

Functional Ecology

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Growth-competition-herbivore resistance trade-offs and the responses of alpine plant communities to climate change

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Summary

1. Climate change is expected to modify current ecological conditions sustaining the coexistence of species within cold-adapted plant communities. It will primarily act upon the existing structure of communities, whose response should depend on the functional differences governing coexistence among alpine species. We postulated that a possible trade-off between *(i)* plant growth in response to temperature, *(ii)* plant competition, and *(iii)* resistance to herbivory, modulates the rate of plant community turnover under climate change.
2. We reviewed the literature investigating functional traits variability within communities along elevation gradients. Despite environmental filtering, our review indicates that interspecific plant functional variation within communities does not necessarily decrease with elevation. While the diversity of traits related to abiotic affinities or competition are well documented, the variability in species resistance to herbivory within communities is poorly known.
3. Using a Lotka-Volterra-based model, we simulated the impact of climate change on plant communities through *(i)* a direct effect on plant growth and competition and *(ii)* an indirect effect via an increase in herbivore pressure. We showed that different shapes of trade-offs between temperature-related growth, competition and resistance to herbivory modulate community turnover under climate change.
4. We documented the existence of two independent trade-offs axes using a detailed dataset of functional traits within two alpine communities in the European Alps. Plant competitive traits (i.e. leaf area and height) were negatively associated to cold tolerance, while traits of the leaf economic spectrum were associated to traits related to the physical resistance to herbivory.
5. We propose that the immediate effect of climate change on alpine plant communities will depend on existing functional variability and how functional axes trade-off with each other. Documenting ecological constraints between plant functional axes should provide indications to anticipate winners and losers in alpine plant communities.

Key-words: Functional community ecology, temperature, competition, stress, global change, plant defences, secondary metabolites, insect herbivores.

Introduction

Climate change is already having pervasive effects on biodiversity across the globe (Grabherr, Gottfried & Pauli 1994; Parmesan 1996; Stange & Ayres 2001; Wilson *et al.* 2004; Hoegh-Guldberg *et al.* 2008; Burrows *et al.* 2011; Pateman *et al.* 2012; Pauli *et al.* 2012a). Species are moving their distribution ranges poleward and upslope because of increasing temperature (Parmesan & Yohe 2003; Hickling *et al.* 2006; Parmesan 2006; Lenoir *et al.* 2008; Chen *et al.* 2011). The asynchronous colonization of new habitats by different species results in novel species co-occurrences, for example; between cold-adapted and more warm-adapted plants (Pauli *et al.* 2012b), between herbivores and new host plants (Singer & Parmesan 1993), or between predators and preys (Harrington, Woiwod & Sparks 1999; Durant *et al.* 2007). Therefore, shifts in environmental conditions following climate change is expected to largely affect ecological and evolutionary trajectories of species confronted with both the modifications of previous interactions or the emergence of new ones (van der Putten *et al.* 2004; Tylianakis *et al.* 2008; Jamieson *et al.* 2012).

Plants have evolved different functional strategies to perform optimally in a given environment (Díaz *et al.* 2016). Acting on species pools, habitat filtering should homogenize the functional structure of plant communities (Kraft *et al.* 2015). On the other hand, within any given plant community, a diversity of strategies exists (Ackerly & Cornwell 2007; Hulshof & Swenson 2010). Indeed, functional divergence among species provide niche differences in resource acquisition among species favouring local coexistence in communities (Bengtsson, Fagerström & Rydin 1994; Silvertown 2004; Leibold & McPeck 2006; Kraft, Valencia & Ackerly 2008). For instance, a plant species might either dominate the canopy to have access to light, or be subordinate and tolerate the shade of other species. In addition to traits governing abiotic tolerance, the coexistence of plant species is thus regulated by their ability to compete with, or benefit, each other (Bengtsson, Fagerström & Rydin 1994; Chesson 2000a). Because coexistence is further favoured by functional trade-offs (Chesson 2000b), understanding the functional divergence among species and how traits are associated with each other is essential to comprehend how species coexist (Kraft, Godoy & Levine 2015), but also how communities will change in a warmer climate (Alexander *et al.* 2016).

An axis of plant coexistence that has been largely understudied is the plant capacity to deal with herbivore attacks (Hulme 1996; Diaz *et al.* 2007; Ishii & Crawley 2011; Ibanez *et al.* 2013; Kempel *et al.* 2015). Herbivores have been shown to impact the structure of plant

communities in several systems (e.g., Milchunas, Sala & Lauenroth 1988; Hulme 1996; Augustine & McNaughton 1998; Carson & Root 2000; Olofsson *et al.* 2004; Hanley & Sykes 2009; Kempel *et al.* 2015). In the context of apparent competition (i.e. indirect competition via a shared enemy, Holt & Lawton 1993; Mooney, Pratt & Singer 2012), divergence in anti-herbivore traits could favour coexistence, at least where herbivore pressure is strong (Kursar *et al.* 2009; Richards *et al.* 2015; Callis-Duehl *et al.* 2017). For instance, Salazar *et al.* (2016) found that, on average, co-occurring species in the genus *Piper* were more likely to differ in secondary chemical composition than expected by chance. Becerra (2007) showed that coexisting *Bursera* plants growing at low elevation tend to be more chemically dissimilar than randomly assigned communities. If a trade-off between competitive abilities and resistance to herbivores exists, equalizing mechanisms can foster species coexistence through a possible investment in either of those strategies but not both. Nonetheless, the shapes of the trade-off between an axis of resistance against biotic attack, of abiotic tolerance and competition have been poorly documented (Agrawal & Fishbein 2006). Considering plant interactions with herbivores in the context of climate change is crucial, since the responses of plant communities to warming with and without herbivores can diverge (Post & Pedersen 2008).

Cold-adapted plant communities, such as in the alpine belt of mountains or in the poles, are expected to be especially vulnerable to climate change (Walker *et al.* 2006). Climate change is forecasted to dramatically impact cold areas through a general decrease in suitable habitats (Parmesan 1996; Parmesan 2006), following the colonisation of shrubs and forests (Dullinger, Dirnbock & Grabherr 2004) together with other competitors from warmer areas (Alexander, Diez & Levine 2015). Yet, climate change may impact alpine plant communities, without the involvement of new players (Harte & Shaw 1995; Niu & Wan 2008; Alexander, Diez & Levine 2015). Warmer temperatures might enhance the metabolism of some, but not all, species, thereby increasing their competitive abilities and dominance (Grace & Tilman 1990; Lambers & Poorter 1992). In addition, climate change could increase the abundance of herbivores and pathogens already present in the alpine zone (Rasmann *et al.* 2014). While there is herbivory from large mammals in the alpine belt, the level of herbivory from insects, which can take up to 30% of the annual biomass in some mountain grasslands (Blumer & Diemer 1996), is lower when compared to the lowlands (Pellissier *et al.* 2016). Pellissier *et al.* (2012; 2014) showed that cold adapted plant species, under more limited herbivory pressure, are chemically less defended against herbivores. Hence, increased herbivory may

impact the structure of alpine plant communities through the preferential feeding of herbivores on the less defended plants (Rasmann *et al.* 2014), which implies possible dominance shifts depending on how plants can defend against herbivore attacks (Klein, Harte & Zhao 2004). The direct impact of climate change on alpine communities should depend on the standing diversity of functional strategies represented and the shape of the correlation between functional traits related to temperature-dependant growth, competition, and defence.

Here, we assembled evidence for the role of within-community interspecific variability and trade-offs in modulating the response of alpine communities to climate change. We reviewed studies documenting the functional variation in communities along elevation gradients. We postulated that despite environmental filtering, alpine communities are functionally diverse, for the traits that structure the three main ecological trade-offs: (i) plant growth in response to temperature, (ii) competitive abilities, and (iii) resistance to herbivore attacks. Second, to evaluate how the structure of the functional trade-offs modulates the responses of alpine plant communities to climate change, we developed a theoretical model simulating climate change, including a direct effect of temperature on plant growth and indirect effects through an increase in plant competition and herbivore pressure. Finally, to corroborate the simulations, we documented the shape of the functional trade-offs among 11 traits associated to temperature growth limit, competition and resistance to herbivory in two alpine grasslands of the western Swiss Alps. We inferred whether the observed structure should promote fast or more limited turnover under climate change. Together, we provide a conceptual framework for predicting how biodiversity will change under climate change and argue for considering the entire functional domain of plants to understand the current and future assembly of plant communities.

Documenting functional diversity in alpine plant communities – a literature survey

Climate change is expected to directly interact with the standing functional variability existing in the alpine plant communities (Fonseca & Ganade 2001; Valencia *et al.* 2015). In a hypothetical situation of a functionally homogeneous assemblage, all species are expected to respond identically to climate change. In contrast, if species vary in their ability to e.g. increase their biomass in response to temperature rise or in their ability to tolerate increased level of competition, responses should be contrasted among species, so that both “winners” and “losers” emerge. The functional diversity within alpine plant communities is expected to be governed by the strong environmental filtering, which should homogenise functional

variations (de Bello *et al.* 2013; Pellissier *et al.* 2013; Read *et al.* 2014). Nevertheless, evidence suggests that a certain degree of functional divergence persists in alpine communities (Spasojevic & Suding 2012; Hulshof *et al.* 2013), likely because of the interplay with other community assembly processes such as niche partitioning (Stubbs & Bastow Wilson 2004), or the evolution of alternative functional designs (Marks & Lechowicz 2006). Here, we reviewed studies investigating functional diversity along elevation gradients and quantified the frequency of positive relative to negative trends. A positive relationship between elevation and functional diversity should suggest niche differentiation, a negative relationship indicates the role of environmental filtering in community assembly processes, while a hump-shaped relationship suggests a mid-domain effect, which can have multiple underlying causes (Grytnes 2003).

We retrieved papers from the ISI Web of Science and the Google search engine. The search was restricted to studies that included a specific comparison of community-level trait variation from low to high elevation in order to infer possible shifts as a result of environmental filtering or niche similarities. In addition, we only included studies that measured community (whole plot)-level interspecific trait-variability with a metric of functional diversity (see Table S1 in Supporting Information). Finally, we recorded positive (+), negative (-) or a hump-shaped (+-) relationships between the functional diversity metrics and elevation.

Overall, we found 22 cases reported in 18 studies that explicitly investigated the variation of functional diversity metrics along an elevation gradient, including functional diversity (FD), functional richness (Fric), functional divergence (Fdiv), functional dispersion (Fdis), functional evenness (Feve), functional attribute diversity (FAD), Rao's quadratic entropy (Rao), and community weighted variance (CWV) (Table S1). While we found the same number of cases showing an increase and a decrease in diversity with elevation (22), the positive and negative relationship was dependent on the metrics used (Chi-square test, $X^2 = 36.5$, $df = 14$, $p\text{-value} = 0.001$). The most significant difference was observed for the functional dispersion index (12 cases were positive versus 1 negative), whereas all other metrics displayed a tendency of being equally distributed in the responses to elevation. Thus, the existing literature suggests a variable response of community functional variation along elevation gradients, but also highlights that high-elevation plants are not necessarily constrained by environmental filtering. Functional variability within communities thus exists

even at high elevation, for traits related to resource sequestration (e.g. LDMC), or competition (e.g. height, SLA).

Trade-offs and community turnover under climate change

We explored how the shape of trade-offs among traits might impact community turnover in response to climate change using a mechanistic model. We postulated that the functional axes of abiotic-dependant growth, tolerance to competition, and resistance to herbivory trade-off with each other and shape the response of communities. Lotka-Volterra models have been used for understanding the structure of communities by including competition among species (Lotka 1920; Volterra 1926). They were originally developed to study intra- and interspecific competition in microorganisms and animals (e.g. Vandermeer 1969), but were rapidly modified to study plant communities (Weiner & Thomas 1986). This family of models allows the investigation of the processes of competition (Bullock, Mortimer & Begon 1995), community invasion (Chesson 2000b; Chesson 2003) and species coexistence (Pacala & Tilman 1994). Using a small set of coefficients, Lotka-Volterra equations can integrate population growth rates together with abiotic and biotic interactions. Such models are predominantly used to explore theoretical conditions of coexistence (Saavedra *et al.* 2017) but can also be used to explore the consequence of climate change on communities (Alexander *et al.*). Here, we explored how different shapes of trade-offs within communities influence their responses to climate change, including a direct physiological effect on species growth, as well as indirect effects associated to an increase in both competition and herbivory.

We developed a model of the response of alpine plant communities to climate change using a set of Lotka-Volterra differential equations. The general approach relies on the use of a Lotka-Volterra model where theoretical traits condition the relative biomass of each species at equilibrium. The differential equation system is defined as the change in biomass of a given species per unit of time. Change in biomass is determined by (i) a growth rate as a function of local temperature conditions relative to species-specific tolerance, (ii) a term of interspecific competition with co-occurring species and (iii) the biomass loss due to herbivory, together with (iv) a term for intra-specific density-dependence. The model is built assuming that the species range limit toward colder conditions is determined by species physiological tolerance (Pellissier *et al.* 2013), but by competition among species when growing in warmer and moister sites, in agreement with ecological theory (Grime 1977;

Vetaas 2002; Alexander, Diez & Levine 2015). The competition term is modelled as the ability of species to tolerate the biomass of co-occurring species. The model is given by the following equation for plants:

$$\frac{dP_i}{dt} = P_i \left[g_i \times (T - T_{min,i}) - c_i P_i - l_i \sum_j P_j - a_i H \right]$$

Where, P_i is the biomass of plant species, while H is the biomass of the herbivore compartment. The term $g_i \times (T - T_{min,i})$ indicates the temperature-dependent relative growth rate of the species that increases linearly with temperature T at a rate g_i and becomes negative for temperature T below $T_{min,i}$, c_i the intraspecific competition rate, l_i the trait indicating the species inherent susceptibility to competition with plant neighbours and a_i the susceptibility to herbivory (i.e. the inverse of resistance). In the model, the growth rate increases linearly with temperature. While most plant species show hump-shaped relationship along the temperature gradient (Pottier *et al.* 2013) and the metabolic activity is expected to saturate at high temperature (Berry & Bjorkman 1980), a linear function represents a good approximation when the model is applied in proximity to species lethal temperatures. The model assumes that the competition imposed on the focal species i , is (1) a function of the total plant biomass (conspecifics and heterospecifics) in the plot together with the susceptibility l_i of the focal species to biomass-related competition, and (2) a function of conspecifics biomass that accounts for the supplementary effect of intraspecific competition and is necessary to stabilize coexistence. The growth g_i is correlated to $T_{min,i}$, so that species growth is reduced for stress tolerant species (Grime 1977). The focal plant species in the community will be attacked by an herbivore compartment H , whose dynamic can be written with the following equation:

$$\frac{dH}{dt} = H \left[M e^{-E/kT} \times \sum_j a_j P_j - m \right]$$

in which the production of the herbivore population biomass depends on the metabolic rate parameter, the amount of plant resources available and plant resistance a_i together with a mortality term m . Metabolic rates increase exponentially with temperature (Brown *et al.* 2004). As a consequence, animals, particularly ectothermic insect herbivores, should display increased metabolic rate under warmer climates (Dillon, Wang & Huey 2010), translating

into higher feeding rates, and damages on plants (DeLucia *et al.* 2012). We modelled insect herbivore metabolism using the Van 't Hoff-Arrhenius relation (Arrhenius 1889). In our illustration, we fixed the values of $M_{\max} = 1$; $T_{1/2} = 2^{\circ}\text{C}$ and herbivore mortality rate to 0.1. In the Arrhenius equation, the Boltzmann's constant k specifies how temperature affects the rate of reaction by changing the proportion of molecules with sufficient kinetic energy (Brown *et al.* 2004). Since, we do not know the value of k , which might vary among insect groups (Chown *et al.* 2007; Irlich *et al.* 2009), we established the values of metabolic rate by defining k so that the temperature of half metabolic rate occurs at 2°C .

We drew randomly 3000 alpine plant species pools of 50 species each, with variable values of $T_{\min,i}$, l_i and a_i within intervals rescaled to $[0;1]$. We applied different ecological constraints on the correlation between the traits values: assuming (1) no trade-offs, (2) pairwise trade-offs (2.i) $T_{\min,i}$ negatively correlated to l_i ; (2.ii) l_i negatively correlated with a_i and (2.iii) $T_{\min,i}$ negatively correlated to a_i ; (3) l_i negatively correlated with $T_{\min,i}$ but positively correlated with a_i and (4) full trade-offs. We then estimated the biomass of each species at equilibrium by running the model simulations for each species pool until the community was stable. We first estimated the state of the community at a site of 1°C . We applied to this community a warming of $+3^{\circ}\text{C}$ to reach a new equilibrium and computed the compositional turnover using the Bray-Curtis dissimilarity index. As a control, we run the same simulations ignoring the effects of herbivory, i.e. fixing $H = 0$. We used an ordinary differential equation using the *ode* solver implemented in R (R Development Core Team 2016) to estimate biomass at equilibrium. Besides comparing changes in beta diversity between T_0 and T_f communities, we quantified species extinctions.

We found marked differences in the expected turnover under different trade-off structures, driven by shifts in species abundance and species extinctions (Figure 1). The median turnover was the lowest, when the species traits of temperature-dependent growth, competition and resistance to herbivory were not constrained by trade-offs (Figure 1). In this situation, where traits are drawn randomly across three functional dimensions, plant species could simultaneously benefit from a temperature-driven growth, while tolerating an increase in both competition and herbivory. In contrast, the median turnover was highest either when there was a trade-off between the susceptibility to herbivory and cold tolerance, and between the susceptibility to competition and susceptibility to herbivory together with cold tolerance. Under those ecological constraints, climate change should promote species turnover via a

combined effect of higher competition and herbivory, causing the replacement of species with low values of T_{min} unable to compete and tolerate high herbivory. Finally, when considering only the effect of plant competition without herbivory, both turnover and extinction were systematically lower except in the case of a trade-off between cold tolerance and competition. Together, the simulations indicated that the shape of the functional trade-off within plant communities modulates their response to climate change.

The model as implemented provided an informative illustration for predicting climate change impacts on communities, but presents nonetheless several limitations. First, we did not account for trait intraspecific variability, which can also influence species coexistence, by modifying competitive interactions (Turcotte & Levine 2016; Chalmandrier *et al.* 2017), and resistance to herbivory (Pellissier *et al.* 2014). Second, in our simplified model, we only considered a unique herbivore compartment, which responds homogeneously to climate change, but not any species-specific differences in plant feeding preferences of the herbivores. In a more complex system, the response of plant communities should depend on feeding preferences of specialist or generalist in present and future communities interacting with a trade-off between physical and chemical resistance (Lankau 2007). Moreover, the results largely depend on the relative effect of plant competition versus the impact of herbivory (e.g. plant tolerance) in the system. The highest levels of turnover were indeed found when resistance to herbivory is included in the trade-off. This was due to the expected cumulative effect of a direct impact of temperature on growth and competition, and an indirect one via the increase in herbivore pressure. However, in real systems, the effect of competition might overwhelm the effect of herbivory, but the relative strength of those factors on plant fitness remains to be quantified (Maron & Crone 2006).

Functional variation and trade-offs – a case study in the Swiss Alps

In the model presented above, we documented how the co-variation between traits related to abiotic-related growth, competition and resistance to herbivory shape plant community turnover under climate change. While several studies documented the functional diversity within plant communities (Table S1), we identified a lack of studies that quantified functional trade-offs within alpine communities, by integrating *(i)* temperature limitation, *(ii)* traits related to competition and *(iii)* resistance to herbivory. We used a dataset of functional traits of two alpine grasslands found in the Swiss Western Alps at 2070 and 2680m a.s.l. for documenting functional co-variation within plant communities. We quantified 11 traits

related to; (i) temperature dependant growth, which was expressed as the cold temperature niche limit of each species (Tmin, Pellissier *et al.* 2013), (ii) competition, including plant size (mean plant height rom the ground), leaf biomass (weight) and leaf area (LA) (iii) leaf economic spectrum, including leaf dry matter content (LDMC), specific leaf area (SLA) and (iv) physical and chemical resistance against herbivores, including leaf toughness, silica content (Si), nutrient content (carbon to nitrogen ratio C/N), and chemical content (number of individual compounds and Shannon chemical diversity indices obtained from a leaf metabolomics survey of all plant species studied (see methods' details in Appendix S1).

To detect the shape of multiple trade-offs, we first submitted the traits \times species populations matrix to a principal component analysis and then remove the variance among site to focus only on the within community variability using a Within-Class analysis (package ade4: Dray & Dufour 2007). Because we collected functional traits at two different sites (2070 and 2268 m a.s.l.), the Within-Class analysis allowed focusing on the functional variation among species within each site in a single analysis. Weight, LA, SLA, LDMC, C/N, leaf toughness, height were log-transformed to avoid distortions. We analysed the correlation of traits to the main axes of trait variance to establish the main functional trade-offs.

Plant species were structured along three main functional axes (Figure 2): (i) the first axis (30% of total variance) opposed species with a high LDMC (axis 1 score= -0.69), leaf toughness (-0.89), leaf silica content (-0.71) and high C/N ratio (-0.68) and high SLA (0.77); this represented an axis of leaf economics and physical defence to herbivore (Wright *et al.* 2004) opposing the taxonomic group of Poales (Figures 2a and 2c) to other clades, in particular Fabaceae; (ii) the second axis (15% of total variance) opposed species with large leaf area (axis 2 score= 0.68), and tall species (0.60) to species with high cold tolerance (0.48); this axis distinguished large species (e.g. Apiaceae) from small species (e.g. Gentianaceae); (iii) the third axis (14% of the total variance) distinguished tall species (axis 3 score=-0.46) from species with a high number (-0.71) and diversity (-0.58) of chemical components. The third axis particularly distinguished Dipsacaeae species and some Rosales species (e.g. *Potentilla* sp.). Together, these results indicate that alpine plant communities are composed of species investing in different functional strategies that co-vary with each other, possibly allowing coexistence (Kraft *et al.* 2015). Specifically, plant ecological strategies were structured along three main axes: i) the leaf economic spectrum opposed to plant

resistance to herbivore, ii) competitive abilities opposed to cold tolerance iii) competitive abilities opposed to species with higher chemical defences.

Discussion

The diversity of functional traits in communities may largely determine their response to climate change. In stressful environments, ecological filtering should impose strong functional trait homogenization (Mayfield, Boni & Ackerly 2009; de Bello *et al.* 2013; Pellissier *et al.* 2013; Kraft, Godoy & Levine 2015), therefore, reducing the variability of possible responses to climate change. Counter to these expectations, we observed that even under harsh climatic conditions, such as at higher elevations, functional divergences among within communities may persist. We suggest that equalizing mechanisms, mediated by trade-offs among the main fitness axes, could foster the maintenance of functional diversity, even in alpine communities (Spasojevic & Suding 2012; Dubuis *et al.* 2013) under processes including competition (Klanderud & Totland 2004; Cadotte & Tucker 2017), facilitation (Choler, Michalet & Callaway 2001; Callaway *et al.* 2002), or herbivory. This existing functional diversity in alpine plant communities will modulate species turnover under climate change, with or without new colonizers.

Our review of the literature indicates that the diversity of plant functional traits in alpine plant communities have been mainly documented along axes related to abiotic tolerance and competition (e.g. Callis-Duehl *et al.* 2017). The diversity of strategies does not necessarily decrease as would be expected under environmental filtering (Table S1). For instance, alpine plants might display various modes of reproduction (Klimešová *et al.* 2008), or different growth forms, for instance with a rhizome, small structure such as cushion forms, or simply a small size (Körner 2003). Moreover, traits related to interspecific competition, such as those associated to resource-use and nutrient uptake strategies (e.g. LDMC, SLA), can show substantial variation in alpine communities. For instance, Spasojevic & Suding (2012) documented only a weak decrease in the diversity of chlorophyll content along a climatic gradient, which suggests that niche differentiation in the canopy is still occurring in alpine communities. As regard to plant defences against biotic attack, despite an average increase in plant palatability with elevation (Descombes *et al.* 2016), some in alpine species may even display a higher constitutive defence level compared to their low-elevation congeneric counterparts (Rasman *et al.* 2014; Pellissier *et al.* 2016). Hence, some alpine species still

present high defence levels, which may make them pre-adapted to future increase in herbivore pressure under warmer temperatures (Pellissier *et al.* 2012). To summarize, environmental filtering above the tree line does not completely homogenise functional diversity within communities (Chalmandrier *et al.* 2017), implying that climate change will have significant variation to act upon.

According to our simulations, the structure of functional trade-offs among different fitness-related axes could constrain the response of plant communities to climate change. Species face the fundamental challenge to trade off investments into multiple functions (Roff & Fairbairn 2007; Agrawal, Conner & Rasmann 2010; Shoval *et al.* 2012). To survive, a plant must be able to germinate, grow and reproduce under specific abiotic conditions, compete for resources such as water or light, and tolerate attacks from herbivores and pathogens.

Moreover, functional trade-offs may include those between competition and stress tolerance (Savage & Cavender-Bares 2013), or between growth and defence (Züst, Rasmann & Agrawal 2015). Using simulations of 3°C warming, we showed that the shape of the functional trade-off determine the rate of community turnover. Under no trade-off constrains, where species performance in growth, competition and resistance to herbivory were randomly assigned, no specific trait combinations that could be favoured under warming conditions were observed. In contrast, under trade-off constraints, an increase in temperature and/or herbivore pressure favours better competitors and/or better-defended plants, which may outcompete the most stress-tolerant ones. Our results parallel empirical evidence showing that alpine communities are highly susceptible to lower elevation competitors (Alexander, Diez & Levine 2015), but also suggest that exclusion could also happen as a result of interaction changes in communities. Documenting the co-variation among traits related to growth, competition and resistance to herbivory is likely central for forecasting the consequences of global change on alpine plant communities.

Usually, functional traits related to herbivore resistance are rarely quantified, nor related to other plant functional traits (Agrawal & Fishbein 2006; Freschet *et al.* 2010; Laughlin 2014). Our analysis included a wide spectrum of plants traits along three main functional axes of climate tolerance, competition and herbivore tolerance. The first axis discriminated species according to species investing in the leaf economic spectrum (e.g. SLA) to tough species with the highest resistance to herbivory. Because SLA is associated to species competitive abilities (Kraft, Godoy & Levine 2015), this axis should relate to the competition-defence trade-off

(McGuire & Agrawal 2005). Along the second axis, we observed that the tallest species were also the ones less tolerant to cold temperatures. Plant species principally distributed in warmer conditions, and whose elevational range barely reaches the alpine belt, are also the most competitive (Alexander, Diez & Levine 2015). Finally, alpine plant species were further segregated along an axis of chemical diversity opposed to plant size. While our analysis of chemical properties remains superficial, as we do not discriminate between molecules that are known to hinder herbivory and other compounds that might be involved in other functions (e.g. mutualism or UV tolerance Rasmann *et al.* 2014), it corroborates the long-standing paradigm that predicts a negative correlation between growth and defences (Herms & Mattson 1992).

What to expect when the observed trade-offs are compared to the simulations? We showed that co-variation between functional trait exists within extant alpine plant communities. Tall competitive species were less tolerant to colder temperature, while those that have fast tissue regeneration were less physically defended against herbivores. In parallel, the simulations indicated that co-variation between temperature related growth and competitive abilities or herbivore tolerance can inflate community turnover under climate change. Hence, independently of the rate between future increase of competition relative to herbivory, we should expect a strong turnover of alpine plant communities under climate change, as long as among-traits trade-offs exists within specie and communities. However, the measured functional traits only represent proxies of competitive abilities (e.g. SLA, height, Kraft, Godoy & Levine 2015) or herbivore tolerance (e.g. toughness, Ibanez *et al.* 2013). In the future, the quantification of demographic traits of species sensitivity to both competitors and herbivores, should allow more confident inferences. Based on the present evidences, we expect that some alpine species will disproportionately benefit from climate change, which may reshape the structure of communities under increased competition and herbivory, even before the possible arrival of new competitors (Alexander, Diez & Levine 2015). Future in-depth analyses on the chemical composition of alpine plants are required to document the role of the independent axis of chemical diversity in species response to abiotic and biotic conditions.

Conclusion

Climate change could have a fast and lasting impact on the existing structure of alpine plant communities (Cannone, Sgorbati & Guglielmin 2007; Engler *et al.* 2011), but this depends on

the existing functional diversity and trait trade-offs. Despite the postulated strong environmental filtering at high elevation, we documented the maintenance of a relatively high level of functional divergence in alpine plant communities (Spasojevic & Suding 2012; Hulshof *et al.* 2013; Callis-Duehl *et al.* 2017). Such functional divergence is structured along correlated axes. Simulations suggest that plant species displaying increased growth under warmer climate, good competitive abilities and resistance to herbivory should increase their dominance in alpine communities and stimulate high species turnover rates. Nevertheless, in the future, studying demographic effects of traits is required to better anticipate how climate change will reshape the structure within alpine plant communities.

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Author's contribution: SR and LP initiated the project, LP, LC and OH performed the model simulations, SR, LP, PD, AK, and ED, collected and analysed the data, all authors wrote the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1. Summary table of functional trait variation along elevation

Appendix S1. Supplementary material and methods for trait sampling

Figure legends

Figure 1. Results of the Lotka-Volterra model. Example of species pool (each species is a black dot) drawn without ecological constraints among traits (a), with pairwise trade-offs (b-d) or with a full tri-partite trade-off (e) and a synergy between competition and resistance to herbivore (f). Expected turnover under simulated climate change considering different trade-offs situations considering or ignoring the effects of herbivory (left and right boxplots for each tradeoff simulation, i.e. *H* and *no H*). The median turnover is highest either when resistance is negatively correlated to cold tolerance, or when competitive ability is associated to resistance but in opposition to cold tolerance. A larger variance in turnover is observed under situations of full trade-off. Extinction is highest especially in cases where the community is composed of numerous species with cold-tolerance abilities, and therefore with low competitive abilities and resistance to herbivory.

Figure 2. Within-site principal Component Analysis. (PCA) analysis representation of major sources of variability among plant species based on the 11 functional traits measured. Panel a) represents the scores of species and traits along axes 1 and 2, while panel b) represent the scores of species and traits along axes 1 and 3. Species scores are coloured according to their affiliations to diverse or note-worthy plants clades found on the studied sites. LA = leaf area; Weight = dry aboveground biomass; Tmin = temperature limit; LDMC = leaf dry matter content; SLA = Leaf mass per area; Tough. = penetration force; Silica = amount of silica per mg dry tissue; C/N = carbon to nitrogen ratio; ChemNb = number of individual compound peaks obtained from the untargeted metabolomics analyses; and ChemDiv = the chemical diversity index based on the abundance of individual peaks per species.

Figures

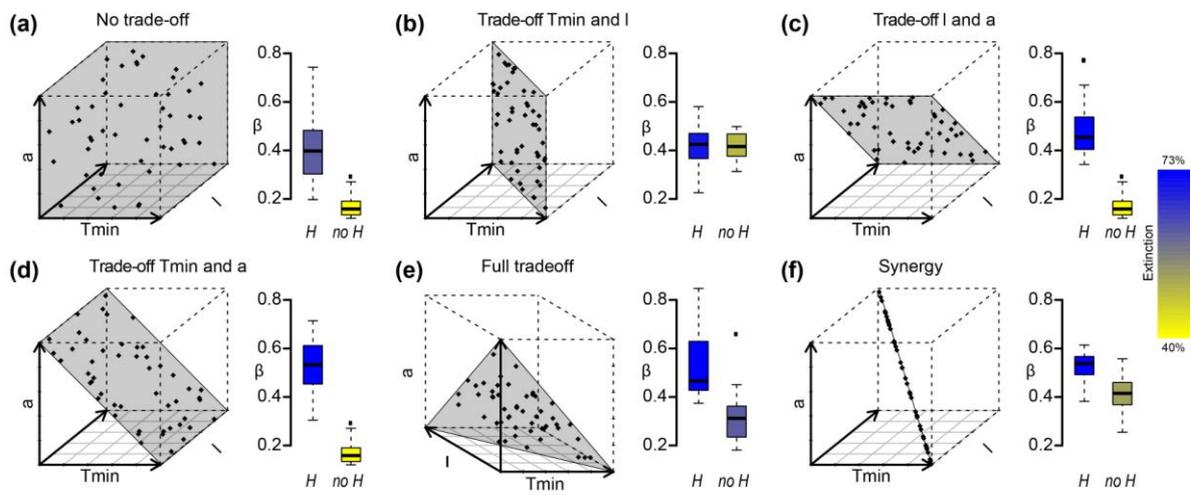


Figure 1

Figure 2

