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Climate modifies response of non-native and native species richness to nutrient enrichment

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Ecosystem eutrophication often increases domination by non-natives and causes displacement of native taxa. However, variation in environmental conditions may affect the outcome of interactions between native and non-native taxa in environments where nutrient supply is elevated. We examined the interactive effects of eutrophication, climate variability and climate average conditions on the success of native and non-native plant species using experimental nutrient manipulations replicated at 32 grassland sites on four continents. We hypothesized that effects of nutrient addition would be greatest where climate was stable and benign, owing to reduced niche partitioning. We found that the abundance of non-native species increased with nutrient addition independent of climate; however, nutrient addition increased non-native species richness and decreased native species richness, with these effects

dampened in warmer or wetter sites. Eutrophication also altered the time scale in which grassland invasion responded to climate, decreasing the importance of long-term climate and increasing that of annual climate. Thus, climatic conditions mediate the responses of native and non-native flora to nutrient enrichment. Our results suggest that the negative effect of nutrient addition on native abundance is decoupled from its effect on richness, and reduces the time scale of the links between climate and compositional change.

1. Introduction

Anthropogenic eutrophication is a global problem [1,2] and leads to a myriad of effects on plant species and ecosystem properties [3–5]. In general, non-native species exhibit greater success than natives under increased nutrient addition [6,7], and often non-native species will increase in abundance and richness in eutrophied communities at the cost of native species [8–10]. This differential response of non-native and native species is related to the tendency of non-native species to have fast growth rates and rapid resource acquisition [11,12], and to exhibit greater biomass increases under increased nutrient addition [6,7]. Increased nutrient addition and climate conditions, however, can have interacting effects on the success of non-native species [13–15]. These effects are influenced by how variation in the mean and heterogeneity of the local environment alters the persistence and establishment of taxa within communities, and the interactions within and among their populations [16]. Further, non-native species differ substantially in their ecological strategies [17,18], potentially leading to varying responses of non-natives to specific combinations of nutrient enrichment and climate conditions. Depending on climate and the extent of nutrient enrichment, non-natives may be excluded by, exclude, or coexist with native species. For example, evidence from studies spanning different regions suggests that the response of non-native species to increased nutrient addition might vary depending on climatic conditions [10,19]. However, it remains unclear (i) whether, on average, non-native species differ from native species in their response to the interaction between nutrient enrichment and climate conditions (mean and variability); and (ii) whether the combined effect of more stable and benign climate conditions and increased nutrients has a net positive effect on non-native species as a group. Because changes in biodiversity (gains and losses) have crucial implications for the functioning of ecosystems across spatial and temporal scales [20], it is pressing that we understand how multiple concurrent environmental changes affect non-native species and invaded natural communities.

Nutrient addition and climate variability may have counteracting effects on the regulation of local diversity, including non-native and native species coexistence. Nutrient enrichment experiments show that eutrophication can reduce diversity by decreasing niche dimensionality and enhancing competitive exclusion via increased light limitation [4,5,8] or other resource limitation [21]. The effects of eutrophication may be dampened by higher plant diversity and functional composition [22]. Climate variability can contribute to the maintenance of diversity as species vary in their responses to climatic conditions [18,23,24]. In contrast, more constant climate conditions may

offer fewer opportunities for temporal niche partitioning [25]. However, the interactive effects of climate mean and variability with nutrient addition on species diversity remain uncertain. Climate-based environmental heterogeneity could offset the negative effects of eutrophication on species coexistence via mechanisms such as the temporal storage effect [26–28], as different species in a community may be favoured at different points in time [16]. Alternatively, climate variability could interact with eutrophication to enhance species invasion by opening colonization windows for species with strategies for high-nutrient resource capture (i.e. weakened biotic resistance, [16]).

Experimental tests suggest that environmental factors can alter the effect that nutrient addition has on a plant's carbon sequestration, nutrient uptake and relative growth rate, ultimately affecting the composition and richness of a community [29–31]. For instance, under elevated temperature and nutrient enrichment, plants respond faster to changes in soil resources and to increased carbon sequestration, leading to changes in community composition [29,31]. Similarly, experimental water and nutrient availability manipulations lead to changes in species richness or cover, suggesting that response to nutrient treatments is influenced by water availability and differs among species [30,32,33]. In addition, trade-offs between water and nitrogen use efficiency have been found across different growth forms (i.e. herbs, shrubs and trees), with the relative position of species on this trade-off affecting their fitness and spatial distribution [30].

In the context of invasion ecology, the few studies that have explicitly explored the relationship between nutrient addition and climate conditions support the hypothesis that interactions between these two factors may cause contrasting trajectories of native and non-native abundance. Evidence from single-site studies suggests that variation in the prevailing environmental conditions affects the abundance of non-native and native species in response to nutrient addition [10,14,15,28]. In nutrient-limited plant communities, for example, higher water availability is not sufficient to enhance exotic species success [34]. Meanwhile, in desert communities, the positive effect that nutrient addition has on exotic species abundance disappears during the driest years [14]. Across sites, Cleland *et al.* [19] showed an increase in exotic species abundance in grasslands around the USA after nitrogen (N) addition. This response was mainly driven by an extreme response to N enrichment at a few sites. Why this was the case is unclear, but local climate conditions may have played a role in determining the effect of eutrophication on non-native abundance. Taken together, these studies demonstrate that the effect of nutrient addition on the relative abundance of non-native plants could vary widely depending on historical climate conditions and the range of climatic variability to which the species in each community are adapted.

Over time, species arrival and local environmental conditions will shape the composition of communities [25,35,36], and species characteristics will determine their success in different abiotic environments (including both mean conditions and variability) [24,25,37,38]. However, nutrient addition modifies environmental conditions, changing the composition of communities and reducing species diversity [4,5,8], often causing losses of rare, native, perennial and N-fixing species [8,39]. Thus, eutrophication represents a new filter, which modifies the identity and abundance of species in communities by selecting for a different combination of
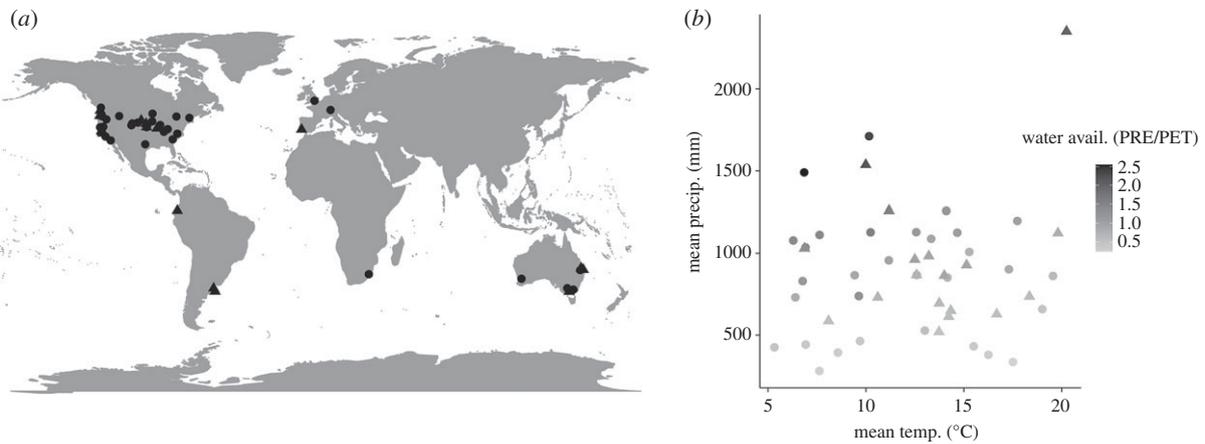
Figure 1. NutNet site locations and climate. Triangles are sites with pre-nutrient (year 0) treatment data only, and circles are sites with both pre-nutrient treatment data and data on the rate of change in richness and abundance of introduced and native species during 3 years of nutrient treatment (years 1–3). (a) Geographical location for study sites. (b) Mean long-term temperature, precipitation and water availability for the sites. The colour gradient in (b) represents water availability; darker colours represent higher water availability.

successful-species characteristics. These eutrophication-related changes in composition may also alter the association between communities and prevalent environmental conditions, either modifying the impact of climatic factors (amount or variability) on these communities, or modifying the time scale at which communities respond to them. This change in the association between environment and communities could have important implications on the response of eutrophied communities to other concurrent environmental changes (e.g. global warming and altered precipitation regimes).

Here, we use data collected as part of the Nutrient Network collaborative research experiment (NutNet, www.nutnet.org; [40]). NutNet has a fully crossed experiment designed to assess the effects of N, phosphorus (P) and potassium plus micronutrient (K) addition on grassland communities world-wide (figure 1a; [40]). NutNet also spans globally relevant climatic gradients, including extreme temperature seasonality and wide gradients in rainfall (figure 1b). We use these data to evaluate whether climatic extremes, means, variances, or both mean and variance of climate conditions most effectively explain the variation and rate of change in the abundance and richness of non-native and native grassland species. We then assess the interactive effects of eutrophication, mean climate, and climate variability on the richness and abundance of non-native species in grassland communities around the world.

2. Methods

(a) Data

We examined plot-level data on species richness (number of species) and abundance (measured as percentage cover by species) by provenance (i.e. non-native or native) collected in 51 grassland sites within NutNet (figure 1a; [40]). We used all 51 sites for the abundance and richness analyses. Only 32 of these sites had at least three years of nutrient addition response data. Therefore, we used this subset to examine the change in abundance and richness of species by provenance in response to the nutrient treatments (figure 1a). If a population was not native to the site in which it was sampled, it was categorized as non-native; if a population was native to the site in which it was sampled, it was categorized as native. The provenance (native/non-native) of each species was determined by experts

at each site. Only sites with at least one non-native species were selected (regardless of their dominance), as sites with no non-native species are uninformative for these analyses.

All sites followed identical treatment and sampling protocols [40]. The nutrient experiment, a factorial addition of N, P and K plus micronutrients, was replicated in three blocks per site. All plots were 5×5 m and annually received 10 g N m^{-2}yr^{-1} as slow-release urea [(NH$_2$)$_2$CO], 10 g P m^{-2} yr^{-1} as triple-super phosphate, [Ca(H$_2$PO$_4$)$_2$], 10 g K m^{-2} yr^{-1} as potassium sulfate [K$_2$SO$_4$]. To avoid toxicity, 100 g m^{-2} yr^{-1} of a micronutrient mix of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%) and Mo (0.05%) was added only in the first treatment year.

The vegetation in all plots was sampled annually, starting in the year prior to the application of nutrients (year 0). The aerial cover of each species rooted within a permanently marked 1 m^2 subplot within each 5×5 m plot was assessed annually at peak biomass. Cover was recorded to the nearest 1%.

We used year 0 (i.e. pre-nutrient treatment data) abundance and richness data for all plots to assess the effect of climate variability on richness and abundance ($n = 51$). Three years of data after nutrient treatment started were used to assess the effect of climate (only control plots), nutrients (all plots) and their interaction (all plots) on rate of change in abundance and richness ($n = 32$). We calculated the abundance of non-native and native species as the % cover from the total for these groups. For the 32 sites for which we had sufficient data to estimate the rates of change in either richness or abundance through time (figure 1), we estimated the rate of change as the log-response ratio between the metric after t years of treatment and the pre-nutrient treatment value ($dR/dt = \log_{10}(R_t/R_0)$) in the same permanently marked plot.

(b) Climate data

For our analyses, we focused on three climate variables: temperature, precipitation and water availability (the balance between potential evapotranspiration and precipitation). Precipitation, temperature and water availability are three of the most common variables used to understand how climate shapes species distributions, diversity and trait variation [24,37,41]. Further, these three variables impact on plants' photosynthetic capacity, growth rates and biomass allocation [41,42]. At the same time, plant traits related to these functions (i.e. traits related to resource capture, water use efficiency and growth rates) tend to differ between non-native and native species [12,43], and vary along gradients on these three climate variables [44].

We obtained monthly climate data for our sites from a 0.5° resolution gridded dataset [45] to explore effects of both means and variability in precipitation, temperature and water availability, as well as number of days with extreme temperature and precipitation events. We defined climate variability as the variance in the climate variable of interest. Water availability was defined using a moisture index (MI) calculated as MI = PRE/PET, where PRE is mean precipitation and PET is Thornthwaite's index of potential evapotranspiration [42]. We quantified mean climate and climate variability over three distinct time scales: within the growing season of species data collection (within season), within the calendar year of species data collection (hereafter, annual climate) and across a long-term record (1961–2000; hereafter, long-term climate). For each year of observation, we defined the growing season of each site as the months with a mean minimum temperature greater than 0.0°C and MI > 0.05 [42].

We calculated extreme events for individual sites by comparing the precipitation or temperature values for every day of every year that species data collection took place with the distribution of rainfall and temperature values of every month from 1961 to 2000. We obtained the daily climate data from the National Center for Environmental Prediction [46]. We defined extreme cold/dry events as the number of days during the species data collection period in which temperature or rainfall was below the first percentile of the 1961–2000 distribution for each site. Likewise, extreme hot/wet events were defined as the number of days in which rainfall or temperature was above the 99th percentile.

(c) Analyses

Our overall aim was to understand whether climate conditions (means, variability and extreme events) interacted with nutrient addition to alter the abundance and richness of non-native and native species, and to test whether this effect differed between these two groups of species. We focused on three response variables: species richness, abundance, and their rate of change (i.e. $dt_{n\ richness}/dt_0$ or $dt_{n\ abundance}/dt_0$, where dt_n represents either abundance or richness after t years of nutrient treatment and dt_0 represents the pre-treatment measure of that metric). Abundance and richness data were derived at the site level. Therefore, we fitted generalized linear models with a negative binomial distribution for richness, and linear models for abundance. Rates of change in richness and in abundance were derived at the plot level, thus we fitted linear mixed-effect models with nested random effects for plot, site and calendar year.

We first evaluated which of a suite of climate variables best explained native and non-native species variation in richness, abundance and their rate of change. All models included a term for provenance (non-native or native), which was allowed to interact with climate (extreme temperature and rainfall events as well as long-term, annual or growing-season water availability, precipitation and temperature means or variances or both; electronic supplementary material, S1). The model for extreme events also included a term for water availability to account for the effect of differences in this variable between sites. This is because differences in water availability between our sites could lead to distinct responses between plant communities to extreme climate events depending on the historical water availability of each site, which have probably shaped the composition of species present at each site. We found strong correlations between some climate variables ($r > 0.7$; electronic supplementary material, S1). To avoid collinearity between these climate variables in the models, if two or more of these variables were present in a model and showed collinearity, we fitted all alternate multivariate models with only one of the collinear variables present (electronic supplementary material, table S1.5). Then we used Akaike information criterion (AIC) to assess what combination of climatic factors best explained each response variable. For each response

variable, we compared the models fitted with ΔAIC values (ΔAIC = $AIC_{model\ i}$ – minAIC, where minAIC is the model with the smallest AIC value). For brevity, we present only results of the models with smallest ΔAIC values.

Next, we developed linear mixed-effect models to establish the relationships between nutrient treatments and the change in richness and abundance of non-native and native species. While these relationships are well known for our sites, and described in full detail elsewhere (see [39]), these relationships can vary in strength among sites within and between studies [14,19,47]. Thus, we used these models to show that the relationship between nutrients and non-native species is robust and present in our dataset, and to provide a comparison for the results from the nutrient and climate interaction tests below. In these models, our response variables were either change in richness or change in abundance. The fixed effects were species provenance, nutrient treatments (N, P, K + micros and all their combinations) and their interactions (graphical representation of these models in electronic supplementary material, figure S2.1 and S2.2). To assess the effect of the nutrient treatments over time, we also included a fixed term in the model for year since the nutrient treatments started. These models included a nested random effect for plot, site and calendar year.

Finally, we tested for the effect of the interaction between climate and nutrient treatment on the rate of change in abundance and richness of non-native and native species. We first selected the best model for the interaction between nutrient treatments and climate using ΔAIC scores as above. Our response variables were rates of change (i.e. either $dR/dt = \log_{10}(R_t/R_0)$ or $dA/dt = \log_{10}(A_t/A_0)$, where R is richness and A abundance). The explanatory variables were species provenance, climate variables, nutrient treatment and three-way interactions between nutrient treatment, species provenance, and each climate variable (electronic supplementary material, table S1.5; graphical representation of these models in electronic supplementary material, figure S2.3 and S2.4). These models included a nested random effect for plot, site and calendar year.

Prior to analyses, we $\log_{10}$ transformed the precipitation data. All data were extracted and analysed using R v. 3.1.1 [48].

3. Results

(a) Effect of climate (no nutrient treatments)

Long-term climate mean and variance were associated with both native and non-native species richness and abundance (electronic supplementary material, table S2.1), often in opposite directions. In both the best and second best models, increased long-term precipitation variance led to increased non-native species richness but reduced native species richness ($p \leq 0.0002$, electronic supplementary material, tables S2.2 and S2.3). The second-best model for richness, which was indistinguishable from the best model based on ΔAIC values (electronic supplementary material, table S2.1), also suggested reduced non-native richness and increased native richness in warmer sites ($p = 0.03$; electronic supplementary material, tables S2.2 and S2.3).

The abundance of non-native and native species (electronic supplementary material, table S2.1) differed in their response to long-term mean precipitation ($p = 0.005$) and long-term variance in precipitation ($p < 0.0001$; electronic supplementary material, table S2.4). Non-native species were more abundant in sites with higher mean precipitation and higher variance in precipitation, whereas the abundance of native species showed the opposite pattern (electronic supplementary material, table S2.5).
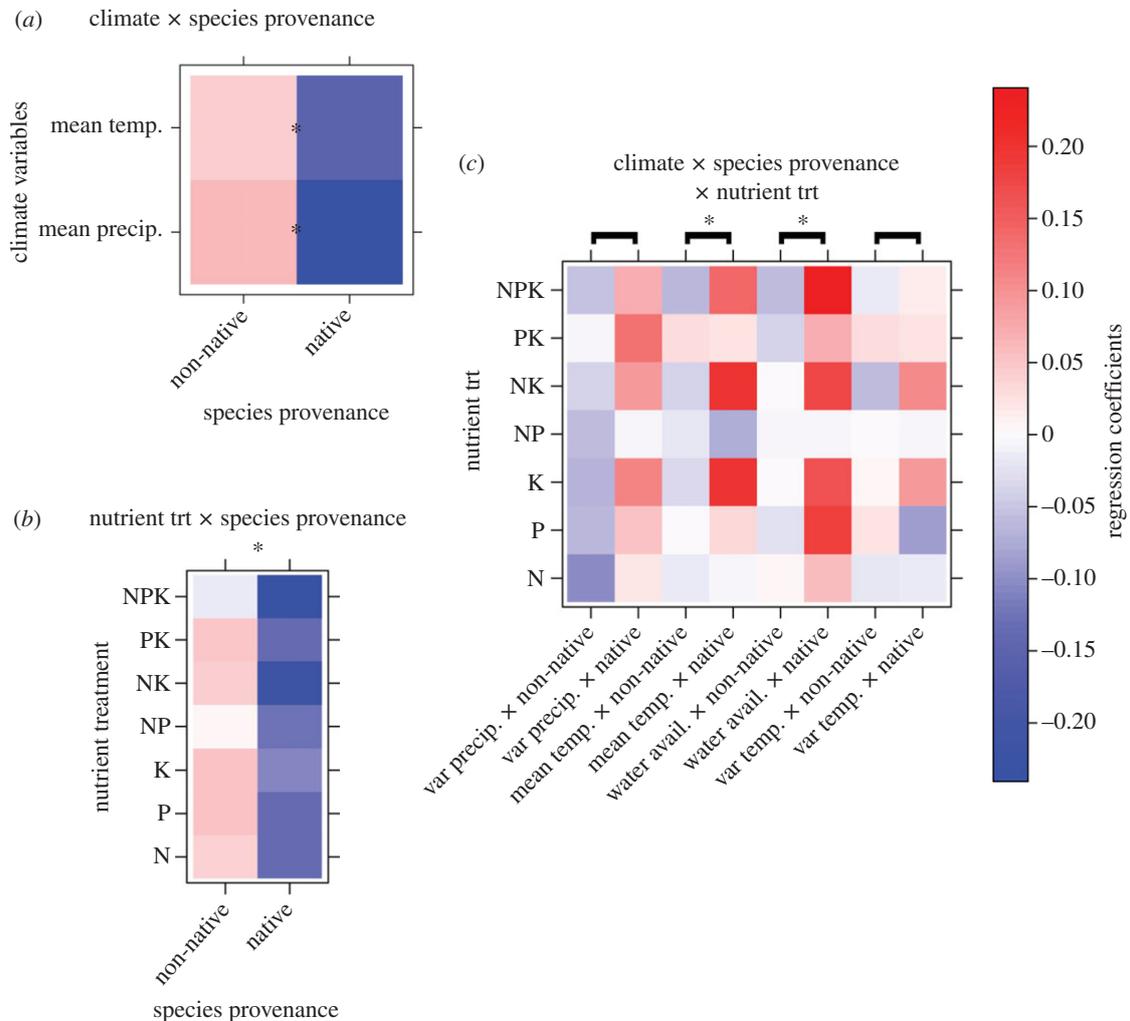
Figure 2. Richness changes of non-native and native species in response to (*a*) climate variables, (*b*) nutrient treatments, and (*c*) the interaction between climate and nutrients. In (*b*), plotted values are the difference in the change in richness for each nutrient treatment (N × P × K factorial) from the change in richness in the control plots. Models in (*a*) and (*c*) were selected using ΔAIC values. Brighter colours represent higher estimates than paler ones; positive estimates are red and negative estimates blue. 'Asterisk' represents significant interactions between species provenance and climate, nutrient treatments, or both.

In control plots, long-term mean climate predicted the rate of change in richness and abundance of non-native and native species (electronic supplementary material, table S2.6). Non-native species richness increased, and native richness was lower in sites with higher long-term mean temperatures ($p = 0.0001$) and long-term mean precipitation ($p < 0.0001$; figure 2*a*; electronic supplementary material, tables S2.7 and S2.8). Similarly, native species declined and non-native species increased in abundance at warmer ($p = 0.0002$) and wetter sites ($p < 0.0001$), whereas the abundance of non-native species increased under these conditions (figure 3*a*; electronic supplementary material, tables S2.9 and S2.10).

(b) Effect of nutrient addition (no climate terms)

Experimental nutrient addition increased the rate of change in richness and abundance of non-native species (figures 2*b* and 3*b*). Richness of non-native and native species declined with years since nutrient addition ($p = 0.01$; electronic supplementary material, tables S2.11 and S2.12). In contrast, the change in relative abundance of species (both native and non-native) was unaffected by the number of years of nutrient addition ($p = 0.38$; electronic supplementary material, tables S2.13 and S2.14).

(c) Interactions between species provenance, climate and nutrient addition

With nutrient addition, changes in richness and abundance of both non-native and native species tended to shift from being predicted by long-term climate to being better predicted by annual climate variables.

First, the effects of nutrient addition on species richness, positive for non-native species and negative for native species (figure 2*b*), were generally more modest in sites that were warmer or wetter (figure 2*c*). Change in native and non-native species richness differed, depending on the nutrient treatments and the climate variable (figure 2*c*), with three-way interactions between species provenance, nutrient treatments and mean temperature ($p = 0.002$), and water availability ($p = 0.0008$; figure 2*c*) demonstrating differential effects of the abiotic environment on native and non-native species. Where annual water availability was high, native species richness generally increased in response to elevated nutrient supply (figure 2*c*). Where annual water availability was high, non-native species richness increased weakly where N was added alone, but declined weakly when N was not added (figure 2*c*). Nutrients and annual temperature affected native and non-native species differently. At warm sites, non-native
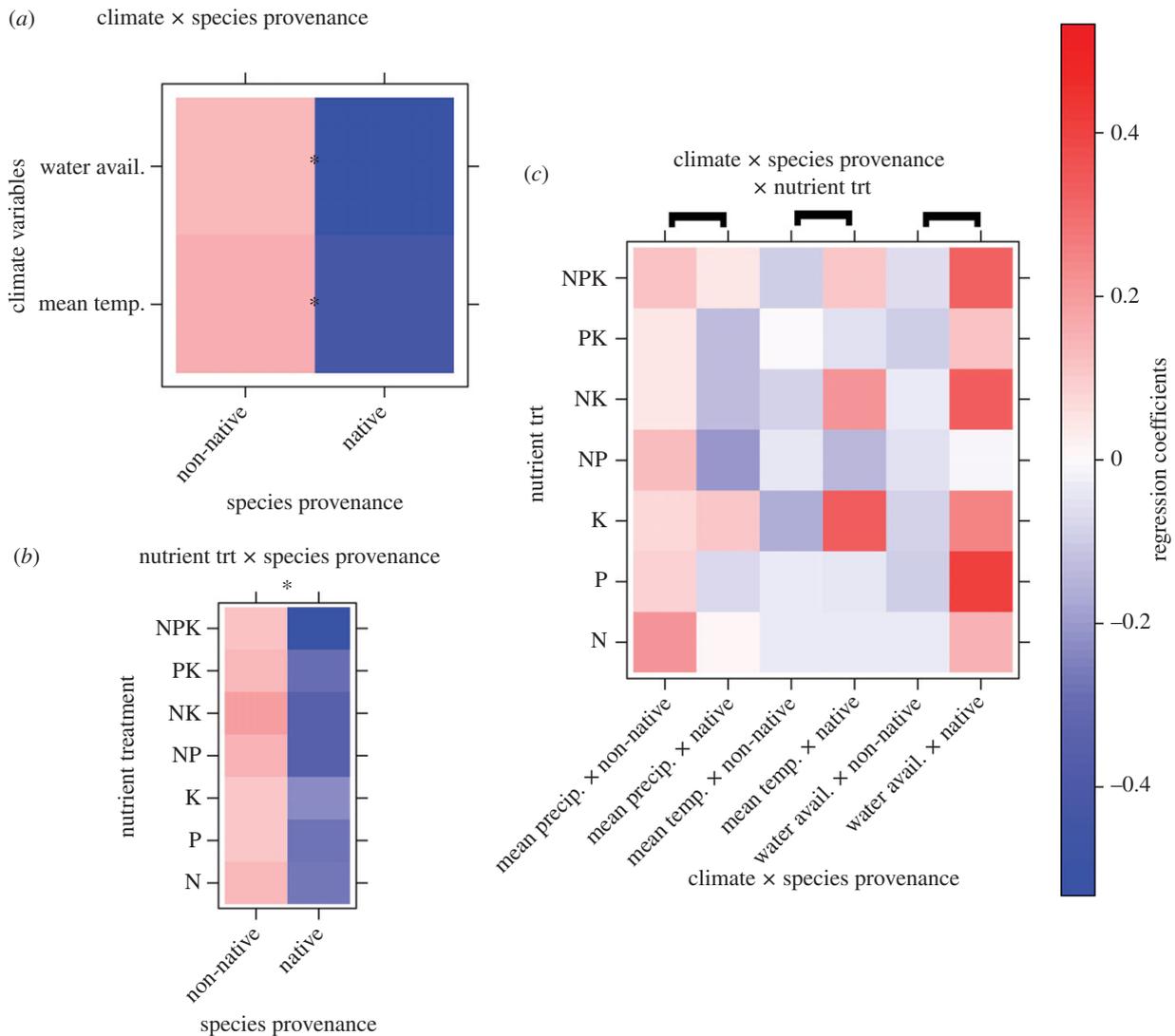
Figure 3. Abundance changes of non-native and native species in response to (a) climate variables, (b) nutrient treatments and (c) the interaction between climate and nutrients. In (b), the values plotted are the differences in the change in abundance for each nutrient treatment (N × P × K factorial) from the change in abundance in the control plots. Models in (a) and (c) were selected using ΔAIC values. Positive estimates are red and negative estimates blue; brighter colours represent higher estimates than paler ones. 'Asterisk' represents significant interactions between species provenance and nutrient treatments, climate variables, or both.

species generally declined under nutrient addition, except when PK was added. Under the same conditions, native species richness increased where K was added (K, NK, NPK; figure 2c), and phosphorus (P, PK and NPK) addition led to weak increases in native richness (figure 2c), whereas N alone and NP addition led to a decrease in native species richness. Across nutrient treatments, increased precipitation variability reduced non-native richness and increased native richness. Increased temperature variability had relatively weak and inconsistent effects on both species groups (figure 2c and electronic supplementary material, table S2.17).

Although addition of nutrients generally increased the abundance of non-natives and reduced natives (figure 3b), the effect of nutrients on the abundance of species in these groups was not altered by climate ($p \geq 0.06$; figure 3c). How-ever, across the nutrient treatments, native species were less abundant at sites with higher mean annual temperature ($p < 0.0001$; electronic supplementary material, table S2.18) and higher water availability ($p = 0.0003$), whereas non-native species increased in abundance with mean temperature and water availability (electronic supplementary material, table S2.19).

4. Discussion

Our results demonstrate that nutrient enrichment changes the time scale at which invaded grassland communities respond to climate. Under nutrient enrichment, changes in abundance and richness of native and non-native species were more related to annual climate, whereas under ambient conditions, long-term climate variables were better predictors. Previous studies across these grassland communities have shown that exotic species are more likely to have annual life histories than native species [39]. Furthermore, nutrient enrichment also increases the abundance of non-native species [7,39]. Thus, the increase in non-native species abundance is probably shift-ing grassland communities towards domination by short-lived species that respond to the environmental conditions over shorter time scales. However, this change in species dominance may not accurately reflect community changes over decadal or longer time scales [29,31]. Nevertheless, our study highlights the importance of considering environmental conditions when assessing the effects of eutrophication on natural commu-nities, as nutrient addition interacts with environmental conditions to determine the trajectory of species richness.

While nutrient addition controlled the abundance of native and non-native species independent of climate, its effect on grassland richness was mediated by climate conditions. In particular, fewer native species were lost in response to nutrient addition in warmer, wetter sites. This is contrary to previous findings that suggest that nutrient enrichment reduces native species richness and increases non-native species richness independently of climate [10,39]. Rare species tend to be lost from communities with nutrient enrichment (particularly N) [8]. Non-native species, when present, are likely to be abundant rather than rare; whereas natives can be either abundant or rare [39]. From this evidence, one would expect that the increase in non-native abundance in the communities in this study would come with a cost to native diversity through the loss of rare species [8]. Contrary to this expectation, our results suggest that the consistent decrease in the abundance of native species might not be primarily owing to declines in rare native species. While we found that native species abundance decreased in nutrient-enriched communities, the negative effects of nutrient enrichment on native species richness were ameliorated in warmer or wetter sites. Thus, the decline in abundance but unchanged richness of native species may reflect a reduction of dominant native species. This increase in evenness could be the result of a high-niche overlap between dominant native and non-native species, with fitness differences favouring abundant non-native species over abundant native competitors [49]. Other mechanisms, such as temporal or spatial niche partitioning, might also be at play among dominant and rare species in these two groups, and warrant further examination.

Annual mean environmental conditions interacted with the nutrient treatments, reducing the net positive effect of eutrophication on the richness of non-native species, and generating a spectrum of scenarios depending on the nutrient treatment and climate variable. In contrast, annual variance in precipitation and variance in temperature affected the change in richness of native and non-native species, independently of nutrient additions. There are several mechanisms that could explain this difference. For instance, greater annual climate variability could ameliorate the effect of competitive exclusion [23,24] caused by the addition of nutrients [50]. Climatic conditions could also reduce competitive exclusion by modifying the strength of the biotic interactions between native and non-native species, weakening the negative effect that nutrient enrichment has on the native taxa. For example, in our nutrient-enriched communities, increased annual water availability could be reducing the intensity of competition between non-native and native species for water and nutrient resources. Climate variability, and the interaction between nutrient enrichment and mean climate conditions could also be promoting species with different resource acquisition strategies; variation in the strength of these environmental factors over time could promote stability in the invaded communities. These mechanisms are not mutually exclusive, and most likely a combination of these mechanisms is acting across these grassland communities, weakening the negative effect of nutrient enrichment on the change in native species richness. Diversity across plant communities worldwide is decreasing with nutrient enrichment, often benefiting non-native species [8,39]. However, across a wide range of communities, non-native species display a wide range of ecological strategies [17] that, depending on local environmental conditions, can lead to different competitive outcomes in their interaction with native species [18], not only to native species loss.

Finally, across broad environmental gradients, native and non-native species differed in their response to climate conditions. This could be due to differences in functional traits between native and non-native species, such as differences in water use efficiency, growth rates or phenology [12,18,43]. At the same time, the association between some of these climate variables and non-native species abundance or richness could also be reflecting a strong association between non-native species and human activity in the invaded communities [51]. It is likely that the association between environmental gradients and native and non-native species response to climate conditions can be attributed to both direct influences of climate on the growth and survival of non-native species and indirect effects, such as association with human activity [51].

5. Conclusion

Using an experimental study replicated with consistent methodology at 32 sites around the world, we have shown that the correlation between climate, nutrient and either change in abundance or richness of grassland plants differs between non-native and native species. The reduced abundance of native species in response to nutrient enrichment is independent of climate conditions. However, annual mean climate conditions mediate the effect that nutrient addition has on change in richness of the two groups of species. Particularly in warmer, wetter sites, climate can partially or fully counteract the increase in richness of non-native species (and loss of natives) that often results from eutrophication. This result from a multi-continent replicated study clarifies our understanding of the effects of nutrient enrichment on non-native species by reconciling previous findings that have suggested that non-native species consistently increase in numbers under eutrophication (especially nitrogen addition; [3,7,39]) with those that have found mixed responses [6,19,47]. Finally, our study demonstrates that by changing the composition of communities, eutrophication may be altering the association between communities and climate, leading to a more rapid time-scale response of the community to climatic fluctuations. This more rapid temporal response has important implications for the future of eutrophied grassland communities in the context of ongoing climate change.

8

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