PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

Macroecological context predicts species' responses to climate warming

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Abstract

Context-dependencies in species' responses to the same climate change frustrate attempts to generalize and make predictions based on experimental and observational approaches in biodiversity science. Here, we propose predictability may be enhanced by explicitly incorporating macroecological context into analyses of species' responses to climate manipulations. We combined vascular plant species' responses to an 8-year, 12-site turf transplant climate change experiment set in southwestern Norway with climate niche data from the observed 151 species. We used the difference between a species' mean climate across their range and climate conditions at the transplant site ("climate differences") to predict colonization probability, extinction probability, and change in abundance of a species at a site. In analyses across species that ignore species-specific patterns, colonization success increased as species' distribution optima were increasingly warmer than the experimental target site. Extinction probability increased as species' distribution optima were increasingly colder than the target site. These patterns were reflected in change in abundance analyses. We found weak responses to increased precipitation in these oceanic climates. Climate differences were better predictors of species' responses to climate manipulations than range size. Interestingly, similar patterns were found when analyses focused on variation in species-specific responses across sites. These results provide an experimental underpinning to observational studies that report thermophilization of communities and suggest that space-for-time substitutions may be valid for predicting species' responses to climate warming, given other conditions are accounted for (e.g., soil nutrients). Finally, we suggest that this method of putting climate change experiments into macroecological context has the potential to generalize and predict species' responses to climate manipulations globally.

KEYWORDS
abundance, Bayesian modeling, biodiversity, climate niche, colonization, extinction, macroecological experiment, range size, transplant, vascular plants

1 | INTRODUCTION

Climate change is altering biotic communities, leading to biodiversity loss and disruptions of ecosystem functions and services. Plants respond to climate change through shifts in leaf and flowering phenology (Buitenwerf et al., 2015; CaraDonna et al., 2014; Heberling et al., 2019; Vandvik et al., 2018; Vitasse et al., 2018) and altered metabolic and growth rates (Dusenge et al., 2019; Reich et al., 2015). Such individual-level responses are likely responsible for ecological consequences such as geographic range expansions and contractions (Chen et al., 2011; Colwell et al., 2008; Dullinger et al., 2012; Kelly & Goulden, 2008) and increased local and global extinction risk (Thomas et al., 2004; Urban, 2015). As species and communities respond to climate change, ecosystem functions and services such as carbon sequestration (Kaplan et al., 2012) and recreation and cultural services (Locatelli et al., 2017; Mace et al., 2012) may be diminished or altered. The climate-driven changes to ecosystems that can harm society necessitate innovative predictive techniques to inform evidence-based management and mitigation decisions.

Climate change experiments and distribution modeling have been key for understanding and predicting the population- and community-level consequences of climate change. For instance, long-term *in situ* warming experiments suggest climate warming will shift vascular plant communities toward more competitive and productive species in a temperate grassland (Fridley et al., 2016) and will increase the dominance of shrubs in a montane temperate grassland (Harte et al., 2015). Turf transplant experiments, where whole plant communities are moved to new sites in the direction of projected climate change, suggest that increased temperatures with climate change may depress the population growth of cold-adapted plant species (Töpper et al., 2018) and that taller, more clonal species will increase in abundance with warming (Guittar et al., 2016). Such climate manipulations are valuable in allowing causal inferences but species' responses can be difficult to generalize as outcomes often vary considerably depending on the abiotic and/or biotic contexts of a particular experiment (Dunne et al., 2004; Vandvik et al., 2020) or species-specific traits or strategies (Fridley et al., 2016). An alternative approach, species distribution modeling, predicts where a species will occur with further climate change based on the species' current/historical distribution and associated climate data (Dyderski et al., 2018; Zhang et al., 2014). Though, unlike experimental approaches, distribution models can generalize and account for uncertainty across many disparate contexts, the observational nature of distribution models and associated extrapolations to future climates makes their validity difficult to test (Early & Sax, 2014).

Some of the challenges of making predictions based on experiments or distribution modeling alone may be overcome by putting climate change experiments into their macroecological context, effectively combining the strengths of both approaches. Climate change experiments are often performed at one site with species that have much broader geographic distributions, encompassing a wide range of climate conditions. We can put an experiment into macroecological context by relating species' responses to climate treatments to their geographic distribution in climate space. For instance, in a nighttime warming and drought experiment, the abundance of species with distributions centered in cooler climates responded more negatively to experimental warming than did species centered in warmer climates (Liu et al., 2018). Additionally, the abundance of species with distributions centered in regions with wetter springs responded more negatively to experimental drought than did species with distributions in drier climates (Liu et al., 2018). Similarly, under climate warming, tree species with distributions centered in colder climates had lower stem growth and net photosynthesis than species with warmer distributions (Reich et al., 2015). These past analyses using species' climate distributions to predict response to experimental climate change have thus far been limited to one or two sites (Liu et al., 2018; Reich et al., 2015). This makes it difficult to disentangle if species' responses to climate treatments depend on site-specific contexts (e.g., soil nutrients, humidity), and more generally to assess if climate distribution-based approaches can be used to generalize context-dependent responses across species, treatments, and sites.

Here, we use a multisite community transplant experiment for a powerful test of how macroecological context performs in predicting species' responses to climate change (Figure 1). We focused on extinction, colonization, and change in abundance (vegetative cover) as measures of species' responses to climate manipulations. Our experiment has 12 sites representing a factorial climate grid with three temperature levels with 4°C variation in mean annual temperature, four precipitation levels spanning 2200 mm in annual precipitation, and contains 151 naturally occurring vascular plant species. Across all sites, intact turfs containing natural plant communities are transplanted toward warmer, wetter, and warmer and wetter climates to experimentally assess responses to projected climate changes. Thus, the experiment has a very large number of distinct climate contrasts between local transplant site climate and the species' climate niche. Previous work in this system found that communities moved warmer, wetter, and both warmer and wetter, experienced higher rates of both extinctions and colonizations compared to local controls, but with considerable variation in the rates of both colonization and extinction (Vandvik et al., 2020). Additionally, species that grow taller and are better lateral spreaders (e.g., have more persistent belowground meristems) increased in abundance after experimental warming (Guittar et al., 2016). We build on this previous research by expanding from single functional traits to using climate niches as a way of integrating multiple traits that interact to determine species' distributions and climate responses.

Rather than using climate niches directly as predictors of species' responses to climate change (e.g., Liu et al., 2018; Reich et al., 2015), we use the difference between the local climate in each experimental site and treatment and each species' climate niche. This makes predictions contextual rather than absolute, allowing generalization of model predictions across disparate biomes and climatic contexts. Similar difference-based models have been used to assess competitive hierarchies (Kunstler et al., 2012) and the predictability of plant
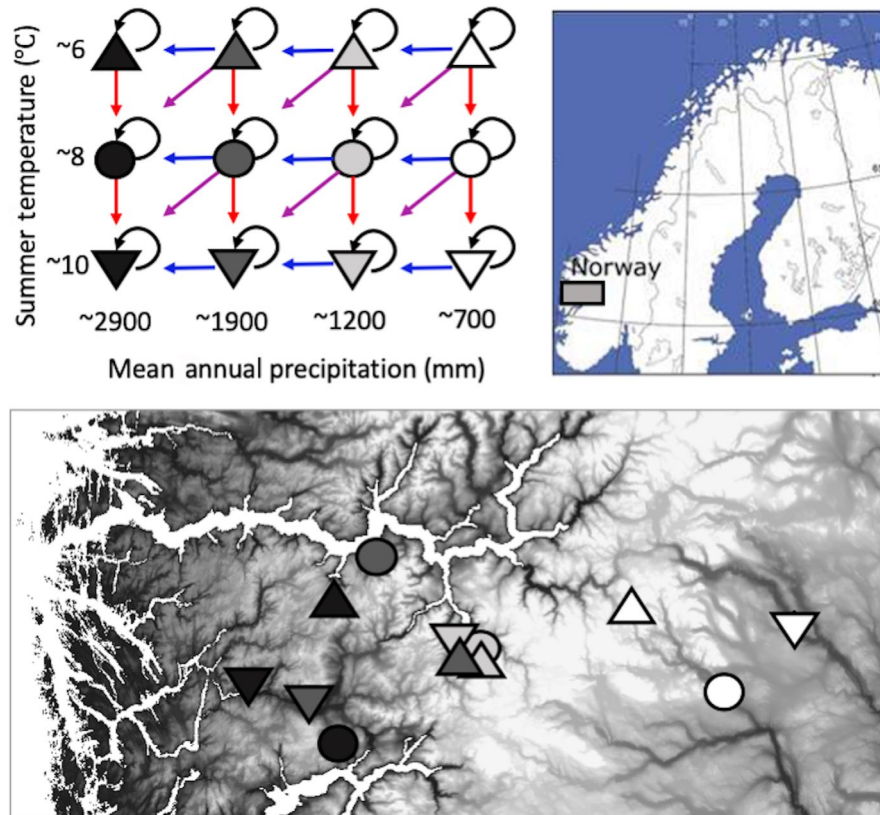
FIGURE 1 Experimental warming and wetting were implemented in a 12-site factorial turf transplant design set in southwestern Norway. The top-right panel places the experimental region in context with Norway and Scandinavia with the gray square. The bottom panel is a close-up of the experimental region with all 12 sites marked by treatments represented in the top left panel. In the bottom panel, lighter colors in the map represent higher elevations, while darker colors are lower elevations. The top-left panel represents the experimental grid setup, where control turfs were left at their site (black arrows, 12 sites), warmed turfs were moved ~2°C warmer in summer temperature (red arrows, eight sites), moved wetter in mean annual precipitation from 500 to 1000 mm (blue arrows, nine sites), or moved both warmer and wetter (purple arrows, six sites). We predict species' responses to these climate treatments by taking the mean climate of their occurrences across Europe (species' climate niche center)

communities through time (Blonder et al., 2017). We predicted that species from progressively warmer and/or wetter ranges relative to the experimental site would increase in abundance and have higher colonization and lower extinction probability in warming and/or wetting treatments. These predictions are intuitive, but not inevitably correct. For example, species may occupy climate microsites that are not represented by coarser measures of climate within a landscape and across their range, in which case climate difference could be unrelated to species' responses to climate change (Ackerly et al., 2020). Additionally, climate differences will not reflect species' physiological adaptations and be poor predictors if species' geographic ranges are largely determined by dispersal and/or biotic interactions and, therefore, do not fill their potential climate space. To capture the potential effects of such other aspects of a species' biology, we used range size (RS) as an alternative predictor of response to climate change, given a species' RS is linked to dispersal ability and/or limiting biotic interactions (Gaston, 1996; Sheth et al., 2020). We expected colonization probability and abundance to increase, and extinction probability to decrease with species' RS in response to warming and/or wetting treatments.

To test these hypotheses, we conducted two sets of analyses. First, we analyzed the full dataset, across all vascular plant species and sites, to investigate how generally climate differences can predict responses to experimental treatments. This general "species-ignorant" analysis is advantageous because it can be used to predict responses within new plant communities and sites, using macroecological context alone. We then performed "species-specific" analyses for species occurring in multiple sites to investigate how climate

differences predicted intraspecific variation in performance. This analysis allows us to assess the variation in species' responses underlying the "species-ignorant" analyses, and to make more accurate species-specific predictions that can be applied to the same species in a different macroecological context.

2 | MATERIALS AND METHODS

2.1 | Turf transplant experiment

In 2009, we implemented a turf transplant experiment across 12 grassland sites in southwestern Norway (Figure 1; Klanderud et al., 2015; Töpper et al., 2018; Vandvik et al., 2020). The regional distribution of the sites created a factorial climatic grid with three summer temperature levels (alpine ~6°C, subalpine ~8°C, boreal ~10°C) and four levels of annual precipitation (~700, 1200, 1900, and 2900 mm) using downscaled climate data from the "normal period" of 1961–1990 (met.no). All other aspects of the sites were similar, including calcareous substrate, south-facing, shallow slopes, and a history of moderate grazing (Klanderud et al., 2015). The experiment was designed to reflect future climate change scenarios for Norway (Hanssen-Bauer et al., 2017; IPCC, 2014), where the climate is expected to get warmer and wetter. Therefore, we factorially moved turfs (intact vegetation communities) from a starting climate to a site that was one "step" warmer in the grid (~2°C, eight site-to-site transplant treatments), one "step" wetter (~600–700 mm, nine site-to-site transplants), or both (six site-to-site transplants, denoted as

"warmer/wetter"), within the climate grid. Each site had five replicate blocks containing one of each transplant treatment as well as two types of control plots—one that was dug up and transplanted back in the same block and one where the vegetation was left intact. After 2015, the local dug up control plots were abandoned, as no evidence of local transplant effects was detected. Blocks were surrounded by electric fencing to protect the experiment but mowed annually to simulate historical grazing. All treatments were randomized within blocks. Each turf was 29 × 29 cm in area and ~10 cm in depth. The inner 25 × 25 cm was analyzed for treatment effects and the outer edge was a buffer for edge effects. We refer to experimental treatments as "controls" and "warmer," "wetter," or "warmer/wetter."

Plant communities were surveyed (visual estimates of percent cover by species) prior to transplanting in the summer of 2009. The vegetation was left to recover in 2010, then surveyed in 2011, 2012, 2013, 2015, and 2017. Nomenclature follows Lid and Lid (2005). Local extinctions were defined by a species being present in the initial (2009) survey but absent in the final survey (2017) and colonizations were species that were absent in the initial survey but present in the final survey. Analyses were performed including all species observed within a plot in the sampling years. Therefore, colonists were counted as "not extinct" in the extinction models and extinctions were counted as "not a colonist" in the colonization models. To examine if this decision altered results, we ran the same analyses dropping colonists for extinction analyses and vice versa for colonization analyses and found the same results, qualitatively (Supporting Information 1). We measured change in cover in the plots with the following equation:

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

where Δc is the change in cover for a given species, s, determined by cover (c) of the species at the final sampling, f, minus the species initial cover, i. We added one to initial and final cover to avoid taking the natural log of zeros. In addition to this main analysis, we analyzed change in cover without extinctions and colonizations (all species present at the beginning and end of the experiment) and found qualitatively similar results (Supporting Information 1).

2.2 | Species' geographic and climate data

For each species (151, after excluding unidentified taxa) in our experiment, we extracted European occurrence data for the years 1950–2019 from the Global Biodiversity Information Facility (GBIF) using the *rgbif* package (Chamberlain & Boettiger, 2017). This resulted in 5,823,882 occurrence records (data available at https://www.gbif.org/occurrence/download/0024756-191105090559680 and https://www.gbif.org/occurrence/download/0024723-191105090559680). We restricted the search to Europe and excluded duplicate records, Greenland, observations east of 50°E, islands south of 29°N latitude, observations clearly from the ocean (27 total),

and observations with coordinate uncertainty greater than 100 km. We restricted our search to Europe to capture populations that are likely most representative/related to the climate niche of the species in our experiment. We ran models using data from the entire globe as well, finding the same results, qualitatively (Table S1.1). We then calculated species' RS in km^2 by projecting their occurrences into the Lambert azimuthal equal area coordinate system and calculating their convex hull from a raster with grid cell length of 50 km (Morueta-Holme et al., 2013). All species had >3 occurrences, allowing for a proper estimate of the convex hull. Ocean area was included to represent the species' potential RS and dispersal ability. We caution that RSs are likely underestimated due to incomplete geographic sampling (Isaac & Pocock, 2015). The occurrence data were biased toward Northwestern Europe with high occurrence density in a few countries (mainly Norway, Sweden, Denmark, Belgium, and the Netherlands), which was expected, given the study areas' location in western Norway at the northwestern edge of Europe. However, to reduce the representation of these highly sampled areas in our species' climate niche estimates, we created a raster grid with cell length equal to 0.0083° and sampled a single representative point from the occurrence data per grid cell. The grid resolution approximates the 30 s resolution of the climate data.

We used geographic occurrences to extract range-wide climate data of the species using the 30 s resolution WORLDCLIM version 2.0 database (Fick & Hijmans, 2017). We used the subsampled occurrence data to extract mean annual temperature (MAT in °C), temperature of the warmest quarter (summer temperature or T_s in °C), and annual precipitation (AP in m). MAT and T_s were highly correlated ($r = 0.87$), so we constructed analyses with only MAT. Additionally, we used data from the Global Aridity and Potential Evapotranspiration Climate Database (Trabucco & Zomer, 2019) for potential evapotranspiration (PET in m, Penman–Monteith equation) and aridity (aridity = AP/PET, unitless) as alternative climate variables, but found that PET was highly correlated with MAT and T_s ($r > 0.98$ and $r > 0.97$, respectively) and aridity was highly correlated with AP ($r > 0.87$). Therefore, we continued analyses with only MAT and AP, as these were the axes of climate variation used for the construction of our experiment. The climate means of subsampled and full occurrence data were highly correlated (all $r = 0.99$). We calculated the mean and median of each climate variable but only used the means in analyses as they were highly correlated (MAT $r = 0.99$, AP $r = 0.96$). We refer to species' mean temperature or precipitation as their "climate niche center."

We then extracted climate data for the experimental sites using the 30 s resolution WORLDCLIM data to stay consistent between climate data source for the experiment and the species' ranges. For each species in each treatment and site, we calculated the "climate difference" or Δ climate variables (i.e., ΔMAT, ΔAP) as the climate niche center minus site climate, using the climate of the destination site for transplant treatment to reflect the species' performance under the experimentally manipulated climate. Climate difference values above zero are cases where a species' climate niche center was hotter or moister than the climate to which the species was

transplanted, while negative values indicate the species' climate niche center was cooler or drier than the experimental climate.

2.3 | Statistical analyses

We assess the predictions of macroecological context with two analyses. First, we ask broadly how climate differences predict responses to treatments of all species while ignoring species' identity to fit a common model of how performance relates to climate differences and transplant treatment. Second, we zoom in to assess explicitly how climate differences predict the responses of individual species that occur in multiple climatic contexts. In all analyses, each data point represents one species in one turf.

2.3.1 | Species-ignorant analyses

To investigate if climate differences predicted species' responses to climate change treatments, we fit models where climate differences were used to predict the response of each population to the turf transplant climate change experiment in each site. For each dependent variable (colonization, extinction, and change in cover), we fit Bayesian hierarchical models (Hobbs & Hooten, 2015) to compare the climate difference variables and RS in their ability to predict responses to climate change manipulations. The combined climate difference model is:

$$
\begin{aligned}
\mu = {}& \text{warmer}_{(0,1)} * \text{wetter}_{(0,1)} * \Delta\text{MAT} * \Delta\text{AP} \\
& + N\left(0, \sigma_{\text{site}}^2\right) + N\left(0, \sigma_{\text{block}}^2\right) + N\left(0, \sigma_{\text{turf}}^2\right) \\
& + N\left(0, \sigma_{\text{species}}^2\right) + N\left(0, \sigma_{\text{family}}^2\right),
\end{aligned}
\tag{1}
$$

where the dependent variable, μ, is fit by the full factorial interaction of the turf transplant treatments (warmer(0,1) and wetter(0,1)) and climate difference variables (ΔMAT and ΔAP). This model fits a total of 16 fixed effect slope and intercept terms. First, there is a global intercept representing the probability of colonization/extinction or change in cover when a species' climate niche center equals site climate (ΔMAT and ΔAP =0) in control plots (warmer(0)*wetter(0)). Next, overall effects of warming (warmer(1)), wetting (wetter(1)), or both (warmer(1)*wetter(1)) are fit with treatment-specific effects (intercepts). Then, to characterize how species with climate niche centers different than the site climate (ΔMAT and/or ΔAP ≠0) change in their probability of colonization/extinction or change in abundance in each of the four treatments, we fit treatment effects with slopes for ΔMAT, ΔAP, and their interaction (12 slopes in total). ΔMAT and ΔAP were left on their original scales (°C for temperature and m/year for precipitation). The other parameters are random (group-level) intercept variance (σ^2) terms that describe the variance in means among groups for turfs (173) nested within block (60), nested within site (12), and species (151) nested in families (42).

We then investigated if species with larger ranges responded positively to climate change treatments with:

$$
\begin{aligned}
\mu = {}& \text{warmer}_{(0,1)} * \text{wetter}_{(0,1)} * \text{RS} + N\left(0, \sigma_{\text{site}}^2\right) \\
& + N\left(0, \sigma_{\text{block}}^2\right) + N\left(0, \sigma_{\text{turf}}^2\right) + N\left(0, \sigma_{\text{species}}^2\right) \\
& + N\left(0, \sigma_{\text{family}}^2\right),
\end{aligned}
\tag{2}
$$

where all of the parameters and variables are the same as in Equation (1), but climate difference variables have been substituted with RS. RS was scaled to have a mean of 0 and standard deviation of 0.5 prior to analysis. Similar to Equation (1), this model contains four intercept parameters representing the effect of treatments on a given dependent variable when RS =0 and four slope parameters characterizing the relationship between RS between a dependent variable for each of the four treatments. Similar models to Equation (2) were run investigating how each climate difference variable (i.e., ΔMAT, ΔAP) alone predicted species' response to the experimental treatments.

Finally, we combined these models to investigate if climate differences and RS explain the same variance in each dependent variable, or if there is added predictive value by incorporating both:

$$
\begin{aligned}
\mu = {}& \text{warmer}_{(0,1)} * \text{wetter}_{(0,1)} * \Delta\text{MAT} * \Delta\text{AP} \\
& + \text{warmer}_{(0,1)} * \text{wetter}_{(0,1)} * \text{RS} + N\left(0, \sigma_{\text{site}}^2\right) \\
& + N\left(0, \sigma_{\text{block}}^2\right) + N\left(0, \sigma_{\text{turf}}^2\right) + N\left(0, \sigma_{\text{species}}^2\right) \\
& + N\left(0, \sigma_{\text{family}}^2\right).
\end{aligned}
\tag{3}
$$

All the parameters and variables are the same as in Equations (1) and (2). Equation (3) fits a total of 20 fixed effect parameters as a combination of Equations (1) and (2) without an interaction of RS and climate differences.

We compared these models using Watanabe–Akaike information criterion (WAIC) and leave-one out cross-validation (LOOCV) to determine which combination of variables best predicted species' responses to climate manipulations while taking into account model complexity (Hooten & Hobbs, 2015). We calculated the criterion with the "loo" package (Yao et al., 2017). For all models, we used vague priors that were normal for slope and intercept terms (N(0, 1E-6)) and gamma priors for random effect variance terms (Γ(0.001, 0.001)). For the dependent variables (μ), colonization and extinction were Bernoulli distributed (0,1) for species within plots while change in cover (Δc_s) was normally distributed. Sample size for each analysis was $n = 4656$, the number of species by turf combinations. We assessed strength and support for a given parameter or relationship based on the posterior probability distribution. For instance, if the probability of a slope (β) term is almost certain to be greater than zero, we note $P(\beta > 0) \sim 1$.

There was little evidence of multicollinearity based on correlations of dependent variables (ΔMAT ~ ΔAP $r = 0.22$; ΔMAT ~ RS $r = 0.51$; ΔAP ~ RS $r = 0.02$). We checked for diversity effects in the results, finding that starting Shannon diversity of a turf had weak to no effect on probability of colonization, extinction, or change in cover (Figure S2.1). Additionally, we ran models of colonization and extinction probability and change in cover from 2009 to 2015 instead of until 2017 as a function of ΔMAT to assess if the last year sampling was an outlier. We found that all the same patterns held,

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only slightly weaker, as to be expected if treatment effects continue to develop over time (Figure S2.3).

2.3.2 | Species-specific analyses

These analyses investigate the variation in species-specific relationships to climate differences that are ignored in the species-ignorant analyses above, and therefore make more robust predictions for specific species. This test is more data-demanding, as it relies on replication at the intraspecific scale. Therefore, we first dropped all species that only occurred at one site (18 species) and/or that had less than 10 observations (37 species), leaving 96 species to model ($n = 4466$). We also dropped experimental treatment as an explanatory factor because it would lower the overall ability to detect species-specific patterns of climate differences by thinning data and power across four treatments. For similar reasons, we did not investigate the interaction of ΔMAT and ΔAP. Species-specific responses over time were modeled as:

$$\mu = \alpha \left[\text{species}_i\right] + \beta \left[\text{species}_i\right] * \Delta \text{MAT} + N\left(0, \ \sigma_{\text{site}}^2\right) + N\left(0, \sigma_{\text{block}}^2\right), \quad (4)$$

where we fit species-specific intercepts ($\alpha[\text{species}_i]$) and slopes ($\beta[\text{species}_i]$) to ΔMAT for each dependent variable, μ, where i is one of the 96 species. We ran the same models for ΔAP by swapping it with ΔMAT in Equation (4). In total, this model fits 192 fixed effects—a species-specific slope (96) and intercept (96). The other parameters are random (group-level) intercept variance (σ^2) terms that describe the variance among blocks (60) nested within sites (12). We ran the

same checks as the other models. Note, parameter estimates for colonization and extinction probability were poor (high uncertainty and poor convergence) for species with low data or never went extinct or colonized over time. We assess parameter support with 68% credibility intervals (CIs) to reflect one standard deviation from the mean on either side, which is less conservative than a 95% CI but more inclusive for these analyses with relatively small sample sizes. We refer to relationships with 68% CIs not including zero as "low uncertainty" for the species-specific analyses.

2.3.3 | Model checks

All models were run in R 3.5.0 (R Core Team, 2018) and implemented with JAGS (Plummer, 2003) in the "R2jags" package (Su & Yajima, 2015). Models were run with three chains for at least 50,000 iterations (first 25,000 burn-in) until the effective sample size for each parameter reached ~3000 and the potential scale reduction factor was close to one ($\hat{R} < 1.01$; Gelman & Rubin, 1992). We inspected traceplots of parameter estimates to ensure good mixing and unique identification. We evaluated model fit with two posterior predictive checks (PPCs): (a) plotting the sum of squared residuals (SSQ) of observed data versus SSQ of data stochastically simulated by the model; and (b) "Bayesian P-values" (Gelman et al., 1996). The first PPC indicates good fit if the plot shows a ball of points centered on a 1:1 line. The "Bayesian P-value" assesses the proportion of observed data SSQ greater than the simulated data SSQ, where good fitting models have values close to 0.5, indicating the model simulates data that approximate the uncertainty in predictions of the

TABLE 1 Model selection results comparing climate differences (ΔMAT and ΔAP) with range size and their combination. ΔWAIC and ΔLOOCV are the differences in information criterion between a given and the best model. *P*-values are "Bayesian *P*-values," which assess if data generated from the model have similar residual error to the observed data. Bayesian *P*-values close to 0.5 represent a properly fitting model

Dependent variable	Model	WAIC	ΔWAIC	LOOCV	ΔLOOCV	Bayesian P-value
Colonization	ΔMAT & ΔAP	4709.7	0.0	4711.3	0.0	0.605
	ΔMAT	4715.2	5.5	4716.7	5.4	0.504
	ΔMAT & ΔAP & range size	4715.7	6.0	4717.4	6.1	0.632
	Range size	4802.3	92.6	4804.5	93.2	0.499
	ΔAP	4823.1	113.4	4825.3	114.0	0.507
Extinction	ΔMAT	4086.2	0.0	4089.2	0.0	0.387
	ΔMAT & ΔAP	4090.0	3.8	4093.2	4.0	0.436
	ΔMAT & ΔAP & range size	4095.1	8.9	4098.5	9.3	0.465
	Range size	4152.7	66.5	4156.9	67.7	0.329
	ΔAP	4189.1	102.9	4193.6	104.4	0.272
ΔCover	ΔMAT & ΔAP	13,828.1	0.0	13,829.4	0.0	0.492
	ΔMAT	13,834.5	6.4	13,835.8	6.4	0.498
	ΔMAT & ΔAP & range size	13,834.9	6.8	13,836.4	7.0	0.497
	Range size	13,950.9	122.8	13,952.7	123.3	0.502
	ΔAP	14,006.7	178.6	14,008.5	179.1	0.499

real data (Gelman et al., 1996). All models passed the PPCs (Table 1 for Bayesian *P*-values of species-ignorant analyses). R code for the analysis is in Supporting Information 3.

3 | RESULTS

3.1 | Species' climate niche centers tend to be warmer and drier than southwestern Norway's fjord habitats

Putting our experiment into a macroecological context revealed that most species in our experiment have distributions that are warmer and drier than our study region. For instance, 93% of controls, 75% of warmer, 90% of wetter, and 73% of warmer/wetter species' observations per turf had ΔMAT greater than 0°C, meaning the temperature niche center of most species present were warmer than our study sites. For ΔAP, 21% of controls, 26% of warmer, <0.001% of wetter, and 0% of warmer/wetter species' observations had ΔAP

greater than 0, meaning the species' precipitation niche centers were drier than the sites.

3.2 | Warm-distributed species were more likely to colonize warmed plant communities

Climate differences were far better than RS in predicting colonization in response to climate change treatments (based on model selection; Table 1). Additionally, climate differences alone outperformed the combination model of climate differences and RS (Table 1), suggesting climate differences and RS explain the same variance in colonization, but RS does so poorly in comparison to climate differences. Colonization probability increased with both increasing ΔMAT and ΔAP, but the strength and uncertainty in these relationships varied across treatments (Figure 2a,b). The probability a species colonized a turf increased more with ΔMAT in the warmer and warmer/wetter treatments ($P(\beta > 0) \sim 1$) than in the wetter and control treatments ($P(\beta > 0) = 0.96$ for both; Figure 2a). Colonization probability
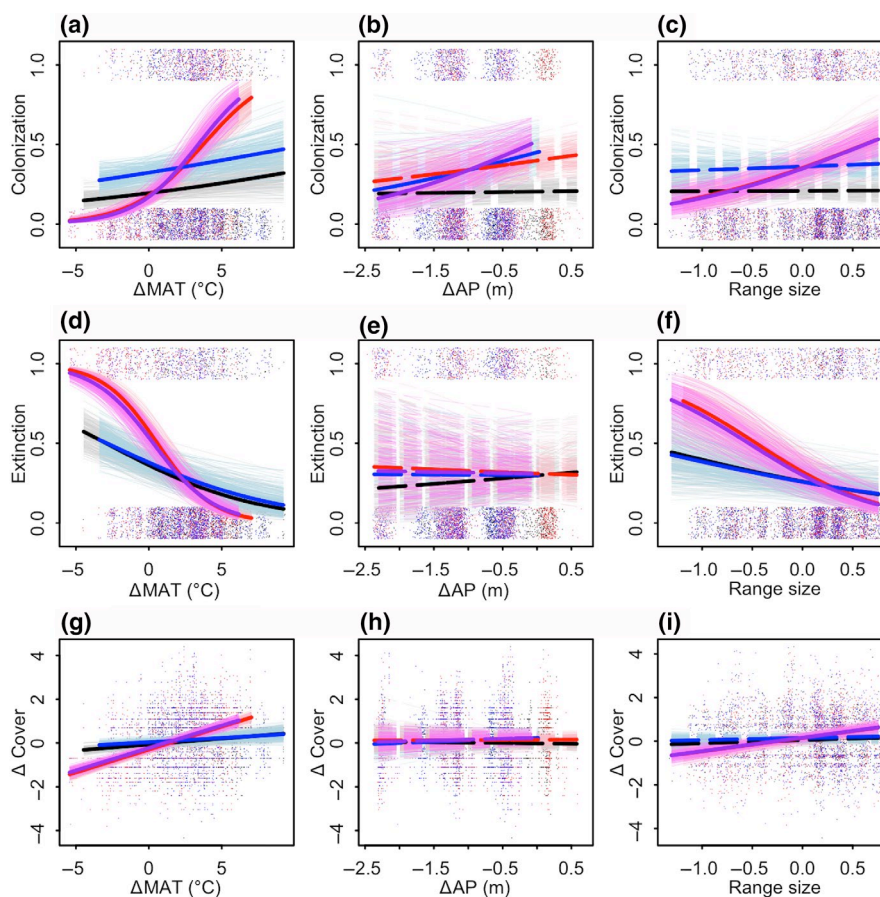

FIGURE 2 Models investigating climate difference (ΔMAT, ΔAP), and range size as predictors of colonization (a–c), extinction (d–f), or change in cover (g–i) in climate change transplant experiments across 12 sites and 151 plant species ("species-ignorant" model). Colors refer to turf treatments, where black represents controls, red represents warmer turfs, blue represents wetter turfs, and purple represents turfs moved both warmer and wetter. Bolded lines are the posterior means and were laid overtop lines representing 200 random draws from the posterior parameter distributions. Dashed lines represent slopes with 95% posterior credibility intervals that include 0. Data points were jittered for visualization in (a)–(f) to avoid overlap. Note, range size is unitless because it was standardized for analysis (see Section 2). These analyses are for main effect patterns of individual climate difference parameters and match that of patterns in the interaction models

increased as ΔAP increased in the wetter, and warmer/wetter turf treatments ($P(\beta > 0) > 0.95$ for both treatments; Figure 2b). Although this was also the case in the warmer and control treatments, there was more uncertainty in this relationship ($P(\beta > 0) = 0.90$ and 0.59, respectively; Figure 2b). The climate difference interaction model additionally suggested that species with niches drier than a site (i.e., more negative ΔAP) had an increased colonization probability in warmer turfs that weakened the positive relationship between ΔMAT with colonization ($P(\beta < 0) \sim 0.97$; Figure 3a; Figure S2.2). Colonization probability increased with increased RS in warmer and warmer/wetter treatments ($P(\beta > 0) > 0.99$ for both), but RS was unrelated to colonization in wetter and control plots ($P(\beta > 0) = 0.66$ and 0.55, respectively; Figure 2c).

3.3 | Species with colder ranges were more likely to go extinct

All models including temperature differences (ΔMAT) were better at predicting local extinctions than the model with RS alone, and, again, model selection suggests that climate differences and RS are explaining the same variation (Table 1). Extinction probability decreased as ΔMAT increased, such that, in warmer and warmer/ wetter treatments, species with temperature niches cooler than a site were almost certain to go extinct ($P(\beta < 0) \sim 1$ for both treatments; Figure 2d). Though the slopes were shallower, the same

pattern was observed in both the wet and control treatments for ΔMAT ($P(\beta < 0) > 0.99$ for both treatments). In contrast, ΔAP did not have a strong relationship with extinction probability in any treatment ($P(\beta < 0) \sim 0.37 < \beta < 0.64$; Figure 2e). There was little evidence for consistent patterns within interaction terms in the climate difference interaction model (Figure 3b; Figure S2.2). Extinction probability decreased with increasing RS and species with the smallest RSs were almost twice as likely to go extinct in warmer/wetter and warmer than in wetter and control treatments (all $P(\beta < 0) > 0.97$; Figure 2f).

3.4 | Species with colder, drier niches decreased in abundance in response to warming

Climate differences were better predictors of abundance change than RS, and as for colonization and extinction, the combination model of climate differences and range suggests they are explaining the same variation (Table 1). Species' abundance increased with increasing ΔMAT and this relationship was steeper in the warmer and warmer/wetter than in control and wetter treatments (all $P(\beta > 0) > 0.99$; Figure 2g). ΔAP was more uncertain in predictions of abundance change over the sampling period regardless of treatment (all treatments $P(\beta > 0) \sim 0.81 > \beta > 0.45$; Figure 2h). Estimates of climate difference interaction effects tended to have high uncertainty (95% CIs include zero) and low effect sizes (Figure 3c; Figure S2.2).
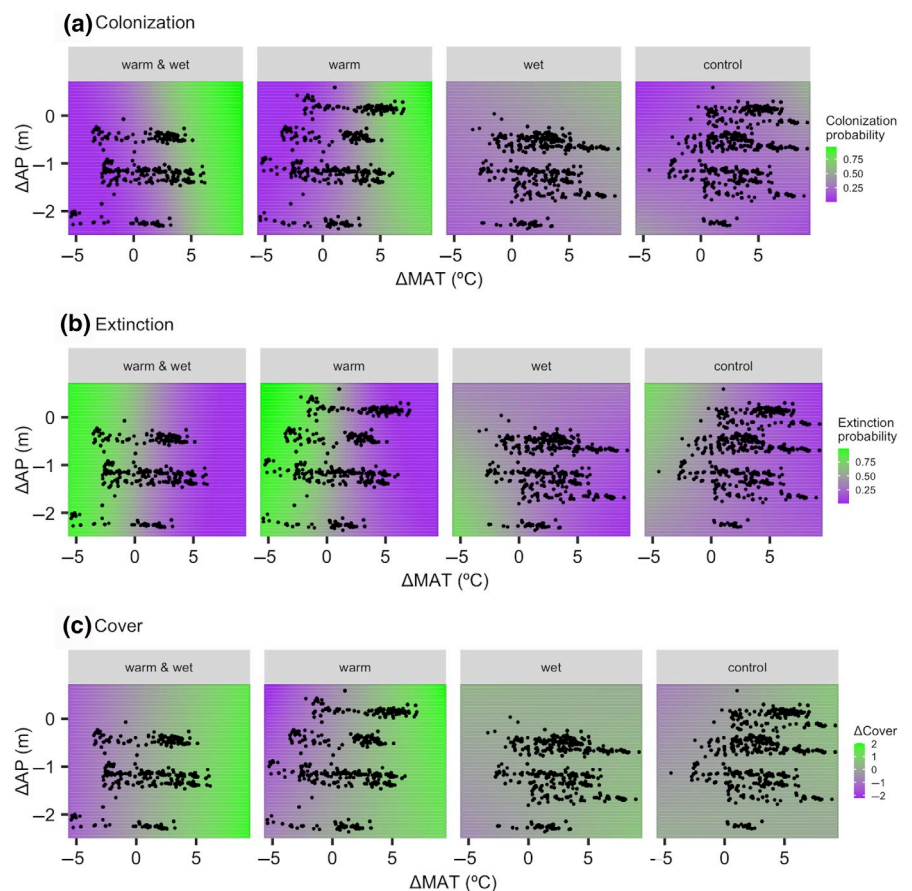

FIGURE 3 Heat-maps of climate difference (ΔMAT and ΔAP) predictions of colonization (a), extinction (b), and ΔCover (c) in each of the experimental treatments in climate change transplant experiments across 12 sites and 151 plant species ("species-ignorant" model). Model predictions of the interaction between ΔMAT and ΔAP are represented by the colored panels. The overlying points show data coverage for ΔMAT and ΔAP combinations. Model predictions should not be considered where they extend beyond the data. Figure S2.2 presents the mean and credible intervals for parameter estimates behind these heat-maps

Species with larger RSs increased in abundance in warmer and warmer/wetter treatments while small-range species decreased in abundance, but this relationship was weak ($P(\beta > 0) \sim 1$ for both treatments; Figure 2i). RS was unrelated to change in abundance for species in wetter and control treatments ($P(\beta > 0) = 0.78$ and 0.87 for control and wetter, respectively; Figure 2i).

3.5 | Species-specific responses follow trends of species-ignorant analysis

Most species showed increased colonization probability, decreased extinction probability, and increased in cover with increasing ΔMAT across sites (Figure 4a,c,e). Species-specific relationships between ΔAP and colonization, extinction, and change in cover tended to have greater uncertainty (more 68% of CIs include zero) and less consistent direction compared to ΔMAT estimates, but species

tended to have higher colonization probability, lower extinction probability, and increased in cover as ΔAP increased (Figure 4b,d,f). Further, summarizing across species with low uncertainty for ΔMAT, 49% of species had positive versus only 14% negative colonization responses to ΔMAT, only 7% had positive versus 64% negative extinction relationships with ΔMAT, and 58% had positive versus only 9% negative changes in cover as a function of ΔMAT (Figure 4a,c,e). Summarizing across species with low uncertainty for ΔAP, 42% had positive versus 17% negative colonization responses to ΔAP, 13% had positive versus 40% negative extinction responses to ΔAP, and 40% had positive versus 16% with negative change in cover as a function of ΔAP (Figure 4b,d,f).

4 | DISCUSSION

Macroecological context matters in the prediction of local plant species' responses to climate change. We found the strongest patterns for temperature context: species with cooler niches relative to the site were more likely to go extinct and to decrease in abundance in response to warming, while species with warmer niches were more likely to colonize and to increase in abundance in warmed turfs. These patterns for temperature context in the analyses across all 151 species ("species-ignorant") were upheld by species-specific analyses exploring patterns within 96 of the more common species. Precipitation context had weaker relationships and was less predictive than temperature context, even in response to wetting treatments in both species-ignorant and -specific analyses. When analyzing species-specific patterns, the plurality of species had higher colonization, lower extinction, and tended to increase in abundance as species' precipitation niche centers approached site precipitation. Temperature differences had much weaker predictive power of dynamics in control turfs, suggesting that species with warmer niches are not universally favored, but that warming is the underlying driver that favors the warm niche species in our experiments. Additionally, species with larger ranges were less prone to extinction, more likely to colonize, and increased in abundance compared to species with smaller ranges. However, these patterns were weaker and less predictive of species' responses to treatments than temperature differences and added nothing to the predictive ability of climate differences, suggesting climate niche relationships, not RS, are driving the patterns among species in colonization, extinction, and abundance dynamics.

Our results suggest that past work, where warmer distributed species outperformed colder distributed species under climate warming at a single site (Liu et al., 2018; Reich et al., 2015) can be generalized to multisite experiments, like our own, and even across different climate change experiments by explicitly incorporating the macroecological context of the study into the analyses. In our system, communities transplanted into a novel climate are converging toward the species composition of controls at that site (Vandvik et al., 2020). Macroecological context predicts that this convergence is the result of cooler niche species going extinct and warmer niche
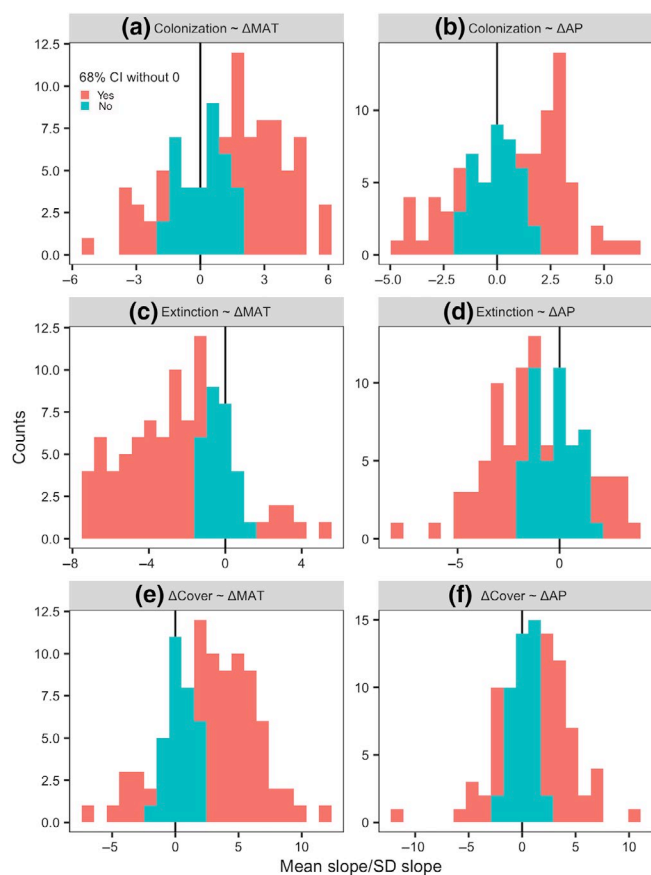

FIGURE 4 Results from analyses of climate difference as a predictor of the response of 96 plant species to climate change treatments across experimental 12 sites ("species-specific" models). Histograms are of mean slope terms divided by their standard deviation from the 68% CI for the species-specific analysis. Panels are separated by which dependent variable (Colonization (a,b), Excitction (c,d), and ΔCover (e,f)) is modeled by which climate difference independent variable (ΔMAT (a,c,e) and ΔAP (b,d,f)). Colors indicate whether the 68% CI included 0 or not. Vertical lines indicate 0

species colonizing and increasing in abundance. Continued warming is likely to favor the expansion of warmly distributed species toward higher latitudes and altitudes at the expense of arctic and alpine plant species, resulting in the latter species' ranges contracting to smaller land area.

Long-term observations of natural vegetation have suggested climate changes over the past decades have driven local extinctions and range expansions (Chen et al., 2011; Kelly & Goulden, 2008). The speed of migration over relatively recent periods suggests species' responses have accelerated with recent climate change (Corlett & Westcott, 2013). On average, boreal, temperate, and alpine areas have seen gains in species richness as low elevation species expand upslope (Pauli et al., 2012; Steinbauer et al., 2018). This upward migration, along with extinction of the coldest adapted species and shifts in dominance toward warmer adapted species, explains thermophilization within natural communities (Gottfried et al., 2012; Román-Palacios & Wiens, 2020; Wiens, 2016). Importantly, our models, both species-ignorant and specific, consistently predicted that all three processes of colonization, extinction, and shifts in abundance favor species from warmer climates, suggesting one process alone is not driving plant community thermophilization (Elmendorf et al., 2015).

The advantage of warm niche species in warmer treatments may come from physiological adaptations to the warmer environment. For instance, plants differ in photosynthetic and thermal strategies related to variable temperature environments (Aparecido et al., 2020; Dusenge et al., 2019; Michaletz et al., 2015, 2016; Perez & Feeley, 2020). Given the variation in temperature-dependent photosynthetic strategies, increased temperature may directly limit the leaf lifetime carbon gain of species with colder niches below needs for maintenance and survival, while warmer niche species gain carbon in excess of maintenance for reproduction. This may drive colder niche species toward extinction in response to warming, while warmer niche species colonize at a higher rate. This hypothesis is speculative, but underlies recent theoretical advances that reframe population and community ecology into economies of leaf carbon gain (e.g., Enquist et al., 2015; Fridley, 2017; Kikuzawa & Lechowicz, 2006; Michaletz et al., 2015). Direct evidence for this mechanism comes from North American tree species, where species with more southern distributions exhibited increased photosynthetic rates with warming that led to greater growth (Reich et al., 2015). Accounting for leaf carbon economies as mechanistic explanations of community dynamics with climate change is a promising area for future research with sweeping ramifications for global vegetation modeling (Kumarathunge et al., 2019).

Novel biotic interactions (e.g., competitors) in the warmer and/or wetter environments likely increase the extinction probability and abundance declines of cold niche species. Distribution modeling suggests that the negative relationship between competition and abundance for a species can intensify in warmer and wetter areas (Lynn et al., 2019; Mod et al., 2014). This is bolstered by experimental evidence that novel competitors in warmer/low elevation plant communities lower survival probability, growth, and reproduction of

focal species more than competitors found in their home communities in the same novel climate (Alexander et al., 2015). Extinctions of the cold niche species in the novel, warmer climates may be due to increased competition from co-occurring species with warmer niches and novel colonists from the community they were transplanted into (Töpper et al., 2018; Vandvik et al., 2020), but variation in these patterns over species and sites has not been previously tied to species' climate niches. While not the focus of this paper, we also found little evidence that community diversity affected the probability of extinction, colonization, or change in abundance (Supporting Information 2), suggesting the identity and/or traits of competitors (Funk & Wolf, 2016; Kunstler et al., 2012) may be more important than the number of competitor species.

Precipitation differences were generally weakly or unrelated to change in extinctions, colonizations, and abundance in turfs transplanted into wetter environments, likely because the sites were wetter than the species' mean niches in almost every case. Our sites occur within oceanic climates, where the lowest annual precipitation is still relatively high, at over 600 mm/year, and these turfs were moved to sites with 1200 mm/year or more. We would expect a greater effect of increased precipitation if the communities were initially water limited. Meta-analysis has shown that precipitation additions in areas with high annual precipitation have little effect on net primary productivity (Wilcox et al., 2017). This suggests that wet communities and ecosystems may not respond to predicted increased annual precipitation with climate change, at least in the short term. However, in the species-specific analyses, we find that a majority of species perform better (higher colonization and lower extinction probability and increased in abundance) when AP at a site was more similar to their niche AP (Figure 4). This was paired with a higher proportion of species having the opposite trend relative to the MAT models, which suggests the weak precipitation difference relationship in the species-ignorant analysis is a result of the variability among species-specific relationships with precipitation differences. Additionally, we suggest that future studies in drier habitats investigate the role of macroecological context predictions using indices more closely linked to the underlying physiological responses, such as PET and aridity. Our system was sufficiently cold and wet that these variables were strongly related to temperature and precipitation, but studies that assess other environmental contexts may find these measures insightful (Fisher et al., 2011).

Range size was not as informative as temperature differences, although species with larger ranges did respond more to warming, but not wetting. A species' RS is determined by a myriad of ecological factors, including environmental tolerances (e.g., climate), tolerance of and/or dependence on biotic interactions (e.g., competition, mutualism), historic factors, and dispersal ability (Gaston, 1996; Sexton et al., 2009; Sheth et al., 2020). If species' RS was a better predictor than climate differences, we could conclude that species' RS captures aspects of the species' ecology and history that are not related, or in addition to their climatic distribution. But this was not the case, potentially because the direct transplantation of

turfs into novel community matrices lowered dispersal barriers to colonization compared with the distances that would be traversed naturally. Additionally, we chose to restrict species' distributions observations to Europe, which will likely underestimate a species' global RS. However, this decision did not impact the overall results (Table S1.1). Although the probability a species goes extinct globally tends to decrease with increasing RS (Brown et al., 1996; Chichorro et al., 2019), our findings suggest that local risk of extinction is more related to a species' climatic niche and more attention should be paid to this dimension of species' ecology.

One of our more surprising results was that even in control and wetter transplant turfs, cold niche species were consistently more likely to go extinct than warm niche species over the 8-year period. We may be detecting the signal of climate change effects outside of treatments (Langley et al., 2018), consistent with considerable warming in this region in recent years (Hanssen-Bauer et al., 2017). Alternatively, extinctions may have increased due to lack of grazing. All sites were located within traditionally grazed landscapes with herbivores excluded to protect experimental infrastructure. Though we control for herbivore effects by mowing the sites, it is possible that the exclusion of large mammalian herbivores could also explain the relatively high background rates of extinction within the plots, although effects of herbivores on plant communities can be variable (Olff & Ritchie, 1998). The strong and consistent pattern revealed by our analyses that cold niche species were the most likely to go extinct suggests that recent climate warming is the most plausible explanation.

There are several caveats to consider for the interpretation and application of this macroecological approach. First, our approach assumes that all populations within a species have the same climate niche. However, detailed studies of *Festuca rubra* in the region have provided evidence of local adaptation of traits associated with the temperature and precipitation grid (Münzbergová et al., 2017; Šurinová et al., 2019). Even with potential local adaptation, our models suggest that species' macroecological context is predictive of their responses to climate change at local sites. Second, there are numerous issues with using data from large archives such as GBIF, including chronic misidentification of species (Nekola et al., 2019) and large geographic bias in the areas typically sampled (Ponder et al., 2001). We expect these issues to be of limited importance to our results because: (i) it is reasonable to assume that misidentifications are spatially unstructured, and so should add minimal error to the climate averages and RSs calculated; and (ii) our GBIF data are spatially biased toward Northwestern Europe, which is expected and even favorable, given this is the most geographically representative area of the experiment. Finally, we focused on the difference between species' climatic niches and site climate when it could be argued that species' climatic niches alone are responsible for the patterns. We maintain that the difference model is more reproducible and globally applicable because it contextualizes the climate niche center to site climate, so that predictions are not contingent on the species-specific climatic niches within the study region and therefore comparable across experiments.

5 | CONCLUSIONS

We have shown that species' responses to a turf transplant climate change experiment are predictable from macroecological context. Species from the warmest distributions relative to local conditions are the most likely to colonize while species with colder distributions than local conditions are the most likely to go extinct. Changes in vegetative cover followed the same pattern: warm niche species increased while cold niche species decreased in abundance. In accordance with reports in many surveys, the results suggest that as climate warming continues, cold-adapted alpine and arctic species are likely to go extinct in favor of upward colonizing, warm-adapted temperate grassland species. Macroecological context, by accounting for the disparity between a species' climate niche and a local site climate, can generalize and predict species' responses to climate change experiments and time series observations across systems.

AUTHOR CONTRIBUTIONS

J.S.L. and V.V. conceived the analysis. V.V. and D.G. designed the field experiment. K.K. and V.V. set up the field experiment and collected the experimental data. R.J.T. managed the experimental data. J.S.L. collected the GBIF data and performed the analyses, and J.S.L. led the writing with contributions from all authors.

DATA AVAILABILITY STATEMENT

Data are available at the Open Science Framework (osf.io) https://doi.org/10.17605/OSF.IO/G8NXM.

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SUPPORTING INFORMATION

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