

Traits help explain species' performance away from their climate niche centre

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Abstract

Aim: Climate change impacts on biota are variable across sites, among species and throughout individual species' ranges. Niche theory predicts that population performance should decline as site climate becomes increasingly different from the species' climate niche centre, though studies find significant variation from these predictions. Here, we propose that predictions about climate responses can be improved by incorporating species' trait information.

Location: Europe.

Methods: We used observations of plant species abundance change over time to assess variation in climate difference sensitivity (CDS), defined as how species performance (colonization, extinction and abundance change) relates to the difference of site climate from the mean temperature and precipitation of each species' range. We then investigated if leaf economics, plant size and seed mass traits were associated with the species' CDS.

Results: Species that performed better (e.g. increased in abundance) towards sites progressively cooler than their niche centre were shorter and had more resource-acquisitive leaves (i.e. lower leaf dry matter content or LDMC) relative to species with zero or the opposite pattern of temperature difference sensitivity. This result supports the hypothesis that if sites cooler than niche centres are more stressful for a species, then shorter stature is advantageous compared with taller species. The LDMC result suggests the environment selects for more resource-acquisitive leaf strategies towards relatively cooler climates with shorter growing seasons, counter to expectations that conservative strategies would be favoured in such environments. We found few consistent relationships between precipitation difference sensitivities and traits.

Main Conclusions: The results supported key a priori foundations on how trait-based plant strategies dictate species responses to climate variation away from their niche centre. Furthermore, plant height emerged as the most consistent trait that varied with species CDS, suggesting height will be key for theory development around species response to climate change.

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KEYWORDS

abundance, biodiversity, body size, climate change, extinction and colonization, functional traits, niche theory, plants

1 | INTRODUCTION

Climate change is reshaping plant communities through increasing extinction risk (Pauli et al., 2012; Urban, 2015), introducing novel colonists through species range expansions (Savage & Vellend, 2015; Steinbauer et al., 2018) and causing shifts in abundance within communities (Gottfried et al., 2012). Climate change experiments often find that moist temperate grassland plant communities shift towards taller, more productive species as climates warm (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Fridley et al., 2016). However, considerable variation among species and communities in their responses suggests that the effects of climate change can be highly context-dependent (Dunne et al., 2004; Vandvik et al., 2020).

Some of the variation in species responses to climate change may be explained by macroecological context: a population's relative environmental position compared with average conditions encountered across the species' range or niche (Lynn, Klanderud, et al., 2021; Reich et al., 2015). Drawing from classical niche theory (Blonder, Moulton, et al., 2017; Hutchinson, 1957), macroecological context predicts that local populations will perform better with climate change if local temperature or precipitation shifts towards conditions more similar to the species' range/niche centres but perform worse if climate shifts away from range centre conditions. This can be assessed by looking at climate differences: the difference between the average climate a species occupies across its geographic distribution (its climate niche centre) and the climate experienced by the local population (Lynn, Klanderud, et al., 2021). For example, in a turf transplant experiment where whole grassland communities were moved to warmer and/or wetter climates, species with climate niches warmer than a given transplant site were less likely to go extinct, more likely to colonize, and increased in abundance compared with species with niches increasingly cooler than their transplant site (Lynn, Klanderud, et al., 2021). Similarly, a single-site warming and drought experiment found that species with warmer summer temperature niches increased in abundance under warming while species with drier spring precipitation niches increased in abundance under drought (D. Liu et al., 2018). Macroecological context thus provides a universalizable framework to assess and predict both population- and community-level variation, that is, differences in response to climate change among species in a given site and/or across sites within a species. Nevertheless, a considerable amount of interspecific variation in species climate responses remains unexplained after accounting for macroecological context.

This additional interspecific variation in macroecological studies of species responses to climate change likely arises from aspects of species life history strategies that are not closely tied to responses to climate. That is, even if species have similar climatic optima, they likely vary in life history and investment strategies for light capture,

tissue quality, reproduction and more (Díaz et al., 2016; Fridley, 2017; Grime, 2006) that are not causally linked to climate but may dictate their performance under different macroecological contexts. For instance, in tree species across the Pacific west of the United States, taller tree species tended to occupy wetter habitats than expected based on models of optimal soil water balance for survival (Bohner & Diez, 2020). This suggests that traits (i.e. height) related to life history strategy outside of those that governed survival responses to climate explained variation in habitat occupancy. Therefore, variation in the magnitude and direction of climate responses across species may partially depend on variation in other traits that relate to their ability to maximize fitness in environments, independent of that site's climate.

Here, we develop a novel modelling framework to test how species' responses to climate variation around their niche centre is associated with plant functional traits. We hypothesize that variation in trait strategies indicative of stress tolerance may in part explain why some species perform better away from their climate niche centre (Dallas et al., 2017; Sporbert et al., 2020). This approach extends the macroecological context framework (see below) to fulfil one of the key aims of functional ecology by explaining how species respond to environmental variation based on their trait strategies (Grime, 2006; Reich, 2014). Our framework is generalizable to other systems and forms of environmental change and, thus, may have broad utility in predicting species vulnerability to various global change drivers.

1.1 | The framework

We first define macroecological context in [Box 1](#), then provide hypotheses for how traits relate species' climate sensitivity in [Table 1](#). A schematic diagram of the framework is provided in [Figure 1](#).

We start with the general assumption that a species' niche centre represents its climate optimum, such that increasing differences in *either* direction represents sub-optimal conditions that reduce performance relative to the niche centre (Brown, 1995). That is, we expect unimodal climate difference sensitivities (CDS; [Box 1](#)). However, in empirical cases where observed climate differences are mostly positive or mostly negative, interpretation is greatly simplified and enables linear investigations on one side of a species' optimum. For example, in our study system (grasslands in south-western Norway), conditions are generally colder and wetter than the estimated niche centres of the species, suggesting we should generally find negative temperature and positive precipitation CDS ([Figure 1b,c](#)). Assuming performance is maximal at the niche centre and given our distribution of niche differences in [Figure 1b](#), a negative temperature CDS means that the species performs worse as site temperature is increasingly cooler than a species' niche centre.

BOX 1 Definitions and interpretation.

Macroecological context is the relation of a site and plant community characteristics to the geographic range and niche characteristics of the species making up the community.

Climate difference is the mean climate variable of a species (niche centre) minus the climate of the site where an individual of the species was observed (i.e. $\Delta\text{climate} = \text{niche climate} - \text{site climate}$). In this study, we focused on mean annual temperature (MAT) and annual precipitation (AP). Negative values mean the site where a species was observed is warmer or wetter than the species' niche centre while positive values indicate the site is cooler or drier than the species' niche centre.

Climate difference sensitivity (CDS) represents the strength and direction of response metric change as climate differences change from negative to positive (Figure 1c). Mathematically, this is the slope from a linear model of climate differences predicting a given response metric. We focus on the direction (positive, zero/unrelated or negative) of CDS. For a given species, positive sensitivity indicates a given response metric increases as climate differences increase, zero sensitivity indicates no relationship between a response metric and climate differences, and negative sensitivity indicates a response metric decreases as climate differences increase from negative to positive.

A positive precipitation CDS means that the species performs better as site precipitation becomes more similar to the species' niche centre.

We assume that species' performances are optimal at their climate niche centres, which are derived from their observed distributions. However, this simplifying empirical assumption requires further scrutiny given dispersal (e.g. Goel & Keitt, 2022), biotic interactions (e.g. Lynn, Miller, & Rudgers, 2021) and other aspects of the abiotic environment (e.g. Moutouama & Gaoue, 2023) will constrain the observed distribution to a subset of possible climates. Ultimately, climate niche centres should be derived from physiological response curves (Michaletz et al., 2015; Perez et al., 2023), but such physiological data are lacking for the vast majority of species. Therefore, using species distributions to estimate climate niche centres is a pragmatic solution that allows testing hypotheses across large numbers of species, given predictions of climate suitability are generally well related to physiological climate performance (VanDerWal et al., 2009).

As outlined above, species vary in the amount of decline or even whether or not performance declines at all away from the niche centre and towards presumably marginal climates (Pironon et al., 2017; Sporbert et al., 2020; but see Britnell et al., 2023; Fristoe et al., 2023). We propose that functional traits may help explain

species' ability to increase performance under non-optimal climate conditions. Specifically, resource acquisitive traits are advantageous in environments that are relatively less stressful (i.e. under non-production limiting conditions) compared with their niche centre, while conservative trait strategies are more advantageous in environments that are relatively more stressful than their niche centre (Grime, 2006). Given these interpretations, we expected species with positive temperature CDSs to have more resource-conservative traits (lower trait values are more conservative) than species with zero or negative CDSs (Figure 1e; Table 1), reflecting a capacity to maintain performance in environments that are increasingly cooler than their niche centre. In contrast, we expected species with positive precipitation sensitivities to have more resource-acquisitive traits (higher trait values are more acquisitive) than the zero and negative precipitation sensitivity species (Figure 1f; Table 1), reflecting the improved performance of species as the precipitation environment becomes relatively drier and hence more like their niche centre. This hypothesis may seem unintuitive given water is often a limiting resource, but this system receives extremely high precipitation annually (sites receiving >3000mm annual precipitation) to the point where cloud cover and lack of sunlight are a greater impediment to productivity than water availability (Seddon et al., 2016). For instance, low-precipitation communities (~800mm) in western Norway tend to have more resource-acquisitive leaves (i.e. higher specific leaf area) than high-precipitation communities (Guittar et al., 2016). We focused on traits from the leaf-height-seed spectrum, which are hypothesized to capture much of the variation in plant life history strategies from fast-growing resource acquisitive, to slow-growing stress-tolerant and small-seeded ruderal strategies (Laughlin et al., 2010; Moles, 2018; Westoby, 1998). Past observational and experimental work supports these a priori predictions and is summarized in Table 1, along with descriptions of the specific traits we test.

2 | METHODS**2.1 | Study design**

We used a 12-site turf-transplant experiment that began in 2009 in southwestern Norway for our observations of species abundance over time (Vandvik et al., 2020). The sites are regionally distributed into a factorial grid with three summer-temperature levels (~6, 8 and 10°C) and four annual precipitation levels (~700, 1200, 1900 and 2900mm) based on downscaled normal period climate data (1961–1990; met.no; coordinates in Table S1.1 in Appendix S1). We transplanted intact grassland plant communities or 'turfs' as treatments either one step 'warmer' (~2°C; eight site-to-site transplants), 'wetter' (~700mm, nine site-to-site transplants) or 'warmer/wetter' (six site-to-site transplants) to factorially isolate the effects of these predicted climate change drivers on plant communities (Hanssen-Bauer et al., 2017). Every site contained local control plots. Over the 10 years since transplanting, the transplanted communities

TABLE 1 Specific hypotheses for how the traits we studied are related to species macroecological context relationships for colonization and abundance change.

Traits and interpretation	Climate difference sensitivity		
	Δ MAT		Δ AP
Resource-acquisitive traits:	-	0	+
• Specific leaf area (SLA): Higher SLA indicates less carbon investment per light capture area (Griffin-Nolan et al., 2019; Guittar et al., 2016; Kichenin et al., 2013; Wilcox et al., 2021)	↑	=	↓
• Leaf nitrogen content (leaf N): Leaves with higher N have higher photosynthetic capacity (Griffin-Nolan et al., 2019; Kichenin et al., 2013; Wilcox et al., 2021)			
• Plant height (H_p): Taller plants can obtain more light (Fridley et al., 2016; Guittar et al., 2016; Venn et al., 2014)			
Resource-conservative traits:	↓	=	↑
• Leaf dry matter content (LDMC): Higher LDMC leaves have more dense tissue (Kichenin et al., 2013; Venn et al., 2014; Wilcox et al., 2021)			
• Leaf thickness (L_{th}): Higher L_{th} leaves are physically stronger (Blonder, Salinas, et al., 2017; Soudzilovskaia et al., 2013; Wilcox et al., 2021)			
• Leaf carbon content (leaf C): Leaves with more carbon have higher structural support (e.g. cell walls) (Peng et al., 2020; Zhao et al., 2014)			
• Leaf C:N: Leaves with higher C:N have more structural support relative to photosynthetic capacity on a mass basis (Zhang, He, et al., 2020; Zhang, Li, et al., 2020)			
• Seed mass (SM): Species with higher SM have higher seedling survival and establishment probability but are generally made in lower numbers (Cheilli et al., 2019; Moles, 2018; Soper Gorden et al., 2016; but see Simpson et al., 2016)			

Note: Predictions for extinctions are flipped. Traits are divided into those for which higher values are considered more resource-acquisitive and associated with higher maximum potential growth rate and those for which higher values are considered more resource-conservative and typically associated with lower maximum potential growth rate. The climate difference sensitivity (CDS) groups are indicated with +, 0, and -, representing positive, zero/null and negative linear relationships with performance, respectively. Our hypotheses for how traits differ between CDS groups are indicated by ↑, =, ↓, signs, which represent whether a group is likely to have higher (↑) or lower (↓) trait values compared with the zero group (=). Support for our trait interpretations and predictions come from the observational and experimental work cited in the 'Traits and interpretation' column.

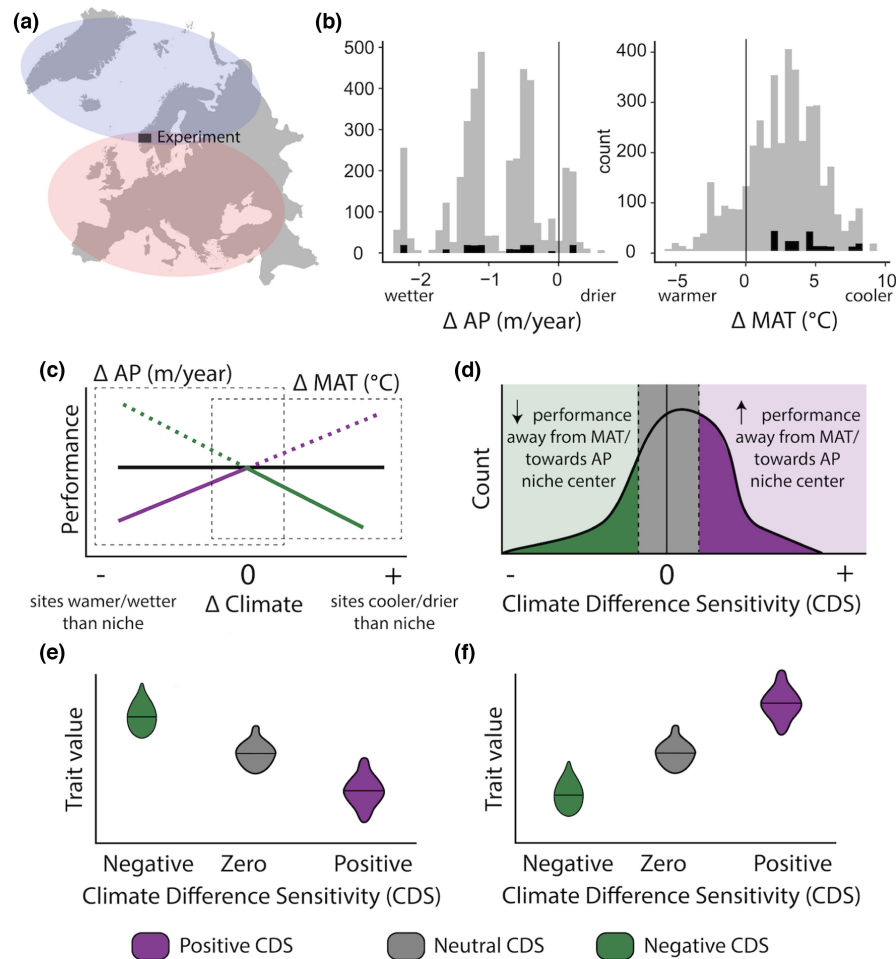


FIGURE 1 Conceptual diagram to demonstrate how we analysed climate difference sensitivity (CDS; Box 1) in relation to species traits. (a) Two hypothetical species with different distributions that both occur in our study region in southwestern Norway. Macroecological context contrasts the characteristics of a species niche with the characteristics of the site where a species is observed as shown in (b), which are the real distributions (histograms) of climate differences of individual species from plots in our data. The black coloured bars are the data from a particular species, *Agrostis capillaris*. We focus on contrasts of species mean annual temperature (MAT) and annual precipitation (AP) niche centres with site MAT and AP as metrics of climate differences ($\Delta MAT = \text{niche} - \text{site temperature}$; $\Delta AP = \text{niche} - \text{site annual precipitation}$). (c) The slope of the relationship between a given performance metric and climate difference for each species is their climate difference sensitivity (CDS). We hypothesize that species performance should decrease away from the centre of their climate niche, and so CDS (slope) should be positive when sites are warmer or wetter than the range centre, and negative when sites are cooler or drier, given the data in (b). Thus, in our case, we predict negative CDS for temperature and positive CDS for precipitation, as indicated by solid versus dashed lines. We propose that traits may be key in explaining why some species do not follow this expected pattern. (d) We then classified the distribution of species CDSs as either negative, zero or positive, based on their slopes and the uncertainty around that estimate (see Figure 2 for real data; this figure is hypothetical). This classification simplifies species CDS into species that do better, worse or are unresponsive as site climates become cooler or more similar in precipitation to their niche centres. The asymmetric distribution in (d) reflects our hypotheses as explained in panel (c). (e and f) Finally, we assessed our hypotheses (Table 1) for what groups of species CDSs would present which trait distributions. Whether we expected a given trait to present either (e) or (f) is dependent on whether the higher trait values are indicative of resource-acquisitive or conservative strategies, whether the CDS is for ΔMAT or ΔAP , and which performance metric (colonization, extinction and abundance change) the CDS represents (Table 1). Note, (c) and the panels following are all hypothetical data and colour labels for each panel are inherited from the legend at the bottom of the figure.

have shifted towards the species composition of their 'destination' sites, albeit with extinction lags (Vandvik et al., 2020). All sites were located on south-facing, shallow slopes with calcareous substrate and grazed, historically (Klanderud et al., 2015). Turfs were $29 \times 29 \times 10$ cm in length, width and depth, and we analysed the inner 25×25 cm for treatment effects, leaving the outer edge as a buffer. Further experimental details can be found in Vandvik et al. (2020).

2.2 | Colonization, extinction and abundance change

We surveyed the plant communities in 2009 with visual estimates of percent cover by species prior to transplantation. After turf recovery in 2010, we resurveyed the turfs in 2011, 2012, 2013, 2015, 2017 and 2019. Plant nomenclature is from Lid and Lid (2005).

Colonizations were counted as species that were absent in a turf in the first survey (2009) but present in the final survey (2019), and extinctions were defined as species present in a turf in the first survey (2009) but absent in the final survey (2019). Change in cover was measured as:

$$\Delta c_s = \ln(c_{s,f} + 1) - \ln(c_{s,i} + 1) \quad (1)$$

With Δc_s as cover change for species, s , in a turf calculated as the natural log (plus one to avoid taking the natural log of zero) of the species final cover, f , minus its initial cover, i . A table of species information found in the survey can be found in Table S1.2 in Appendix S1.

2.3 | Species range and climate data

For each species in the dataset (151 excluding unidentified species), we downloaded occurrence records from 1950 to 2019 across Europe from the Global Biodiversity Information Facility (Occdownload Gbif.Org, 2019a, 2019b) with the *rgbif* package (Chamberlain & Boettiger, 2017). We followed Lynn, Klanderud, et al. (2021) for GBIF data cleaning methods. Briefly, we subsampled occurrence records to represent a species occurrence once per a grid cell of $\sim 1 \times 1$ km or ~ 30 s resolution rasterized grid and extracted climate data for these occurrences from the 30s resolution WORLDCLIM v 2.0 database. We focused on mean annual temperature (MAT in $^{\circ}\text{C}$) and annual precipitation (AP in m/year) because of their widespread availability and strong correlation in our system with other climate variables such as potential evapotranspiration. We then took the mean of MAT and AP across the species' occurrences to estimate a species' 'climate niche centre'. Mean and median niche centres were highly correlated ($r > .9$ for both MAT and AP). We also used WORLDCLIM data to extract MAT and AP data for the experimental destination sites to stay consistent between site and species' climate data sources. Finally, we calculated 'climate differences' or ΔMAT and ΔAP as a species' niche centre minus the site climate (Box 1).

2.4 | Functional trait data

Trait data were collected in natural plant communities outside of the experimental plots in 2016 at all 12 sites. We sampled the most abundant species cumulatively making up $\sim 80\%$ of local, natural vegetative cover to constrain sampling effort. Some additional trait data were collected in 2017 to fill gaps. Traits were measured using standard protocols (Pérez-Harguindeguy et al., 2013) on 10 replicate individuals spaced ~ 2 meters apart per species per site and all measurements were taken from flowering, sun-exposed and healthy individuals. Full details on trait measurements of vegetative height (H_v ; cm), specific leaf area (SLA; cm^2/g), leaf dry matter content (LDMC; g/g), leaf thickness (L_{th} in mm), leaf nitrogen (leaf N; %mass), leaf carbon (leaf C; %mass) and leaf C:N ratio (%/%) and seed mass (SM in

g/1000 seeds without dispersal tissues from Royal Botanic Gardens Kew, 2021) can be found in the Appendix S1. Our analyses aimed at assessing species-level trait variation, but if there is more variation among individuals of a species than between, interpretations of mean traits would be questionable. Variance partitioning analyses suggest this was not the case (Appendix S1).

2.5 | Statistical analyses

Testing our hypotheses required two steps: (1) fit the 'species-specific' macroecological context models, and (2) investigate how traits are associated with the direction of macroecological predictions. We only included species with trait data ($n=85$). We used three response metrics: colonization, extinction and abundance change (Δc). Colonization and extinction probability were Bernoulli distributed, and Δc was normally distributed.

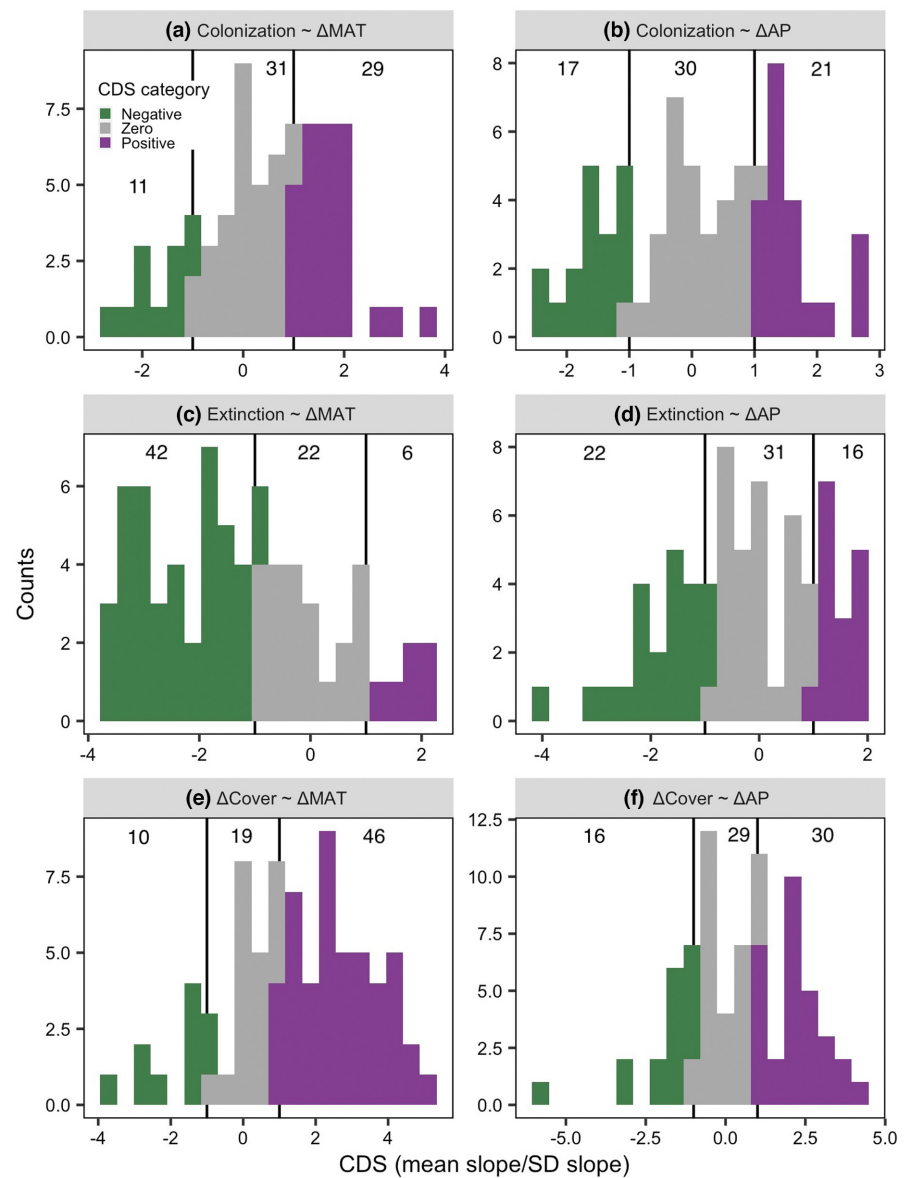
For step 1, we fit models with species-specific slope and intercept parameters relating climate differences to a response metric (cf. Figure 1c). Each data point represents one species per turf. This species-specific analysis is data demanding. We, therefore, dropped species that did not occur at multiple sites (< 2 sites; three species) and/or had too little data (< 10 observations; seven species), leaving 75 species for analysis. Additionally, transplant treatment effects were not included in the model because it further thinned power across treatments and because the main pattern of interest is how species respond to climate differences, regardless of the source of these differences. As mentioned above, a key effect of transplantation is expanding the set of temperature and precipitation environments a species experiences (Lynn, Klanderud, et al., 2021). The model was specified as:

$$\mu = \alpha[\text{species}_i] + \beta[\text{species}_i] * \Delta\text{MAT} + N(0, \sigma^2_{\text{site}}) + N(0, \sigma^2_{\text{block}}) \quad (\text{step 1}) \quad (2)$$

where μ is one of the three response metrics linearly predicted by species i ($[\text{species}_i]$) with an intercept (α) and slope (β , or climate difference sensitivity/CDS) describing how species performance relates to a climate difference metric (either ΔMAT or ΔAP). The model included site and block as group-intercept variance terms (σ^2).

For each species, we took the mean slope (β or CDS) posteriors generated from step 1 and classified them by direction (positive or negative) and uncertainty (degree of posterior overlap with zero). The uncertainty was classified based on the inner 68% or $\pm 1\text{SD}$ of the posterior slope estimate. If the 68% interval included zero, the sensitivity was classified as zero/unrelated. If the 68% interval did not include zero, it was further classified by its direction as either positive or negative. We simplified CDS into a directional classification rather than analysing raw slope values because (1) raw slope values as measures of strength are contingent on historical and environmental factors unassociated with climate differences (e.g. priority effects), and (2) the magnitude of the slopes may be dependent on where in the climate difference spectrum the species' were sampled and, therefore, may be unreliable as a precise measure of CDS but useful for general

FIGURE 2 Distributions of species climate sensitivities (step 1) used in the functional trait analyses. Histograms show the mean slope divided by their standard deviation to reflect if the posterior distribution overlaps 0 at the 68% credibility interval. CDSs were classified as 'Negative' if the CDS was less than -1, 'Positive' if the CDS was greater than 1 and 'Zero' if the CDS was between -1 and 1. These boundaries are marked by vertical lines and CDS colours for all panels are in the legend of (a). Panels are ordered by performance metric colonization (a, b), extinction (c, d) and abundance change or 'ΔCover' (e, f) modelled by climate differences (ΔMAT (a, c, e) and ΔAP (b, d, f)). Numbers above the histogram bars label the number of species that fall into a given CDS classification.



characterizations of directional responses. We focused on slopes and not intercepts from the model because the slope represents how a species is predicted to respond to climate change away from its niche centre, while the intercepts represent a species' base performance when a site's climate is equal to the species' niche centre. Slopes and intercepts were also highly correlated (all $r \sim .7$ or greater). Additionally, some species had parameters that failed to converge (failed model checks; see below) in step 1 for colonization and extinction and were dropped for analyses in step two (final counts per analysis in Figure 2).

In step 2, we tested if the direction (negative, zero/unrelated, positive) of species climate difference sensitivities (CDS) for each response metric were associated with different trait strategies (cf., Figure 1e,f):

$$\text{trait}_m = \alpha_m * \text{CDS (step 2)} \quad (3)$$

where values of a trait, m , were analysed as a function of species' CDS direction (factor with levels negative, zero/unrelated, positive) with

intercepts, α_m . We investigated these relationships for all eight traits in Table 1, but only reported height, LDMC, leaf C:N and seed mass in the main text with full results in Appendix S2. All trait data were normally distributed with natural log transformation. Additionally, we checked that our interpretation of CDSs as moving away from niche centre for temperature and towards niche centre for precipitation was justified with analyses removing climate difference observations below ΔMAT and above ΔAP zero/niche centre line, finding similar results in Appendix S3.

All models were fit with Bayesian methods (Hobbs & Hooten, 2015) in JAGS (Plummer, 2003) in the 'R2jags' package (Su & Yajima, 2015) in R 4.0.3 (R Core Team, 2020). Model specifications and checks can be found in Appendix S1. Bayesian analyses produce posterior probability distributions of parameters allowing for probabilistic statements on the strength and direction of a term (e.g. probability a slope term, β , is greater than zero given as $P(\beta > 0) = 0.99$). We additionally calculated the joint probability distribution (degree of overlap) between posteriors of negative and positive CDSs to

assess their degree of difference (in percentages) when one or the other had a large amount of support for being different from the zero CDS.

3 | RESULTS

Species climate difference sensitivities spanned the full range of negative, zero and positive for each of the different performance metrics and climate variables (Figure 2), but the distribution of CDSs did not meet our expectations. Temperature CDSs suggested most species performed better (positive colonization and cover, negative extinction CDS) in sites cooler than their niche centre, while precipitation CDSs were more evenly distributed (Figure 2). While not consistent with our expectation from niche theory, this broad distribution of CDSs increased the power for testing associations between traits and CDSs (Figure 2 for trait sample sizes).

3.1 | Temperature climate difference sensitivity and traits

Results for all three-response metrics (i.e. colonization, extinction, abundance change) were consistent with our predictions for height, but opposite of expectations for LDMC and with little relationship of other traits to temperature difference sensitivities (Table 1). Species with higher colonization probability at sites cooler than their niche centre (positive CDSs) were shorter and had higher LDMC compared with species that decreased in colonization probability in sites cooler than their niche centre (negative CDSs). Specifically, species for which colonization probability increased as sites became cooler than their niche centres (i.e. with increasing ΔMAT), were, on average, $\sim 40\%$ shorter ($P(\beta < 0) \sim 1$) and had $\sim 20\%$ lower LDMC ($P(\beta < 0) \sim 0.98$) than species with zero CDS (Figure 3a; Table 2). This trait difference was especially substantial for height which overlapped by only 9% between positive and negative temperature CDS species. In contrast, there was high overlap between negative and positive CDS species for LDMC ($\sim 50\%$) even though the LDMC of negative CDS species was not different from the zero CDS species ($P(\beta < 0) \sim 0.74$). Differences in other traits among CDS groups were more variable, but species with positive CDS had lower leaf C:N than the zero CDS species ($P(\beta < 0) \sim 0.92$).

Similarly, shorter species and species with more resource-acquisitive leaf strategies had decreased extinction probability as sites became cooler than their niche centres, which only supported our height hypothesis (Table 1). Species that had lower extinction probability as temperature differences increased (negative CDSs) were 46% shorter ($P(\beta < 0) \sim 0.99$), had 28% lower LDMC ($P(\beta < 0) \sim 1$) and 14% lower leaf C:N ($P(\beta < 0) \sim 0.98$) than species with zero CDS (Figure 3b; Table 2). There was little overlap between negative and positive CDS species in height, LDMC and leaf C:N (all $< 16\%$). Additionally, species with positive extinction CDS tended to be taller but with higher uncertainty ($P(\beta > 0) \sim 0.85$).

Again, supporting height but not leaf hypotheses (Table 1), shorter species and species with more resource-acquisitive leaf strategies increased in abundance as sites became cooler than species' niche centres. Species that increased in cover as temperature differences increased were 73% shorter ($P(\beta < 0) \sim 0.99$) and had 26% lower LDMC ($P(\beta < 0) \sim 1$; Figure 3c; Table 2). Species with positive temperature CDS for cover were different from negative CDS species for height and LDMC (both $< 8\%$ overlap).

3.2 | Precipitation climate difference sensitivity and traits

Species colonization-precipitation CDSs were weakly related to traits at best, which was counter to our hypotheses (Table 1) and consistent across response metrics. With height, species that decreased in colonization ability as sites became drier and more similar to their niche centre (negative CDSs) were, on average, 24% shorter than ($P(\beta < 0) \sim 0.90$) and species with positive CDSs were 29% taller than ($P(\beta > 0) \sim 0.90$) species with zero CDS (Figure 4a; Table 2), which generally supported predictions (Table 1). The probability that positive and negative precipitation CDS species overlapped in height was only $\sim 10\%$. Together, this suggests that taller species had increasing colonization probability while shorter species had decreasing colonization probability as site precipitation became more like their niche centre precipitation.

In contrast to our predictions (Table 1), species with lower seed mass had an increased chance of going extinct as site precipitation moved from wetter to more like species' niche centres. Species with higher extinction probability as precipitation differences increased had 175% lower seed mass than species with zero extinction CDS for precipitation ($P(\beta < 0) \sim 0.99$; Figure 4b; Table 2). However, there was $\sim 25\%$ overlap in seed mass for species with positive and negative extinction CDS for precipitation, even though negative CDS was not very different from zero CDS species for seed mass ($P(\beta < 0) \sim 0.80$). Species with positive extinction CDS for precipitation also had higher leaf C:N ($P(\beta > 0) \sim 0.89$) than zero CDS species, though this pattern had high uncertainty.

Species that increased abundance as site precipitation became more similar to their niche centre were taller ($P(\beta > 0) \sim 0.95$), had higher LDMC ($P(\beta > 0) \sim 0.97$), higher leaf C:N ($P(\beta > 0) \sim 0.93$) and higher seed mass ($P(\beta > 0) \sim 0.97$; Figure 4b; Table 2). However, all of these traits except for height overlapped greatly with traits of the species negative precipitation CDS for cover (lowest overlap among them was leaf C:N at $\sim 46\%$) and the direction of these trait differences from the zero CDS species was the same for positive and negative CDS groups (Figure 4c). Together, this suggests the only consistent pattern emerging for precipitation CDS was species that increased abundance as sites went from wetter to more like species' niche centres were taller than other species, supporting our hypothesis (Table 1).

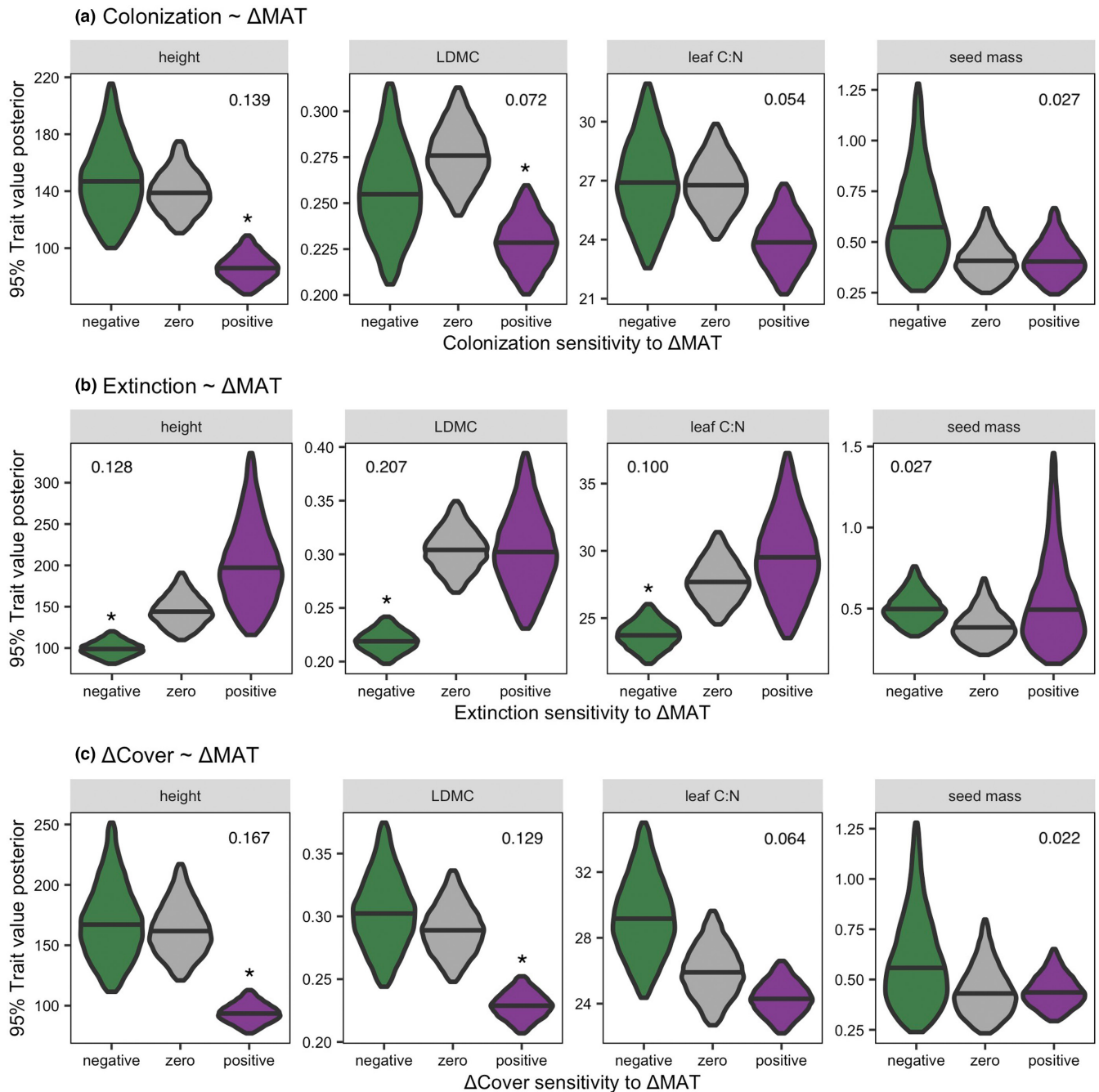


FIGURE 3 Mean trait values for species with positive, zero or negative (a) colonization, (b) extinction and (c) abundance change or ' Δ Cover' climate difference sensitivities (CDSs) for temperature. Violins represent the density of the 95% posterior estimates for a given trait with the midline representing the median posterior value. Panel titles label the traits with units of height in cm, leaf dry matter content (LDMC) in g/g, leaf carbon to nitrogen ratio (leaf C:N) is a unitless ratio (%/%) and seed mass in g/1000 seeds. Asterisks (*) indicate a given CDS is different from the zero group at the 95% credibility level (see Table 2). Numbers in each panel are Bayesian R^2 values.

4 | DISCUSSION

Relating functional traits to climate difference sensitivities yielded several novel insights: (1) shorter species and species with more resource-acquisitive leaves displayed higher performance in sites increasingly cooler than their niche centre, (2) temperature

sensitivity was more related to trait strategies than precipitation sensitivity, and (3) plant vegetative height (body size) was the most consistent trait for understanding species climate difference sensitivities. Generally, these results supported our a priori hypotheses for height (Table 1), but not for leaf or seed traits, as we discuss below.

TABLE 2 Summary statistics for analyses of how climate difference sensitivity (CDS) groups are related to traits.

Performance metric	Climate variable	Trait	Climate difference sensitivity			R ²
			Negative	Zero	Positive	
Colonization	MAT	Height	0.054 (0.59)	3.841	-0.480 (0.00)	.139
		LDMC	-0.080 (0.26)	-1.287	-0.190 (0.02)	.072
		Leaf C:N	0.005 (0.52)	3.288	-0.115 (0.08)	.054
		Seed mass	0.344 (0.76)	-0.901	-0.007 (0.49)	.027
	AP	Height	-0.272 (0.10)	4.734	0.254 (0.90)	.093
		LDMC	0.001 (0.50)	-1.381	0.042 (0.66)	.023
		Leaf C:N	-0.035 (0.36)	3.228	0.074 (0.79)	.038
		Seed mass	0.008 (0.51)	-0.997	0.407 (0.85)	.036
Extinction	MAT	Height	-0.379 (0.02)	4.972	0.312 (0.85)	.128
		LDMC	-0.328 (0.00)	-1.191	-0.007 (0.49)	.207
		Leaf C:N	-0.156 (0.02)	3.322	0.064 (0.69)	.100
		Seed mass	0.264 (0.77)	-0.960	0.248 (0.65)	.027
	AP	Height	-0.056 (0.39)	4.782	-0.075 (0.37)	.022
		LDMC	-0.061 (0.27)	-1.380	0.0489 (0.67)	.030
		Leaf C:N	0.014 (0.56)	3.193	0.117 (0.89)	.045
		Seed mass	-0.303 (0.20)	-0.560	-1.010 (0.01)	.099
ΔCover	MAT	Height	0.030 (0.55)	5.088	-0.549 (0.00)	.167
		LDMC	0.045 (0.63)	-1.242	-0.233 (0.01)	.129
		Leaf C:N	0.119 (0.85)	3.255	-0.064 (0.22)	.064
		Seed mass	0.255 (0.69)	-0.843	0.014 (0.51)	.022
	AP	Height	-0.02 (0.46)	4.640	0.298 (0.95)	.060
		LDMC	0.103 (0.83)	-1.470	0.173 (0.97)	.060
		Leaf C:N	0.022 (0.60)	3.186	0.118 (0.93)	.050
		Seed mass	0.531 (0.90)	-1.188	0.674 (0.97)	.067

Note: Estimates are sorted by performance metrics, climate difference variables and traits. The estimates are presented by how much trait values for the 'negative' and 'positive' CDS groups differ from the 'zero' CDS, indicated by the sign. The parentheses in the negative and positive CDS columns refer to the probability that the posterior distribution of the estimate is greater than 0 ($P(\beta > 0)$). Estimates that have 95% credibility intervals that do not overlap 0 and are different from the 'zero' CDS group are bolded. Finally, we present a Bayesian R² for each model (see Section 2). All trait estimates were log transformed. See Figures 3 and 4 for predicted trait means from these analyses.

4.1 | Does species' performance peak away from their temperature niche centre?

A surprising and novel result from our analyses in step 1 is that species performance generally peaked in sites cooler than their niche centre rather than near their niche centre (Figure 2a,c,e). This aligns, through new methodology, with a growing body of evidence that species do not perform best towards either their geographic or climatic niche centre (Dallas et al., 2017; Pironon et al., 2017; Sporbert et al., 2020). We offer three non-mutually exclusive hypotheses for this result that deserve more attention in future work. First, species' climate optima are likely cooler than can be estimated from current distributions because (a) species current ranges are lagging behind the pace at which the climate has already changed (Alexander et al., 2018; Svenning & Sandel, 2013), and (b) many species have not yet recolonized the total habitable climate space that has been left open since the last glacial

maximum (Knight et al., 2020; Normand et al., 2011). Both mechanisms suggest an underfilling of species' potential cold range edge in their global distribution that would result in the 'optimum cooler than centre' pattern. Second, intensified biotic interactions may limit the performance of a species near the centre of their fundamental niche (Louthan et al., 2018; Lynn, Miller, & Rudgers, 2021), representing a truncation of the fundamental niche to the realized niche (Hutchinson, 1957). Finally, species performance in a given temperature environment is dependent on other niche dimensions like nutrient availability (Chapin & Shaver, 1985). Therefore, both characterizations of species temperature niche and observations within our sites may be confounded by failing to consider other niche dimensions. The multidimensional and interacting niche requirements and histories of species will inevitably disrupt attempts to generalize by simplifying investigations down to a few aspects of their niche (e.g. temperature). Nevertheless, the level of predictive success that such simplified models can achieve should

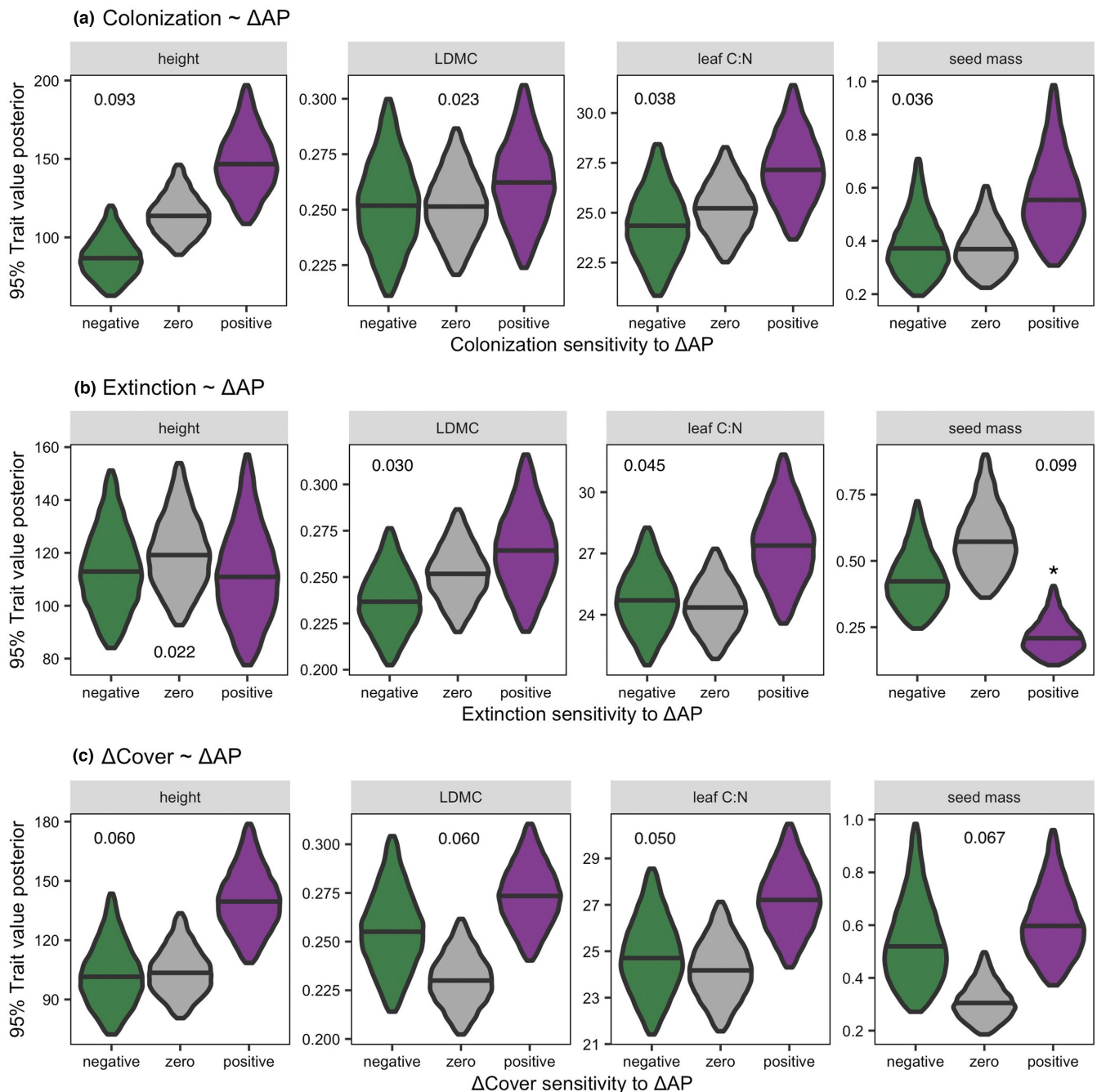


FIGURE 4 Mean trait values for species with positive, zero or negative (a) colonization, (b) extinction and (c) abundance change or 'ΔCover' CDSs for precipitation. Violins represent the density of the 95% posterior estimates for a given trait with the midline representing the median posterior value. Panel titles label the traits with units of height in cm, leaf dry matter content in g/g, leaf carbon to nitrogen ratio (leaf C:N) is a unitless ratio (%/%) and seed mass in g/1000 seeds. Asterisks (*) indicate a given CDS is different from the zero group at the 95% credibility level (see Table 2). Numbers in each panel are Bayesian R^2 values.

inspire confidence that our base assumptions are on track and general prediction is obtainable.

One possible caveat to our interpretation is that the range of temperatures and environments investigated outside the species' niche centres was narrow relative to the breadth of environments a species occupies across their entire range. Expanding the climate range of performance observations is a key next step in assessing this framework. Furthermore, progress in predicting species responses

to warming using their temperature niche will come from increased measurements of physiological performance over temperature gradients (Michaletz et al., 2015; Perez et al., 2023; Reich et al., 2015; Yamori et al., 2014) which will better characterize a species niche. Our work presented here can serve as the prior information to inform such physiologically based investigations and assess/resolve the issues of using observed distributions to infer a species' niche characteristics.

4.2 | Plant height, body size and prediction under climate change

The consistent relationship of plant vegetative height with climate difference sensitivities adds to a large and growing body of evidence that organismal body size is a key determinant of species' climate distributions and responses. Taller and larger sized plants tend to have greater competitive effect within a community (Grime, 1973), suggesting that the lower performance of taller species in sites cooler than their niche centre in our system may reflect a stress tolerance-competitive ability tradeoff and their relative competitive dominance in the communities under optimal abiotic conditions. The strong pattern that shorter species performed better in sites increasingly cooler than their niche centre suggests that shorter stature is an advantage in cooler, more stressful temperature environments (Körner, 2016). This and past work supports this hypothesis (Table 1), given both experimental (Guittar et al., 2016) and observed warming (Bjorkman et al., 2018) drive height increases via species turnover within communities. Body sizes' utility in predicting species responses to climate change holds across biomes and taxonomic groups (Fuller et al., 2021; Gardner et al., 2014; Ma et al., 2021; Pardee et al., 2022; Sheridan & Bickford, 2011). These firm correlational bedrocks of plant height/body size and climate change responses should move into developing and testing more mechanistic theoretical models of how climate change will drive shifts in communities and ecosystems (Choi et al., 2016; Schramski et al., 2015).

4.3 | Lower leaf investment favoured in relatively colder environments?

We hypothesized that species with more resource-conservative leaves (e.g. high LDMC) would perform better as sites became increasingly cooler than their niche centre (Table 1). Conservative, high LDMC leaves generally relate to higher cold tolerance (Ladwig et al., 2018) while species with resource-acquisitive leaves have higher photosynthesis and growth rates (Kazakou et al., 2006; Wright et al., 2004) and are better poised to take advantage of a favourable climate. Our unexpected finding of a relative advantage of low LDMC species in cooler than niche centre climates may be the result of short growing seasons and potentially high nutrient environments selecting for cheap, fast, deciduous leaves. Plants occupying higher elevations with shorter growing seasons can have lower LDMC leaves than plants in lower elevations (Venn et al., 2014) and lower LDMC species senesce earlier than high LDMC leaves (Bucher & Römermann, 2021). High-nutrient environments tend to select for lower LDMC leaves because the advantage of investing carbon to protect mineral nutrients in leaves is low if replacing the nutrients is easy (Daou et al., 2021). Given long dormant periods and high nutrient availability, the optimal strategy for species in environments colder than their niche centre may be low-LDMC, resource-acquisitive leaves. We further hypothesize that these physiological

advantages of low LDMC leaves in sites cooler than their range centre may confer a competitive advantage over other species at the sites with more conservative leaves (Dong et al., 2020; Kunstler et al., 2016). Testing this hypothesis would require cross-range transplant experiments paired with nutrient additions and models of competitive hierarchies, where a given species' performance is modelled by the difference between its trait value and its competitors (Kunstler et al., 2012).

4.4 | Seed mass was not strongly associated with species climate difference sensitivities

Seed mass, as an estimate of maternal resource investment without dispersal, was generally unrelated to climate difference sensitivities, counter to our hypotheses (Table 1). Globally, seed mass across species tends to increase with temperature and precipitation (Moles et al., 2014), suggesting that greater seed mass can lead to greater establishment and survival probability in environments with high competition for light (DeMalach et al., 2019; Westoby, 1998). Instead, we found weak evidence that smaller seeded species had greater extinction probability as site precipitation became more like their niche centre. This result was contrary to our main hypothesis, though evidence from the literature is mixed on how seed mass relates to a species climate response (Table 1). Past work has shown that species vary considerably in their optimal temperature and precipitation for germination (Gya et al., 2023; Vandvik et al., 2017), and other work suggests that optimal germination temperatures do not necessarily relate to a species' distribution (Marques et al., 2014). Seed mass' lack of relation to climate difference sensitivities, even in models of colonization, may stem from disparities between the climate where a species occurs and the narrower weather window when a species germinates. Additionally, species in this system exhibit a range of clonal reproduction strategies that may be more important for recruitment dynamics than seed strategies (Guittar et al., 2016), further explaining the lack of differences among species in seed mass with CDS.

4.5 | Traits are unrelated to species precipitation difference sensitivity

We found less support that traits were related to precipitation difference sensitivities—a simple vote count of how many relationships had 95% CIs that did not include zero across all traits and models (24 total) for precipitation versus temperature was one versus 10, respectively. Almost all the species (88%) had ranges that were drier than our sites, suggesting that precipitation variation in this oceanic region (~800–4400 precipitation mm/year) is a relatively minor driver of vegetation dynamics (reviewed in Wilcox et al., 2017). Nevertheless, we found weak evidence that taller species increased in abundance and had higher colonization probability as site precipitation became more like their niche centre

precipitation. These results are in slight contrast with evidence that higher precipitation favours taller, larger bodied plants (Liu et al., 2019), but support our hypothesis that taller stature confers a competitive advantage at a species niche centre (Table 1). This further suggests that the extremely high precipitation found in our study system may actually act as a stressor that shortens growing season length via snowpack (Rixen et al., 2022) and may restrict photosynthetically active radiation via clouds (Nijp et al., 2015), rather than leading to higher productivity (Knapp et al., 2017; Seddon et al., 2016) and more competition for light. Therefore, given the extremity of this system, the precipitation results should not be extrapolated globally and sensitivity to precipitation deserves more study in other systems. Additionally, root traits may be better positioned to determine plant water use strategies than the aboveground traits we assessed (Li et al., 2017; Zwicke et al., 2015).

4.6 | Limitations

There are several caveats to consider when interpreting our results. First, because of data limitations, we assumed that the effects of climate transplant treatments were contained in climate difference estimates. This assumption is false in absolute terms, given that transplants also change the plant, herbivore, pollinator, etc. community in which a turf is embedded. Nevertheless, prior work suggests that this simplifying assumption is reasonable (Lynn, Klanderud, et al., 2021; Vandvik et al., 2020). It was impossible to include transplant climate treatments explicitly as a factor in the intraspecific models because it would thin data so that patterns of species responses with climate differences would be undetectable.

Second, the climate grid restricted the climate difference range observed for species, such that we only assessed CDS on one side of the species' temperature/precipitation niche. This may obscure patterns such as non-linearities. Additionally, the lack of full climate difference sampling for a species (e.g. maximum spanned $\Delta\text{MAT} \sim 6^\circ\text{C}$) may explain our surprising finding that many species perform better away from their niche centre, given we may not be sampling the extremes of a species possible climate difference. However, as stated above, there is growing evidence that species do not perform best at their niche centre (e.g. Sporbert et al., 2020), and our trait analysis may provide part of the explanation. Our modelling framework is well suited to any species performance observations over time and would benefit from testing across a greater spatial extent that encompasses the full spectrum of species' climate differences (e.g. Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012).

Finally, while a strength of our study is that it is based on trait data collected from within the study system, our trait data were obtained from individuals in the natural communities outside of the observed turfs (except for seed data), which could have two consequences. Given the prominence of intraspecific trait variation within

and across communities along environmental gradients (Siefert et al., 2015), trait values measured in one site may not reflect the trait expression of the individuals in permanent resampling plots in another site. We recognize that finer-grained trait data (e.g. site specific) might increase predictive power, but such data are difficult and time-consuming to obtain and thus would not be useful in making broad-scale predictions of responses to climate change. Additionally, intraspecific variation in our system was less than interspecific variations (Appendix S1), suggesting our trait sampling protocols provided useful data for prediction, as we found. Alternatively, past work suggests that traits may be most useful when viewed as syndromes of species measured in a common environment that reflect differences across species (Fridley et al., 2016; Grime et al., 1997; Reich, 2014; Shipley et al., 2016). However, this trait screening method would have been logistically and financially difficult in our system given the number of potential species (> 140).

5 | CONCLUSIONS

Generally, shorter plant species with more resource-acquisitive leaves had higher performance as sites became cooler than their niche centres. We found little evidence that seed mass was related to species climate difference sensitivities. Additionally, trait relationships to precipitation difference sensitivities were generally weaker than to temperature differences. Importantly, the results support the foundations of functional trait ecology (Shipley et al., 2016) and suggest the functional approach can be valuable for predicting future community and ecosystem responses to global change. The results provide a novel, mechanistic, trait-based explanation for the recent and puzzling findings that species do not perform best in their expected climatic optima. Furthermore, we suggest that this analysis framework is adaptable to any dataset with spatial/environmentally distributed observations of species performance over time that can be paired with traits. Expanding this framework to other systems is crucial to fully assess its potential as a tool for conservation.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13718>.

DATA AVAILABILITY STATEMENT

Data are available at Dryad (<https://doi.org/10.5061/dryad.63xsj3v69>) and code for all analyses can be found on GitHub (<https://github.com/jslynn33/macrocontext-and-traits>).

For peer review: <https://datadryad.org/stash/share/WbpdEhb2B8VC7JC3HDBxIRwoPQOdnCiYCbAv1Ja5bc>.

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REFERENCES

- Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M. A., Pauchard, A., Rabitsch, W., Rew, L. J., Sanders, N. J., & Pellissier, L. (2018). Lags in the response of mountain plant communities to climate change. *Global Change Biology*, 24(2), 563–579. <https://doi.org/10.1111/gcb.13976>
- Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S. A., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C., Forbes, B. C., Georges, D., Goetz, S. J., Guay, K. C., Henry, G. H. R., HilleRisLambers, J., Hollister, R. D., Karger, D. N., Kattge, J., Manning, P., ... Weiher, E. (2018). Plant functional trait change across a warming tundra biome. *Nature*, 562(7725), 57–62. <https://doi.org/10.1038/s41586-018-0563-7>
- Blonder, B., Moulton, D. E., Blois, J., Enquist, B. J., Graae, B. J., Macias-Fauria, M., McGill, B., Nogué, S., Ordonez, A., Sandel, B., & Svenning, J.-C. (2017). Predictability in community dynamics. *Ecology Letters*, 20(3), 293–306. <https://doi.org/10.1111/ele.12736>
- Blonder, B., Salinas, N., Patrick Bentley, L., Shenkin, A., Chambi Porroa, P. O., Valdez Teixeira, Y., Violle, C., Fyllas, N. M., Goldsmith, G. R., Martin, R. E., Asner, G. P., Díaz, S., Enquist, B. J., & Malhi, Y. (2017). Predicting trait-environment relationships for venation networks along an Andes-Amazon elevation gradient. *Ecology*, 98(5), 1239–1255. <https://doi.org/10.1002/ecy.1747>
- Bohner, T., & Diez, J. (2020). Extensive mismatches between species distributions and performance and their relationship to functional traits. *Ecology Letters*, 23(1), 33–44. <https://doi.org/10.1111/ele.13396>
- Britnell, J. A., Zhu, Y., Kerley, G. I. H., & Shultz, S. (2023). Ecological marginalization is widespread and increases extinction risk in mammals. *Proceedings of the National Academy of Sciences of the United States of America*, 120(3), e2205315120. <https://doi.org/10.1073/pnas.2205315120>
- Brown, J. H. (1995). *Macroecology*. University of Chicago Press.
- Bucher, S. F., & Römermann, C. (2021). The timing of leaf senescence relates to flowering phenology and functional traits in 17 herbaceous species along elevational gradients. *Journal of Ecology*, 109(3), 1537–1548. <https://doi.org/10.1111/1365-2745.13577>
- Chamberlain, S., & Boettiger, C. (2017). R python, and ruby clients for GBIF species occurrence data. *PeerJ PrePrints*. <https://doi.org/10.7287/peerj.preprints.3304v1>
- Chapin, F. S., & Shaver, G. R. (1985). Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, 66(2), 564–576. <https://doi.org/10.2307/1940405>
- Chelli, S., Simonetti, E., Wellstein, C., Campetella, G., Carnicelli, S., Andreetta, A., Giorgini, D., Puletti, N., Bartha, S., & Canullo, R. (2019). Effects of climate, soil, forest structure and land use on the functional composition of the understorey in Italian forests. *Journal of Vegetation Science*, 30(6), 1110–1121. <https://doi.org/10.1111/jvs.12792>
- Choi, S., Kempes, C. P., Park, T., Ganguly, S., Wang, W., Xu, L., Basu, S., Dungan, J. L., Simard, M., Saatchi, S. S., Piao, S., Ni, X., Shi, Y., Cao, C., Nemani, R. R., Knyazikhin, Y., & Myneni, R. B. (2016). Application of the metabolic scaling theory and water-energy balance equation to model large-scale patterns of maximum forest canopy height: Large-scale modeling of maximum forest height patterns. *Global Ecology and Biogeography*, 25(12), 1428–1442. <https://doi.org/10.1111/geb.12503>
- Dallas, T., Decker, R. R., & Hastings, A. (2017). Species are not most abundant in the Centre of their geographic range or climatic niche. *Ecology Letters*, 20(12), 1526–1533. <https://doi.org/10.1111/ele.12860>
- Daou, L., Garnier, É., & Shipley, B. (2021). Quantifying the relationship linking the community-weighted means of plant traits and soil fertility. *Ecology*, 102(9), e03454. <https://doi.org/10.1002/ecy.3454>
- DeMalach, N., Ron, R., & Kadmon, R. (2019). Mechanisms of seed mass variation along resource gradients. *Ecology Letters*, 22(1), 181–189. <https://doi.org/10.1111/ele.13179>
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529(7585), 167–171. <https://doi.org/10.1038/nature16489>
- Dong, K., Xu, Y., Hao, G., Yang, N., Zhao, N., & Gao, Y. (2020). Both vacant niches and competition-trait hierarchy are useful for explaining the invasion of *Caragana microphylla* into the semi-arid grassland. *Plant and Soil*, 448(1–2), 253–263. <https://doi.org/10.1007/s11104-020-04429-z>
- Dunne, J. A., Saleska, S. R., Fischer, M. L., & Harte, J. (2004). Integrating experimental and gradient methods in ecological climate change research. *Ecology*, 85(4), 904–916. <https://doi.org/10.1890/03-8003>
- Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., Collier, L. S., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Fosaa, A. M., Gould, W. A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D. S., Hofgaard, A., Jarrad, F., Jónsdóttir, I. S., ... Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time: Warming effects on tundra vegetation. *Ecology Letters*, 15(2), 164–175. <https://doi.org/10.1111/j.1461-0248.2011.01716.x>
- Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Dorrepaal, E., Elumeeva, T. G., Gill, M., Gould, W. A., Harte, J., Hik, D. S., Hofgaard, A., Johnson, D. R., Johnstone, J. F., Jónsdóttir, I. S., Jorgenson, J. C., ... Wipf, S. (2012). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, 2(6), 453–457. <https://doi.org/10.1038/nclimate1465>
- Fridley, J. D. (2017). Plant energetics and the synthesis of population and ecosystem ecology. *Journal of Ecology*, 105(1), 95–110. <https://doi.org/10.1111/1365-2745.12693>
- Fridley, J. D., Lynn, J. S., Grime, J. P., & Askew, A. P. (2016). Longer growing seasons shift grassland vegetation towards more-productive species. *Nature Climate Change*, 6(9), 865–868. <https://doi.org/10.1038/nclimate3032>
- Fristoe, T. S., Vilela, B., Brown, J. H., & Botero, C. A. (2023). Abundant-core thinking clarifies exceptions to the abundant-center distribution pattern. *Ecography*, 2023(2), e06365. <https://doi.org/10.1111/ecog.06365>
- Fuller, A., Mitchell, D., Maloney, S. K., Hetem, R. S., Fonsêca, V. F. C., Meyer, L. C. R., van de Ven, T. M. F. N., & Snelling, E. P. (2021). How dryland mammals will respond to climate change: The effects of body size, heat load and a lack of food and water. *Journal*

- of *Experimental Biology*, 224(Suppl 1), jeb238113. <https://doi.org/10.1242/jeb.238113>
- Gardner, J. L., Amano, T., Mackey, B. G., Sutherland, W. J., Clayton, M., & Peters, A. (2014). Dynamic size responses to climate change: Prevailing effects of rising temperature drive long-term body size increases in a semi-arid passerine. *Global Change Biology*, 20(7), 2062–2075. <https://doi.org/10.1111/gcb.12507>
- Goel, N., & Keitt, T. H. (2022). The mismatch between range and niche limits due to source-sink dynamics can be greater than species mean dispersal distance. *The American Naturalist*, 200(3), 448–455. <https://doi.org/10.1086/720420>
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Benito Alonso, J. L., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, M. R., Kazakis, G., Krajčí, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., ... Grabherr, G. (2012). Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2(2), 111–115. <https://doi.org/10.1038/nclimate1329>
- Griffin-Nolan, R. J., Blumenthal, D. M., Collins, S. L., Farkas, T. E., Hoffman, A. M., Mueller, K. E., Ocheltree, T. W., Smith, M. D., Whitney, K. D., & Knapp, A. K. (2019). Shifts in plant functional composition following long-term drought in grasslands. *Journal of Ecology*, 107(5), 2133–2148. <https://doi.org/10.1111/1365-2745.13252>
- Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, 242(5396), 344–347. <https://doi.org/10.1038/242344a0>
- Grime, J. P. (2006). *Plant strategies, vegetation processes, and ecosystem properties* (2nd ed.). Wiley.
- Grime, J. P., Thompson, K., Hunt, R., Hodgson, J. G., Cornelissen, J. H. C., Rorison, I. H., Hendry, G. A. F., Ashenden, T. W., Askew, A. P., Band, S. R., Booth, R. E., Bossard, C. C., Campbell, B. D., Cooper, J. E. L., Davison, A. W., Gupta, P. L., Hall, W., Hand, D. W., Hannah, M. A., ... Whitehouse, J. (1997). Integrated screening validates primary axes of specialisation in plants. *Oikos*, 79(2), 259. <https://doi.org/10.2307/3546011>
- Guittar, J., Goldberg, D., Klanderud, K., Telford, R. J., & Vandvik, V. (2016). Can trait patterns along gradients predict plant community responses to climate change? *Ecology*, 97(10), 2791–2801. <https://doi.org/10.1002/ecy.1500>
- Gya, R., Geange, S. R., Lynn, J. S., Töpfer, J. P., Wallevik, Ø., Zernichow, C., & Vandvik, V. (2023). A test of local adaptation to drought in germination and seedling traits in populations of two alpine forbs across a 2000 mm/year precipitation gradient. *Ecology and Evolution*, 13(2), e9772. <https://doi.org/10.1002/ece3.9772>
- Hanssen-Bauer, I., Førland, E. J., Haddeland, I., Hisdal, H., Mayer, S., Nesje, A., Nilsen, J. E. Ø., Sandven, S., Sandø, A. B., Sorteberg, A., & Ådlandsvik, B. (2017). *Climate in Norway 2100 – A knowledge base for climate adaptation* (free No. 1/2017; climate in Norway 2100, pp. 1–47). Miljø-Direktoratet Norge. <https://www.miljodirektoratet.no/globalassets/publikasjoner/M741/M741.pdf>
- Hobbs, N. T., & Hooten, M. B. (2015). *Bayesian models: A statistical primer for ecologists*. Princeton University Press.
- Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427.
- Kazakou, E., Vile, D., Shipley, B., Gallet, C., & Garnier, E. (2006). Covariations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology*, 20(1), 21–30. <https://doi.org/10.1111/j.1365-2435.2006.01080.x>
- Kichenin, E., Wardle, D. A., Peltzer, D. A., Morse, C. W., & Freschet, G. T. (2013). Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology*, 27(5), 1254–1261. <https://doi.org/10.1111/1365-2435.12116>
- Klanderud, K., Vandvik, V., & Goldberg, D. (2015). The importance of biotic vs. abiotic drivers of local plant community composition along regional bioclimatic gradients. *PLoS One*, 10(6), e0130205. <https://doi.org/10.1371/journal.pone.0130205>
- Knapp, A. K., Ciais, P., & Smith, M. D. (2017). Reconciling inconsistencies in precipitation–productivity relationships: Implications for climate change. *New Phytologist*, 214(1), 41–47. <https://doi.org/10.1111/nph.14381>
- Knight, C. A., Blois, J. L., Blonder, B., Macias-Fauria, M., Ordóñez, A., & Svenning, J.-C. (2020). Community assembly and climate mismatch in late quaternary eastern north American pollen assemblages. *The American Naturalist*, 195(2), 166–180. <https://doi.org/10.1086/706340>
- Körner, C. (2016). Plant adaptation to cold climates. *F1000Research*, 5, 2769. <https://doi.org/10.12688/f1000research.9107.1>
- Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S. J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J. H. C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., ... Westoby, M. (2016). Plant functional traits have globally consistent effects on competition. *Nature*, 529(7585), 204–207. <https://doi.org/10.1038/nature16476>
- Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N. E., Kattge, J., & Coomes, D. A. (2012). Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: Implications for forest community assembly. *Ecology Letters*, 15(8), 831–840. <https://doi.org/10.1111/j.1461-0248.2012.01803.x>
- Ladwig, L. M., Damschen, E. I., Martin-Blangy, S., & Alstad, A. O. (2018). Grasslands maintained with frequent fire promote cold-tolerant species. *Journal of Vegetation Science*, 29(3), 541–549. <https://doi.org/10.1111/jvs.12635>
- Laughlin, D. C., Leppert, J. J., Moore, M. M., & Sieg, C. H. (2010). A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology*, 24(3), 493–501. <https://doi.org/10.1111/j.1365-2435.2009.01672.x>
- Li, H., Liu, B., McCormack, M. L., Ma, Z., & Guo, D. (2017). Diverse below-ground resource strategies underlie plant species coexistence and spatial distribution in three grasslands along a precipitation gradient. *New Phytologist*, 216(4), 1140–1150. <https://doi.org/10.1111/nph.14710>
- Lid, J., & Lid, D. T. (2005). *Norsk flora (Norwegian flora)*. Samlaget.
- Liu, D., Peñuelas, J., Ogaya, R., Estiarte, M., Tielbörger, K., Slowik, F., Yang, X., & Bilton, M. C. (2018). Species selection under long-term experimental warming and drought explained by climatic distributions. *New Phytologist*, 217(4), 1494–1506. <https://doi.org/10.1111/nph.14925>
- Liu, H., Gleason, S. M., Hao, G., Hua, L., He, P., Goldstein, G., & Ye, Q. (2019). Hydraulic traits are coordinated with maximum plant height at the global scale. *Science Advances*, 5(2), eaav1332. <https://doi.org/10.1126/sciadv.aav1332>
- Louthan, A. M., Pringle, R. M., Goheen, J. R., Palmer, T. M., Morris, W. F., & Doak, D. F. (2018). Aridity weakens population-level effects of multiple species interactions on *Hibiscus meyeri*. *Proceedings of the National Academy of Sciences of the United States of America*, 115(3), 543–548. <https://doi.org/10.1073/pnas.1708436115>
- Lynn, J. S., Klanderud, K., Telford, R. J., Goldberg, D. E., & Vandvik, V. (2021). Macroecological context predicts species' responses to climate warming. *Global Change Biology*, 27(10), 2088–2101. <https://doi.org/10.1111/gcb.15532>
- Lynn, J. S., Miller, T. E. X., & Rudgers, J. A. (2021). Mammalian herbivores restrict the altitudinal range limits of alpine plants. *Ecology Letters*, 24(9), 1930–1942. <https://doi.org/10.1111/ele.13829>
- Ma, C.-S., Ma, G., & Pincebourde, S. (2021). Survive a warming climate: Insect responses to extreme high temperatures. *Annual Review of Entomology*, 66(1), 163–184. <https://doi.org/10.1146/annurev-ento-041520-074454>

- Marques, A. R., Atman, A. P. F., Silveira, F. A. O., & de Lemos-Filho, J. P. (2014). Are seed germination and ecological breadth associated? Testing the regeneration niche hypothesis with bromeliads in a heterogeneous neotropical montane vegetation. *Plant Ecology*, 215(5), 517–529. <https://doi.org/10.1007/s11258-014-0320-4>
- Michaletz, S. T., Weiser, M. D., Zhou, J., Kaspari, M., Helliker, B. R., & Enquist, B. J. (2015). Plant thermoregulation: Energetics, trait–environment interactions, and carbon economics. *Trends in Ecology & Evolution*, 30(12), 714–724. <https://doi.org/10.1016/j.tree.2015.09.006>
- Moles, A. T. (2018). Being John Harper: Using evolutionary ideas to improve understanding of global patterns in plant traits. *Journal of Ecology*, 106(1), 1–18. <https://doi.org/10.1111/1365-2745.12887>
- Moles, A. T., Perkins, S. E., Laffan, S. W., Flores-Moreno, H., Awasthy, M., Tindall, M. L., Sack, L., Pitman, A., Kattge, J., Aarssen, L. W., Anand, M., Bahn, M., Blonder, B., Cavender-Bares, J., Cornelissen, J. H. C., Cornwell, W. K., Díaz, S., Dickie, J. B., Freschet, G. T., ... Bonser, S. P. (2014). Which is a better predictor of plant traits: Temperature or precipitation? *Journal of Vegetation Science*, 25(5), 1167–1180. <https://doi.org/10.1111/jvs.12190>
- Moutouama, J. K., & Gaoue, O. G. (2023). Effects of range and niche position on population dynamics of a tropical plant. *Ecology*, 104, e3990. <https://doi.org/10.1002/ecy.3990>
- Nijp, J. J., Limpens, J., Metselaar, K., Peichl, M., Nilsson, M. B., van der Zee, S. E. A. T. M., & Berendse, F. (2015). Rain events decrease boreal peatland net CO₂ uptake through reduced light availability. *Global Change Biology*, 21(6), 2309–2320. <https://doi.org/10.1111/gcb.12864>
- Normand, S., Ricklefs, R. E., Skov, F., Bladt, J., Tackenberg, O., & Svenning, J.-C. (2011). Postglacial migration supplements climate in determining plant species ranges in Europe. *Proceedings of the Royal Society B: Biological Sciences*, 278(1725), 3644–3653. <https://doi.org/10.1098/rspb.2010.2769>
- Occdownload Gbif.Org. (2019a). *Occurrence download* (p. 548705285) [Darwin Core archive]. The Global Biodiversity Information Facility. <https://doi.org/10.15468/DL.KGT63R>
- Occdownload Gbif.Org. (2019b). *Occurrence download* (p. 2984632) [Darwin Core archive]. The Global Biodiversity Information Facility. <https://doi.org/10.15468/DL.TEJ1MJ>
- Pardee, G. L., Griffin, S. R., Stemkovski, M., Harrison, T., Portman, Z. M., Kazenel, M. R., Lynn, J. S., Inouye, D. W., & Irwin, R. E. (2022). Life-history traits predict responses of wild bees to climate variation. *Proceedings of the Royal Society B: Biological Sciences*, 289(1973), 20212697. <https://doi.org/10.1098/rspb.2021.2697>
- Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Benito Alonso, J. L., Coldea, G., Dick, J., Erschbamer, B., Fernández Calzado, R., Ghosn, D., Holten, J. I., Kanka, R., Kazakis, G., Kollár, J., Larsson, P., Moiseev, P., Moiseev, D., Molau, U., ... Grabherr, G. (2012). Recent plant diversity changes on Europe's mountain summits. *Science*, 336(6079), 353–355. <https://doi.org/10.1126/science.1219033>
- Peng, A., Klanderud, K., Wang, G., Zhang, L., Xiao, Y., & Yang, Y. (2020). Plant community responses to warming modified by soil moisture in the Tibetan plateau. *Arctic, Antarctic, and Alpine Research*, 52(1), 60–69. <https://doi.org/10.1080/15230430.2020.1712875>
- Perez, T. M., Andino, J. E. G., Rivas-Torres, G., & Feeley, K. J. (2023). Climate constrains photosynthetic strategies in Darwin's daisies: A test of the climatic variability and jack-of-all-trades hypotheses. *The American Naturalist*, 201(1), 78–90. <https://doi.org/10.1086/721957>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61(3), 167. <https://doi.org/10.1071/BT12225>
- Pironon, S., Papuga, G., Villellas, J., Angert, A. L., García, M. B., & Thompson, J. D. (2017). Geographic variation in genetic and demographic performance: New insights from an old biogeographical paradigm: The Centre-periphery hypothesis. *Biological Reviews*, 92(4), 1877–1909. <https://doi.org/10.1111/brv.12313>
- Plummer, M. (2003). *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*. Proceedings of the 3rd international workshop on distributed statistical computing, 124, 125.
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Reich, P. B., Sendall, K. M., Rice, K., Rich, R. L., Stefanski, A., Hobbie, S. E., & Montgomery, R. A. (2015). Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. *Nature Climate Change*, 5(2), 148–152. <https://doi.org/10.1038/nclimate2497>
- Rixen, C., Høye, T. T., Macek, P., Aerts, R., Alatalo, J., Andeson, J., Arnold, P., Barrio, I. C., Bjerke, J., Björkman, M. P., Blok, D., Blume-Werry, G., Boike, J., Bokhorst, S., Carbognani, M., Christiansen, C., Convey, P., Cooper, E. J., Cornelissen, J. H. C., ... Zong, S. (2022). Winters are changing: Snow effects on Arctic and alpine tundra ecosystems. *Arctic Science*, 8, 572–608. <https://doi.org/10.1139/AS-2020-0058>
- Royal Botanic Gardens Kew. (2021). *Seed Information Database (SID) (Version 7.1)*. <http://data.kew.org/sid/>
- Savage, J., & Vellend, M. (2015). Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography*, 38(6), 546–555.
- Schramski, J. R., Dell, A. I., Grady, J. M., Sibly, R. M., & Brown, J. H. (2015). Metabolic theory predicts whole-ecosystem properties. *Proceedings of the National Academy of Sciences of the United States of America*, 112(8), 2617–2622. <https://doi.org/10.1073/pnas.1423502112>
- Seddon, A. W. R., Macias-Fauria, M., Long, P. R., Benz, D., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, 531(7593), 229–232. <https://doi.org/10.1038/nature16986>
- Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, 1(8), 401–406. <https://doi.org/10.1038/nclimate1259>
- Shiple, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, 180(4), 923–931. <https://doi.org/10.1007/s00442-016-3549-x>
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., L. Dantas, V., Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., ... Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18(12), 1406–1419. <https://doi.org/10.1111/ele.12508>
- Simpson, A. H., Richardson, S. J., & Laughlin, D. C. (2016). Soil-climate interactions explain variation in foliar, stem, root and reproductive traits across temperate forests. *Global Ecology and Biogeography*, 25(8), 964–978. <https://doi.org/10.1111/geb.12457>
- Soper Gorden, N. L., Winkler, K. J., Jahnke, M. R., Marshall, E., Horkey, J., Hudelson, C., & Etterson, J. R. (2016). Geographic patterns of seed mass are associated with climate factors, but relationships vary between species. *American Journal of Botany*, 103(1), 60–72. <https://doi.org/10.3732/ajb.1500295>
- Soudzilovskaia, N. A., Elumeeva, T. G., Onipchenko, V. G., Shidakov, I. I., Salpagarova, F. S., Khubiev, A. B., Tekeev, D. K., & Cornelissen, J. H. C. (2013). Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proceedings*

- of the National Academy of Sciences of the United States of America, 110(45), 18180–18184. <https://doi.org/10.1073/pnas.1310700110>
- Sporbert, M., Keil, P., Seidler, G., Bruelheide, H., Jandt, U., Ačić, S., Biurrun, I., Campos, J. A., Čarni, A., Chytrý, M., Čušterevska, R., Dengler, J., Golub, V., Jansen, F., Kuzemko, A., Lenoir, J., Marcenò, C., Moeslund, J. E., Pérez-Haase, A., ... Welk, E. (2020). Testing macroecological abundance patterns: The relationship between local abundance and range size, range position and climatic suitability among European vascular plants. *Journal of Biogeography*, 47(10), 2210–2222. <https://doi.org/10.1111/jbi.13926>
- Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A. D., Breiner, F. T., Burg, S., Czortek, P., Dawes, M. A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V. A., ... Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556(7700), 231–234. <https://doi.org/10.1038/s41586-018-0005-6>
- Su, Y.-S., & Yajima, M. (2015). *R2jags: Using R to Run "JAGS"*. <https://CRAN.R-project.org/package=R2jags>
- Svenning, J.-C., & Sandel, B. (2013). Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany*, 100(7), 1266–1286. <https://doi.org/10.3732/ajb.1200469>
- Urban, M. C. (2015). Accelerating extinction risk from climate change. *Science*, 348(6234), 571–573. <https://doi.org/10.1126/science.aaa4984>
- VanDerWal, J., Shoo, L. P., Johnson, C. N., & Williams, S. E. (2009). Abundance and the environmental niche: Environmental suitability estimated from niche models predicts the upper limit of local abundance. *The American Naturalist*, 174(2), 282–291. <https://doi.org/10.1086/600087>
- Vandvik, V., Elven, R., & Töpper, J. (2017). Seedling recruitment in sub-alpine grassland forbs: Predicting field regeneration behaviour from lab germination responses. *Botany*, 95(1), 73–88. <https://doi.org/10.1139/cjb-2016-0022>
- Vandvik, V., Skarpaas, O., Klanderud, K., Telford, R. J., Halbritter, A. H., & Goldberg, D. E. (2020). Biotic rescaling reveals importance of species interactions for variation in biodiversity responses to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 117(37), 22858–22865. <https://doi.org/10.1073/pnas.2003377117>
- Venn, S., Pickering, C., & Green, K. (2014). Spatial and temporal functional changes in alpine summit vegetation are driven by increases in shrubs and graminoids. *AoB Plants*, 6, plu008. <https://doi.org/10.1093/aobpla/plu008>
- Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, 199(2), 213–227. <https://doi.org/10.1023/A:1004327224729>
- Wilcox, K. R., Blumenthal, D. M., Kray, J. A., Mueller, K. E., Derner, J. D., Ocheltree, T., & Porensky, L. M. (2021). Plant traits related to precipitation sensitivity of species and communities in semiarid shortgrass prairie. *New Phytologist*, 229(4), 2007–2019. <https://doi.org/10.1111/nph.17000>
- Wilcox, K. R., Shi, Z., Gherardi, L. A., Lemoine, N. P., Koerner, S. E., Hoover, D. L., Bork, E., Byrne, K. M., Cahill, J., Collins, S. L., Evans, S., Gilgen, A. K., Holub, P., Jiang, L., Knapp, A. K., LeCain, D., Liang, J., Garcia-Palacios, P., Peñuelas, J., ... Luo, Y. (2017). Asymmetric responses of primary productivity to precipitation extremes: A synthesis of grassland precipitation manipulation experiments. *Global Change Biology*, 23(10), 4376–4385. <https://doi.org/10.1111/gcb.13706>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. <https://doi.org/10.1038/nature02403>
- Yamori, W., Hikosaka, K., & Way, D. A. (2014). Temperature response of photosynthesis in C3, C4, and CAM plants: Temperature acclimation and temperature adaptation. *Photosynthesis Research*, 119(1–2), 101–117. <https://doi.org/10.1007/s11220-013-9874-6>
- Zhang, J., He, N., Liu, C., Xu, L., Chen, Z., Li, Y., Wang, R., Yu, G., Sun, W., Xiao, C., Chen, H. Y. H., & Reich, P. B. (2020). Variation and evolution of C:N ratio among different organs enable plants to adapt to N-limited environments. *Global Change Biology*, 26(4), 2534–2543. <https://doi.org/10.1111/gcb.14973>
- Zhang, K., Li, M., Su, Y., & Yang, R. (2020). Stoichiometry of leaf carbon, nitrogen, and phosphorus along a geographic, climatic, and soil gradients in temperate desert of Hexi corridor, Northwest China. *Journal of Plant Ecology*, 13(1), 114–121. <https://doi.org/10.1093/jpe/rtz045>
- Zhao, N., He, N., Wang, Q., Zhang, X., Wang, R., Xu, Z., & Yu, G. (2014). The altitudinal patterns of leaf C:N:P stoichiometry are regulated by plant growth form, climate and soil on Changbai Mountain, China. *PLoS One*, 9(4), e95196. <https://doi.org/10.1371/journal.pone.0095196>
- Zwicke, M., Picon-Cochard, C., Morvan-Bertrand, A., Prud'homme, M.-P., & Volaire, F. (2015). What functional strategies drive drought survival and recovery of perennial species from upland grassland? *Annals of Botany*, 116(6), 1001–1015. <https://doi.org/10.1093/aob/mcv037>

BIOSKETCH

Joshua S. Lynn is an ecologist interested in integrating information across scales to make predictions on species responses to global change. The authors are part of the 'Between the Fjords' working group and are generally interested in global change ecology with a focus on plants in mountain landscapes.

Author contributions: J.S.L. conceived of the analyses in collaboration with D.E.G. and V.V. V.V. and D.E.G. designed the experiment. K.K. and V.V. set up the experiment and collected the data. R.G. collected the trait data and made the conceptual figure. R.J.T. managed the experimental data. J.S.L. gathered the GBIF data and performed all analyses. J.S.L. drafted the manuscript with input from all authors.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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