Journal of Vegetation Science

Journal of Vegetation Science IAVS

RESEARCH ARTICLE OPEN ACCESS

Successful Alien Plant Species Exhibit Functional Dissimilarity From Natives Under Varied Climatic Conditions but Not Under Increased Nutrient Availability

Marija Milanović[1,2] | Jonathan D. Bakker[3] | Lori Biederman[4] | Elizabeth T. Borer[5] | Jane A. Catford[6] | Elsa Cleland[7] | Nicole Hagenah[8] | Sylvia Haider[9] | W. Stanley Harpole[2,10,11] | Kimberly Komatsu[12] | Andrew S. MacDougall[13] | Christine Römermann[2,14,15] | Eric W. Seabloom[5] | Sonja Knapp[1,2] | Ingolf Kühn[1,2,10]

[1]Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Halle, Germany | [2]German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany | [3]University of Washington, School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA | [4]Iowa State University, Department of Ecology, Evolution, and Organismal Biology, Ames, Iowa, USA | [5]Department of Ecology, Evolution, and Behavior, University of Minnesota, St Paul, Minnesota, USA | [6]Department of Geography, King's College London, London, UK | [7]Ecology, Behavior & Evolution Department, University of California, La Jolla, California, USA | [8]Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Pretoria, South Africa | [9]Institute of Ecology, Leuphana University of Lüneburg, Lüneburg, Germany | [10]Geobotany and Botanical Garden/Institute for Biology, Martin Luther University Halle-Wittenberg, Halle, Germany | [11]Department of Physiological Diversity, Helmholtz Center for Environmental Research – UFZ, Leipzig, Germany | [12]Biology Department, University of North Carolina at Greensboro, Greensboro, North Carolina, USA | [13]Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada | [14]Plant Biodiversity, Institute of Ecology and Evolution, Friedrich-Schiller University, Jena, Germany | [15]Senckenberg Institute for Plant Form and Function Jena (SIP), Jena, Germany

Correspondence: Marija Milanović (milanovicmarija712@gmail.com)

Received: 10 July 2024 | **Revised:** 1 March 2025 | **Accepted:** 4 March 2025

Co-ordinating Editor: Alicia Teresa Rosario Acosta

Funding: MM gratefully acknowledges the support of iDiv funded by the German Research Foundation (DFG–FZT 118, 202548816), iDiv Flexpool project iCon (Analyzing plant invasions in their environmental context). Konza Prairie LTER funding from NSF 2025849, NSF 1440484, NSF 0823341, NSF 0218210.

Keywords: exotic species | grasslands | invasive species | leaf functional traits | nutrient addition | nutrient network (nut net) | plant traits

ABSTRACT

Aims: The community composition of native and alien plant species is influenced by the environment (e.g., nutrient addition and changes in temperature or precipitation). A key objective of our study is to understand how differences in the traits of alien and native species vary across diverse environmental conditions. For example, the study examines how changes in nutrient availability affect community composition and functional traits, such as specific leaf area and plant height. Additionally, it seeks to assess the vulnerability of high-nutrient environments, such as grasslands, to alien species colonization and the potential for alien species to surpass natives in abundance. Finally, the study explores how climatic factors, including temperature and precipitation, modulate the relationship between traits and environmental conditions, shaping species success.

Location: In our study, we used data from a globally distributed experiment manipulating nutrient supplies in grasslands worldwide (NutNet).

Methods: We investigate how temporal shifts in the abundance of native and alien species are influenced by species-specific functional traits, including specific leaf area (SLA) and leaf nutrient concentrations, as well as by environmental conditions such as climate and nutrient treatments, across 17 study sites. Mixed-effects models were used to assess these relationships.

Sonja Knapp and Ingolf Kühn shared last authorship.

Results: Alien and native species increasing in their abundance did not differ in their leaf traits. We found significantly lower specific leaf area (SLA) with an increase in mean annual temperature and lower leaf Potassium with mean annual precipitation. For trait–environment relationships, when compared to native species, successful aliens exhibited an increase in leaf Phosphorus and a decrease in leaf Potassium with an increase in mean annual precipitation. Finally, aliens' SLA decreased in plots with higher mean annual temperatures.

Conclusions: Therefore, studying the relationship between environment and functional traits may portray grasslands' dynamics better than focusing exclusively on traits of successful species, per se.

1 | Introduction

Alien species can spread rapidly and dominate plant communities. However, these highly successful species represent a tiny fraction of all species that are introduced into a new habitat. A general understanding of what separates these few highly successful species would allow for more effective risk assessment of introduced species and control of newly introduced species (Gallagher et al. 2015). Abundant alien species, which we define as those whose presence in a region is attributable to human actions, deliberate or inadvertent, that enabled them to overcome biogeographical barriers (Pyšek et al. 2020). Alien plant species may successfully establish and spread in new habitats due to their advantageous traits, including faster growth rates, shorter life spans, elevated leaf nutrient levels, higher seed production, enhanced dispersal ability, greater specific leaf area (SLA), and rapid germination (Ordonez et al. 2010; Leishman et al. 2007; Ordonez 2014; Gallagher et al. 2015). Taken together, these traits may reflect differences in resource conservation (nutrient use/leaf traits/lifespan) and resource acquisition (root-shoot biomass ratio, leaf traits) between aliens and natives, where different trait values were recorded in invading aliens compared to co-occurring native species (Funk 2013). The functional differences of species from different regions may improve alien species' chances of success in new environments, allowing them to acquire more resources, increase in abundance, and outcompete other species (Pyšek and Richardson 2007; Van Kleunen et al. 2010; Divíšek et al. 2018).

While the success of alien species may depend on species traits, studying functional traits in isolation without considering environmental conditions misses the important role of abiotic and biotic context on trait selection (Kambach et al. 2023; Golivets et al. 2024). Among other factors, environmental filters (such as climate, land use, and nutrient supply) or human selection might lead to functional similarity between native and alien species, where a set of traits necessary for survival and reproduction will be consistent across species of different origins. In contrast, alien species' success may also depend on being distinct from the native community (Fargione et al. 2003). Thus, trait similarity (via environmental filtering) and trait dissimilarity (via limiting similarity of coexisting species; MacArthur and Levins 1967; Abrams 1983) present important mechanisms in invasion ecology (Catford et al. 2009; Enders et al. 2020). Alien species that are functionally distinct from natives may occupy areas with variable environmental conditions (Knapp and Kühn 2012; Gross et al. 2013; Milanović et al. 2020; Golivets et al. 2024) or outperform local species as climatic conditions change (Pyšek and Richardson 2007). However, Ordonez et al. (2010) found no difference in the trait-environment relationship between native and alien species, presumably because under distinct environmental conditions, both alien and native plants are required to feature a set of traits essential for survival and success.

Field experiments have shown that plant community composition (La Pierre and Smith 2015; Harpole et al. 2016; Komatsu et al. 2019), vegetation cover (Seabloom et al. 2015), and community functional properties (Firn et al. 2019; Broadbent et al. 2020) can dramatically change following nutrient addition. Leishman et al. (2007) found that slower-growing native species dominated in areas with low nutrient availability, but community composition shifted toward fast-growing alien species in disturbed, nutrient-rich environments. Similarly, studies show that species with traits related to fast growth and high nutrient content, photosynthetic rate, or biomass (Funk et al. 2016) were dominant and appeared to be facilitated by increased nutrient availability. The effect of nutrients on trait expression is particularly pronounced for traits related to growth, such as SLA and leaf formation rate (La Pierre and Smith 2015; Heckman et al. 2016), although Firn et al. (2019) found an opposing effect where SLA of plant communities remained relatively constant with nutrient additions. Increases in nutrient quantities are an important driver of plant invasions in grasslands (Seabloom et al. 2015; Funk et al. 2016), and they can be used as model habitats for the main mechanisms behind biological invasions. In contrast, low nutrient availability is predominantly favorable for native species.

Studying the impact of herbivore exclusion on invasion success is crucial because herbivores can limit the spread of alien species by feeding on them, while their absence may allow non-native plants to flourish, particularly in nutrient-enriched environments. Since invasive species often escape their natural herbivores, they may experience reduced grazing pressure, enabling them to capitalize on resource availability without the trade-offs associated with high palatability and rapid growth (Blumenthal 2006).

In our study we performed success-based comparisons of co-occurring alien and native plant species, including functional traits and site-based parameters (temperature, precipitation, nutrient additions, and herbivore exclusion), using a high-resolution, large-extent, worldwide grassland experiment NutNet (Nutrient Network). Including context dependency (reflected in the trait-environment relationships), we assessed the trait-environmental relationship's impact on species success (observed as an increase in species cover over time). Context dependency (or 'mechanistic context dependence' defined by Catford et al. 2022) describes the difference in strength or sign of the relationship between studied variables under different conditions. Accordingly, the interaction of traits may be crucial to explain the success of alien species (Küster et al. 2008). Likewise, an interaction effect of an environmental variable (e.g., temperature, nutrients) can alter the effect of the explanatory variable (species trait) on a response variable (increase in species cover which was a proxy for species success), demonstrating the ecological process. Specifically, in our paper, the following questions are addressed: (Q1) Do traits differ between successful native and alien species? (Q2) Do species traits predict species responses to nutrient addition, herbivore exclusion or distribution along climatic gradients? (Q3) Does the success of native or alien species depend on trait-environment relationships?

2 | Methods

2.1 | NutNet Experimental Design & Site Info

In our study, we used data from the Nutrient Network (NutNet, http://www.nutnet.org/), a globally distributed, herbivore exclusion and nutrient addition experiment replicated in grassland sites across multiple geographical regions (North America, Europe, Africa, and Australia). Our study included only NutNet sites with alien and native species present, with a minimum of 3 years of nutrient addition of essential plant nutrients (N, P, and K) and an unfertilized control. Based on these criteria, our study covers 17 sites (detailed information on sites in Appendix S1) distributed in five biogeographical regions: central plains (North America, four sites), montane west (North America, three sites), Pacific coast (North America, six sites), Atlantic coast (North America, one site), and Australia (three sites) and spanning a variety of ecosystems, including mountain grasslands, shrub steppes, shortgrass and tallgrass prairies, and savannas. Climatic information (mean annual temperature-MAT and mean annual precipitation-MAP) for every site (2007–2020) was retrieved from the WorldClim Global Climate database at a 1 km spatial resolution (version 1.4; http://www.worldclim.org; values ranging for MAP: 262–1898 mm, and for MAT: 5.5°C–18.4°C; Hijmans et al. 2005).

At each of the 17 sites (Borer et al. 2014), nutrients were applied to all treatment plots at the following rates: 10 g N/m^2/year as time-release urea, 10 g P/m^2/year as triple super phosphate, and 10 g K/m^2/year as potassium sulfate. Treatment plots include either one added nutrient (N, P, K), combinations of nutrients (NP, NK, PK, NPK) or plots with a fence for herbivore exclusion (180 cm in height) and plots with a fence and NPK additions. Most of the NutNet sites have three replicate blocks divided into 10 plots measuring 5 m × 5 m each, resulting in a total of 30 plots per experimental site (control and one of the nutrient treatments and/or herbivore exclusion; details on experimental design in Appendix S2).

2.1.1 | Change in Species Cover Over Time (Species Success)

Species abundances were quantified annually (up to 13 years post-treatment) at peak biomass at each site starting in the year preceding the application of experimental treatments (pretreatment year) and species cover was estimated to the nearest 1% within a 1-m^2 subplot in each plot. The cover of each species (list of species Appendix S3) in a permanently marked 1 × 1 m quadrat was estimated visually, and the cover estimates were used for detecting species-level responses to treatment. Several sites with distinct growth periods had the cover estimated at two time points, and species were assigned the maximum cover across both sampling times.

Species origin (native or alien) was determined by the principal investigator of the site checked using national flora databases. To investigate the success of species of different origins (native and alien), we performed linear regressions for every species and every treatment plot, where species cover was a response variable and the year of cover data collection (2007–2021) was the explanatory variable. Coefficients (changes in slope) from the model were used to represent change (increase or decrease) in every species' maximum cover over the period of observation and were used as a response variable in the following analyses.

2.1.2 | Leaf Traits Measurements

For leaf trait measurements (SLA and leaf nutrients (N, P, K)), we selected the most dominant species within each plot and collected leaves once following the application of nutrient treatments. For each species selected for leaf trait analysis in each plot, we randomly selected five fully developed leaves with little to no signs of herbivore damage from five mature individuals. Sampling followed the standardized protocols detailed by Firn et al. (2019). All leaves from each species in each plot were combined to measure leaf area. Depending on the resources available at each site, leaf area (mm^2) was measured using leaf area meters or using a flatbed scanner (Epson perfection V300) and the image analysis software ImageJ. Thereafter, all leaves were dried at 60°C for 48 h and then weighed (dry weight; g). SLA was calculated as the leaf area divided by the dry weight. SLA was calculated for all five leaves collected from each species in each plot at every site. Dried leaves were then ground, bulked per plot and per species, and analyzed for leaf nutrient concentrations. The leaf Nitrogen content was determined using a LECO TruMac, which is based on a combustion technique

TABLE 1 | Mixed effect model results for trait-origin model (includes interaction between traits (leaf Potassium (leaf K), leaf Phosphorus (leaf P), SLA and leaf nitrogen (leaf N)), and origin (ORG) as predictors and change in species cover over time as a response variable).

	Estimate	Std. Error	df	*t*
(Intercept)	0.016	0.308	78.1	0.956
Leaf K:ORG (Alien[a])	0.685	0.384	1102.8	1.784
Leaf P: ORG (Alien)	−0.450	0.324	1102.79	−1.385
SLA:ORG (Alien)	−0.605	0.312	983.87	−1.929
Leaf N:ORG (Alien)	−0.183	0.348	796.29	−0.528

Note: The table includes estimated coefficients, standard error, degrees of freedom (df) and *t* value.
[a]Reference for origin—native species.

TABLE 2 | Mixed effect model results for trait-environment model (includes interaction between traits (leaf Potassium (leaf K), leaf Phosphorus (leaf P), SLA and leaf Nitrogen (leaf N)), and climate (mean annual temperature-MAT, mean annual precipitation-MAP) or treatment (TRT: Nitrogen (N), phosphorus (P), potassium (K) and Fence), as predictors and change in species cover over time as a response variable—fixed effect).

	Estimate	Std. Error	df	*t*
(Intercept)	−0.22	0.55	635.5	−0.403
SLA:MAT	−1.05	0.34	583.5	−3.070
SLA:MAP	−0.16	0.21	830.6	−0.751
MAT:Leaf N	−0.11	0.29	912.8	−0.371
MAP:Leaf N	−0.15	0.21	903.9	−0.697
MAT:Leaf K	−0.02	0.28	995.6	−0.060
MAP:Leaf K	−0.45	0.23	1043	−1.994
MAT:Leaf P	0.10	0.23	1046	0.451
MAP:Leaf P	0.03	0.18	1050	0.166
Leaf N:TRT(FENCE)	0.18	0.80	1030	0.223
Leaf N:TRT(K)	−0.01	0.73	1023	−0.009
Leaf N:TRT(N)	−0.41	0.79	1025	−0.517
Leaf N:TRT(NK)	−0.36	0.71	1025	−0.501
Leaf N:TRT(NP)	0.06	0.72	1028	0.078
Leaf N:TRT(NPK)	0.01	0.73	1029	0.014
Leaf N:TRT(NPK + FENCE)	0.10	0.73	1032	0.143
Leaf N:TRT(P)	0.11	0.68	1026	0.157
Leaf N:TRT(PK)	0.48	0.71	1030	0.664
Leaf K:TRT(FENCE)	0.31	1.06	1028	0.296
Leaf K:TRT(K)	0.75	0.97	1025	0.776
Leaf K:TRT(N)	0.45	0.91	1035	0.496
Leaf K:TRT(NK)	−0.10	0.91	1028	−0.111
Leaf K:TRT(NP)	1.72	0.98	1025	1.738
Leaf K:TRT(NPK)	0.30	0.98	1035	0.303
Leaf K:TRT(NPK + FENCE)	0.27	1.03	1028	0.260
Leaf K:TRT(P)	0.11	0.94	1029	0.120
Leaf K:TRT(PK)	0.32	0.91	1026	0.351
Leaf P:TRT(FENCE)	1.07	1.03	1033	1.034
Leaf P:TRT(K)	0.20	1.09	1025	0.188
Leaf P:TRT(N)	0.39	1.15	1029	0.342
Leaf P:TRT(NK)	1.20	1.11	1028	1.081
Leaf P:TRT(NP)	−0.33	0.86	1023	−0.379
Leaf P:TRT(NPK)	−0.09	0.86	1034	−0.109
Leaf P:TRT(NPK + FENCE)	0.30	0.91	1027	0.330
Leaf P:TRT(P)	−0.16	0.84	1042	−0.194
Leaf P:TRT(PK)	−0.08	0.92	1042	−0.086

(Continues)

TABLE 2 | (Continued)

	Estimate	Std. Error	df	*t*
SLA:TRT(FENCE)	0.17	0.76	1039	0.215
SLA:TRT(K)	−0.39	0.72	1022	−0.544
SLA:TRT(N)	−0.01	0.77	1017	−0.015
SLA:TRT(NK)	0.04	0.77	1024	0.052
SLA:TRT(NP)	−1.36	0.75	1023	−1.796
SLA:TRT(NPK)	1.10	0.73	1027	1.506
SLA:TRT(NPK + FENCE)	0.84	0.71	1053	1.171
SLA:TRT(P)	0.06	0.76	1025	0.078
SLA:TRT(PK)	−0.45	0.78	1020	−0.569

Note: The table includes estimated coefficients, standard error, degrees of freedom (df) and *t* value.

that uses thermal conductivity relative to pure gas and provides accurate and precise results (nitrogen values vary <0.02). The leaf Potassium and Phosphorus concentrations were determined using laser ablation inductively coupled plasma mass spectrometry after Duodu et al. (2015) with the following exceptions: the internal standard was not added, but carbon was measured; the most abundant naturally occurring element was used; and no extra pulverizing was performed beyond that required for carbon and nitrogen analysis, which consisted of placing a sample and a 2-mm-diameter tungsten carbide ball inside 2-mm plastic centrifuge vials, followed by grinding for 15 min using a TissueLyser. Leaves (approximately 0.2 g) were compressed in a hydraulic dye, which produced a pellet approximately 5 mm across and 2 mm tall. These pellets were glued to a plastic tray in groups of ~100 and placed inside the laser chamber. A New Wave 193-nm excimer laser with a TrueLine cell was connected to an Agilent 8800 inductively coupled plasma mass spectrometer. The laser beam was 65 μm in diameter and rastered across a length of approximately 500 μm for approximately 50 s, 5 times per sample with a 30-s washout or background between rasters. The laser fluence at the laser exit was approximately 2 J/cm^2 and the repetition rate was 7 Hz. The National Institute of Standards and Technology National Bureau of Standards peach leaves and National Institute of Standards and Technology National Bureau of Standards spinach were used as monitoring standards; these were analyzed every third sample (15 rasters) for moderately close sample-standard bracketing. The average and standard deviation of each element in each sample were calculated and reported following the method presented by Longerich et al. (1996) using Iloite data reduction software.

2.2 | Statistical Analyses

2.2.1 | Data Standardization and Multicollinearity

Explanatory variables were standardized to zero mean and unit standard deviation. We tested for multicollinearity among explanatory variables (traits, mean annual temperature and precipitation) using the function *corrplot*. We recorded correlation coefficients ($r<|0.7|$, Dormann et al. 2013) for all leaf traits, as well as between temperature and precipitation. We found that all predictors had low correlation coefficients (range 0.18–0.44) and so were included in the analysis.

2.2.2 | Mixed Effect Models

To investigate the relationship between species success with traits and/or environmental predictors, we fit several mixed-effect models (LME). The first model ('trait-model', Q1) includes the change in species cover over time as a response variable, all of the four species traits, and origin as fixed effects, their two-way interactions, and 1|site/block as a random effect. Further, we tested if traits predict species change (regardless of their origin) in cover under different environments. The corresponding LME included change in species cover over time as response and trait-environment interactions as predictors (nutrient additions, herbivore exclusion, temperature and precipitation, Q2). The final model tests (Q3) the trait-environment relationships of native and alien species, with change in species cover over time as a response and fixed effects include traits, origin, environment (climate—mean annual temperature (MAT) and mean annual precipitation (MAP), and nutrient treatments and herbivore exclusion), and all three-way interactions. We used the *lmer* function (package lme4) to fit mixed-effect models for all research questions (Q1, Q2, Q3). To check for assumptions, we inspected the residuals in the diagnostic plots of each model. The data analysis was performed using R, version 4.3.1 (R Core Team 2017).

3 | Results

3.1 | Species Success and Traits of Alien and Native Species (Q1)

We found no statistically significant differences in the leaf traits of successful aliens and natives (Table 1), based on the trait model (Q1) that included all leaf traits and species origin (as fixed effects) with change in species cover over time as a response variable. The trait-origin model explained 10.5% of the variance (conditional R^2) of which 1.3% can be explained by fixed effects (marginal R^2, Appendix S4a).

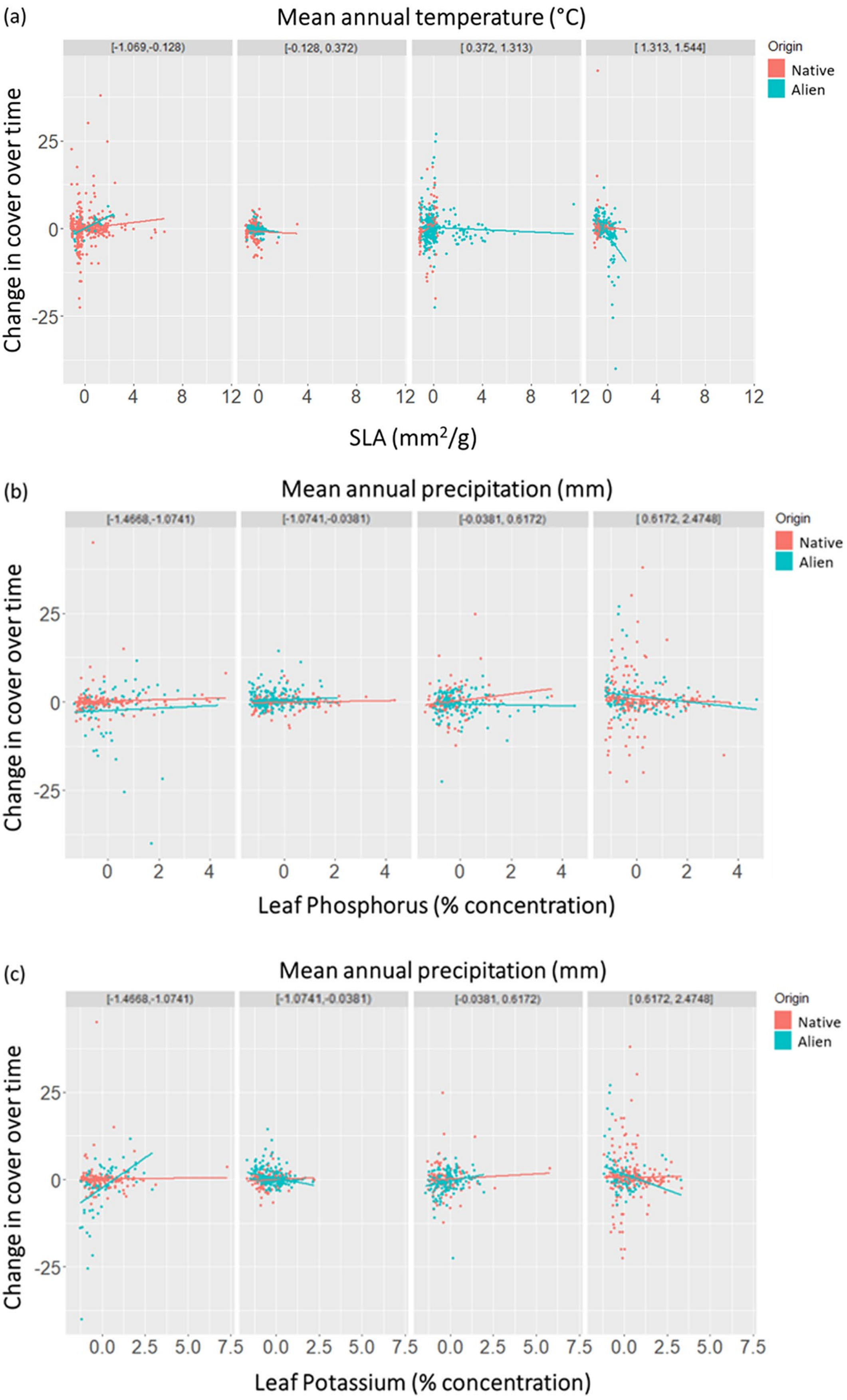

FIGURE 1 | Legend on next page.

FIGURE 1 | Scatter plots illustrating the variation in cover change of native and alien species as a function of leaf trait values under differing mean annual temperature (MAT) and precipitation (MAP) conditions. The y-axis represents the change in species cover per plot, while the x-axis shows trait values (specific leaf area (SLA), leaf phosphorus (Leaf P), and leaf potassium (Leaf K)). Points and trend lines are color-coded by species origin: Red represents native species, and blue represents alien species. Grid cells indicate categories of scaled temperature and precipitation increases. Panel (a) depicts the three-way interaction between SLA, MAT, and species origin; panel (b) highlights the interaction between leaf phosphorus, MAP, and species origin; and panel (c) shows the interaction between leaf potassium, MAP, and species origin.

3.2 | Species Success and Trait-Environment Relationships (Q2)

The trait-environment model shows how trait-environment relationships relate to species' success, irrespective of their origin. The trait-environment model explained 13% of the variance (conditional R^2) of which 6.1% was explained by fixed effects (marginal R^2, Appendix S4b). We found that species with higher SLA (coefficient = −1.05, Table 2) were significantly less successful as site-level mean annual temperature increased. Similarly, species with higher amounts of leaf Potassium were less successful at sites with higher mean annual precipitation (coefficient = −0.45, Table 2).

3.3 | Species Success and Trait-Environment Relationships of Alien and Native Species (Q3)

The trait-environment model included leaf traits, climate (MAT/MAP), all nutrient treatments, and origin with change in species cover over time as a response variable (as a fixed effect). The trait-environment model explained 22% of the variance (conditional R^2) of which 15% is explained by fixed effects (marginal R^2; see Appendix S4c for a full summary). We found that compared to natives, successful aliens tend to contain more leaf Phosphorus (coefficient = 0.88, Figure 1b, Table 3), but leaf Potassium declines in aliens with increasing mean annual precipitation (coefficient = −2.21, Figure 1c, Table 3). Finally, compared to natives, the SLA of alien species declines with increasing mean annual temperature (coefficient = −2.35, Figure 1a, Table 3).

4 | Discussion

In this study, we analyzed the success of co-occurring native and alien species by examining both species-specific and site-based parameters. Incorporating a range of factors, including species traits, climate, and nutrient content, is critical for understanding these dynamics. The success of alien species is often explained through contrasting hypotheses, which can be based on the distinct trait spaces these species occupy in comparison to native species (Enders and Jeschke 2018). One set of hypotheses focuses on alien species being functionally dissimilar from native species ('competitive-relatedness hypothesis', 'try harder', 'limiting similarity hypothesis', 'phenotypic divergence' (Crawley et al. 1996; Cahill Jr. et al. 2008)), i.e., having niches with specific environmental profiles (Pyšek and Richardson 2007; Divíšek et al. 2018). Contrasting hypotheses ('pre-adaptation hypothesis', 'habitat filtering hypothesis', 'phenotypic convergence', 'fit with locals') relate to alien success and illustrate how the same general strategies may lead to similar traits that allow alien and native species to coexist under local environmental conditions (Ordonez et al. 2010). In our results, we found support for both standpoints, and that alien and native species share traits and can be functionally distinct (on different scales and for multiple traits).

We observed that specific leaf area (SLA) and leaf nutrient levels were comparable across species of different origins, indicating functional similarity. However, specific leaf area (SLA), leaf Phosphorus, and leaf Potassium varied between successful native and alien species across different climatic conditions. Specific leaf area is one of the most commonly used traits in invasion ecology; yet, the majority of studies have found contrasting results. For example, studies have found that higher SLA values can be beneficial for alien species (Mathakutha et al. 2019; Divíšek et al. 2018; Ordonez and Olff 2013), as well as that greater SLA may lead to a competitive disadvantage in aliens (Feng et al. 2019; Feng and van Kleunen 2016; Kunstler et al. 2016; Kraft et al. 2015). Successful aliens tend to conserve acquired resources, exhibit higher stress tolerance (particularly water), lower metabolic and photosynthetic rates, and are long-lived, slow-growing species (Wright et al. 2004; Poorter and Bongers 2006; Vellend et al. 2014). The conflicting results for SLA highlight the importance of accounting for the role of environmental conditions in mediating trait effects on species success. Although we observed evidence of trait differences between successful alien species and native species under varying climatic conditions, leaf traits did not exhibit significant variation outside of specific environmental contexts. This indicates that species success is context-dependent. Hess et al. (2020) argue that functional differences between species are often not found, particularly when there are multiple co-occurring alien species. Further, a meta-analysis by Price and Pärtel (2013) revealed that the importance of functional dissimilarity for species success diminishes in more established and natural habitats, while it plays an important role in experimental setups. Studies so far (shown in a meta-analysis done by Leffler et al. 2014) have shown that functional differences are context-dependent, where other mechanisms may explain the success of invasive species. Thus, introducing climatic information within the plots revealed that the variation in most of the leaf traits we studied is relevant to species' success under different environmental conditions.

Previous studies provide evidence that alien plant species outperform native species along climatic gradients (e.g., warm and dry conditions, Pyšek et al. 2005) as well as in environments with enhanced soil nutrients (Zhao et al. 2020). In examining the relationship between traits and climate, we found that precipitation significantly interacted with leaf nutrient concentrations, while successful alien species exhibited lower specific leaf area (SLA) values compared to natives in warmer temperatures.

TABLE 3 | Mixed effect model results for traits-environmental model (includes interaction between traits (leaf Potassium (leaf K), leaf Phosphorus (leaf P), SLA and leaf Nitrogen (leaf N)), origin (ORG) and climate (mean annual temperature-MAT, mean annual precipitation-MAP) or treatment (TRT: Nitrogen (N), phosphorus (P), potassium (K) and Fence), as predictors and change in species cover over time as a response variable—fixed effect).

	Estimate	**Std. Error**	**df**	***t***
(Intercept)	0.49	0.72	780.56	0.68
SLA:TRT(FENCE):ORG (Alien[a])	−0.90	1.60	981.09	−0.56
SLA:TRT(K):ORG (Alien)	1.06	1.50	952.95	0.70
SLA:TRT(N):ORG (Alien)	0.07	1.65	946.87	0.04
SLA:TRT(NK):ORG (Alien)	0.59	1.63	957.49	0.36
SLA:TRT(NP):ORG (Alien)	−0.15	2.03	963.32	−0.07
SLA:TRT(NPK):ORG (Alien)	−2.33	1.58	958.55	−1.47
SLA:TRT(NPK + FENCE):ORG (Alien)	−0.14	1.60	985.77	−0.08
SLA:TRT(P):ORG (Alien)	−0.19	1.59	960.25	−0.12
SLA:TRT(PK):ORG (Alien)	0.39	1.64	953.02	0.24
Leaf N:TRT(FENCE):ORG (Alien)	−1.65	1.70	971.50	−0.97
Leaf N:TRT(K):ORG (Alien)	−0.75	1.54	951.26	−0.48
Leaf N:TRT(N):OORG (Alien)	−0.09	1.65	959.05	−0.05
Leaf N:TRT(NK):ORG (Alien)	−0.29	1.51	957.98	−0.19
Leaf N:TRT(NP):ORG (Alien)	−2.44	1.49	961.21	−1.63
Leaf N:TRT(NPK):ORG (Alien)	−0.41	1.52	962.44	−0.27
Leaf N:TRT(NPK + FENCE):ORG (Alien)	−1.23	1.50	964.53	−0.82
Leaf N:TRT(P):ORG (Alien)	−0.12	1.42	958.56	−0.08
Leaf N:TRT(PK):ORG (Alien)	−0.42	1.46	969.12	−0.29
Leaf P:TRT(FENCE):ORG (Alien)	2.34	2.20	961.02	1.06
Leaf P:TRT(K):ORG (Alien)	1.29	2.25	957.52	0.57
Leaf P:TRT(N):ORG (Alien)	0.92	2.43	964.04	0.38
Leaf P:TRT(NK):ORG (Alien)	−0.10	2.26	960.12	−0.04
Leaf P:TRT(NP):ORG (Alien)	2.25	1.78	959.50	1.26
Leaf P:TRT(NPK):ORG (Alien)	0.73	1.80	960.93	0.40
Leaf P:TRT(NPK + FENCE):ORG (Alien)	0.87	1.90	977.28	0.46
Leaf P:TRT(P):ORG (Alien)	0.34	1.76	957.58	0.19
Leaf P:TRT(PK):ORG (Alien)	1.87	1.92	972.10	0.97
Leaf K:TRT(FENCE):ORG (Alien)	−1.40	2.30	958.90	−0.61
Leaf K:TRT(K):ORG (Alien)	−0.83	2.07	963.14	−0.40
Leaf K:TRT(N):ORG (Alien)	−0.24	2.04	958.55	−0.12
Leaf K:TRT(NK):ORG (Alien)	−0.42	1.98	958.42	−0.21
Leaf K:TRT(NP):ORG (Alien)	2.34	2.13	967.30	1.09
Leaf K:TRT(NPK):ORG (Alien)	1.05	2.05	961.26	0.51
Leaf K:TRT(NPK + FENCE):ORG (Alien)	−0.55	2.18	966.75	−0.25
Leaf K:TRT(P):ORG (Alien)	−0.96	2.04	959.49	−0.47

(Continues)

TABLE 3 | (Continued)

	Estimate	Std. Error	df	*t*
Leaf K:TRT(PK):ORG (Alien)	−2.52	1.95	960.33	−1.29
SLA:ORG (Alien):MAT	−2.34	0.93	960.56	−2.52
SLA:ORG (Alien):MAP	0.65	0.54	503.02	1.21
Leaf N:ORG (Alien):MAT	−0.01	0.64	921.42	−0.01
Leaf P:ORG (Alien):MAT	−1.05	0.59	991.17	−1.77
Leaf K:ORG (Alien):MAT	1.34	0.69	992.91	1.94
Leaf N:ORG (Alien):MAP	0.81	0.57	938.66	1.41
Leaf P:ORG (Alien):MAP	0.87	0.44	991.86	1.96
Leaf K:ORG (Alien):MAP	−2.20	0.60	992.11	−3.63

Note: The table includes estimated coefficients, standard error, degrees of freedom (df) and *t* value. The full model summary (including random effects) is shown in the Appendix S4c.
[a]Reference for origin – native species.

As a result, in warmer sites, native species with higher SLA tend to be more successful. SLA interactions with climate in grasslands can, however, often be genus- or species-dependent (Liu et al. 2017). This might explain the inconsistent results from the majority of current research, where climate is significantly correlated to SLA (e.g., negative association in Wright et al. (2004), or positive association in Poorter and Bongers (2006)). We found a significant relationship between SLA and environmental factors, and these results are in line with a previous study by Catford et al. (2019) where species with higher SLA were more successful at spreading to new plots while those with lower SLA had higher long-term occupancy rates (i.e., high SLA is advantageous in earlier stages and lower SLA is gaining in importance in the long term).

Chen et al. (2013) found that climatic factors, such as precipitation, significantly influence the availability of soil nutrients and are a primary driver of leaf nutrient levels, and this relationship was particularly pronounced in Phosphorus content. Elevated levels of leaf Phosphorus in herbaceous plant species are indicative of enhanced growth potential (Tecco et al. 2010). This phenomenon may result from the increased availability of effective soil nutrients, which is influenced by rising precipitation levels. Consequently, this can lead to higher tissue Phosphorus concentrations, as diminished soil moisture in drier sites can restrict nutrient uptake (Wood et al. 2005). Thus, successful alien species demonstrate enhanced phosphorus acquisition in wetter sites by effectively utilizing available phosphorus resources. This enhanced nutrient uptake facilitates more rapid growth rates when compared to native species. In contrast to leaf Phosphorus, leaf Potassium concentrations in successful alien species decreased as precipitation increased. Meier and Leuschner (2014) demonstrated similar results, as leaf Potassium concentrations decline with increasing precipitation, indicating a potential limitation of potassium for plant growth in moist environments.

Firn et al. (2019) found no significant relationship between SLA and soil nutrients and that, conversely, leaf nutrients were the only traits that responded to an increase in soil nutrient supplies. However, in our study, no evidence of trait differences between native and alien species was observed, suggesting functional similarity between species of different origins under conditions of elevated soil nutrients. The ability of successful alien plant species to perform similarly to natives under high-nutrient conditions might be related to their area of origin. Most of the alien species at our sites have been introduced from Eurasia, where these species have been preadapted to increased nutrient rates due to 10,000 years of continuous arable farming. Successful species, regardless of their origin, occupy nutrient-rich plots that allow them to secure adequate soil nutrients for rapid growth. This results in thinner and larger leaves, which enhance light capture and contribute to greater competitive ability, provide benefits in resource capturing, allocation of metabolic components, higher photosynthetic rates, and rapid growth (Reich et al. 1999; Wright et al. 2004; Vellend et al. 2014; Rosbakh et al. 2015; Mathakutha et al. 2019).

The divergence of the effects that climate and nutrient additions have on aliens' and natives' leaf traits confirms the complexity of studying species' success. The success of alien species due to their functional dissimilarity from native species can be evident under specific environmental conditions (Milanović et al. 2020). However, Drenovsky et al. (2012) concluded that dominant native and alien species show functional similarity as a response to changes in resource availability. Further, Cleland et al. (2011) found that native and alien species' traits were context-dependent (traits varied between sites) and that aliens that became successful had a set of traits pre-adapting them to the novel environmental conditions. Thus, it is necessary to further study species trait sets and to include multivariate relationships of traits with soil nutrients and climate (e.g., nutrient availability may change with precipitation and temperature). In particular, habitat conditions can be decisive factors in filtering successful species and their traits (Lembrechts et al. 2017; Kambach et al. 2023).

Our findings have important implications for understanding the main mechanisms behind the success of alien plant species in grasslands. We show that trait and environmental aspects, as well as their interactions, affect species' success, suggesting that including both components is necessary since aliens showed functional similarity and dissimilarity from co-occurring native flora. We conclude that, independent of the environment, natives and aliens tend to be similar in leaf nutrients on both local and global scales. However, the functional dissimilarity, reflected in differences in SLA between natives and aliens under different environmental conditions, can help in explaining the success of plant invasions in grasslands.

Author Contributions

M.M. developed and framed research questions, analyzed data, and wrote the paper. I.K., S.K., and C.R. developed and framed research questions and contributed to paper writing. S.H., E.T.B., E.C., J.D.B., L.B., E.W.S., K.K., N.H., J.A.C., S.H., and A.S.M. contributed with data (as NutNet site and project coordinators) and paper writing.

Acknowledgments

This work was conducted using data from the NutNet collaborative experiment, funded at the site scale by individual researchers, and coordinated with funding from NSF to E.T.B. and E.W.S. (NSF-DEB-1042132 and NSF-DEB-1234162). We thank the Minnesota Supercomputer Institute for hosting project data. The authors thank QUT's Central Analytical Facilities (CARF), part of the Institute of Future Environment (IFE), for use of their facilities to analyze leaf nutrient concentrations. Open Access funding enabled and organized by Projekt DEAL.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in Zenodo with the unique identifier: https://doi.org/10.5281/zenodo.14944000.

References

Abrams, P. 1983. "The Theory of Limiting Similarity." *Annual Review of Ecology and Systematics* 14, no. 1: 359–376. https://doi.org/10.1146/ANNUREV.ES.14.110183.002043.

Blumenthal, D. M. 2006. "Interactions Between Resource Availability Andenemy Release in Plant Invasion." *Ecology Letters* 9: 887–895. https://doi.org/10.1111/j.1461-0248.2006.00934.x.

Borer, E. T., W. S. Harpole, P. B. Adler, et al. 2014. "Finding Generality in Ecology: A Model for Globally Distributed Experiments." *Methods in Ecology and Evolution* 5, no. 1: 65–73. https://doi.org/10.1111/2041-210X.12125.

Broadbent, A. A., J. Firn, J. M. McGree, et al. 2020. "Dominant Native and Non-native Graminoids Differ in Key Leaf Traits Irrespective of Nutrient Availability." *Global Ecology and Biogeography* 29, no. 7: 1126–1138. https://doi.org/10.1111/geb.13092.

Cahill, J. F., Jr., S. W. Kembel, E. G. Lamb, and P. A. Keddy. 2008. "Does Phylogenetic Relatedness Influence the Strength of Competition Among Vascular Plants?" *Perspectives in Plant Ecology, Evolution and Systematics* 10, no. 1: 41–50. https://doi.org/10.1016/j.ppees.2007.10.001.

Catford, J. A., R. Jansson, and C. Nilsson. 2009. "Reducing Redundancy in Invasion Ecology by Integrating Hypotheses Into a Single Theoretical Framework." *Diversity and Distributions* 15, no. 1: 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x.

Catford, J. A., A. L. Smith, P. D. Wragg, et al. 2019. "Traits Linked With Species Invasiveness and Community Invasibility Vary With Time, Stage and Indicator of Invasion in a Long-Term Grassland Experiment." *Ecology Letters* 22, no. 4: 593–604. https://doi.org/10.1111/ele.13220.

Catford, J. A., J. R. Wilson, P. Pyšek, P. E. Hulme, and R. P. Duncan. 2022. "Addressing Context Dependence in Ecology." *Trends in Ecology & Evolution* 37, no. 2: 158–170. https://doi.org/10.1016/j.tree.2021.09.007.

Chen, Y., W. Han, L. Tang, Z. Tang, and J. Fang. 2013. "Leaf Nitrogen and Phosphorus Concentrations of Woody Plants Differ in Responses to Climate, Soil and Plant Growth Form." *Ecography* 36, no. 2: 178–184. https://doi.org/10.1111/j.1600-0587.2011.06833.x.

Cleland, E. E., C. M. Clark, S. L. Collins, et al. 2011b. "Patterns of Trait Convergence and Divergence Among Native and Exotic Species in Herbaceous Plant Communities Are Not Modified by Nitrogen Enrichment." *Journal of Ecology* 99, no. 6: 1327–1338. https://doi.org/10.1111/j.1365-2745.2011.01860.x.

Crawley, M. J., P. H. Harvey, and A. N. D. A. Purvis. 1996. "Comparative Ecology of the Native and Alien Floras of the British Isles." *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 351, no. 1345: 1251–1259. https://doi.org/10.1098/rstb.1996.0108.

Divíšek, J., M. Chytrý, B. Beckage, et al. 2018. "Similarity of Introduced Plant Species to Native Ones Facilitates Naturalization, but Differences Enhance Invasion Success." *Nature Communications* 9, no. 1: 4631. https://doi.org/10.1038/s41467-018-06995-4.

Dormann, C. F., J. Elith, S. Bacher, et al. 2013. "Collinearity: A Review of Methods to Deal With It and a Simulation Study Evaluating Their Performance." *Ecography* 36, no. 1: 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Drenovsky, R. E., A. Khasanova, and J. J. James. 2012. "Trait Convergence and Plasticity Among Native and Invasive Species in Resource-Poor Environments." *American Journal of Botany* 99, no. 4: 629–639. https://doi.org/10.3732/ajb.1100417.

Duodu, G. O., A. Goonetilleke, C. Allen, and G. A. Ayoko. 2015. "Determination of Refractive and Volatile Elements in Sediment Using Laser Ablation Inductively Coupled Plasma Mass Spectrometry." *Analytica Chimica Acta* 898: 19–27. https://doi.org/10.1016/j.aca.2015.09.033.

Enders, M., F. Havemann, F. Ruland, et al. 2020. "A Conceptual Map of Invasion Biology: Integrating Hypotheses Into a Consensus Network." *Global Ecology and Biogeography* 29, no. 6: 978–991. https://doi.org/10.1111/geb.13082.

Enders, M., and J. M. Jeschke. 2018. "A Network of Invasion Hypotheses." In *Invasion Biology: Hypotheses and Evidence*, 49–59. CAB International. https://doi.org/10.1002/ecs2.2146.

Fargione, J., C. S. Brown, and D. Tilman. 2003. "Community Assembly and Invasion: An Experimental Test of Neutral Versus Niche Processes." *Proceedings of the National Academy of Sciences* 100, no. 15: 8916–8920. https://doi.org/10.1073/pnas.1033107100.

Feng, Y., T. D. Fouqueray, and M. van Kleunen. 2019. "Linking Darwin's Naturalisation Hypothesis and Elton's Diversity–Invasibility Hypothesis in Experimental Grassland Communities." *Journal of Ecology* 107, no. 2: 794–805. https://doi.org/10.1111/1365-2745.13061.

Feng, Y., and M. van Kleunen. 2016. "Phylogenetic and Functional Mechanisms of Direct and Indirect Interactions Among Alien and Native Plants." *Journal of Ecology* 104, no. 4: 1136–1148. https://doi.org/10.1111/1365-2745.12577.

Firn, J., J. M. McGree, E. Harvey, et al. 2019. "Leaf Nutrients, Not Specific Leaf Area, Are Consistent Indicators of Elevated Nutrient Inputs." *Nature Ecology & Evolution* 3, no. 3: 400–406. https://doi.org/10.1038/s41559-018-0790-1.

Funk, J. L. 2013. "The Physiology of Invasive Plants in Low-Resource Environments." *Conservation Physiology* 1, no. 1. https://doi.org/10.1093/conphys/cot026.

Funk, J. L., R. J. Standish, W. D. Stock, and F. Valladares. 2016. "Plant Functional Traits of Dominant Native and Invasive Species in

Mediterranean-Climate Ecosystems." *Ecology* 97, no. 1: 75–83. https://doi.org/10.1890/15-0974.1.

Gallagher, R. V., R. P. Randall, and M. Leishman. 2015. "Trait Differences Between Naturalized and Invasive Plant Species Independent of Residence Time and Phylogeny." *Conservation Biology* 29, no. 2: 360–369. https://doi.org/10.1111/cobi.12399.

Golivets, M., S. Knapp, F. Essl, et al. 2024. "Future Changes in Key Plant Traits Across Central Europe Vary With Biogeographical Status, Woodiness, and Habitat Type." *Science of the Total Environment* 907: 167954. https://doi.org/10.1016/j.scitotenv.2023.167954.

Gross, N., L. Börger, R. P. Duncan, and P. E. Hulme. 2013. "Functional Differences Between Alien and Native Species: Do Biotic Interactions Determine the Functional Structure of Highly Invaded Grasslands?" *Functional Ecology* 27, no. 5: 1262–1272. https://doi.org/10.1111/1365-2435.12120.

Harpole, W. S., L. L. Sullivan, E. M. Lind, et al. 2016. "Addition of Multiple Limiting Resources Reduces Grassland Diversity." *Nature* 537, no. 7618: 93–96. https://doi.org/10.1038/nature19324.

Heckman, R. W., J. P. Wright, and C. E. Mitchell. 2016. "Joint Effects of Nutrient Addition and Enemy Exclusion on Exotic Plant Success." *Ecology* 97, no. 12: 3337–3345. https://doi.org/10.1002/ecy.1585.

Hess, M. C., E. Buisson, R. Jaunatre, and F. Mesléard. 2020. "Using Limiting Similarity to Enhance Invasion Resistance: Theoretical and Practical Concerns." *Journal of Applied Ecology* 57, no. 3: 559–565. https://doi.org/10.1111/1365-2664.13552.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. "Very High Resolution Interpolated Climate Surfaces for Global Land Areas." *International Journal of Climatology: A Journal of the Royal Meteorological Society* 25, no. 15: 1965–1978. https://doi.org/10.1002/joc.1276.

Kambach, S., F. M. Sabatini, F. Attorre, et al. 2023. "Climate-Trait Relationships Exhibit Strong Habitat Specificity in Plant Communities Across Europe." *Nature Communications* 14, no. 1: 712. https://doi.org/10.1038/s41467-023-36240-6.

Knapp, S., and I. Kühn. 2012. "Origin Matters: Widely Distributed Native and Non-native Species Benefit From Different Functional Traits." *Ecology Letters* 15, no. 7: 696–703. https://doi.org/10.1111/j.1461-0248.2012.01787.x.

Komatsu, K. J., M. L. Avolio, N. P. Lemoine, et al. 2019. "Global Change Effects on Plant Communities Are Magnified by Time and the Number of Global Change Factors Imposed." *Proceedings of the National Academy of Sciences of the United States of America* 116, no. 36: 17867–17873. https://doi.org/10.1073/pnas.1819027116.

Kraft, N. J., O. Godoy, and J. M. Levine. 2015. "Plant Functional Traits and the Multidimensional Nature of Species Coexistence." *Proceedings of the National Academy of Sciences* 112, no. 3: 797–802. https://doi.org/10.1073/pnas.1413650112.

Kunstler, G., D. Falster, D. A. Coomes, et al. 2016. "Plant Functional Traits Have Globally Consistent Effects on Competition." *Nature* 529, no. 7585: 204–207. https://doi.org/10.1038/nature16476.

Küster, E. C., I. Kühn, H. Bruelheide, and S. Klotz. 2008. "Trait Interactions Help Explain Plant Invasion Success in the German Flora." *Journal of Ecology* 96, no. 5: 860–868. https://doi.org/10.1111/j.1365-2745.2008.01406.x.

La Pierre, K. J., and M. D. Smith. 2015. "Functional Trait Expression of Grassland Species Shift With Short-and Long-Term Nutrient Additions." *Plant Ecology* 216: 307–318. https://doi.org/10.1007/s11258-014-0438-4.

Leffler, A. J., J. J. James, T. A. Monaco, and R. L. Sheley. 2014. "A New Perspective on Trait Differences Between Native and Invasive Exotic Plants." *Ecology* 95, no. 2: 298–305. https://doi.org/10.1890/13-0102.1.

Leishman, M. R., T. Haslehurst, A. Ares, and Z. Baruch. 2007. "Leaf Trait Relationships of Native and Invasive Plants: Community-and Global-Scale Comparisons." *New Phytologist* 176, no. 3: 635–643. https://doi.org/10.1111/j.1469-8137.2007.02189.x.

Lembrechts, J. J., J. M. Alexander, L. A. Cavieres, et al. 2017. "Mountain Roads Shift Native and Non-native Plant species' Ranges." *Ecography* 40, no. 3: 353–364. https://doi.org/10.1111/ecog.02200.

Liu, M., Z. Wang, S. Li, X. Lü, X. Wang, and X. Han. 2017. "Changes in Specific Leaf Area of Dominant Plants in Temperate Grasslands Along a 2500-Km Transect in Northern China." *Scientific Reports* 7, no. 1: 10–780. https://doi.org/10.1038/s41598-017-11133-z.

Longerich, H. P., S. E. Jackson, and D. Günther. 1996. "Inter-Laboratory Note. Laser Ablation Inductively Coupled Plasma Mass Spectrometric Transient Signal Data Acquisition and Analyte Concentration Calculation." *Journal of Analytical Atomic Spectrometry* 11, no. 9: 899–904. https://doi.org/10.1039/ja9961100899.

MacArthur, R., and R. Levins. 1967. "The Limiting Similarity, Convergence, and Divergence of Coexisting Species." *American Naturalist* 101, no. 921: 377–385. https://doi.org/10.1086/282505.

Mathakutha, R., C. Steyn, P. C. le Roux, et al. 2019. "Invasive Species Differ in Key Functional Traits From Native and Non-invasive Alien Plant Species." *Journal of Vegetation Science* 30, no. 5: 994–1006. https://doi.org/10.1111/jvs.12772.

Meier, I. C., and C. Leuschner. 2014. "Nutrient Dynamics Along a Precipitation Gradient in European Beech Forests." *Biogeochemistry* 120: 51–69. https://doi.org/10.1007/s10533-014-9981-2.

Milanović, M., S. Knapp, P. Pyšek, and I. Kühn. 2020. "Trait–Environment Relationships of Plant Species at Different Stages of the Introduction Process." *NeoBiota* 58: 55–74. https://doi.org/10.3897/neobiota.58.51655.

Ordonez, A. 2014. "Functional and Phylogenetic Similarity of Alien Plants to Co-Occurring Natives." *Ecology* 95, no. 5: 1191–1202. https://doi.org/10.1890/13-1002.1.

Ordonez, A., I. J. Wright, and H. Olff. 2010. "Functional Differences Between Native and Alien Species: A Global-Scale Comparison." *Functional Ecology* 24, no. 6: 1353–1361. https://doi.org/10.1111/j.1365-2435.2010.01739.x.

Ordonez, A., and H. Olff. 2013. "Do Alien Plant Species Profit More From High Resource Supply Than Natives? A Trait-Based Analysis." *Global Ecology and Biogeography* 22, no. 6: 648–658.

Poorter, L., and F. Bongers. 2006. "Leaf Traits Are Good Predictors of Plant Performance Across 53 Rain Forest Species." *Ecology* 87, no. 7: 1733–1743. https://doi.org/10.1890/0012-9658(2006)87[1733:ltagpo]2.0.co;2.

Price, J. N., and M. Pärtel. 2013. "Can Limiting Similarity Increase Invasion Resistance? A Meta-Analysis of Experimental Studies." *Oikos* 122, no. 5: 649–656. https://doi.org/10.1111/j.1600-0706.2012.00121.x.

Pyšek, P., P. E. Hulme, D. Simberloff, et al. 2020. "Scientists' Warning on Invasive Alien Species." *Biological Reviews of the Cambridge Philosophical Society* 95, no. 6: 1511–1534. https://doi.org/10.1111/brv.12627.

Pyšek, P., V. Jarošík, M. Chytrý, Z. Kropáč, L. Tichý, and J. Wild. 2005. "Alien Plants in Temperate Weed Communities: Prehistoric and Recent Invaders Occupy Different Habitats." *Ecology* 86, no. 3: 772–785. https://doi.org/10.1890/04-0012.

Pyšek, P., and D. M. Richardson. 2007. "Traits Associated With Invasiveness in Alien Plants: Where Do We Stand?" *Biological Invasions*: 97–125. https://doi.org/10.1007/978-3-540-36920-2_72007.

Reich, P. B., D. S. Ellsworth, M. B. Walters, et al. 1999. "Generality of Leaf Trait Relationships: A Test Across Six Biomes." *Ecology* 80, no. 6: 1955–1969. https://doi.org/10.1890/0012-9658(1999)080[1955:GOLTRA]2.0.CO;2.

Rosbakh, S., C. Römermann, and P. Poschlod. 2015. "Specific Leaf Area Correlates With Temperature: New Evidence of Trait Variation at the

Population, Species and Community Levels." *Alpine Botany* 125: 79–86. https://doi.org/10.1007/s00035-015-0150-6.

Seabloom, E. W., E. T. Borer, Y. M. Buckley, et al. 2015. "Plant Species' Origin Predicts Dominance and Response to Nutrient Enrichment and Herbivores in Global Grasslands." *Nature Communications* 6, no. 1: 7710. https://doi.org/10.1038/ncomms8710.

Tecco, P. A., S. Díaz, M. Cabido, and C. Urcelay. 2010. "Functional Traits of Alien Plants Across Contrasting Climatic and Land-Use Regimes: Do Aliens Join the Locals or Try Harder Than Them?" *Journal of Ecology* 98, no. 1: 17–27. https://doi.org/10.1111/j.1365-2745.2009.01592.x.

Van Kleunen, M., E. Weber, and M. Fischer. 2010. "A Meta-Analysis of Trait Differences Between Invasive and Non-invasive Plant Species." *Ecology Letters* 13, no. 2: 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x.

Vellend, M., D. S. Srivastava, K. M. Anderson, et al. 2014. "Assessing the Relative Importance of Neutral Stochasticity in Ecological Communities." *Oikos* 123, no. 12: 1420–1430. https://doi.org/10.1111/oik.01493.

Wood, T. E., D. Lawrence, and D. A. Clark. 2005. "Variation in Leaf Litter Nutrients of a Costa Rican Rain Forest Is Related to Precipitation." *Biogeochemistry* 73: 417–437. https://doi.org/10.1007/s10533-004-0563-6.

Wright, I. J., P. B. Reich, M. Westoby, et al. 2004. "The Worldwide Leaf Economics Spectrum." *Nature* 428, no. 6985: 821–827. https://doi.org/10.1038/nature02403.

Zhao, C. Y., Y. Y. Liu, X. P. Shi, and Y. J. Wang. 2020. "Effects of Soil Nutrient Variability and Competitor Identify on Growth and Co-Existence Among Invasive Alien and Native Clonal Plants." *Environmental Pollution* 261: 113894. https://doi.org/10.1016/j.envpol.2019.113894.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.