., 2021; Wright et al., 2004). We can name three principal functional trade-offs at the above and below-ground that are orthogonal to each other: plant size, fast vs. slow, do-it-yourself vs. outsourcing (Bergmann et al., 2020; Díaz et al., 2016; Weigelt et al., 2021). Along the **plant size** (tall or short) dimension species and communities differ in their plant growth potential. Along the **fast vs. slow** trade-off, species and communities with low leaf mass per area (LMA), low root tissue density (RTD), high leaf nitrogen content (LNC) and high root nitrogen content (RNC) are exploitative with a fast growth strategy. They tend to have high respiration and photosynthesis rates per unit mass, thus they exploit the light better through their larger light-intercepting leaves and higher investment of nitrogen in photosynthetic proteins (Onoda et al., 2017). Yet, they cannot sustain these faster photosynthetic rates for a long time and thus, have shorter life cycles. Species and communities with low root tissue density (RTD) and high root nitrogen content (RNC) expand the roots faster to exploit the nutrients better, however they are short-lived because the roots are less resistant to stress (Freschet et al., 2021) Conversely, conservative species are slow and steady and thus more resilient. Along the **do-it-yourself vs. outsourcing** trade-off, plants either explore water and nutrients themselves by increasing their specific root length (SRL) or invest carbon in their fungi partners and host them in their wider roots (i.e. wider root diameter). In fact, mycorrhiza helps enhance the stomatal conductance and water use efficiency in drought conditions (Augé et al., 2015). Here, it is also important to acknowledge that there is some contradicting evidence on to what extent RTD is orthogonal to the SRL and root diameter (Carmona et al., 2021; de Vries et al., 2016). In my thesis, I focus on above-ground traits (Figure 3, green boxes) to i) understand the species demographic success under warming (Chapter 2) and ii) reveal signals of community assembly mechanisms through their diversity patterns (Chapter 3). I further focus both on

above- and below-ground traits (Figure 3, at community level in order to understand the shifts in functional strategies and how they cascade to ecosystem functioning.

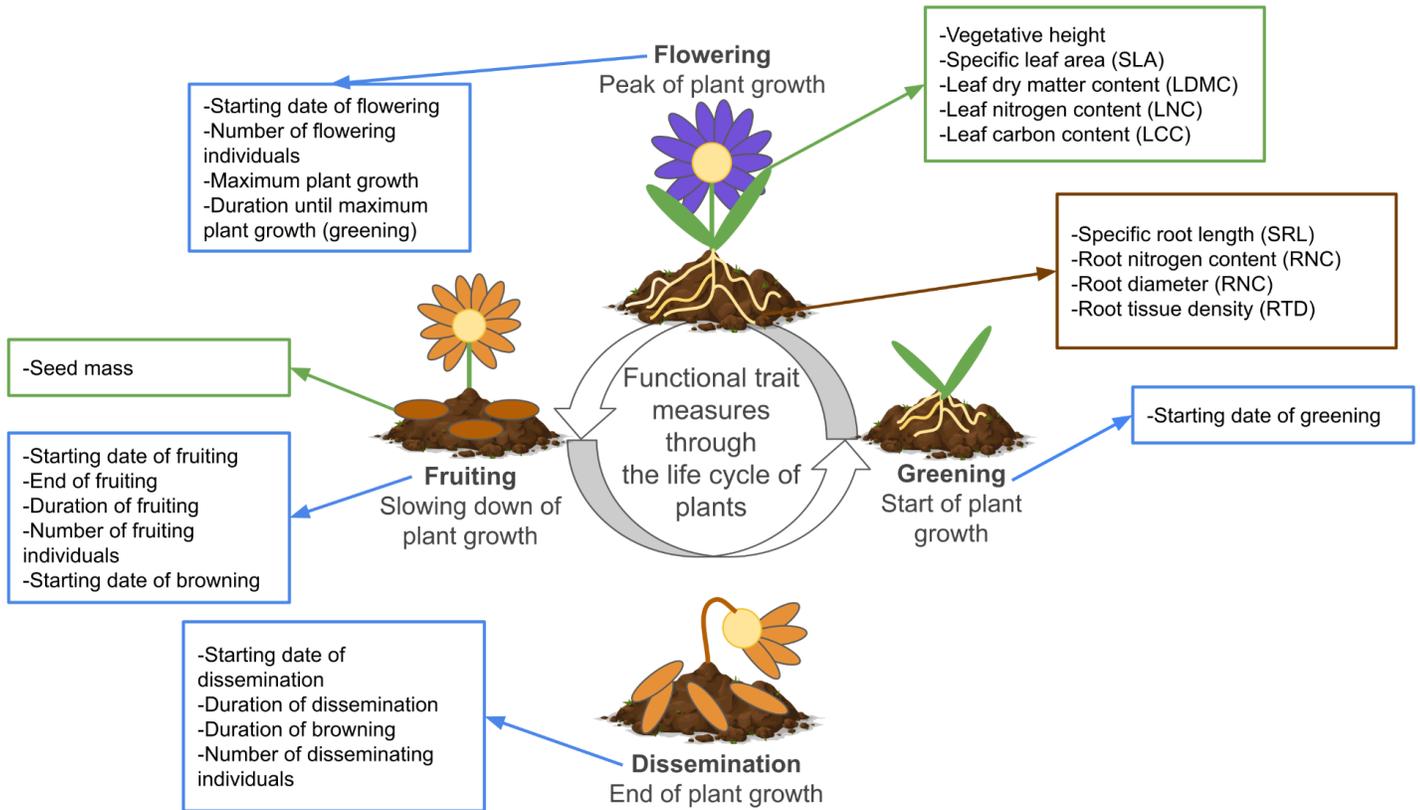


Figure 3: Measuring the phenological (blue boxes) and morpho-physiological functional traits at the above-(green boxes) and below-ground (brown boxes) along the different stages of plant life and growth. All these functional traits served as a toolbox in my thesis in order to understand species and communities' response to warming and drought.

2.2. Individual and population level responses

Reproduction, mortality and migration are the three most fundamental demographic processes underlying population dynamics. All three happen at the individual or population level thus making this scale key to understanding plants' responses to warming and drought. There are three possible ways of individuals and their populations to respond to increasing temperatures

(Figure 6A): They (i) acclimate (or adapt via evolution; but this is out of scope in my thesis) their phenological and morpho-physiological functional traits (Box 1) so that reproduction and survival exceed mortality, (ii) die or (iii) move, which for plants means that they disperse their seeds to more suitable sites. However, tracking seeds and measuring plants demography and acclimation in traits are very costly in species-rich communities. As these processes happen at the individual and population level (i.e. with intraspecific variability), I will detail them under this section even so I partly used species level information (i.e. ignoring intraspecific variability, e.g. in functional traits) in my thesis.

2.2.1 Acclimation: To what extent functional traits are plastic?

Plants can survive climate change by adapting to the new conditions. However, climate change is rapid and may exceed the rate of adaptation by evolutionary processes in long-lived plants. Therefore survival may depend on phenotypic plasticity in morphology and physiology (Fox et al., 2019; Nicotra et al., 2010). Phenotypic plasticity describes the potential variability in the expression of phenotypes of the same genotype in dependence on environmental conditions and it may or may not be permanent throughout an individual's lifespan. Phenotypic plasticity can help an individual or a population to acclimate to changing abiotic conditions. When acclimation is triggered following an environmental cue, it is a rapid mechanism for the survival of a single individual that can result in plastic rescue (Snell-Rood et al., 2018) and can assure a long-term demographic success that can be “beyond just buying time” (Fox et al., 2019). For example, plasticity in leaf traits can allow populations to shift their leaf traits in response to warming in order to better acclimate to the new conditions (Henn et al., 2018). Interestingly, it is not necessarily the traits with the most intraspecific variability that are the most plastic (Henn et al., 2018). **Thus, to what extent are functional traits (Box 1) plastic?**

A meta-analysis of reciprocal transplant experiments on various life history, morphological and physiological traits showed that not all studied traits were showing plastic responses yet **phenological life history traits (e.g. flowering day or performance) were the most plastic traits when abiotic conditions changed** (Palacio-López et al., 2015). Another global scale meta analysis recently found that of above- and below-ground plant traits related to morphology, physiology, allocation, size and performance were showing plastic responses under climatic or non-climatic (e.g. competition, light and nutrients) treatments, and non-climatic treatments caused even stronger plastic responses (Stotz et al., 2021). Among climatic treatments, temperature was leading to the strongest plasticity response after watering. Plant height, SLA and above- and below-ground plant growth were among the most plastic traits. Additionally, they

provided evidence on the drivers and limits of global phenotypic plasticity. They found that mean annual temperature and precipitation were good predictors of plasticity in plant traits and physiological plasticity decreased in colder and drier conditions. They concluded that species from stressful conditions may not be able to show plastic responses under climate warming, for example in the case of alpine plants. Moreover, it seems like resource-conservative species — despite their tolerance to stress — show less phenotypic plasticity under changing conditions (Stotz et al., 2022).

2.2.2. Acclimation of phenology to warming & drought

One of the main drivers of phenology is temperature (Piao et al., 2019). On one hand, accumulated temperature (e.g. growing degree days) allows the advancement of plant growth from greening to reproduction. For example, insufficient accumulated temperature prevents the fruit maturation which apparently sets the limits of plant' northern ranges (Chuine, 2010). On the other hand, chilling is necessary to break the dormancy and lack of it, limits flower formation or leaf unfolding which explains the plant limits at the southern range (Chuine, 2010). In fact, plants enter into dormancy in early spring and autumn under low temperature and short photoperiod which inhibits their plant growth and chilling is required to break it (Flynn & Wolkovich, 2018). Once the dormancy is broken, with increasing temperatures and photoperiod, plant growth advances. A certain amount of temperature is required to further initiate the reproductive stage of plant life. In the mountains, snow cover dynamics also are in interplay with temperature, especially the soil temperature. Earlier snowmelt might expose plants to freezing temperatures too early in the season. As an escape mechanism from such an early exposure to freezing, plants also exhibit photoperiod control of spring phenology (Körner, 2003). Photoperiod also controls for browning: decreasing photoperiod as the growing season advances gives the cues for senescence (Piao et al., 2019; Serrano-Bueno et al., 2021). Start of browning is also tightly linked to soil moisture: reduced soil moisture can induce earlier browning (Estiarte & Peñuelas, 2015; Wang et al., 2020).

Changes in phenology is one of the most well documented consequences of climate warming (Parmesan, 2006; Parmesan & Yohe, 2003; Piao et al., 2019). In fact, this is not very surprising: On one hand, since the neolithic times humans have learned to track the phenology of plants in order to adjust their agricultural practices. On the other hand, plasticity in phenology can be one of the first responses to be triggered following an environmental cue because as

shown above plants are following already very tightly the environmental cues (Nicoltra et al., 2010).

One of the most dominant and consistent plastic responses of phenology to climate warming is the earlier spring phenology (Piao et al., 2019), flowering phenology in particular (Parmesan & Hanley, 2015) based on calendar dates. For example, the rate of advancement of leaf unfolding in Europe is 3 days/decade (1969–1998) in one study and 4.2 days/decade (1982–2011) in another that look at different three species and time periods (Piao et al., 2019). In the US and China, rates are lower (with 0.9 days/decade) and higher (5.5 days/decade), respectively.

As for autumn phenology, it is the “neglected” season (Gallinat et al., 2015). Yet, there is accumulating evidence on its delay as a global pattern (Parmesan & Hanley, 2015). Piao et al. (2019) notes from worldwide phenological observatories that the average delay rate of leaf coloring is 0.1 days/decade in Europe and 2.9 days/decade in China between 1982–2011. As we can see, the magnitude of phenological plasticity is dependent on the region, species and period. It is important to note that the advancement rate is not the same along this period with a decreasing rate after 2000. Even though Piao et al. (2019) is cautious in providing explanations, it is possible that accelerated warming might be catching up with the limits of phenological plasticity. Hence, it is still crucial to investigate the impact of future climate warming on phenology.

As for below-ground phenology, it is the “neglected” compartment (Radville et al., 2016). Above-mentioned drivers of plant growth phenology at the above-ground are also important for the below-ground plant-growth. Yet, interestingly, there is an observed asynchrony between above- and below-ground phenology (Schwieger et al., 2019). Root growth phenology seems to be earlier, longer and highly variable among species compared to phenology of the above-ground plant growth (McCormack et al., 2015; Radville & Eissenstat, 2016; Steinaker et al., 2009). (Schwieger et al., 2019) suggested that these differences can be due to i) root phenology being more dependent on the soil temperature compared to leaf phenology that is more dependent on the air temperature, ii) roots' dependence on leaves for carbon allocation that is also driven by the temperature. The asynchrony between above- and below-ground plant growth phenology is important to consider in the context of climate warming, especially if we want to understand how biomass is altered at the both compartments. Yet, studies on root growth phenology are limited with some evidence on earlier root growth (Sullivan & Welker,

2005). (Radville et al., 2016) further hypothesized that root growth phenology will be mainly driven by the moisture considering the drought-induced root growth cessation.

2.2.3. Acclimation of morpho-physiological functional traits to warming & drought

The three main axes of functional trade-offs at the above and below-ground compartments are (see also Box 1): plant size, fast vs. slow economic spectrum and do-it-yourself vs. outsourcing strategies. Along a stress gradient, different functional strategies are dominant at the stressful and benign end of the gradient. In stressful conditions, we would in general expect that i) plants are limited in plant growth and thus are rather small, ii) they need to be resilient and conservative and are thus slow growing species, iii) they invest in fungi associations to withstand stressful conditions and are thus outsourcing (Table 1). However, defining stress for plants is a multidimensional problem and an increase in one yet a decrease in another stress factor could lead to contrasting results (Myers-Smith et al., 2019). Hence, we need to examine the drivers of morpho-physiological functional traits and possible plastic responses for the stress gradients that seem particularly relevant under climate change.

In the context of my thesis, I consider three stress gradients that could explain different functional strategies in plants: temperature, moisture and soil nutrient gradients and I summarize these responses in Table 1. The first two are direct changes in abiotic conditions due to climate change. Changes in soil nutrients are triggered both by direct effects of climate change and also indirectly through changes in plants (Figure 1 & 5). Interestingly, increased temperature and decreased soil moisture and soil nutrients under climate change have potentially opposing effects on functional traits (Tabel 1). Hence, responses to climate change depend on if the water is a limiting factor in the ecosystem (Myers-Smith et al., 2019) and if the soil nutrients change with direct and indirect effects under warming and drought.

Table 1: Plant functional trade-offs along temperature, moisture and soil nutrient stress gradients with example references. Arrows indicate the increasing or decreasing trend along with changes that are expected to be seen under climate change. Blue arrows show hypothesized trends with an overall consensus in existing studies. Red arrows show hypothesized trends but with more contrasting evidence. (VH: Vegetative height, LMA: leaf mass per area, LNC: leaf nitrogen content, RNC: root nitrogen content, RTD: Root tissue density, SRL: specific root length, RD: root diameter)

	Increasing temperature	Reference	Decreasing moisture	Reference	Increasing soil nutrients	Reference
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Plant size	VH		(Crawford et al., 2012; Joswig et al., 2022; Kempainen et al., 2021; Romero-Montepaone et al., 2021)		(Blumenthal et al., 2020; Joswig et al., 2022; Kempainen et al., 2021; Onoda et al., 2017)		(Freschet et al., 2018)
		Tall plants can maintain the carbon balance between increased transpiration and photosynthesis and they can cool down under high temperatures.	Under drought stress, short plants can invest more carbon into leaves (rather than height) to maintain turgor pressure. Also investing more to root depth than height might be more advantageous for water search in soil.	Tall plants can exploit better the nutrient rich soils.			
Fast-slow trade-off	LMA		(Joswig et al., 2022; Kempainen et al., 2021; Simpson et al., 2016) but see (Wright et al., 2005)		(Blumenthal et al., 2020; Joswig et al., 2022; Kempainen et al., 2021; Onoda et al., 2017; Simpson et al., 2016)		(Joswig et al., 2022; Martinez-Almoyna et al., 2020; Simpson et al., 2016; Weil et al., 2021)
		Plants with low LMA have low carbon cost per leaf area and thus can maintain higher photosynthesis and growth rate when the conditions are favorable.	Plants with high LMA can invest in thicker cell walls to maintain turgor pressure and increase leaf resilience as a drought tolerance strategy.	Plants with low LMA can maintain faster growth and thus higher nutrient uptake.			
	LNC		(Joswig et al., 2022; Kempainen et al., 2021; Wright et al., 2005)		(Joswig et al., 2022; Kempainen et al., 2021; Onoda et al., 2017) but see (Wright et al., 2005)		(Joswig et al., 2022; Martinez-Almoyna et al., 2020; Weil et al., 2021)
		Plants that invest more in photosynthetic enzymes (high N content) can maintain higher photosynthetic rates.	Cell walls accommodate less N than photosynthetic enzymes. Under drought, plants that have thicker cell walls (high LMA) have less LNC.	Plants in nutrient rich soils can maintain higher N uptake and metabolize more N in the leaves.			
	RNC		(Freschet et al., 2021; Scheurwater et al., 2002) but see (Laughlin et al., 2021)		(Freschet et al., 2021; Scheurwater et al., 2002) but see (Laughlin et al., 2021)		(Freschet et al., 2018, 2021)
		Plants that maintain faster growth rate can uptake higher amounts of N (nitrate) from soil and metabolize it directly in the roots. However, for graminoids RNC might not increase	Plants with a drought tolerance strategy maintain slower growth rates which might decrease the N uptake and reduction.	Plants where the soils are rich in plant- available N can uptake better.			

		with faster nutrient uptake because nitrate is also metabolized in shoots.					
	RTD		(Simpson et al., 2016) But see (Laughlin et al., 2021).		But see (Laughlin et al., 2021)		(Simpson et al., 2016)
		In the absence of freezing damage to cells, plants can maintain a faster growth rate without investing in root tissues.	Plants with high RTD can resist cellular damage under drought.	Plants can maintain faster growth in nutrient rich soils and thus invest less in root tissues for their persistence.			
Do-it-yourself vs. outsourcing trade-off	SRL		But see (Laughlin et al., 2021; Simpson et al., 2016)		(Augé et al., 2015; Laughlin et al., 2021; Simpson et al., 2016)		(Simpson et al., 2016) but see (Freschet et al., 2021)
		Plants invest more in root length per mass because under benign conditions they do not need to invest carbon in collaborative interactions but a do-it-yourself strategy is more beneficial.		Plants invest less in root length but more in diameter to accommodate more fungi in the roots to enhance stomatal conductance and water use efficiency.		Plants invest less in root length but more in diameter to accommodate more fungi in the roots to better exploit the nutrient rich soils.	
	RD		But see (Laughlin et al., 2021)		But see (Laughlin et al., 2021)		
		Plants invest less in root diameter because under benign conditions they do not need to invest carbon in collaborative interactions but a do-it-yourself strategy is more beneficial.		Plants invest more in diameter to accommodate more fungi in the roots to enhance stomatal conductance and water use efficiency.		Plants invest more in diameter to accommodate more fungi in the roots to better exploit the nutrient rich soils.	

In summary, in response to warming and drought plants are expected to acclimate in their morpho-physio-phenological traits. **Changes in phenological traits are mostly affected by temperature and may be one of the first responses to be triggered. Changes in**

morpho-phenological traits require a thorough investigation as warming and drying in summer can result in responses in traits towards opposing directions.

2.3. Species level responses

2.3.1 Ignoring intraspecific variability

Even though we know that individual trait values may deviate from species averages, for example due to phenotypic plasticity, we often measure the changes in functional traits at species level. Firstly, this is due to the way we used to think in ecology in terms of species rather than individuals as within species diversity was for long rather a neglected notion and only received increasing interest in the last two decades (Westerband et al., 2021). Secondly, it is due to the difficulty in tracking individuals, especially in the plant kingdom. As soon as measuring intraspecific trait variability came into focus, it was revealed that variability within species can be comparable to variability between species (Messier et al., 2010) and that it is driven by abiotic and biotic gradients (Westerband et al., 2021). However, intraspecific variability also depends on the focal traits, species and spatial scales (Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Albert, Thuiller, Yoccoz, Soudant, et al., 2010) (Kuppler et al., 2020). First studies neglected the belowground department but it was recently shown that results hold for root traits: (Weemstra et al., 2021) and (Defrenne et al., 2019; Kumordzi et al., 2019; Weemstra et al., 2021) found that intraspecific trait variation in root traits depends on species identity. **Since general patterns across species and environments still remain relatively obscure in intraspecific trait variation, we may hypothesize that species level traits are sufficient proxies for identifying patterns along stress gradients.** In fact, there are various open source databases that are available per ecosystem of interest that could help us to capture well the functional traits of a species in a certain habitat (Bjorkman, Myers-Smith, Elmendorf, Normand, Zamin, et al., 2018; Kattge et al., 2020). For example, in arctic tundra, they found that trait-temperature relationship had the same direction (i.e. Table 1) when measured interspecifically (i.e. through abundance weighted mean) or intraspecifically (Myers-Smith et al., 2019).

2.3.2 Winner and loser species under climate change

Failure of acclimation in functional traits can also be observed at species level. Increased mortality at individual level drives species to extinction or successful migration of individuals results in colonizing species. In fact, It has always been predicted that increased temperature and drought will eventually reach the physiological limits of plants in some regions and the ones

that will not be able to “migrate” will become extinct (Harrison, 2020). However, observations are not always in line with this hypothesis. It seems like the global plant biodiversity decline is less than 0.1 % and conveys a lot of uncertainty both in the numbers and the causes (i.e. the causes are not always attributable to climate warming) (Vellend et al., 2017). At a local scale, studies reported both decreasing and increasing species diversity under climate change (Vellend et al., 2017). This is probably because the starting abiotic conditions are important. For example, it is projected that in arctic and temperate habitats species richness is likely to increase and in (sub)tropical regions rather to decrease with climate change (Sommer et al., 2010). Vellend et al. (2017) reviewed results from experimental warming (1-2°C) and found region-dependent patterns. For example, when the warming effect was coupled also with drought the species richness was reduced in a shrubland (Peñuelas et al., 2007). However, in tundra ecosystems there was no change at all in species richness after 20 years of experimental warming (Elmendorf et al., 2012). **Overall, it is not clear if this net zero change is an outcome of the balance between extinctions and colonizations or stability in species demographics.**

Largely stable patterns in species richness under climate warming do not mean that species do not suffer (or benefit) from climate warming. In fact, before species extinctions or migration, we may observe changes in species abundances under warming. **More importantly, monitoring species abundance changes may help us to catch early warning signals of possible local extinctions or expansions and enable better forecasts of demography under future climate warming** (Ehrlén & Morris, 2015). Yet, unfortunately, such studies are scarce or limited to certain regions for species rich communities. For example, in mountains, (Rumpf et al., 2018) found that winners overall outnumbered losers but that losers were overrepresented among high-elevation species. Or, in tundra ecosystems, increased abundance of shrubs and graminoids is an observed phenomenon (Myers-Smith et al., 2019). Whereas in alpine ecosystems, graminoids' abundance decreased (Ganjurjav et al., 2016) or increased (Hu et al., 2021; Liu et al., 2018) but decreased for forbs (Ganjurjav et al., 2021; Hu et al., 2021; Liu et al., 2018). However, it is not clear in these studies if there is a balance between the winners and losers in terms of species identities or magnitude of changes.

In summary, measuring the changes in functional traits at species level can help us to reveal general patterns in response to warming and drought. In response to acclimation failure, we can determine the extinct species. Moreover, determining the changes in abundances early on can be the early warning signals of such extinction events.

2.4. Community scale responses

Changes in species turnover and relative abundances ultimately restructure plant communities. This has two main consequences (**Figure 6B**): i) species' interactions at local scale re-establish, altering the dominant processes that assemble the communities (Gilman et al., 2010), ii) species with functional traits that are already adapted to the new abiotic and biotic conditions increase in their abundance, while others decrease (Soudzilovskaia et al., 2013) and ultimately shift the dominant functional strategies in the communities (Bjorkman, Myers-Smith, Elmendorf, Normand, Weiher, et al., 2018; Kempainen et al., 2021; Lachaise et al., 2022).

2.4.1. Changes in community assembly processes under warming and drought

2.4.1.1. Filtering framework

The “filtering framework” is the dominant framework to conceptualize the determinants of process behind community assembly from a regional species pool that built in the past through evolution and dispersal barriers ((Keddy, 1992)). These filters can be abiotic constraints and biotic interactions (e.g. competition). Abiotic filters select for species that are adapted to the local environmental conditions. This process forms the local species pool. Species that can also co-exist with the other species are selected from the local species pool in a local community.

Abiotic and biotic filters are expected to leave specific patterns in the functional trait structure of communities (Fig. 1.A.) (Keddy, 1992; McGill et al., 2006). On the one hand, if environmental conditions are very selective they should lead to trait convergence by filtering out the limited number of viable functional strategies (Cornwell et al., 2006). On the other hand, when competition increases with functional similarity (i.e. symmetric competition), we should observe trait divergence as coexisting plants must find distinct functional strategies to reduce competition for limited resources (e.g. water, nutrients) (MacArthur & Levins, 1967). Competition can also lead to convergent traits due to hierarchical competition, when certain functional strategies have the ultimate competitive advantage while others are excluded. Such trait hierarchies are shown to be established especially in the case of competition for light (Kunstler et al., 2012; Mayfield & Levine, 2010).

2.4.1.2. Stress gradient hypothesis for community assembly processes

The relative strength of these filters may change along a stress gradient — for example, from warm, wet and nutrient-rich conditions to cold, dry and nutrient-poor conditions — (Figure 4).

According to the stress gradient hypothesis, at the benign end of the gradient, competitive interactions are prevalent and at the stressful end of the gradient abiotic filters are more severe and biotic interactions can become facilitative (Bertness & Callaway, 1994; Louthan et al., 2015). For example, in stressful conditions, species are already limited in their resource use strategies and photosynthetic activity and they cannot be competitive at the same time (Bricca et al., 2022) or there is less need to be competitive as the stress is already limiting the resources so they can even facilitate each other (Bertness & Callaway, 1994). In fact, the origin of the stress-gradient hypothesis dates back to Darwin (1859):

“When we travel southward and see a species decreasing in numbers, we may feel sure that the cause lies quite as much in other species being favored as in this one being hurt. So it is when we travel northward; but in a somewhat lesser degree, for the number of species of all kinds, and therefore of competitors, decreases northward; hence in going northward, or in ascending a mountain, we far oftener meet with stunted forms, due to the directly injurious action of climate, than we do in proceeding southward or in descending a mountain. When we reach the arctic regions, or snow-capped summits, or absolute deserts, the struggle for life is almost exclusively with the elements (p. 69).”

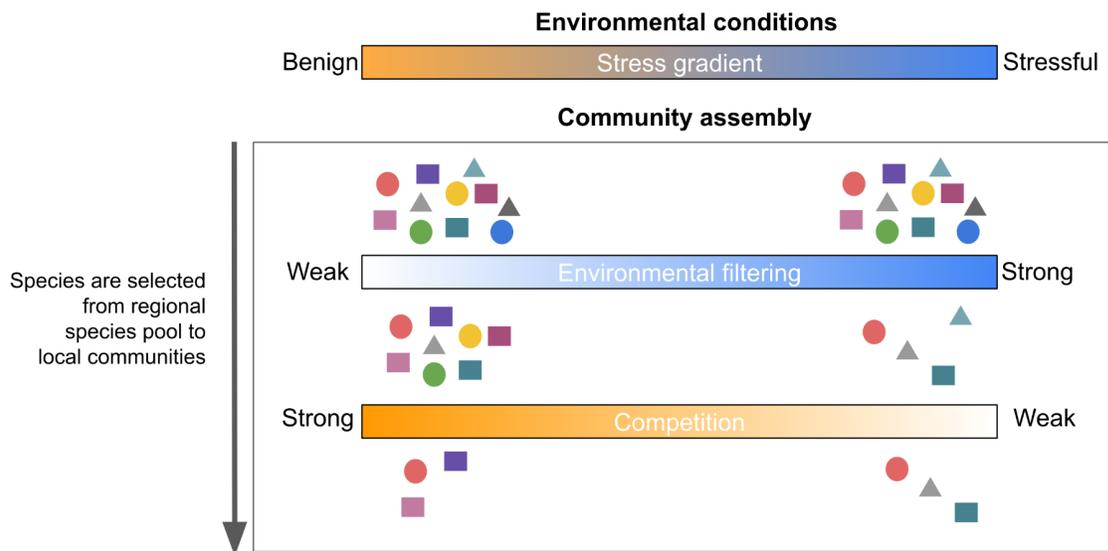


Figure 4: Changes in the strength of different filters that select for species from a regional pool to local communities along a stress gradient. Colored shapes represent different species. For simplicity, here I only chose to show species diversity however note that these filters act also on species abundances.

Combining the filtering framework and the stress gradient hypothesis we expect to find low trait diversity in stressful conditions (cold and dry) and high trait diversity (if competition is symmetric) or low trait diversity (if competition is hierarchic) in benign conditions (warm and wet). For example, a recent continent-wide study found that in European grasslands, highest trait diversity in communities in intermediate to warm temperature conditions (Boonman et al., 2021). There is also evidence suggesting that precipitation can be a more important determinant of functional diversity than temperature in dry grasslands (Moradi & Oldeland, 2019). **However, pinpointing to a specific community assembly process through these patterns is not easy** because i) one pattern can indicate two different processes (e.g. functional convergence can indicate both environmental filtering and hierarchical competition) and/or ii) a dominant process can mask the weaker one (e.g. strong environmental filtering masking symmetric competition). For example, (May et al., 2013) found trait convergence at both ends of a stress gradient in a Mediterranean-desert transition ecosystem with drought at one end and high productivity at the other end. In an alpine tundra ecosystem, (Spasojevic & Suding, 2012) found functional divergence for some traits and convergence for others at the stressful end of the environmental gradient. Besides, they also found increased functional diversity in height and leaf area at the benign end of the gradient, yet it remained unclear if it is a signal of competition for light or a facilitation among alpine plants.

Under warming and drought, we would expect that communities' assembly processes change, however the direction of change will depend on the limiting factors in the system (May et al., 2013; Moradi & Oldeland, 2019). On one hand, warming increases the energy input in the system thus the productivity which might increase competition and release the environmental filter, on the other hand, increased summer drought stress may decrease competition and increase environmental filtering. To disentangle the different hypotheses we require conceptual developments of contrasting (and thus more detailed) diversity patterns under environmental filtering vs. competition.

In summary, climate change restructures taxonomic and functional community composition and the underlying processes of assembly. The challenge of revealing these processes along stress gradients through functional diversity still persists. **Yet, overcoming this challenge is of utmost importance if we wish to understand the changes in community assembly under warming and drought.**

2.4.2. Changes in community level functional strategies under warming and drought

Species with functional traits that are already adapted to the new abiotic and biotic conditions increase in their abundance, while others decrease (Soudzilovskaia et al., 2013) and ultimately drive the dominant functional strategies in the communities (Bjorkman, Myers-Smith, Elmendorf, Normand, Weiher, et al., 2018; Kemppinen et al., 2021; Lachaise et al., 2022). The expected shifts under warming and drought are already detailed in Table 1 and Chapter 4 is dedicated for this question. Here, I would rather elaborate on to what extent the individual and species level functional strategies scale up to the community level (i.e. community weighted mean traits, CWM).

Conceptually, there are several hypotheses supporting the idea that trade offs scale up from individuals and species to communities. The CWM-optimality hypothesis assumes that processes constraining local functional diversity to environmental conditions (i.e. environmental filtering) are predominant and makes the prediction that species are more likely to occur where their trait values are more similar to the community weighted mean traits (Muscarella & Uriarte, 2016). This is consistent with the idea that niche partitioning along resource gradients can be the primary driver of species distributions and community diversity patterns (Pickett & Bazzaz, 1978). However, in addition to environmental filtering there may also be a biotic filter (Bertness & Callaway, 1994). The strength and the type of biotic interactions behind this filter are supposed to depend both on environmental conditions and the species involved (e.g., stress gradient hypothesis). While some biotic interactions (such as hierarchical competition for light) are supposed to result in low trait diversity within local communities, others (such as symmetric competition) are supposed to increase local trait diversity (Münkemüller et al., 2020). When biotic filters and transient dynamics do not only affect trait variance but also kurtosis and skewness (Gross et al., 2021), CWM may not only get less clear due to high variance but may also shift in comparison to CWM expected under an environmental filter only. These conceptual considerations are well reflected in varying results across literature where some studies show that upscaling from individual and species level to the community level does work well (Bjorkman, Myers-Smith, Elmendorf, Normand, Weiher, et al., 2018; Myers-Smith et al., 2019) and others show strong local variability in traits measured locally (Jung et al., 2014). The rule of thumb seems to be that the stronger the environmental filter (and the weaker biotic processes leading to trait divergence) the better we can upscale to the community level.

2.5. Changes in ecosystem functioning under warming and drought

Climate warming and drought directly changes ecosystem functions such as productivity, decomposition, pollination and bacterial communities due to changes for example in energy input (Figure 6D) but also indirectly through the changes in plants and their functional composition (Figure 6E) (Yang et al., 2020). On the one hand, direct warming effects generally enhance growth, decomposition rates, bacterial biomass, yet increase pollinator diversity and abundance (Table 2). Drought has rather opposite effects on these ecosystem functions. On the other hand, changes in plants (species turnover, functional traits and changes in abundances) cascade to ecosystem functioning. In Table 2, I summarize these effects.

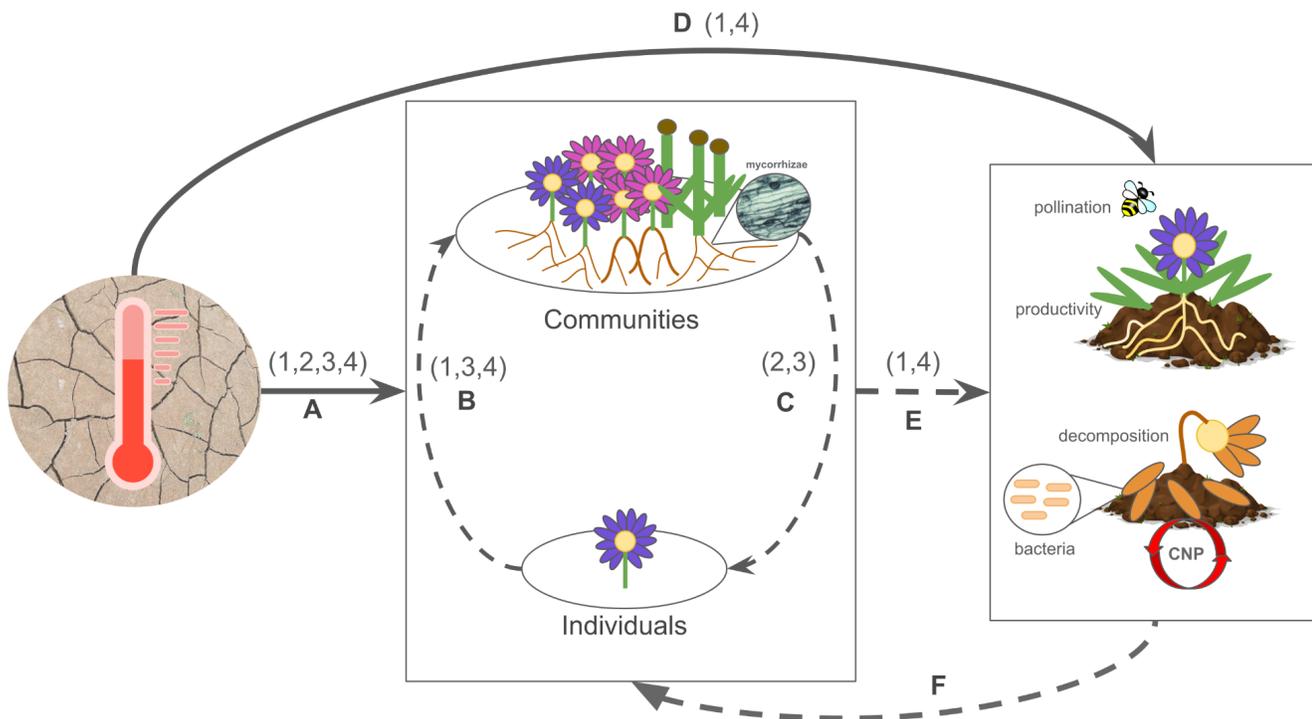


Figure 5: Direct (solid arrows, A,D) and indirect (dashed arrows, B,C,E,F) effects of climate warming and drought on individuals, communities and ecosystem functioning. **A.** Direct effects of climate warming and drought on individuals and communities. **B.** Changes in individual scale processes like demography and plasticity in functional traits cascade to communities and change the assembly and functional strategies of the communities. **C.** Some species gain further advantage under warming and drought because they have competitive advantage. Some species are suffering even more under the increased competition. **D.**

Warming and drought affects ecosystem functioning directly but changes in the community and individual functional traits cascade to ecosystem functioning too (**E**). Altered nutrient dynamics and soil organisms further feedback to plants (**F**). Numbers in parentheses indicate in which chapter I was interested in these direct or indirect effects of climate warming and drought.

Table 2: Direct effects of warming and drought and indirect effects via changes in plants through different processes on ecosystem functioning.

	Direct warming effects		Direct drought effects		Indirect effects via changes in plants (under warming only)	
Above-ground productivity (AGP)	↑	(Bjorkman, Myers-Smith, Elmendorf, Normand, Weiher, et al., 2018; Hagedorn et al., 2019; Rustad et al., 2001; Wu et al., 2011, 2012)	↓	(Wu et al., 2011)	↑	(Bjorkman, Myers-Smith, Elmendorf, Normand, Weiher, et al., 2018; Yang et al., 2020)
	Higher energy input, longer growing seasons increase the plant growth that ultimately increases the above-ground productivity.		Drought inhibits photosynthesis thus above-ground plant growth.		Species turnover: Upslope or northward colonizers are usually tall species that increase the above-ground productivity overall.	
Below-ground productivity (BGP)	↑	(Hagedorn et al., 2019; Yang et al., 2020)	↓	(Deng et al., 2021; Gherardi & Sala, 2020)	↑	(Yang et al., 2020)
	Higher energy input, longer growing seasons increase the plant growth that ultimately increases the below-ground productivity. However the ratio BGP/AGP		Below-ground productivity decreases with drought, however the ratio BGP/AGP increases in drought in order to decrease the transpiration		Morpho-physiological functional traits: Increase in the fast-growing species may enhance further the root growth.	

	decreases as plants allocate more to above-ground to benefit from increased energy input.		through leaves but also increase the capacity to reach water through long roots.			
Soil nutrients	↑	(Grogan & Chapin, 2000; Hagedorn et al., 2019; Rustad et al., 2001; Wu et al., 2012)	↑ ?	(Deng et al., 2021)	↑	(Deng et al., 2021; Hagedorn et al., 2019; Rumpf et al., 2018)
	Soil nutrients in the soil increase due to increase in N mineralization and increase in decomposition.		Retarded mineralization yet higher stability of dissolved organic matter the soil N content might increase.		Morpho-physiological functional traits: Increase in fast-growing species abundances with high nitrogen content and/or nitrophilous species increase the litter N and enhanced decomposition can increase the soil N content.	
Decomposition	↑	(Grogan & Chapin, 2000; Hopkins et al., 2012; Stuble et al., 2019)	↓	(Deng et al., 2021)	↓ ?	(Handa et al., 2014; Mori et al., 2020; Porre et al., 2020)
	Warming enhances the microbial activity that increases the decomposition rates.		Drought inhibits the microbial activity that decreases the decomposition rates.		Morpho-physiological functional traits: Increase in species abundance with fast leaf traits may increase the decomposition rates. Species turnover: homogenization of the plant communities may decrease the decomposition rates	
Pollination	↓	(Sánchez-Bayo & Wyckhuys, 2019; Soroye et al., 2020; van Klink et al., 2020)	↓	(Hung et al., 2021)	↓	(Ganuza et al., 2022; Gérard et al., 2020)
	Abundance and diversity of pollinators decrease with warming.		Abundance and diversity of pollinators decrease with drought		Phenology: Changes in flowering phenology creates a phenological mismatch between plants and pollinators. Functional groups: It seems like warming favors graminoids but not forbs. Decrease in the demographic performance of flowering plants can cause a decrease in pollinators.	

Bacterial biomass	↑	(Chen et al., 2016)	↓	(Deng et al., 2021)	↑	(Yergea u et al., 2007)
	Bacterial biomass increases with warming.		Bacterial biomass decreases (especially in relation to fungi biomass).		Morpho-physiological functional traits: Abundance increase in fast-growing species can further enhance the bacteria.	

As much as it is a challenge to disentangle the direct effects of warming and drought from indirect ones via changes in plants, it is an important task to accomplish to understand if these indirect effects can buffer, slow down or enhance the direct effects on ecosystem functioning.

3. Transient dynamics of plants under warming

As I emphasized above, different scales of biological organization of plants may acclimate to climate warming with different timing and magnitude (Figure 1&2). We can explicitly study the timing and magnitude of these dynamic responses over time. In fact, once abiotic and biotic conditions change, plants do not pass immediately from one stable state to another but rather they first show a number of intermediate (transient) responses (Hastings, 2004; Hastings et al., 2018). So far, the ultimate aim in climate change biology was to determine the long-term changes in plants under warming. However, we now know that studying transient dynamics is essential for multiple reasons. First, transient states can last long and over time periods relevant for conservation and political decisions (Morozov et al., 2020). (Hastings et al., 2018) conceptualize the cases of long transient phenomena in two forms: i) a state remains transient because the change is slow yet would be faster under just slightly different conditions, ii) a state remains transient because it is attracted from one direction yet repelled from others. Secondly, the transient state can inform us on the final state before it is too late (i.e. early warning signal). For example, in the case of adaptive plasticity, we can observe a “Matthew effect” as initial advantages would accumulate to an ultimate advantage at a final state (Fox et al., 2019). **However, in the case of an impairment at any biological organization, we can catch the early warning signals of a tipping point** (Scheffer et al., 2001, 2009).

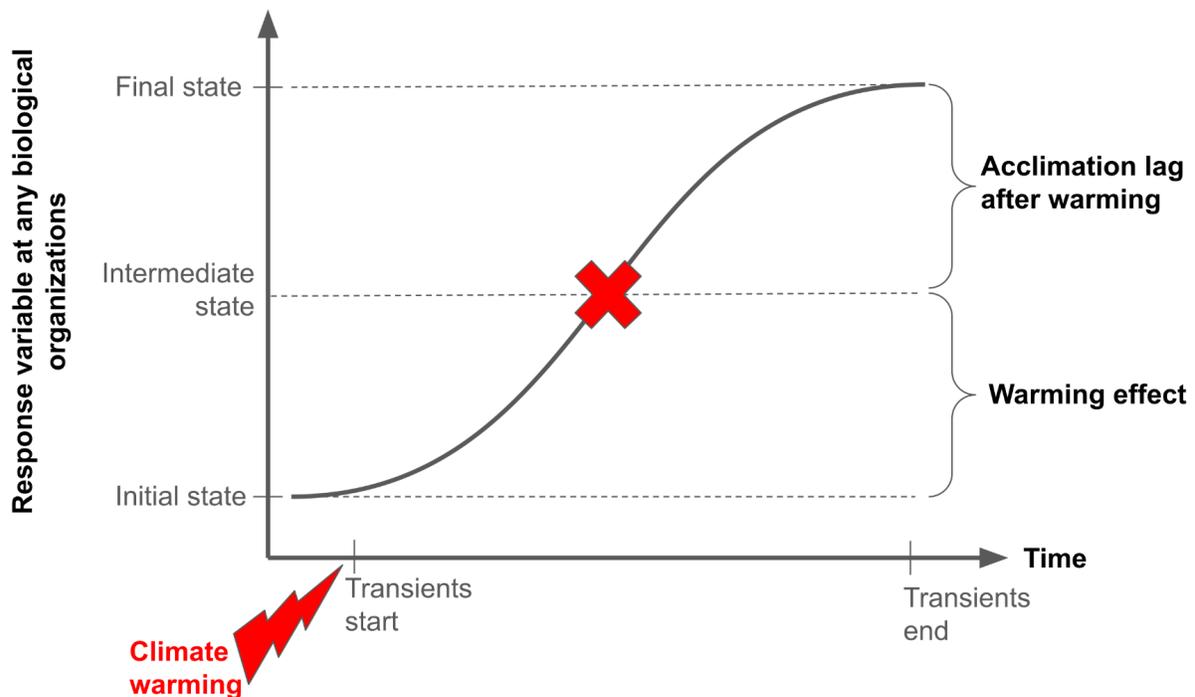


Figure 6: Plants' trajectory of acclimation to climate warming. Transient dynamics start with the climate warming from an initial state of the response variable at any biological organization to a final state. Along the transients, we can measure the responses of the intermediate (transient) states. We can characterize and quantify the warming effect as the difference between the initial and intermediate states. We can characterize and quantify the acclimation lags as the difference between the final and intermediate states.

We can study the transient dynamics of any biological organization under warming and associated effects through its trajectory of acclimation (Figure 6). We can construct such a trajectory if we have a proxy of the initial and final states and if we can measure the intermediate responses over time once the plants are warmed and dried. Any response variable (related to any biological organization) can acclimate immediately to the new conditions and reach the final state. Yet, this is often not the case. Response variables will often give an intermediate response between the initial and final states and will not acclimate completely to the new conditions. Thus, acclimation lags will remain. We can quantify the amount of acclimation to the new conditions (i.e. how much the plants change under warming?) as the difference between the initial and intermediate states which is the “warming effect”. We can further quantify the remaining lag between the final and intermediate state (i.e. how much more change is needed to reach the final state?) which is the “acclimation lag after warming”.

Acclimation lags can remain because the response given by plants i) may simply be not enough for a complete acclimation or ii) can be divergent meaning that not in the expected direction towards the final state (Bektaş et al., 2021).

In order to characterize acclimation trajectories and quantify warming effects and acclimation lags, we can build on a controlled field experiment that simulates realistic warming and drought scenarios on plant communities. My thesis builds on such an experiment in which alpine plant communities and their associated soil were transplanted to warmer environments and then observed over the following years (“AlpagesVolants”, see Box 2). Here comes **“the power” of the whole community transplant experiments** (Nooten & Hughes, 2017): i) we can track the changes in plants as soon as climate change is introduced, ii) we can approximate direct and indirect effects of climate warming as we can warm the plant communities as a whole with their soils and microbial associates and follow the timing of different responses, iii) we can investigate the effect of new competitors from a well adapted species pool due to species entering the warmed plots from outside of the experiment (Yang et al., 2018).

Box 2: Whole community transplant experiments to study transient dynamics in a *in situ* laboratory

Mountains are important biodiversity hotspots and they sustain important ecosystem services. Moreover, mountains provide an on-field laboratory for us to study the effect of climate on plants and ecosystem functions as along the elevational gradients temperature changes sharply. Whole community transplant experiments take advantage of this unique nature of mountains. We can simulate climate warming on the plant communities by transplanting them to lower altitudes to very close sites in airline distance (warmed communities; Figure 7A, orange triangles). This way we can assure that precipitation and bedrock are largely equivalent, yet the main environmental factor that changes is the temperature. Additionally, by transplanting the home and target communities (Figure 7A, purple diamonds and yellow squares, respectively) in their original habitat, we can control for the transplantation effect and assure that comparisons between warmed, home and target communities cancel out the transplantation effect.

Transplant experiments can help us reveal the trajectory of acclimation to warming (Figure 6 & 7). In fact, warmed and control communities represent different stages of acclimation (Figure 7B). Home communities are not exposed to warming thus, they represent the initial state before the transients start. When transplanted, warmed communities enter a transient state and plants show a number of intermediate responses that we can track and measure. Finally, after a certain amount of time warmed communities will acclimate completely to warming or they will be invaded by the species from the target communities: At some point in time, they will be indistinguishable from the target control communities. Hence, target control communities represent the final state of the transient dynamics. Once this trajectory of acclimation is defined, we can quantify the warming effects and acclimation lags in plants' responses (Figure 7C). The amount of change after experimental warming can be quantified by the difference between home control and warmed communities (i.e. Warming effect). The amount of change that is needed to be able to reach the complete acclimation can be quantified by the difference between the warmed and target control communities (i.e. Acclimation lag after warming).

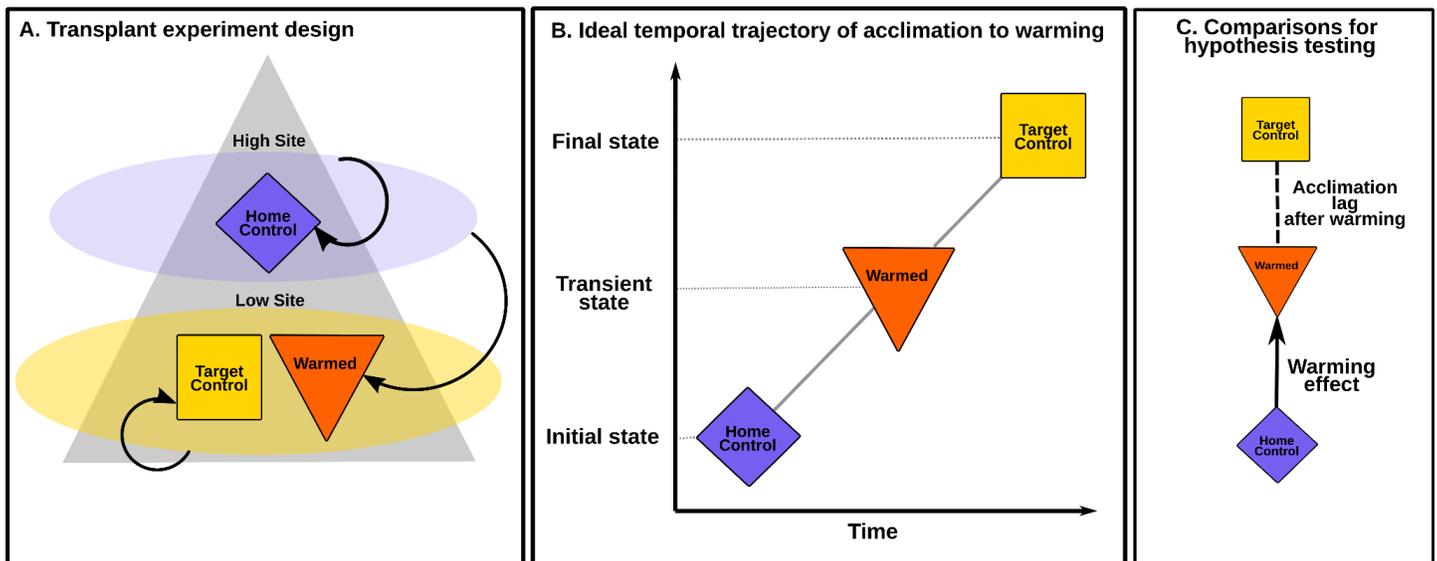


Figure 7: Transplant experiment design (A). Along an elevational gradient, communities are transplanted to a lower site to simulate climate warming (Warmed communities, in orange triangles). Target (yellow squares) and home (purple diamonds) communities are transplanted in their original sites in order to control for the transplantation effect. **Ideal temporal trajectory of acclimation to warming (B).** Communities in a transplant experiment can represent different stages of acclimation to warming. Initial state is represented by the home control communities. Warmed communities are in a transient state after the transplantation and after a certain amount of time they will either completely acclimate to the new

conditions or they will be colonized by the species at the target site, hence the final state can be represented by the target control communities. **Comparisons for hypothesis testing (C).** By comparing home control to warmed communities we can quantify the warming effect. By comparing warmed to target control communities, we can quantify the acclimation lags after warming.

4. Climate warming at a biodiversity hotspot: European Alps

High mountains inhabit a great species diversity due to various evolutionary (Rahbek et al., 2019) and ecological processes (Körner, 2021a). Tectonic uplifts and erosion that formed mountains have also created strong environmental gradients for species. Populations that were isolated by geographic barriers, glaciers, and microhabitats (i.e. specific climate and soil conditions) evolved into new species (Rahbek et al., 2019). Körner (2021) assumes that there exist roughly 10 thousand flowering alpine plants (almost 4 % of known plants). Following the extreme high mountain conditions, alpine plants are physiologically and morphologically adapted to low-temperature extremes, strong diurnal temperature variations, dehydration due to freezing, and high exposure to solar radiation (Körner, 2021b). Hence, it has always been important in climate change ecology to understand how such cold-adapted plants are responding (and will continue to respond) to climate warming. Considering the recent IPCC report showing that climate warming is (and will continue to be) accelerated in the European Alps (Intergovernmental Panel on Climate Change (IPCC), 2022), we need to understand how alpine plants will react to future climate warming if we wish to conserve them (Figure 8).

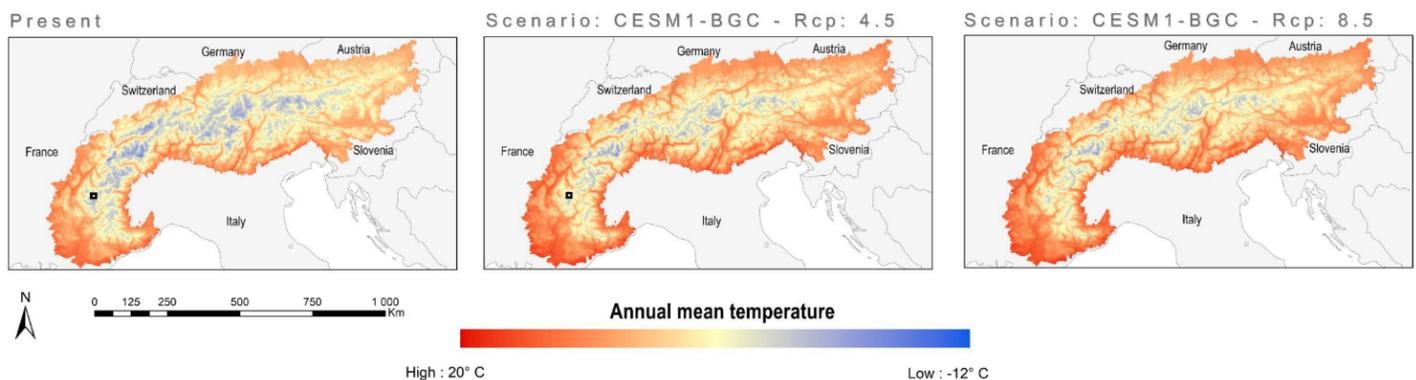


Figure 8: Present and future (by the end of the century) annual mean temperature in European Alps. Middle and right figures show the future annual mean temperature according to an intermediate and

pessimistic climate mitigation scenario (Rcp 4.5 & 8.5). (Figure by Julien Renaud and projections taken from (Karger et al., 2017)).

An important characteristic of mountains are the steep environmental gradients over relatively small spatial scales. On the responses of mountain plants to warming, one of the first hypotheses was that plants will be “migrating” upward at the mountains to follow their climatic niche under warming (Grabherr et al., 1994; Parmesan & Yohe, 2003). However, this would mean that high mountain plants might not be able to migrate higher up due to lack of suitable habitat (e.g. lack of suitable soils, high slopes or simply end of mountains) or they might be “invaded” by low altitude plants. **Consequently, they would not only suffer from climate warming but also from restriction of their abiotic and biotic niche.** Since then, there is accumulating evidence on this hypothesis (Gottfried et al., 2012; Pauli et al., 2012). Hence, alpine plants might be at the edge of extinction. However, we can only fully understand this phenomenon if we know how the alpine plants respond to climate warming at different scales of biological organization.

The steep environmental gradients at small spatial scales do not only influence potential response trajectories of plant communities and their functioning as a response to climate change but they also provide *in situ* laboratories. Observatories allow to study close-by ecosystems under distinct climatic conditions and transplant experiments allow to simulate climate change while keeping much of the additional abiotic environment (more or less) constant (Box2).

5. Main thesis questions and chapter specific questions

My aim in this Ph.D., is to understand the direct and indirect effects of climate warming and drought on alpine grasslands. Towards this understanding I investigate transient responses of warmed alpine plants at different biological scales (Figure 5, Box 2). The overarching questions of this thesis are: **1) How are individuals, communities and ecosystem functioning affected directly by experimental warming and drought (Chapters 1-4)? 2) Do acclimation lags remain after experimental warming and drought (Chapters 1,3,4)? 3) How are plants indirectly affected by experimental warming and drought via biotic interactions (Chapter 2,3)? 4) How are ecosystem functions indirectly affected by experimental warming and drought via changes in plants (Chapters 1,4)?**

More specifically in Chapter 1, I focus on the acclimation of phenological functional traits at species and community level. I specifically ask: i) Did mountain grassland phenology completely

acclimate in their phenological traits over 3 years of warming? ii) Was acclimation lags due to divergent or insufficient warming effects? In Chapter 2, I focus on the demographic responses of the alpine species through their changes in relative abundances and the colonizing species from the subalpine species. I specifically ask: i) Which alpine species lose or win under the simulated climate warming? What determines the decrease (loser) or increase (winner) in relative abundance under warming? iii) Is there a difference between alpine winners from the original communities and winners colonizing from a subalpine species pool? In Chapter 3, I focus on disentangling the community assembly processes in mountain grasslands and their changes under warming. I specifically ask: i) What are the community assembly processes and their relative importance in mountain grasslands? ii) How the community assembly processes change in mountain grasslands under experimental warming? iii) Are these changes due to species turnover or species' local abundance changes? In Chapter 4, I focus on the changes in the whole community functional strategies at the above- and below-ground and how these changes cascade to ecosystem functioning. I specifically ask: i) Can we disentangle fast vs. slow and do-it-yourself vs. outsourcing trade-offs in mountain grassland communities? ii) Do functional strategies change under warming and drought? iii) How do the warming induced shifts in plant strategies affect above- and below-ground ecosystem functions?

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**Chapter 1:
Lags in phenological
acclimation of
mountain grasslands after
recent warming**

RESEARCH ARTICLE

Lags in phenological acclimation of mountain grasslands after recent warming

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Abstract

1. In the current biodiversity crisis, one of the crucial questions is how quickly plant communities can acclimate to climate warming and longer growing seasons to buffer the impairment of community functioning. Answering this question is pivotal especially for mountain grasslands that experience harsh conditions but provide essential ecosystem services to people.
2. We conducted a reciprocal transplant experiment along an elevation gradient (1,920 m vs. 2,450 m) in the French Alps to test the ability of plant species and communities to acclimate to warming and cooling. For 3 years, we measured weekly the timing of phenological events (e.g. start of flowering or greening) and the length of phenological stages linked to demographic performance (e.g. lengths of flowering or greening periods).
3. We found that warming (and cooling) changed the timing of phenological events strongly enough to result in complete acclimation for graminoids, for communities in early and mid-season, but not at all for forbs. For example, warming resulted in later greening of communities and delayed all phenophases of graminoids. Lengths of phenological stages did not respond strongly enough to climate change to acclimate completely, except for graminoids. For example, warming led to an acclimation lag in the community's yearly productivity and had a strong negative impact on flowering of forbs. Overall, when there was an acclimation failure, responses to cooling were mostly symmetric and confirmed slow acclimation in mountain grasslands.
4. *Synthesis.* Our study highlights that phenological plasticity cannot prevent disruption of community functioning under climate warming in the short term. The failures to acclimate after 3 years of warming signals that species and communities underperform and are probably at high risk of being replaced by locally better-adapted plants.

KEYWORDS

climate change, global change ecology, mountain grasslands, NDVI, phenology, reciprocal transplant, transient dynamics, warming experiment

1 | INTRODUCTION

Climate warming is altering the biodiversity and functioning of mountain grasslands. Plant communities will not immediately restructure to adjust to new air and soil temperatures and associated changes in growing season length and snow cover (Carlson et al., 2017; Choler, 2015; Gobiet et al., 2014) but will show a number of transient responses (Hastings et al., 2018) that are susceptible to lag behind climate warming (Alexander et al., 2018). Plastic responses of plant phenotypes are prone to be triggered before species' abundance distributions and, finally, community composition change (Nicotra et al., 2010). By monitoring these transient dynamics, we can identify the short-term acclimation lags, that is, the difference between the current state to the one completely accustomed to a new climate, that can temporarily disrupt ecosystem functions and services and can serve as early warning signals of long-term degradations. Quantifying and characterizing acclimation lags in addition to the responses to warming are pivotal to understand how strongly adjusting plant species and communities are still underperforming in comparison to well-adapted ones, how prone they are to be replaced and outcompeted by better-adapted ones and how strongly ecosystem processes are impaired (Ryo et al., 2019; Ström et al., 2011).

Among plastic responses to warming, plant phenology is one of the first to be triggered (Bellard et al., 2012; Parmesan & Hanley, 2015; Shen et al., 2015). Phenology refers to the timing and duration of events in species' plant growth and reproduction over the year including budburst, flowering, seed production and browning. Phenology strongly affects demographic performance, community assembly and functions (Ackerly et al., 2000; Richardson et al., 2013). As climate warming does not only result in higher mean temperatures but also in changed snow cover regimes and earlier starts and longer durations of growing seasons, it will affect different aspects of plant phenology in different periods of the season. In the short term, phenology can allow acclimation of plant communities, particularly for their main functions such as productivity (Carlson et al., 2017; Piao et al., 2019). However, many questions on the transient responses of mountain plant phenology to warming remain open: Do early- or late-season phenological stages acclimate the fastest? How much time is required to close acclimation lags? Are species plastic in their responses or does acclimation require a restructuring of community composition? It will depend on the answers to these questions which species and ecosystem functions can prevail under climate warming. Therefore, we need to effectively measure phenological responses to realistic warming scenarios and use informative phenological indicators and ways to characterize acclimation lags.

Plant phenology and its response to warming climate is a globally long-studied phenomenon with different experimental methods and at different organism levels (Piao et al., 2019; Winkler et al., 2019; Wolkovich et al., 2012). For mountain grasslands, experimental warming showed an advancement in greening, flowering and fruiting but a delayed browning at community level (Meng et al., 2019). However, even so community-level phenological

responses often resemble species-specific responses to warming (Diez et al., 2012), species with different characteristics still show idiosyncratic responses (Arft et al., 1999; Dunne et al., 2003; Li et al., 2016; Smith et al., 2012; Wang, Meng, et al., 2014). Yet, it has been suggested that responses can potentially be generalized at the growth-form level (Arft et al., 1999; Dunne et al., 2003; Oberbauer et al., 2013). For example, graminoids and forbs are likely to give different responses as they differ in functional and reproductive strategies (Reich et al., 2003; Shen et al., 2015; Siebenkäs et al., 2015).

Both at community level and at species level, a plethora of indicators have been suggested to track changes in phenology for different periods in the season and to approximate different demographic processes (Table 1). Consequently, these indicators can respond differently to warming. Therefore, a comprehensive study of warming effects and acclimation lags requires not only to combine species- and community-level measures but also to integrate different indicators to have the most complete overview on phenological changes. Here, we refer to indicators that capture the start, end or pace of phenological stages as proxies for the timing of plant growth and reproduction (time-related indicators, Table 1) and we refer to indicators that capture the length of phenophases (e.g. length of greening or flowering) and the number of individuals passing to a certain phenophase as proxies of demographic performance (performance-related indicators, Table 1).

For time-related indicators, warming generally leads to an earlier and quicker onset of phenophases in early-season while late-season responses are much more variable (Parmesan & Hanley, 2015). We are not aware of acclimation lag studies but expect faster acclimation to warming in the early season as it has been shown that plants are plastic in adjusting the leaf out to changes in snow cover dynamics (Choler, 2015; Körner, 1999). In contrast, high mountain grassland plants are adapted to short growing seasons and we expect that adjusting to longer season lengths may be more difficult than to start the season earlier. For performance-related indicators, warming leads to more plant growth but also more idiosyncratic species-specific responses, for example, to either decreases or increases in reproductive performance (Aldridge et al., 2011; Carlson et al., 2017; Li et al., 2016; Liu et al., 2012). Additionally, while climate warming might generally improve conditions for plant growth, it is often associated with lower snow cover protection and more frequent exposure to freezing events due to early snowmelt which may limit some species (Choler, 2015). In contrast to time-related indicators, we expect performance-related indicators to be more limited by physiological constraints, to be less plastic and thus, be much slower in adjusting (Baptist et al., 2010).

Hitherto, warming studies have mainly focussed on a single type of indicator (Aldridge et al., 2011; Li et al., 2016; Meng et al., 2019; Wang, Meng, et al., 2014; Wang, Ottlé, et al., 2014) (but see counter examples: Wang et al., 2020; Wang, Wang, et al., 2014) and quantified phenological changes as a response to warming (i.e. the warming effect; Piao et al., 2019; Shen et al., 2015; Wolkovich et al., 2012) but rarely measured acclimation lags (Ryo et al., 2019). Measuring

TABLE 1 Grouping of phenological indicators and their representation at different levels. Shading indicates the focal organism level. (g: indicator related to plant growth; r: indicator related to reproductive period; please refer to the main text for further explanation of their calculation and interpretation)

			Level	
Indicators			Community-level	Species-level
Phenology	Time related	Days after maximum plant growth	g	
		Days before maximum plant growth	g	
		Greening speed	g	
		Browning speed	g	
		Ratio mid-season days	g	
		Days until mean flowering day		r
		Days until mean fruiting day		r
		Days until mean dissemination day		g
		Performance related	Annual plant growth	g
	Early plant growth		g	
	Mid-season plant growth		g	
	Late plant growth		g	
	Flowering length			r
	Fruiting length			r
	Max % flowering			r
	Max % fruiting			r
	Max % dissemination			g

acclimation lags is a challenge as it requires to identify the adjusted community state after complete acclimation (Visser & Both, 2005).

Here, we suggest a combination of a transplant experiment with a conceptual framework to measure transient warming and cooling effects and acclimation lags in mountain grasslands (Figure 1). We added cooling effects to test for reciprocity and to find out whether the acclimation to new thermal conditions in mountain grasslands is generally a slow phenomenon (Crous, 2019). Our reciprocal transplant experiment along an elevation gradient simulates three degrees of warming and longer growing seasons hence, a realistic warming scenario for the Alps for this century (see projections for RCP4.5 and 8.5 scenarios: Jacob et al., 2014; Vorkauf et al., 2021). We transplanted alpine communities 500 m downwards to subalpine conditions to simulate climate warming (Figure 1A, AlpineWarmed) and, reciprocally, we transplanted subalpine communities 500 m upwards (Figure 1A, SubalpineCooled). We controlled for transplantation effects at both sites with control plots (Figure 1A, AlpineControl and SubalpineControl respectively). We suggest measuring warming (or cooling) effects by comparing AlpineControl to AlpineWarmed plots (or SubalpineControl to SubalpineCooled plots, Figure 1C).

To measure acclimation lags we assume that plants in control plots are in equilibrium with climatic conditions. To justify this assumption despite ongoing climate change, we argue that (a) the historical climate warming is a slow- and long-term phenomenon compared to the experimental manipulation and thus negligible in comparison (Table S3), and (b) the ongoing climate change has not induced yet a trend of longer growing seasons even though this is an expected phenomenon (Jacob et al., 2014; Wang et al., 2021). Moreover,

results would only be more extreme if we had transplanted communities from long-term climate equilibrium. Acclimation lags can then be measured by comparing where the state of AlpineWarmed plots (or SubalpineCooled plots) is relative to the shortest trajectory of acclimation which we define here as the shortest distance between states of AlpineControl and SubalpineControl plots (Figure 1B,D). We suggest two measurements (Figure 1D): Acclimation lags can be big either because little acclimation has been achieved yet and the still to cover distance is much larger than the distance already covered (deficient acclimation) and/or because transient adjustments deviate in direction from the shortest trajectory to complete acclimation (deviating acclimation). Theoretically, we expect that in the very long-term lags will close and compared plots will be indistinguishable.

Combining a species to community scale approach, a multi index approach for phenology and our conceptual framework, we asked whether: (a) mountain grassland phenology completely acclimated in timing and performance over 3 years of warming; (b) the lag in acclimation was due to deficient and/or divergent warming effects and (c) the transient responses to warming and cooling were symmetric.

2 | MATERIALS AND METHODS

2.1 | Experimental design

The experiment was implemented close to the Col du Lautaret (45°02'04"N 06°24'18"E) in the French Alps in September

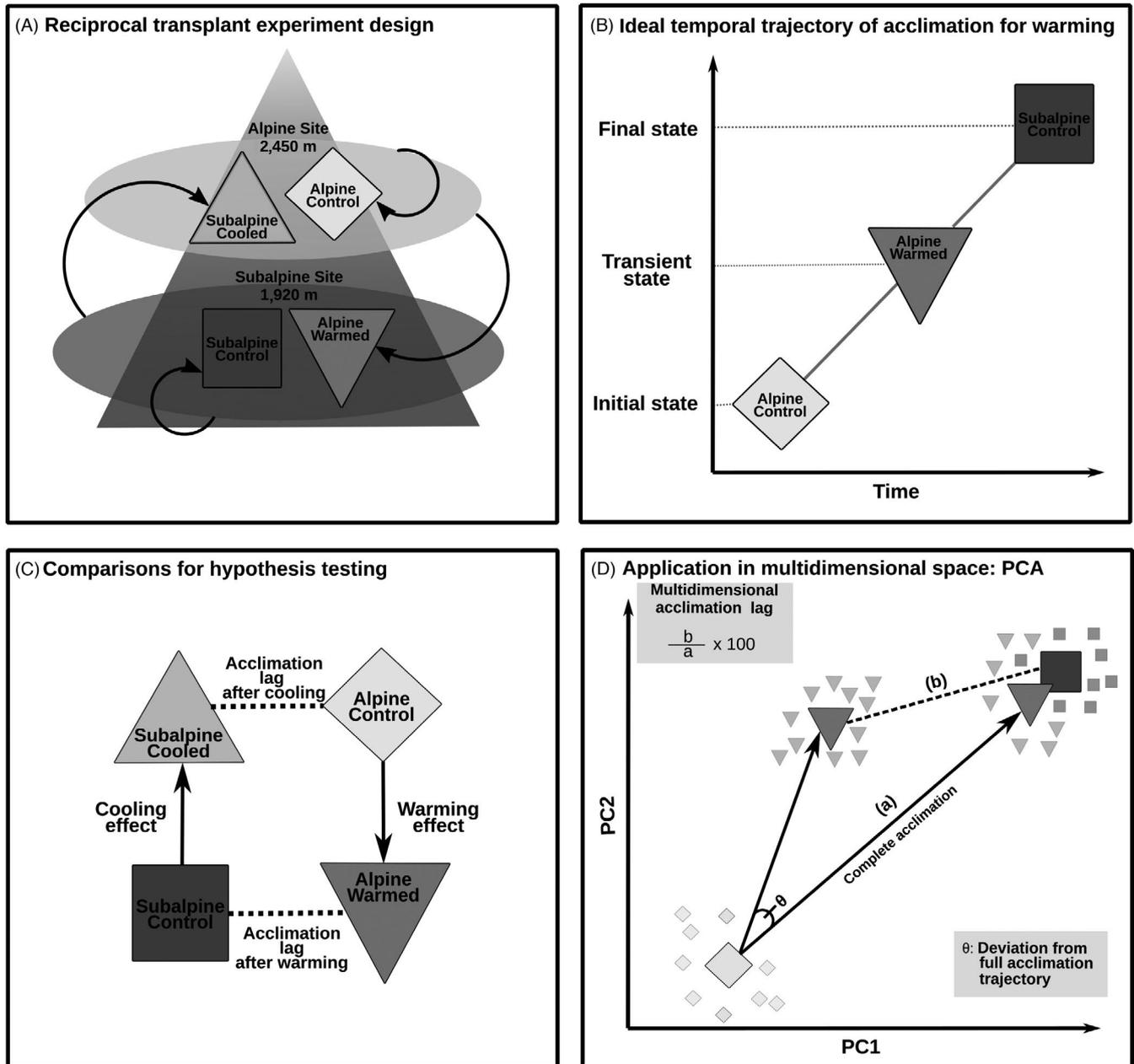


FIGURE 1 (A) Schematic representation of the reciprocal transplant experiment. Arrows indicate the destination of the transplantation. (B) Ideal temporal trajectory of acclimation to warming and the representation of the states (initial, transient and final) of the transplanted plots under the assumption that initial (final) states are at equilibrium under alpine (subalpine) conditions. (C) Treatment effects and associated comparisons of plots (custom contrast setting). Arrows indicate cooling or warming effects. Dotted lines indicate acclimation lags. For the warming effect, AlpineWarmed is contrasted to AlpineControl. For the cooling effect, SubalpineCooled is contrasted to SubalpineControl. For the acclimation lag after warming, SubalpineControl is contrasted to AlpineWarmed. For the acclimation lag after cooling, AlpineControl is contrasted to SubalpineCooled. (D) Application of the framework to real data based on a principal component analysis (PCA) in order to identify a warming effect, an acclimation lag, and a deviation from the full acclimation trajectory

2016 (Figure 1A). The translocation sites are the subalpine site 'Lautaret' (45°04'00"N 06°41'90"E) at 1,920 m altitude and the alpine site 'Galibier' (45°05'44"N 06°40'06"E) at 2,450 m altitude. Sites are close to each other (~2 km airline distance), have a similar orientation (south-east at alpine and south-south-west at subalpine site), bedrock (base-riched flysch) and soil (dystric cambisols). During the observation period (autumn

2016–autumn 2019), average annual soil temperature at the subalpine site was 3.2°C warmer than at the alpine site (and days with similar temperatures at the two sites were very rare), average July soil temperature was 3.1°C warmer and snow-free season was 58.7 days longer (Table S1; Figure 2A). At the subalpine site, plant communities were mainly dominated by the graminoids *Patzkea paniculata*, *Carex sempervirens* and *Festuca*

nigrescens, and the forbs *Centaurea uniflora*, *Helianthemum nummularium* and *Meum athamanticum* (Figure S13). At the alpine site, plant communities were mainly dominated by the graminoids *Carex sempervirens*, *Festuca nigrescens* and *Poa alpina*, and the forbs *Potentilla aurea*, *Trifolium alpinum* and *Geum montanum* (Figure S13). Overall, the dominant graminoid species in AlpineControl and SubalpineControl plots makeup to 22.5% and 26.5% of relative abundance respectively. All plant communities were dominated by perennial species.

In 2016, to simulate the effect of warming on alpine grasslands, we transplanted 10 replicates 4 m² blocks of vegetation with at least 20 cm of their intact below-ground parts and the surrounding soils from the alpine to the subalpine site (AlpineWarmed plots in the following). For transport, each block was cut in 4 × 1 m² sub-blocks that were re-assembled in their original composition when re-planted. To simulate the effect of cooling on subalpine communities, 10 intact 4 m² blocks of vegetation and soils were transplanted from the subalpine to the alpine site (SubalpineCooled plots). To control for the transplantation stress, we also horizontally transplanted 10 intact 1 m² blocks at both the subalpine and the alpine sites (SubalpineControl plots and AlpineControl plots respectively). Around the turfs we placed water permeable root barriers to avoid root ingrowth from the natural vegetation around the plots. At both sites, cattle and sheep were kept out by electric fences.

2.2 | Defining the growing season

We considered the start and end of phenological events always relative to the start of the growing season and the end of the growing season respectively (Table S1). This choice assures that (a) plots in different sites and years are comparable and (b) we compare the direct phenological response rather than the differences in calendar dates (Johansson et al., 2013). We defined the start (end) of the growing season as the first date when the normalized difference vegetation index (NDVI) based on Moderate Resolution Imaging Spectroradiometer (MODIS) remote-sensed data was above (below) 0.1 and the locally measured daily soil temperature was above (below) 1°C (Choler, 2015, 2018; Figure 2). For the remote-sensing data (RS-based NDVI), we downloaded the MOD09Q1 surface reflectance products corresponding to tile h18.v4 (40–50°N, 0–15.6°E) from the Land Processes Distributed Active Archive Center (LP DAAC). We used surface reflectance in the red and near-infrared to calculate the 250-m-resolution NDVI 8-day times series corresponding to the two sites. The RS-based NDVI time-series data were BISE (Best Index Slope Extraction) corrected, gap-filled with cubic spline interpolation and smoothed using the Savitzky–Golay filter (Choler, 2015). For the local soil temperature measurements, we equipped the two sites with standalone soil temperature data loggers (Hobo pendant UA; Onset Computer Corporation) buried at 5 cm below-ground. We smoothed daily soil temperature time series with cubic spline interpolation.

2.3 | On site measurements and phenological indicators

2.3.1 | Community-level

We tracked the phenology at community level using NDVI as a measurement of greening and a proxy for photosynthetic activity and plant growth (Myneni & Williams, 1994; Figure 2C). We measured NDVI in each treatment sub-block (10 × 4 × 1 m² sub-blocks for AlpineWarmed and for SubalpineCooled) and in each control block (10 × 1 m² blocks for AlpineControl and SubalpineControl) with three measurement repetitions once (twice at maximum growth) per week during the growing seasons of the years 2017, 2018 and 2019. We took the measurements with a Decagon ProCheck spectral reflectance sensor for NDVI with 630 nm (red) and 800 nm (near-infrared) spectral irradiance. The measurements were taken at clear sky from 9 a.m. to 4 p.m. during on the same day for both sites. We derived indicators from the NDVI curves over the growing season independently for each year, treatment sub-blocks, control blocks and replicates. We gap-filled the time series (i.e. the other days of the week) using cubic smoothing spline interpolation and smoothed using Savitzky–Golay filter (Choler, 2015).

Based on these time series, we calculated several indicators. These indicators were based on the definition of seasons within the whole growing season: (a) early season as the period starting from the onset of the growing season to the last day when the NDVI values were below the 90% of the maximum NDVI, (b) mid season as the period when the NDVI values stayed above 90% of the maximum NDVI and (c) late season as the period between the first day where NDVI values dropped below 90% of the maximum NDVI until the offset of the growing season. A threshold choice of 80% of maximum NDVI was also tested and it did not affect the results (unpublished). While the start and end of growing seasons were identified with MODIS remote-sensed data, we were able capture the unique phenological dynamics in plant growth of each plot repetition by (a) starting NDVI measurements right after the snow melt when the field site was accessible, (b) identifying the maximum NDVI based on field measurements for each plot.

We calculated time-related indicators as (Table 1): (a) the days from the start of the growing season until 90% of the maximum plant growth (greening days), (b) greening speed as the rate of increase in the NDVI values (i.e. from 0.1 of onset value to 90% of maximum NDVI value) during early season (Equation 2), (c) ratio of mid-season days to growing season days, (d) days after 90% of the maximum plant growth until the end of the growing season (browning days) and (e) browning speed as the rate of decrease in the NDVI values (from 90% of maximum NDVI value to 0.1 of offset value) during late season (Equation 1).

$$\text{Greening speed} = \left| \frac{0.9 \times \max \text{NDVI} - 0.1}{\text{Greening days}} \right|, \quad (1)$$

$$\text{Browning speed} = \left| \frac{0.1 - 0.9 \times \max \text{NDVI}}{\text{Browning days}} \right|. \quad (2)$$

We calculated performance-related indicators as proxies for biomass production and plant growth as the areas under NDVI curves for each season (Table 1): (a) early plant growth, (b) mid-season plant growth, (c) late plant growth and (d) annual (i.e. whole growing season) plant growth.

2.3.2 | Species-level

We tracked the phenology of focal dominant species (Table S2) in one sub-block of each treatment block ($20 \times 1 \text{ m}^2$ sub-blocks in total) and in each control block ($20 \times 1 \text{ m}^2$ blocks in total) every week during the growing seasons of 2017, 2018 and 2019. The selected dominant species for the blocks with subalpine origin (SubalpineControl and SubalpineCooled) were *Patzkea paniculata*, *Carex sempervirens*, *Festuca nigrescens*, *Centaurea uniflora*, *Helianthemum nummularium* and *Meum athamanticum*. The selected species for the blocks with alpine origin (AlpineWarmed and AlpineControl) were *Carex sempervirens*, *Festuca nigrescens*, *Poa alpina*, *Potentilla aurea*, *Trifolium alpinum* and *Geum montanum*. We focus here on the flowering, fruiting and dissemination phases as they reflect both early- and late-season plant growth and reproduction phenologies. For each treatment sub-block and control block and each species, we determined the phenophases of 10 randomly selected individuals (or the maximum number of individuals available when <10, see Table S2 for percentage of observations when <10 individuals were observed). During the peak of the growing season, we increased the frequency of NDVI and phenology measurements to two times a week.

To reduce observation bias, we determined the start of the phenophase for a species as the average of (a) the last date when no individuals of the given species in the given phenophase were observed and (b) the first date when the individuals of the given species in the given phenophase were observed (vice versa for the end of phenophase; Li et al., 2016). In case this averaging is not possible for the fact that the start or end of a phenophase were exactly the start or the end of the observation period on the field, the latter dates were taken.

We calculated time-related indicators as the days from the start of the growing season until the mean date of the phenophase (Table 1; Moussus et al., 2010).

We calculated performance-related indicators as (Table 1): (a) the maximum ratio of individuals in the phenophase to the number of sampled individuals (maximum 10) and (b) length of the phenophase as the number of days between the onset and the end of the phenophase. (Li et al., 2016). We excluded the length of the dissemination period from our study as we could not collect the data over the whole dissemination period.

2.4 | Statistical analyses

For our sets of phenological indicators (community- vs. species-level and time vs. performance related), we analysed four different treatment effects (Figure 1C): (a) a warming effect by comparing

AlpineWarmed to AlpineControl plots, (b) a cooling effect by comparing SubalpineCooled to SubalpineControl plots, (c) an acclimation lag after warming by comparing SubalpineControl to AlpineWarmed plots and (d) an acclimation lag after cooling by comparing AlpineControl to SubalpineCooled plots. We conducted all the statistical analyses on R (R Core Team, 2017).

First, we tested the different treatment effects for each phenology indicator independently using linear mixed effects models (NLME R package). At the community level, we took the median of the measurement repetitions to avoid including measurement errors due to the handheld NDVI sensor. We considered treatment (custom contrast setting of above-explained comparisons, Figure 1C) and year as fixed effects and subplot identity nested in plot identity as random effect. At the species level, we accounted for treatment, year and functional group (forbs or graminoids) as fixed effects and block and species identity as random effects. As we conducted multiple tests, we adjusted the *p*-values with multivariate *t*-distribution adjustment within the EMMEANS package in R (Lenth, 2016). Here, we discuss the common responses of forbs and graminoids, and report the species-specific responses in the Appendix (Figure S1).

Second, in order to summarize results for timing- versus performance-related phenological indicators, we performed six different principal component analyses (PCAs) for time-related versus performance-related indicators for communities, forbs and graminoids. We visualized the first two components of each PCA in the Appendix (Figures S4–S6). For further analyses we determined the number of significant principal components (PCs) with Horn's parallel analysis in the R package PARAN (Dinno, 2018; Franklin et al., 1995; Figure S12). As a result, we retained the first two PCs. For community-level PCAs two PCs were necessary to well capture the variation, and for species-level PCAs one PC was sufficient. Then calculated (a) the multidimensional acclimation lag (here 'multidimensional' refers to the multiple indicators and the one or two PC axes describing their variation) as the percentage of the remaining acclimation relative to the complete acclimation (Figure 1D), (b) the deviation from the shortest acclimation trajectory as the angle between the shortest acclimation trajectory and the warming effect (Figure 1D) with the shortest acclimation trajectory being the Euclidean distance between AlpineControl and SubalpineControl plots. In the case of two significant PCs (i.e. community level), we calculated the Euclidean distances with the *dist* function within the STATS package and the angles with the *Angle* function within the LEARNGEOM package in R (Briz-Redón & Serrano-Aroca, 2018). In the case of a single significant PC (i.e. species level), angles were set either to 0° (i.e. on the acclimation trajectory) or to 180° (opposite direction of the acclimation trajectory).

For interpretation, we speak of 'acclimation lag' or 'deficient warming effect' if we found a significant difference between SubalpineControl and AlpineWarmed or AlpineControl and SubalpineCooled and of 'complete acclimation' otherwise. We speak of a divergent warming or cooling effect if the observed trajectory deviates from the shortest trajectory of complete acclimation. Importantly, acclimation lags can be much higher than 100% when

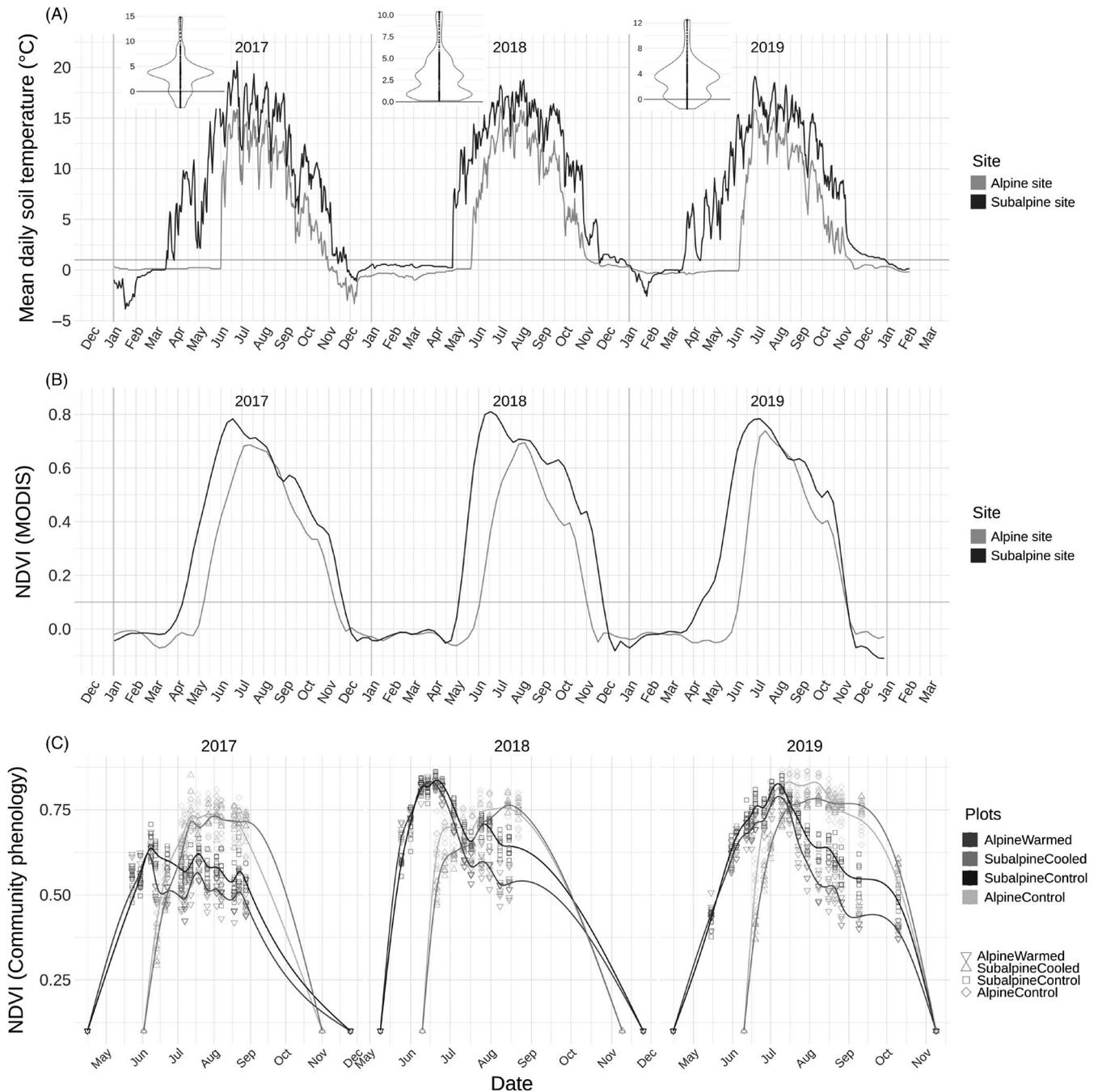


FIGURE 2 (A) Soil temperature with daily soil temperature differences between the two sites for each year in the violin plots, (B) NDVI from MODIS remote-sensed data and (C) on-site NDVI plot measurements of alpine and subalpine sites. (A) and (B) were used to identify the growing seasons. (C) Transparent data points are on-site NDVI measurements for each plot. NDVI curves are daily means of interpolated and smoothed on site NDVI measurements for each treatment and control plots (see Section 2 for details)

the distance to the optimally adapted community is not narrowing down over time but is instead increasing during the transient dynamics. This can either happen when the adjustment response goes in the ‘wrong’ direction or when the adjustment response goes in the ‘right’ direction but then overshoots largely. We consider that the acclimation lags in warming and cooling are symmetrical when they have almost the same (i.e. maximum 10% difference) multidimensional acclimation lag.

3 | RESULTS

3.1 | Was phenology completely acclimated after 3 years of warming?

In a first step, we summarized results for the six sets of indicators (Table 1, combinations of community, forbs, graminoids with time related and performance related) and depending on whether at least

one indicator per set showed a significant acclimation lag, we give further details in upcoming sections.

After 3 years of warming, the phenology of communities and focal species did not completely acclimate, with the exception of graminoids (Figure 3). For time-related indicators (Figure 3A), we observed complete acclimation to warming in most cases, especially during early-season and flowering. However, late-season phenology (i.e. days after maximum plant growth) for communities and fruiting phenophase for forbs showed a significant acclimation lag.

For performance-related indicators (Figure 3B), we observed significant acclimation lags under warming except for the graminoids. Both annual and mid-season plant growth for communities and flowering phenophase (i.e. both flowering length and max % flowering) for forbs failed to reach complete acclimation.

3.2 | Was the warming effect on phenology deficient and/or divergent?

Both deficient and divergent warming effects were responsible for the observed acclimation lags (Figure 4). However, lag size and deviation angle were dependent on the focal organism level and phenological indicators.

For time-related indicators, the community-level acclimation lag was relatively small, 10%, and deviated only slightly from the shortest trajectory, 5° (Figure 4). With warming and longer season length (Figure 2; Table S1), alpine community plant growth in the early season slowed down and communities took longer to reach their maximum plant growth (compared to AlpineControl). In late season, communities decreased browning speed and increased browning days (i.e. days after maximum plant growth) but failed to acclimate to the complete use of the late-season which constitutes the major part of the acclimation lag. Interestingly, plant communities could only acclimate their greening speed to longer season length in the third year but failed to do so in the first 2 years after transplantation (Figure S6a). At the species level, forbs did not only fail to close the acclimation lag due to the absence of any warming effect (Figures 3a and 4), but they even increased the lag by responding in the 'wrong' direction (i.e. 180° away from the shortest trajectory to complete acclimation. Specifically, fruiting for the AlpineWarmed species started earlier than for the SubalpineControls in all 3 years after the transplantation.

For performance-related indicators, the community-level acclimation lag was relatively large, 26%, but deviated only moderately from the shortest trajectory, 15° (Figure 4). Thus, even if communities could increase their performance during early and late season, their underperformance in the most important mid season resulted

in an important acclimation lag (Figure 3). In addition, this acclimation lag tended to increase over years (Figure S7a). Forbs showed an even bigger acclimation lag (685%) because they responded in the 'right' direction but exceeded far beyond the acclimation state. Notably, such large lags occur because the original distance between the phenology of alpine and subalpine plants was small and the response is measured relative to this original distance (Figure 4). This was especially the case for reproduction in the indispensable flowering stage (length of flowering period and number of individuals reaching this phenophase; Figure 3).

3.3 | Were acclimation lags in warming and cooling symmetric?

Acclimation lags in warming and cooling were not always symmetric. However, the strongest acclimation lags caused by warming (i.e. performance-related indicators for communities and forbs and time-related indicators for forbs) were symmetric for cooling (Figure 4; Figures S4 and S5).

For time-related indicators, cooling caused a larger acclimation lag and stronger deviation from the shortest trajectory than warming at the community level. Forbs were on the shortest acclimation trajectory after cooling in contrast to their deviating response to warming response but the sizes of acclimation lags were similar (Figure 4).

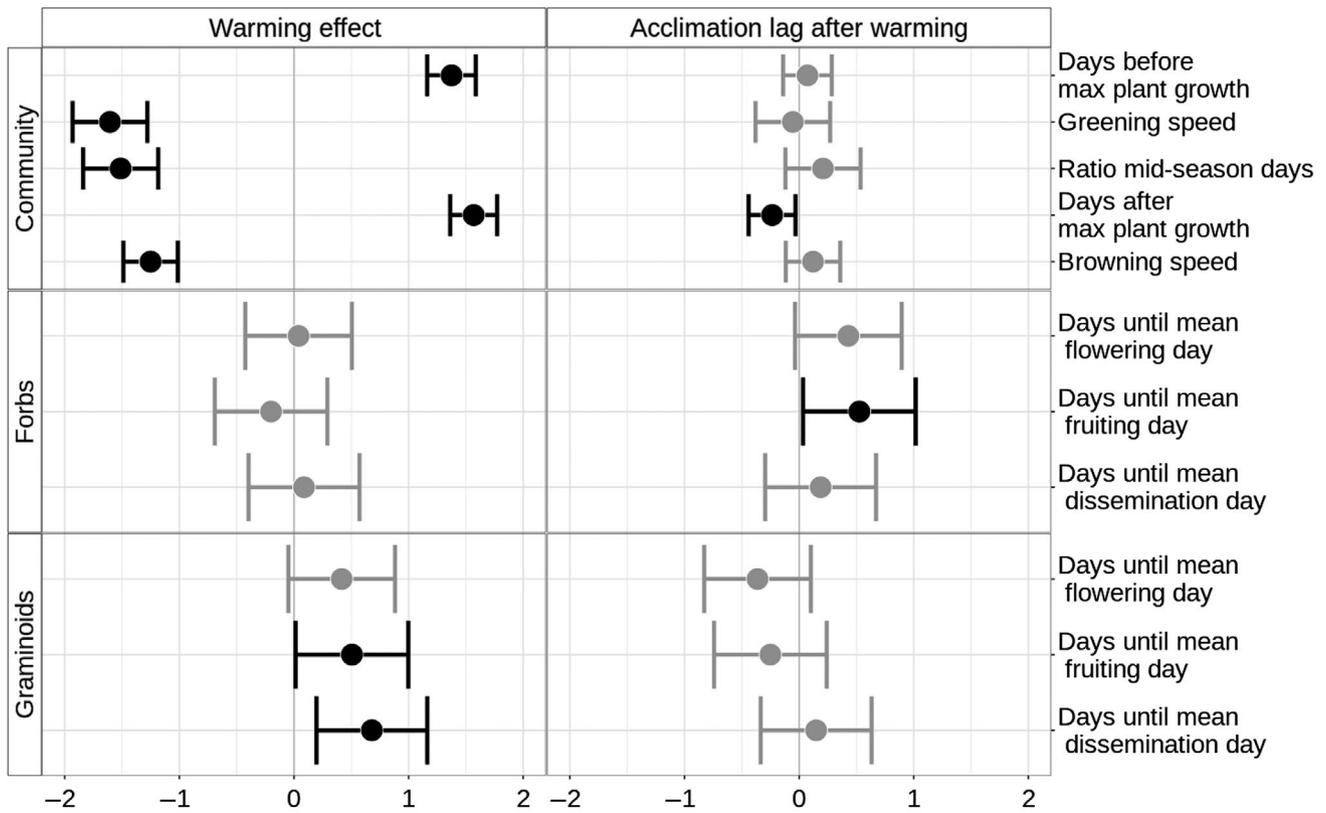
For performance-related indicators, at the community level, acclimation lags and deviations from shortest trajectories were comparable to warming and cooling (Figure 4; Figure S5a). After cooling, annual and mid-season plant growth could acclimate completely but early- and late-season plant growth failed to acclimate (Figure S3b). Forbs suffered even more from cooling than from warming and this was true for lag size and deviation from shortest trajectories. This trend holds for graminoids even though their acclimation lags were not significant.

4 | DISCUSSION

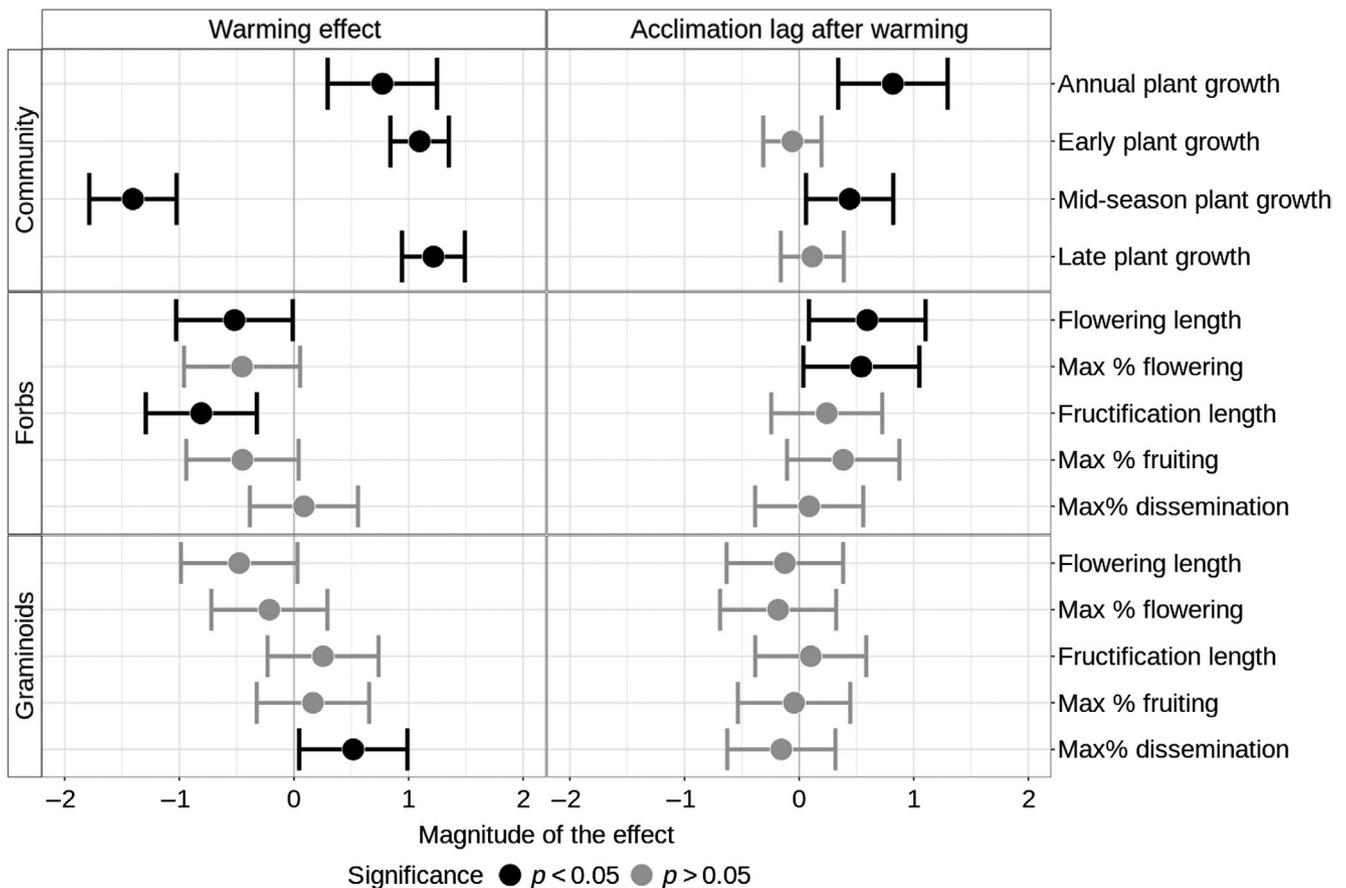
The phenology of mountain grasslands is known to strongly respond to climate change but so far little was known about remaining acclimation lags. Here, we built on our conceptual framework and a reciprocal transplant experiment to unravel whether phenological responses to warming and cooling follow the shortest trajectories to complete acclimation and how big remaining lags to complete acclimation are. We found that important aspects of phenology did not acclimate after 3 years of warming. This suggests that the projected climate warming is exceeding the limits of phenological plasticity of the here studied

FIGURE 3 Standardized effect sizes as the magnitude of warming effect and acclimation lag after warming at each focal organism level (community-level, species-level forbs and graminoids) for (A) timing of events and (B) performance related phenological indicators. Significant results are shown in black. Error bars represent 95% confidence intervals. Warming effect: AlpineWarmed-AlpineControl. Acclimation lag after warming: SubalpineControl-AlpineWarmed. For time-related indicators, positive warming effects indicate delayed phenology

(A) Timing of events



(B) Performance



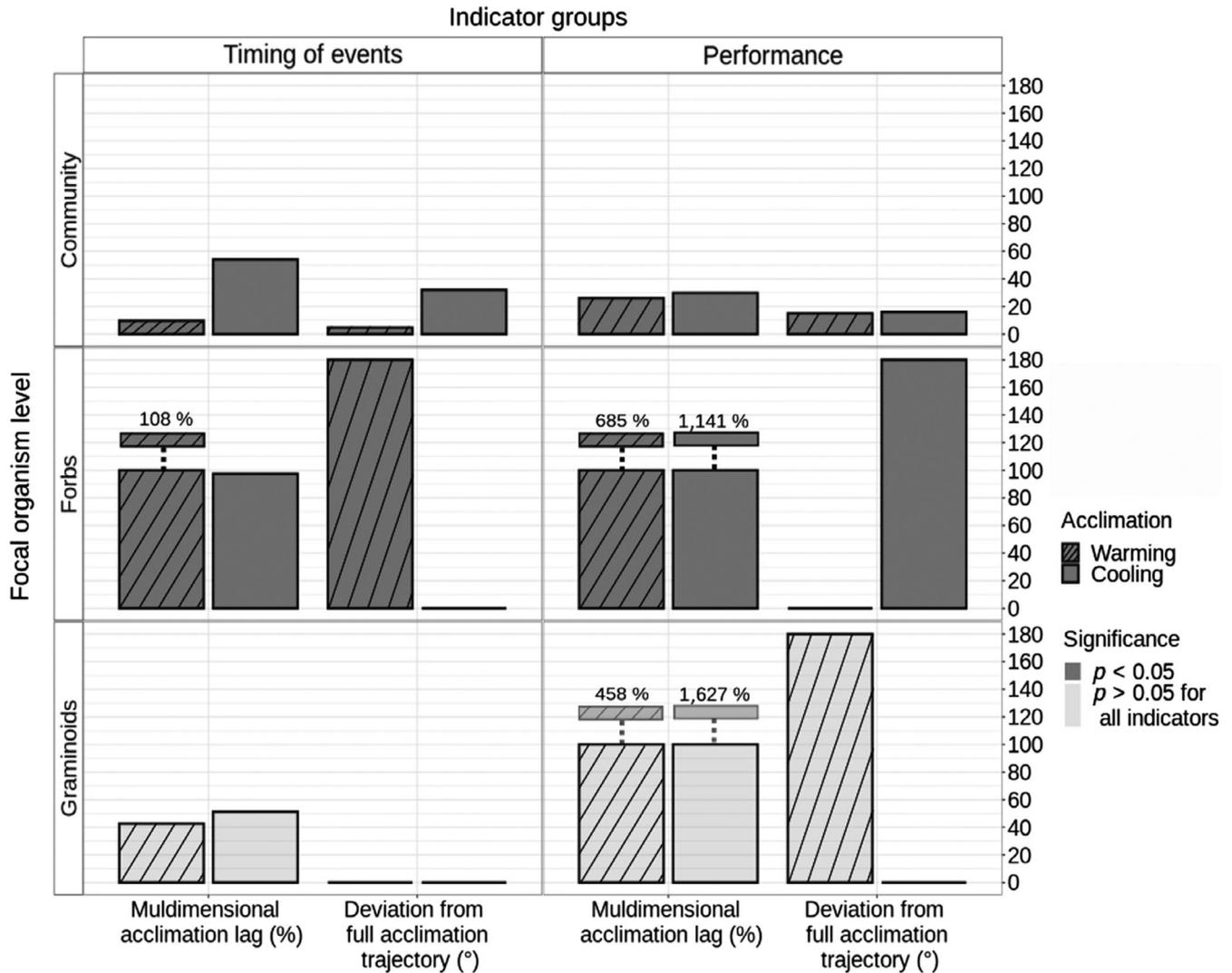


FIGURE 4 Multidimensional acclimation lag and the deviation from full acclimation trajectory for both indicator groups (timing of events and performance) and all organism levels (community-level, species-level forbs and graminoids). Acclimation for warming and for cooling are shown in stripes and solid bars, respectively. When all the indicators fully acclimate, they are shown in light grey (insignificant acclimation lag in the contrast analysis, see Figure 2)

grasslands. This was especially true for indicators that are key for demographic performance and thus success. Forbs and overall community phenology were most affected, while graminoids coped overall well with climate changes. Importantly, even though we observed strong warming effects, they were not strong enough to lead to complete acclimation and we also found that transient dynamics largely deviated from the shortest trajectory to acclimation, especially for forbs. Finally, the symmetry between acclimation lags under warming and cooling underlines that important phenological processes adjust too slowly. This might indicate that the functioning of mountain grasslands under the threat of climate change can be reversible in the short term.

4.1 | Timing of phenological events

Earlier works found that climate warming led to earlier phenology (experimental warming: Meng et al., 2018, 2019; review on existing

studies: Parmesan & Hanley, 2015; review on alpine ecosystem: Winkler et al., 2019) and faster plant growth (Wang et al., 2020). In apparent contradiction, our climate warming experiment promoted later phenology (i.e. later maximal plant growth, later starts of fruiting and dissemination periods of graminoids) and slower early-season increase in growth (i.e. slower greening speed). These warming effects allowed complete acclimation of the early- and mid-season timing of phenology to subalpine conditions for graminoids and communities. One major reason for this difference with other studies is that we used the growing season start and not calendar days as a reference (Johansson et al., 2013). Our main arguments for this choice are that the snow-free growing season is a major driver of alpine ecosystems (Choler, 2015), that plants physiologically respond to the first frost free days and that thus the comparison among study sites is ecologically less meaningful when it is based on calendar days. Another reason for our results is that with our in situ transplant experiment, we did not only manipulate temperature but

also the expected accompanying changes in snow cover and growing season length (Choler, 2015). In fact, once we calculated the warming effect on greening days based on calendar days, we found an advancement too (i.e. 24.85, with $p < 0.001$ according to two sample t test) but this reflects mainly the advancement of snow melt.

Our results are consistent with apparent strategies of alpine communities: alpine conditions force plants to squeeze life cycles in shorter growing seasons (Körner, 1999) and induce faster plant growth right after the snow melt that is later in the year and thus, plants experience higher air temperatures directly after the snowmelt (Jonas et al., 2008). Yet, with warming and longer growing seasons (just as in subalpine conditions), snowmelt is earlier, the protective effect of snow cover is lost and thus, lower air temperatures are accompanied by potential spring freezing events that together slow down plant growth in the early season and can kill flower buds and leaves of frost-sensitive species (Choler, 2018; Inouye, 2000, 2008). For the end of the growing season, we found in concordance with Wang et al. (2020) that plant communities could not sustain the high mid-season plant growth rates. Potential explanations are warming-associated increases in drought stress (Wang et al., 2020) (i.e. even though the airborne estimated water balance of precipitation and evapotranspiration is comparable between sites, *unpublished results*) or inherent allocation trade-offs (Johansson et al., 2013).

In sum, alpine plant communities adjusted well to warmer conditions and higher uncertainties at the beginning of the growing season but could not fully achieve their adaptation to faster cycles at the end of the growing season.

4.2 | Phenological indicators linked to performance

In our experiment, the warming of grasslands increased yearly plant community growth (i.e. photosynthetic activity approximated by NDVI curves) which is consistent with several earlier studies (Cao et al., 2015; Carlson et al., 2017; Wang et al., 2012; Yang et al., 2019) but in contradiction to Wang et al. (2020). Our observed yearly increase was due to increased early and late plant growth, despite reduced mid-season plant growth. While our early-season results coincide with those of Wang et al. (2020), they differ for the mid and late season (i.e. no change and decrease). Reasons might be the fact that they (a) could only record for 2°C of warming and (b) defined early and late seasons on the basis of months rather than considering yearly differences in seasonal dynamics (i.e. interannual differences in start and end of growing season). Here, we suggest that (a) when 3°C is exceeded, a negative warming effect can be imposed on mid-season community performance and (b) it is important to consider interannual differences in identifying the seasons and warming effects on them.

Interestingly, in our experiment these strong warming effects were mostly due to short-term responses of the communities, such as phenotypic plasticity, and not due to compositional changes of plant communities. As most species in our observed grasslands were perennials, limited species turnover took place in the first 3 years after transplantation (Figure S8).

Going a step further than merely describing the warming effect, we also showed that the significant increase in growth was not sufficient to close the acclimation lag completely. In other words, better-adapted grassland species originating from the subalpine area take better advantage of the more favourable climate and grow better over the year. In line with these results, it has already been shown that a positive demographic response to warming is not always able to prevent extinction (Sheth & Angert, 2018). The reason for the remaining acclimation lag is probably functional traits of subalpine communities (e.g. height, specific leaf area) being better adapted to the favourable climate than those of alpine communities.

The community-wide warming effects on growth do not necessarily translate into increased reproductive performance at the species-level (Doak & Morris, 2010). Earlier studies found idiosyncratic warming effects on reproductive performance at the species level. Some found an increase (Iler et al., 2019; Kudernatsch et al., 2008; Li et al., 2016), no change at all (Dorji et al., 2020) or a decrease (Aldridge et al., 2011; Gugger et al., 2015; Liu et al., 2012) depending on species and ecosystem and others identified species-specific responses (Wang, Wang, et al., 2014; Winkler et al., 2019). In our study, we could relate the species-specific responses to growth forms with forbs failing to acclimate to warmer conditions (i.e. shorter flowering period, fewer individuals flowering) but alpine graminoids performing as well as subalpine graminoids in warmer, subalpine climate. This is in line with independent Ellenberg indicator values (i.e. categorical values indicating the species' abiotic niche; (Bartelheimer & Poschlod, 2016) suggesting that the dominant forbs in our study system are much less tolerant to variation in temperature (and moisture) than the dominant graminoids (Figure S9). Specifically, we argue that problems of forbs to acclimate could be linked to: (a) disrupted vernalization (i.e. flower bud formation depends on low temperatures, especially during winter; (Liu et al., 2012), (b) more allocation of resources to somatic growth than to reproduction (Johansson et al., 2013; Liu et al., 2012), (c) shading created by graminoids that have the potential to grow taller than forbs.

The observed acclimation lag of forbs in flowering performance is prone to cascade to the other trophic levels, specifically to associated pollinators (Gezon et al., 2016) and thus to further disrupt functioning of warmed alpine communities. In addition, responses specific to growth form may also cause a community composition shift in favour of graminoids. This is in line with a recent global review on the ecological flexibility of graminoids in their climate and habitat range, their success in establishment and dispersal and ecological competitiveness due to their functional and physiological traits (Linder et al., 2018). Yet, such shift in communities also risks the well-being of the whole multitrophic network and ecosystem functioning through further reduction of pollination services (Burkle et al., 2013; Gezon et al., 2016). In our study site, we already found indications of a significant acclimation lag in pollinator diversity after 3 years of warming (Figure S10).

The short-term community-level and growth form-specific results point to expected long-term responses of mountain grasslands (Pironon et al., 2017), including range shifts and restructuring of communities.

With warming, we know that some plant communities will be able to track their climatic niche and some will not, either due to migration failures or the absence of niche space on mountain tops (Alexander et al., 2015, 2016; Matteodo et al., 2013). In a scenario where subalpine plant communities can track their climate but alpine communities remain within their current niche, alpine species may not be able to increase their demographic performance either in plant growth or in reproduction fast enough and will thus be outcompeted by the subalpine species (Alexander et al., 2015, 2016). The increase in community plant growth and the competitive exclusion of slower-growing alpine species will also change plant–soil feedbacks. According to the ‘fast–slow’ plant economics spectrum, faster growth is associated with more exploitative plant traits (and thus, functional strategies), especially under favourable environmental conditions (Martinez-Almoyna et al., 2020; Reich, 2014). Such an above-ground functional strategy shift towards the faster part of the economic spectrum will affect the micro-organisms involved in plant litter composition (e.g. higher bacteria:fungi ratio), will change their ecosystem functions (e.g. faster nutrient cycling) and will then feedback to the plant communities, potentially further accelerating changes (Bardgett & Wardle, 2010).

4.3 | Divergent warming effects

It has been recently highlighted that perturbations to an ecosystem's steady state can trigger transient responses of ecological relevance (Mari et al., 2017). The question is not only how long it will take until the new steady state is reached but also how strongly responses are initially amplified before decaying towards a final state. Here we demonstrate that warming effects, especially on the phenology of alpine forbs, can be not only divergent (Ryo et al., 2019) but can lead phenology far away from any acclimation. In line with a previous long-term study (Wu et al., 2012), we found a similar but weaker response at the community level. Overall, determining the divergent responses can inform us on the long-term trajectory of the warming effect, and can serve as an early warning signal for negative impacts on ecosystem functioning (Scheffer et al., 2009). For example, fine scale NDVI measurements on communities are relatively easy to implement and according to our results, monitoring only for community productivity can serve for early detecting shifts in communities and ecosystem functioning.

4.4 | Symmetry between acclimation lag after warming and cooling

We found most of the acclimation lags after warming and cooling to be symmetric, indicating some plasticity in phenological responses to climate change that is, however, not sufficient for short-term acclimation to realistic warming scenarios. We conclude that slow phenological acclimation to new thermal conditions is a general phenomenon for mountain plant communities. Notably, for some phenological indicators (i.e. timing of community growth and flowering performance of forbs), the acclimation lag after cooling was

significantly wider than for warming. It has been suggested earlier that for mountain grasslands, physiological limits at the cold thermal range edge are much more pronounced than at the warm edge (Pellissier et al., 2013). In addition, it has been shown that a major driver of the warm edge is competition (Alexander et al., 2015), which has not yet started to act at its full force in our experiment. However, decrease in flowering performance both with warming and cooling indicates that flowering phenology is highly sensitive at both ends of the thermal limits (Li et al., 2016; Wang, Meng, et al., 2014).

The question of symmetry might also have practical implications. With the advancing research on climate warming, the reversibility of the warming effect at many levels is still an open debate (Scheffer et al., 2001). The symmetric response between acclimation lag after warming and cooling can also inform us on the reversibility of the impacts of warming. Here, it seems like most of the warming impacts especially on above-ground productivity and flowering performance can be reversible in the short-term. However, we also acknowledge that these observed transient responses might be buffered by the ones at different levels or can even lead to other cascading effects or critical transitions.

5 | CONCLUSIONS

With our reciprocal transplant experiment on mountain grasslands, we revealed that community- and species-level phenological responses to climate warming were not enough for their complete acclimation to their new conditions in the short term, except for graminoids. These phenological acclimation lags probably impair other ecosystem functions, such as pollination and plant–soil feedbacks. Short-term acclimation lags, and especially strong deviations from acclimation trajectories, may also hint at long-term impairment of ecosystem functions and restructuring of communities. This emphasizes the importance of characterizing the size and direction of acclimation lags in upcoming global change research.

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CONFLICT OF INTEREST

The authors do not have any conflicts of interest to declare.

AUTHORS' CONTRIBUTIONS

B.B., W.T. and T.M. conceived the ideas and designed the methodology and led the writing of the manuscript; P.C. substantially helped with the interpretation of the results and design of the conceptual framework; A.S. and T.M. organized the fieldwork; M.-P.C., J.R., A.S. and T.M. established the protocol; J.R. managed the database; B.B., R.D.V., J.R. and M.-P.C. collected the data; B.B. analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.3r2280ggb> (Bektaş et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Chapter 2:

**Climate warming losers in
alpine grasslands are cold
adapted, drought intolerant
and smaller
[yet less conservative] than
their neighbors**

Climate warming losers in alpine grasslands are cold adapted, drought intolerant and smaller [yet less conservative] than their neighbors

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Abstract

Before vulnerable species become extinct under global warming, they are likely to change their local abundances. If these shifts in abundances are early warning signals, they also lead to community restructuring and alter ecosystem functions. Identifying winner and loser species under global warming is thus crucial should we want to mitigate future long-term impacts. Here, focussing on alpine grassland plants, we identified and characterized the winners and losers over five years of experimental warming based on changes in abundances. We found that there were more losers than winners and that relative losses generally exceeded gains. As expected, loser species were characterized as cold-adapted and drought-intolerant. They also were less conservative and smaller than their neighbors indicating that being the most conservative and tall was a beneficial competitive strategy. In contrast to the alpine winners, subalpine species successfully immigrating from outside of the plots tended to be more exploitative and moisture loving. These results highlight that typical alpine plants are losing in three ways under climate change. First, they suffer directly from new stress conditions, second, they suffer indirectly from shifts in competitive pressure in their natural communities and finally, as a potential extinction debt, they are threatened by the arrival of subalpine species.

Introduction

Climate is changing particularly rapidly in the European Alps: soil temperature is rising, summer droughts are becoming more frequent, and snow is melting earlier (Kotlarski et al., 2022; Scherrer et al., 2022). Some plant species are benefitting from more benign growth conditions due to longer growing seasons and higher energy input (Wang et al., 2020). Instead, others suffer from additional stress such as increased drought stress and more frequent early-spring freezing events (Dolezal et al., 2020). As a result the composition of many alpine grassland communities changed substantially over the last decades (Pauli et al., 2012). However, at the species level, it is still not clear which species will be the long-term losers of warming in these systems (Jacob et al., 2014). More importantly, if we can identify and understand the characteristics that make species a loser, we may better protect them in the future.

Mountain plant species can respond in several ways to climate warming: They can i) show adaptive plasticity, ii) “migrate” upslope, or iii) go extinct. While there is evidence that mountain plants show adaptive plasticity under warming for example in phenological (Bektaş et al., 2021; Stuble et al., 2021) and functional traits (Henn et al., 2018), it is still a matter of debate whether these mechanisms can protect them from warming in the long run and prevent species extinctions in local communities (Block et al., 2020; Cotto et al., 2017). Upward migration may provide an escape especially for species from lower elevations, but these migrating species then threaten species from higher elevations through competition (Körner, 2003; Parmesan & Yohe, 2003). Therefore, it is important to distinguish between species that successfully resist climate change locally and those that successfully invade novel communities and contribute to the homogenisation of ecosystems. For the moment, mountain summits get richer (Pauli et al., 2012; Steinbauer et al., 2018; Wipf et al., 2013) and local extinctions are so far rarely documented (Nomoto & Alexander, 2021; Rumpf et al., 2019). However, in situ changes of mountain species abundances in rich communities have rarely been tracked so far. An exception is the study of (Rumpf et al., 2018) who identified species winning and losing in abundance and range size in the European Alps under current climate warming based on community relevés. Although they could not directly show that climate change was the driving force as they relied on resampling of historical surveys, they found that winners overall outnumbered losers but that losers were overrepresented among high-elevation species. The challenge is thus to build a stronger identification and characterisation of loser and winner species in terms of abundance shifts to catch the early warning signals of possible species extinctions and assure better alpine biodiversity conservation.

Warming experiments, specifically whole community transplant experiments, might thus be particularly useful to determine winners and losers of climate warming because we can track the transient dynamics once the plants are warmed. However, addressing this question with such experiments remains a challenge, especially in mountain grasslands. Firstly, a recent study showed that changes in species' abundances in control communities could sometimes exceed the changes in treatment communities (Langley et al., 2018). Even without an experimental treatment, communities and populations are dynamic, succession and recovery after disturbance can continue several years and they can respond strongly to interannual climate effects (Langley et al., 2018). Secondly, perennial species that are dominant in mountain grasslands and are generally resilient to intra and interannual environmental variations may only slowly respond to warming treatments (Grime et al., 2008). Thirdly, measuring abundance shifts only between two years might not only result from experimental warming but also from interannual variations. For example, in two warming experiments at the same location but with a different timeline, Block et al. (2020) and Visakorpi et al. (2022) investigated species cover changes between the first and third experimental years: the former found more losers than winners and the latter found that the number of losers and winners were almost the same. This demonstrates that transient dynamics, interannual climatic variations and long life cycles may bias results. Hence, it is crucial to measure the multi-year trends in species' demographic changes under experimental warming relative to their interannual dynamics in control communities.

Once winner and loser species are identified, the crucial following question is why some species win and others lose under climate warming. The common strategy to answer this question is to investigate whether the demographic response of species to their abiotic environment and their biotic interactions with their neighbors could be predicted through their functional traits (Table 1). This assumes that traits are good proxies of eco-physiological characteristics (Onoda et al., 2017; Reich, 2014). For instance, observation-based studies found evidence that warm-adapted (Gottfried et al., 2012) and tall species in tundra ecosystems (Bjorkman, Myers-Smith, Elmendorf, Normand, Weiher, et al., 2018) increase their abundances under climate warming. Additionally, (Soudzilovskaia et al., 2013) found that species with conservative (i.e. high leaf mass per area and thick leaves) traits tend to increase in abundance in alpine ecosystems under ongoing warming, likely due to their better efficiency in surviving water deficit. However, despite the use of traits, the mechanisms behind these patterns still remain obscure. Are winner

species already pre-adapted to warmer and more dry conditions (i.e. they have the right combination of traits) or do species get a competitive advantage over their neighbors in acquiring light or soil nutrients more quickly under the novel conditions or both? Answering this key question has not received much attention so far since most studies investigating abundance changes due to climate change did not investigate proxies of biotic interactions explicitly. Yet, investigating whether there is a signal of hierarchical competition detectable through patterns of trait hierarchy between species and their neighbors should help disentangle the two mechanisms (Conti et al., 2018; Kunstler et al., 2012; Rixen et al., 2022).

Here, we addressed the above-mentioned challenges based on a multi-year transplantation experiment of alpine grasslands, simulating a 3°C warming, a temperature change expected in these mountains by the end of this century (Intergovernmental Panel on Climate Change (IPCC), 2022). In concordance with climate change predictions, our warming treatment also increased drought stress during summer in the alpine communities. We specifically asked: i) Which alpine species lose or win under the simulated climate warming? ii) What determines the decrease (loser) or increase (winner) in relative abundance under warming? iii) Is there a difference between alpine winners from the original communities and winners colonizing from a subalpine species pool?

Methods

Study site and experimental design

We performed a large transplant experiment in the French Alps in September 2016 (Bektaş et al., 2021) to simulate climate warming and a resulting increase in drought stress by moving plots from an alpine to a subalpine site. The alpine site “Galibier” (45°05'44"N 06°40'06"E at 2450 m altitude) and the subalpine site “Lautaret” (45°04'00"N 06°41'90"E at 1920 m altitude) are close to each other (~2km airline distance), have a similar orientation (South-East at alpine and South-South-West at subalpine site), bedrock (base-riched flysch) and soil (dystric cambisols). At the alpine site, communities were dominated by *Trifolium alpinum*, *Potentilla aurea*, *Plantago alpina*, *Carex sempervirens subsp. Sempervirens* and *Poa alpina*. At the subalpine site, communities were dominated by *Patzkea paniculata subsp. paniculata*, *Festuca nigrescens*, *Carex sempervirens subsp. sempervirens*, *Festuca laevigata*, and *Plantago maritima subsp. serpentina*. We transplanted 10 replicates of 4m² turfs of vegetation with at least 20-30 cm of their intact belowground parts and the surrounding soils from the alpine to the

subalpine site (AlpineWarmed plots). For the transport, each turf was cut in 4 x 1m² pieces and then reassembled in their original composition when re-planted. To control for the transplantation stress, we also horizontally transplanted 10 intact 1m² turfs at the alpine site (AlpineControl plots). Control and warmed plots were in close proximity of a few meters. Around the turfs, we placed water-permeable root barriers to avoid root ingrowth from the surrounding natural vegetation. At both sites, cattle and sheep were excluded by electric fences. More details on the experimental design can be found in Bektaş et al. (2021). During the years (2017, 2018 and 2021) of data collection, average annual soil temperature at the subalpine site was 3.53°C warmer than at the alpine site, average July soil temperature was 3.11°C warmer and the snow free season was 56 days longer. In 2021, average summer moisture was 13 % (+/-1 %) lower in AlpineWarmed than in AlpineControl plots.

Vegetation surveys

At the peak of plant growth (July 2017, 2018 and 2021), we identified and counted all individuals that touched a 4mm metal stick (here after, pinpoint) at equally spaced points (10 cm distance) in both warmed plots (300 points per 4m² plots) and control (100 points per 1 m² plots). Individuals that could be identified only at the genus level were excluded from further analysis (2 % of 30,891 individuals touching the pinpoint). The pinpoint counts were performed on a square metallic grid which allowed us to know the exact position of pinpoints and identified individuals. Overall, 100 different species were recorded across the three years of sampling. To avoid that stochasticity or measurement errors bias results we excluded 23 very rare species that were present only in a single year and in less than five AlpineControl plots (e.g. *Vaccinium myrtillus* present only in a single plot in 2017) and another species that passed the rareness criterion but was extinct in the control plots after 2017 (*Polypogon viridis*) and thus remained with 76 species. We identified i) 29 colonizers as species that appear in AlpineWarmed communities but were never present in AlpineControl communities and ii) four extinct species as species that were absent from AlpineWarmed but present in AlpineControl communities in 2021 in more than five plots .

Calculating changes in abundance trends due to warming

We excluded colonizer species from the analysis of abundance changes as they were not part of the original communities but subalpine species. As number of pinpoints differ between warmed and control plots, we calculated the abundance of a species *i* relative to the number of pinpoints in a plot *j*:

$$\text{Relative abundance}_{i,j} = \left(\frac{\text{number of pinpoints in } j \text{ where } i \text{ is present}}{\text{number of pinpoints in } j} \right) \times 100 \quad (\text{Eq. 1})$$

For each of the 47 alpine species, we built a linear mixed-effects model (LMM) with relative abundance as the response variable, treatment (AlpineControl or AlpineWarmed), experimental year (as a numeric variable) and their interaction as fixed effects and repetition as a random effect (Fig. 1C & D). From each species-specific model, we extracted the interaction effect between treatment and years and used it in the following analyses to describe the change in temporal abundance trends due to warming (“change in abundance” hereafter). In other words, if species gain less (or lose more) over time in AlpineWarmed than in AlpineControl, then the interaction effect is negative meaning that warming leads to a relative abundance loss compared to the control (note that abundances can still be increasing in both treatments as long as the increase is lower in AlpineWarmed than in AlpineControl), and vice versa. Finally, we identified species with significant positive interaction terms as winners and species with significant negative interaction terms as losers. All analyses were run with the `nlme` and `emmeans` package in R (Lenth, 2022; Pinheiro et al., 2022; R Core Team, 2022).

Intrinsic characteristics: Functional traits and Landolt indicator values

We considered two categories of species’ traits known as good proxies of species’ eco-physiological characteristics: Species functional traits that can be directly measured at the individual level and are available at the species level from trait databases (vegetative height, leaf dry matter content, leaf carbon to nitrogen ratio and specific leaf area), and Landolt indicator values that summarize expert knowledge on the abiotic limits of species (“thermophily” captured by the Landolt’s temperature indicator and “moisture-requiring” captured by Landolt’s moisture indicator (Bartelheimer & Poschlod, 2016). We extracted functional trait data from our in-house trait measurements (Brun et al., 2022; Thuiller et al., 2014) (<https://originalps.osug.fr/>) and complemented the missing data from the TRY database (Kattge et al., 2020) and the Tundra Trait database (Bjorkman, Myers-Smith, Elmendorf, Normand, Zamin, et al., 2018). These interspecific traits were measured mostly in mountain grasslands and in the case of a lack of data, we completed them by prioritizing similar ecosystems such as mountains or tundra. We log-transformed and standardized all traits (mean $\mu = 0$, standard deviation $\sigma = 1$, Fig. S2). Weigelt et al. (2021) and (Díaz et al., 2016) showed that vegetative height on one hand, and traits linked to a conservative-exploitative strategy trade-off (called “conservative dimension” hereafter), on the other hand, are two different dimensions of plant functional strategies that

together capture well all above ground trait variations. To calculate values for the conservative dimension, we built a principal component analysis (PCA) from leaf dry matter content, leaf carbon to nitrogen ratio, and specific leaf area (Fig. S3). Horn's parallel analysis (`paran` package in R) confirmed that the first PCA axis was significant and sufficient to represent trait variation along the conservative dimension (Franklin et al., 1995) and explained enough variation to be useful (53%, Fig. S3). We thus kept two functional trait dimensions: vegetative height, which relates to the growth capacity and competitive advantage for light acquisition, and our first PCA axis as a conservative dimension which represents plants' nutrient and water acquisition strategies (Table1, Fig. S4). Among our 76 identified loser and winner species, there were still some species lacking trait values (3% for the temperature indicator and the moisture indicator, none for vegetative height, 12% for the conservative dimension). We filled these remaining gaps with the mean of the corresponding trait values across all species for which trait data were available.

Table 1: Trait variables that potentially determine the change in abundance under warming and drying (in brackets the variable name used in the following), associated mechanisms, and hypotheses. Conservative dimension: integrated trait from leaf dry matter content, specific leaf area, and leaf carbon to nitrogen ratio.

Variables	Mechanism tested		Hypotheses (loser species are ...)	References
	Intrinsic characteristics: Adaptation to new conditions	Extrinsic characteristics: Hierarchical competition with neighbors		
Landolt temperature indicator (Thermophilly)	X		... cold-adapted	(Gottfried et al., 2012; Rumpf et al., 2018)
Landolt moisture indicator (Moisture-requiring)	X		... drought intolerant	(Visakorpi et al., 2022)

Vegetative height (Vheight)	X	X	... shorter and thus have problems to i) cool down under heat , ii) gain the extra light needed to maintain their carbon balance under warming or iii) compete for light	(Bjorkman, Myers-Smith, Elmendorf, Normand, Weiher, et al., 2018; Crawford et al., 2012; Kunstler et al., 2012; Romero-Montepaone et al., 2021)
Conservative dimension (Conservative)	X	X	... either more conservative and thus slow in growth and nutrient acquisition or more exploitative and thus less drought tolerant	(Blumenthal et al., 2020; Onoda et al., 2017; Soudzilovskaia et al., 2013; Visakorpi et al., 2022)

Extrinsic characteristics: Trait hierarchies in closest neighborhood

Not only species trait values *per se* but also the difference to the neighbors can determine a species success. Species that are taller than their neighbors should have better access to light and may have a competitive advantage (Kunstler et al., 2012). Similarly, species with more exploitative traits than their neighbors should outcompete them in benign conditions while species that are more conservative than their neighbors should outcompete them under stressful conditions (Wright et al., 2004). We tested these patterns of trait hierarchies for all 43 non-extinct alpine species and for the 29 alpine colonizers in AlpineWarmed communities in 2021. First, we calculated for each individual and trait (vegetative height and conservative dimension) the mean trait difference between the focal individual and all individuals in the close neighborhood (i.e. touching the same pinpoint or one of the four pinpoints in 10 cm distance). We then calculated the median per species and trait as an indicator of the species' prevalent positions in the two trait hierarchies. Higher values mean higher positions, i.e. the species tends to be taller (i.e. Vheight hierarchy hereafter) and/or more conservative (i.e. conservative hierarchy hereafter) than its neighbors.

Statistical analyses

We tested how the change of abundance due to warming (i.e. losing and winning tendencies) depended on species intrinsic and extrinsic characteristics and their interaction with linear models for all alpine species except for extinct species for which we had no trait hierarchy information. To avoid problems of multicollinearity, we kept conservative hierarchy in the variable list but removed conservative dimension as the two were highly correlated ($r=0.96$). All other variables could remain in the model (variation inflation factor <5).

We then build a global linear regression model with abundance change as response variable and thermophily, moisture-requiring, vegetative height, height hierarchy, conservative height (5 main effects) and all their two-way interactions as explanatory variables (10 interaction effects). To determine variable importances, we adopted a multimodel inference approach (Burnham & Anderson, 2007) which is based on modeling all possible sub-models from the global model (dredge function in MuMIn package) (Symonds & Moussalli, 2011). We favored this approach instead of a stepwise regression to avoid i) over-complicated models, ii) optimizing for a single solution (i.e. several combinations of variables —sometimes with completely different variables— are likely to give similar AIC or BIC, but only one will be selected as the ‘optimal’ solution), and iii) strong a priori hypotheses that could be conflicting due to different effects of warming and drought. The variable importance was then calculated as the sum of all the Akaike weights w_i (Eq.3) of sub-models where the variable was present.

$$W_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r)} \quad (\text{Eq. 3})$$

$$\Delta_i = AIC_i - \min AIC \quad (\text{Eq. 4})$$

where AIC_i is the AIC of the sub-model i , and $\min AIC$ is the smallest AIC value in the set of models. w_i (between 0-1) is thus considered to be the probability of a sub-model being the best approximated model. The more a variable is involved in sub-models with strong w_i , the more important it is. This approach based on sets of multiple sub-models is far more robust than inferring variable importance based on a single stepwise selected model (Burnham & Anderson, 2007).

Results

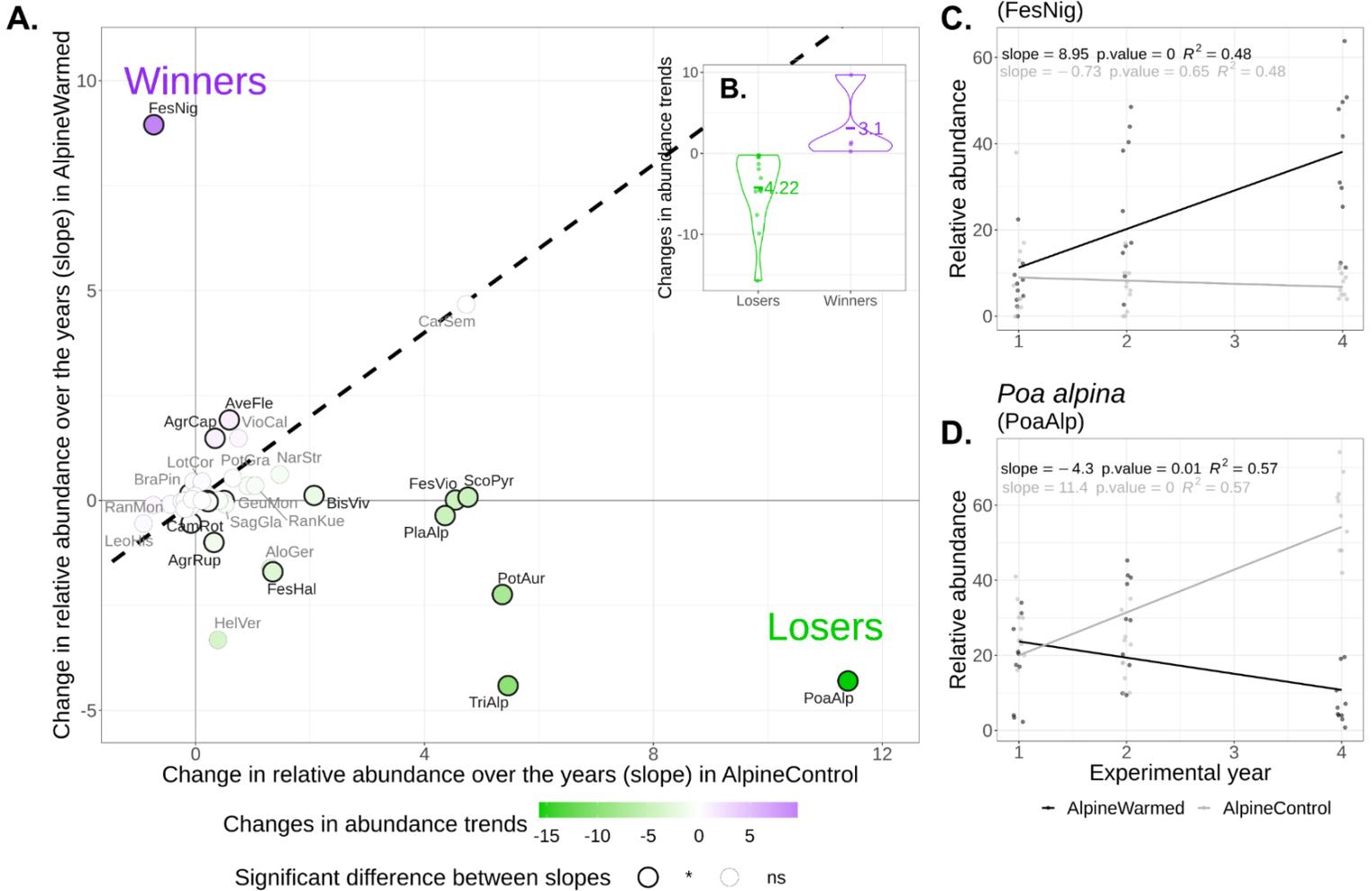


Fig. 1: Loser (green) and winner (violet) alpine plants under experimental climate warming. **A.** Change in relative abundance over the years (slope) in AlpineControl communities vs. in AlpineWarmed communities. All the species that have a significantly lower (higher) slope in AlpineWarmed communities than in AlpineControl communities were identified as loser (winner) species (in black contour). Changes in abundance trends were calculated for each species as the difference between the slopes in AlpineWarmed and AlpineControl communities. Stronger green (violet) indicates a stronger losing (winning) trend. **B.** Changes in abundances for each category only for species that are identified as winners (losers) (i.e. significant difference between slopes). The mean values are indicated on the violin plots. **C.** An example of a winner: Its relative abundance significantly increased over the years in AlpineWarmed communities while it was constant in AlpineControl. **D.** An example of a loser: its relative abundance decreased in AlpineWarmed communities while it increased in AlpineControl communities.

Which alpine species lose or win under the simulated climate warming?

Among 47 alpine species, we identified 13 significant losers (with one of them extinct) and 4 significant winners (i.e. significant negative and positive interaction effects between years and treatment, respectively, Fig. 1A). There were not only more loser species but absolute abundance decrease (-4.22 ± 1.26) was higher than absolute increase (3.10 ± 2.27) (Fig. 1B). For example, the winner *Festuca nigrescens* (FesNig) significantly increased in relative abundance (slope = 8.95) in AlpineWarmed communities while it was constant in AlpineControl (Fig. 1C). *Poa alpina* (PoaAlp) significantly decreased in relative abundance (slope = -4.3) in AlpineWarmed communities while it increased (slope = 11.4) in AlpineControl. *Myosotis alpestris* went extinct in all AlpineWarmed but had an increasing trend (slope = 0.21) in AlpineControl. The other three extinct species were no significant losers as their abundance was decreasing in AlpineControl as well.

What determines abundance changes under warming?

According to the multimodel inference, the most important intrinsic species characteristics linked to a decrease in abundances under warming was cold-adaptation (i.e. low thermophily, most important variable), moisture requirement (4th most important variable) and being small (5th most important variable, Fig. 2). The two trait hierarchies were similarly important as the intrinsic species characteristics, with abundances decreasing under warming for species surrounded by neighbors with more conservative strategies (2nd most important variable) and by taller species (3rd most important variable, Fig. 2). Notably, interactions between species characteristics did not seem important for explaining abundance changes under warming thus underlining that there were no trade-offs in addition to the already considered height and conservation dimensions.

Is there a difference between alpine winners and subalpine colonizers?

As we only observed 4 significant winner species, statistical comparisons between winners from the original alpine communities and the 29 colonizers from the newly surrounding subalpine site are limited. However, some differences in species characteristics are striking: While alpine winners tend to be conservative and more conservative than their neighbors as well as drought tolerant, subalpine colonizers are exploitative species and more exploitative than their closest neighbors as well as moisture lovers (Fig. 3).

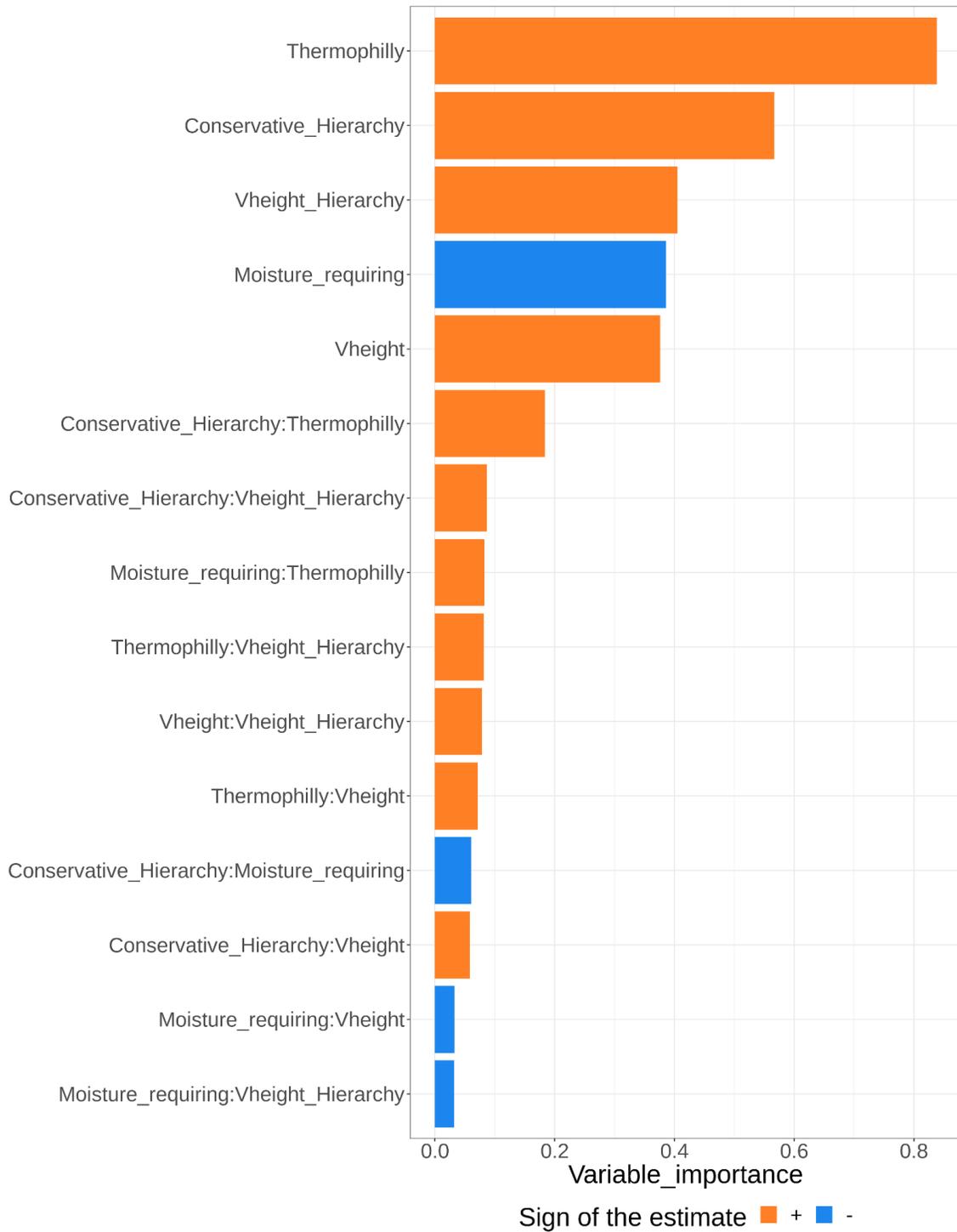


Fig. 2: Variable importance in explaining the changes in abundance trends under warming. Positive (in orange) and negative (in blue) coefficient estimates of the averaged model after multimodel inference are shown. Thermophilly: Landolt temperature indicator, Moisture-requiring: Landolt moisture indicator, Vheight: Vegetative height, Conservative:

Integrated trait of specific leaf area, leaf dry matter content, leaf carbon nitrogen ratio;
 Hierarchy: Functional difference between species and its closest neighbors (positive values indicate that species are at the top of the hierarchy, for example the species is taller and/or more conservative than its neighbors.)

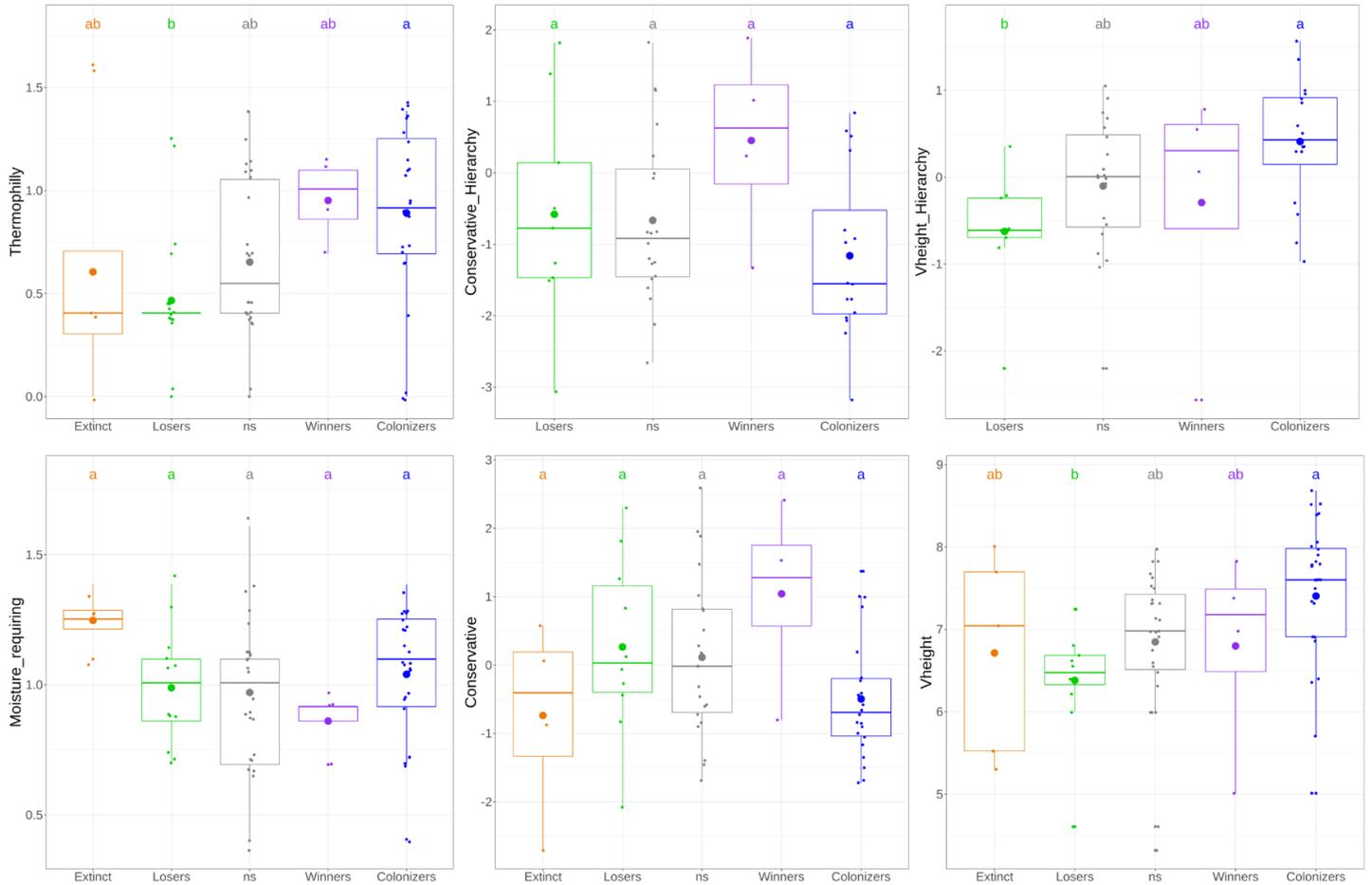


Fig. 3: Intrinsic and extrinsic characteristics of extinct species (orange), losers (green), winners (violet), colonizers (blue) and species with no significant change in abundances (ns, gray). Mean values per category are indicated with a larger point. The letters indicate results from Tukey's test. Note that extinct species do not have hierarchies as they were absent in the AlpineWarmed plots.

Discussion

Climate will be hotter and drier in the future but who will be the losers and winners of these changes? Here, we experimentally simulated these changing climatic conditions in alpine grasslands and found that many more alpine plant species will be losers than winners and that abundance decreases will be stronger than increases. Losses will be especially strong among cold-adapted and moisture loving species that are smaller and less conservative than their closest neighbors. However, in addition to the few winning alpine species there are a number of new species from subalpine grasslands that may colonize. While the few winning alpine species were conservative and drought resistant, the many novel colonizers were exploitative and moisture lovers, thus showing an entirely different functional strategy. The fate of alpine grassland species will thus depend not only on their own ability to acclimate to the new climate and to the changing game of competition in their familiar neighborhood, but also on their ability to withstand novel competitors.

Climate change in alpine grasslands is strong and known to affect plant community diversity and structure. But any determination of winners and losers needs to disentangle high interannual climate variations (Körner, 2003) from multi-year trends as well as trends caused by warming from other background trends (e.g. due to increased nitrogen atmospheric deposit and higher atmospheric carbon dioxide). An additional challenge is that species are perennial and may cushion stress in the short term by their reserves. Here, we compared abundance trends over years in control communities to those in warmed and dried communities. Indeed, we found that without this control we would have created completely misleading results (Langley et al., 2018). For example, *Festuca violacea* (FesVio) may have been falsely identified as a winner as its relative abundance increases under experimental warming. However as its abundance increases even more in its original alpine conditions this species is rather a loser.

Based on our careful determination of winners and losers we could then show that more alpine plants suffer than benefit from warming (13 losers, with 1 of them extinct, vs. 4 winners) and that average relative abundance decrease was stronger than increase. However, in addition, 29 subalpine species from lower altitudes were able to colonize the warmed plots underlining that not species richness itself but rather the alpine life form will be compromised by warming. In line with these results, earlier observational studies found that many mountain species can profit from changing conditions by increasing their abundances and, to a smaller degree, extending their ranges (Rumpf 2018), thus increasing species diversity at mountain tops (Steinbauer et al.,

2018). However, the higher the altitude the less profit the species originally occurring here and alpine species lose (Rumpf 2018). So far, despite abundance and range losses, alpine species seem to resist (Steinbauer et al., 2018) and extinctions have only been occasionally documented (Nomoto & Alexander, 2021; Rumpf et al., 2019). Yet, many researchers assume that these observations are transient (Alexander et al., 2018; Svenning & Sandel, 2013) and present an extinction debt (Tilman et al., 1994) with extinctions just temporally lagging behind abundance losses (Block et al., 2022; Losapio et al., 2021; Nomoto & Alexander, 2021; Watts et al., 2022). Such lags could occur i) due to the longevity of many species, ii) due to interannual variability and iii) because indirect effects through changing competition landscapes require the competitors to arrive before they can outcompete less well adapted species (Nomoto & Alexander, 2021). In our experiment, subalpine species were in the meadows just next to the warmed turfs and indeed 29 subalpine species were able to successfully colonize the warmed alpine plots. Potentially due to this accelerated speed up in novel competition landscapes we also observed the extinction of four species (even so only one of them was a significant loser indicating that the others were already rare in alpine conditions), thus, supporting the hypothesis of an extinction debt.

Changes in abundances are not only potential early warning signals for extinction debts but they can cascade to multitrophic interactions and ecosystem functions especially if they are linked to community trait shifts. As expected, we found that winning and losing was closely linked to traits and trait hierarchies. Cold-adapted, moisture-loving and short alpine species suffered the most under experimental warming. This is in line with previous studies that revealed a thermophilization phenomenon in the European Alps (Gottfried et al., 2012; Gritsch et al., 2016). Coherent with the fact that conditions got not only warmer but also drier in our experiment, losing was linked to being a moisture lover and extinct species were even stronger moisture lovers than surviving losers. Such interdependencies of multiple stress factors, such as warming and drought, have already been highlighted in other studies (Myers-Smith et al., 2019). Finally, short species suffer as they cannot i) enhance evaporative leaf cooling (Crawford et al., 2012) and/or grow taller in order to protect reproductive organs from heated soils, and ii) access enough light to counterbalance the negative carbon balance due to enhanced respiration and inhibited photosynthesis under warming and drought (Romero-Montepaone et al., 2021).

We found that, besides these physiological limits, loser species were also suffering from inferior positions in trait hierarchies with their direct neighbors. Such signals of competitive interactions

were in magnitude equally important as intrinsic traits thus supporting literature underlining the role of novel competitive landscapes in climate change responses (Alexander et al., 2015). In our experiment we found that losing alpine species were smaller (and less conservative) than their direct neighbors, indicating that light (as well as water and nutrient) acquisition under stress became more important limiting factors. While our data strongly support the conclusions related to height hierarchy, results for the conservative hierarchy need to be interpreted with care as this extrinsic characteristic is strongly correlated to the intrinsic conservative dimension. The message that conservative strategies are beneficial remains even if it is difficult to say whether this is due to abiotic or biotic filtering or both. Previous studies showed already that conservative leaf traits can be a winning strategy under warming (Bjorkman, Myers-Smith, Elmendorf, Normand, Weiher, et al., 2018; Soudzilovskaia et al., 2013; Visakorpi et al., 2022). In fact, conservative leaf traits can help to better acquire nutrients under warming-associated stress such as early exposure to freezing events and drought (Weil et al., 2021). For example, investing in thicker and stiffer cell walls help sustaining turgor under drought (Blumenthal et al., 2020; Onoda et al., 2017). Interestingly, while the typical alpine winner in our experiment was more conservative and taller than the neighbors, the typical subalpine colonizer was exploitative and still taller. This different winning strategy made subalpine colonizers more successful than alpine winners. In fact, increased community vegetation height, migration of taller species towards arctic and demographic success of tall species are already observed phenomena under warming (Bjorkman, Myers-Smith, Elmendorf, Normand, Weiher, et al., 2018; Elmendorf et al., 2012). If loser species are already suffering under subtle changes in their natural neighborhoods due to increased abundances of taller neighbors, they may be under risk of extinction once the upslope migration of even taller and more exploitative lowland plants is accelerated under future climate warming.

It remains an interesting question why strategies between alpine winners and subalpine colonizers differ. A potential answer could be that alpine species can only acclimate in the limits of their phenological plasticity and may not be able to reach the optimal strategy developed by the better preadapted subalpine colonizers. For example, it was shown in earlier studies that graminoids can outperform forbs under experimental warming due to their higher phenological plasticity (Bektaş et al., 2021). Indeed, the best three winners in our study were graminoids (including *Festuca nigrescens* (FesNig) , also a species studied in (Bektaş et al., 2021)) . However, we also found significant losers in graminoids (e.g. *Festuca violacea* (FesVio) and *Poa alpina* (PoaAlp)) and a significant winner in forbs (*Antennaria dioica* (AntDio)).

Nevertheless, phenological plasticity may contribute to demographic acclimation at species level but it is probably not the only determining factor and it may not lead to an optimal strategy (Block et al., 2020). This raises the question of if the identified alpine winners are perhaps only transient winners until subalpine colonizers are abundant enough to take over?

Our study can be further improved for understanding the factors of losing and winning tendencies. Firstly, here we only assessed the importance of species' above-ground traits, however root traits could also play an important role in species' demographic success especially under drastic environmental changes. For example, species that are highly collaborative with their fungi associates can also be resilient. Secondly, in this study, we do not account for intraspecific variability and plasticity in functional traits. Species that are not plastic in their functional traits to acclimate to new environmental conditions might also be losers of climate warming.

Conclusion

While other work has shown that mountain vegetation can even profit from climate warming in terms of increased species richness and winner species, here we highlight that this is not the case for alpine grasslands. Alpine plant losses clearly outnumbered gains. Results highlight that these losses and gains may be driven by both the adaptation of functional traits to the new climate and shifts in competitive hierarchies. Thus, climate warming does not only mean that we risk losing species but we will also lose parts of the functional setup, such as cold-adapted, short species and the specific ecosystem functions that they provide. Approaches that can provide early warning signals of these potential losses are thus of utmost importance for predicting and protecting alpine plant life.

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Chapter 3:

A spatially explicit trait-based approach uncovers changes in assembly processes under warming

A spatially explicit trait-based approach uncovers changes in assembly processes under warming

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Abstract

Understanding the reassembly of plant communities under climate warming requires deciphering the processes behind observed diversity patterns. Here, we introduce a novel framework that integrates spatially explicit sampling and plant trait information linked to resource acquisition strategies to quantify the strength of community assembly processes. More specifically, by accounting for the spatial distance between individuals, our framework allows disentangling the potential signals of environmental filtering from those of biotic interactions and symmetric competition from hierarchical competition. Applying it to an elevational transplant experiment in the French Alps, we found joint signals of environmental filtering and symmetric competition in subalpine and alpine communities. Signals of environmental filtering were generally stronger in alpine than in subalpine communities and warming significantly reduced this filter for most traits. Signals of competition dependent on traits and treatments. Symmetric competition was prevalent in alpine communities (in vegetative height and seed mass), while subalpine communities showed signals of both symmetric (in leaf dry matter content) and hierarchical competition (in specific leaf area and leaf carbon to nitrogen ratio). Warming increased the signal of competition (increasing strength for vegetative height and adding a competition signal for leaf dry matter content). Our framework highlights the importance of explicitly accounting for spatial distances for disentangling diversity patterns linked to different assembly processes in plant communities.

Introduction

Climate change alters the composition and functioning of plant communities (Harrison, 2020; IPBES, 2019). In particular, it affects plant individuals directly but also indirectly through changes in their biotic neighbors: Winners will continue losing their less adapted neighbors that decline in abundance or become extinct (Román-Palacios & Wiens, 2020; Urban, 2015). Moreover, new plant species will become neighbors due to asynchronous and species-specific range shifts, such as in mountains (Alexander et al., 2015; Rumpf et al., 2018). The interplay between the direct effects of climate change and the induced changes in biotic interactions is thus key to fully understand and predict future plant communities' reshuffling. However, we are still far from being able to disentangle the signals of jointly acting environmental and biotic processes behind observed diversity patterns (Münkemüller et al., 2020).

According to the original community assembly framework, environmental and biotic processes filter which species from a regional species pool can succeed in local communities (Keddy, 1992). These filters are expected to leave specific patterns in the functional trait structure of communities (Fig. 1.A.; Keddy, (1992); McGill et al. (2006)). On the one hand, environmental filtering should lead to trait convergence by selecting for the limited number of viable functional strategies (Cornwell et al., 2006). On the other hand, when competition increases with functional similarity (i.e. symmetric competition) we should observe trait divergence as coexisting plants must find distinct functional strategies to reduce the competition for limited resources (e.g. water, nutrients, and light; MacArthur & Levins (1967)). For plants a multitude of processes exist that may lead to limiting similarity. For example, a required resource like nitrogen exists in different forms in the soil. Some plant species (e.g. with thinner and strongly branching roots) have a root system well equipped for direct access to the inorganic nitrogen pool while others with opposite traits invest in the collaboration with mycorrhizae and thus, in the indirect access to the organic nitrogen pool (Weigelt et al., 2021). Similarly, trade-offs between acquisition

strategies are important: A trade-off between light acquisition and biomass allocation strategies allows the coexistence of tall and short species in herbaceous communities (Hirose & Werger, 1995) and a trade-off between light and nutrient acquisition strategies can lead to divergent patterns of species' nitrogen contents (Hirose & Werger, 1994).

Despite its vast applications, the original community assembly framework was criticized early on. Firstly, it was argued that expectations should not be oversimplified. For example, competition can lead to convergent traits due to hierarchical competition, when certain functional strategies have the ultimate competitive advantage while others are excluded. Such trait hierarchies are shown to be established especially in the case of competition for light (Kunstler et al., 2012; Mayfield & Levine, 2010). As to the environmental filtering, it can lead to divergent traits under strong small-scale environmental heterogeneity (Willis et al., 2009). Secondly, the framework is insufficient to reveal simultaneously acting assembly processes (Münkemüller et al., 2020). Thirdly, assembly processes depend on spatial scales and different processes are likely to act at different scales. While it is difficult to identify the most relevant scales, different scale choices can lead to contradictory results (Cavender-Bares et al., 2006; Chalmandrier et al., 2017; Münkemüller et al., 2012). In fact, instead of reflecting species coexistence patterns, the chosen scale of the analysis might only reflect co-occurrence patterns which are not enough to unravel assembly processes (Blanchet et al., 2020). For example, biotic filters may be overlooked if distances between studied individuals are too large. Despite the awareness that scale can be the key in revealing community assembly rules and in addressing the above-mentioned issues, attempts to develop a spatially-explicit approach are so far limited to either comparing two opposing scales (Carboni et al., 2013; Cavender-Bares et al., 2006) or to adhoc manipulations of the dataset and/or species pool (Bello et al., 2013; Chalmandrier et al., 2017)) with the exceptions of Trisos et al. (2014) and Xu et al. (2021) who however did not develop a stringent spatially-explicit framework. In addition, if relevant scales

for environmental and biotic filters are unknown, we require a continuous spatially-explicit sampling protocol and trait-based diversity analysis to disentangle assembly processes.

Here, we developed such a spatially continuous trait-based framework of community assembly (Box 1). By studying the relationship between spatial and functional distances between focal and neighbor individuals, we detected the signals of dominant processes acting at community scale and disentangled signals of environmental filtering from those of biotic interactions and symmetric competition from hierarchical competition. We applied our framework to a two-year transplant experiment in mountain grasslands where both environmental filtering and competition filters are expected to act in concert (Scherrer et al., 2019) and their relative strengths should depend on the severity of the environmental stress (Bertness & Callaway, 1994; Louthan et al., 2015; Sundqvist et al., 2013). We tested the following hypotheses using functional traits related to stress tolerance and competitive ability:

(H1) Environmental filtering is stronger in alpine than in subalpine grasslands due to more severe alpine conditions (i.e. colder air and soil temperature, freezing events and shorter growing season);

(H2) Competition is stronger in subalpine than in alpine grasslands due to more benign conditions and higher productivity.

(H3) With climate warming the strength of environmental filtering weakens and the strength of biotic filtering strengthens. We expect the opposite for cooling. As weak or temporally changing environmental and biotic filters may rather induce abundance changes than local extinctions or colonizations, we expect that all patterns are stronger when they are not only based on presence-absences but are weighted by local

abundances (Hu et al., 2021; J. Wang et al., 2021). This should be especially the case for the transplanted communities as they are still adjusting to new conditions in a transient phase.

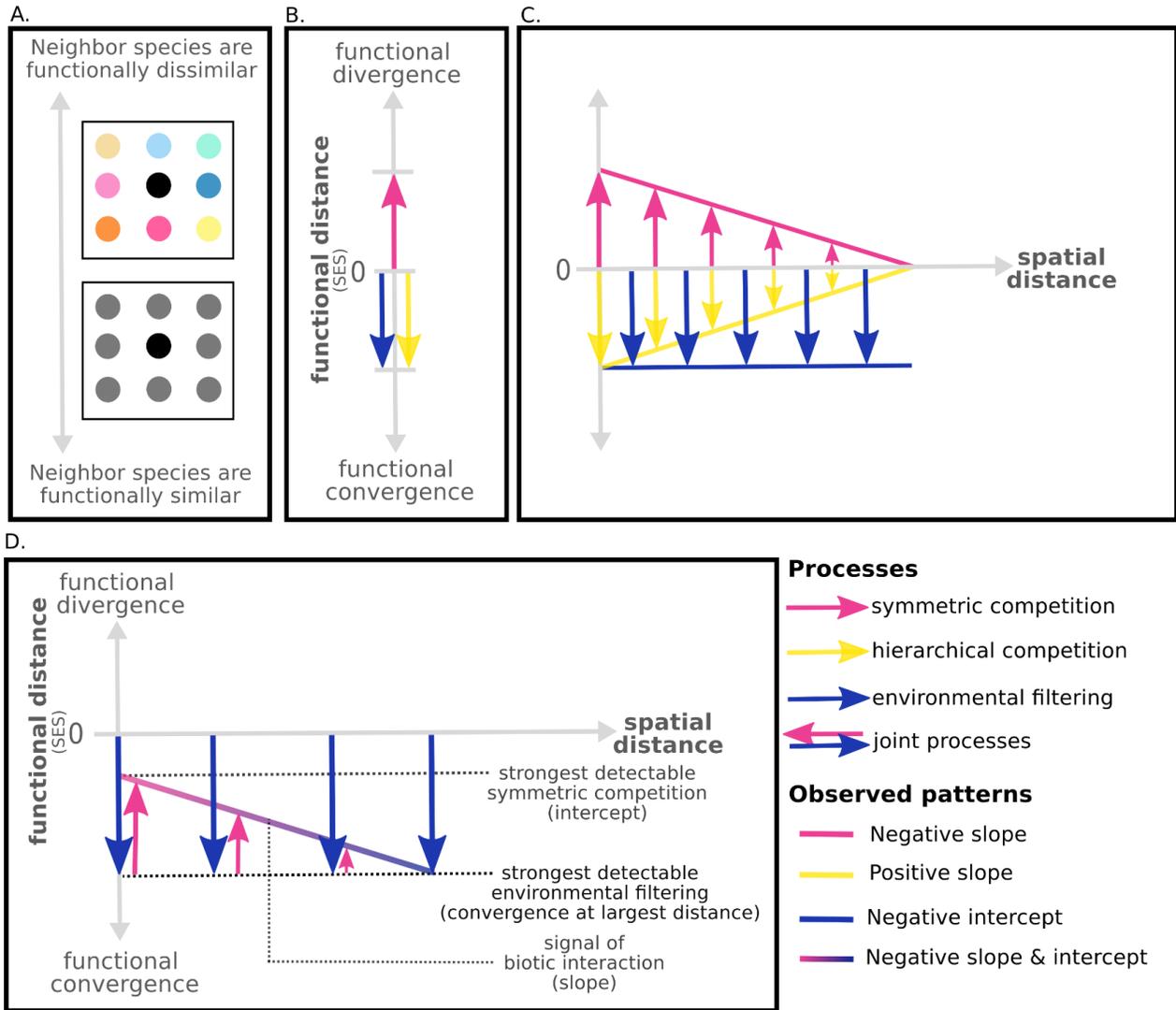


Fig. 1: Spatially explicit trait-based framework to disentangle community assembly processes. In all the conceptual diagrams, the x-axis indicates the spatial distance and the y-axis indicates the functional distance between focal individuals and its neighbors standardized by randomizations (i.e. SES, see Eq. 3). A functional distance below (above) 0 is a tendency towards functional convergence (divergence). **A.** By observing different functional diversity patterns in a community we can understand processes behind community assembly. As the focal and neighbor species become functionally less (more) similar, the functional distance between the focal and its neighbors increases (decreases). **B.** The original framework of

community assembly aims to disentangle processes behind functional patterns by studying only the functional distance between focals and their neighbors. This framework does not integrate spatial distances and thus, cannot disentangle simultaneously acting processes. **C.** In a spatial distance-based framework the signal of environmental filtering remains constant with increasing spatial distance while the effect of biotic interaction is fading away. **D.** An example of a pattern when different processes are in interplay (here environmental filtering and symmetric competition characterized by limiting similarity) but patterns can be disentangled by distance-dependent analyses. Environmental filtering is constantly strong but the closer individuals the stronger the effect of limiting similarity. We used three indices to summarize these regressions: (i) a significant slope indicates a signal of potential biotic interactions, (ii) the intercept represents the functional diversity estimate at the smallest possible distance between neighbors where the effect of competition is strongest (i.e. stronger symmetric competition leads to stronger limiting similarity) and (iii) the predicted value at the largest neighborhood distance is expected to show the strongest effect of environmental filtering as competition should be weakest here.

Box 1: A spatially explicit trait-based community assembly framework

We built our framework on two basic assumptions: i) Environmental filtering is constant in small and homogeneous community plots (i.e. is distance independent); ii) Interaction strength between plant individuals decreases with spatial distance (i.e. is distance dependent). We propose to quantify variation in functional trait distances between a focal individual and its neighbors along increasing neighborhood distances (Thuiller et al., 2010). We use standardized effect sizes (SES, i.e. standardized by means and standard deviations of randomized communities, see Eq. 3) as functional distances such that positive values indicate trait divergence, negative values trait convergence and values around zero random patterns (Gotelli & Graves, 1996). Plotting the resulting trait distances against spatial distances helps to disentangle jointly acting processes. A negative intercept and non-significant slope may reflect a signal of strong environmental filtering and no biotic interaction (Fig. 1.B. blue line). A significant slope may indicate a signal of any kind of biotic interaction (Fig. 1.B. pink and yellow line). In the case of competition, we can tease apart hierarchical vs. symmetric competition. A negative slope may indicate symmetric competition because the closer the individuals are, the more they

limit the functional similarity of the others (Fig. 1.B. pink line). A positive slope may indicate hierarchical competition because the closer the individuals are, the more they are functionally clustered around the most competitive strategy (Fig. 1.B. yellow line). However, environmental filtering and biotic interactions can act jointly. For example, the interplay of a strong environmental filter and symmetric competition may result in a negative slope and mostly trait convergence (Fig. 1.C.). At the smallest spatial distance, competition is strongest. While the simultaneously acting environmental filter pulls diversity to convergence, functional similarity is limited to the value at which species can still coexist under full competition. If species get any more similar, one will outcompete the other. Thus, the intercept in Fig. 1.C. quantifies the strength of symmetric competition (i.e. the stronger the symmetric competition the smaller the limit to similarity). Further, at spatial distances that are too large for biotic interactions, the environmental filter acts alone. Convergent patterns at this spatial distance thus quantify the strength of environmental filtering. The question of how large this spatial distance needs to be can be answered by expert knowledge or by observing how convergence responds to increasing spatial distances and at which spatial distance it reaches a plateau. Although the intercept and the diversity at the largest measured spatial distance do not necessarily reflect the sheer strength of each assembly process, they are useful to compare relative strengths of filters between communities with different environmental conditions or climate change treatments.

Note that competition and facilitation signals cannot be easily disentangled with this framework because facilitation is also distance dependent and can cause both convergence or divergence (Münkemüller et al., 2020). Additional assumptions and analyses are required to identify facilitation. In this study, we performed an additional spatial aggregation analysis that suggested that signals of facilitation are absent (Appendix S1). Moreover, if the assumption of homogeneous plots does not hold, a positive slope between spatial and functional distances could also signal micro-scale environmental filtering (Conti et al., 2017; Willis et al., 2009; Xu et

al., 2021).

In this specific application, we focused on detecting dominant processes acting at the scale of a diverse community. It is possible that processes important only for a subpart of the community or jointly acting processes with weaker effects on diversity patterns are overlooked (Chalmandrier et al., 2022). In that particular case, our framework is flexible to be applied to subparts of the communities to reveal processes at finer scales. In addition, more refined null models in the calculation of SES values can be used to remove a pattern expected from a given process and to test if, after this, there is an additional signal in the data that could be linked to additionally acting but weaker processes (Hardy, 2008). Finally, other types of functional relationships between traits and performance (i.e. unimodal functions) can be explored through the use of specific indices (e.g. trait differences for trait hierarchies, Kunstler et al. 2012) and be interpreted in the light of their spatial distance dependency following our framework.

Methods

Experimental design

The reciprocal transplant experiment was conducted in the French Alps (Col du Lautaret - 45°02'04"N 06°24'18"E), in September 2016 (Bektaş et al., 2021). The subalpine site "Lautaret" (45°04'00"N 06°41'90"E at 1920 m altitude) and the alpine site "Galibier" (45°05'44"N 06°40'06"E at 2450 m altitude) are close to each other (~2km airline distance), have a similar orientation (South-East at alpine and South-South-West at subalpine site), bedrock (base-riched flysch) and soil (dystric cambisols). In 2018, the year of data collection, average annual soil temperature at the subalpine site was 2.9°C warmer than at the alpine site, average July soil temperature was 2.8 °C warmer and snow free season was 48 days longer. At the alpine site,

communities were dominated by *Trifolium alpinum*, *Potentilla aurea*, *Plantago alpina*, *Carex sempervirens* subsp. *Sempervirens* and *Poa alpina*. At the subalpine site, communities were dominated by *Patzkea paniculata* subsp. *paniculata*, *Festuca nigrescens*, *Carex sempervirens* subsp. *sempervirens*, *Festuca laevigata*, and *Plantago maritima* subsp. *serpentina*. In 2016, to simulate the effect of warming on alpine grasslands, we transplanted 10 replicates of 4m² blocks of vegetation with at least 20 cm of their intact belowground parts and the surrounding soils from the alpine to the subalpine site (AlpineWarmed plots). For the transport, each block was cut in 4 x 1m² subblocks and then reassembled in their original composition when re-planted. To simulate the effect of cooling on subalpine communities, 10 intact 4 m² blocks of vegetation and soils were transplanted from the subalpine to the alpine site (SubalpineCooled plots). To control for the transplantation stress, we also horizontally transplanted 10 intact 1m² blocks at both the subalpine and the alpine sites (SubalpineControl plots and AlpineControl plots, respectively). Within the same site, control and treatment plots are in close proximity within a few meters. Around the turfs, we placed water permeable root barriers to avoid root ingrowth from the natural vegetation around the plots. At both sites, cattle and sheep were excluded by electric fences and grazing is not simulated. There were no soil disturbances due to burrowing animals or erosion due to slope. More details on the experimental design and the changes in the communities due to experimental warming can be found in Bektaş et al. (2021).

Vegetation surveys

At the peak of the plant growth (July 2018), we identified and counted all species that touched a 4mm metal stick (here after, pinpoint) at equally spaced points (~10cm distance) in both the treatment (400 points in total for each repetition) and control (100 points in total for each repetition) plots. Species that could be identified only at genus level were excluded from the further analysis (5% of 21166 identified individuals). The pinpoint counts were performed on a square grid which allowed us to know the exact position of pinpoints.

Defining focal and neighbor species

All identified and counted species at a pinpoint were considered as focal individuals (AlpineControl: 2267, SubalpineControl: 3109, AlpineWarmed: 9198, SubalpineCooled: 5440). For each focal individual, we constructed four different neighborhoods at different distances to the focal, starting at 10cm (i.e. individuals touching the focal pinpoint and pinpoints at 10cm distance) and then increasing distances (i.e. the 20cm neighborhood ring consisted of the individuals touching pinpoints at $>10\text{cm}$ and $\leq 30\text{cm}$ and so forth). Pre-analyses showed that the 40cm neighborhood ring was a good compromise (i.e. competition signals were sufficiently reduced and there were enough focal pinpoints for which the most distant neighborhood was still in the experimental plots) (Appendix Fig. S12). Conspecifics were taken out from a focal's neighborhood as they could be the same individuals if touching the same pinpoint or clones if in close proximity. As the methods we use are sensitive to sample sizes, within each neighborhood we subsampled 20 individuals 20 times with replacement and we made all the calculations within these sub-neighborhoods. We chose the number of individuals to subsample so that we would not lose more than 15% of the pinpoints at the smallest neighborhood in any of the treatments. The abundances of the neighbors within sub-neighborhoods were estimated as the total pinpoint touches within the sub-neighborhood (i.e. all touches at all pinpoints in this sub-neighborhood). We only included focal-neighborhood combinations for which more than 80% of the neighbors had functional trait information and for which the entire neighborhood was within the grid. While the number of focal-neighborhood combinations decreased with increasing neighborhood distance this way, these adjustments did not change the overall shape of the trait distributions and thus, the remaining species represented well the trait space at each neighborhood distance (Appendix Fig. S1).

Regional species pool

We extended our regional species pool beyond the list of species in the experiment to be able to account for all species in the catchment area and thus all species available to enter the local communities (Carstensen et al., 2013). The regional species pool (787 species) included species from i) our experimental sites, ii) botanical surveys from the long-term monitoring program ORCHAMP along the elevational gradient of the transplant experiment (i.e. from 1920m to 2700m at 5 different sites, <https://orchamp.osug.fr/sites/5>), and iii) botanical surveys (i.e. 747387 observation points) from the Alpine National Botanical Conservatory (CBNA; <http://www.cbn-alpin.fr/>) taken within a 5km buffer around the experimental sites. As our experimental sites are grasslands, we excluded shrubs, trees and understory herbs from the pool to avoid a signal of an additional habitat filtering process.

Table 1: Selected plant functional traits. Synthesized from (Martinez-Almoyna et al., 2020; Saatkamp et al., 2019; Venn et al., 2014).

Trait	Function <i>(high trait values result in ...)</i>	Species interactions <i>(high trait values result in ...)</i>
Vegetative height	More photosynthetic growth, higher contribution to community productivity	Stronger competition for acquiring light and creating shade to neighbors
Specific leaf area (SLA)	More photosynthetic growth, higher contribution to community productivity, more intolerance to harsh environmental conditions	Stronger competition for acquiring light and creating shade to neighbors
Leaf dry matter content (LDMC)	More resistance to harsh environmental conditions and disturbance	Slower resource acquisition
Leaf carbon nitrogen ratio (CN)	More resistance to infertile soils	Slower resource acquisition
Seed mass	More intolerance to harsh conditions in the soil	Higher competitive advantage in establishment

Interspecific functional trait data

We considered five different traits that reflect different functional plant strategies and competitive strength within communities (Table 1). We also considered an integrative trait of vegetative height, specific leaf area (SLA) and leaf dry matter content (LDMC). These three traits represented the multidimensional trait space of the species pool well (Appendix Fig. S4). We log-transformed and then we transform the trait values so that they follow a normal distribution with the Gaussianize function for skewed heavy-tails in LambertW package (Goerg, 2022). (Appendix Fig. S5). We extracted the interspecific functional trait data from our in-house trait measurements (Brun et al., 2022; Thuiller et al., 2014) available in the Androsace database (<https://originalps.osug.fr/>) and complemented the missing data for all the traits in Table 1 from the TRY database (Kattge et al., 2020) and the Tundra database (Bjorkman, Myers-Smith, Elmendorf, Normand, Zamin, et al., 2018). We detailed the data selection and manipulation processes from these databases in Appendix S2.

Species with no trait information at all were removed (3.8 % of the regional pool) and formed the updated species pool. As they were used together for the integrative trait, vegetative height, SLA, LDMC were only calculated for those species for which all three traits were available (619 species, 82% of the updated species pool). Leaf CN ratio and seed mass were calculated based on 525 and 476 species (69% and 63% of the updated species pool), respectively. Based on species relative abundances, the coverage of the trait data in the experimental communities were above 97% for all traits (Appendix Fig. S3).

Functional distances

Some research suggests that environmental filters are more important to determine species presence or absence, while biotic interactions rather affect species' abundances (Boulangéat et al., 2012). In addition, transient dynamics of communities under change may first respond by abundance changes and only in the long-term by extinctions and colonization events. To

account for this, we calculated two metrics, an abundance-weighted (Eq.1) and a unweighted (Eq.2) mean functional distance between a focal and its neighbors according (Thuiller et al., 2010):

$$WMDN = \frac{\sum_{i=1}^N w_i \times d_i}{\sum_{i=1}^N w_i} \quad (\text{Eq.1})$$

$$MDN = \frac{\sum_{i=1}^N d_i}{N} \quad (\text{Eq. 2})$$

where N is the number of neighbor species, w_i is the relative abundance of the neighbor species i , d_i is the functional distance between the focal and the neighbors i . The functional distance was calculated as the Euclidean distance between focals and their neighbors for each single trait and for the integrated trait.

Null model

Our null hypothesis was that “*observed neighbors of a species are randomly selected from the regional species pool.*” For this we randomized the pinpoint x species abundance matrix used to identify neighborhoods by randomly switching observed species names with species names from the species pool. We then calculated for all focals and all sub-neighborhoods functional distances for observed and randomized data. As these functional distances were calculated at 20 sub-neighborhoods, we later took the median to have a single value for each focal species at each neighborhood distance size for observed and randomized data. We calculated the standardized effect size (SES) for each individual and at each neighborhood distance based on median values as follows:

$$SES = \frac{Metric_{observed} - mean(Metric_{Null})}{sd(Metric_{Null})} \quad (\text{Eq. 3})$$

Negative (positive) values of SES indicate that focal individuals are functionally more similar (dissimilar) to their neighbors than expected by chance (i.e. functional convergence vs. functional divergence).

Statistical analyses

First, we tested for significant patterns of functional convergence and divergence of focals independently for each neighborhood distance and for all metrics, traits, and experimental treatments. We used the two-sided Wilcoxon signed-rank test (*wilcoxon.test* in R) to test if the focal individuals' SES values were significantly different from zero in order to control for multiple testing (Bernard-Verdier et al., 2012).

Independently for all metrics, traits, experimental treatments, we built linear mixed-effects regression models with spatial distances as explanatory variables, SES functional distances as responses and repetition plots as random effects (*lme4* package in R). In functional distance calculations, neighborhoods overlapped. We corrected for this by weighing each observation by its pinpoints' nonoverlap ratio within its plot. We calculated the latter as follows:

$$1 - \frac{Overlap_{ij}}{\sum_{i=1}^N Overlap_{ij}} \quad (\text{Eq.4})$$

where *Overlap* is the number of overlaps of a pinpoint *i* with any of the neighborhoods in repetition plot *j* and *N* is the number of pinpoints within the same repetition plot. We calculated predictions with the *lmerTest* and the *ggeffects* package. We used slope, intercept and the predicted value at the largest neighborhood distance to summarize these regressions and to interpret them according to our framework (Fig. 1.C.).

We did not rely on significance tests of the regression models as we cannot be sure that our measured functional distance values are normally distributed and independent from each other. We thus repeated the entire analyses we did on 100 random species compositions, using the same null model as described above. We then compared intercepts and slopes of these “test” data with our observed data and based the significance test on this (Appendix Fig. S9 & S10). We detected the potential signal of any biotic interaction through a significant slope between spatial and functional distances. Before identifying the biotic interactions at a finer scale, we further checked if there is a potential signal of facilitation in our system with an additional spatial aggregation analysis (Appendix S3-Fig. S6). Once we confirmed that a signal of facilitation is absent, we also identified the potential processes behind competition at a finer scale: a negative slope can signal symmetric competition and a positive slope can signal hierarchical competition. We quantified the relative strength of competition through the intercept as it estimates the functional distance at the smallest spatial distance between neighbors where the effect of competition is expected to be strongest (see Box 1, Fig. 1).

To test H1 & H2, we compared the above-mentioned metrics between AlpineControl and SubalpineControl communities. To test H3, we compared AlpineWarmed communities to AlpineControl and SubalpineControl (Bektaş et al., 2021) with the expectation that warmed communities showed a transient response between AlpineControl and SubalpineControl communities. Moreover, to better understand how abundances influence results, we compared regression results for WMDN (abundance weighted) and MDN (presence-absence based). Lastly, we compared warming and cooling effects to see if they are symmetric. We conducted all the statistical analyses in R (R Core Team, 2021).

Results:

Patterns of alpine and subalpine control plots are mostly congruent with stress gradient hypothesis

At all neighborhood distances, SES values (WMDN and MDN) indicated that focals were functionally more similar to their neighbors than expected by chance (i.e. significant functional trait convergence; Appendix Fig. S7). A few exceptions existed for SLA and one for leaf CN ratio for SubalpineControl and Cooled communities (Appendix Fig. S7).

AlpineControl and SubalpineControl communities showed different signals of competition (Fig. 2). AlpineControl communities had significant negative slopes in integrated trait, vegetative height and seed mass whereas SubalpineControl communities showed significant positive slopes in SLA and leaf CN ratio and a significant negative slope in LDMC (Fig. 2). Thus, we detected a signal of limiting similarity due to symmetric competition in AlpineControl (via integrated trait, vegetative height and seed mass) and in SubalpineControl (via LDMC) communities (Fig. 1). Additionally, we detected a signal of hierarchical competition in SubalpineControl communities (via SLA and leaf CN ratio, Fig. 1).

AlpineControl communities had a significant negative intercept in integrated trait, vegetative height, SLA and LDMC whereas SubalpineControl communities had only a single significant negative slope in integrated trait. Alpine communities showed environmental filtering when subalpine communities did not and for the integrated trait, alpine communities showed stronger environmental filtering than subalpine communities (i.e. at the largest neighborhood distance, focals were functionally more similar to their neighbors than expected by chance, i.e. convergence). Moreover, where AlpineCommunities did not have a signal of biotic interaction, SubalpineCommunities had.

Overall, while jointly acting assembly processes were present for alpine communities for the same traits, for subalpine communities we did not detect jointly acting assembly processes for the same traits.

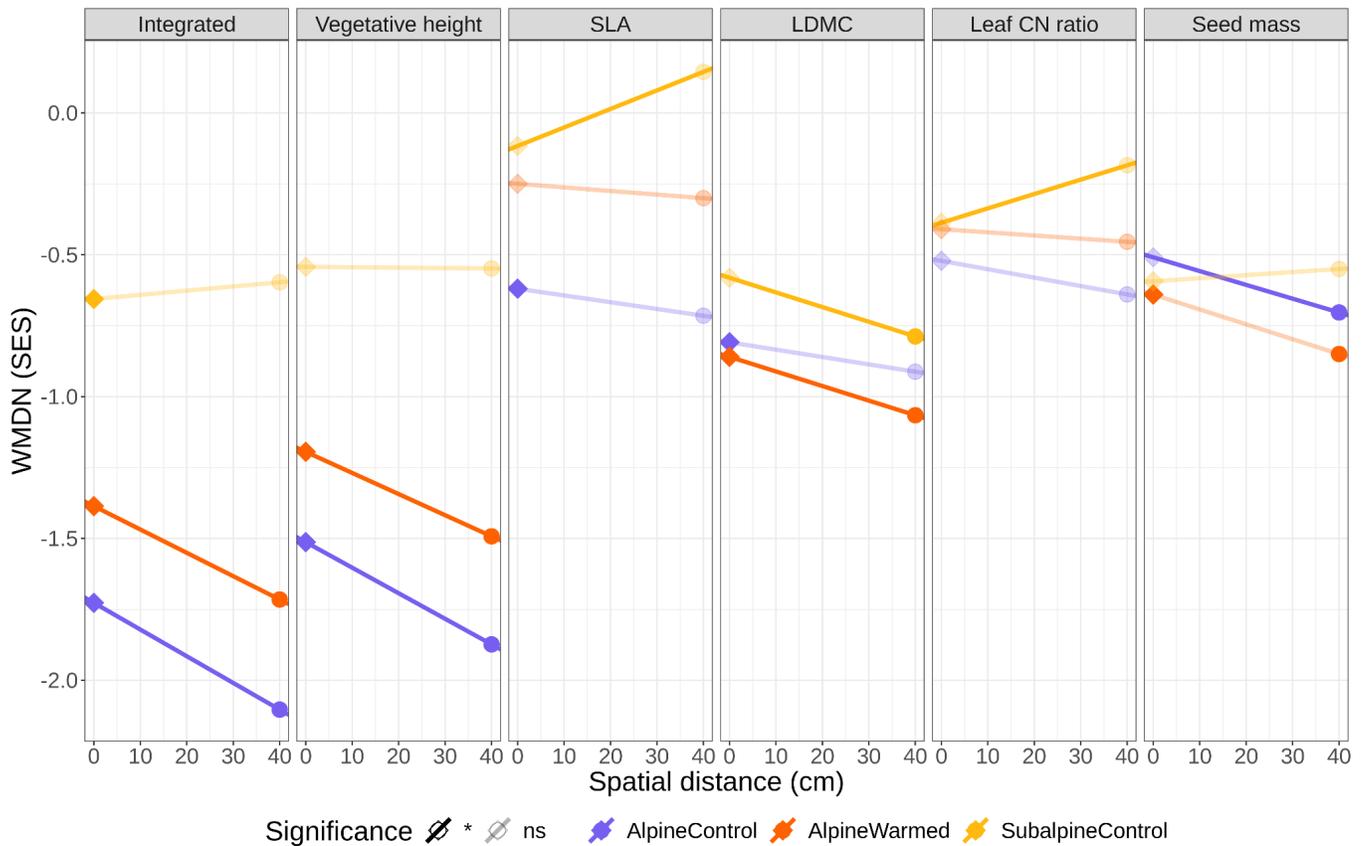


Fig. 2: Changes in SES of functional distances (WMDN) with increasing spatial distances as predicted by the linear mixed effect regressions. A significant slope is a signal of biotic interaction. A significant intercept is a signal of environmental filtering (diamond). The intercept quantifies the strongest detectable biotic interaction if there is any. The predicted value at the largest distance is the strongest detectable environmental filtering (circle). We identified these terms as significant for observed communities if their values are higher or lower than 5% of the values calculated for 100 test communities. Non-significant terms are transparent. Integrated: combination of vegetative height, SLA & LDMC, SLA: Specific leaf area, LDMC: Leaf dry matter content, CN: Leaf carbon nitrogen ratio. (n.s: non-significant, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$)

Community reassembly mechanisms under climate warming

AlpineWarmed communities showed significant negative slopes in integrated trait, vegetative height and LDMC and significant negative intercepts in integrated trait, vegetative height, LDMC and seed mass (Fig. 2). In fact, AlpineWarmed communities were in a transient state where observed relationships between functional and spatial distances were in between the two

controls with the exception of LDMC and seed mass (Fig. 2).

Under warming, some signals of assembly processes appeared and some others were lost (Fig. 2). In comparison to AlpineControl communities, while a signal of symmetric competition appeared for LDMC, it was lost for seed mass. Additionally, while a signal of environmental filtering was lost for SLA, it appeared for seed mass. Hence, we evaluated the changes in relative strengths of these assembly processes when signals were present in both AlpineControl and AlpineWarmed communities (Fig. 3). In line with H3, for integrated trait and vegetative height, AlpineWarmed communities showed most of the time potentially weaker environmental filtering and slightly stronger competition than AlpineControl communities (Fig. 3). Yet, the environmental filtering increased for LDMC under warming.

Changes in local abundances pronounce the warming effect

Including abundance information (WMDN) or not (MDN) to calculate functional distances did not drastically change the general conclusions (Fig. 3). Still, as expected, the warming effect was more pronounced when changes in abundances were taken into account for the integrated trait and for the vegetative height (i.e. only in signals of environmental filtering) but not for LDMC.

Warming and cooling effects on community assembly processes were asymmetric

Surprisingly, none of the regression indices (i.e. slopes and intercepts) were significant for SubalpineCooled communities except for LDMC (Appendix Fig. S10). With cooling, environmental filtering increased for LDMC, a weaker response than of warming (Fig. 3).

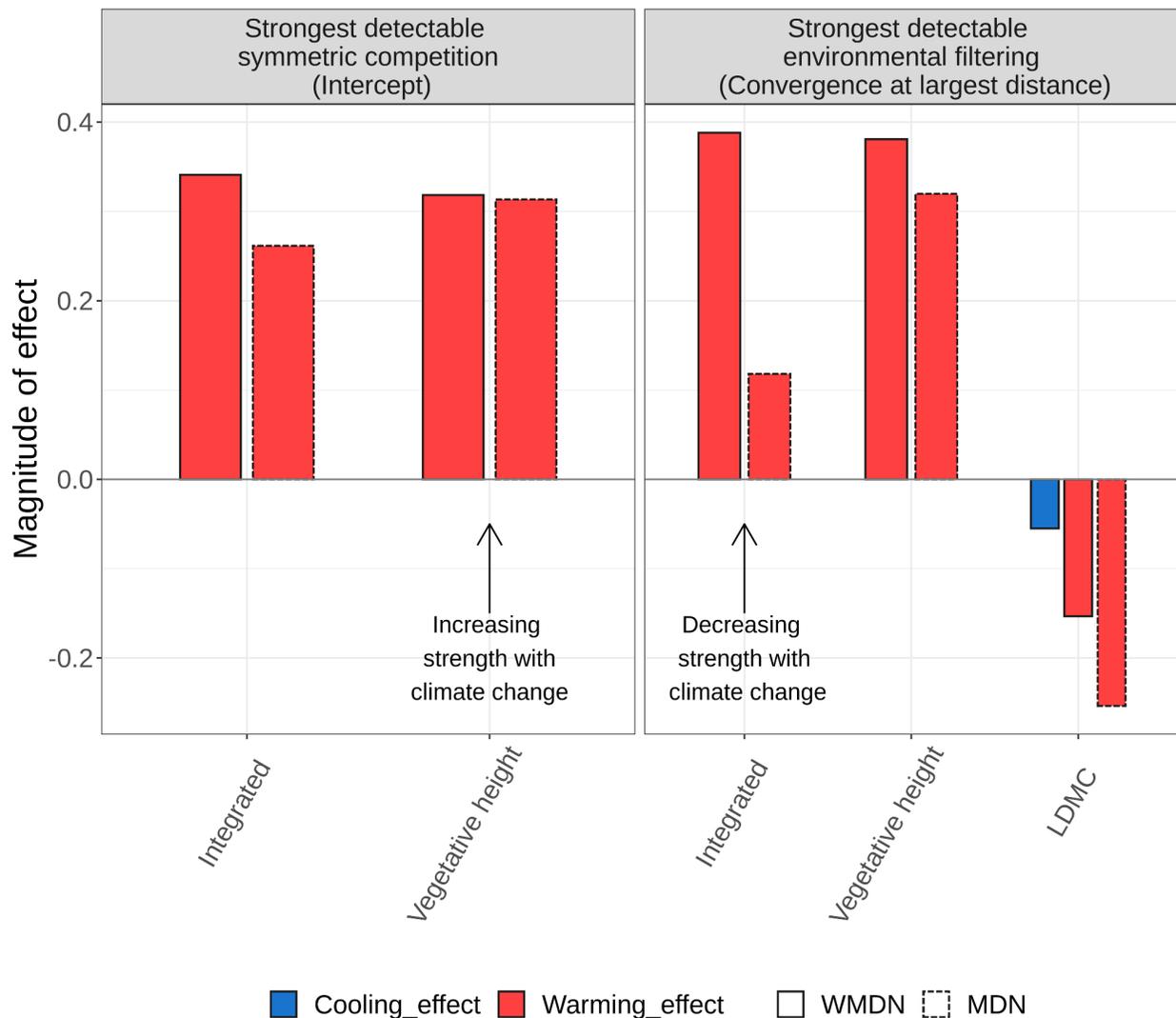


Fig. 3: Effect of warming and cooling on the regression indices of integrated trait, vegetative height and LDMC when the indices are shown to be significant (Fig. 2). Warming effects are estimated as the difference of regression indices between AlpineWarmed and AlpineControl communities, either under the consideration of abundances (WMDN) or only under consideration of presence/absences (MDN). Cooling effects are estimated as the difference between SubalpineCooled and SubalpineControl communities (only WMDN). a) The intercept of the regression (as the strength of strongest detectable symmetric competition where the distance between individuals is close to zero and the limiting similarity between neighbors is the strongest) and b) the regression-based estimate of SES (see Box 1 and Fig. 2) at the largest studied distance (as a potential signal of the strongest detectable environmental filtering where biotic interaction should be negligible) *Note:* Changes in indices can only be interpreted in combination with the knowledge of the original values. a) Positive intercept differences mean that intercepts moved closer to zero which could indicate increasing symmetric competition with

climate change (and vice versa). b) Positive differences of functional distances at largest spatial distance mean that these values moved closer to zero which could indicate a decrease in environmental filtering with climate change.

Discussion

Today, we require more than ever a method that can disentangle jointly acting processes in communities under ongoing climate change and that is sensitive to reveal the beginning of restructuring processes. Here, we introduced such a conceptual framework and demonstrated its efficacy. Through the unique combination of our spatially-explicit trait based framework and a reciprocal transplant experiment, we disentangled signals of joint assembly processes. Signals of environmental filtering and competition were omnipresent in the functional diversity patterns of alpine and subalpine grasslands. Under control conditions —consistent with the stress gradient hypothesis — environmental filtering was the major structuring force in the stressful alpine site, whereas competition was most of the time only present signal for various traits. Two years of experimental warming led to a shift of structuring assembly processes through the appearance of new processes or changes in strength of already present processes. Responses to cooling were either non-significant or weaker when present.

Interplay of assembly processes in mountain grasslands

The unveiled interplay of environmental and biotic signals in our study was consistent with theoretical expectations (Chalmandrier et al., 2013), as well as demographic studies (Hülber et al., 2011) and on-site observations (Klanderud et al., 2015) in alpine ecosystems. Alpine communities showed signatures of strong environmental filtering and of symmetric competition in integrated trait and vegetative height. However, environmental filtering was detected many more times under stressful alpine conditions where short growing seasons, low number of growing degree days, and nutrient limitation impose strong restrictions to successful functional strategies (Chalmandrier et al., 2017; Martinez-Almoyna et al., 2020; Midolo et al., 2021; Weil et

al., 2021). In contrast, in benign subalpine conditions, we did not detect any signal of environmental filtering (except for the integrated trait) and we detected signals of hierarchical (via SLA and leaf CN ratio) and symmetric (via LMDC) competition in subalpine communities when these signals were absent in alpine conditions.

While previous work suggests that facilitation can replace competitive interactions in stressful conditions (Kikvidze et al., 2005; Michalet et al., 2006), we did not find any potential signals of facilitation in the alpine site (Appendix S3). However, harsh abiotic conditions do not necessarily lead to facilitative interactions (e.g. (Maestre et al., 2005) for drylands) and our results confirm earlier studies showing that competitive interactions can prevail in alpine environments (Hülber et al., 2011; Klanderud, 2010; Zhou et al., 2019). It is also important to note that cushion plants which are known to foster facilitation as nurse plants were not abundant in our study site.

Warming and cooling induce community reassembly

In our experiment, we warmed and cooled perennial grassland communities that are adapted to strong intra- and inter-annual climatic variability. Thus, we expected only moderate responses to warming and cooling after only two years of treatment. Nevertheless, our framework allowed us to even detect these small shifts in the relative importance of community assembly processes.

As expected, under warming, we found strong evidence for a release from environmental constraints and increasing strength of symmetric competition for vegetative height and even loss of environmental filtering signal for SLA. However, a signal of environmental filtering appeared for seed mass and its strength increased for LDMC. Moreover, a signal of symmetric competition appeared for LDMC and was lost for seed mass. For LDMC, this can be explained by the personal observations on the field that warming was potentially accompanied by an increased drought stress. For seed mass, reasons are less clear.

Interestingly, as signals of changes in assembly processes were much stronger in abundance than in presence-absence based analyses for the integrated trait and vegetative height, we concluded that most shifts in community assembly started by changing abundance structures and not by mere colonization or extinction events. For warming, this result is in congruence with earlier observational studies that found an increase of abundances of thermophilic (Rumpf et al., 2018) and tall (Bjorkman, Myers-Smith, Elmendorf, Normand, Weiher, et al., 2018) species under increasing annual temperatures. However, for competition a previous transplant experiment on tundra communities found that biotic interactions were key determinants of colonization and extinction already during the first four years of warming (Vandvik et al., 2020). Interestingly, in this study graminoids were the key drivers of these responses. In our site, long-lived plant species are dominating the alpine communities and competition effects may thus be slower (Bektaş et al., 2021; Compagnoni et al., 2021; Morris et al., 2008). However, warming effects were more pronounced for LDMC with presence-absence than abundance based analysis. This could be an indication that warming-associated drought is driving the extinction and colonization events, for example by eliminating drought intolerant species and allowing colonization of exploitative species. Overall, functional divergence as a result of climate warming may be one of the processes behind the observed patterns of increasing species' richness on mountain summits and thus requires further investigation under current climate change (Steinbauer et al. 2018).

In contrast to warming, signals of any assembly processes were most of the time absent for cooled subalpine communities. More constraining environmental filters like cooling may lead to stronger convergence only with time lags as individuals from perennial species with energy storage in their root systems may still tolerate some years of maladaptation. If at the same time the new winner-species are becoming more abundant, then diversity may even slightly diverge temporally.

Towards a spatially explicit trait-based community assembly framework

Our novel spatially explicit trait-based community assembly framework allowed us to uncover small shifts in the relative importance of environmental and biotic processes in community reassembly even after short-term climate warming. Simply applying the traditional filtering approach to our climate change experiment would have revealed functional convergence for all plots at all spatial scales. This could have misled to the interpretation that environmental filtering is the only structuring force in these communities. However, explicitly including the relationships between functional and spatial distances not only allowed identifying the important role of symmetric competition but also the changing importance of environmental filtering. The simplicity of our framework in quantifying the relative importance of environmental and biotic processes can be used to compare different conditions along environmental gradients and different experimental treatments in multifactorial experiments.

Here, we have paved the way for future applications of this framework but some challenges still remain. First, our framework is well adapted to disentangle environmental filtering from biotic interactions and more specifically, symmetric competition from hierarchical competition. However, it can neither disentangle facilitation from competition nor hierarchical competition from small-scale environmental heterogeneity (see introduction and Box 1). For these questions, additional analyses such as co-occurrence tests (Appendix S3) and small scale environmental measures of microhabitats are required (Conti et al., 2017). Second, the choice of the regional species pool depends on the research question (Münkemüller et al., 2020). Our species pool was spatially and habitat wise restricted to our experimental sites and should thus already account for evolutionary and large distances-related processes (e.g. dispersal). Other species pools and null models are commonly used to refine assembly tests and these methodological advances can be easily integrated in the calculation of SES values in our framework. Third, we chose a linear relationship between spatial and functional distances to be

able to extract easily comparable and comprehensible parameters. In reality, this relationship may not be linear, but logistic or threshold driven (Morlon et al., 2008; Thuiller et al., 2010). Our main conclusions will not be affected by this choice as we solely compare effects between different treatments of the same type of communities. However, it could be interesting in itself to better quantify the relationship between the strength of biotic interactions and the spatial distance in highly diverse communities, such as mountain grasslands (e.g. at which spatial distance does the signature of biotic interactions completely fade away?). Such questions have been previously studied (Adler et al., 2010; Chu & Adler, 2015; Silander & Pacala, 1985) but many questions still remain (Graco-Roza et al., 2021), especially in species-rich communities where different species can maintain biotic interactions at different spatial distances.

Above-ground structures that influence the distance dependency of biotic interaction may be easy-to-measure traits but belowground interactions are much more challenging to study not only because little is known about specific root traits but also because microbial associates will play an important role in distance-decay patterns. Fourth, how much we can learn from applying this framework depends first and foremost on the trait data used in the study. Here, we used species-specific measures of aboveground traits from trait databases. If finances and time allow, it could be highly valuable to include on-field trait measurements to be able to further investigate the role of species-specific phenotypic plasticity to warming in reshaping the communities under climate change (Henn et al., 2018). Moreover, by including belowground root traits, we could better account for trade-offs between light and nutrient acquisition and additional strategy gradients such as “do-it-yourself vs. outsourcing” (Weigelt et al., 2021).

Finally, we acknowledge that a massive data collection is needed for this framework. This may not be optimal in the context of global change research, especially if we would like to i) cover large spatial scales to provide representative results, ii) have multiple repetitions during or between years to capture transient responses relevant for society and iii) integrate plastic responses of species traits to account for ecosystem adaptability. However, a possible future

solution for this problem may be community composition tracking with fine resolution hyperspectral imagery (Sarić et al., 2022; Thomson et al., 2021; Z. Wang et al., 2020). From these images we can potentially extract the information of in-situ functional information and spatial distances between individuals in a community and can compare many communities over space and time.

Conclusion

Through our spatially explicit trait-based approach, we paved the way for a novel framework in community ecology that addresses simultaneously many major issues of the original framework of assembly processes. We used the basic but fundamental knowledge, that species coexistence depends not only on their functional but also spatial distance, to unravel the processes acting together in plant communities. The unique combination of our framework with a reciprocal community transplant experiment in the French Alps allowed us to test the framework on assembly processes in mountain grasslands and their restructuring under climate change. We identified environmental filtering and symmetric competition acting in concert in alpine communities, and hierarchical or symmetric competition shaping the subalpine communities, a result that is congruent with the stress gradient hypothesis. Our framework has shown to be useful and sensitive enough to capture reassembly dynamics that affect primarily abundance structure, and less species turnover. We believe that the simplicity and flexibility of our framework will allow future studies to answer theoretical questions in community ecology and to better understand the effects of global change on community restructuring.

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Chapter 4:

**Plant functional strategies
acclimate quickly to *in situ*
warming but may no longer
provide all their ecosystem
functions**

Plant functional strategies acclimate quickly to *in situ* warming but may no longer provide all their ecosystem functions

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Abstract

The response of the plant kingdom to climate change is recognized as one of the fundamental mediators of environmental change. But until now, little is known about how plant functional strategies respond to *in situ* climate warming and how these responses cascade to shifts in ecosystem functioning.

Here, we simulated three degrees of climate warming and increased summer drought on alpine grassland communities by transplanting them to subalpine conditions. We investigated whether the variation of above and belowground plant functional traits could be summarized by the common large-scale functional strategy tradeoffs and tested for warming effects and acclimation lags on these revealed tradeoffs. Finally, we analyzed whether shifts in functional strategy trade-offs cascaded to proxies of ecosystem functioning.

Even at community-level, we found two orthogonal tradeoffs that well represented trait variation, with leaf mass per area, leaf nitrogen content and root nitrogen content varying along a fast vs. slow economic spectrum, and specific root length and root diameter along a do-it-yourself vs. outsourcing tradeoff. Subalpine control communities were slower and more outsourcing than alpine control communities, indicating that water stress was limiting at lower altitudes.

Surprisingly, warmed alpine communities fully acclimated their functional strategies already after five years of warming. Functional strategy shifts cascaded to all measured ecosystem functions. We thus lose in these communities the plant strategies and functions typical for alpine conditions. However, sometimes warming disrupted the linkage between plant strategies and functions found in control communities. For example, while outsourcing increased below-ground productivity in alpine control communities, it decreased it in warmed alpine communities.

Our study highlights that measuring shifting plant strategies in communities under change can not only provide early warning signals for vegetation change but can also help to better understand resulting shifts in ecosystem functions. Moreover, during the transient dynamics of acclimation the tight linkage between functional strategies and function provision may become temporarily interrupted, which may be a relevant problem in our ever changing world.

Introduction

Plant functional traits are essential predictors of plant performance (Adler et al., 2014; Falster et al., 2018; Soudzilovskaia et al., 2013) and ecosystem functioning under climate change (Violle et al., 2007). Using trait-based approaches, ecologists have achieved great advances in identifying trade-offs that underpin ecological strategies in large-scale distributions of plant species (Violle et al., 2012). They have also shown that changes in these plant functional strategies can cascade in the ecosystem to functions such as above and belowground productivity, decomposition and to microbial community composition (Suding et al., 2008). However, how plant functional strategies shift over time in local communities under ongoing climate change and how strongly these shifts affect ecosystem functions is less clear.

Functional traits are not independent of each other. At the individual level, physiological trade-offs arise from the allocation of limited resources for one purpose or another. Accordingly, at the species level, only a few plant functional strategies (i.e. successful trait combinations) along these essential trade-offs have proven evolutionarily viable in vascular plants (Díaz et al., 2016). Whether or not these individual and species level functional strategies scale up to the community level (i.e. to combinations of abundance weighted mean community trait values), may depend on the underlying community assembly rules (Chalmandrier et al., 2017; Read et al., 2014; Rosbakh et al., 2015) and evidence thus is variable (Holdaway et al., 2011; Lachaise et al., 2022; Wüest et al., 2018). Moreover, most studies supporting the idea of a few key trade-offs in plant functional trait variability focused on large spatial scales and thus included stark environmental gradients. However, if we are to use functional strategy shifts to better understand and early recognize vegetation responses to climate change we need to establish these trade-offs at small spatio-temporal scales.

The first trade-off identified from leaf traits was named leaf economic spectrum (Reich, 2014; Wright et al., 2004) as it can be interpreted through economic theory with not money but

nutrients, carbon and water as resources. Plants invest either in high leaf mass per area (LMA), low leaf dry matter content (LDMC) and high leaf nitrogen content (LNC) —a fast-growing but short-lived strategy— or in opposite leaf traits —a slow-growing but long-lived strategy. The “fast” strategy improves plant fitness under benign environmental conditions and on fertile soils while the “slow” strategy is better adapted to stressful conditions such as high altitudes (Table 1, Appendix Table S1). Plant vegetative height was suggested as a second dimension, with some species investing in early reproduction and staying small and others in becoming tall and thus in strong competitiveness for light (Price et al., 2014). Only recently, Bergmann et al. (2020) used a global root dataset and was able to integrate belowground traits in the large-scale analyses of plant functional strategies. They showed that some root traits fall within the leaf economic spectrum, supporting the idea of a whole plant fast-slow economic spectrum (Poorter et al., 2014), with plants with high root nitrogen content (RNC) at the “fast” end and plants with opposing root traits at the “slow” end of the trade-off. Secondly, they revealed an orthogonal and root-specific trade-off that can be described along do-it-yourself vs. outsourcing strategies. Plants either invest in high values of specific root length (SRL) to take up water and nutrients directly or they invest in wider root diameters to host fungal partners and indirectly increase their nutrient uptake. The “do-it-yourself” strategy improves plant fitness in soils with easily available nutrients and the “outsourcing” strategy performs better when nitrogen exists in not readily available forms for plants or if there is increased abiotic stress, such as drought stress (Augé et al., 2015; Laughlin et al., 2021). For some traits it is still under discussion whether they belong to one or the other trade-off, for example for root tissue density (Carmona et al., 2021; de Vries et al., 2016). Both the fast-slow and the outsourcing vs. do-it-yourself trade-offs are tightly linked to ecosystem functions. At the fast end of the economic spectrum, plant productivity is higher than at the low end. Nutrient-rich and easy to decompose litter accelerates microbial activity and shifts communities towards bacteria dominated (vs. fungi dominated) and thus fast growing copiotroph microbial communities, finally resulting in more fertile soils than at the slow end (Strickland & Rousk, 2010). At the outsourcing end of the collaboration trade-off, plant-mycorrhizal associations lead to better nutrient uptake and more fertile soils and can improve plant growth under stress such as drought (Santander et al., 2017).

Under accelerating climate change in the European Alps with increasing air and soil temperatures, more frequent summer droughts and earlier snow melts (Kotlarski et al., 2022; Scherrer et al., 2022), these plant functional strategies are expected to change with important impacts on the associated ecosystem functions (Table 1). On the one hand, climate warming

increases growing season lengths and energy input. This may push alpine ecosystems from stressful to more benign conditions: we may expect a shift towards faster and do-it-yourself plant functional strategies (Table 1). On the other hand, droughts and the reduced protection from constant snow cover in periods with freezing temperatures increase physiological stress: we may thus expect a shift towards slower and outsourcing strategies. For example, (Stanisci et al., 2020) explained a dominant slow strategy in their drier subalpine grassland sites with the need to overcome water stress and the dominant fast strategy in the colder alpine sites with the need to counterbalance the shorter growing season lengths with faster growth. Accordingly, a recent review study on climate warming effects showed that shifts in leaf traits depend on whether water is limiting in the system or not (Myers-Smith et al., 2019). Moreover, results differed between studies focussing on individuals vs. communities, on observations vs. experiments and on spatial vs. temporal data (Myers-Smith et al., 2019).

Here, we are interested in shifts of plant functional strategies and ecosystem functions in an alpine grassland that is water limited. We included both leaf and root traits at the community level and locally studied temporal changes after five years of experimental warming. More specifically we asked: i) Can we disentangle fast vs. slow and do-it-yourself vs. outsourcing trade-offs in our small scale experiment? ii) Do functional strategies differ between treatments? iii) How do the warming induced shifts in plant strategies affect above- and below-ground ecosystem functions?

Table 1: Plant functional trade-offs along temperature, moisture and soil nutrient stress gradients with example references. Arrows indicate the increasing or decreasing trend for each trait as a response to different abiotic drivers. Blue arrows show hypothesized trends with an overall consensus on existing studies. Red arrows show hypothesized trends but with some contrasting evidence. (LMA: leaf mass per area, LNC: leaf nitrogen content, RNC: root nitrogen content, SRL: specific root length, RD: root diameter). An extended version of this table with an explanation of the hypotheses can be found at the general introduction of the thesis on Table 1.

		Increasing temperature	Decreasing moisture	Decreasing soil nutrients
Economic (fast-slow) spectrum	LMA	 (Joswig et al., 2022; Kemppinen et al., 2021; Simpson et al., 2016) but see (Wright et al., 2005)	 (Blumenthal et al., 2020; Joswig et al., 2022; Kemppinen et al., 2021; Onoda et al., 2017; Simpson et al., 2016)	 (Joswig et al., 2022; Martinez-Almoyna et al., 2020; Simpson et al., 2016; Weil et al., 2021)

	LNC	↑ (Joswig et al., 2022; Kemppinen et al., 2021; Wright et al., 2005)	↓ (Joswig et al., 2022; Kemppinen et al., 2021; Onoda et al., 2017) but see (Wright et al., 2005)	↓ (Joswig et al., 2022; Martinez-Almoyna et al., 2020; Weil et al., 2021)
	RNC	↑ (Freschet et al., 2021; Scheurwater et al., 2002) but see (Laughlin et al., 2021)	↓ (Freschet et al., 2021; Scheurwater et al., 2002) but see (Laughlin et al., 2021)	↓ (Freschet et al., 2018, 2021)
Collaboration spectrum	SRL	↑ But see (Laughlin et al., 2021; Simpson et al., 2016)	↓ (Augé et al., 2015; Laughlin et al., 2021; Simpson et al., 2016)	↑ (Freschet et al., 2021)
	RD	↓ But see (Laughlin et al., 2021)	↑ But see (Laughlin et al., 2021)	↓

Methods

Study site and experimental design

To simulate climatic warming of 3°C and linked water limitation in the French Alps, we moved alpine grassland plots 500m down an elevational gradient in September 2016 (Bektaş et al., 2021). The alpine site “Galibier” (45°05'44"N 06°40'06"E at 2450 m altitude) and the subalpine site “Lautaret” (45°04'00"N 06°41'90"E at 1920 m altitude) are close to each other (~2km airline distance), have a similar orientation (South-East at alpine and South-South-West at subalpine site), bedrock (base-riched flysch) and soil (dystric cambisols). At the alpine site, communities are dominated by *Trifolium alpinum*, *Potentilla aurea*, *Plantago alpina*, *Carex sempervirens subsp. Sempervirens* and *Poa alpina*. At the subalpine site, communities are dominated by *Patzkea paniculata subsp. paniculata*, *Festuca nigrescens*, *Carex sempervirens subsp. sempervirens*, *Festuca laevigata*, and *Plantago maritima subsp. serpentina*. We transplanted 10 replicates of 4m² turfs of vegetation with at least 20 cm of their intact belowground parts and the surrounding soils from the alpine to the subalpine site (AlpineWarmed plots). For the transport, each turf was cut in 4 x 1m² pieces and then reassembled in their original composition when re-planted. Around the turfs, we placed water-permeable root barriers to avoid root ingrowth

from the natural vegetation. To control for the transplantation stress, we also horizontally transplanted 10 intact 1m² blocks at the alpine site (AlpineControls) and at the subalpine site (SubalpineControls), respectively. At both sites, cattle and sheep were excluded by electric fences. More details on the experimental design can be found in Bektaş et al. (2021).

In 2021, the year of data collection, average annual soil temperature at the subalpine site was 4.24°C warmer than at the alpine site, average July soil temperature was 2.85°C warmer and snow free season was 48 days longer. The average summer soil moisture was significantly lower in AlpineWarmed than in AlpineControl plots (12.73 +/- 1.05 %, Fig. S1). In 2020, we also measured soil nutrients. Soil nitrate concentration as the plant-available nitrogen did not differ between control and treatment plots (Fig. S1), but soil P concentration decreased significantly with warming (84.97 +/- 23.43 mg/kg, Fig. S1).

Community-level leaf traits

We calculated community level leaf traits using plant relevés and trait databases. Plant relevés were sampled at the peak of the growing season in 2021. We identified and counted all individuals that touched a 4mm metal stick (here after, pinpoint) at equally spaced points (10cm distance) in both the treatments (300 points per plot) and the controls (100 points per plot). Individuals that could be identified only at the genus level were excluded from further analysis (2 % of 13,952 identified individuals). We calculated species relative abundances for each plot and each species by dividing the number of pinpoints each species touched by the total number of pinpoints.

We then extracted interspecific functional leaf traits for all sampled species from our in-house trait measurements (Brun et al., 2022; Thuiller et al., 2014) available in the Androsace database (<https://originalps.osug.fr/>) and complemented the missing data from the TRY database (Kattge et al., 2020) and the Tundra trait database (Bjorkman et al., 2018). For each plot, we then calculated the community weighted mean (CWM) of the log-transformed traits as the product of relative abundance and trait value summed up over all species.

Community-level root traits

Due to low coverage of root traits in the databases we measured community level root traits in situ using root ingrowth cores (Freschet et al., 2021). In September 2020, we planted two soil ingrowth cores (15cm deep, 5cm diameter, plastic mesh size of 3mm) in each plot. We filled the cores with river sand as a standardized root ingrowth medium, let the cores one year in place

and resampled them in September 2021, merging the two samples of one plot into a single ziplock bag. Directly after sampling, we (i) washed the samples to separate fine roots from sand, (ii) weighed the fresh mass of the fine roots, (iii) scanned them to obtain measures of root diameter, length and volume (WinRhizo software, REF), (iv) dried them 72 hours at 65°C for 72 hours and weighed the dry mass and (v) measured root nitrogen content. We calculated specific root length (SRL) as the ratio of root length to root dry mass, and root tissue density (RTD) as the ratio of root dry mass to volume. We log transformed all root trait measurements in order to have a distribution of the values closer to Gaussian. Root cores in one SubalpineControl were missing. Hence, we gap-filled the values with the mean of the nine other replicates of SubalpineControl plots.

Ecosystem functions

We focussed on above- and belowground functions that are tightly linked to plant communities: Above- and belowground productivity, decomposition of recalcitrant (rooibos tea) and labile (green tea) litter (Keuskamp et al., 2013), and 16S rRNA gene copy number as a proxy for bacterial biomass as it is correlated with the shift from more copiotrophic to more oligotrophic microbial communities (REF). We used dry mass of fine roots as a proxy of annual belowground biomass. As a proxy of annual aboveground biomass production, we measured in each plot in each week of the growing season the Normalized Difference Vegetation Index (NDVI) with Decagon ProCheck spectral reflectance sensor and estimated the area under the NDVI curve from the snowmelt to snowfall in 2021 (Bektaş et al., 2021). We placed green and red teabags (Keuskamp et al., 2013) beneath the soil surface in each plot close to the soil ingrowth cores in September 2020, let the teabags one year in place, resampled them in September 2021, dried them for 48h at 70°C and measured their dry mass. From this we calculated the decomposition rate as the difference of the initial dry mass of the teabag and the measured dry mass in 2021 divided by the initial dry mass. We performed quantitative PCR (qPCR) on dry root and sand samples in order to quantify 16S rRNA gene copy number as a proxy for bacterial biomass. We log-transformed and standardized all measurements in order to have a distribution of the values closer to Gaussian and to be able to compare them.

Statistical analyses

To disentangle fast vs. slow and do-it-yourself vs. outsourcing trade-offs in our small scale experiment, we built a principal component analysis (PCA) on all leaf (LMA, LDMC, LNC) and root (i.e. SRL, RD, RNC) traits related to our two focal trade-offs (Table 1 & Fig. S4). We then

tested with Horn's parallel analysis if two dimensions were adequate to represent the variation in these traits (Franklin et al., 1995). We left out RTD from the analysis as the literature on its interdependence with SRL is not clear and also in our study it was highly correlated to SRL ($r = -0.85$) (Carmona et al., 2021; de Vries et al., 2016). Finally, we wanted to see if these dimensions could be captured by the hypothesized trade-offs. We thus run an independent PCA per tradeoff (i.e. one for LMA, LDMC, LNC, RNC (Fig. S3) and one for RD and SRL), extracted the first principal components and projected them on the original PCA on all traits to check if they were orthogonal to each other. For all further analyses we use these two first principal components as variables representing the two trade-offs. We performed the PCA and parallel analysis with FactoMineR and paran package in R, respectively (Dinno, 2018; Lê et al., 2008).

To assess if functional strategies differ between treatments, we built two independent linear regressions to explain the two trade-offs with the three treatment levels (AlpineControl, SubalpineControl, AlpineWarmed) and applied post hoc tests to identify significant differences between treatments. To correct for multiple testing we adjusted the p-values with the multivariate t-distribution adjustment in the emmeans package (Lenth, 2022). We interpret a significant difference (i) between AlpineControl and SubalpineControl as a strategy difference along the elevational gradient, (ii) between AlpineControl and AlpineWarmed as a warming effect and (iii) between SubalpineControl and AlpineWarmed as an acclimation lag after 5 years of warming (Bektaş et al., 2021).

To assess if the warming induced shifts in plant strategies affect above- and below-ground ecosystem functions, we used only data from AlpineControl and AlpineWarmed and built independent linear regressions for our focal ecosystem functions in dependence on treatment, the two trade-off variables and their two-way interactions. We selected the most parsimonious models (backward stepwise selection with Akaike information criterion (AIC, step function in R) and determined the importance of the selected variables based on difference in AIC between the models with and without the focal variable.

Results

Can we disentangle the two trade-offs in our small scale experiment?

We found that two axes were sufficient to explain the variation in our focal traits that are theoretically linked to the fast vs. slow and the do-it-yourself vs. outsourcing trade-offs (Fig. 1 and Horn's parallel analysis, Fig. S4). Plotting the two first principal components from separate

PCAs for the two trade-offs showed that the fast vs. slow and the do-it-yourself vs. outsourcing trade-offs were almost orthogonal to each other (Fig. 1, dashed lines). We thus use these derived variables to represent the two trade-offs in the further analyses.

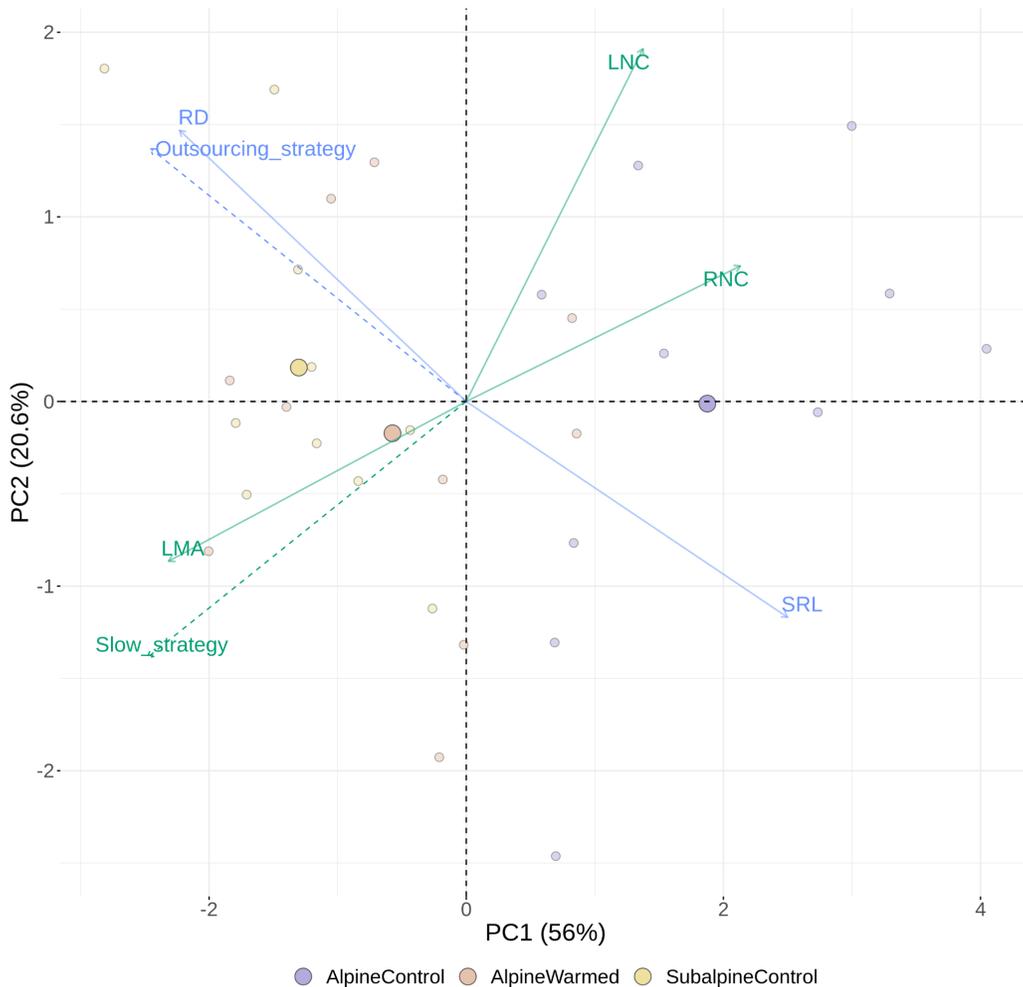


Figure 1: Community-level functional trait space with fast vs. slow and do-it-yourself vs. outsourcing trade-offs of the experimental plots. Fast vs. slow trade-off is constructed from LNC, RNC and LMA (in green). Do-it-yourself vs. outsourcing is constructed from SRL and RD (in purple). (LNC: leaf nitrogen content, LMA: leaf mass per area, RNC: root nitrogen content, SRL: specific root length, RD: root diameter)

Do functional strategies differ between treatments?

Strategies along both trade-offs differed significantly along the elevation gradient (AlpineControl vs. SubalpineControl), alpine communities significantly shifted their strategies after warming (AlpineControl vs. Alpine Warmed) and they shifted them enough to fully acclimate to the new climatic conditions (AlpineWarmed vs. SubalpineControl, Fig. 2). While alpine plant communities

tended towards faster and do-it-yourself strategies, subalpine communities and warmed alpine communities tended towards slower and more outsourcing strategies.

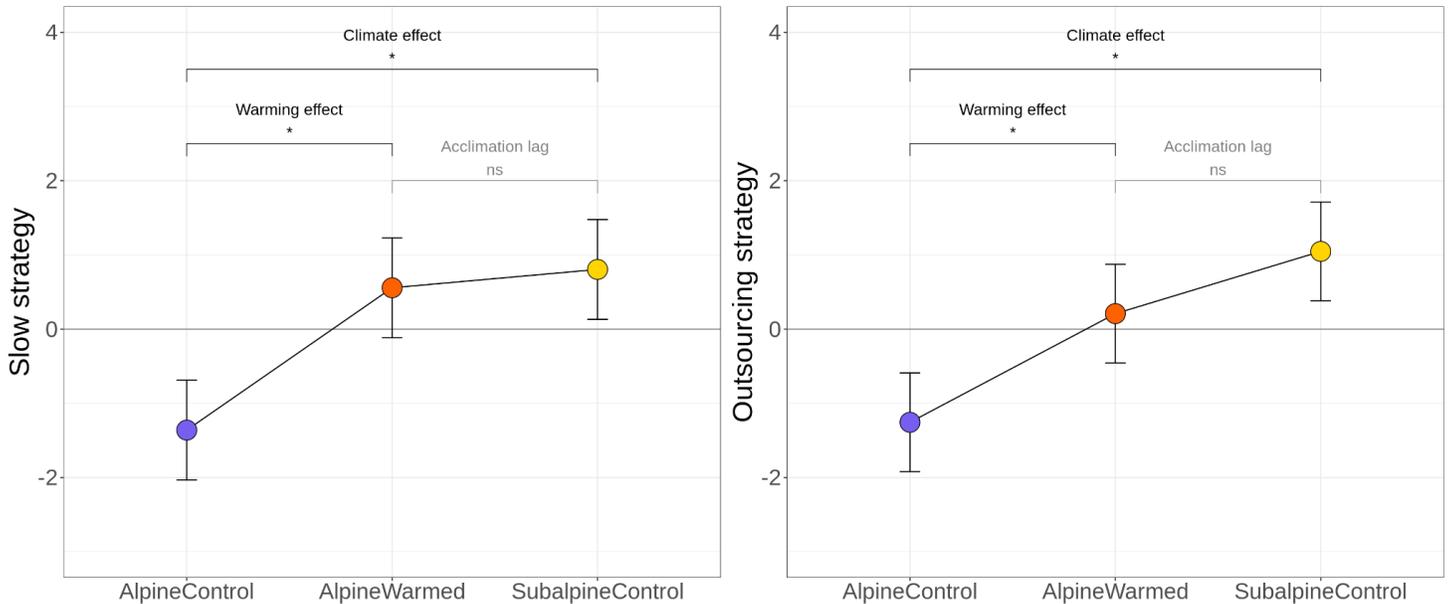


Figure 2: The position of the treatment and control plots on the fast vs. slow (left) and do-it-yourself vs. outsourcing (right) trade-offs. Positive values indicate slow and outsourcing strategies. Different comparisons and their significance is indicated above. Significant (p -value < 0.05) comparisons are in black. Error bars represent 95% confidence intervals.

How do the warming induced shifts in plant strategies affect ecosystem functions?

Belowground productivity and bacterial biomass in roots were moderately explained by treatments and plant functional strategies (26% and 20% explained variation) and aboveground productivity, red tea bag decomposition, green tea bag decomposition and bacterial biomass in sand (74%, 60%, 55%, and 53% explained variation) were very well explained (Fig. 3). Treatment was always an important explanatory variable (Fig. 3). Importantly, all ecosystem functions were in addition influenced by at least one plant functional trade-off thus indicating that changes in community-level functional strategies cascade to ecosystem functions (even so the effect was very small for the labile litter decomposition, Fig. 3). While belowground productivity was overall increased with outsourcing, it decreased with outsourcing in warmed communities (Fig. 3, 4A). A potential reason for this could be that while communities acclimated their overall outsourcing strategy to warming, this strategy shift was driven by a fully acclimated SRL but, though important for productivity, RD was strongly lagging behind (i.e. no significant warming effect and thus no acclimation, Fig. 4 B & C). Similarly to belowground productivity, aboveground

productivity was overall increased with faster functional strategies under control conditions but it tended towards a decrease with faster strategies in warmed communities (Fig. 3, 5A). However, for aboveground productivity this could not be explained by a desynchronized response of traits linked to the fast-slow trade-off (Fig. 5 B, C & D). Decomposition of recalcitrant litter (red teabag) was largely improved by outsourcing and slightly improved by fast strategies alone. In warmed communities, the positive effect of outsourcing was even stronger. Bacterial biomass as an indicator of copiotroph and thus faster microbial communities in roots was increased by fast plant functional strategies. Bacterial biomass in sand was increased by fast and do-it-yourself plant functional strategies. In warmed communities, the positive effects of outsourcing were even stronger.

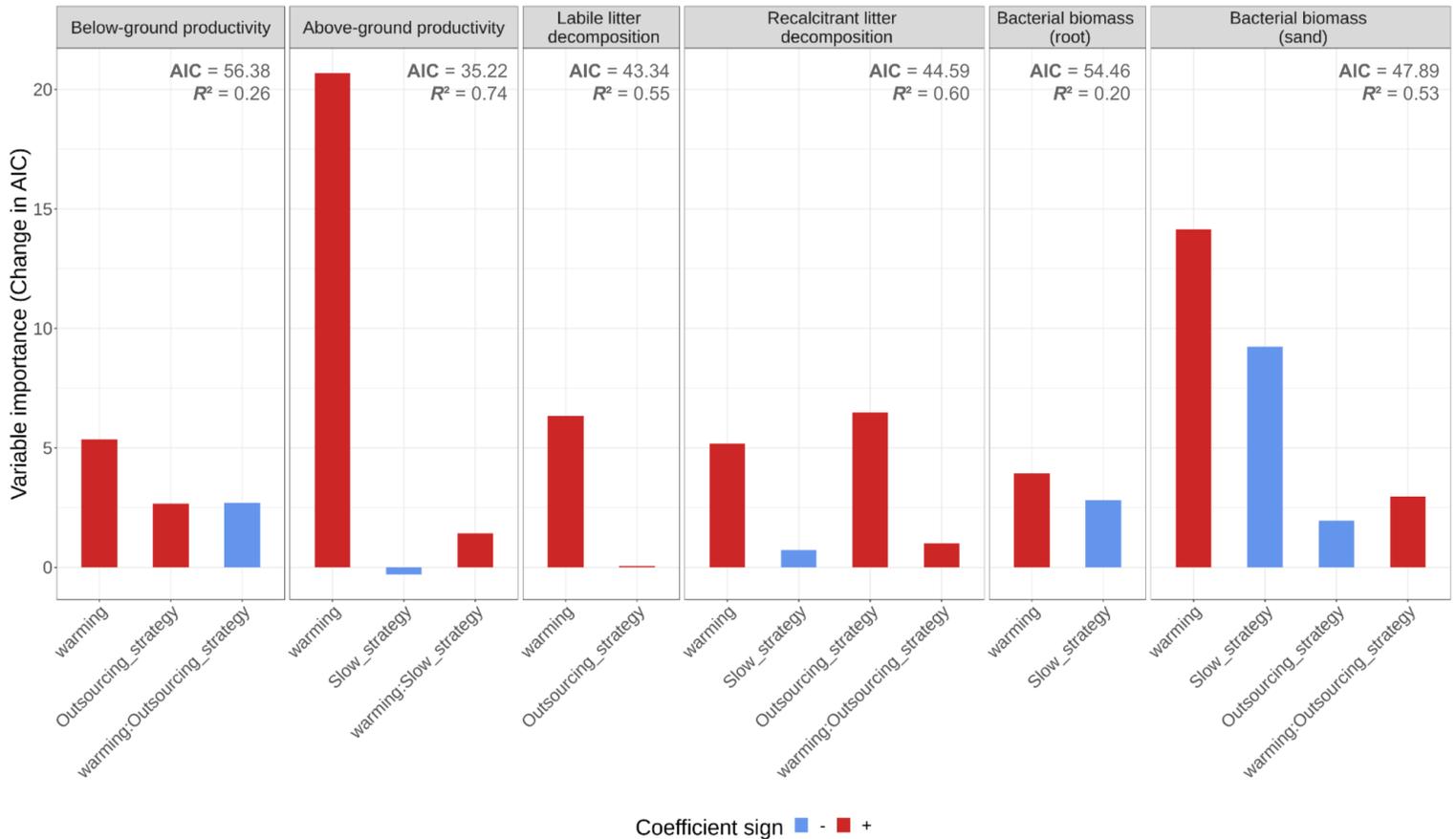


Fig. 3: Variable importance of the most parsimonious models for each ecosystem function. The variable importance is calculated as the difference in AIC between the reduced model when the variable is eliminated and the most parsimonious model. AIC and R^2 scores of the models are indicated for each function.

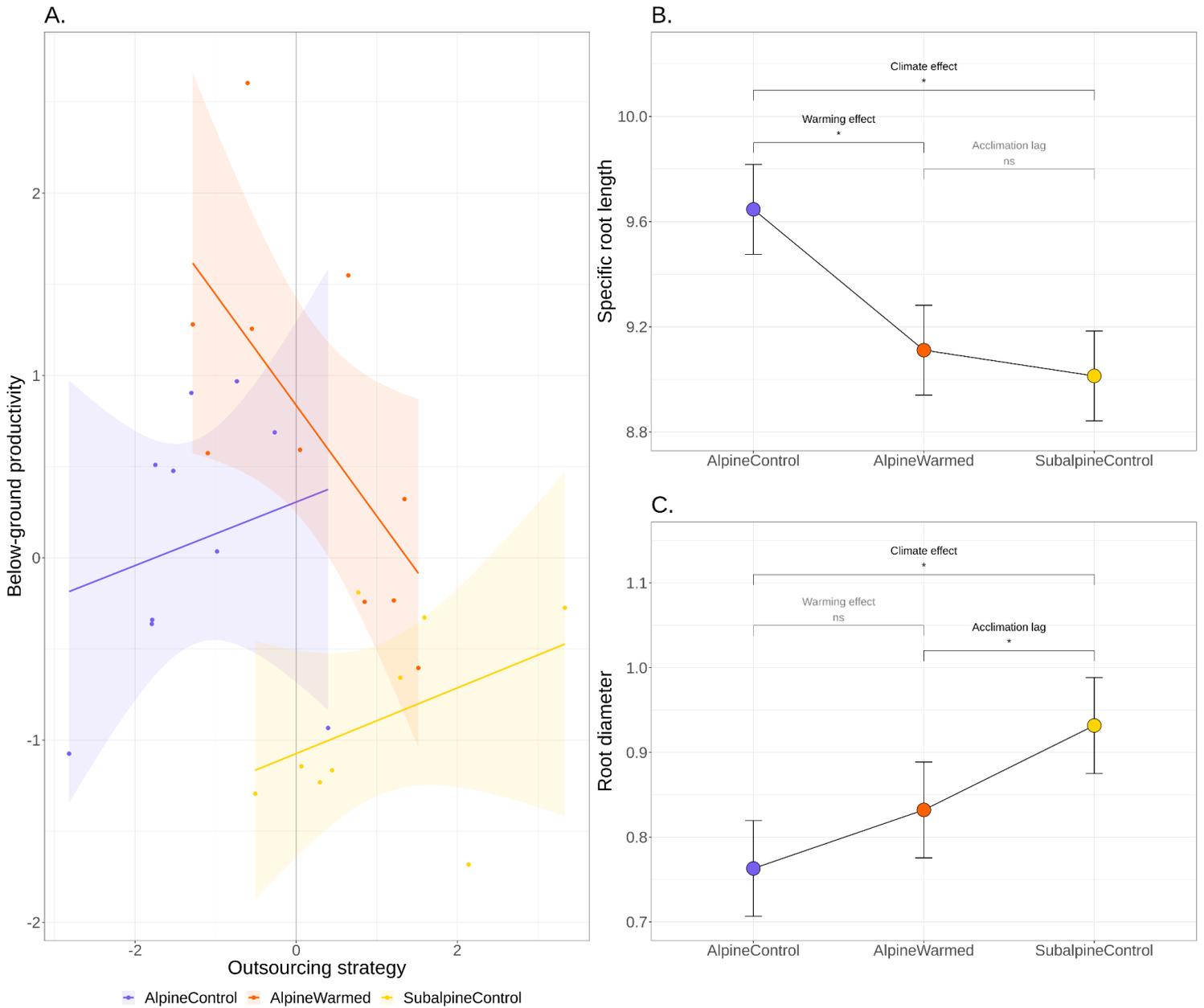


Fig. 4: **A.** Change in below-ground productivity with the outsourcing strategy for AlpineControl (purple) and AlpineWarmed (orange) plots. Mean specific root length (**B.**) and mean root diameter (**C.**) as components of the collaboration spectrum. Different comparisons and their significance is indicated above. Significant (p -value < 0.05) comparisons are in black. Error bars represent 95% confidence intervals.

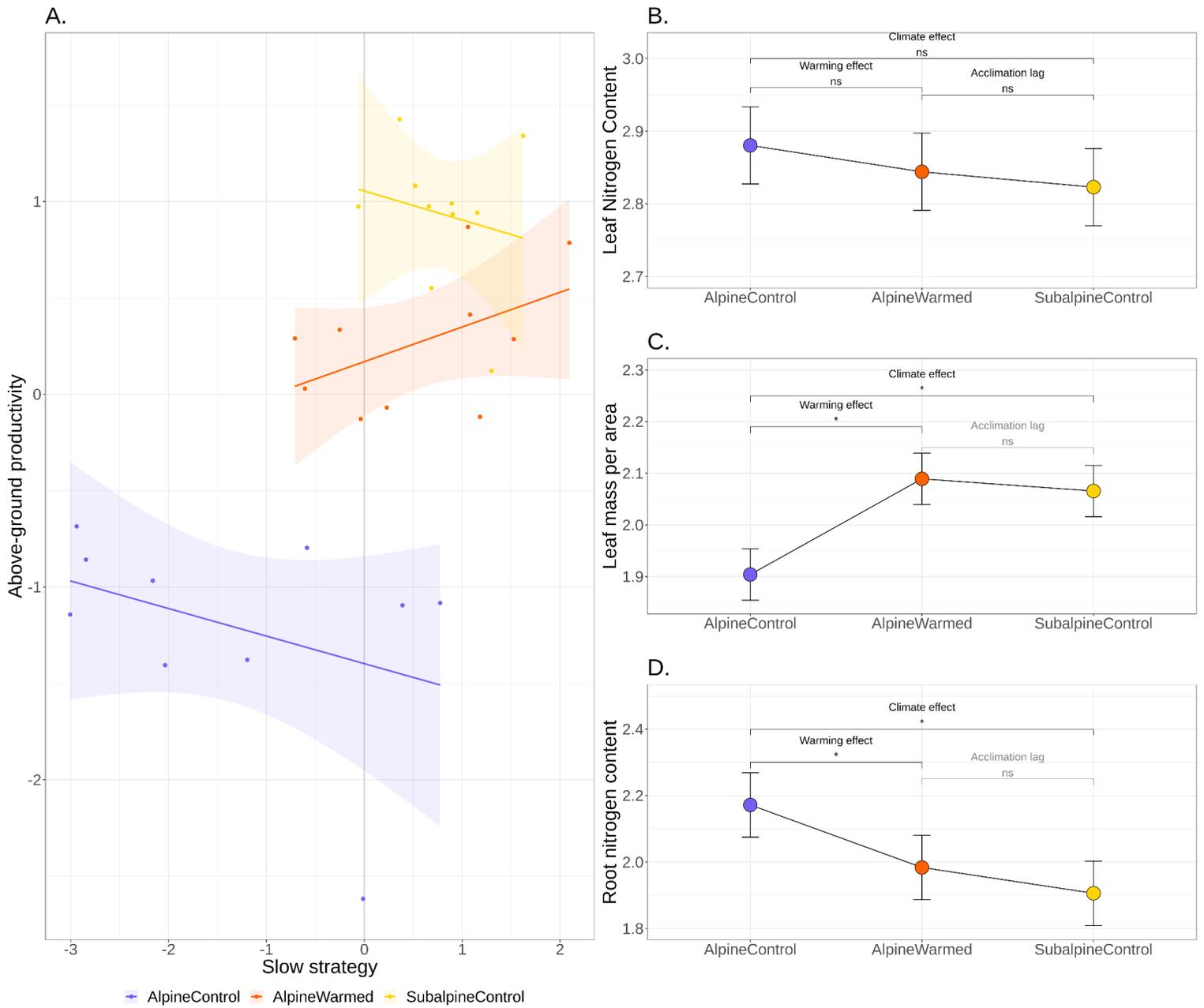


Figure 5: A. Change in above-ground productivity with the slow strategy for AlpineControl (purple) and AlpineWarmed (orange) plots. Mean leaf nitrogen content (B.), leaf mass per area (C.) and (D.) root nitrogen content as components of the collaboration spectrum. Different comparisons and their significance is indicated above. Significant (p -value < 0.05) comparisons are in black. Error bars represent 95% confidence intervals.

Discussion

The response of the plant kingdom to climate change is recognized as one of the fundamental mediators of environmental change with shifts in plant communities cascading further to both the brown and the green food web. Here we studied the responses of plant functional strategies to in situ climate warming and the cascading effects of these responses on related ecosystem functions. We observed quick warming effects and full acclimation in the two dominant strategy tradeoffs. Shifts in trade offs cascaded to plant above- and below-ground productivity, litter decomposition in the soil and a functional shift in microbial communities. We thus lose in these communities the plant strategies and functions typical for alpine conditions. In addition, at least for one function, a plant strategy successful under control conditions (i.e. outsourcing) was not able any more to increase its function (i.e. belowground productivity) under transient warming conditions. Such interruptions of links between plant strategies and ecosystem functions under transient dynamics may be problematic in a world that is constantly warming.

Species' orthogonal trade-offs upscale to communities

We showed that in our small scale, community-level experiment, fast vs. slow and do-it-yourself vs. outsourcing trade-offs explained trait variation well. Like shown earlier in large-scale observations on species distributions along stark environmental gradients, these two dimensions were orthogonal to each other and sufficient to represent plant functional strategies (Bergmann et al., 2020; Weigelt et al., 2021). To our knowledge, there is so far a single study that investigated the presence of orthogonal trade-offs in leaf and root traits at community level and our results are in line with this study (Lachaise et al., 2022). Here, in addition, we showed that this framework of orthogonal trade-offs can be particularly useful in determining stress for plants and studying ongoing climate change on shifts in plant functional strategies.

Moisture determines the functional strategies in mountain grasslands

Alpine communities were faster and more do-it-yourself communities compared to subalpine communities and under warming, alpine communities quickly became slower and more outsourcing and had fully acclimated after five years. From the perspective of temperature and soil nutrients (Table 1), we rather expected that subalpine and warmed communities would exhibit faster and more do-it-yourself strategies compared to alpine communities as in the subalpine site both the energy input and above-ground productivity are higher (Fig. 4,5). However, this was not the case (Fig. 2). In fact, communities showed that the prevailing stress

gradient was the increased summer drought (and/or potentially decreased soil nutrients, Fig. S1) and responses to transplantation were rather driven by drought effects and/or decrease in soil P (Table 1). Such drought responses were reported earlier (Lachaise et al., 2022; Laughlin et al., 2021) as mycorrhiza supports plant growth under drought stress (Augé et al., 2015) and have a slower strategy to withstand drought (Table 1).

Complete acclimation in functional strategies

That alpine communities acclimated already after five years of experimental warming, was surprising as our experimental communities are dominated by perennial species that are known to be resistant to abiotic changes. Results from a sister study on our experiment can explain how this fast response was possible. They showed that abundance changes in warmed communities were more important than extinctions (only 5 out of 100 alpine species) and colonization events (29 subalpine species but with very low abundances) (Bektaş et al. 2022, unpublished). It seems like the turnover in alpine communities under warming is built up by abundance changes and phenotypic plasticity. However, from a closer look within the do-it-yourself vs. outsourcing trade-off, this trait turnover was not “perfect” in alpine warmed communities: Root diameter did not acclimate completely while specific root length did (Fig. 4). This might indicate either a temporal decoupling between root traits even if they belong to the same trade-off or a complete decoupling due to changes in abiotic conditions (Laughlin et al., 2017). As discussed below such disruptions may have impacts on resulting ecosystem functions.

Changes in functional strategies cascade to ecosystem functions

While warming affected both functional strategies and ecosystem functioning directly, the latter was affected also indirectly through the shifts in functional strategies. Looking at the main effects of the functional strategies, first allowed us to assess the “expected” links between the functional strategies and ecosystem functioning in alpine communities. However, the interaction effects between warming and functional strategies revealed some disruptions probably due to transient dynamics under warming.

In alpine communities, an outsourcing strategy was associated with an increased belowground productivity and decomposition (particularly the recalcitrant litter) but a decrease in bacterial biomass. Outsourcing is prone to favor fungi dominance as the recalcitrant litter decomposition is associated with fungi communities (Daebeler et al., 2022; Hoppe et al., 2016) and this

strategy should normally pay off as an increase in the below-ground productivity. However, under warming, the relationship between an outsourcing strategy and ecosystem functions was altered. Recalcitrant litter decomposition and bacterial biomass were further enhanced with increased outsourcing but below-ground productivity decreased. There can be several explanations to this: i) it could be that plants' investment to fungi did not really pay off as the fungi abundance was still not enough and microbial communities need more time to adjust so as the below-ground productivity, ii) fungi and bacteria communities are actually facilitating each other (Boer et al., 2005), iii) due to presence of a double stress gradient (decreased moisture but increased nutrients), there is an increase in both microbial communities.

A slow strategy was associated with a decrease in bacterial biomass, recalcitrant litter decomposition and above-ground productivity. This is in line with the expectations that slow functional traits are associated with slow ecosystem functioning, nutrient turnover and less productivity (Reich, 2014) and supports our hypothesis that the water is the limitation in this system. However, interestingly, under warming the relationship between the above-ground productivity and the slow strategy changed to become positive. Having in mind that warming explained the increase in above-ground productivity best, it could be that slow communities further invest in plant size through plasticity in order to increase photosynthetic activity and escape competition for light.

Limitations and perspectives

Investigating the plastic and demographic responses to climate warming is important in order to have a full picture of the thermal acclimation in alpine communities (Nicoitra et al., 2010). Here, we captured the plastic responses in root traits and abundance driven responses in leaf traits. Our study would benefit further from measuring the plasticity also in leaf traits, especially as we suspect that the plasticity in functional traits is important for the responses of ecosystem functions. Moreover, our study indicated a possible temporal decoupling between plant investment in fungi and fungi abundance under warming. Hence, it would be important to study explicitly the changes in microbial communities and their temporal dynamics in order to understand such multitrophic mismatches.

Conclusion

In this study, we confirmed that fast vs. slow and do-it-yourself vs. outsourcing orthogonal trade-offs upscale to community level and vary with climatic conditions in mountain grasslands.

Tracking the transient dynamics of these strategies under warming allowed us to detect their rapid acclimation. Our study highlights the importance of multiple stressors in altitudinal gradients and that the warming associated effects such as drought and changes in nutrient dynamics can lead the direction of the responses rather than the temperature change alone. The cascading effects between functional strategies and ecosystem functioning and the impairment of their link under warming show that studying the transient dynamics of functional traits can serve as early warning signals.

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Discussion

During my thesis, I focused on revealing the direct and indirect effects of climate warming and associated drought on plants at different biological scales, their trajectory of acclimation and cascading effects to ecosystem functions. I chose the alpine grasslands as a case study primarily because of their intrinsic value in plant biodiversity and secondly, because mountains are *in situ* laboratories that allowed me to set up a transplant experiment to simulate climate warming on plant communities. In the introduction I asked the following questions **1) How are individuals, communities and ecosystem functioning affected directly by experimental warming and drought** (Chapters 1-4)? **2) Do acclimation lags remain after experimental warming and drought** (Chapters 1,3,4)? **3) How are plants indirectly affected by experimental warming and drought via biotic interactions** (Chapter 2,3)? **4) How are ecosystem functions indirectly affected by experimental warming and drought via changes in plants** (Chapters 1,4)? In the following sections, I will be answering the four main questions of my thesis through the key findings from each chapter. The summary of these answers can be found in Table 3. Later, I will be discussing the limitations of my thesis and potential ways to improve them.

1. Direct effects of warming and drought

Throughout each chapter we first focussed on the direct effects of warming and drought (Table 3, red arrows). This effect was studied by comparing AlpineControl communities to AlpineWarmed communities. The large majority of *in situ* warming experiments is focussing on this effect. First, we investigated the warming effect on phenological indicators related to timing and demographic performance in plant growth at community level and reproduction at species level after three years of experimental warming (Chapter 1). In response to warming and drought in alpine grasslands, i) the timing of phenological events was delayed, ii) plant growth was enhanced for communities yet iii) reproductive performance decreased for forbs. **Thus, overall alpine plant growth responded to the additional energy input available at the subalpine site. Warming clearly affected forbs and graminoids differently.** While forbs did not show any plasticity in timing of flowering and fruiting, graminoids' fruiting was delayed and thus well suited for the longer growing season length at the subalpine site. While forbs' flowering and fruiting duration decreased, graminoids showed no negative effect of transplantation on reproductive performance. These results showed that some plants were quicker to respond to

warming in their phenology and to profit from the advantages (e.g. more energy input) of the new conditions while others suffered more from the added stress (e.g. drought) and that these responses were linked to growth forms. Yet, could we already see changes in abundances and species distributions of alpine plants? Was it possible to identify winners and losers? Were there already extinct species and colonizer subalpine species in the warmed alpine communities? And finally, were there characteristics that made a species a winner, loser, extinct or colonizer that were more fine than rough classifications in life forms? We answered these questions by tracking the changes in species' abundance trends through five years of experimental warming and drought (Chapter 2). **Among 47 alpine species, we identified 13 significant losers and 4 significant winners and losses generally exceeded gains.** One of these losers, *Myosotis alpestris*, was an extinct species which had an increasing trend in AlpineControl communities. Additionally, we detected three other extinct species that already had a decreasing trend in abundance in AlpineControl which may be linked to the fact that **our control communities are not constant but are influenced by "background global warming"**. Moreover, there were 29 subalpine species that could already colonize the AlpineWarmed communities. Thus, overall our results supported observational studies showing that alpine plant life is in danger not least by downhill species moving upwards, successfully colonizing and potentially outcompeting the alpine species already suffering from the direct climate change effects. Losers were the ones that could not withstand the direct effects of warming and drought: they were cold-adapted and drought-intolerant. They were also shorter and on average less conservative than winners. In contrast to the alpine winners, subalpine colonizers tended to be more exploitative and moisture-loving. These results underlined that the changing competition landscapes may become even more rough for alpine species when subalpine species start to arrive and colonize because they are even better adapted than the alpine winners. Changes in species' abundance trends based on their functional traits pointed out that communities were already restructuring due to the direct effects of warming and drought. Hence, we could detect adjustments in the community assembly mechanisms early on. Thus, we assessed the changes in community assembly processes after 2 years of experimental warming and drought (Chapter 3). For this, we first developed a spatially explicit trait-based community assembly framework that is useful to i) detect jointly acting community assembly processes, ii) disentangle environmental filtering from biotic interactions and hierarchical competition from symmetric one, iii) reveal changes in these processes under climate change. Through our novel framework, we detected changes in functional diversity patterns that are attributable to changes in community assembly processes under climate change. Experimental climate change weakened environmental filtering and

increased competition for some traits and for some others, signals of processes appeared or lost. We also detected a release in environmental filtering through changes in diversity patterns of vegetative height, SLA and leaf C/N and an increased environmental filtering through the changes in diversity patterns of LDMC. **This showed that communities were restructuring based on both i) increased energy input and nutrients in the system and ii) water that was becoming a limiting factor in the warmed communities.** Findings from all chapters indicated that not only individuals but also communities were reacting very quickly to warming and drought. Hence, we finally asked if the **whole communities' functional strategies and ecosystem functions were already changing under warming and drought and increasing strength of competition.** We answered these questions after 5 years of experimental warming and drought and found that **communities became overall more conservative (slow) and outsourcing.** A response that was in agreement with the characteristics forming an alpine winner but not with those making a subalpine colonizer successful. This highlights that warmed communities are already strongly affected by direct warming effects and also by indirect effects via changed competition landscapes within their alpine communities. However, indirect effects via changed competition landscapes with entirely new species lag far behind and that the characteristics of these species are different than those of alpine winners may indicate larger future changes. Even so, first colonizers indicate potential future directions, community level processes and functions are not yet affected.

In summary, individuals, species and communities in alpine grasslands were very quick (1-5 years) to react directly to warming and drought even though these reactions were not always positive. As much as communities were highly plastic as a whole (Chapter 1) and even though extinction events were rare (Chapter 2), very sharp changes in abundance trends drove the quick responses in community functional shifts and assembly processes (Chapter 3 & 4). **These were early warning signals of warming and drought effects in alpine grasslands, however the question remains: "Were these responses transient?"**

2. Transient dynamics and acclimation lags

I believe that one of the strongest points of my thesis was the fact I could track the transient dynamics under warming and drought and provide answers to the above question. To do so, I developed a framework (Box 2) in the context of transplant experiments. First, comparing the alpine and subalpine control communities allowed me to define the trajectory of acclimation to warming. Second, comparing the warmed alpine communities (through a transplantation to

subalpine conditions) to subalpine control communities allowed me to decipher the acclimation lags. Throughout the chapters, I could characterize and quantify the acclimation lags that remained due to not yet sufficient acclimation or even warming responses that were diverging from the direct trajectory to a fully acclimated state. First, we found that phenology acclimated fully in their plant growth and reproduction timing except that browning and fruiting for forbs lagged behind (Chapter 1). However, as much as communities increased their plant growth substantially, this was not enough to close the acclimation lags. In addition, forbs reproductive performance showed a divergent warming response hence warmed alpine forbs lagged behind the subalpine forbs even more than when they started their acclimation. Graminoids were fully acclimated to new conditions. **This shows that alpine forbs under warming are less performant than the subalpine forbs and thus, they might not be able to withstand the competition with them once they colonize the warmed communities.** Second, we found that community assembly mechanisms were also showing transient responses under warming and drought (Chapter 3). In experimental communities, environmental filtering (via patterns in integrated trait and vegetative height) was still stronger than of subalpine communities and increased strength in environmental filtering for LDMC was actually a divergent response that was not on the acclimation trajectory. Moreover, while the hierarchical competition was present in subalpine communities, we detected no such signal in experimental communities. Moreover, the strength of symmetric competition detected via the patterns in LDMC remained higher for subalpine communities than for experimental communities. **This shows that subalpine communities have highly competitive species and even some being at the top of their hierarchy and that alpine communities that are less driven by competition may suffer from these colonizers.** After we found out that acclimation lags remained in plant growth, reproductive performance of some plant functional groups and community assembly mechanisms (Chapter 4), we investigated if whole community functional strategies acclimated after five years of warming. Surprisingly, by shifting towards a more conservative (slow) and outsourcing strategies, communities acclimated completely after 5 years of warming. However, acclimation lags remained for some ecosystem functions (Chapter 4, Appendix Fig. S8). In fact, the acclimation lag in above-ground productivity after three years of warming and drought (Chapter 1) was persistent even after 5 years of warming and drought (Chapter 4) due to insufficient warming effect. On the other hand, below-ground productivity had a nonsignificant warming effect (even with a divergent tendency) and thus, acclimation lag remained.

In summary, **as much as the responses of plants to warming and drought were rather fast, this did not mean that it was always sufficient or in the direction of the acclimation trajectory.** Completed acclimation in community functional strategies shows that changes in species abundances in the above-ground and plasticity in the below-ground are powerful mechanisms of acclimation to climate change. Remaining acclimation lags in plant growth, community assembly and ecosystem functions could be due to i) multiple stress factors (warming and drought) that are pulling the system in different directions (Hastings et al., 2018), iii) feedbacks between different processes notably plant-soil feedbacks (PSF) (van der Putten et al., 2013; Weil et al., 2021), iv) indirect effects of warming and drought through plant-plant interactions, notably competition.

3. Indirect warming effects via changes of biotic interactions

Warming and drought affect the plants and ecosystem functions indirectly through plant-plant interactions. Here, we tried to reveal the competition effect on demographic performance (Chapter 2) and community assembly (Chapter 3). First, we showed that losers were shorter (and maybe less conservative) than their neighbors (i.e. they were at the bottom of their hierarchy). Thus, they were suffering both because of their traits that were not preadapted to the new conditions and competition as they were surrounded by species that are coping relatively well with warming and drought effects. We further showed that with warming competition strength increased in vegetative height and a signal of competition appeared in LDMC (Chapter 3). However, both of these signals were symmetric competition. Recently, (Chalmandrier et al., 2022) showed that as much as symmetric competition through limiting similarity can be the driving force of the community assembly, hierarchical competition can still favor some tall species with high SLA. In fact, short loser species in our experimental communities that suffer due to competition with taller neighbors constitute still a small subpart of these communities (i.e. there were 26 species with constant abundances along five years of treatment).

In summary, competition between plants is an important mechanism that determines which plants suffer further under warming and drought and that restructures the communities as a whole. These findings together with acclimation lags in plant growth and vegetative height (Table 1) reveal that alpine communities that suffer under climate warming are particularly vulnerable to highly competitive species from lower altitudes. In fact, we already detected the first subalpine colonizers in AlpineWarmed communities that were even taller and even higher at the light competition hierarchy than alpine winners (Chapter 2). In addition, they were more

exploitative than winners and even more exploitative than their neighbors. This might indicate that even alpine winners are at risk of being outcompeted by colonizers in the future.

4. Cascades to ecosystem functioning

Not only plants but also ecosystem functioning is affected by climate warming. These effects can be direct, for example by changed nutrient turnover rates due to changed temperatures, but also indirectly through the functional characteristics of plants. In my thesis, I studied different ecosystem functions, ranging from those with very tight connections to plants such as above and belowground plant productivity, to those that link plants with other trophic levels, such as pollination aboveground and bacterial biomass belowground, towards those that are involved in processes of plant-soil feedbacks such as decomposition. For aboveground productivity, we assessed the effects of plasticity in plant growth and shifts in community functional strategies on above-ground productivity (Chapter 1 & 4). We found that the changes in functional strategies had only a minor importance in increased above-ground productivity (Chapter 4). Together with the findings in Chapter 1, it seems like plasticity is the driving force of the above-ground productivity rather than the species abundance changes or turnover. In the below-ground, increased specific root length and a slight increase in root diameter resulted in an enhanced productivity. We additionally assessed the pollinator diversity under warming and drought and we found that subalpine communities attract more pollinators than AlpineWarmed communities (Chapter 1). This was probably due to the fact that flowering duration and number of flowering individuals in SubalpineControl communities were higher than AlpineWarmed communities. Moreover, shifts in functional strategies cascaded to bacterial biomass: bacterial biomass decreased as the communities got conservative (slow).

In summary, the effect of warming and drought on ecosystem functions in alpine grasslands is a complex phenomenon due to both direct and indirect effects. It is clear that changes in plant communities cascade to ecosystem functioning, however how the ecosystem functions notably changes in nutrient dynamics feedback to plant communities remains as an open question within the scope of my thesis.

Table 3: Summary of warming and drought effects (red arrow), acclimation lags (orange arrow), competition effects (green arrow) and cascading effects to ecosystem functioning (blue arrow) found in different patterns of plant performance and characteristics (lines) at different levels of biological organization (columns) in this thesis. Upwards arrows represent a positive warming effect, a remaining acclimation lag, signal of increased competition and positive effect on ecosystem functioning, respectively and vice versa for downwards pointing arrows. Numbers in parentheses indicate the different chapters of the thesis.

	Individuals		Species				Communities
	Forbs	Graminoids	Extinct species	Losers	Winners	Colonizers	
Reproductive performance	↓↑↑(1)	⇒⇒(1)	?				?
Plant growth performance	?	?	?				↑↑↑(1)
Vegetative height	?	?	↓(2)	↓↓(2)	↑↑(2)	↑↑(2)	⇒(4)↑(4)↑(3)
Conservative leaf traits	?	?	↓(2)	↓↓(2)	↑↑(2)	↓(2)	↑(4)⇒(4) ↑(3)↑(4)
Outsourcing root traits	?	?	?				↑⇒↑(4)

▬ Direct warming and drought effect
 ▬ Acclimation lag
 ▬ Competition effect
 ▬ Cascade to ecosystem functions

Overall, in alpine grasslands, warming and drought effects are strong yet not always enough to completely acclimate to the new conditions. In general, this makes the alpine species and communities vulnerable to more performant subalpine colonizers once the upslope migration will be accelerated. We saw that plants at different biological scales were quick to react to experimental warming and drought. We recorded changes in phenology already one year after the transplantation and changes in species abundances already two years after the transplantation that cascade to community assembly mechanisms already. However, extinction and colonization events were recorded five years after the transplantation. It thus seems like changes in phenology and species abundances precedes the species turnover. Moreover, we detected that community level functional strategies were already acclimated and ecosystem

functioning responded strongly after one year and continued to respond strongly after five years for productivity. This shows that the cascading effects are rather quick between biological scales and can enhance the warming effects. In fact, direct effects were not necessarily quicker than the indirect effects as we already detected changes in plant-plant interactions and plant-pollinator interactions within two years and plant-soil microbes interactions after five years. So, **what threats does the future hold for alpine plants? Or even are there any threats at all? Yes, threats still persist.** 1) We already recorded extinct species when it was only the beginning of colonization events. We suspect that extinctions will speed up with the accelerated colonizations. Even the winner species that were once benefitting from the climate change can suffer later once novel competitors arrive (Alexander et al., 2015; Block et al., 2022). 2) We showed a homogenization in the functional traits and ecosystem functions as warmed alpine communities are resembling more and more to the subalpine communities. 3) We showed that there is a desynchrony between community functional strategies and ecosystem functions, yet we do not know to what extent these will further impair the functions and feedback to the plants. 4) Warming comes with drought and thus, it is even harder to predict the responses of multiple stressors. As the associated drought is also driven by the plants' evapotranspiration, we do not know how they will further feedback each other.

5. Limitations

There are a couple of limitations to my thesis and here, I would like to discuss three of them: i) methodological limitations regarding the experimental setup, ii) problems with disentangling plant-soil feedbacks and iii) ignoring plasticity in functional traits and evolutionary processes.

5.1. Methodological limitations

With my thesis, I showed that warming experiments, notably whole community transplant experiments, are powerful tools to assess the trajectory of thermal acclimation. Our setup allowed us to i) simulate a warming scenario that is realistic for the upcoming century in mountain grasslands, ii) introduce equally the warming associated effects such as expected changes in the snow cover dynamics, extension of growing seasons and early exposure to freezing events, iii) compare the warmed communities with their state in their original (home) climate and with their state in the future climate once the acclimation is completed, iv) change both the abiotic and biotic conditions and assess indirect effects of climate warming. However, each of these strengths of the experiment might also have some shortcomings. Firstly, despite the fact that the degree of warming that we introduced here was a realistic scenario, we know

that the changes will not be as quick as introduced with the experiment (Block et al., 2022). Hence, it is important to understand if these responses that we recorded are on the trajectory of potential responses of a gradual change in temperature. For example, Block et al. (2022) recently showed by coupling a transplant experiment with a demographic model that responses to quick experimental warming might miss intermediate responses under gradual climate warming because there could be species that benefit from moderate climate warming. Secondly, one of the warming associated effects that we introduced was the drought. As much as increased summer drought is an expected change in the future in the mountains, on one hand, it is hard to create a realistic scenario of future precipitation (Korell et al., 2020). On the other hand, it is a challenge to disentangle the warming and drought effects. For example, (Wolkovich et al., 2012) found that the warming experiments underpredict the change in plant phenology (in comparison to observation based studies), potentially due to an artifact of drier soils due to experimental manipulation. In our experiment, we chose the sites where annual precipitation was comparable yet experimental warming caused also a decrease in soil moisture (potentially due to increased evapotranspiration of plants) in an expected direction: AlpineWarmed soils were as dry as SubalpineControl soils (Chapter 4, Appendix Fig. S1), hence I do not think that it was an artifact. However, within the scope of my thesis, we only interpreted the drought effect through the directions of shifts in functional traits and strategies (Chapter 4). In the future, the drought effects should be more thoroughly investigated. Thirdly, comparing the AlpineControl to SubalpineControl allowed us to reveal the acclimation trajectory and comparing AlpineWarmed to SubalpineControl allowed us to reveal acclimation lags. To my knowledge, there are only a couple of studies that adopt a similar approach (Palacio-López et al., 2015) though with a less emphasis on ecological processes such as acclimation lags (Midolo & Wellstein, 2020). However, I acknowledge that the assumptions defining the acclimation trajectory are strong ones. Here, I would like to elaborate on two of them: i) We assume that both initial (AlpineControl) and final (SubalpineControl) states are already at equilibrium, at the same stage of their succession, experience same soil legacy effects and not subject to already initiated climate warming (or they are affected the same way). As our study is comparative, when these effects are the same magnitude, we are able to take them into account but when they are different in magnitude, it is hard to control. ii) We assume that after a sufficient time, AlpineWarmed communities will be functionally indistinguishable from SubalpineControl communities either because they will completely acclimate or they will be colonized by the subalpine species. I think that the latter is an assumption that is realistic within the experimental setup, however can be unrealistic in the natural context as it assumes that all

the subalpine species will be able to migrate upslope. Fourthly, even though the experiment allows us to change biotic conditions and assess indirect effects of climate warming, these changes in the biotic conditions may not always be realistic. Besides that we exposed warmed communities to migration from subalpine plants (maybe in an unnatural way), the same is true for organisms from other multitrophic groups such as grazers, pollinators and soil macrofauna. Hence, in the future, it is important to understand to what extent the AlpineWarmed communities are colonized by subalpine organisms in general. Lastly, my thesis covers a timeline of five years. It is only natural to ask if this timeline is enough to conclude on the warming effects in alpine plant communities and if these effects will be different than of the long term impairments. For example, (Wu et al., 2012) showed that the warming effects recorded especially for ecosystem functioning in the short-term can be reversed later due to N and species losses under warming that inhibited productivity in the long-term (after 10 years of warming). As much as the short-term responses can be reversed in the long-term, this does not mean that the short-term responses are less important because i) they can inform us on the starting point of the transients which can ultimately define the long-term trajectory (Fox et al., 2019; Hastings, 2004), ii) they can still provide early warning signals of catastrophic shifts in the ecosystem functioning (e.g. the desynchrony that we recorded with the community functional strategies and ecosystem functions) (Scheffer et al., 2001), iii) the systems can stay in long-term transients for a long time (Hastings et al., 2018) and thus, they can still harm the ecosystem services in a lifetime of a human being.

5.2. Plant-soil feedbacks

As we showed in Chapter 4, experimental warming changes in the ecosystem functioning towards faster cycles and more productive communities. All these changes eventually cascade to nutrient availability and change the interactions between soil organisms and plants. In fact, we already found that there is a decrease in soil P concentration and an increasing tendency in soil N concentration under warming. Moreover, increase in the bacterial biomass and the communities that are becoming more outsourcing and thus, can host more mycorrhiza if available are the first indications of changes in soil micro communities and their interaction with plants. As much as we revealed the direct and indirect effects of climate warming and drought on plants in alpine grasslands (Figure 6, arrows A-E), here we lack the indirect effects via soil biota and functioning on plants (Figure 6, arrow F). Here, I will briefly explain different PSF chains and which parts of my thesis could have been improved by incorporating them.

During their growth, plants alter the soil conditions through nutrient dynamics and soil communities. Eventually, these alterations in return feedback on plant growth and survival (van der Putten et al., 2013). **One important feedback chain is the fungal-based vs. bacteria-based nutrient cycle via plant litter quality** (Hobbie, 2015). Fast growing (exploitative) species' litter is high quality organic matter with low C:N ratios and low lignin concentration. Such litters stimulate bacterial-dominated food webs associated with enhanced decomposition and fast cycling of nutrients. The resulting fertile soils feedback to these fast-growing plant species and promote them further. In contrast, slow-growing (conservative) species have litter with opposing qualities that favors the growth of fungi which are typically associated with low rates of nutrient turnover. The resulting infertile soils feedback to these slow-growing plant species and promote them further. For example, in Chapter 2, we found that being conservative (slow-growing) was a winning strategy under experimental warming and drought. It could be that these species with low nutrient requirements initiated positive PSF by producing low-quality litter, driving the nutrients towards depletion and thus, outcompeting the faster-growing species (Bennett & Klironomos, 2019). In Chapter 4, we also saw that the whole community strategy was shifting towards a slow growth. We also saw that as much as the bacterial biomass increased with direct effects of warming, as the communities got slower they also had less bacterial biomass. Hence, the questions stand: **1) Are there a fungal-based PSF in alpine communities? 2) If yes, can exploitative subalpine colonizers defeat this PSF? 3) If yes, how long does this process take?**

Despite the complexity of PSF, we can substantially enlarge our understanding on the effects of climate warming and drought on plants, soil nutrient dynamics and communities and on their interactions. PSF are particularly important in the context of transient dynamics because they can buffer, slow down or accelerate the effects of climate warming and drought on plants. More specifically, we can understand if they can change the timing of acclimation and cause (or prevent) acclimation lags.

5.3. Adaptive plasticity in functional traits

Plasticity in functional traits in response to climate warming and drought can be “beyond buying time” and can assure the long-term success of the alpine plants (Fox et al., 2019). As much as plastic responses can be indications of long-term acclimation to new conditions, this largely depends on the evolutionary processes that are in play, in other words if the plasticity will be

adaptive or not. Here, I will briefly mention i) when the plasticity can be adaptive, and ii) in which chapters, we could have assessed if the plasticity was adaptive in mountain grasslands.

We can mention three types of plastic responses that can determine if it is adaptive or not: developmental switch, general physiological responses to stress, and developmental selection. When the response is a developmental switch, it is evolved along exposures to “ancestral” environments (e.g. shade-avoidance in plants can be an example here (Franklin, 2008)). As they are evolved in specific environments, they are less likely to be relevant (or adaptive) in abrupt or extreme environmental changes. Inherited general physiological responses to stress that evolved for a wider range of environments may enhance the survival of individuals in various novel environments and thus, may remain adaptive (e.g. heat resistance granting also resistance to osmotic stress (Snell-Rood et al., 2018; Wang et al., 2004)). Plasticity induced by novel environments within the individuals’ lifetime is defined as developmental selection and it is very likely to be adaptive. This response is observed mainly for morphological structures such as leaves, stems, flowers, and roots (de Kroon et al., 2005). For example, roots grow deeper in search of water or plants grow taller, or leaves grow wider in search of light. There can be responses that might be determined by a combination of these processes. Changes in the plant’s life cycle events might be one of them.

In fact, we do not know if the phenological plasticity that we recorded in Chapter 1 were adaptive or not. Moreover, along with my thesis, I primarily used interspecific functional traits and never measured the plasticity in morpho-physiological traits at population level. However, it is not easy to measure adaptive plasticity. (Palacio-López et al., 2015) suggested that trait plasticity can be adaptive if the traits are showing plasticity under changing conditions towards the trait values of the species that are already adapted in these conditions. They were able to identify if the plasticity was adaptive or not and its direction through reciprocal transplant experiments because they had the trait values of the species from “origin/home” (i.e. from where they are transplanted) and “destination/target” (i.e. to where they are transplanted). Thus, they showed that among the plastic traits, 49.4% showed complete adaptive plasticity, 19.5% adaptive plasticity (with lags remaining), and 31% nonadaptive plasticity (diverging from the plasticity trajectory). Even though life history traits including phenological traits were the most plastic ones, they were also the most divergent thus non-adaptive.

Hence, our findings require an improvement through an analysis of adaptive plasticity at population level for morpho-physio-phenological traits. For this, we would need to measure plasticity in functional traits at individual level. This would also be an opportunity to fill in the knowledge gaps on Table 1 (i.e. all the question marks at individual and species level). By measuring the plastic responses of functional traits under warming, we can further understand if winners/losers/colonizers/extinct species and different functional groups differ in their plasticity in functional traits. Investigating especially the plastic responses of winners and colonizers would be the first step to understand if the plastic responses under warming are adaptive or not.

6. Perspectives

In this section, I will suggest ways to improve the above-mentioned limitations on i) methodology and ii) incorporating PSF.

6.1. Methodological limitations: improving the warming experiment & combining warming experiments with observation studies and process-based models

The methodological limitations that I stated above are an important reminder that no method is perfect in the climate change ecology because the interactions between drivers, biological scales, multitrophic groups and responses under climate warming are just too complex. Being aware of the limitations is of course first important for improving warming experiments but also is a big opportunity to combine different methods in ecology and take advantage of the strengths of each of them. Here, the improvements that I will suggest will be first based on how to improve the current warming experiment, second on how to improve the analyses by combining different methods in ecology such as observation based studies and process-based modeling approaches.

First, I criticized the fact that the change that we introduced within our experiment can be too quick. To understand if a gradual change and these drastic responses that we recorded are in the same direction, I will suggest two improvements: assessing the effects i) of the intermediate warming scenario and ii) through an observation based study. For the first one, in 2021, we replicated our transplant experiment in the same area (Col du Lautaret) and Alpe d'Huez but with an intermediate site this time which would simulate a warming of 1.5°C on alpine grassland communities. Moreover, on our sites, there is another experiment that simulates warming on communities with open-top-chambers and we know that open top chambers are rather

conservative and can only warm the communities around 1.5°C in alpine and arctic habitat (Yang et al., 2018). Thus, we can examine the responses of a moderate climate warming on alpine grasslands through these alternative setups. For the second one, we can take advantage of a parallel setup that is an observatory in the French Alps (ORCHAMP-Observatoire spatio-temporel de la biodiversité et du fonctionnement des socio-écosystèmes de montagne). ORCHAMP has monitoring sites at various points of elevational gradient around the French Alps with five different subsites at each point that are 200m of altitude apart. There is an ORCHAMP elevational gradient in the valley where we also conduct our experiments and our sites coincide with ORCHAMP subsites too. Elevational gradients help us to understand the effects of changes in abiotic and biotic conditions on plants through space-for-time substitution. Hence, with this study, we can understand if a gradual change in temperature and soil moisture affect the plants in the same direction that we recorded in our experiment.

Second, I criticized that within the scope of my thesis we could not differentiate the warming and drought effects. For this, I would suggest two improvements: i) designing a sub-experiment by adding water at a sub-part of our plots and comparing the responses between with and without water addition treatments, ii) disentangling the effects of warming from drought through the ORCHAMP observatory. For example, (Weil et al., 2021) already showed by using the data from ORCHAMP network that climate water stress (a satellite based measurement) has a direct link with plants and is negatively correlated with above-ground productivity and positive with root depth while the growing degree days has a positive effect on above-ground productivity. We can further improve our understanding on the effect of soil moisture on plants in the mountain grasslands through on-site soil moisture measurements.

Third, I criticized the assumptions for defining the trajectory of acclimation and the accessibility of the subalpine colonizers to our warmed communities. One important argument was that maybe we are creating an “unrealistic” scenario where all the subalpine species can access warmed communities. Here, there are multiple processes in play for both alpine and subalpine plants. For alpine plants, as I showed in my thesis, their demographic and assembly dynamics change under warming based on their functional traits. For subalpine plants, we do not know which species will not be able to acclimate (or adapt in the long-term) to warming and thus, will be able to migrate upslope or become extinct. Thus, we do not know how the alpine communities will be further affected by the successful migrator colonizer subalpine species. As the processes and their interactions are rather complex here, I think that we can benefit from a

process-based approach (Block et al., 2022; HilleRisLambers et al., 2013; Urban et al., 2013). We would need a spatially and temporally explicit dynamic vegetation model that takes into account i) species' habitat suitability, ii) demography, iii) dispersal and iv) competition for light and soil nutrients. FATE-HD is such a process-based model (Isabelle et al., 2014). We can spatially augment our warming experiment to a landscape scale with FATE-HD and temporally track vegetation dynamics of alpine and subalpine communities along a century-long warming. This way, we can also reveal the relative importance of demographic changes in the communities due to warming and the competition effect between the alpine species and with the subalpine colonizers.

In summary, the future research on revealing direct and indirect effects of warming on alpine grassland communities would benefit substantially from a methodologically holistic approach. By combining experimental, space-for-time substitution and modeling methods, we can decrease their disadvantages to minimum when they are used alone and disentangle better the direct effects from indirect ones and warming effects from drought.

6.2. Improving our understanding in plant-soil feedbacks for climate change ecology

As I introduce above, PSF has three important components: plants, nutrient dynamics and soil organisms. As much as we provided some first results on the change of nutrient dynamics and soil microorganisms (notably, bacteria), first, our research should be improved by having a thorough *in situ* analysis on both of them. Here, I will first suggest how to improve our understanding on soil microorganisms and on PSF in general.

Firstly, we know that soil organisms' diversity are affected directly by changes in energy input in the ecosystem, yet this effect differs among different multitrophic groups such as parasites, decomposers and plant symbionts that could have different impacts on the ecosystem functioning and PSF (Calderón-Sanou et al., 2022). Hence, at one hand, we should first understand how warming and drought alters the diversity and relative abundance of soil organisms. We can achieve this for example by detecting the soil organisms' diversity through DNA metabarcoding (Calderón-Sanou et al., 2020) together with quantitative PCR in order to have a proxy of changes in abundances of certain groups (Jian et al., 2020). For PSF, it would be important to understand the diversity and abundance changes plant symbiotes, mycorrhiza, natural enemies of the plant fungi-associates (Bennett & Klironomos, 2019). For ecosystem

functioning, it would be important to understand the diversity and abundance of fungi and bacteria decomposers and detritivores as their relative abundance can provide further insights if the ecosystem is going towards faster or slower cycles.

Secondly, we need to disentangle different feedback loops in PSF and their changes under warming and drought. In the above section, I introduced two examples of PSF (Figure 6). We can disentangle the first one on nutrient dynamics again through the process-based model approach with FATE-HD. FATE-HD has a separate sub-module that simulates the competition for soil nutrients. More specifically, along their life cycle, species contribute to the soil nutrient pool based on their litter quality and tolerate the soil nutrients based on their tolerance range. By coupling our warming experiment with FATE-HD, we can understand i) the relative importance of the competition through soil nutrients in shaping the communities, ii) how changes in plants under warming drive the soil nutrients pool and iii) how the changes in soil nutrient pools feedback further to the vegetation dynamics. The second example PSF was on the competition between plants through their soil community associates. This would require a modeling approach that is at a finer scale that incorporates both the plant demography and soil microbial density. Such models between two plant species have been widely used, however modeling competition with PSF in species rich communities still remains as a challenge (Ke & Miki, 2015).

In summary, due to complexity in PSF, revealing the impact of warming and drought on them and their impact on plants in return would be difficult only with an experimental approach. However, coupling our findings with different modeling approaches would be an important step to overcome this challenge and contribute to our understanding of PSF in general and in climate change ecology.

Conclusion

During my thesis, I focused on revealing the direct and indirect effects of climate warming and associated drought on plants at different biological scales, their trajectory of acclimation and cascading effects to ecosystem functions. I chose the alpine grasslands as a case study primarily because of their intrinsic value in plant biodiversity and secondly, because mountains are *in situ* laboratories that allowed me to set up a transplant experiment to simulate climate warming on plant communities. Overall, the variability in the timing and functional forms of climate change responses at different biological scales led to losses of functionality, such as for plant-pollinator interactions or exploitation of plant-mycorrhizal interactions. As much as the

warming effects were strong, many responses to climate warming are not sufficient for full acclimation. Thus, the threats for alpine plants persist. Alpine grasslands are getting increasingly homogenized and losing the distinctive features of the high and harsh environment at all levels of organisms. I expect that these threats will accelerate even more in the future with more competitive colonizers that move upslope at the mountains. In the future, I aim to improve this research by combining different approaches in ecology such as observation-based studies and process-based modeling approaches. This way I believe, I can disentangle more complex species interactions at the above- and below-ground and feedbacks between the plants, soil communities and ecosystem functioning.

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Appendix

Appendix for Chapter 1

Table S1: Soil temperature, growing season (GS) lengths, start and end dates of alpine and subalpine sites

Year	Site	Soil temperature (°C) annual	Soil temperature (°C) july	GS length	Season start	Season end
2017	alpine	3.74	12.35	152	2017-06-02	2017-11-01
2017	subalpine	7.16	16.02	224	2017-04-15	2017-11-25
2018	alpine	4.42	13.85	152	2018-06-10	2018-11-09
2018	subalpine	7.34	16.66	200	2018-05-09	2018-11-25
2019	alpine	3.88	13.40	152	2019-06-10	2019-11-09
2019	subalpine	7.14	16.17	208	2019-04-15	2019-11-09

Table S2: Focal species' descriptive table

Species	Growth form	Origin	Flower onset	Observations (%) <10 individuals	Cover class	Ellenberg moisture indicator	Ellenberg moisture indicator variation	Ellenberg temperature indicator	Ellenberg temperature indicator variation
<i>Geum montanum</i> L.	forb	alpine	May	66.83	2	3.0	small variation (I)	1.5	small variation (I)
<i>Potentilla aurea</i> L.	forb	alpine	June	2.51	3	2.5	small variation (I)	1.5	large variation (II)
<i>Trifolium alpinum</i>	forb	alpine	June	1.13	4	2.5	small variation (I)	1.5	small variation (I)
<i>Poa alpina</i> L.	graminoid	alpine	June	2.13	2	3.5	large variation (II)	1.5	large variation (II)
<i>Carex sempervirens</i> Vill.	graminoid	both	June	1.32	4	2.0	small variation (I)	1.5	small variation (I)
<i>Festuca nigrescens</i> Lam.	graminoid	both	June	2.32	4	2.5	large variation (II)	2.5	large variation (II)
<i>Centaurea uniflora</i>	forb	subalpine	July	10.65	3	2.0	small variation (I)	2.0	small variation (I)
<i>Helianthemum nummularium</i> (L.) Miller	forb	subalpine	June_May	4.64	2	2.0	small variation (I)	1.5	small variation (I)
<i>Meum athamanticum</i> Jacq.	forb	subalpine	May	1.63	3	2.5	small variation (I)	2.5	small variation (I)
<i>Patzkea paniculata</i> (L.) G. H. Loos	graminoid	subalpine	June	7.02	4	2.0	small variation (I)	3.0	small variation (I)

***Flower onset** according to the local plant functional trait database *Androsace* (Thuiller et al., unpublished)

****Observations (%)**: Percentage of observations when only less than 10 individuals are recorded over the total number of observations along the whole growing season.

*****Cover class** according to Braun-Blanquet classes (2: 6-25%, 3: 26-50%, 4: 51-75% cover). Inventories were done at each site in 2016.

Thuiller et al. (unpublished) *Androsace* Plant Functional Traits Database, Laboratoire d'Ecologie Alpine, 38610 Gières, France
 Braun-Blanquet J., Roussine N. & Nègre R., (1952) Les groupements végétaux de la France méditerranéenne. Dir. Carte Group.
 Vég. Afr. Nord , CNRS, 292 p.

Table S3: Changes in annual air and soil temperature (°C) and in community-level phenological indicators (NDVI). Historical changes are between 1960-2016 for temperature and between 2000-2016 for phenological indicators. Experimental changes are between 2016 observed data and average of three-years experimental outputs. The last column shows how much change was already taken due to ongoing climate warming in comparison to the experimental warming. The sign difference indicates that the changes are in different directions.

Indicator	Historical change (HC)	Experimental change (EC)	HC relative to EC (%)
Annual air temperature	1.20000	NA	NA
Annual soil temperature	0.80000	3.20000	25.00
Growing Season Length	0.73383	48.61855	1.51
Annual plant growth	4.78956	17.90705	26.75
Early plant growth	4.35445	4.22724	103.01
Late plant growth	-1.14368	18.68990	-6.12
Mid-season plant growth	1.65843	-4.93400	-33.61
Greening speed	-0.00121	0.00056	-216.07
Browning speed	0.00098	-0.00218	-44.95
Greening days	7.30226	6.56413	111.24
Browning days	-6.94135	49.42147	-14.05
Mid-season ratio	-0.00087	-0.09379	0.93

*Daily mean air temperature data were extracted from SAFRAN–CROCUS–MEPRA meteorological model developed by Météo-France for the French Alps. NDVI data were extracted from MODIS remote sense time series data for historical changes. Changes were calculated from predicted values of a linear model between indicator values and years. Remote sense data were prepared and phenological indicators were calculated in the same way as it was elaborated on the main manuscript. Annual air temperature for EC is missing as the experimental measurements have gaps in the data to damaged probes on the field site.

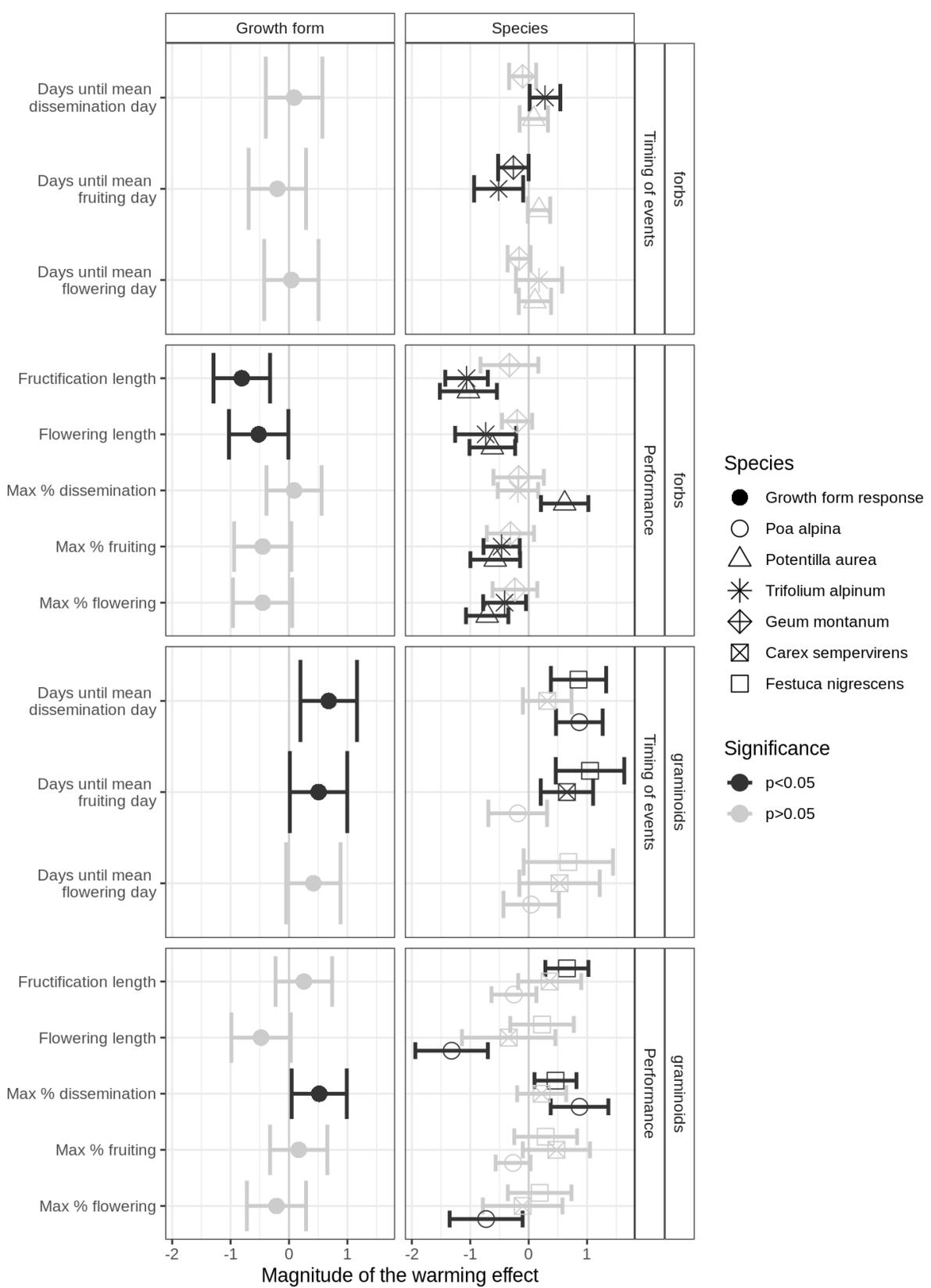


Figure S1: Standardized effect sizes as the magnitude of warming effect for timing and performance related indicators and for each growth form and each species. Significant results are shown in black. Error bars represent 95% confidence intervals. Warming effect: AlpineWarmed-AlpineControl.

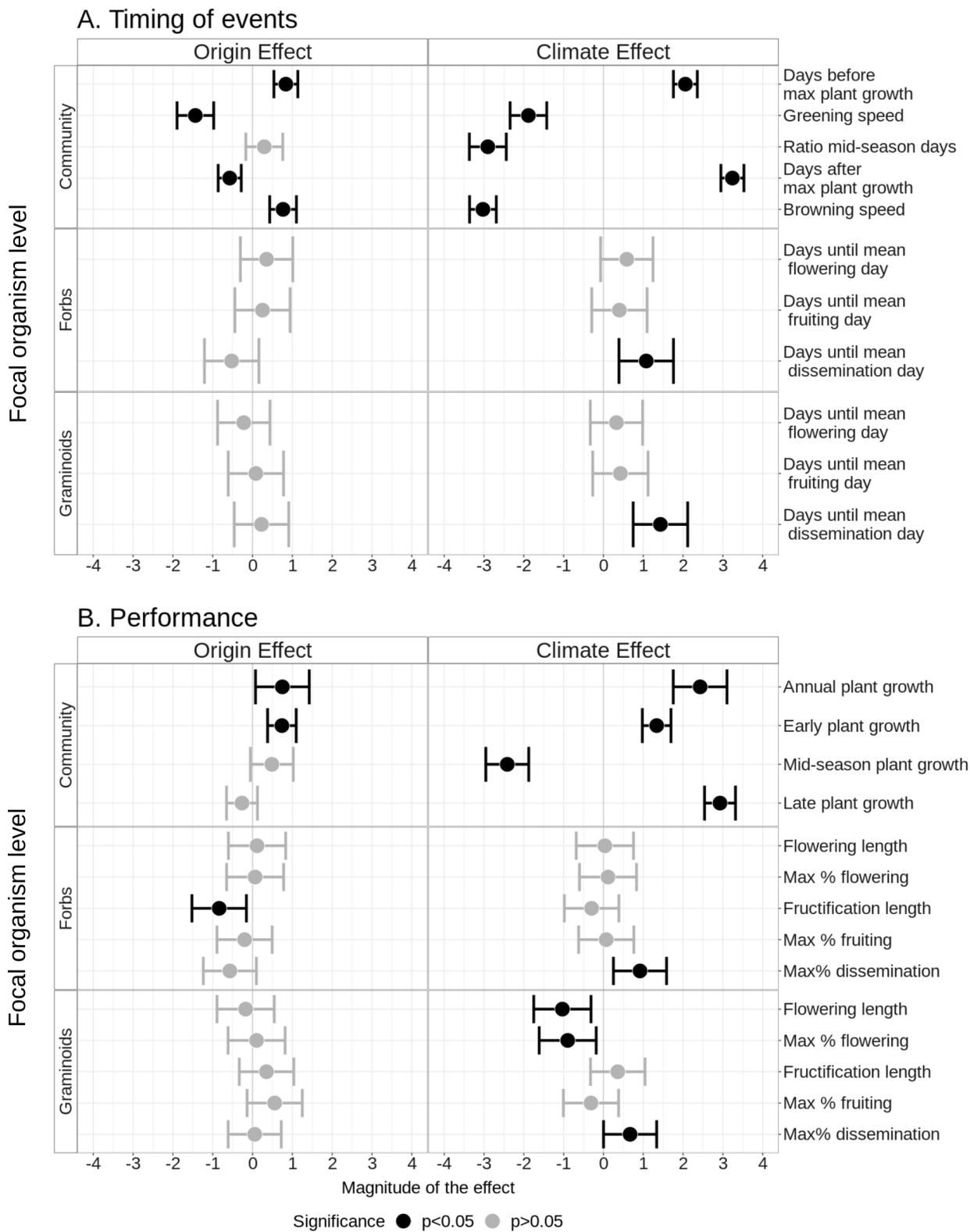
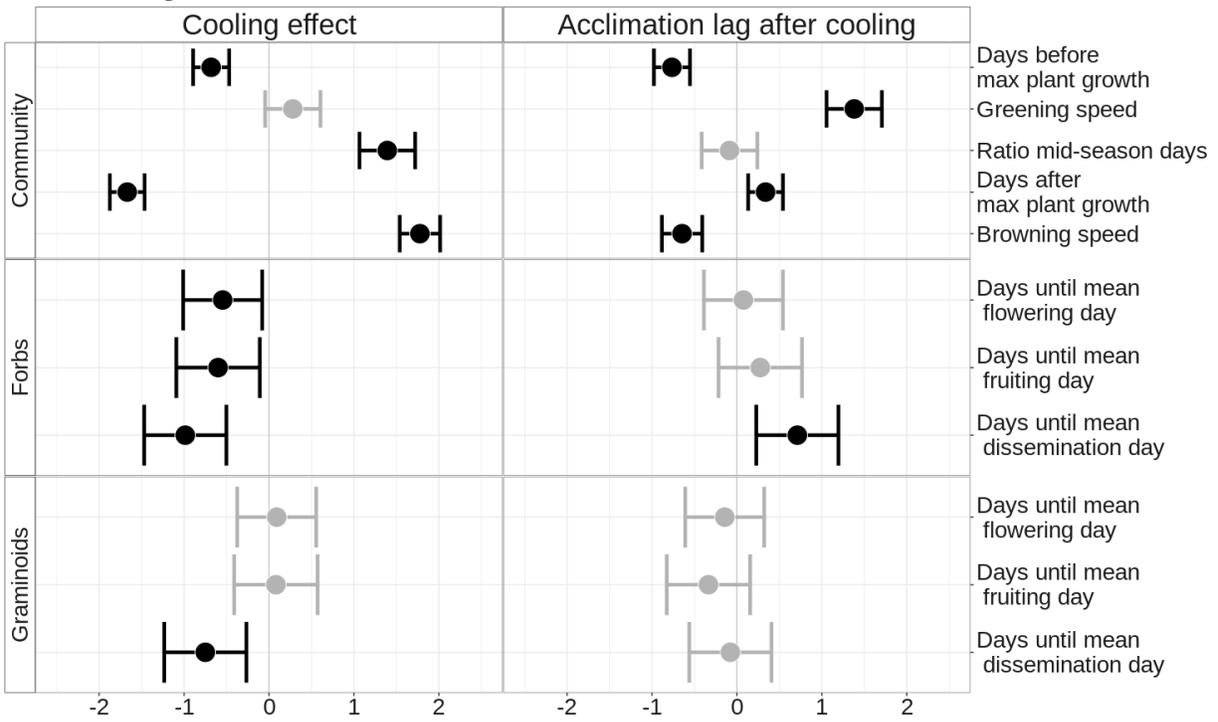


Figure S2: Standardized effect sizes as the magnitude of origin and climate effects at each focal organism level (community level, species level forbs and graminoids) for **(A)** timing of events and **(B)** performance related phenological indicators. Significant results are shown in black. Error bars represent 95% confidence intervals. Origin effect: Subalpine origin - Alpine origin; Climate effect: Subalpine site - Alpine site.

A. Timing of events



B. Performance

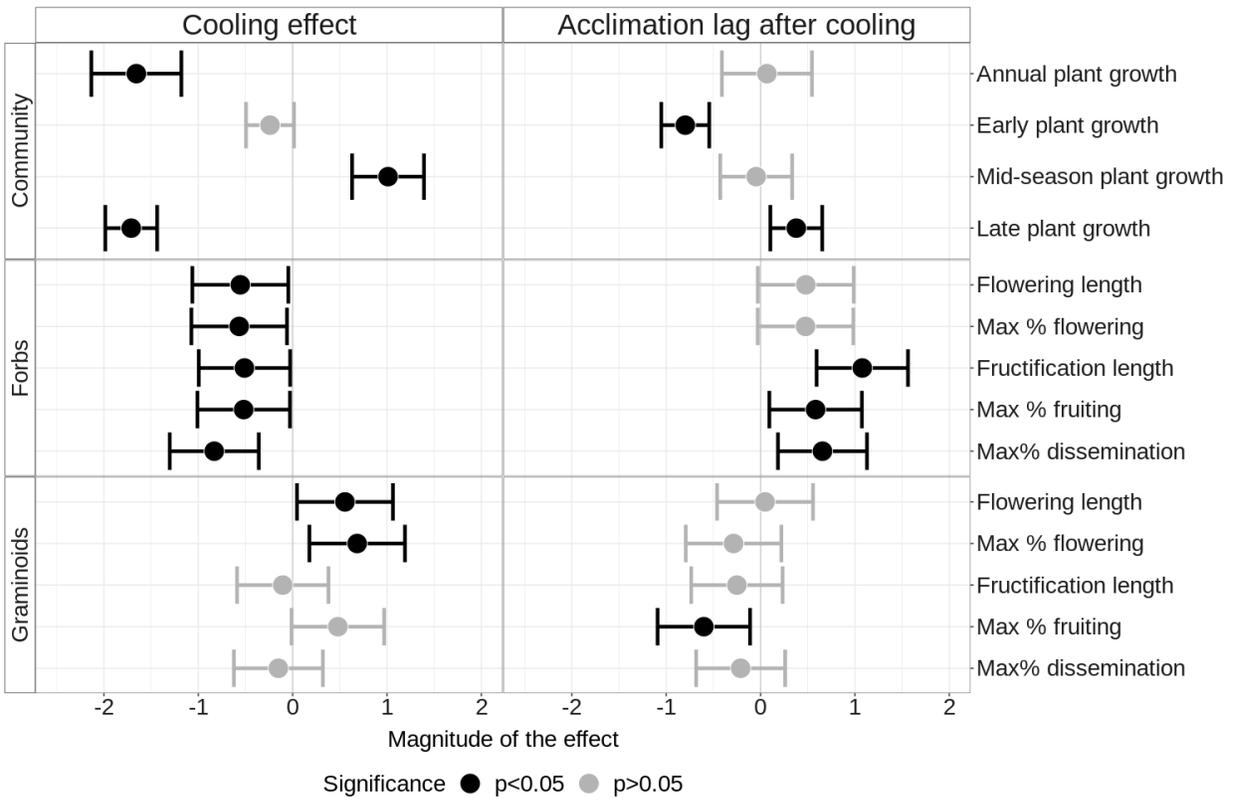
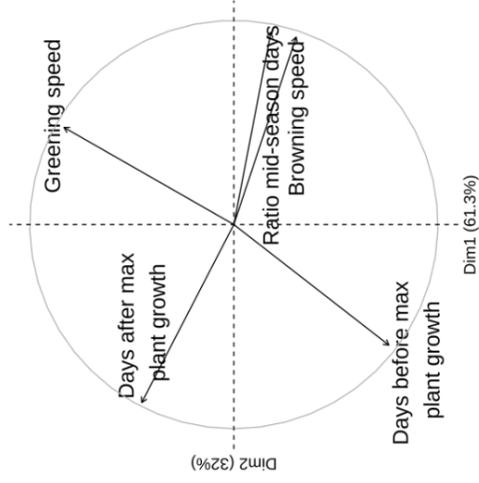
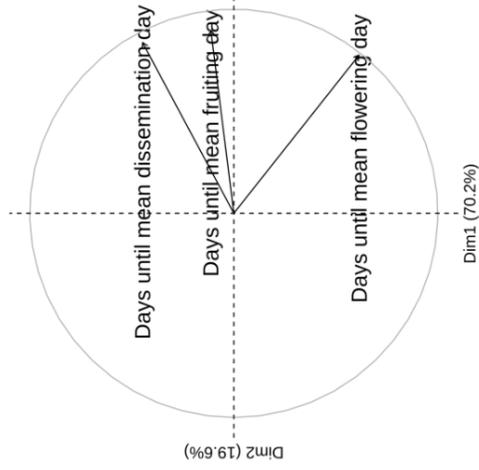


Figure S3: Standardized effect sizes as the magnitude of cooling effect and acclimation lag after cooling at each focal organism level (community level, species level forbs and graminoids) for **(A)** timing of events and **(B)** performance related phenological indicators. Significant results are shown in black. Error bars represent 95% confidence intervals. Warming effect: AlpineWarmed-AlpineControl. Acclimation lag after warming: SubalpineControl-AlpineWarmed.

A) Community



B) Forbs



C) Graminoids

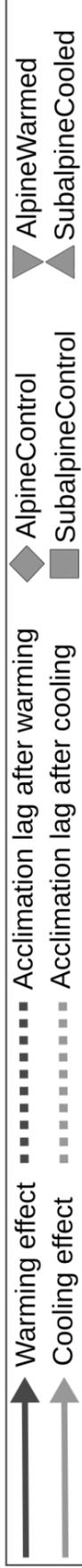
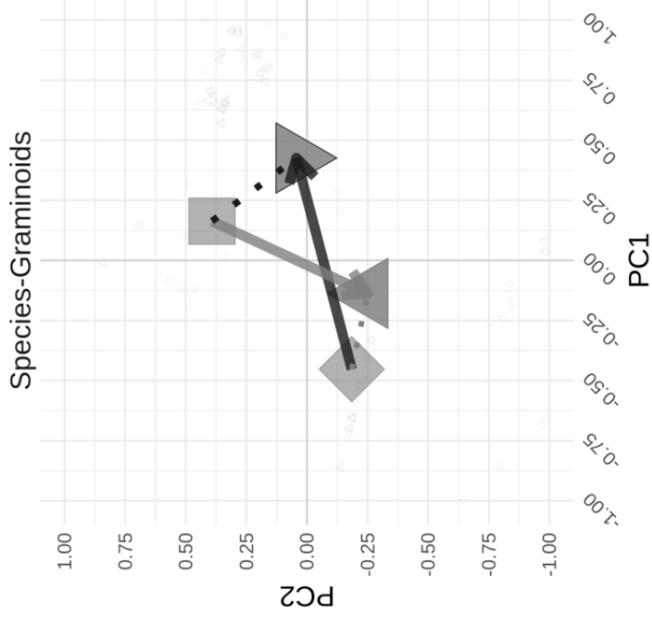
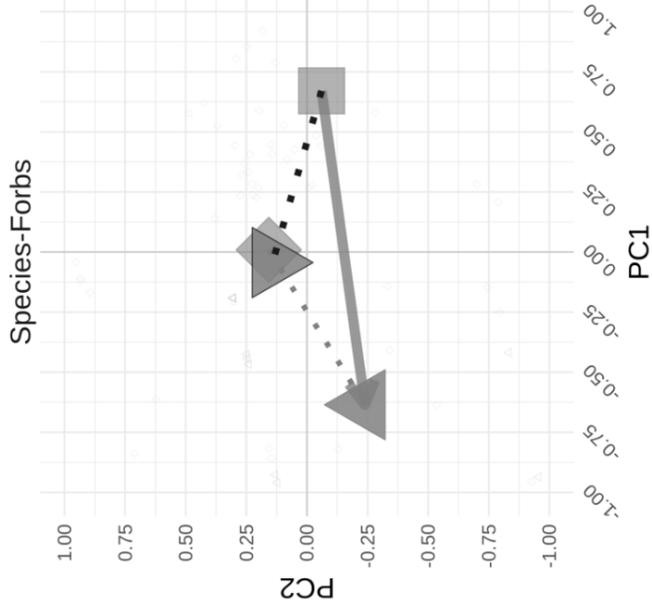
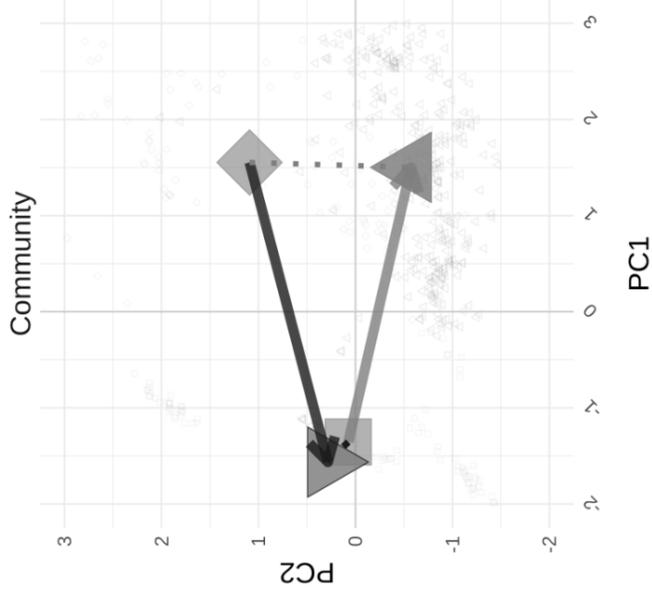
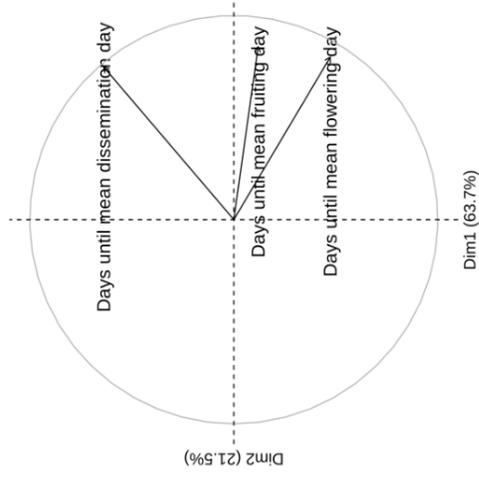
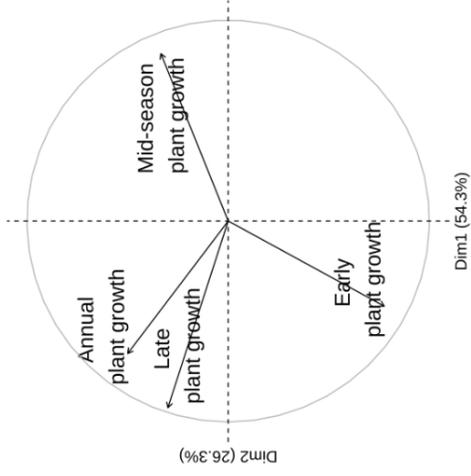
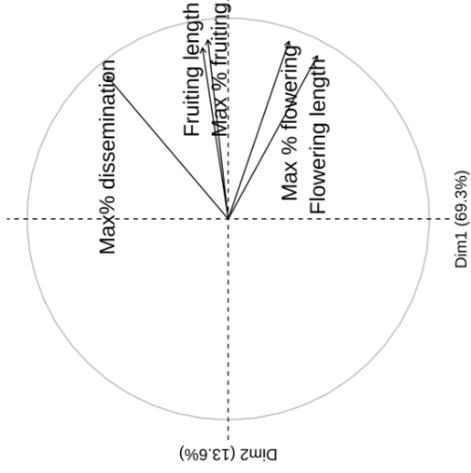


Figure S4: Differences in timing related phenological indicators (plotted in a two-dimensional PCA space) between two treatments and controls (AlpineWarmed, SubalpineCooled, AlpineControl and SubalpineControl) at the community (A) and the species level (forbs (B) and graminoids (C)). Straight arrows highlight warming (AlpineWarmed-AlpineControl) or cooling effect (SubalpineCooled-SubalpineControl) and dotted lines the acclimation lag after warming (SubalpineControl-AlpineWarmed) or cooling (AlpineControl-SubalpineCooled). Here, the responses over 3 years were shown (diamond: AlpineControl, square: SubalpineControl, inverse triangle: AlpineWarmed, triangle: SubalpineCooled). For further analyses, the first two PCs were selected from (A) and only the first PC from (B) and (C).

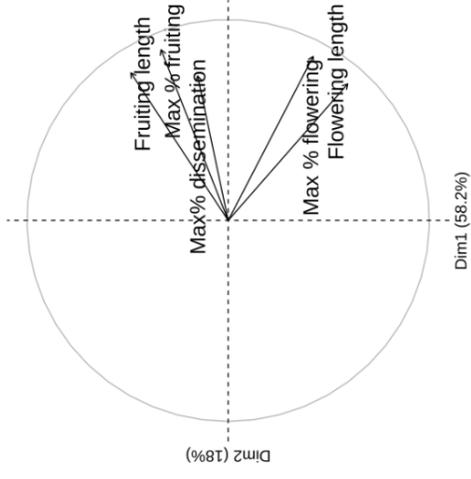
A) Community



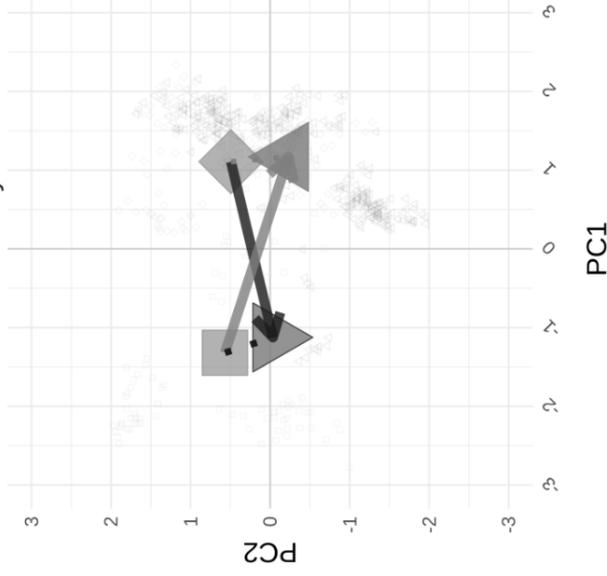
B) Forbs



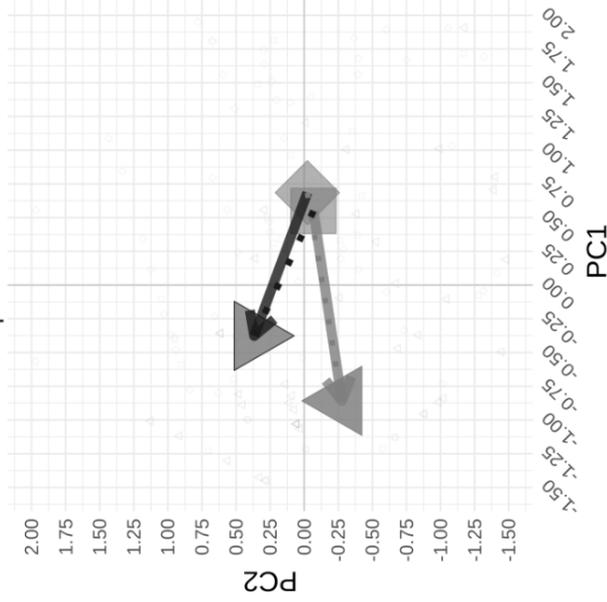
C) Graminoids



Community



Species-Forbs



Species-Graminoids

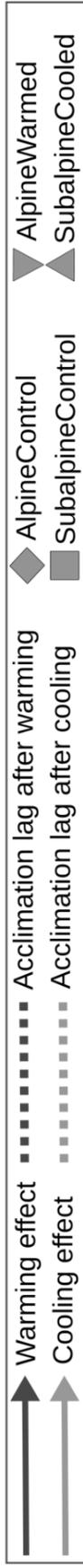
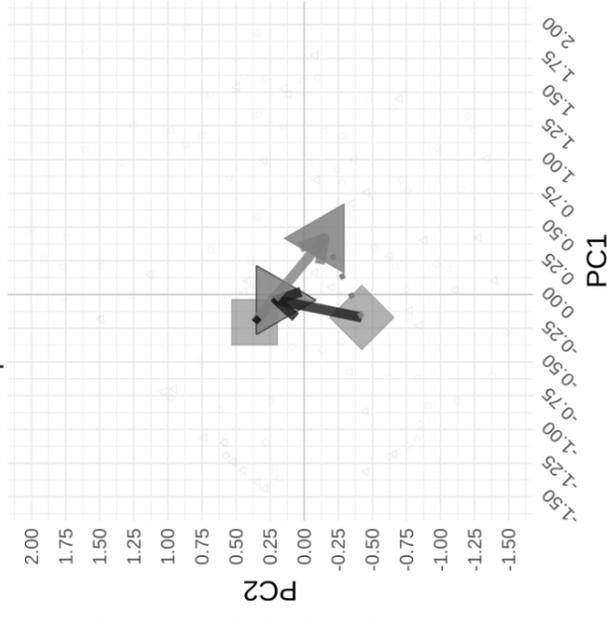
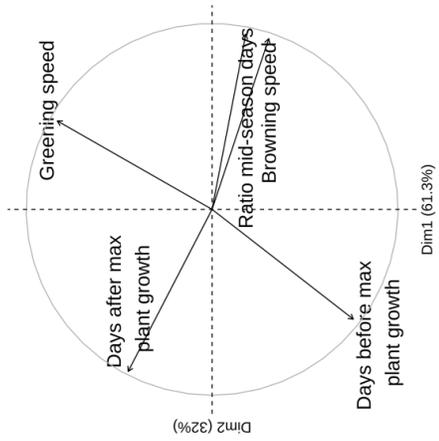
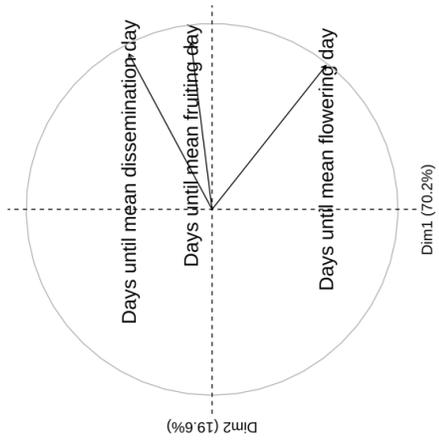


Figure S5: Differences in performance related phenological indicators (plotted in a two-dimensional PCA space) between two treatments and controls (AlpineWarmed, SubalpineCooled, AlpineControl and SubalpineControl) at the community (A) and the species level (forbs (B) and graminoids (C)). Straight arrows highlight warming (AlpineWarmed-AlpineControl) or cooling effect (SubalpineCooled-SubalpineControl) and dotted lines the acclimation lag after warming (SubalpineControl-AlpineWarmed) or cooling (AlpineControl-SubalpineCooled). Here, the responses over 3 years were shown (diamond: AlpineControl, square: SubalpineControl, inverse triangle: AlpineWarmed, triangle: SubalpineCooled). For further analyses, the first two PCs were selected from (A) and only the first PC from (B) and (C).

A) Community



B) Forbs



C) Graminoids

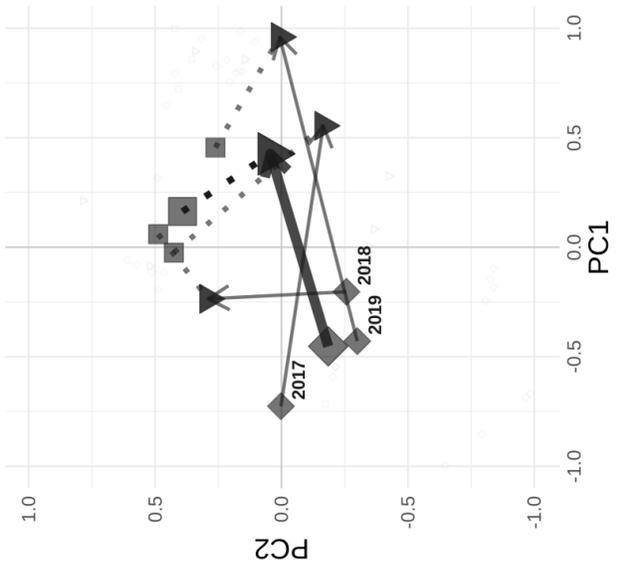
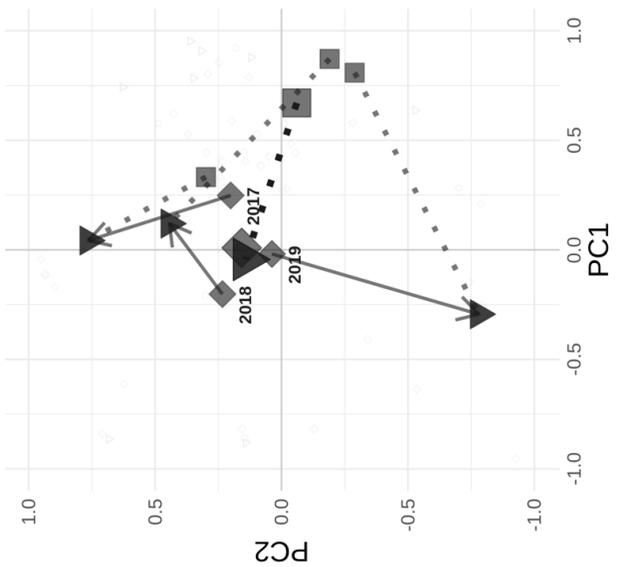
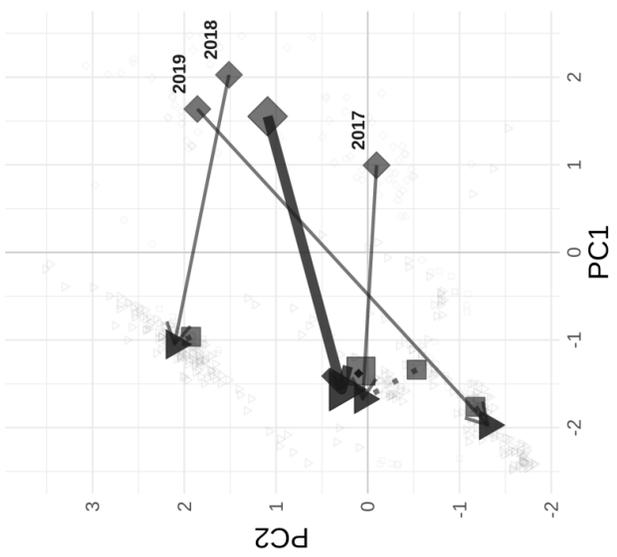
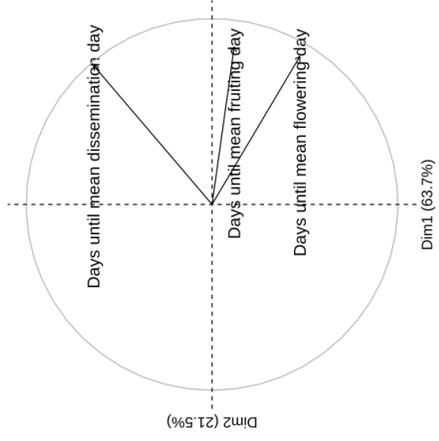
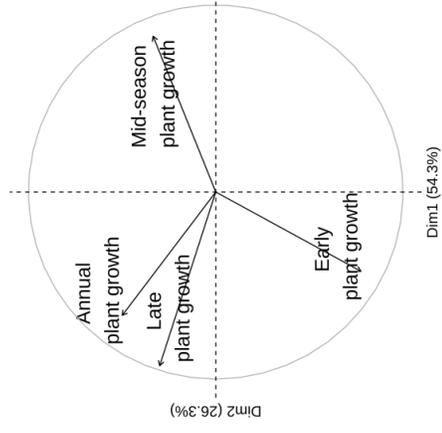
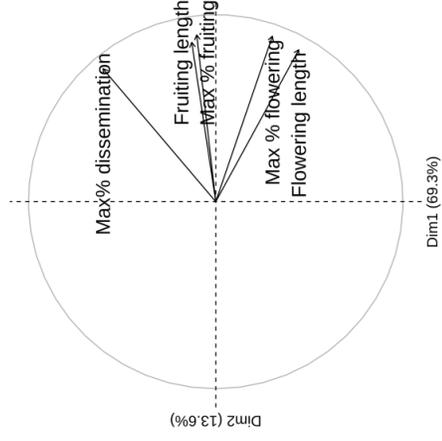


Figure S6: Differences in timing related phenological indicators (plotted in a two-dimensional PCA space) between the three treatments (AlpineWarmed, AlpineControl and SubalpineControl) at the community (A) and the species level (forbs (B) and graminoids (C)). Straight arrows highlight warming effect (AlpineWarmed-AlpineControl) and dotted lines the acclimation lag after warming (SubalpineControl-AlpineWarmed). Thicker lines indicate the overall response for three years. Thinner lines indicate annual response. (diamond: AlpineControl, square: SubalpineControl, inverse triangle: AlpineWarmed). For further analyses, the first two PCs were selected from (A) and only the first PC from (B) and (C).

A) Community



B) Forbs



C) Graminoids

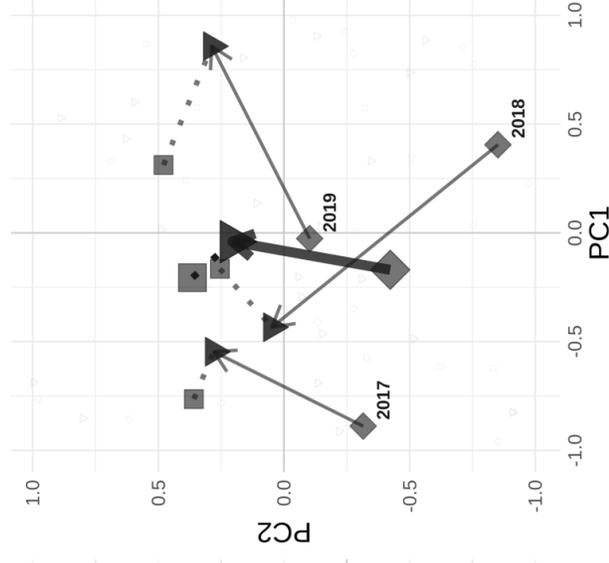
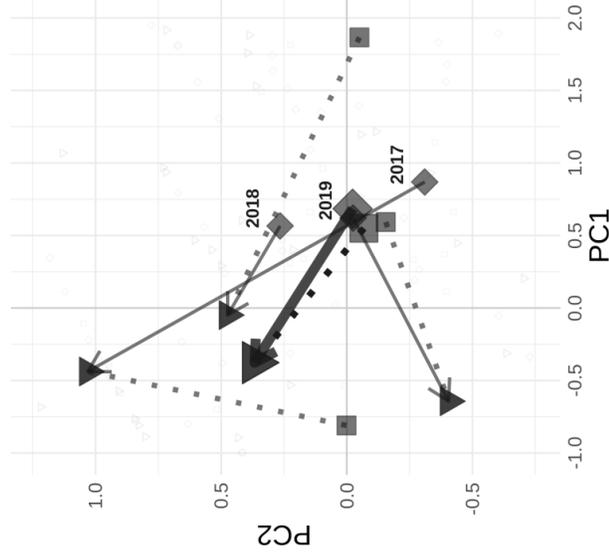
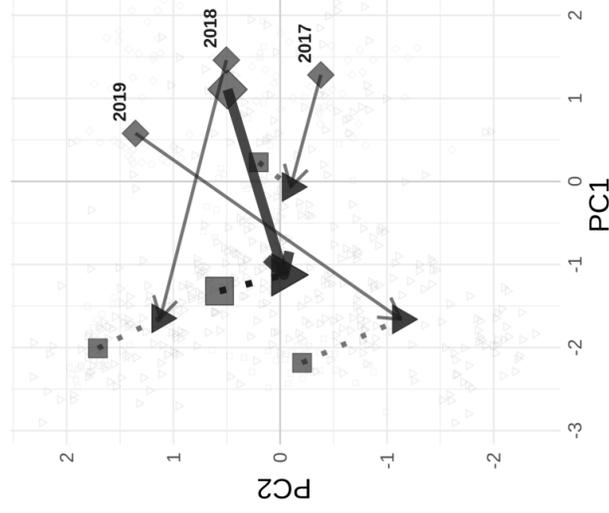
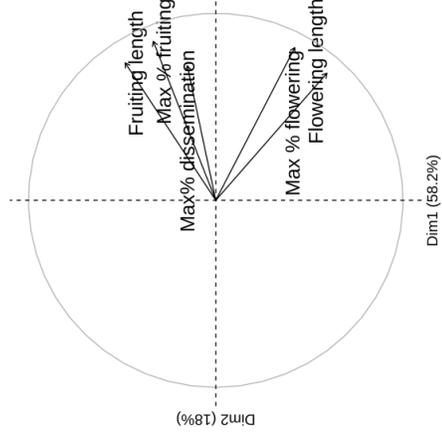


Figure S7: Differences in performance related phenological indicators (plotted in a two-dimensional PCA space) between the three treatments (AlpineWarmed, AlpineControl and SubalpineControl) at the community (A) and the species level (forbs (B) and graminoids (C)). Straight arrows highlight warming effect (AlpineWarmed-AlpineControl) and dotted lines the acclimation lag after warming (SubalpineControl-AlpineWarmed). Thicker lines indicate the overall response for three years. Thinner lines indicate annual response. (diamond: AlpineControl, square: SubalpineControl, inverse triangle: AlpineWarmed). For further analyses, the first two PCs were selected from (A) and only the first PC from (B) and (C).

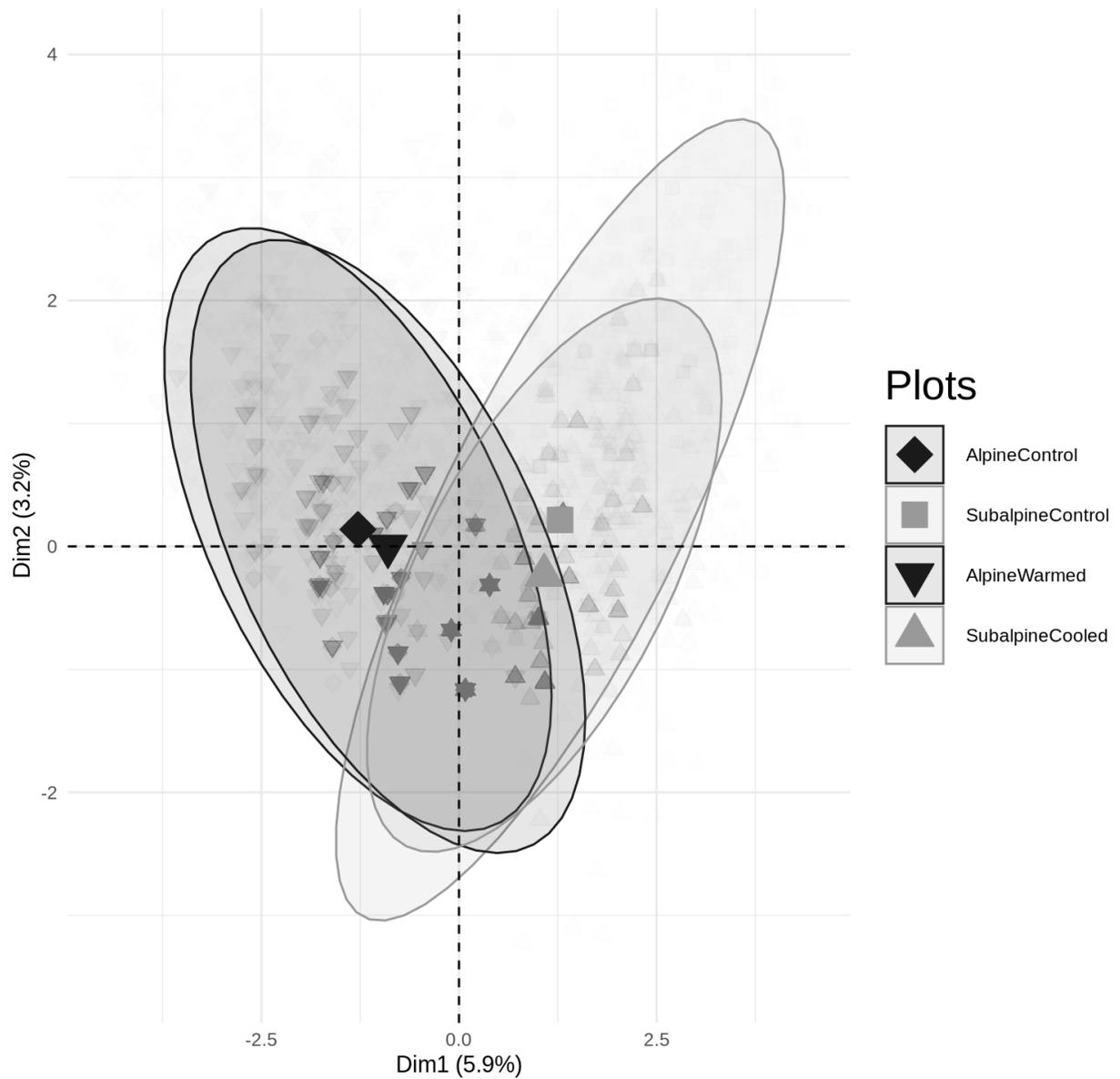


Figure S8: Principal component analysis (PCA) of community composition from abundance data collected in 2018 of dominant species in both alpine and subalpine sites. (diamond: AlpineControl, square: SubalpineControl, inverse triangle: AlpineWarmed, triangle: SubalpineCooled).

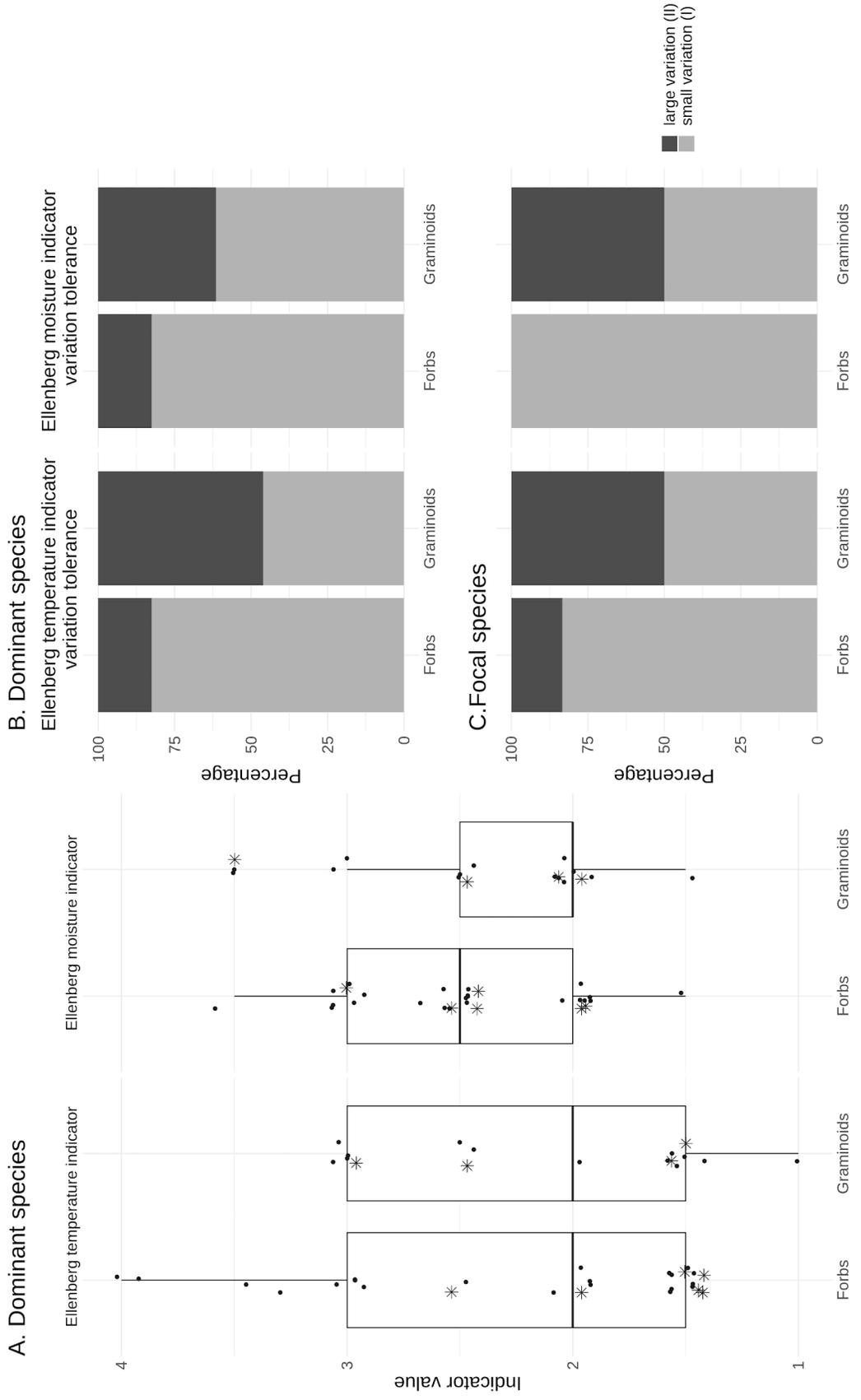


Figure S9: (A) Ellenberg temperature and moisture indicator values of dominant species in alpine and subalpine site. The values of the focal species are shown in star. Percentages of number of species that can tolerate small or large variation in their Ellenberg temperature and moisture indicator values (B) for dominant species and (C) for focal species in both sites and (C) for focal species in the study.

Appendix S10: Cascading acclimation lag: From phenological indicators to flower visiting insects

Grassland phenology can have strong impacts on pollination services. As we found that warmed alpine forbs' communities flowered less often, for shorter time periods and tendentially earlier than subalpine forbs' communities (Figure 2), we asked whether this had any cascading effect on flower visiting behavior of insects.

To answer this question we observed insects visiting flowers in the AlpineWarmed, AlpineControl and SubalpineControl plots between June and September in 2019. Observations were limited to conditions favourable for insect visits, i.e. between 10:00 and 13:00 and only if it was warm enough, not too cloudy (either $> 13^{\circ}\text{C}$ if less than half of the sky was covered with clouds or $> 15^{\circ}\text{C}$ otherwise) and not too windy (maximum 29.5 km/h). Each week (and twice at the peak of growing season) we spent 10 minutes at each of 8 randomly chosen replicates of each treatment to observe flower visits (summing up to a total of 1400 observation minutes). We counted all insects that visited a flower within a 1 m² focal area during this standardized time period. We only identified main insect groups following the guidelines of the public science UK PoMS, Pollinator Monitoring Scheme (<https://www.ceh.ac.uk/our-science/projects/pollinator-monitoring>) because the observations were done by non-expert interns.

Pollinator visits per minute were generally quite low (AlpineControl: 0.34, AlpineWarmed: 0.04, SubalpineControl:0.2, SubalpineCooled: 0.32). We found strong site-specific effects on pollinator communities, with more flies and small insects ($<3\text{mm}$) in AlpineControl plots and more *Coleoptera* and *Hymenoptera* species in SubalpineControl plots. Overall, AlpineControl plots tended to attract slightly more visits than SubalpineControl plots. Due to these site specific differences, we focus on acclimation lags comparing AlpineWarmed and SubalpineControl plots that are at the same site and thus available to the same pollinator community. Our main results show that the flowers in AlpineWarmed plots were visited by a significantly less diverse group of insects and also had a tendency to be overall less visited than the SubalpineControl plots (Figure S10).

As AlpineWarmed and Subalpine Control plots are at the same location (randomly placed at the site) and have been observed at the same moment, differences in flower visiting insects are clearly due to plot-level vegetation differences. We conclude that reduced flower numbers, shorter flowering periods and premature flowering are among the main drivers of impaired flower visiting of insects creating a cascading acclimation lag from plant phenology to insect pollination.

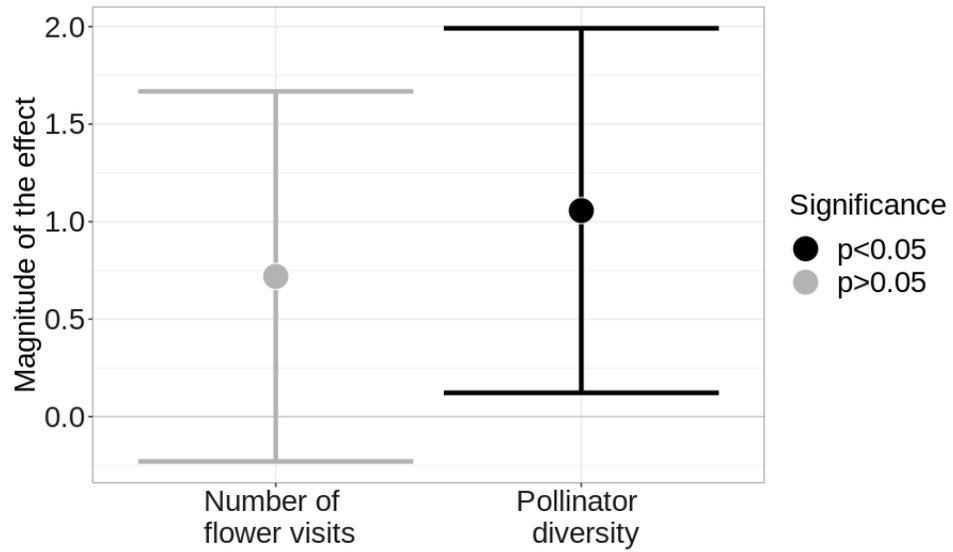


Figure S.10: Acclimation lags after warming (Standardized effect sizes of the difference between SubalpineControl and AlpineWarmed). Significant results are shown in black. Error bars represent 95% confidence intervals.

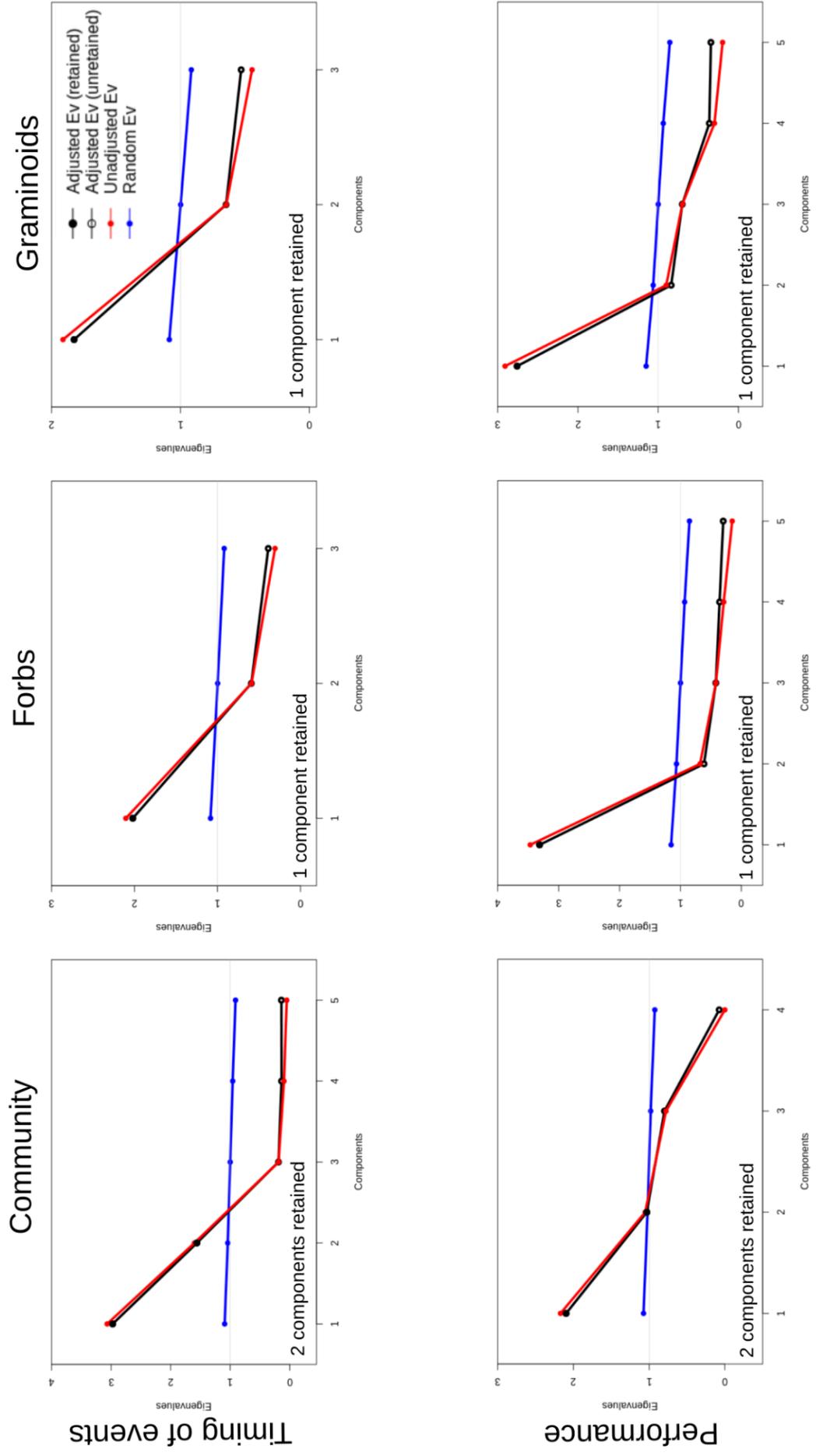


Figure S12: Results from Horn's parallel analysis to select the number of principal components from each PCA (Appendix Figure S4-7).

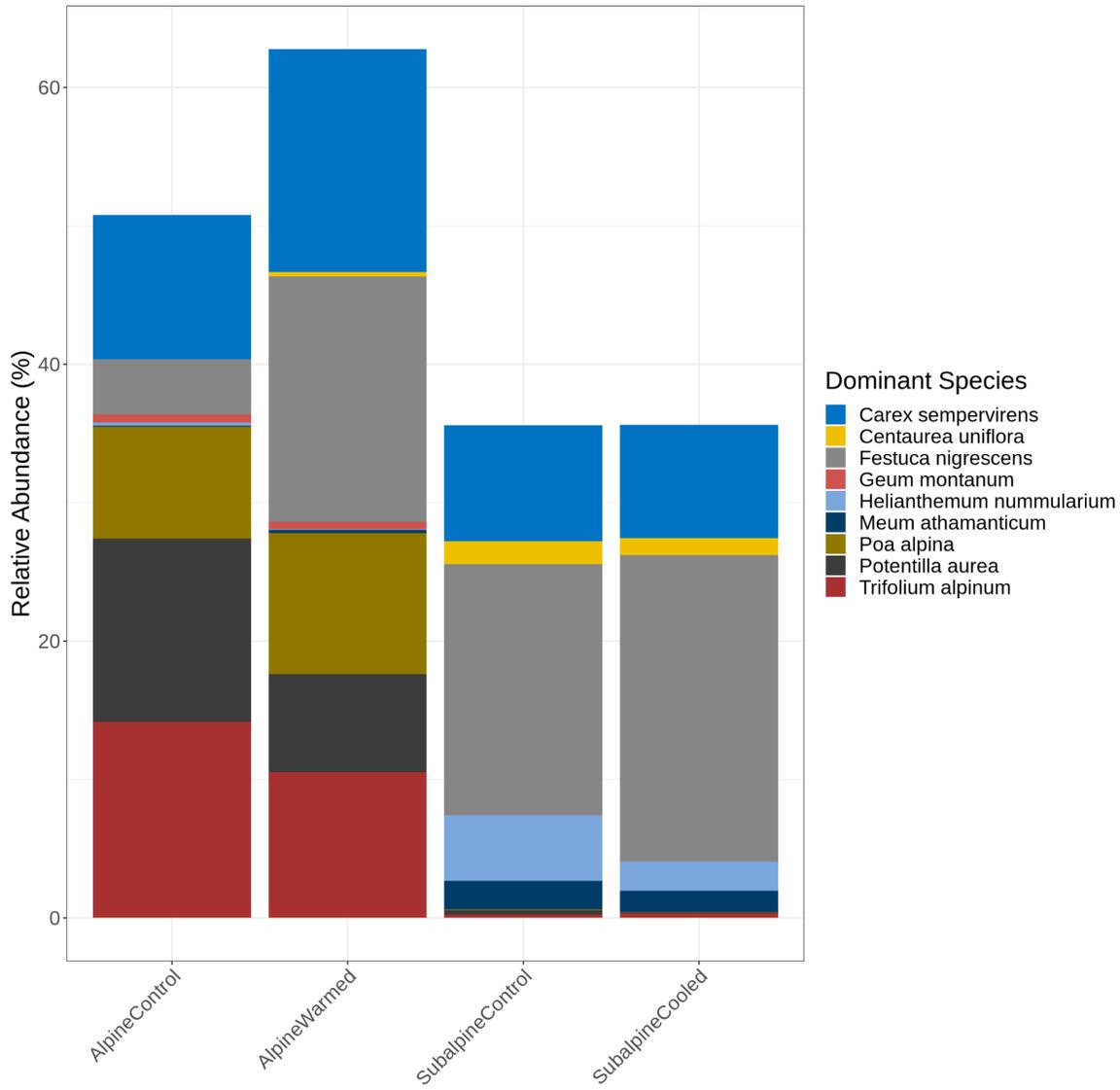


Figure S13: Relative abundances (%) of dominant species in the different experimental plots. These are calculated from a separate dataset of species abundances collected in 2018, i.e. two years after the transplantation.

Appendix for Chapter 2

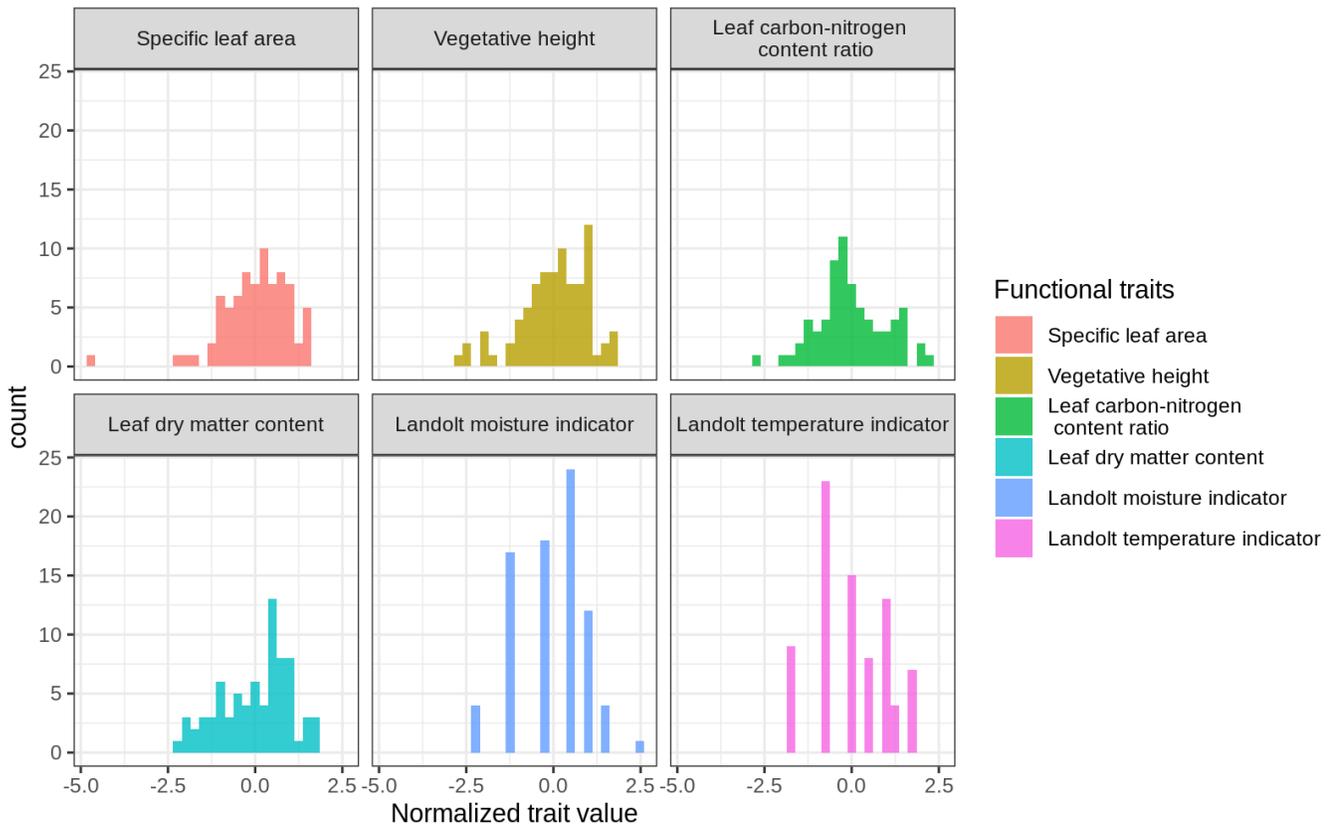


Fig. S2: Log-transformed and standardized (mean $\mu = 0$, standard deviation $\sigma = 1$) trait distributions of the species in the AlpineWarmed plots.

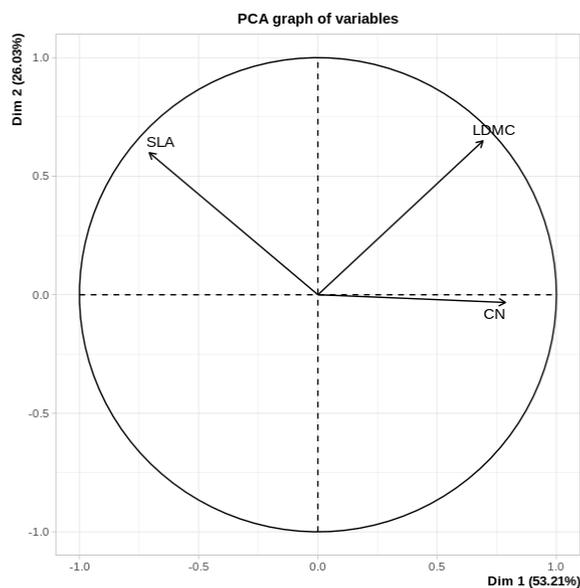
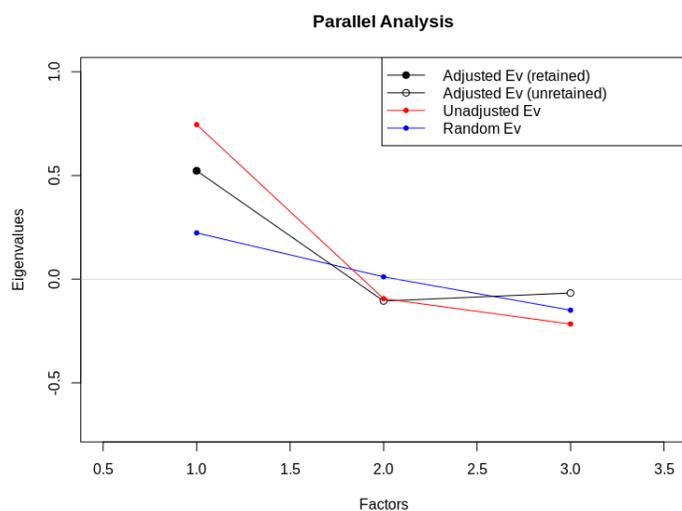


Fig. S3: Horn's parallel analysis (left) on the principal component analysis (PCA) (right) on specific leaf area (SLA), leaf dry matter content (LDMC), and leaf carbon and nitrogen ratio (CN) with species in the AlpineWarmed plots. We extracted the first principal component of this PCA in line with the results of the parallel analysis to construct the conservation dimension (see Methods section in the main text for further details.)

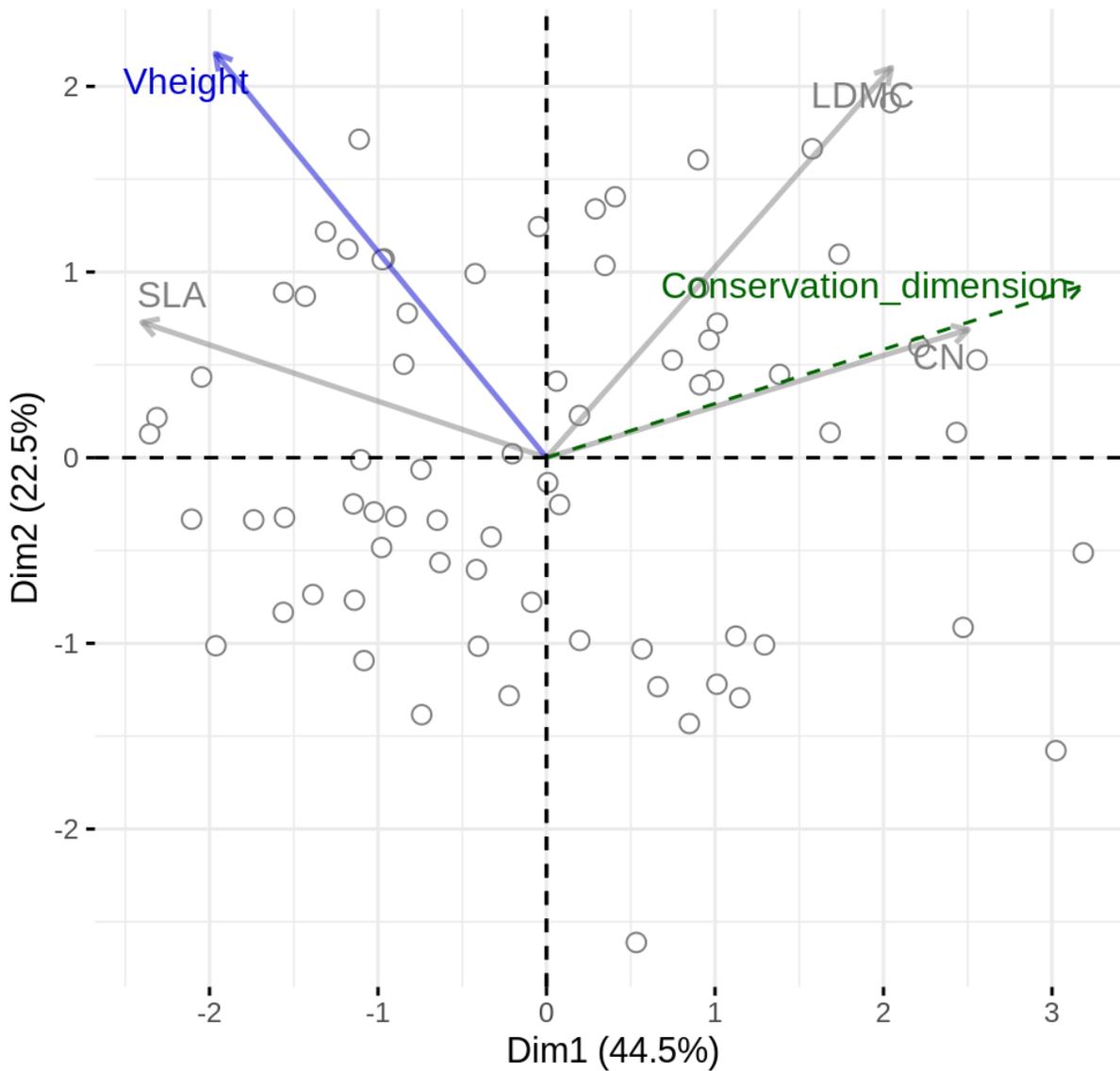


Fig. S4: Principal component analysis (PCA) on vegetative height (Vheight), specific leaf area (SLA), leaf dry matter content (LDMC), and leaf carbon and nitrogen ratio (CN) with species (each dot on the figure) in the AlpineWarmed plots. The conservation dimension is the first axis of the PCA constructed from SLA, LDMC and CN as shown on Fig. S3 is also projected on the figure in green.

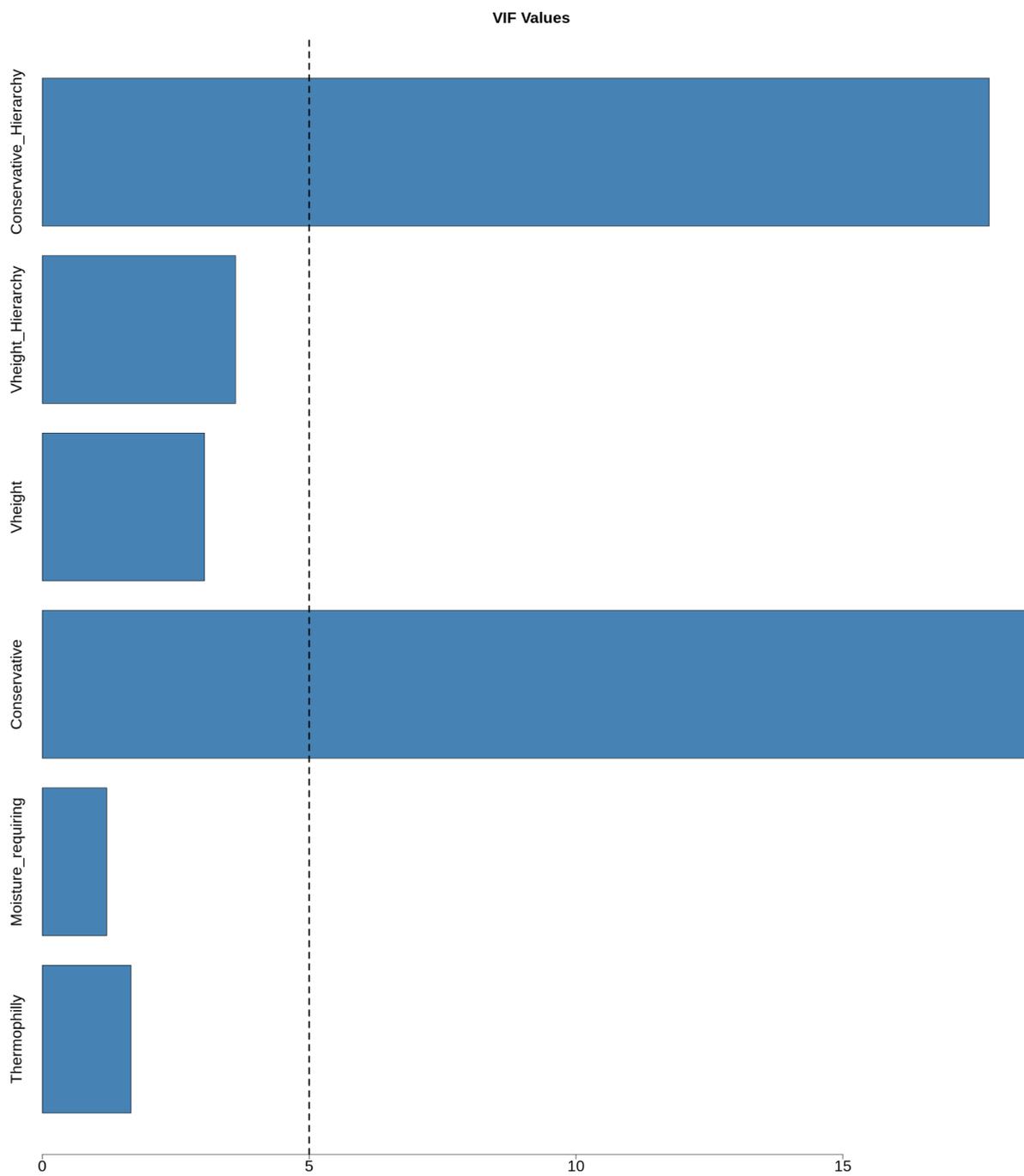


Fig. S5: Variation inflation factor (VIF) to check the multicollinearity between functional traits and hierarchy patterns. VIF = 5 threshold is indicated with a dashed line.

Appendix for Chapter 3

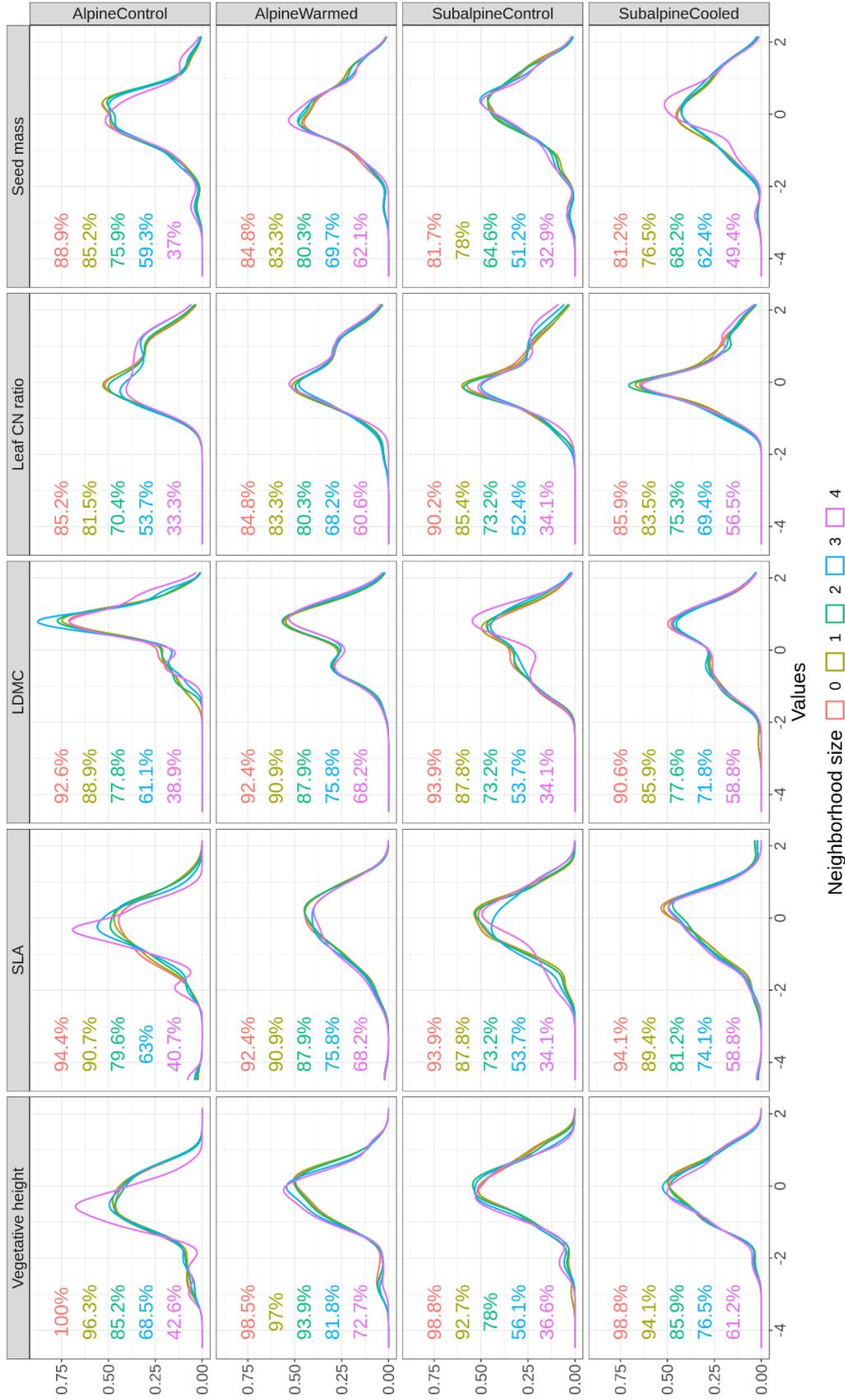


Fig. S1: Functional trait distributions of the focal species at each neighborhood level and the percentage of the remaining focal species after the methodological adjustments as indicated in the main manuscript. Percentages are given in relation to the number of species observed on the field (AlpineControl: 54, AlpineWarmed: 66, SubalpineControl: 82, SubalpineCooled: 85). The overall shape of the trait distributions are very well preserved even if the percentage of the species that are kept decrease sharply at the largest neighborhood size.

Appendix S2: Completing the trait data with TRY and Tundra databases.

When our alpine traits database *Androsace* lacked the trait information for our species in the experimental and regional pools, we extracted the missing traits from TRY and Tundra databases. From both databases, we included the data with an error risk 2 or less. In order to assess climate bias on the trait measurements in the TRY database, we subsetted the data from mountain and high latitude observatories. These data sources were "Niwot Alpine Plant Traits", "Italian Alps Plant Traits Database", "Abisko & Sheffield Database", "European North Russia", "Alaska Peatland Experiment PFT values", "Tundra Plant Traits Database", "Rocky Mountain Biological Laboratory WSR/gradient plant traits" (here after "TRY(primary)"). Hence, we had two sub datasets TRY(all) & Tundra and TRY (primary) & Tundra. We compared the trait distributions of the common species from *Androsace*, TRY(all) & Tundra and TRY (primary) & Tundra (Figure S1). For each trait, we compared the differences between the means of the distributions of both sources to *Androsace* with a custom contrast analysis in the *emmeans* package in R. None of the comparisons were significant but the difference between *Androsace* and TRY (primary) & Tundra was smaller than all datasets merged except for vegetative height. As a result of this comparison, we chose to prioritize the usage of TRY (primary) & Tundra for all traits when available except for vegetative height (Table S1). For vegetative height, we took the data from all datasets merged.

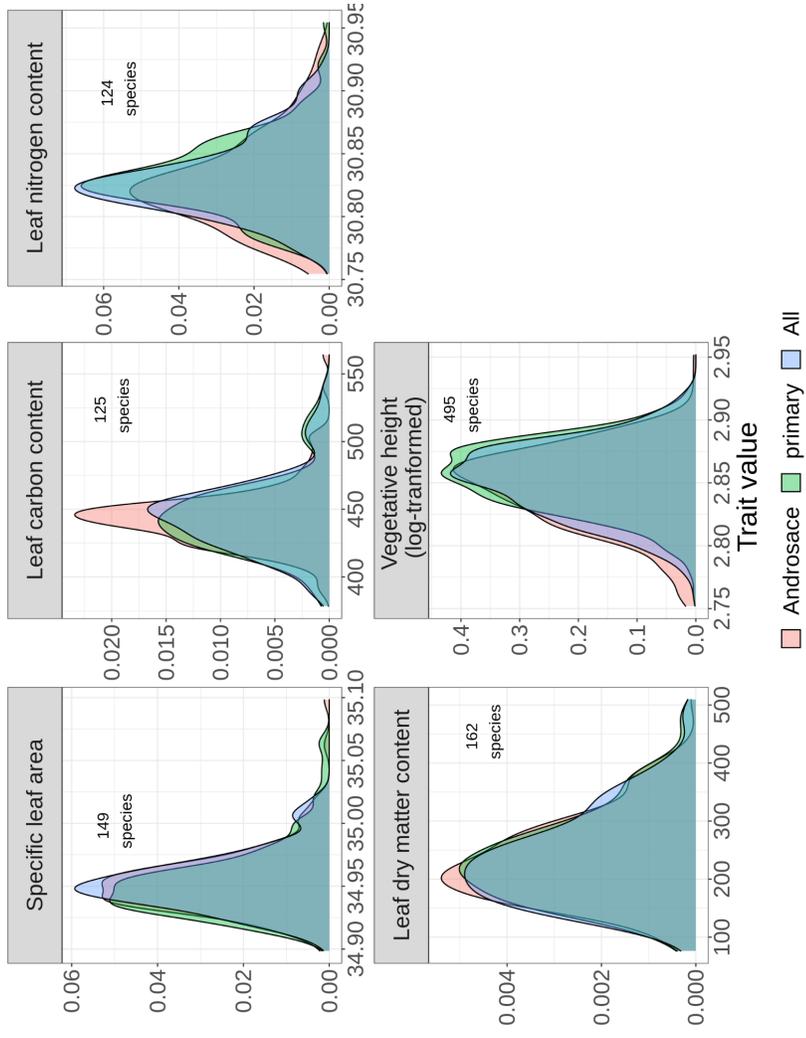
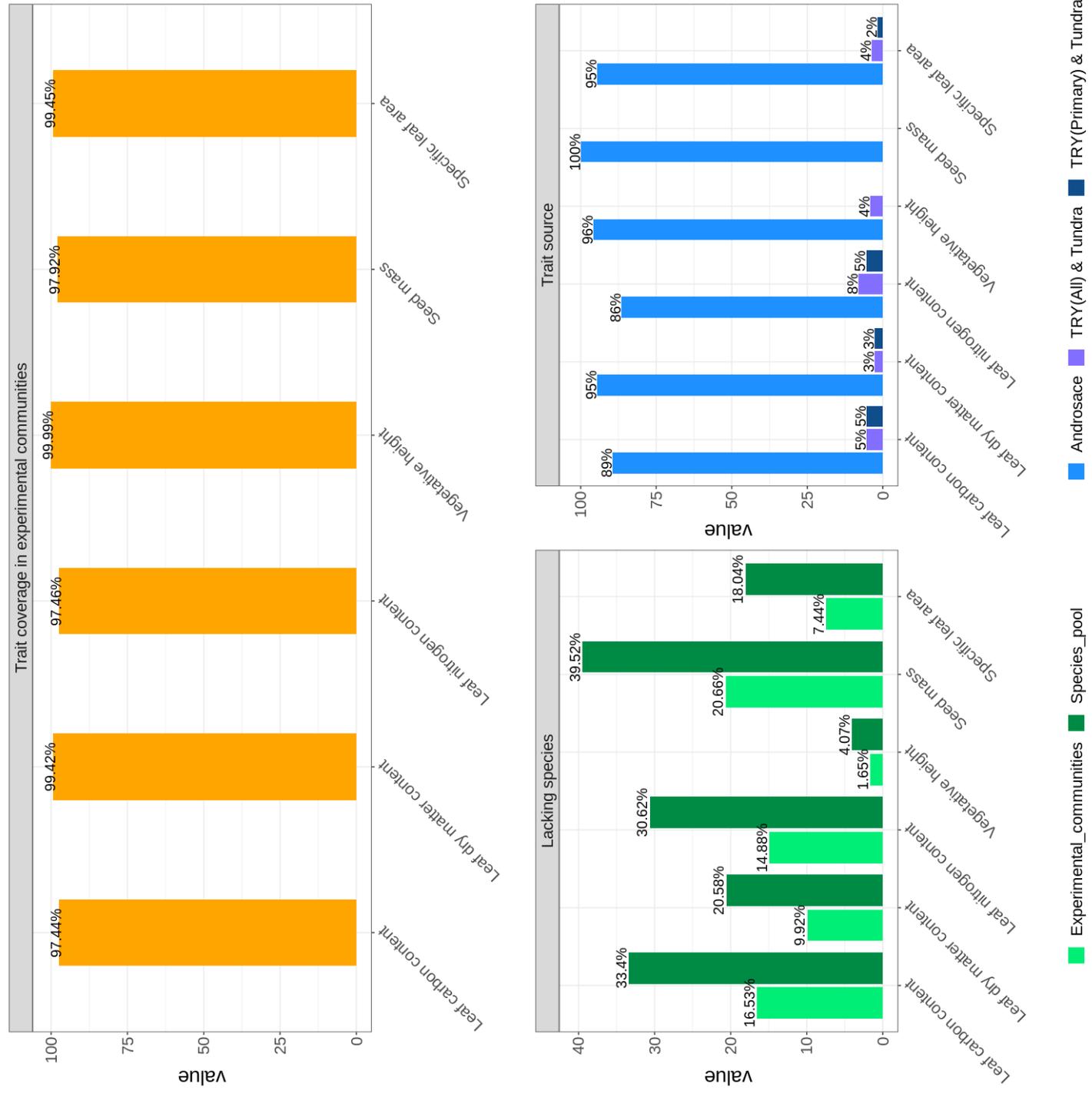


Fig. S2: Trait distributions of the common species with each trait dataset Androsace, TRY (primary) & Tundra and TRY(all) & Tundra.

Table S1: Results of the contrasts analysis of trait distributions. The significant differences are highlighted.

contrast	trait	estimate	Significance	SE	df	Lratio	p.value	lower.CL	upper.CL	Significance.1
Androsace-Primary(TRY & Tundra)	Vegetative height (log-transformed)	-0.320044087813614	p<0.05	0.0580696607712884	1482	-5.511382080810436	8.38064967423335e-08	-0.448627285046835	-0.1914608905803925	p<0.05
Androsace-All(TRY)	Vegetative height (log-transformed)	-0.180454887214779	p<0.05	0.0580696607712884	1482	-3.107558832236233	3.74071918415331e-03	-0.309038084448003	-0.0518716899815554	p<0.05
Androsace-Primary(TRY & Tundra)	Specific leaf area	0.358138125301927	p>0.05	0.99858491117598398	444	0.358645640530226	9.10627888217432e-01	-1.857958669922090	2.5742349205259436	p>0.05
Androsace-All(TRY)	Specific leaf area	0.257054728034886	p>0.05	0.99858491117598430	444	0.257418998632644	9.52695085598334e-01	-1.959042067189138	2.4731515232589101	p>0.05
Androsace-Primary(TRY & Tundra)	Leaf carbon content	-0.740424356251353	p>0.05	3.4754189726623888	372	-0.213046070725723	9.673000061084206e-01	-8.457965027419776	6.9771163149170716	p>0.05
Androsace-All(TRY)	Leaf carbon content	-1.451267078886710	p>0.05	3.4754189726623839	372	-0.417580467363033	8.81194953736253e-01	-9.168807750055123	6.26627359222817037	p>0.05
Androsace-Primary(TRY & Tundra)	Leaf nitrogen content	-1.076009476504080	p>0.05	0.9767149587604161	369	-1.101661714969209	4.38093562616382e-01	-3.244976953870412	1.0929580008622515	p>0.05
Androsace-All(TRY)	Leaf nitrogen content	-0.790662264707847	p>0.05	0.9767149587604110	369	-0.809511779886435	6.31322406056529e-01	-2.959629742074167	1.3783052126584734	p>0.05
Androsace-Primary(TRY & Tundra)	Leaf dry matter content	-3.758756022802298	p>0.05	8.7999661384550230	483	-0.427133009793855	8.76111152739368e-01	-23.282940717862580	15.7654286722579826	p>0.05
Androsace-All(TRY)	Leaf dry matter content	-1.425258920600824	p>0.05	8.7999661384550443	483	-0.161961864190883	9.80940553077061e-01	-20.949443615661153	18.0989257744595022	p>0.05
Androsace-Primary(TRY & Tundra)	Seed mass	0.3540666666624999	p>0.05	1.7450375715155835	21	0.202899165269828	9.70332877729387e-01	-3.7823668328308042	4.4905016615580404	p>0.05
Androsace-All(TRY)	Seed mass	0.3540666666625000	p>0.05	1.7450375715155841	21	0.202899165269828	9.70332877729387e-01	-3.7823668328308043	4.4905016615580431	p>0.05

Fig. S3: Trait coverage in experimental communities and in the species pool as in the cumulative sum of species' relative abundances for which the traits are available (above), percentage of species that are still lacking in the experimental communities and in the species pool (bottom left), trait sources as in percentage of species in the species pool (bottom right).



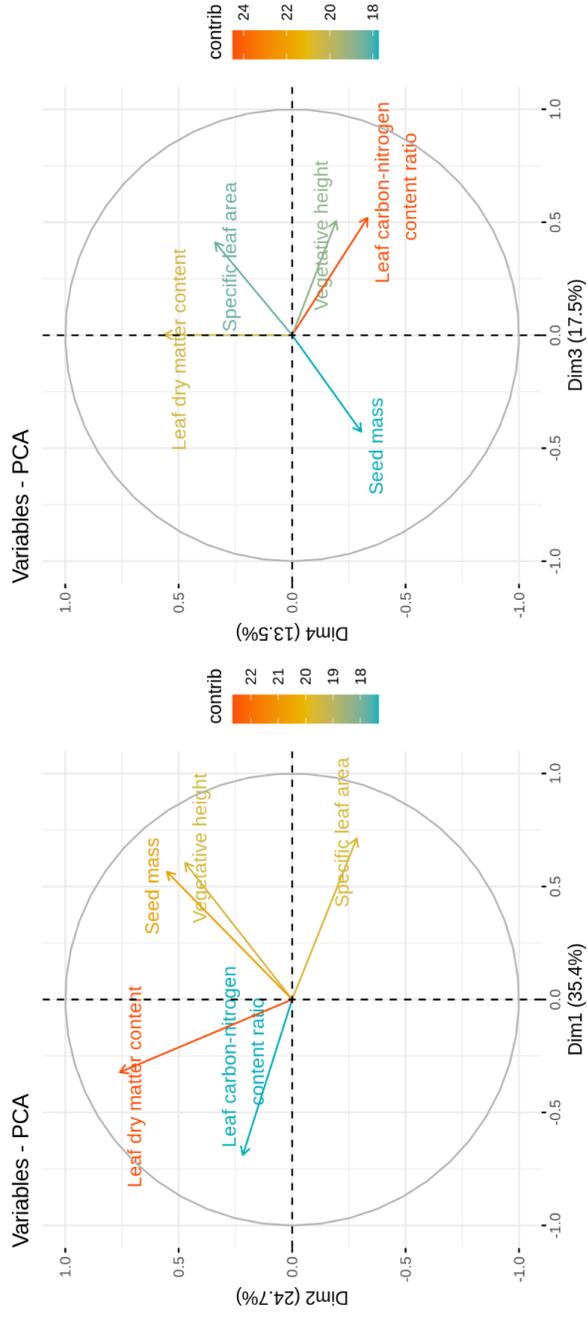


Fig. S4: Principal component analysis for the traits available in the regional species pool. Color code: contribution to the principal components.

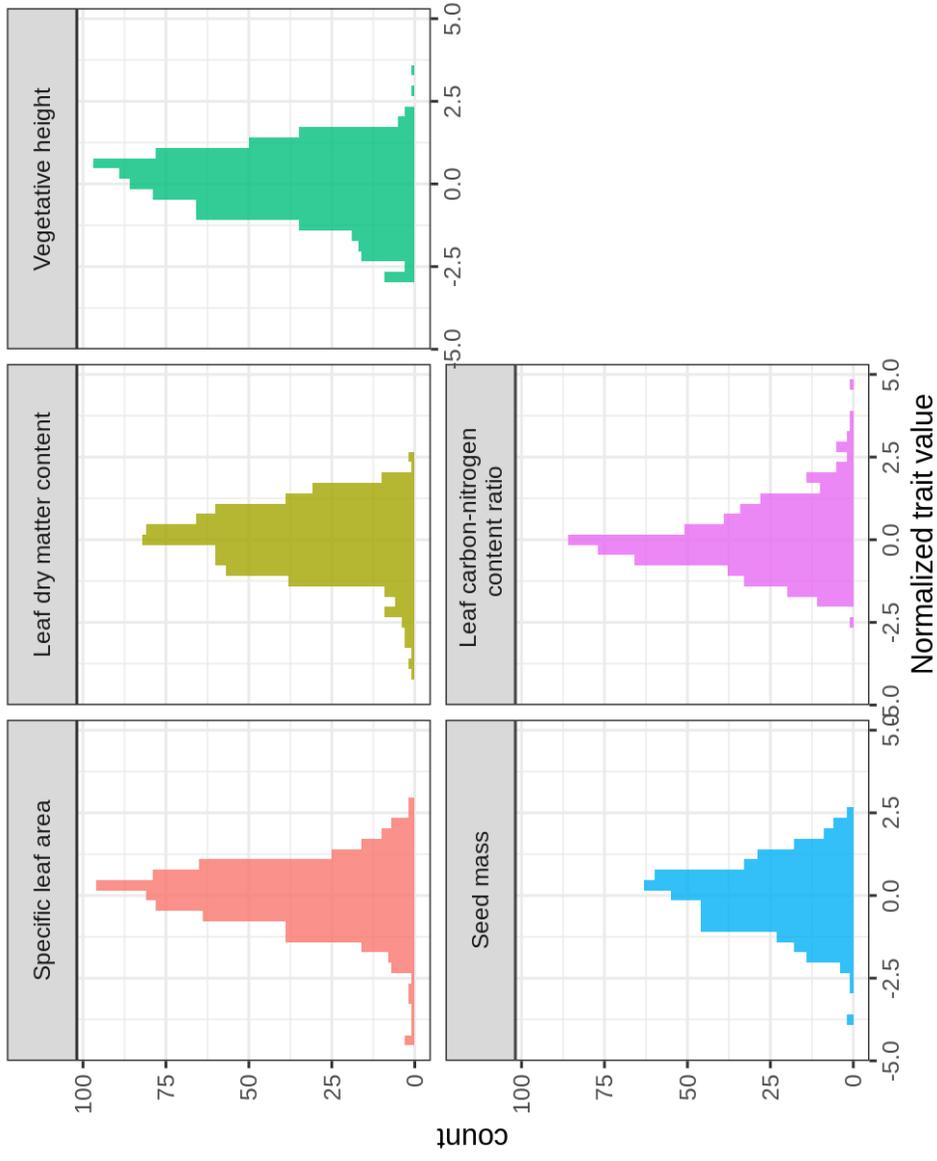


Fig. S5: Log-transformed and gaussianized (for skewed heavy tails) trait distributions in the regional species pool.

Appendix S3: Species coexistence patterns in experimental communities

To capture the signatures of facilitative interaction between species, we investigated species pairwise coexistence patterns. We expected to see species coexisting more than expected if they are facilitating each other (Gallien et al. 2018). At smallest spatial scale where species touched the same pinpoint (see Methods section in the main manuscript), we calculated the species pairwise coexistence scores as follows:

$$I_{jk} = \frac{2 \times N_{jk}}{N_j + N_k}$$

where N_{jk} is the number of pinpoints where species j and k coexist N_j is the number of pinpoints where species j exist N_k is the number of pinpoints where species k exist.

We randomized 500 times the sites list of the coexisting species for a given focal species and calculated $I_{jk-null}$. We calculated standardized effect sizes of the species pairwise coexistence scores as follows:

$$SES_{jk} = \frac{I_{jk-observed} - mean(I_{jk-null})}{sd(I_{jk-null})}$$

Where sd is the standard deviation of the null scores.

For each treatment group, we conducted a Wilcoxon signed-ranks test with the alternative hypothesis that SES of species pairwise coexistence scores are greater than 0. The p.value of the test results for all treatment groups were 1. Hence, we concluded that species do not coexist more than expected and facilitation was not observed in these communities (Figure S3).

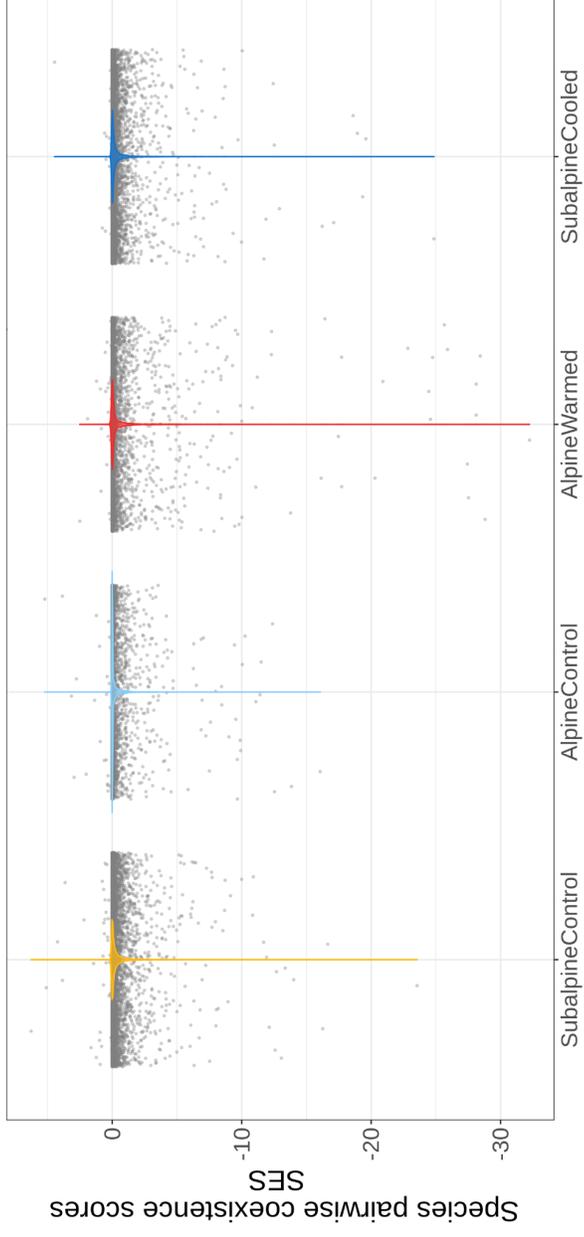


Fig. S6: SES of species pairwise coexistence scores for all the experiment groups.

References:

Gallien, L. et al. 2018. Frequency and intensity of facilitation reveal opposing patterns along a stress gradient. - *Ecol. Evol.* 8: 2171–2181.

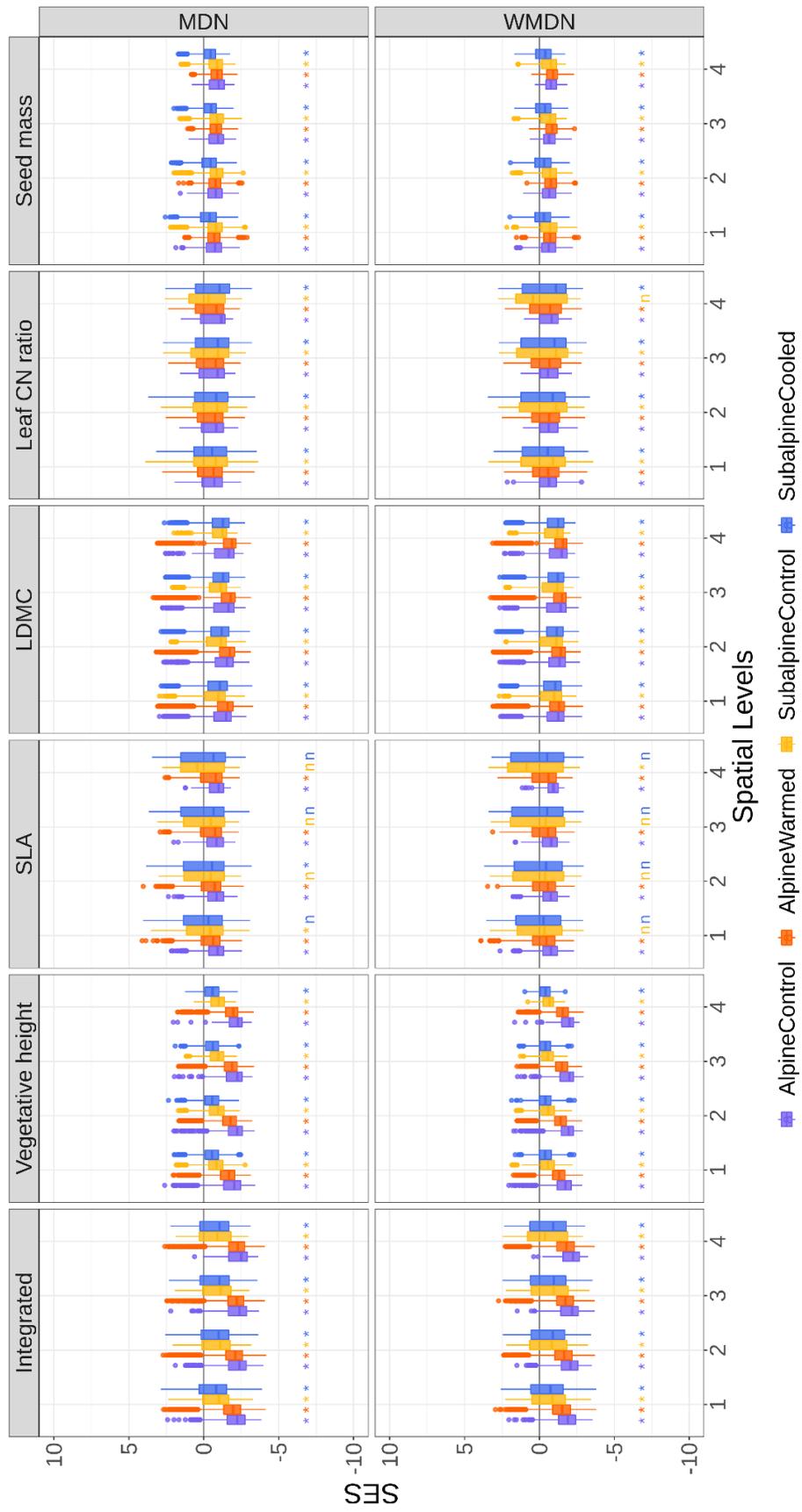


Fig. S7: Standardized effect sizes of functional distances between focal individuals and their neighbors at each neighborhood size for all experiment groups. Results of two-sided Wilcoxon signed-ranks test are noted below the boxplots (n: non-significant, *: p>0.05)

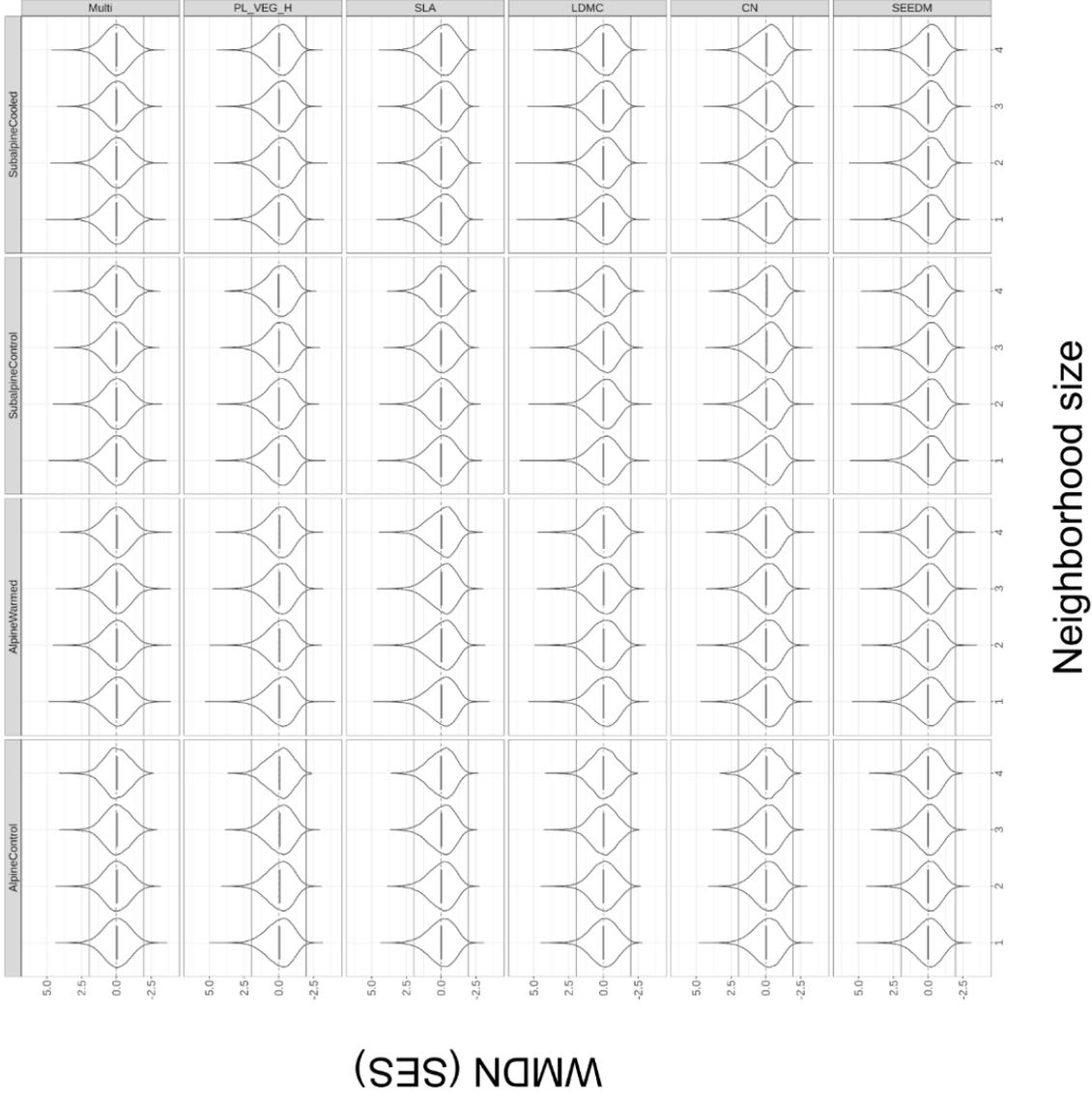


Figure S8: WMDN(SES) of 100 test communities at different neighborhood sizes and all the traits (integrated, vegetative height,

specific leaf area, leaf dry matter content, leaf CN ratio and seed mass, respectively in rows).

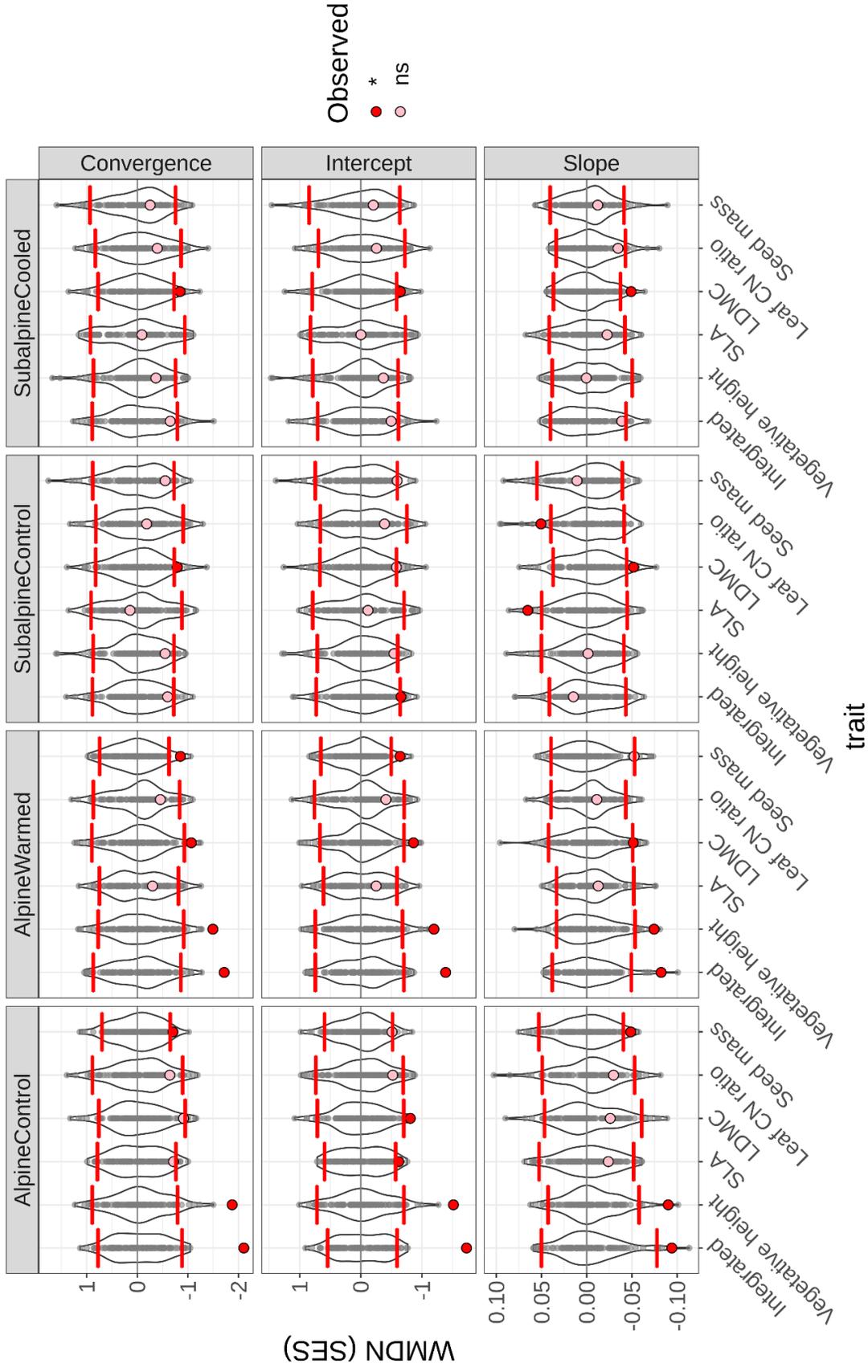


Fig. S9: Defining the significance of slopes, intercepts and convergence at the largest spatial distance for observed communities for WMDN (SES). We identified these terms as significant for observed communities if their values are higher or lower than 5% of the values calculated for 100 test communities.

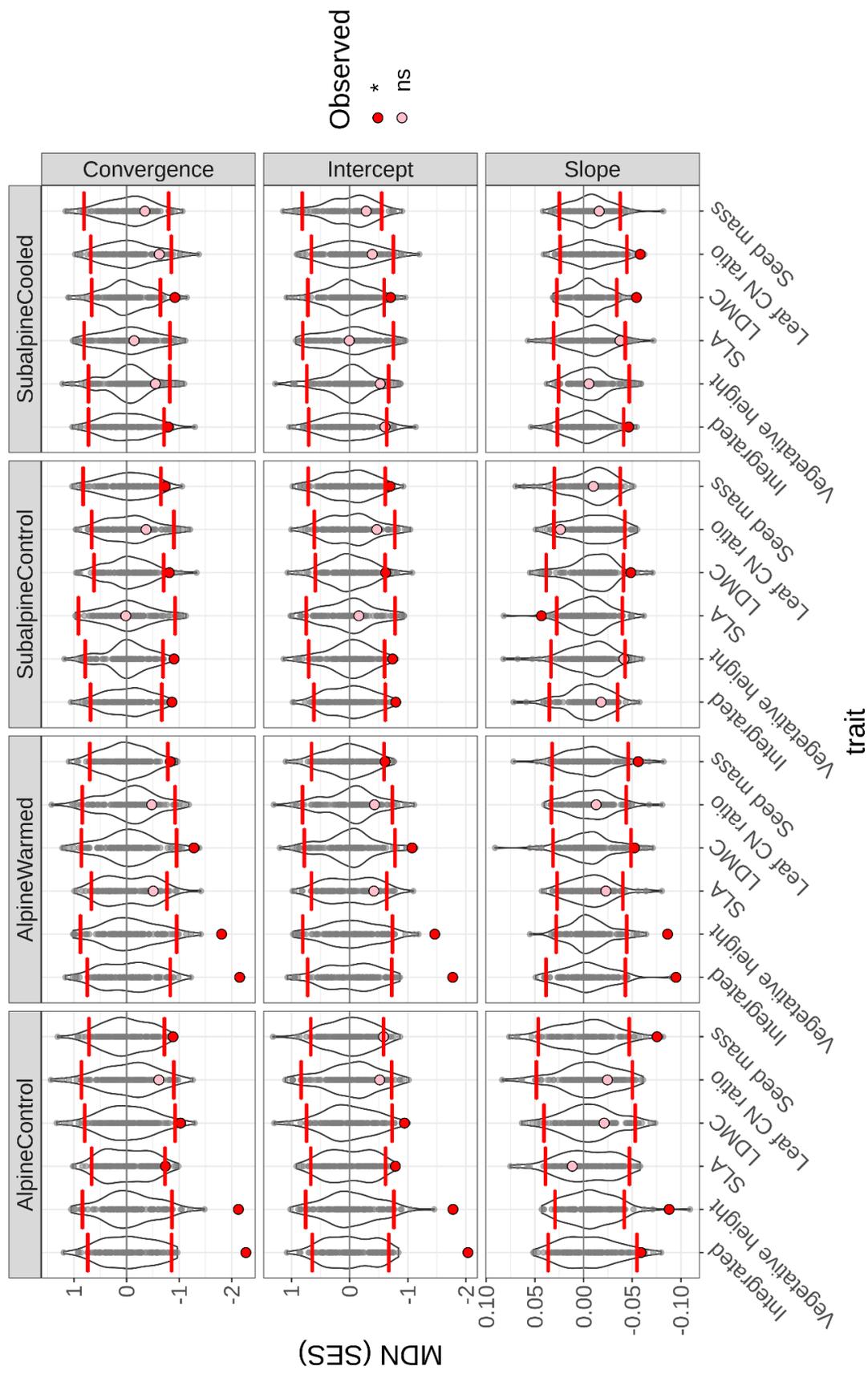


Fig. S10: Defining the significance of slopes, intercepts and convergence at the largest spatial distance for observed communities for MDN (SES). We identified these terms as significant for observed communities if their values are higher or lower than 5% of the values calculated for 100 test communities.

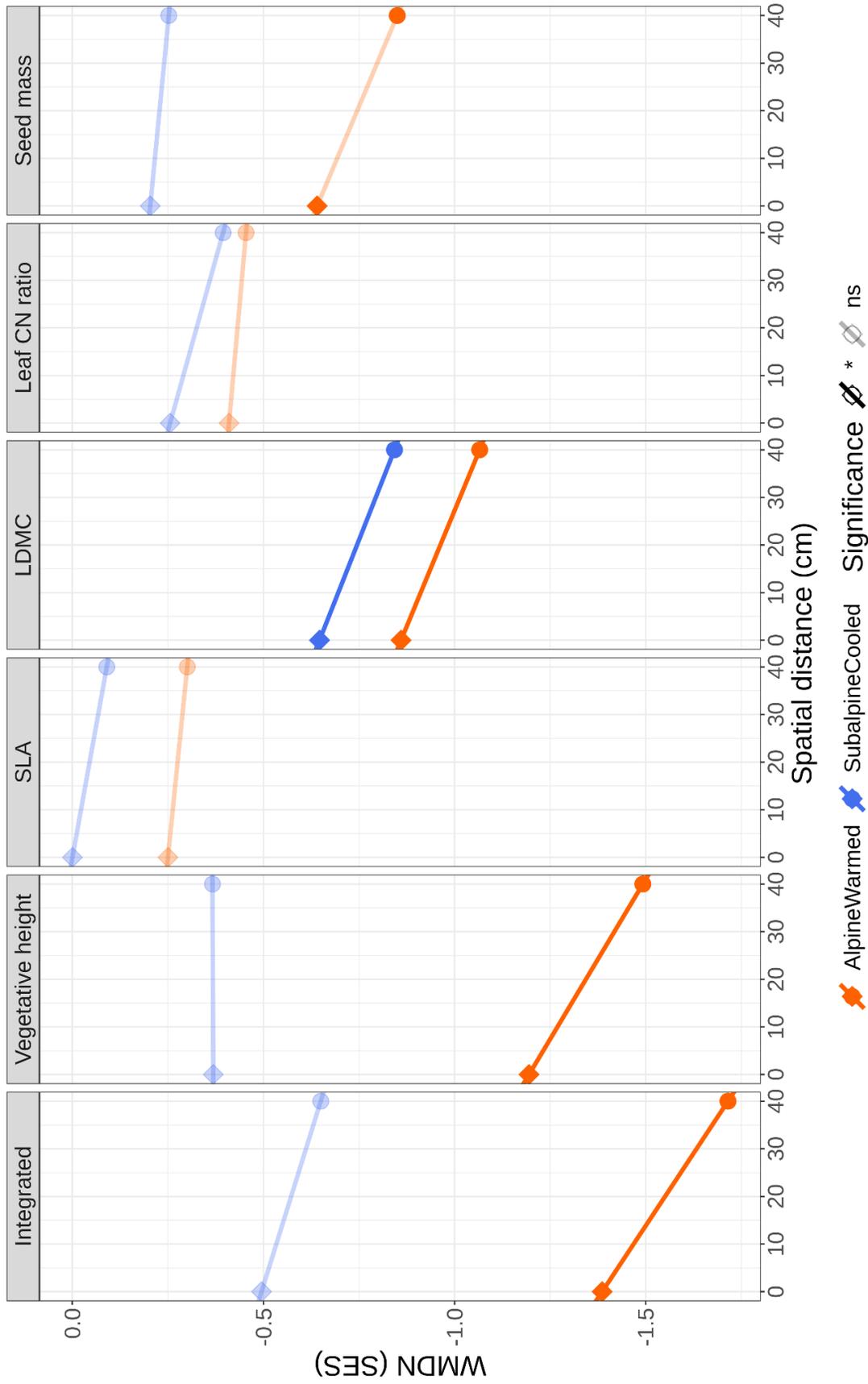
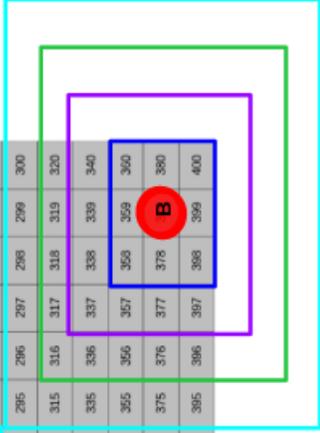


Fig. S11: Changes in SES of functional distances (WMDN) with increasing spatial distances as predicted by the linear mixed effect regressions. A significant slope is a signal of biotic interaction. A significant intercept is a signal of environmental filtering (diamond). The

intercept quantifies the strongest detectable biotic interaction if there is any. The predicted value at the largest distance is the strongest detectable environmental filtering (circle). We identified these terms as significant for observed communities if their values are higher or lower than 5% of the values calculated for 100 test communities. Non-significant terms are transparent. Integrated: combination of vegetative height, SLA & LDMC, SLA: Specific leaf area, LDMC: Leaf dry matter content, CN: Leaf carbon nitrogen ratio. (n.s: non-significant, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$)

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140
141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160
161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
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201	202	203	204	205	206	207	208	209	210	211	212	213	214	215	216	217	218	219	220
221	222	223	224	225	226	227	228	229	230	231	232	233	234	235	236	237	238	239	240
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281	282	283	284	285	286	287	288	289	290	291	292	293	294	295	296	297	298	299	300
301	302	303	304	305	306	307	308	309	310	311	312	313	314	315	316	317	318	319	320
321	322	323	324	325	326	327	328	329	330	331	332	333	334	335	336	337	338	339	340
341	342	343	344	345	346	347	348	349	350	351	352	353	354	355	356	357	358	359	360
361	362	363	364	365	366	367	368	369	370	371	372	373	374	375	376	377	378	380	380
381	382	383	384	385	386	387	388	389	390	391	392	393	394	395	396	397	398	399	400



● Focal individual's position and zero neighborhood size
■ First neighborhood size
■ Second neighborhood size
■ Third neighborhood size
■ Fourth neighborhood size

Fig. S12: Illustration of the definition of focal individual and neighborhoods on a treatment plot with 400 pinpoints. Red dot represents the position of the focal individual and the smallest neighborhood. Different colored squares represent different sizes of neighborhoods. Focal individual A's neighborhoods at all sizes remain within the borders of the plot thus, the focal individual A remains in the analysis at all neighborhood sizes. Focal individual B's zero and first neighborhoods only remain in the borders of the plot, thus focal individual B is excluded from the analysis only at second, third and fourth neighborhood sizes.

Appendix for Chapter 4

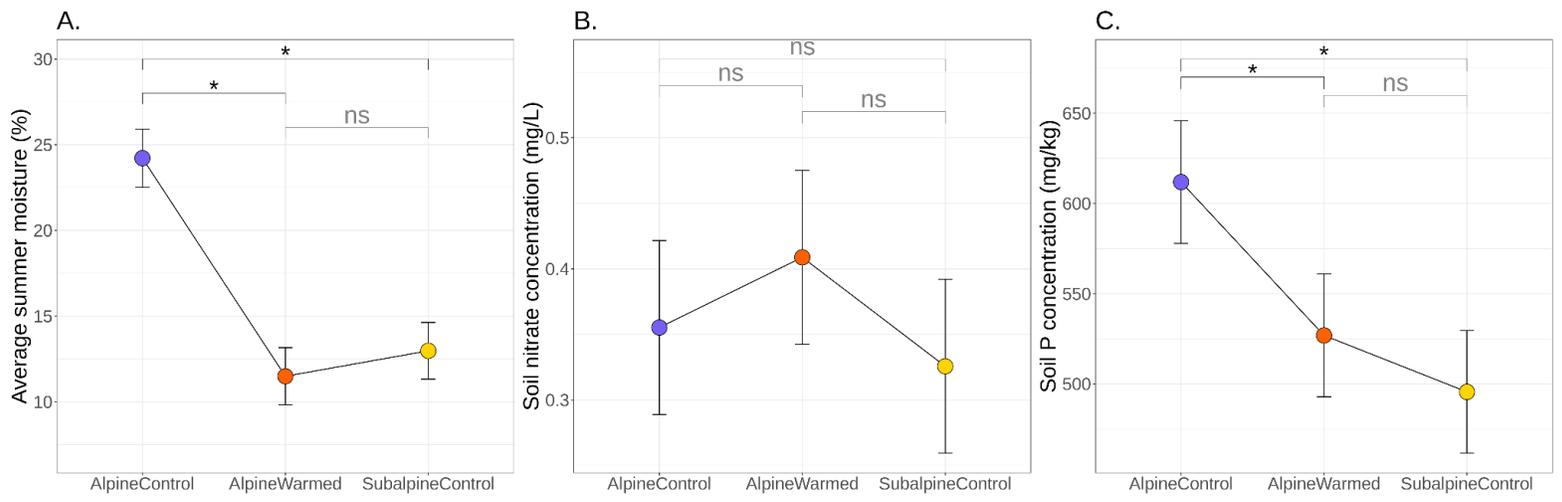


Fig. S1: Average summer moisture (A.), soil nitrate concentration (B.) and soil P concentration (C.) measured directly in the experimental plots. Significant comparisons (p -value < 0.05) are indicated in black. Error bars represent 95% confidence intervals.

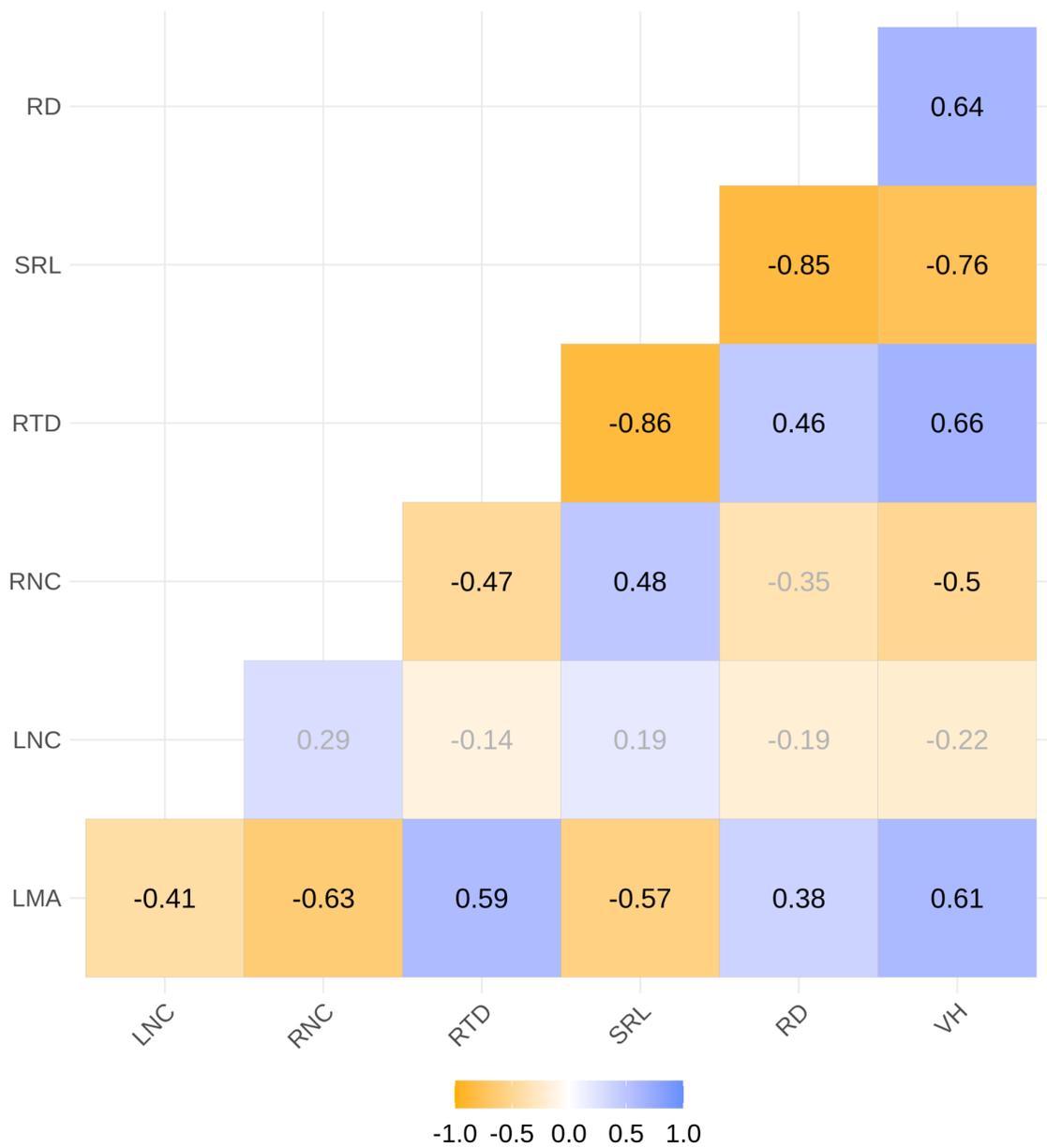


Fig. S2: Pearson correlation coefficient between the community-level functional traits. The color gradient indicates the strength of correlation coefficient. Significant correlations are written in black.

(LNC: leaf nitrogen content, LMA: leaf mass per area, RTD: root tissue density, RNC: root nitrogen content, SRL: specific root length, RD: root diameter, VH: vegetative height)

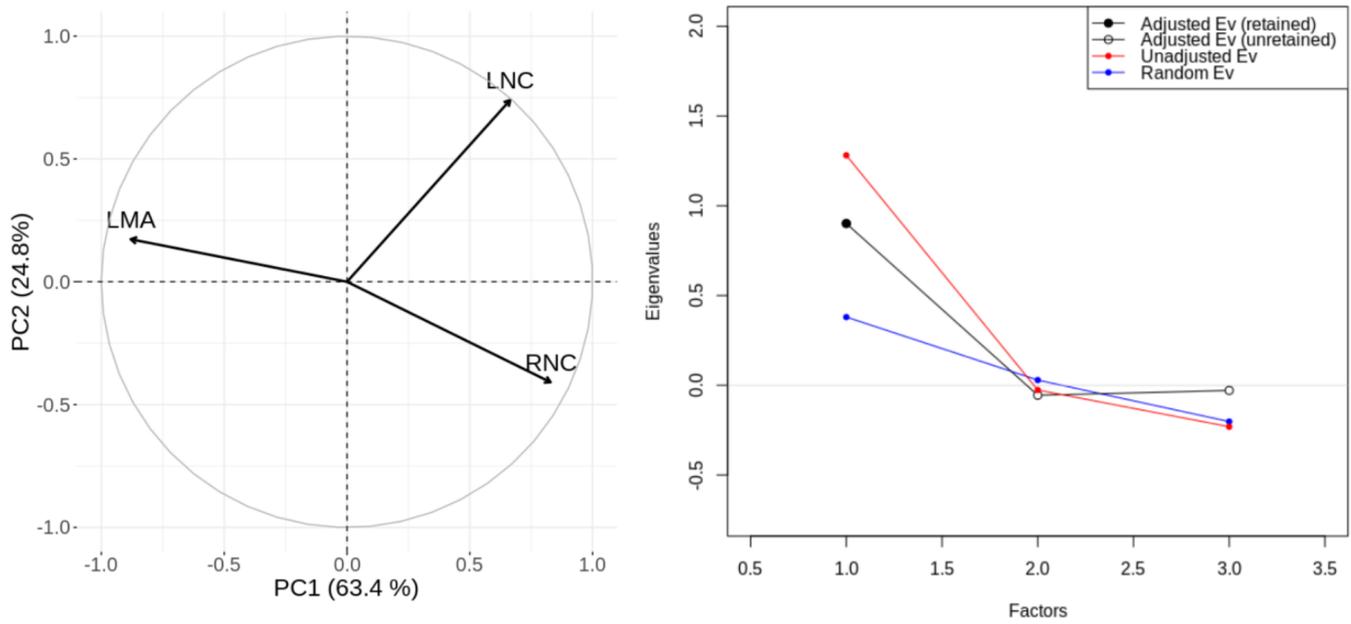


Fig. S3: Principal component analysis (PCA) of community-level functional traits of conservation spectrum (left) and Horn's parallel analysis on the PCA to determine the significant principal components (right). Positive adjusted eigenvalues indicate dimensions to retain. Here, only one principal component is retained.

(LNC: leaf nitrogen content, LMA: leaf mass per area, RTD: root tissue density, RNC: root nitrogen content)

Parallel Analysis

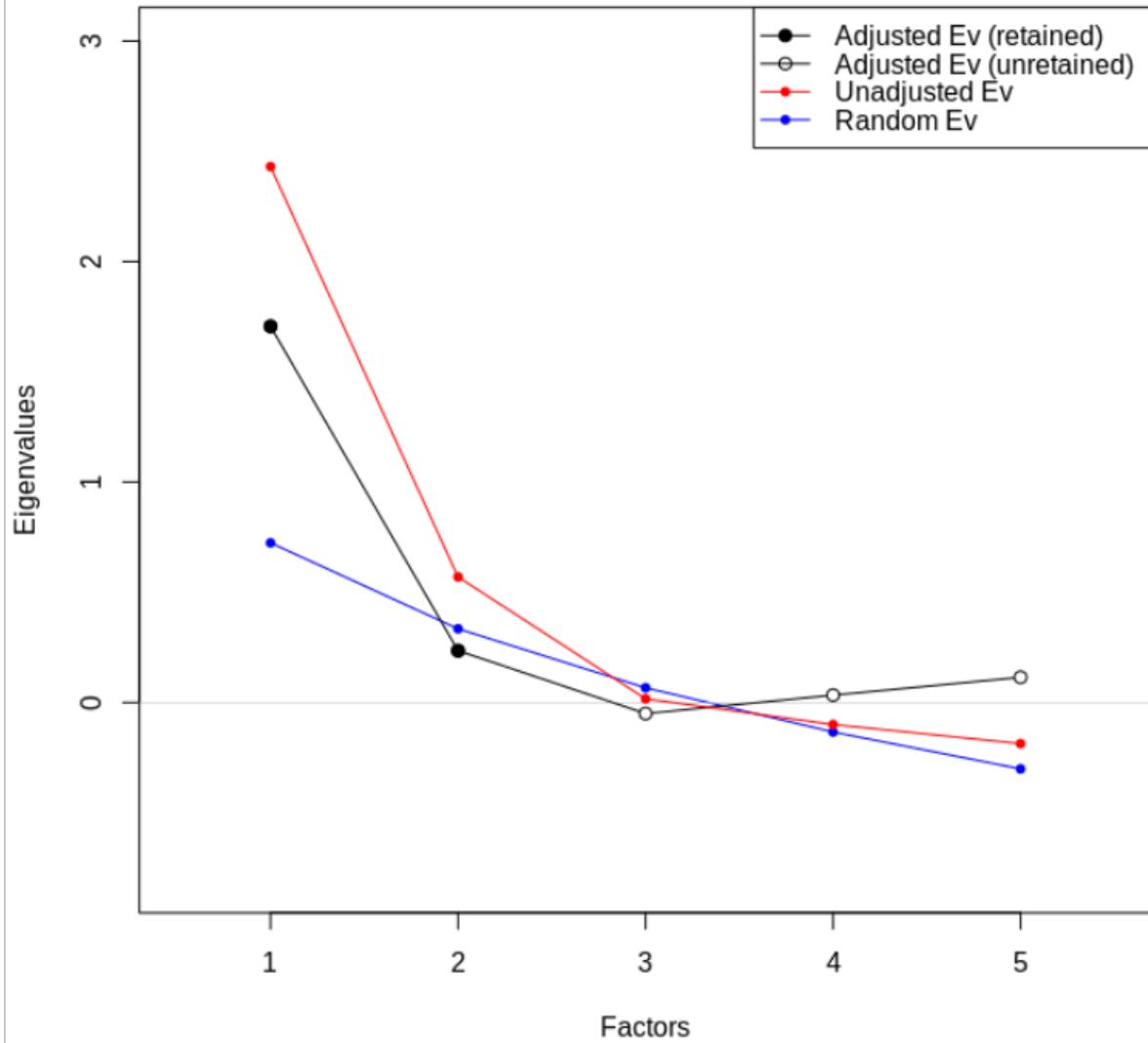


Fig. S4: Horn's parallel analysis on the principal component analysis built from all the community-level functional traits (Table 1 in the main text). Positive adjusted eigenvalues indicate dimensions to retain. Here, the first two principal components are retained.

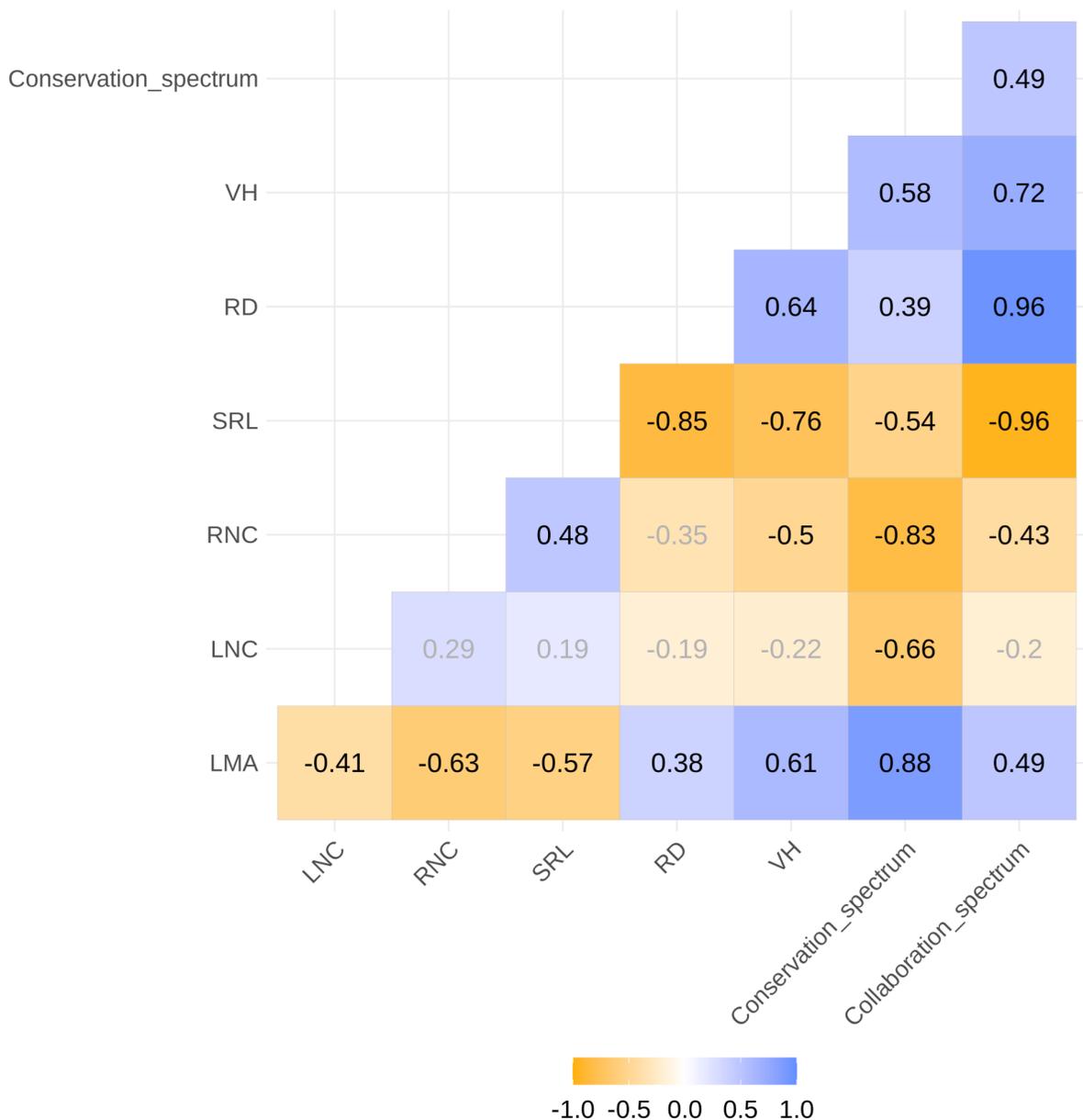


Fig. S5: Pearson correlation coefficient between the community-level functional traits, conservation and collaboration spectra. The color gradient indicates the strength of correlation coefficient. Significant correlations are written in black. Conservation spectrum is constructed from the first principal component of a PCA from LNC, LMA and RNC. Collaboration spectrum is constructed from the first principal component of a PCA from SRL and RD. (LNC: leaf nitrogen content, LMA: leaf mass per area, RNC: root nitrogen content, SRL: specific root length, RD: root diameter, VH: vegetative height)

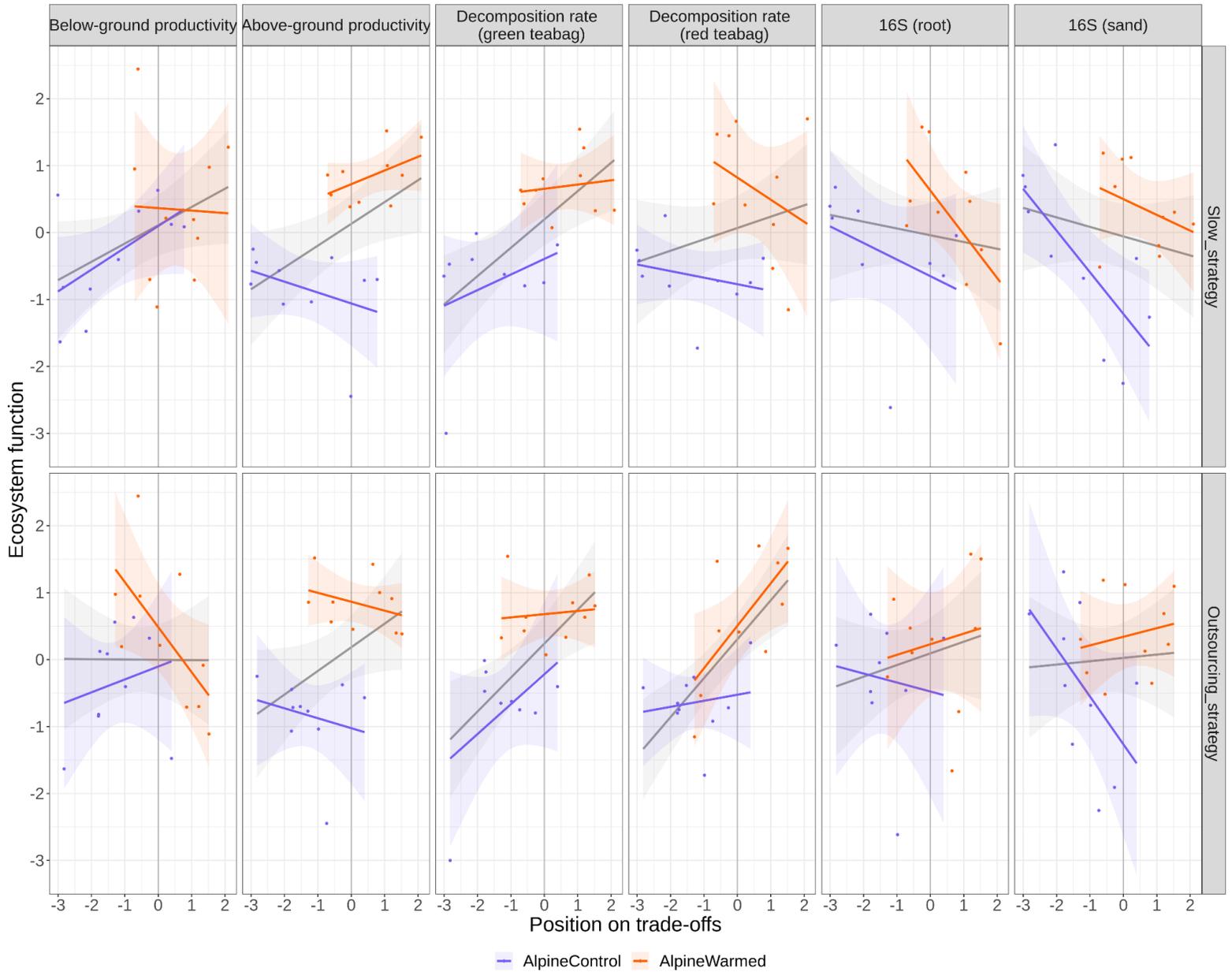


Fig. S6: Change in the ecosystem functions with functional trade-offs for AlpineControl (purple), AlpineWarmed (orange) and all (gray) plots. Positive values indicate slow and outsourcing strategies.

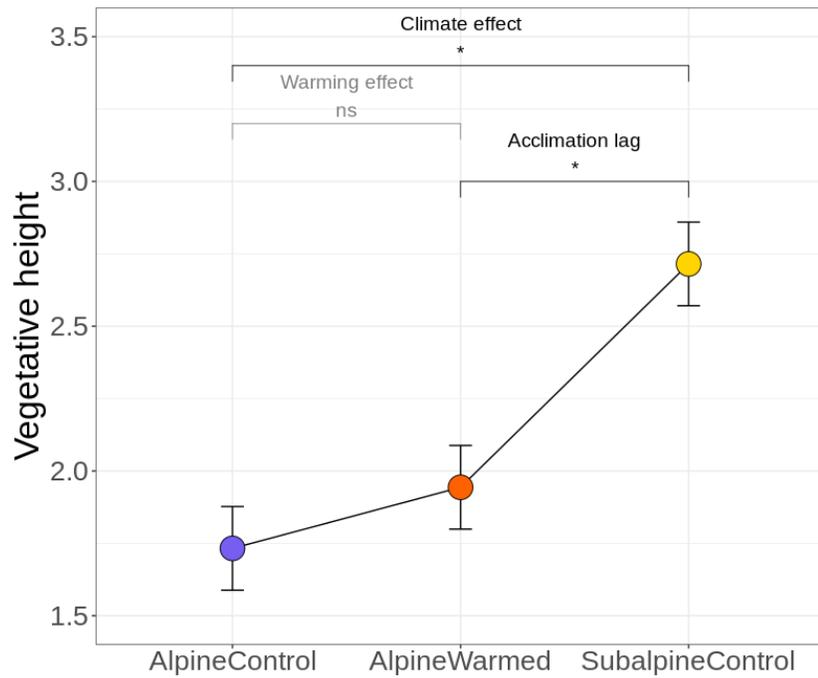


Fig. S7: Climate effect, warming effect and acclimation lag in vegetative height

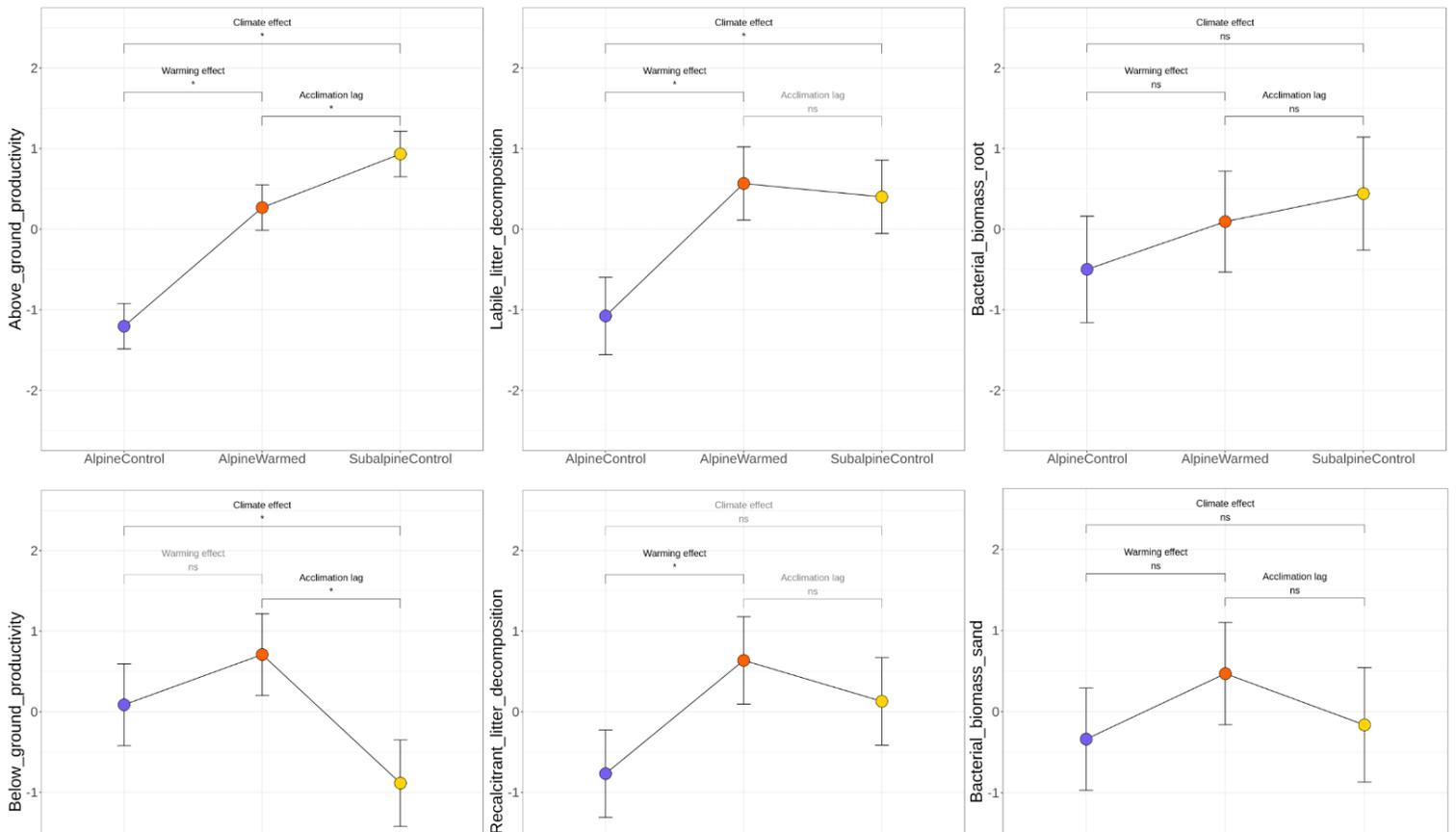


Fig. S8: Climate effect, warming effect and acclimation lag in ecosystem functioning