OIKOS

Research article

Increases in functional diversity of mountain plant communities is mainly driven by species turnover under climate change

Max A. Schuchardt[1], Bernd J. Berauer[2], Anh Le Duc[1], Johannes Ingrisch[3], Yujie Niu[1], Michael Bahn[3] and Anke Jentsch[1]

[1]Department of Disturbance Ecology, Bayreuth Center of Ecology and Environmental Research, University of Bayreuth, Bayreuth, Germany
[2]Institute of Landscape and Plant Ecology, Department of Plant Ecology, University of Hohenheim, Germany
[3]Department of Ecology, University of Innsbruck, Innsbruck, Austria

Correspondence: Max A. Schuchardt (max.schuchardt@uni-bayreuth.de)

Oikos
2023: e09922
doi: 10.1111/oik.09922
Subject Editor: Bente J. Graae
Editor-in-Chief: Pedro Peres-Neto
Accepted 27 June 2023

Warming in mountain regions is projected to be three times faster than the global average. Pronounced climate change will likely lead to species reshuffling in mountain plant communities and consequently change ecosystem resilience and functioning. Yet, little is known about the role of inter- versus intraspecific changes of plant traits and their consequences for functional richness and evenness of mountain plant communities under climate change. We performed a downslope translocation experiment of intact plant-soil mesocosms from an alpine pasture and a subalpine grassland in the Swiss and Austrian Alps to simulate an abrupt shift in climate and removal of dispersal barriers. Translocated plant communities experienced warmer and dryer climatic conditions. We found a considerable shift from resource conservative to resource acquisitive leaf-economy in the two climate change scenarios. However, shifts in leaf-economy were mainly attributable to species turnover, namely colonization by novel lowland species with trait expressions for a wider range of resource use. We also found an increase in vegetative height of the warmed and drought-affected alpine plant community, while trait plasticity to warming and drought was limited to few graminoid species of the subalpine plant community. Our results highlight the contrast between the strong competitive potential of novel lowland species in quickly occupying available niche space and native species' lack of both the intraspecific trait variability and the plant functional trait expressions needed to increase functional richness under warming and drought. This is particularly important for the trailing range of many mountain species (i.e. subalpine zone) where upward moving lowland species are becoming more abundant and abiotic climate stressors are likely to become more frequent in the near future. Our study emphasizes mountain plant communities' vulnerability to novel climates and biotic interactions under climate change and highlights graminoid species as potential winners of a warmer and dryer future.

Keywords: alpine grassland, functional diversity, invasion, species turnover, traitspace, translocation

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Introduction

Mountain regions are known to warm three times faster than global average temperatures (Pepin et al. 2015, IPCC 2021). The highest deviations from global average occur during the winter and lead to an elongation of the growing season (Körner 2021). There is general agreement that mountain plant species 1) adapt to novel climates through intraspecific plasticity (Rixen et al. 2022), 2) track their optimal climatic niche to higher elevations (Steinbauer et al. 2018) or nearby 'escape-refugia' (Scherrer and Körner 2011, Körner and Hiltbrunner 2021) or 3) lag behind climatic changes due to a high rate of inertia and thus likely blur local extinction patterns (Dullinger et al. 2012, Alexander et al. 2018, Nomoto and Alexander 2021).

Observational studies in mountain regions have so far reported a lack of native species replacement by novel lowland species. Still, some observational studies in mountain plant communities have found a thermophilisation of species (Lamprecht et al. 2018, Steinbauer et al. 2020) or a reduction in range size and abundance of cold-adapted species (Rumpf et al. 2018, Steinbauer et al. 2022). In contrast, many experimental studies (Alexander et al. 2015, Meineri et al. 2020, Vandvik et al. 2020, Margreiter et al. 2021) suggest that competitive pressure on native mountain species is likely increasing under climate change due to novel plant-to-plant interactions affecting the biotic niche (Eltonian dimension (Elton 1926)). Increasing competition by novel lowland species in combination with native species loss will likely affect ecosystem structure and functioning. Moreover, plant growth in cold biomes is traditionally known to be restricted by temperature and growing season length, which results in low nitrogen (N) mineralization rates (Grogan and Chapin 2000, Huber et al. 2007) and N availability (Mayor et al. 2017). Such a narrow abiotic niche (Grinnellian dimension (Grinnell 1917)) mostly favors species with a rather resource conservative growth strategy (Körner 2021). However, mineralization rates are expected to increase under climate warming (Wang et al. 2016, Salazar et al. 2020). Warming in combination with the climate change-induced elongation of the growing season is likely increasing the abiotic niche of mountain ecosystems – when not restricted by water availability. Climate models predict that precipitation patterns in the European Alps will change along with climate warming (Mastrotheodoros et al. 2020, Böhnisch et al. 2021), especially in its seasonal distribution with an elevated risk of summer drought for many subalpine areas (Spinoni et al. 2018, IPCC 2021, Stephan et al. 2021). The likely increased drought risk for mountain regions is especially important as the effects of warming and drought have been found to be opposing (De Boeck et al. 2016, Volk et al. 2021). While warming alone generally releases mountain plant communities from abiotic limitations, drier conditions increase abiotic stress. Various studies have shown contradictory results from the interactive effect of warming and drought compared to warming alone. As an example, De Boeck et al. (2016), Berauer et al. (2019), Schuchardt et al. (2021) and Niu et al. (2023) found large die-backs of native species resulting from the synergistic impacts of warming and drought. In particular, De Boeck et al. (2016) found that heat spells combined with drought had strong effects on the aboveground productivity of alpine plant communities, while heat spells alone had no significant impact. A follow up study in the same experiment (De Boeck et al. 2018) found strong legacy effects of combined warming and drought in mountain grassland communities shifting community structure post-drought (Klanderud et al. 2015, Rosbakh et al. 2017, Collins et al. 2022a, Müller and Bahn 2022). Environmental filters, such as the drought imposed in the De Boeck et al. (2018) study, select individuals based on their responses and thus help shape community structures which have specific functional trait compositions (Keddy 1992, Lavorel and Garnier 2002).

Functional trait expressions are descriptive indicators of growth and resource use strategy of single plant species and the communities they assemble. The range of trait expressions, from acquisitive to conservative, observed within a plant community can thus be used as a description of niche space available to the species within it. Niche space will be affected by climate change mainly through the modification of resource availability and the arising shifts in competitive outcomes between species. Functional diversity is a valuable measure to quantify resource use complementarity and niche dynamics (Dehling and Stouffer 2018, Ceulemans et al. 2019). The impact of climate change on plant communities' functional diversity and the resulting changes in plant resource-use strategies remains poorly explored (Díaz et al. 2016, Carmona et al. 2021). This is especially true for cold biomes and mountain ecosystems (de Bello et al. 2013, Bjorkman et al. 2018, Thomas et al. 2020, Asplund et al. 2022, Rixen et al. 2022). Mountain plant communities' functional diversity may be low because of large-scale environmental filtering due to limited resource availability (e.g. short growing seasons) which leads to high functional evenness and trait convergence sensu de Bello et al. (2013). Such limited resource availability results in a conservative growth strategy (dominated by species with low specific leaf area (SLA), high leaf dry matter content (LDMC), and a small stature (Körner 2021)) with plant-to-plant interactions being more facilitative than competitive (Callaway et al. 2002, Körner 2021). On the other hand, climate warming may relieve mountain plant communities from limited resource availability, thus expanding available abiotic niche space (Rumpf et al. 2018, Hagedorn et al. 2019). An abiotic niche space expansion will likely cause niche filling through 1) intraspecific plasticity of native species (single species niche divergence) as a consequence of limitation-relief (Bolnick et al. 2011, Rixen et al. 2022) or 2) novel lowland species filling up unoccupied niche space bringing novel trait expressions (Alexander et al. 2015, Munson and Sher 2015, Nomoto and Alexander 2021) – both processes increase functional diversity (Zanzottera et al. 2020).

High functional diversity – that is, greater variation in resource use than species diversity (Craven et al. 2016) – has been shown to enhance ecosystem functions such as productivity (Tilman et al. 1997, Díaz and Cabido 2001, Hooper et al. 2005, Chanteloup and Bonis 2013, Brun et al. 2019) and the stability of productivity through time (Polley et al. 2013, Craven et al. 2016). Furthermore, increased functional diversity was found to enhance resilience to disturbances like droughts (Hallett et al. 2017, Craven et al. 2018) or resilience to colonization by novel species (Dukes 2001, Cavieres 2021). The three key measures to assess functional diversity are: 1) functional richness – the spread of trait values across species within a plant community (occupied trait space); 2) functional evenness – the degree to which species biomass is distributed in the niche space and 3) functional divergence – the abundance-weighted, species-specific distance from the center of gravity (the mean of all species) in the functional space indicating the degree of resource use differentiation across species (Villéger et al. 2008, Mouillot et al. 2013). So far, little is known about how climate change in mountain regions will alter these measures of functional diversity and their underlying ecological processes. As an example, intraspecific trait variation (ITV) was found greater in species with large range sizes and lower median elevations (Rixen et al. 2022). High ITV likely leads to an increased capability to respond to climate warming (Jónsdóttir et al. 2022). In contrast, small ranged species are expected to suffer from climatic changes as their ability to track climate change is limited through low ITV. The general uncertainty how single species perform in future communities is complicated by the upslope shift of novel lowland species, which bring novel functional trait expressions into mountain communities and may render any trait plasticity of the native species negligible, as well as the interacting, sometimes antagonistic, effects of the expected changes in temperature, water availability, and length of growing season with climate change.

Mountain plant communities with low functional richness, high functional evenness, and low functional divergence are likely more vulnerable to climate change, as buffering of extremes (through trait complementarity) is limited and unoccupied trait space may be available for competing colonizers (Dukes 2001, Vetter et al. 2018, Haider et al. 2022). In a study across 117 vegetation surveys, Bjorkman et al. (2018) found that temperature-driven changes in plant trait expressions were generally strong across the tundra and alpine biome with soil moisture being direction-decisive. Further, this study found a biome-wide increase in vegetative height, decreases in LDMC, and increases in leaf nitrogen and SLA, mainly because of species turnover due to colonization of available niche space by novel species. These shifts from rather resource conservative towards more resource acquisitive trait expressions under climate change are supported by leaf economic theory (Wright et al. 2004, Reich 2014) and by findings from Read et al. (2014), van Zuijlen et al. (2021) and Stanisci et al. (2020), with the latter two additionally highlighting the importance of local soil moisture.

To test the interactive effect of warming and drought on shifts in mountain species trait expressions, the role of novel species in filling unoccupied trait niches, and their implications on functional diversity, we have translocated plant-soil mesocosms from the European Alps downslope to a warmer and drier climate. The translocation of plant communities outside their maternal environments creates an experimentally abrupt shift in climate conditions, simultaneously manipulating temperature and precipitation, and removes dispersal barriers. This approach combines future abiotic stressors and novel biotic interactions for many mountain species at the trailing edges of their range where both climate change and novel competitive outcomes are expected to be the most severe. After five years of exposure to the novel climate, we measured the traits of 1551 leaves of all present species to elucidate dynamics in resource-use strategy via functional richness, evenness, and divergence. In situ measured traits are a valuable asset to account for intraspecific trait variation, which is often ignored when using data-base derived trait means across various study sites and habitats with different life histories (Albert et al. 2011, Bolnick et al. 2011). Our study addresses three questions: 1) how will community biomass and species-specific trait expressions respond to the net effect of interacting warming and drought? 2) to what degree are observed shifts in trait expressions driven by intraspecific trait variation of native species and by turnover and the arrival of novel lowland species? 3) how will functional richness, functional evenness and functional divergence respond to the net effect of interacting warming and drought?

Material and methods

Experimental setup

In the spring of 2016, 36 intact plant-soil mesocosms were extracted from two experimental sites for downslope translocation (for detailed methods see Berauer et al. 2019). Plant communities from the high elevation site Furka (2440 m a.s.l.; Switzerland) represent alpine pasture vegetation (*Caricetum curvulae*; dominated by perennial species) (Hefel and Stöcklin 2010), while communities from the subalpine site Stubai (1850 m a.s.l.; Austria) belong to an extensively managed, semi natural subalpine grassland (*Trisetum flavescentis*; dominated by perennial species) (Bahn et al. 2009, Ingrisch et al. 2018). At the high and mid elevation site, one set of mesocosms (n = 9) was reburied as a climatic control, while another set of mesocosms (n = 9) was translocated downslope to Bayreuth (350 m a.s.l.; Germany), a typical lowland semi-natural grassland community *Arrhenatheretum elatioris* which provides the novel matrix community for warmed plant communities (Fig. 1). Plant-soil communities were 30 cm in diameter and 25 cm in depth, representing a volume shown to be sufficient to study community responses and interactions in small statured grasslands (Milbau et al. 2007) while maintaining belowground processes. Each experimental site was fenced to avoid grazing. Aboveground biomass (AGB) was harvested yearly at peak biomass.

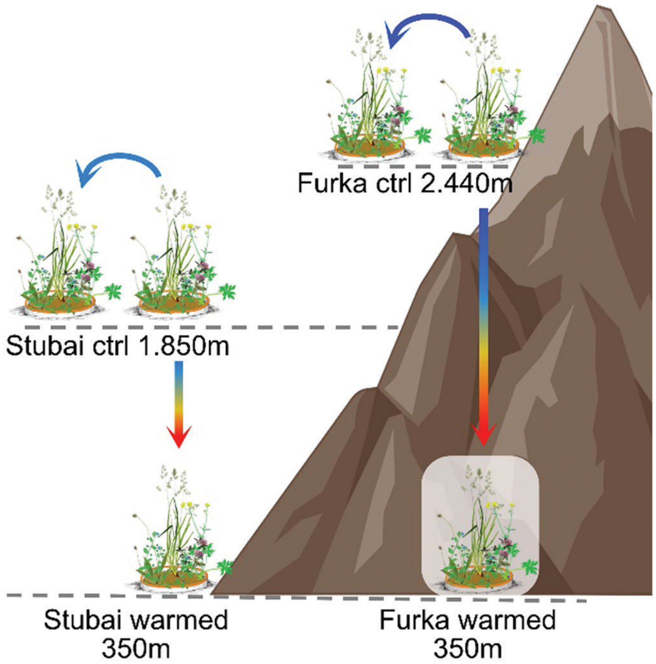

Figure 1. Experimental setup. Two mountain plant communities originating from different elevations (alpine Furka and subalpine Stubai) were reburied at site of origin as climatic control (blue arrows) and translocated downslope to Bayreuth (350 m) to simulate climate change (red arrows). Each translocation direction was replicated nine times.

Climatic parameters

The translocation scenarios represent changes of various climatic parameters such as mean annual temperature (MAT), mean annual precipitation (MAP), growing season air temperature, growing season precipitation, and growing degree days (GDD). All parameters were derived from on-site climate stations at 2 m as these represent the longest continuous time series of available climatic data but note the atmospheric decoupling described in Körner and Hiltbrunner (2018). Soil moisture was derived from horizontally installed soil moisture sensors (EcH2O 5-TM, Decagon Devices Inc., USA; EcH2O Em50, Decagon Devices Inc., USA) at −5 cm in one mesocosms at each respective experimental site (Supporting information).

Both climate change scenarios presented here are quantified as the deviation of growing season temperature at the climatic control site of origin and the recipient lowland site. Plant communities translocated from Furka to Bayreuth ($\text{Furka}_{\text{warm}}$) were exposed to a warming treatment of + 4.4°C and communities translocated from Stubai to Bayreuth ($\text{Stubai}_{\text{warm}}$) to a warming of + 3.3°C (Table 1). Five-year mean growing season precipitation was 181 mm at Furka, 397 mm at Stubai, and 166 mm at Bayreuth (note that growing season length is shorter at Furka and Stubai compared to Bayreuth; Supporting information). The number of growing degree days during the growing season increased by a factor of 4.2 for $\text{Furka}_{\text{warm}}$ and by a factor 1.4 for $\text{Stubai}_{\text{warm}}$. The start of the growing season was defined as the fifth day of five consecutive days with a mean daily air temperature higher than 5.0°C. This early season temperature threshold has been shown to primarily drive the green-up of grassland species (Scherrer and Körner 2010, Guo et al. 2018). In this study, the end of growing season was defined by the day of biomass harvest varying across sites.

Aboveground biomass

AGB of individual mesocosms was harvested in 2020, 3 cm above ground, at site-specific peak biomass (from low to high elevation sites: 29 June, 20 July, and 1 August) directly after trait measurements. AGB was sorted to species, dried at 60°C to constant weight (> 48 h) and weighed (Berauer et al. 2019, Halbritter et al. 2020). Each species was assigned a treatment level resident status ('native' or 'novel') based on whether the species occurred within any experimental mesocosm of the same origin in the year of experimental setup (2016). We defined all species present in 2016 across the 18 mesocosms per site of origin as 'native' to the respective

Table 1. Geographic and climatic characteristics of study sites from low to high elevation. Total values are calculated for the period of experimental exposure (2016–2020). Growing season start defined as the fifth day of five consecutive days with a mean daily air temperature at 2 m ≥ 5°C and end of growing season as the day of biomass harvest. Data shown was calculated from on-site weather station data. For details on the annual precipitation regime and soil moisture in mesocosms see the Supporting information.

			Experimental site (country)		
			Bayreuth (D)	Stubai (A)	Furka (CH)
Geography	Elevational belt		Colline	Subalpine	Alpine
	Coordinates		49°55′16″N 11°34′55″E	47°07′44″N 11°18′19″E	46°34′36″N 08°25′17″E
	Elevation (m a.s.l.)		350	1850	2440
Climate	Long-term mean	MAT (°C)	8.2	3.0	-0.5
		MAP (mm)	724	1097	1600
	$\bar{x}$ Growing degree days (heat sum)	Total	2155	1344	403
		Growing season	885	623	210
	$\bar{x}$ Temperature (°C) exposure	MAT	9.58	6.94	0.35
		Growing season	13.2	9.87	8.8
	$\bar{x}$ Precipitation (mm) exposure	MAP	608	1031	1096
		Growing season	166	397	181

community. In three cases (*Geranium sylvaticum*, *Gentiana punctata* and *Sibbaldia procumbens*) community native species were assigned as 'novel'. We made these decisions using local expert knowledge and adjusted the species status accordingly (e.g. perennial species first seen in the second year of experiment due to low AGB in the year of setup as a result of the disturbance by the translocation itself). All species names were checked according to the Global Biodiversity Information Facility (GBIF 2021). We excluded biomass that we could not assign to a species (e.g. a single senesced leaf) but these cases were extremely rare and AGB amounts negligible (< 0.001 g).

Plant functional trait measurements

Following the handbook of Pérez-Harguindeguy et al. (2013), we sampled 3–5 leaves from 1–3 individuals (limited by the amount of available individuals per replicate) per species for each mesocosm (replicate) in summer 2020, for a total of 1551 leaf-samples across two climatic control communities and two warmed and drought-affected communities with each treatment replicated nine times. Fresh leaves were scanned (Portable Area Meter LI-3000C), stored in moist and cooled conditions until processing, and weighed within 48 h of sampling. We collected dry weight of single leaves after a minimum of 48 h at 60°C in the drying oven. Additionally, vegetative height (not lifted, excluding inflorescence) was measured for each individual where leaf-samples were taken.

Data analyses

Single traits across treatments

To calculate shifts in SLA and LDMC between climatic control and climate change scenarios, we collected a total of 1551 leaf-samples at an individual level (up to three individuals per species and mesocosm). Additionally, we measured vegetative height at an individual level. To test overall trait expression shifts across all species between treatments, we used linear mixed effect models with the respective trait value as response variable, treatment as fixed effect, and mesocosm-ID, individual, and species as random effects. In a separate model, we split the fixed effect 'treatment' into the three levels, 'native ctrl', 'native warmed' and 'novel warmed', to test the effect of 'resident status' on plant communities in the climate change scenarios. Next, we conducted a post hoc Tukey HSD to compare respective trait values of plants in the climate change scenario (levels: 'native warmed' and 'novel warmed') to trait values of the native community (level: 'native control') at site of origin.

We did not measure individual specific AGB but sorted biomass on a species level per mesocosm. To meet lme-model assumptions, we transformed AGB values of both sites of origin using 'Tukey's Ladder of Powers' in the *transformTukey()* function (Mangiafico 2022). For AGB we used the same lme-model structure and Tukey HSD post hoc test as for the other traits but used only mesocosm-ID and species as random effects.

To explore species-specific shifts in trait values (ITV) of native species in the climate change scenarios compared to native species remaining at the respective climatic control site, we used the same linear mixed effect model structure as above but ran single models for selected species. In all models, we analyzed both sites of origin separately as they consisted of two (ecological and botanical) different mountain plant communities (alpine versus subalpine).

Functional diversity analysis

To examine the functional diversity of mountain plant communities, we averaged the following three traits: vegetative height as well as LDMC and SLA. First, we averaged the respective trait values to the level of an individual (mean out of 2–5 leaves). Second, we averaged trait values to the level of a mesocosm (mean out of up to three individuals) and third to a treatment level (mean out of nine mesocosms for each respective experimental treatment). We did not measure specific AGB for individuals, but sorted biomass on a species level per mesocosm. Thus, we used averaged species-specific AGB out of nine mesocosms in each experimental treatment.

To examine if individual plant species shifted their functional diversity, measured by their growth form (stature and leaf-economics), upon translocation, we used the 'mFD' package (Magneville et al. 2022) to both calculate and evaluate functional spaces of single experimental treatments. We used Euclidean distances to calculate trait-based distances between single species. In this step, all four traits were equally weighted. We found the minimum mean absolute deviation (mad = 0.015) between the trait-based distances and the space-based distance in a three-dimensional space (Supporting information) with no negative eigenvalues (Maire et al. 2015). Thus, presented indices are computed in a 3D space. Next, we correlated the PCoA (Principal coordinates analysis) axis with underlying traits using linear regression models of the *mFD::traits.faxes.cor()* function (Supporting information). Further, we calculated the three fundamental functional diversity indices: functional richness, functional divergence and functional evenness (Mason et al. 2005, Villéger et al. 2008) using the *mFD::alpha.fd.multidim()* function. Here, functional richness was defined as the volume of the convex hull shaped by the species of single treatments (i.e. the filled functional space). Thus, functional richness increases as a function of a community's trait value variability values as a result of species' trait expression. Functional evenness was defined as the regularity of species abundance distribution in the functional space using the minimum spanning tree (MST) method linking all species present in a treatment. Thus, functional evenness decreases if vertex species (species with extreme trait values) are widely spread throughout functional space, indicating a wide range of resource use strategies. Functional divergence was defined as the abundance-weighted species-specific distance from the center of gravity (mean of all species) in the functional space (Villéger et al. 2008). For instance, if the most abundant species are vertex species (with extreme trait values), functional divergence and consequently niche differentiation is high.

All data analyses were performed within the R programming environment (ver. 4.2.1, www.r-project.org).

Results

Community trait responses and native species loss

Compared to their climatic control sites, we found no effect for AGB but increases in vegetative height ($p < 0.001$), decreases in LDMC ($p = 0.02$), and increases in SLA ($p < 0.001$) across all warmed and drought-affected species and replicates in the alpine plant community originating from Furka. The observed shifts in vegetative height, LDMC and SLA for the warmed and drought-affected alpine plant community were mainly driven by novel species (species not present in the initial plant community). We found increases in native and novel species' vegetative height ($p_{native} < 0.001$; $p_{novel} < 0.001$), decreases in novel species LDMC ($p_{native} = ns$; $p_{novel} < 0.01$) and increases in novel species SLA ($p_{native} = ns$; $p_{novel} < 0.001$) for the warmed and drought-affected alpine plant community compared to native species at the climatic control site (Fig. 2A).

Compared to their climatic control site, we found no effect of warming and drought on community AGB, vegetative height, LDMC, or SLA across all species and replicates in the subalpine plant community originating from Stubai (note some different species-specific responses in Fig. 4). Nevertheless, we detected leaf-trait expression differences between the group of novel species growing under the

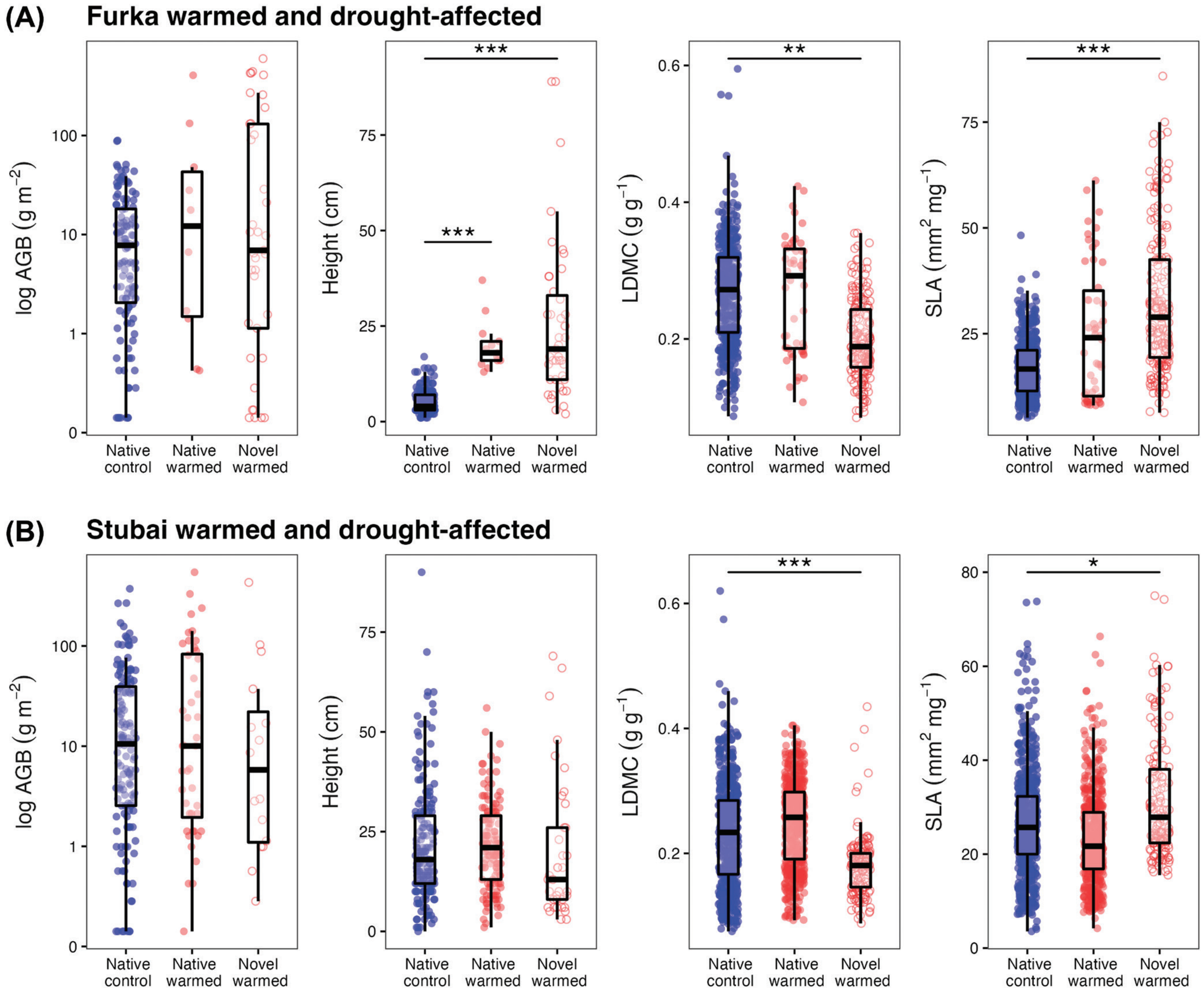

Figure 2. Plant functional trait responses between two climate change scenarios and their respective climatic control site. Shown are individual specific trait values across nine mesocosms per climatic treatment (1150 individual leaves in total). (A) Trait responses of the alpine plant community originating from Furka experiencing a + 4.4°C growing season temperature increase and (B) trait responses of the subalpine plant community originating from Stubai experiencing a + 3.3°C growing season temperature increase. Asterisks indicate significant trait shifts compared to native species at control site ($p < 0.05$*; $p < 0.01$**; $p < 0.001$***). Note different axis scales across panels.

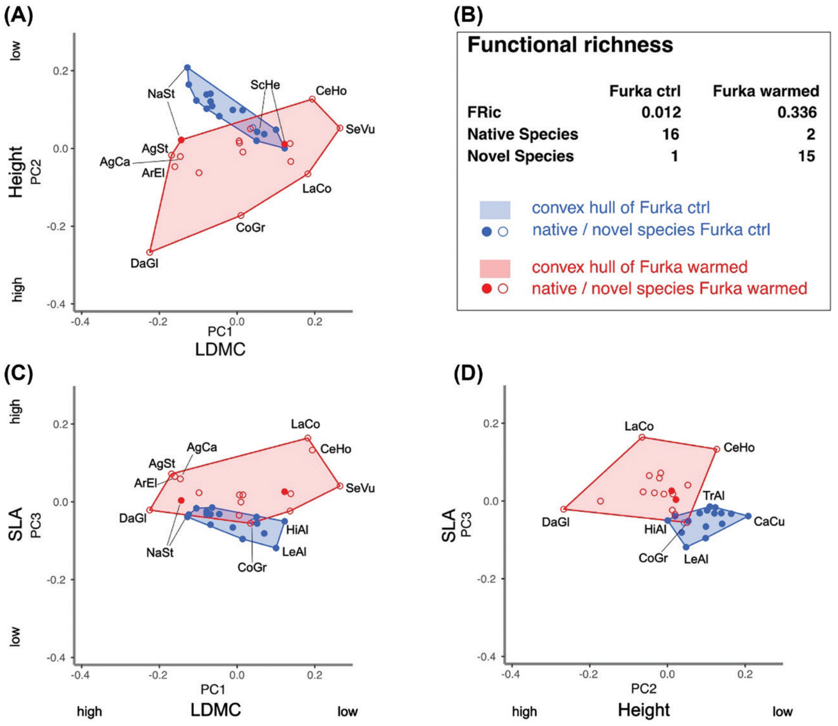

Figure 3. Effect of warming and drought on the functional richness (FRic) of the alpine plant community. FRic (defined as the convex hull volume) in the climatic ctrl (blue) and in the climate change scenario (red). Compared to the climatic control site, functional richness increased as species present in the warmed plant community showed a higher variability in vegetative height, aboveground biomass, LDMC and SLA (wide range from minimum to maximum expanding the volume of the occupied trait space). Indices were computed in a three-dimensional space. Filled dots and circles indicate if a species was native or novel to the initial plant community. Species abbreviation only of selected species (Supporting information).

climate change scenario and the native species growing at the subalpine control site. For novel species in the warmed and drought-affected subalpine plant community, we found significant decreases in LDMC ($p_{native} = ns$; $p_{novel} < 0.001$) and increases in SLA ($p_{native} = ns$; $p_{novel} = 0.03$) compared to native species growing at the site of origin (Fig. 2B).

Across all replicates originating from the alpine community Furka, we found strong species turnover (loss of native species and colonization of novel species) with 16 native and one novel species at $Furka_{ctrl}$ and two native and 15 novel species at $Furka_{warm}$ (Fig. 3B). For the subalpine community from Stubai, we found 20 native species at $Stubai_{ctrl}$ and 10 native and eight novel species at $Stubai_{warm}$ (Fig. 4B).

Functional richness

For both climate change scenarios of the two mountain plant communities, we found an increase in functional richness compared to their respective climatic control site. Occupied trait space (i.e. functional richness) expanded under warming as previously unoccupied niche space was colonized by mainly novel vertex species (note symbol shape depending on resident status in Fig. 3, 4).

Furka warmed and drought-affected

Functional richness increased by 28-fold (Fig 3B) in $Furka_{warm}$ compared to $Furka_{ctrl}$, indicating the use of unoccupied niche space in the climate change scenario. Compared to $Furka_{ctrl}$, functional richness increased as species present in the translocated plant community showed a higher variability in vegetative height, aboveground biomass, LDMC, and SLA (a wide range from minimum to maximum expands the volume of the occupied trait space).

This is supported by strong species turnover and replacement of native species by novel species ($n_{native} = 2$ in 2020; *Nardus stricta* and *Scorzoneroides helvetica* while $n_{novel} = 15$). Functional richness increased mainly through the expansion of occupied trait space due to the increase in the community's vegetative height and AGB (mainly explained by PC 2; Supporting information) driven by novel vertex species (Fig. 2A, 3A). Novel fast-growing species like *Senecio vulgaris*, *Cerastium holosteoides* and *Lapsana communis* occupied the trait space of low LDMC (mainly explained by PC1; Supporting information) while novel graminoid species like *Agrostis stolonifera*, *Agrostis capillaris*, *Arrhenatherum elatius* and *Dactylis glomerata* occupied the trait space of high LDMC, indicating rather resource conservative growth (Fig. 3C). Both native species persisting until the end of the experiment, *Nardus stricta* and *Scorzoneroides helvetica*, increased their vegetative heights ($p_{NarStr} = 0.002$; $p_{ScoHel} < 0.001$) showing trait plasticity under warming and drought. SLA of *Scorzoneroides helvetica* increased ($p = 0.04$) while *Nardus stricta* remained

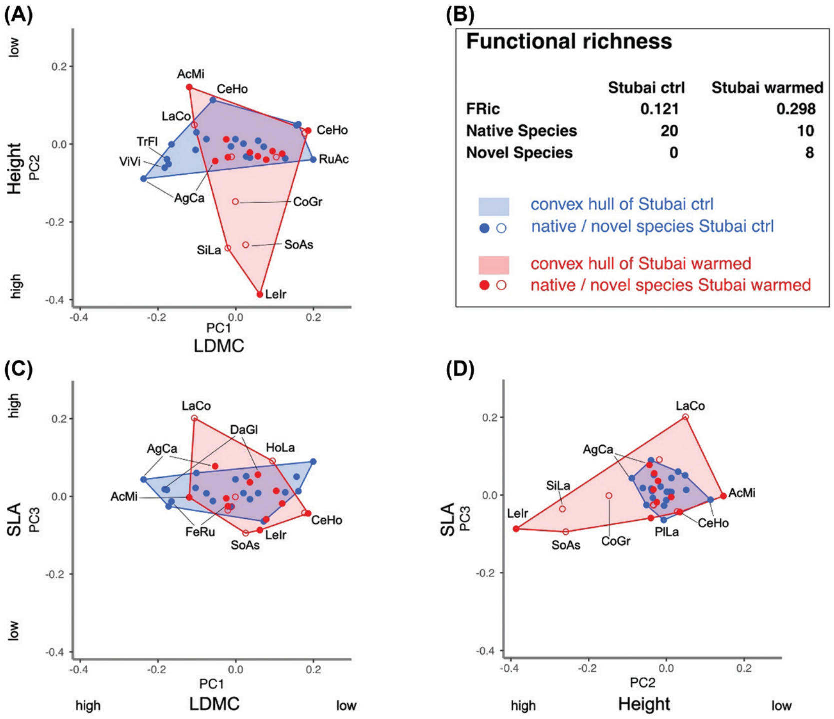

Figure 4. Effect of warming and drought on the functional richness (FRic) of the subalpine plant community. FRic (defined as the convex hull volume) in the climatic ctrl (blue) and in the climate change scenario (red). FRic increased as species present in the warmed plant community mainly showed a higher variability in vegetative height and aboveground biomass (indicated by PC2) compared to the plant community remaining at the climatic control site. Indices were computed in a three-dimensional space. Filled dots and circles indicate if a species was native or novel to the initial plant community. Species abbreviation only of selected species (Supporting information).

resource conservative, with high LDMC and low SLA level in Furka$_{warm}$.

Stubai warmed and drought-affected

We found a 2.5-fold increase in functional richness in the Stubai$_{warm}$ treatment with eight out of 18 species being novel species (Fig 4B). Functional richness mainly increased due to the vegetative height of the two novel species, *Sonchus asper* and *Silene latifolia*, and the native species *Leucanthemum ircutianum* (three minimum vertices of PC2) and *Achillea millefolium* (the maximum vertex of PC2; Fig. 4A). The increase in functional richness can be explained by two novel species (*Sonchus asper* and *Lapsana communis*) occupying the opposite extremes of PC3 (mainly displaying SLA Fig. 4C). These species increase the convex hull volume of Stubai$_{warm}$, but not the mean community SLA across all warmed and drought-affected species, rather driving the significant increase in SLA between the groups 'native control' and 'novel warmed' (Fig. 2B). We found a strong decrease in LDMC for the traditionally resource conservative graminoids surviving through the end of the experiment (*Agrostis capillaris* $p < 0.001$; *Dactylis glomerata*, $p < 0.01$; *Festuca rubra*, $p < 0.001$) in Stubai$_{warm}$ compared to Stubai$_{ctrl}$. This indicates niche divergence towards a more opportunistic, resource acquisitive, and thus rapid growth in the climate change scenario through trait plasticity of these three species. Importantly, the two other species originally occupying the resource conservative space of high LDMC at Stubai$_{ctrl}$ (*Vicia villosa* and *Trisetum flavescens*) were no longer present in Stubai$_{warm}$ at the end of the experiment.

Functional evenness

Both mountain plant communities experiencing climate change decreased their functional evenness compared to their respective climatic control site. Minimum spanning tree (mst) values increased in both climate change scenarios, with increased numbers indicating complementary resource use strategies across species (Furka$_{warm}$ versus Furka$_{ctrl}$ = 0.55-fold increase; Stubai$_{warm}$ versus Stubai$_{ctrl}$ = 0.74-fold increase; Table 2, Supporting information). Branch length of the 'minimum spanning tree' in the Furka$_{warm}$ treatment was mainly elongated, indicating a decrease in functional evenness, by one native species *Cerastium holosteoides* and the novel

Table 2. Functional diversity measures and species numbers of climatic control and respective climate change scenarios. Calculated values are based on mesocosm average trait values and are shown in Supporting information in more detail.

	Stubai ctrl	Stubai warmed	Furka ctrl	Furka warmed
Functional evenness	0.603	0.444	0.711	0.393
Functional divergence	0.881	0.767	0.774	0.916
Native species number	20	10	16	2
Novel species number	0	8	1	15

vertex species *Senecio vulgaris*, *Lapsana communis*, *Collomia grandiflora* and *Dactylis glomerata* (Supporting information). Branch length of the 'minimum spanning tree' in the Stubai$_{\mathrm{warm}}$ treatment was mainly elongated by the native forb *Leucanthemum ircutianum* and the two novel, tall growing vertex species *Sonchus asper* and *Silene latifolia* in addition to *Lapsana communis* as a novel small statured vertex species of PC2 (Supporting information).

Functional divergence

Plant communities at both the climatic control sites and climate change scenarios showed high values of functional divergence (Table 2, Supporting information) indicating a high degree of niche differentiation and thus low resource competition. This is likely because both frequent and rare species (size of points indicates abundance) are found to be vertex species in the trait space. We found small but contrasting differences in functional divergence between the two mountain plant communities under climate change and their climatic control. Functional divergence increased slightly by a 1.18-fold in Furka$_{\mathrm{warm}}$ and decreased slightly by a 0.87-fold in Stubai$_{\mathrm{warm}}$. In Furka$_{\mathrm{warm}}$, functional divergence tended to increase as vertex species with high abundance were found further away from the center of gravity (mean of all species), indicating a higher degree of niche differentiation with climate change. In Stubai$_{\mathrm{warm}}$, functional divergence tended to decrease as species with high abundance were located closer to the center of gravity compared to Stubai$_{\mathrm{ctrl}}$, indicating a tendency of niche convergence with climate change.

Discussion

Species adaptation to novel climates and novel species colonization are key components affecting plant community functional diversity, and thus functioning, under climate change. In a translocation experiment, we found consistent leaf-trait responses across two climate change scenarios using two different grassland types (alpine and subalpine). Leaf-trait expressions shifted from more resource conservative to resource acquisitive growth for both the alpine and the subalpine plant community. This was mainly driven by the appearance of novel species in the climate change scenarios and was rarely attributable to a plastic shift in resource use of native species. The assumed underlying mechanism, the experimentally induced extreme shift in climate conditions, favored the colonization of novel lowland species since native species seemed to lack trait expressions (e.g. big fast-growing leaves or high stature) suitable for quickly occupying niche space freed by the climate change scenarios. Novel species colonization drove patterns of three main functional diversity measures. After extreme climate change, we observed 1) a strong increase in functional richness – likely due to the (temporary) co-existence of community native and novel lowland species expanding occupied trait space, 2) a decrease in functional evenness – due to increased interspecific resource use complementarity and 3) varying responses of functional divergence depending on the degree of niche differentiation among species.

Native species loss and trait responses

In contrast to findings by Cui et al. (2018), Volk et al. (2021) and Haider et al. (2022), we did not find shifts in aboveground biomass following climate change. The previously mentioned studies found that increases in aboveground productivity were correlated with increases in temperature and peaked at sites with medium temperature increases and no water limitation. These insights highlight the adaptation of mountain species to high daytime canopy temperatures and the often-ignored atmospheric decoupling of air and tissue temperature (sensu Körner and Hiltbrunner 2018). While most mountain species can translate higher temperatures into increased AGB, our study reveals that the net-effect of warming and drought did not lead to changes in AGB. This finding is circumstantial – only fifth year AGB data consisting of surviving native and novel species is presented. We assume that previously lost native species experienced a decrease in abundance over time, highlighting the vulnerability of many mountain species to severe climate change. This pattern is supported by Steinbauer et al. (2020) that found decreases in cold adapted species cover and richness on mountain tops. The strong species turnover and native species loss found in our experiment align to the tendency of strong changes in abiotic conditions, namely the interaction of warming and drought, to drive species loss (De Boeck et al. 2016). Previous studies in our experimental setup have found very large diebacks of community native species (Berauer et al. 2019) and strong colonization by novel species with replacements becoming stronger with increasing climatic distance to the site of origin and time (Schuchardt et al. 2023a). In a common garden experiment, Haider et al. (2022) found that survival and flowering probability of the invasive forb *Senecio inaequidens* decreased with increasing climatic distance to the source population. Their finding is similar to Cui et al. (2018) who report mortality rates of 90–100% of the study species *Viola biflora* upon translocation outside the present species range. Consistent with the extensive literature highlighting native species loss following climate change, the severe climatic changes in our study led to the gradual loss of native species through time with novel lowland species propagule presence in the matrix accelerating the colonization by novel species. This is especially important as novel species dominated the shift in leaf-trait expressions towards a more resource acquisitive trait expression in the year of trait measurements (the end of the experiment).

Leaf-trait expressions shifted from rather resource conservative at control sites towards resource acquisitive in the two climate change scenarios. While this pattern was significant for all species present in the warmed and drought-affected alpine plant community (including the two native species), these shifts were only significant for novel species colonizing the warmed and drought-affected subalpine plant community as the surviving native species (n = 10) did not show a plastic response. The increases in SLA and decreases in LDMC we observed under warmed and drought-affected climate conditions are consistent with findings from various studies focusing on warming alone. As an example leaf economic theory (Wright et al. 2004, Reich 2014) suggests that leaf-economy shifts towards a more resource acquisitive growth under warming. This pattern has been observed in a cold-biome wide meta studies (Bjorkman et al. 2018), various field studies (Stanisci et al. 2020, Rixen et al. 2022) and experiments (Meineri et al. 2020, van Zuijlen et al. 2021). Our findings, combined with the consistency of previous studies in finding strong shifts in trait expressions due to species turnover under warming, highlight three important insights: 1) the lack in many mountain plant species of trait expressions that would increase colonization resistance under climate change (i.e. big and fast growing leaves or high seed output to occupy free niche space), 2) novel species bring along novel trait expressions which offer competitive advantages over native trait expressions (e.g. bigger and faster growing leaves) and 3) for many mountain species, intraspecific trait variation to adapt to novel climates is limited or overshadowed when novel species are present. Our observed shifts in intraspecific trait values were limited to a few graminoid species in the subalpine plant community and the two surviving native species in the alpine plant community (*Nardus stricta* and *Scorzoneroides helvetica*) with all trait expressions converging towards the novel matrix community (i.e. growing more resource acquisitive).

Furthermore, we found no significant increase in vegetative height for plant communities originating from the subalpine grassland Stubai when translocated downslope. Here, the lack of shifts in vegetative height for native and novel species was likely due to the absence of a dense plant community matrix at the warming and drought-affected site, reducing the need to grow vertically when AGB could spread horizontally. Contrary to the pattern in the subalpine plant communities, we found an increase in vegetative height for both native and novel species in the alpine communities. While the latter is not surprising, the increase in vegetative height of the two surviving species may point towards intraspecific trait variation as an underlying mechanism for survival under climate change (Henn et al. 2018, Rixen et al. 2022).

Functional diversity responses upon abrupt climate change

Theory (stress-gradient hypothesis sensu Bertness and Callaway (1994) and Maestre et al. (2009) and) states that interspecific competition decreases with elevation and plant-to-plant interactions become facilitative rather than competitive in alpine plant communities (Callaway et al. 2002). Thus, we expected low functional richness at both climatic control sites (as most community members share similar trait expressions) and an increase in functional richness with climate change (Harpole and Tilman 2007). We found a strong increase in functional richness in both climate change scenarios with the stronger effect for the translocated alpine plant community indicating that mainly warming and species turnover was driving the pattern as the effect of drought would have selected species with rather resource conservative trait expressions (Reich 2014). The underlying mechanism of the observed shift towards more resource acquisitive trait expression under warming and drought was mainly attributable to the (temporary) co-existence of species from different environments (the alpine or subalpine in addition to lowland), which used an overall wider range of resources (i.e. expressed as functional richness or niche space). Mountain communities are known to be more susceptible to colonization under changed climatic conditions, especially after soil disturbances (Haider et al. 2022), as they lack the competitive trait expressions to fill available niche space post-disturbance (Meineri et al. 2020). It has been shown that gaps in such communities can be quickly exploited by novel species (Dukes 2001, Milbau et al. 2013, Haider et al. 2022, Schuchardt et al. 2023a). Given the consistency of studies finding high colonization rates after soil disturbance and abrupt shifts in climate conditions, it is not surprising that we found a strong increase in functional richness due to trait space expansion in our experiment. In our study, severe climatic change led to community disturbance effects comparable to those of soil disturbances in other studies (i.e. a significant removal of native species). Consequently, this indicates two contrasting processes affecting community structure and functioning of future mountain plant communities. First, high colonization susceptibility (openness, weak biotic filter) of resident mountain plant communities will likely favor fast growing, opportunistic novel species over native species, increasing the systems' vulnerability to climate change and disturbances (Lembrechts et al. 2016, 2018, Nomoto and Alexander 2021). This is especially important at a species' trailing edge (where climatic change and novel biotic interactions are the most severe) or disturbed habitats, such as the sides of roads or trails where novel species' seeds are either already present in the matrix or vectored by humans or cattle. Second, the weak biotic filter of mountain plant communities may also facilitate native species migration to higher elevations (Lembrechts et al. 2018, Steinbauer et al. 2018) or nearby escape habitats (Körner and Hiltbrunner 2021) likely contributing to the system's high inertia (Tilman et al. 1994, Alexander et al. 2018, Figueiredo et al. 2019).

In our study, only few species showed the ability to adapt to novel climates and make use of available resources by growing more resource acquisitive e.g. *Scorzoneroides helvetica* in Furka$_{\text{warm}}$ and *Agrostis capillaris*, *Dactylis glomerata* and *Festuca rubra* in Stubai$_{\text{warm}}$. The ability to shift towards more resource acquisitive trait expression among these species indicates intraspecific plasticity allowing species to track experimentally induced changes in climatic conditions, highlighting plasticity as an important mechanism to persist within plant communities (Henn et al. 2018). Even though only a few surviving species were able to shift their trait values, these trends align with Rixen et al. (2022) who show that species with larger range sizes were found to have greater intraspecific trait variation, which likely increases survival under climate change. Conversely, two other resource conservative species (*Vicia villosa* and *Trisetum flavescens*) and two small statured species (*Prunella vulgaris* and *Trifolium repens*) present at the subalpine control site died over the course of the experiment at Stubai$_{\text{warm}}$ (data not shown but see Schuchardt et al. 2023a). This pattern likely indicates that species in the climate change scenarios had to adapt by growing taller in stature with more resource acquisitive leaves (increasing SLA and decreasing LDMC) or were outcompeted by novel species with a locally adapted resource acquisitive growth. For species originating from the alpine pasture Furka, the abrupt climate change combined with the 2018 central Europe-wide drought (Bastos et al. 2020) was likely too severe for survival (see the Supporting information for soil moisture depletion in mesocosms over the duration of the experiment), especially as these highly specialized species lack fast enough plastic responses to quickly fill available niche space. This assumption is supported by another study in the same experiment (Schuchardt et al. 2023a) showing that the loss of native species was gradual and that novel species colonization only began in 2019 after the central Europe-wide drought of 2018. Since the study presented here lacks the temporal resolution and consists of a single trait measurement at the end of the experiment, we cannot prove whether lost species showed intraspecific responses to warming and drought before going locally extinct.

We found contrasting patterns in functional divergence across the two warmed mountain plant communities. While species resource use strategies diverged for the alpine plant community in the climate change scenario, functional divergence decreased for the subalpine plant community (i.e. resource use became more even across species). These two contrasting signals are likely due to a high degree of niche differentiation of novel annual species colonizing the alpine plant communities (bringing along a higher variance in trait expressions in addition to higher proportional AGB contributions) while species contributing to major parts of the subalpine communities' productivity shared similar resource use traits (low variation in LDMC and SLA; Supporting information). This is particularly interesting as graminoid species in both climate change scenarios shifted their resource use towards the center of gravity (the mean of all species) instead of remaining in a resource conservative unoccupied niche, indicating strong species-specific competition tradeoffs and likely differences in resource uptake between graminoids and tall growing forbs. While forbs likely draw resources (e.g. nutrients and water) from deeper soil layers, graminoid species are known for an increased nutrient uptake flexibility through a shallow but dense rooting system (Rosbakh et al. 2017), likely enhancing graminoids' climate change resilience but making them vulnerable to shifts in precipitation regimes (Bardgett et al. 2014, Kübert et al. 2019, Mackie et al. 2019). This observation highlights that hidden (belowground) traits likely allow the co-existence of species occupying similar aboveground niches, a mechanism that to date remains poorly explored.

Implication for mountain plant communities

Our experimental approach was unique in that we created scenarios with a strong increase in temperature, a decrease in available moisture, and the presence of novel lowland species to explicitly push mountain plant communities beyond their climatic envelopes and introduce novel biotic interactions. Consequently, our results shed some light on how mountain plant communities could respond to the net effect of climate change. We were able to highlight that the often-overlooked interaction of warming and drought pushed both mountain plant communities beyond a threshold of resistance, creating a window of opportunity for novel lowland species to colonize. The interaction of warming, drought, and the presence of many novel species in the matrix is a realistic scenario for many species at their current trailing edge, where upward moving lowland species are already present as future competitors. Today, these lowland species may be present with low abundances (at their leading edge), but their competitive potential once climate change-induced gaps are created was found to be strong in this study. In nature, the co-existence of native and upward moving lowland species will likely lead to a transient state of increased functional richness which does not necessarily indicate an increase in ecosystem function or stability but rather a shift in the community use of available resources (increased functional richness) to avoid competition (high divergence). Additionally, our study shows that an abundance weighted measure like functional divergence may primarily indicate that dominating species avoid competition while it is ignoring species turnover of small statured or less abundant species (loss of native and colonization of lowland species) happening in the background. Thus, we highlight the need for more studies exploring in situ species turnover along a time series under severe climatic change. We conclude that mountain plant communities' vulnerability to climate change is higher than previously reported, especially once their threshold of resistance to drought is crossed.

Alternative viewpoints

So far, species turnover in mountain plant communities has rarely been reported under natural conditions. Translocation studies like Cui et al. (2018), have found strongest species turnover rates under the most severe climatic changes. By using a very steep translocation gradient in our study, we intentionally pushed mountain plant communities beyond their climatic envelopes. It is likely that the study design overestimates the ability of lowland species to track climate change to higher elevations by completely removing dispersal barriers and excluding native mountain species seed rain from the matrix, which should be addressed in future studies with addition of native species seeds. Our approach, mimicking a severe future scenario, provoked strong species turnover resulting in the collapse of the alpine community. Our observed collapse is currently lacking in most previous translocation studies as they use less severe, 'closer future' scenarios based on true elevational gradients with intermediate steps (De Boeck et al. 2018, Nomoto and Alexander 2021). But which approach mimics a ‘realistic’ future scenario? We need to understand the consequences of crossing thresholds of persistence, especially knowing that many ecological responses are non-linear and threshold triggered (Collins et al. 2022b). A compartmentalization of climatic stressors ignores the interactive impacts of climate change. Rather than attempting to disentangle the effects of warming, drought, and novel species presence our approach studies the ‘net effect of climate change’ which should be picked up in future studies.

Funding – We are grateful to the Federal Ministry of Education and Research (BMBF) for funding this research (SUSALPS; grant number: FKZ 031B0516C). This study is also part of AJ’s research project MindTheGap! financed by the Upper Franconian Trust (Oberfrankenstiftung; grant number: OFS FP00237). YN is a Humboldt fellow funded by the Alexander von Humboldt-Foundation. Open Access funding enabled and organized by Projekt DEAL.

Author contributions

Max A. Schuchardt: Data curation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Bernd J. Berauer**: Data curation (supporting); Formal analysis (supporting); Supervision (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Anh Le Duc**: Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Johannes Ingrisch**: Data curation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Yujie Niu**: Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Michael Bahn**: Funding acquisition (supporting); Project administration (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Anke Jentsch**: Conceptualization (lead); Data curation (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (lead); Project administration (lead); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.79cnp5j1m (Schuchardt et al. 2023b).

Supporting information

The Supporting information associated with this article is available with the online version.

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