

Why are non-native plants successful? Consistently fast economic traits and novel origin jointly explain abundance across US ecoregions

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Summary

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- Are non-native plants abundant because they are non-native, and have advantages over native plants, or because they possess 'fast' resource strategies, and have advantages in disturbed environments? This question is central to invasion biology but remains unanswered.
- We quantified the relative importance of resource strategy and biogeographic origin in 69 441 plots across the conterminous United States containing 11 280 plant species.
- Non-native species had faster economic traits than native species in most plant communities (77%, 86% and 82% of plots for leaf nitrogen concentration, specific leaf area, and leaf dry matter content). Non-native species also had distinct patterns of abundance, but these were not explained by their fast traits. Compared with functionally similar native species, non-native species were (1) more abundant in plains and deserts, indicating the importance of biogeographic origin, and less abundant in forested ecoregions, (2) were more abundant where co-occurring species had fast traits, for example due to disturbance, and (3) showed weaker signals of local environmental filtering.
- These results clarify the nature of plant invasion: Although non-native plants have consistently fast economic traits, other novel characteristics and processes likely explain their abundance and, therefore, impacts.

Introduction

Dominance by non-native plants has been observed in ecosystems around the world (Lowe *et al.*, 2000). For example, across 64 globally distributed grassland sites, non-native plant species were six times as likely as native species to be dominant (> 80% relative cover; Seabloom *et al.*, 2015). Because impacts of non-native species are driven by their high abundance (Le Maitre *et al.*, 2011; Bradley *et al.*, 2019; Pearse *et al.*, 2019), understanding why they become abundant remains a central question in invasion biology (Catford *et al.*, 2009; Gioria *et al.*, 2023).

One common explanation for the success of non-native species is that they have been disproportionately introduced from the world's pool of fast growing species, with traits that enable them to thrive in disturbed environments (Davis *et al.*, 2000; MacDougall *et al.*, 2018). Tradeoffs between 'slow' traits that confer stress tolerance and 'fast' traits that confer rapid resource acquisition and processing occur globally, in all types of ecosystems, and among both native and non-native species (Wright *et al.*, 2004; Ordonez *et al.*, 2010; Reich, 2014). Many non-native and invasive species have traits associated with rapid resource acquisition and growth, including high leaf nitrogen (N), leaf phosphorus,

specific leaf area (SLA), and maximum photosynthetic rate (Pyšek & Richardson, 2007; van Kleunen *et al.*, 2010). Non-native species also tend to benefit from anthropogenic changes that increase resource availability and to be common in disturbed and eutrophied habitats, suggesting that fast economic traits might contribute to their high abundance (Chytrý *et al.*, 2008; Bradley *et al.*, 2010; Gonzalez *et al.*, 2010; Pyšek & Chytrý, 2014). Thus, it is possible that successful non-native species are simply fast growing species in environments increasingly favorable to them (Davis *et al.*, 2011).

To date, most comparisons between traits of native and non-native species have been at the scale of regional and global species pools. We know less about whether trait differences are also present within local plant communities, the scale at which such differences could matter for plant performance (Carboni *et al.*, 2016; Hulme & Bernard-Verdier, 2018). Because traits are often constrained by environmental filtering (Muscarella & Uriarte, 2016; Bruelheide *et al.*, 2018), native and non-native species may have similar traits at any given location (Leishman *et al.*, 2010; Funk *et al.*, 2016). Although there are multiple examples of non-native species with faster economic traits than co-occurring native species, these patterns are not universal, and are partially due to differences in functional group and life history (Funk & Vitousek, 2007; Leishman *et al.*, 2007; Ordóñez & Olff, 2013; Funk *et al.*, 2016; Garbowski *et al.*, 2024). Key unanswered questions are how consistently non-native species have fast economic traits relative to the native species with which they co-occur locally, and to what degree these faster traits underlie high non-native plant abundance.

An alternative explanation for non-native species' high abundance is that their novel biogeographic origin provides them with specific advantages over native species (Saul & Jeschke, 2015; Buckley & Catford, 2016). Being non-native may help plants in a variety of ways (Catford *et al.*, 2009; Gioria *et al.*, 2023). For example, the enemy release hypothesis suggests that a lack of natural enemies can help non-native species compete against native species still burdened by their own enemies (Maron & Vila, 2001; Saul & Jeschke, 2015). The evolutionary imbalance hypothesis suggests that non-native species from regions with long evolutionary histories may have acquired beneficial traits not present among native species, as suggested for invasive plants in forests of the eastern United States (Catford *et al.*, 2009; Fridley, 2012; Frisvold *et al.*, 2023).

These and related hypotheses predict that non-native species will benefit from their biogeographic origin and therefore increase in abundance relative to co-occurring native species. However, despite many examples of abundant non-native species, it remains unclear whether such patterns are the norm (Lowe *et al.*, 2000; Chytrý *et al.*, 2008; Seabloom *et al.*, 2015). It is also not clear whether observations of high non-native species abundance are attributable to specific advantages stemming from their biogeographic origin or to other characteristics, such as fast resource strategies. Key unanswered questions are how often non-native species are more abundant than (1) co-occurring native species and (2) co-occurring native species with similar economic traits.

Understanding the relative contributions of fast resource strategies and biogeographic origin to non-native plant abundance is

needed not only to better understand invasion but also to guide management. If non-native species are simply fast growing plants in favorable environments, they can be treated like other fast growing plants (Davis *et al.*, 2011). Appropriate remedies might focus on reducing disturbance and resource availability (Perry *et al.*, 2010). By contrast, if non-native species are abundant because of their biogeographic origin, they should be treated cautiously (Buckley & Catford, 2016). Appropriate remedies would then focus on specific effects of origin, such as the use of biological control to counter effects of enemy release (Maron & Vila, 2001).

Here, we combine an extensive dataset of plant abundance (69 441 plots) across the United States (Petri *et al.*, 2023) with leaf economic trait data from the TRY database (Kattge *et al.*, 2020) to disentangle the roles of biogeographic origin and resource strategy in non-native plant success (Fig. 1). We first compare the leaf N, SLA, and leaf dry matter content (LDMC) of native and non-native species, for all species within each ecoregion, and for species co-occurring within plots (communities). We then compare abundance between native and non-native species and test whether differences in abundance can be explained by differences in their traits. To do this, we model the abundance of individual species within plots as a function of species origin, species trait value, and the community-weighted mean (CWM) trait value of the other species in each plot. This approach assumes that CWM trait values are constrained by environmental filtering (Muscarella & Uriarte, 2016) and uses them to provide an expected level of abundance given a species' trait value. In other words, the traits of the other abundant species in a community provide information about a focal species' expected abundance given its traits. For simplicity, we use 'fast' and 'slow' to refer to the position of both species and communities (plot CWMs) on the leaf economic spectrum.

Our null hypothesis is that non-native species are similar to native species in both their traits and their abundance. We test three hypotheses about whether and why non-native species may differ in abundance from native species (Fig. 2a).

H1: *Faster resource strategy – Relative to native species, non-native species have faster leaf economic traits (H1a) but similar abundance when trait–abundance relationships are statistically controlled (H1b).*

Native/non-native trait differences may be more pronounced at ecoregion than plot scales if environmental filtering constrains the range of plant traits present within a local community (Funk *et al.*, 2016).

H2: *Biogeographic origin – Non-native species are more abundant than native species even when trait–abundance relationships are statistically controlled.*

This pattern would suggest the importance of biogeographic origin.

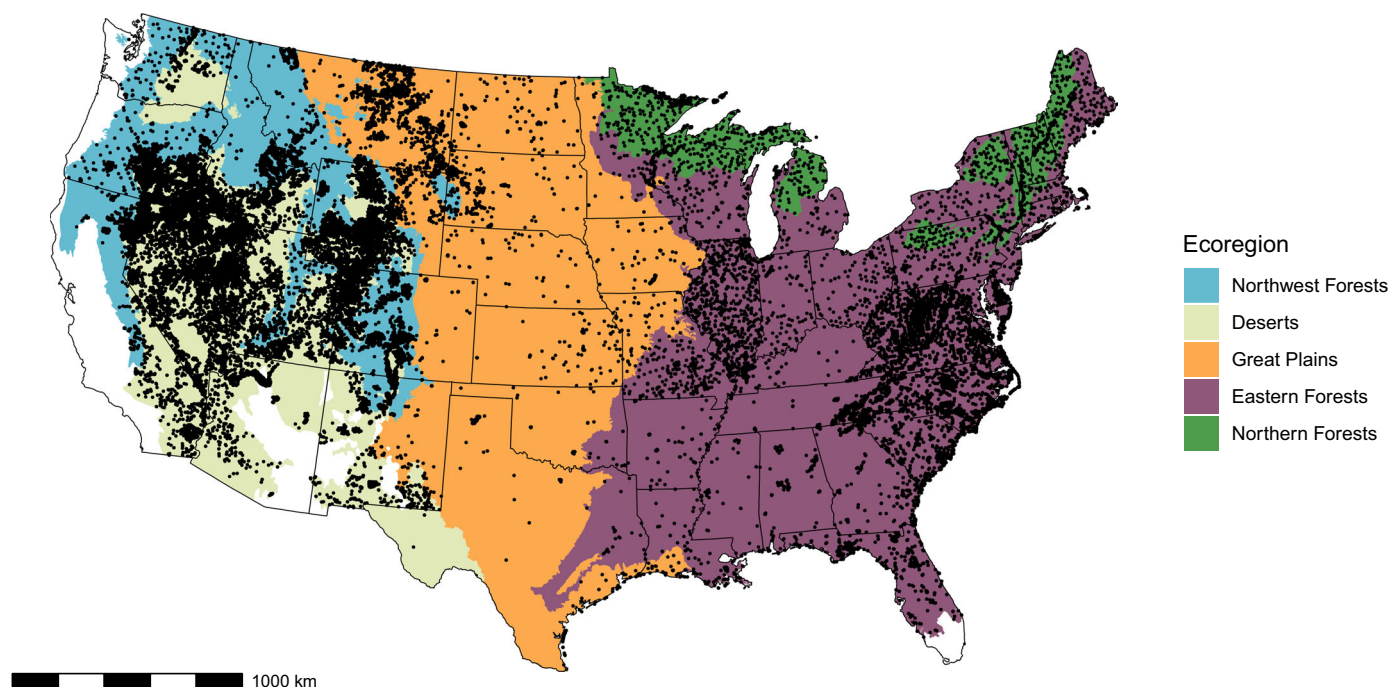


Fig. 1 Locations of plots and ecoregions. Analyses included 69 441 plots (black dots), across five Level 1 ecoregions (colored regions) within the conterminous United States.

H3: *Biogeographic origin among fast species – Non-native species with fast economic traits are more abundant than native species with fast economic traits when trait–abundance relationships are statistically controlled.*

This pattern would be expected if non-native species benefit more from being fast, for example due to higher nutrient use efficiency (Penuelas *et al.*, 2010), than native species.

These hypotheses about how non-native species' abundance and traits compare to those of native species in turn lead to predictions across plots. Faster resource strategies (H1) should lead to non-native species with abundance patterns similar to those of fast native species. Advantages stemming from biogeographic origin should lead to non-native species being more abundant than native species, either irrespective of species traits (H2), or primarily among fast non-native species (H3; Fig. 2b).

Materials and Methods

Data compilation and harmonization

We compiled plant cover data from the SPCIS database as described in Petri *et al.* (2023), including from the following sources: Bureau of Land Management Landscape Assessment Inventory and Monitoring Database, Carolina Vegetation Survey, Forest Inventory and Analysis Program, Illinois Natural History Survey Critical Trends Assessment Program, National Ecological Observatory Network (NEON, 2019), National Park Service Inventory & Monitoring Data, National Wetland Condition Assessment, Virginia Natural Heritage Program, West

Virginia Natural Heritage Program. Each of these datasets provides plant cover data for all species at particular locations, collected using plot surveys or line point intercept surveys. Species origin (native or non-native) and growth form (graminoid, forb, subshrub, shrub, tree, vine, and others) were added at the continental United States scale from the USDA Plants Database (<https://plants.usda.gov/home>), with adjustments as described in Petri *et al.* (2023). This approach focuses on intercontinental invasions and does not capture variation in species traits or performance associated with range shifts within the United States.

From the SPCIS dataset, we focused on data collected in five United States Level 1 Ecoregions (Fig. 1), which we judged to contain sufficient data (> 1000 plots) for meaningful abundance comparisons between native and non-native species: Northwest Forests ($n = 8326$ plots), North American Deserts ($n = 25\,687$ plots), Great Plains ($n = 5040$ plots), Eastern Temperate Forests ($n = 27\,847$ plots), and Northern Forests ($n = 2580$ plots). Together, these regions account for 94% of land area within the conterminous United States, and include 87% of the taxa (11 280 taxa) and 83% of the plots ($n = 69\,441$ plots) within the SPCIS database. These regions describe broad differences in vegetation type that could influence abundance differences between native and non-native species. Historical and current disturbance regimes also vary widely among ecoregions, with ongoing agricultural disturbances, such as soil tillage, common in the Great Plains, and parts of the Northwest and Eastern Forests, and changes in fire and grazing regimes in the Deserts (Mack & Thompson, 1982; Theobald *et al.*, 2025).

It is also important to note that the sampling designs that underlie our dataset, while created to effectively sample across large

H0 (null): Non-native species (gray) are similar to native species (black) in both traits and abundance.

H1 (Faster resource strategy): Non-native species (blue) have “faster” economic traits (H1a) than native species but have similar abundance to native species given their traits (H1b).

H2 (Biogeographic origin): Non-native species (orange) are more abundant than native species with similar economic traits.

H3 (Biogeographic origin among fast species): Fast non-native introduced species (yellow) are more abundant than fast native species with similar economic traits.

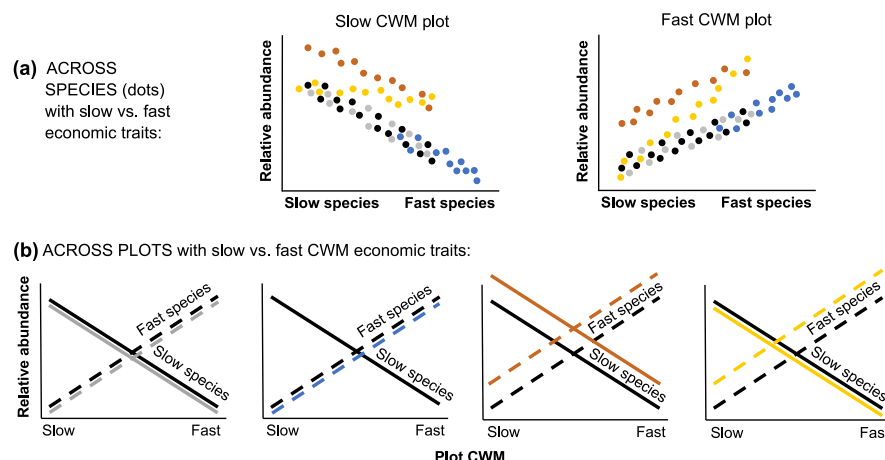


Fig. 2 Hypotheses. The relative abundance of native and non-native species may vary in multiple ways across species and plots with slow vs fast economic traits (slow vs fast species and plots, respectively). (a) Across all species in a plot, abundance is expected to depend on environmental filtering, as indicated by the match between an individual species' traits and the community-weighted mean (CWM) traits of the other species in the plot (Muscarella & Uriarte, 2016). For example, a recently disturbed plot with high resource availability is likely to be dominated by species with high leaf nitrogen (N) (fast species), and therefore have high CWM leaf N (a fast CWM plot). (b) Consequently, the abundance of a given focal species should depend on the interaction between its leaf N and the CWM leaf N of the other species in the plot. Fast species should be more abundant in fast CWM plots than in slow CWM plots and vice versa. These expectations are shown for native species in the black points (a) and black lines (b). Non-native species may then differ from these expectations by having faster traits (H1), or greater abundance than expected given their traits (H2, H3).

landscapes, do not combine to represent a full random sampling of the five ecoregions (Petri *et al.*, 2023). For example, some areas are particularly well sampled (e.g. Illinois), while others are under sampled (e.g. the southern Great Plains). In addition, some data sources focus on relatively pristine areas, such as the National Parks or areas away from human disturbances (e.g. Virginia Natural Heritage Program). Such sampling limitations could have led to different and, in some areas, lower relative abundance of non-native species than would be observed in the ecoregions as a whole.

Species abundance was measured as the relative percent cover of species. This metric is relevant to the impact of non-native species, comparable across locations, and independent of scale (Catford *et al.*, 2012). For plots where multiple vegetation strata (e.g. understory, shrub, and canopy) were measured, absolute percent cover was summed across strata for each taxon. We then calculated relative cover for each species in each plot as $\text{cover}_{\text{species}} / \text{cover}_{\text{total}}$. For plots measured in multiple years, we retained only the most recent survey data.

We added species-level data from the TRY database (Kattge *et al.*, 2020) for three different leaf economic traits that are indicative of a species' resource strategy: SLA, leaf N, and LDMC. These correlated traits capture different leaf functions that contribute to the leaf economic spectrum (Wright *et al.*, 2004). Leaves with greater area per unit mass (higher SLA), more chlorophyll (higher leaf N), or less structural tissue (lower LDMC) can achieve higher photosynthesis per unit investment, and therefore faster growth (Reich, 2014). Conversely, these traits incur costs, such as shorter tissue lifespans and less resistance to herbivory and drought.

We used the Taxonomic Name Resolution Service (<https://tnrs.biendata.org/>) to match species names. Trait values > 4 SD from the species, genus, or family mean trait values were

omitted (Kattge *et al.*, 2011). SLA measurements of leaves with and without petioles were included. We averaged individual trait measurements to the species level. Relying on species-level trait data reflects an assumption that much of the relevant variation in traits occurs at the species level (Shipley *et al.*, 2016). Intraspecific trait variation across environments or species' native vs non-native ranges may also influence the relative abundance of native and non-native species (Felker-Quinn *et al.*, 2013; Westerland *et al.*, 2021), but could not be included given available data. Taxa for which origin could not be determined were not included. We calculated CWM trait values for individual plots as the sum across species of each species' trait value multiplied by its relative cover. We omitted plots for which trait values were available for < 80% of total cover. Trait data were available for 19%, 26%, and 16% of species for Leaf N, SLA, and LDMC, respectively. However, because trait data were more frequently available for common vs rare species, the 80% threshold for plot inclusion was met for larger proportions of plots: 39 339 (leaf N), 22 872 (LDMC), and 44 217 (SLA), out of 69 441 total plots.

Analysis of trait differences between native and non-native species (H1a)

To compare trait values for the entire observed flora of each ecoregion, we fit linear models with species-level averages for each focal trait as the response variables and included species origin, ecoregion, origin $\times$ ecoregion, and growth form as fixed effects. Analyses were conducted in the GLMMTMB package in R (Brooks *et al.*, 2017). To ask whether native and non-native species differed in their traits at the plot scale, we used linear mixed models

with the plot-level average trait values of native or non-native species as the response variable. These analyses were limited to plots containing both native and non-native species and for which trait data were available for at least one species of each origin. Predictor variables included fixed effects of species origin, ecoregion, origin $\times$ ecoregion, and growth form, and a random intercept for plot. Trait values were ln-transformed before analysis.

Analysis of abundance differences between native and non-native species

To test whether non-native species differed in abundance from native species within the same plant communities, we first fit a model that did not account for traits. This model provided a reference point for interpreting subsequent models that did incorporate traits. We fit a linear mixed model in *glmmTMB* with the relative abundance of each species in each plot as the response variable and predictor variables including origin $\times$ ecoregion, growth form, and random intercepts for plot and species.

Analysis of trait-dependent abundance differences between native and non-native species (H1b, H2, H3)

To test our hypotheses about whether non-native species are more abundant than functionally similar native species (H2 or H3), or whether their abundance simply reflects faster traits (H1b), we used CWM traits to provide an expected level of abundance for each species in each plot. Specifically, we fit linear mixed models with the response variable being the relative abundance of each species in each plot, and the predictor variables including species origin, the trait value of the focal species (for which cover was being analyzed), and the CWM trait value for all other species within the plot. Assuming that traits are filtered by environmental conditions (Muscarella & Uriarte, 2016; Bruelheide *et al.*, 2018), a focal non-native species should have greater abundance in a particular plot if its trait value is similar to the average trait value of the other vegetation within the plot (X-shaped pattern in Fig. 2b). These models also included growth form, interactions between origin, species traits, and CWM traits, and random intercepts for plot and species. Separate models were fit for each ecoregion.

Using the above models, we tested H1, H2, and H3 by comparing the abundance of non-native species to the abundance of native species with similar leaf economic traits. Specifically, we predicted the abundance of native and non-native species for the 5th, 50th and 95th percentiles of the distribution of individual leaf economic traits across all species, and compared the resulting patterns to the hypothesized patterns in Fig. 2. For simplicity, we focus primarily on one trait, leaf N, in the main text and show results for SLA and LDMC in the [Supporting Information](#).

We fit Bayesian regression models, using the *BRMS* package in R (R Core Team, 2024) to call *STAN*, software that uses Hamiltonian Monte Carlo to estimate parameters (Stan Development Team, 2023). To improve model performance, we standardized the response variable, log relative abundance, by subtracting the

mean and dividing by the SD. Default noninformative priors in the *BRMS* package were used, and initial values of zero ($\text{init} = '0'$) were used to improve convergence. Model convergence was assessed using the Gelman–Rubin statistic, and visual examination of three independent chains, for 5000 posterior samples of the model (including 2500 warmup samples). The significance of individual parameters was assessed using posterior distributions to calculate probabilities that parameters were greater than or less than zero, and are reported in the [Supporting Information](#).

Results

Trait comparisons

Non-native species had higher leaf N and SLA and lower LDMC than native species (i.e. faster for all traits) both within species pools for each ecoregion (Fig. 3a,c,e; Supporting Information Table S1) and within plots (Fig. 3b,d,f; Table S2). These differences were significant for each trait in every ecoregion, supporting H1a. In contrast to our expectations based on environmental filtering at local scales, however, the magnitude of the trait difference between native and non-native species was similar within ecoregions and within plots: On average, non-native species had 22% higher leaf N and 26% higher SLA at both ecoregion and plot scales, 13% lower LDMC within ecoregions, and 15% lower LDMC within plots. Traits also differed between ecoregions. In particular, SLA was highest in Northern and Eastern Forests and lowest in Deserts (Fig. 3d).

Abundance differences without traits

In models comparing the abundance of non-native species to native species within the same communities without including traits, abundance differences varied widely between ecoregions. Non-native species were more abundant than native species in Deserts and Great Plains, similar in abundance to native species in Northwest Forests, and less abundant than native species in Northern and Eastern Forests (Fig. 4a, Table S3). Rank-abundance curves indicated that these differences were broad based and did not depend on a few extremely abundant species (Fig. S1).

Trait-dependent abundance differences

Models that included leaf N revealed that the interaction between focal species leaf N and CWM leaf N of nonfocal species differed for native and non-native species (Fig. 5). Among native species, results matched expectations based on environmental filtering: Species with high leaf N (95th percentile) tended to be most abundant in plots with high CWM leaf N, while species with low leaf N (5th percentile) tended to be most abundant in plots with low CWM leaf N. By contrast, non-native species showed little signal of environmental filtering: Species with low leaf N often increased in abundance with increasing CWM leaf N, in some cases more so than species with high leaf N. Plots with higher

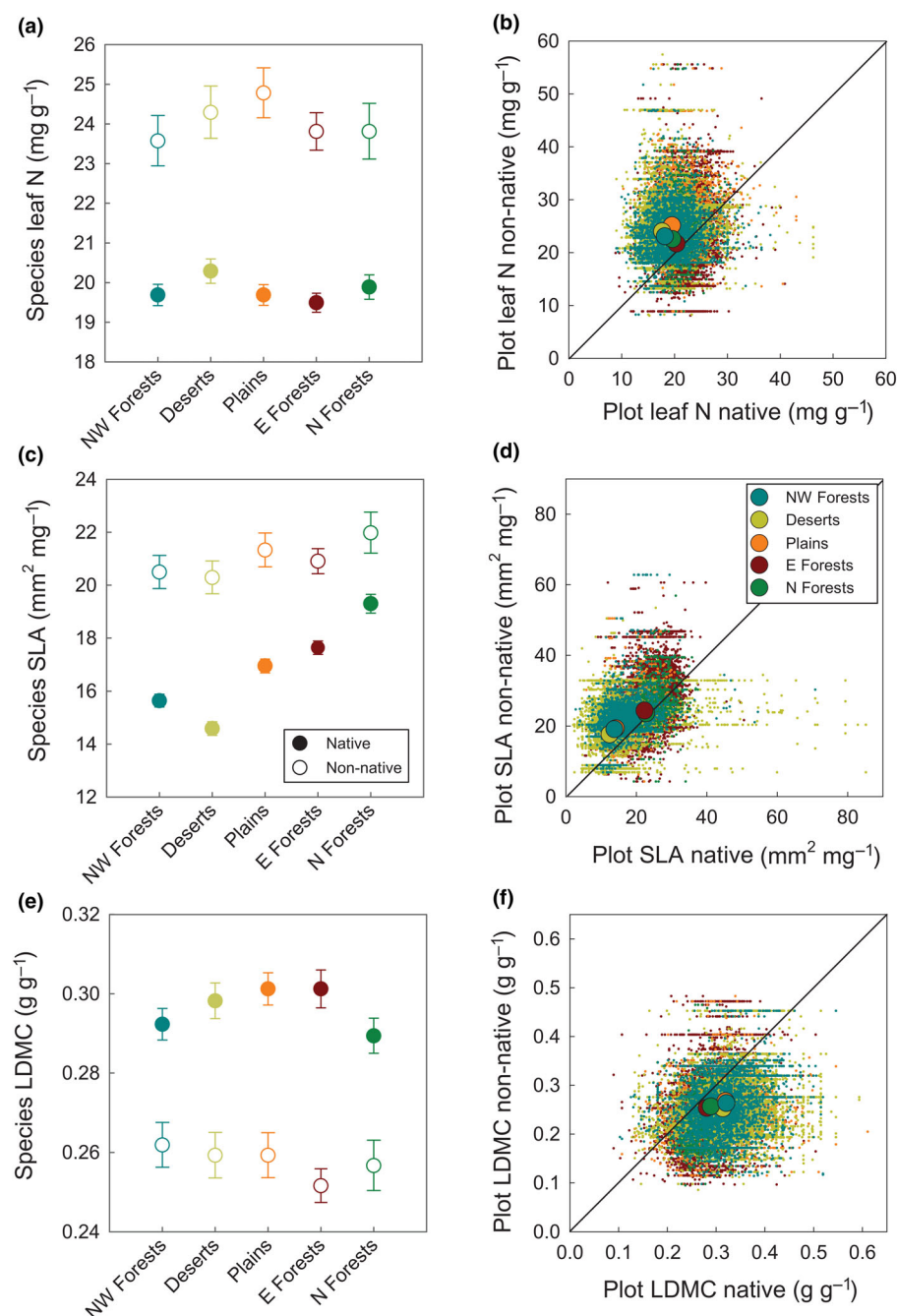


Fig. 3 Trait differences between native and non-native species. Non-native species had faster leaf economic traits than native species both for all species observed within ecoregions (a, c, e) and within plots (deviations from 1 : 1 line in b, d, f). Ecoregion-scale comparisons depict marginal mean trait values ($\pm$ SE) from linear models that included origin $\times$ ecoregion and growth form as fixed effects. Plot-scale comparisons depict mean trait values of native species vs mean trait values of non-native species for individual plots (small points; $n = 32\,328$ (b), $32\,860$ (d), and $29\,064$ (e) plots), and marginal mean trait values (large points) from linear mixed models that included origin $\times$ ecoregion and growth form as fixed effects, and plot as a random effect (Supporting Information Table S2). Non-native species had faster traits in most plots, including higher leaf nitrogen (N), higher specific leaf area (SLA), and lower leaf dry matter content (LDMC) in 77%, 86%, and 82% of plots, respectively. Contrasts between native and non-native species were significant for all ecoregions both at the ecoregion scale ($P < 0.002$) and at the plot scale ($P < 0.0001$).

CWM leaf N are those dominated by fast species (with high leaf N) and likely occur in areas with high resource availability.

Comparing abundance between native and non-native species with similar leaf N, regional patterns were qualitatively similar to those observed without including traits: Non-native species were generally more abundant than native species in the Deserts and Great Plains (providing partial support for H2) and less abundant in Forested ecoregions (Figs 4b, 6). These differences also depended on species and community leaf N. Among species with high leaf N, non-native species had more consistent abundance advantages in the Great Plains and Deserts (partially supporting H3) and smaller abundance disadvantages in Northwest Forests

and Eastern Forests. Non-native species with low or medium leaf N also increased in abundance relative to native species with increasing CWM leaf N in most ecoregions (Figs 4b, 6).

To depict and test our primary hypotheses, Figs 2 and 5 compare native and non-native species with similar leaf N. However, non-native species' faster economic traits (Fig. 3) could further contribute to their abundance, particularly in fast CWM plots. To test this possibility, we compared predicted origin effects on abundance: (1) at the same trait values for native and non-native species (percentiles based on the distribution of leaf N across all species; Fig. 6, 'Same traits'), and (2) at separate trait values for native and non-native species (percentiles based on their

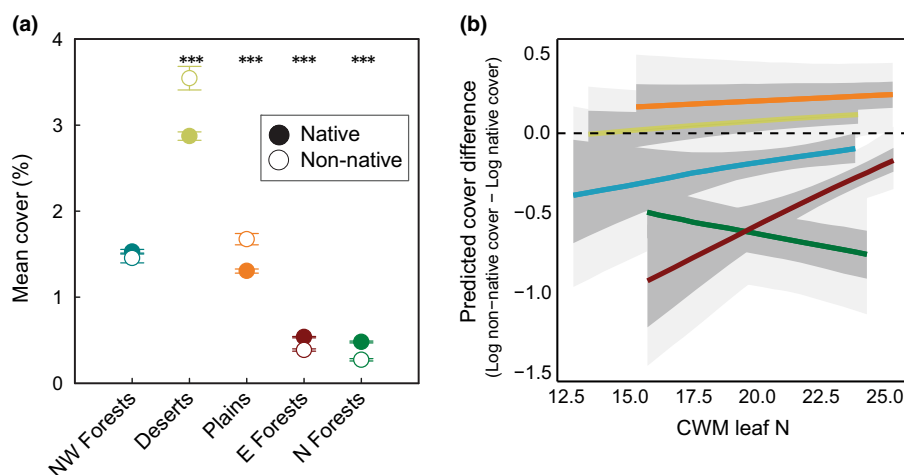


Fig. 4 Differences in relative cover by biogeographic origin and ecoregion in models with and without leaf nitrogen (N). (a) Predicted cover of native and non-native species as a function of origin and ecoregion. Models also included growth form and random intercepts for species and plot. Points depict back transformed marginal means (± 1 SE; within points in most cases). Asterisks indicate significant contrasts ($P < 0.001$) between native and non-native species within ecoregions ($n = 1411$ 627 species cover observations across 69 441 plots; See Supporting Information Table S3 for statistical results and Fig. S1 for rank-abundance curves). (b) Predicted differences in abundance between non-native species and co-occurring native species as a function of origin and community-weighted mean (CWM) leaf N of nonfocal species. Separate Bayesian models for each ecoregion also included species leaf N, interactions between origin, species leaf N, and CWM leaf N, as well as growth form, and random intercepts for plot and species. Estimates are for the median species-level leaf N across all species. Shading indicates 50% (dark gray) and 95% (light gray) credible intervals. See Figs S2 and S3 for statistical results; $n = 660$ 278 species observations across 39 339 plots.

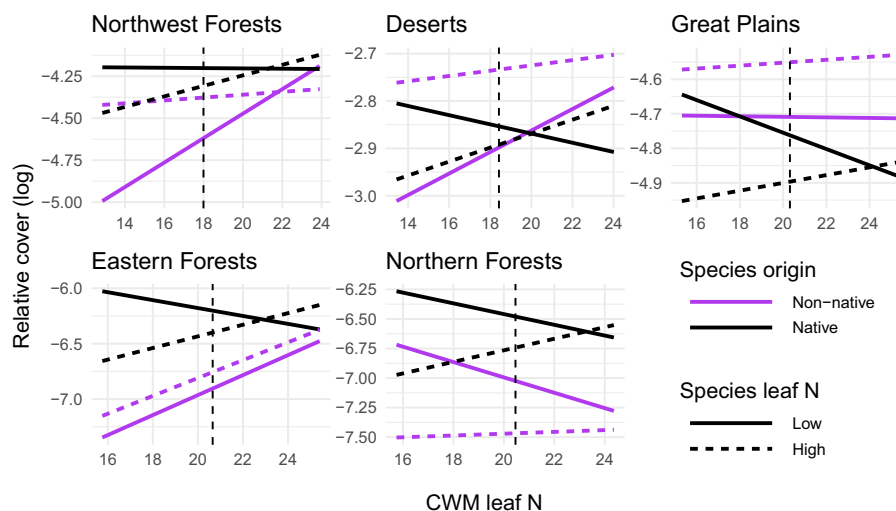


Fig. 5 Abundance comparisons, including leaf nitrogen (N). A focal species' relative cover depended on the three-way interaction between the species' origin, its leaf N, and the community-weighted mean (CWM) leaf N of other species within the same plot. Solid and dashed lines denote estimates for the 5th (solid) and 95th (dashed) percentiles of the distribution of leaf N across all species. Vertical dotted lines represent the median CWM leaf N in each ecoregion. Environmental filtering was apparent for native species in all ecoregions as indicated by more positive slopes for species with higher leaf N (X-shaped patterns created by solid and dashed black lines; Fig. 2). By contrast, non-native species often had higher cover in plots with greater CWM leaf N, irrespective of species leaf N (positive slopes for both solid and dashed purple lines). Non-native species were also more abundant relative to native species among species with high leaf N (dashed purple vs dashed black lines) than among species with low leaf N (solid purple vs solid black lines) in most ecoregions and communities. Parameter estimates in Supporting Information Figs S2 and S3; $n = 660$ 278 species observations across 39 339 plots.

respective distributions of leaf N; Fig. 6; 'Typical traits'). Non-native species' relatively high leaf N led to slightly higher predicted abundance in the Northwest Forests, Deserts, and Great

Plains and lower predicted abundance in Northern Forests. These differences were small, however, compared with the overall differences in abundance.

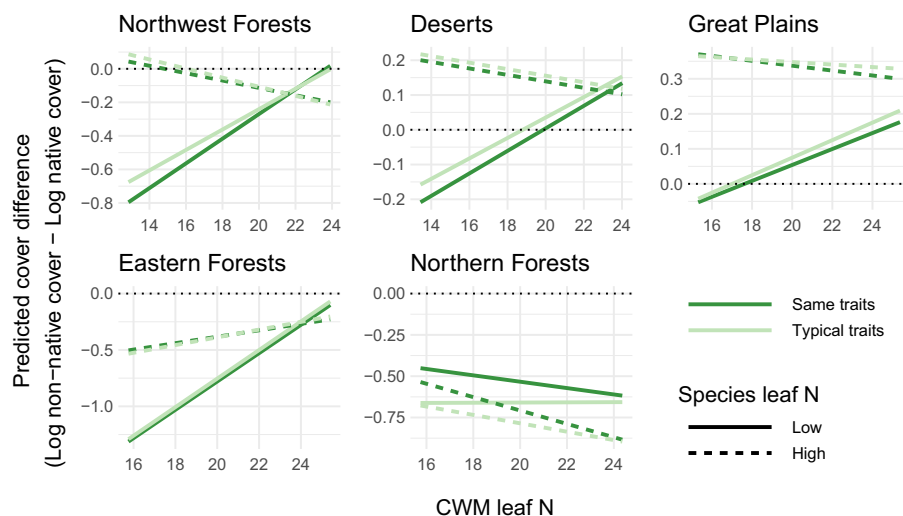


Fig. 6 Sensitivity of abundance differences to trait distributions. Differences in predicted abundance between non-native species and co-occurring native species depended on the trait distributions used in the prediction. Lines denote estimates for the 5th ('low', solid lines) and 95th ('high', dashed lines) percentiles of the distribution of leaf nitrogen (N) across all species ('Same traits', dark green; as in Fig. 5) or across native species and non-native species separately ('Typical traits', light green). Thus, 'Same traits' models compare non-native species to native species with similar leaf N, while 'Typical traits' models compare typical non-native species to typical native species. The fact that non-native species had faster traits ('Typical traits') led to somewhat higher relative abundance in the Northwest Forests, Deserts, and Great Plains and somewhat lower relative abundance in Northern Forests. For both 'Same' and 'Typical' traits, non-native species abundance was usually higher, relative to native species, among species with high leaf N. Among species with low leaf N, the relative abundance of non-native species increased with increasing community-weighted mean (CWM) leaf N in most ecoregions. $n = 660\,278$ species observations across 39 339 plots.

Results were consistent when including LDMC rather than leaf N (reversed in sign because low LDMC indicates fast species): Lower species-level or community-level LDMC often increased the abundance of non-native relative to native species in most ecoregions (Figs S4–S8). By contrast, results for models including SLA, which influences not just resource economics but also shade tolerance (Hodgson *et al.*, 2011), differed in some ecoregions. With SLA, there was less evidence for environmental filtering among native species and more variation among ecoregions in the effects of species and community-level traits (Figs S9–S13).

Discussion

Despite decades of research into the mechanisms underlying plant invasion, the relative contributions of resource strategy and biogeographic origin have not previously been quantified. Combining leaf economic trait data with measurements of plant abundance in communities across the United States, we learned that non-native species are very different from native species in their traits and abundance. Non-native species had faster economic traits than native species in most plant communities – higher leaf N and SLA, and lower LDMC. Non-native species also had distinct patterns of abundance, even when accounting for trait–abundance relationships, suggesting that they are not simply fast species growing in favorable environments. However, the traits of both focal species and their communities influenced the success of non-native species. In the Deserts and Great Plains, non-native species were more abundant than similar native species, particularly for focal species with fast traits, suggesting the importance

of biogeographic origin. By contrast, non-native species were less abundant than similar native species in forested ecoregions. Non-native species were often most abundant relative to similar native species in communities with fast CWM traits, which may indicate reliance on colonization opportunities.

Hypothesis 1a – faster traits

Studies of regional species pools have typically found non-native species to have faster traits than native species (Grotkopp & Rejmánek, 2007; Pyšek & Richardson, 2007; Ordóñez *et al.*, 2010). However, studies within communities have been less consistent, finding that non-native species had faster traits (Ordóñez & Olff, 2013; Garbowski *et al.*, 2024), similar traits (Leishman *et al.*, 2007; Funk *et al.*, 2016), or slower traits (Funk & Vitousek, 2007) than co-occurring native species. Across plant communities, regions, and spatial scales in the United States, our results show a remarkably consistent pattern of faster traits for non-native than native species. These trait differences were present in most plant communities (e.g. 77% of 32 398 plots for leaf N), and were similar in magnitude within regional floras and communities (Fig. 3). These results support H1a (faster resource strategy), but not the expectation that environmental filtering limits trait differences within communities.

Consistently faster traits among non-native than native species within communities could be explained by several processes. Recent disturbance or eutrophication could have changed environmental filters, selecting for faster species among new colonizers (including non-native species) than among extant species (Díaz *et al.*, 1999; Funk *et al.*, 2008). Local trait distributions could

also reflect regional trait distributions if propagule pressure strongly influences non-native species abundance (Colautti *et al.*, 2006). Finally, fast non-native species could have advantages not shared by slower non-native species, as suggested by evidence for H3 (to be described later; Fig. 5). Irrespective of the cause, these results quantify the substantial overlap between the categories of non-native species and fast growing or weedy species (Wright *et al.*, 2004; van Kleunen *et al.*, 2010), both within regional floras and within communities. Furthermore, the fact that trait differences are common within local communities makes it possible that such differences influence the relative abundance of native and non-native species within those communities.

Abundance differences without traits

Non-native species were not consistently more abundant than native species; rather, they were more abundant in the Great Plains and Deserts, similar in abundance in Northwest Forests, and less abundant in Northern and Eastern Forests (Fig. 4a). The high relative abundance of non-native species in the Great Plains matches previous findings across a set of 62 grasslands around the world (Seabloom *et al.*, 2015), but comparable results for forested and desert regions have not been available.

Hypotheses 0 and 1b – similar abundance given traits

Native and non-native species had very different associations with the CWM traits of the nonfocal species in the same plots, contradicting H0 (Figs 2b, 5). For native species, those with high leaf N became more abundant as CWM leaf N increased, and vice versa, as expected if traits are filtered by environmental conditions (Muscarella & Uriarte, 2016; Bruehlheide *et al.*, 2018). Thus, high CWM leaf N, which may indicate a resource-rich plot, such as a disturbed area or a wetland, favored focal native species with high leaf N. Conversely, low CWM leaf N, which may indicate a resource-poor plot, such as an arid or shaded area, favored native species with low leaf N.

By contrast, non-native species, even those with lower leaf N, were often most abundant in plots where other species had higher leaf N (Fig. 5). This unexpected pattern could be caused by greater colonization opportunities in plots with high CWM leaf N (e.g. due to disturbance), which are important for expanding populations of non-native species (Davis *et al.*, 2000; Häkkinen *et al.*, 2023).

Given native and non-native species' distinct patterns of abundance, there was only limited support for H1b, that non-native species with fast resource strategies have abundance patterns that are typical for such species (Fig. 2b; Davis *et al.*, 2011). In Northwest Forests, native and non-native species with high leaf N were similar in abundance (Fig. 5). In addition, non-native species' higher leaf N appeared to be beneficial in the Northwest Forests, Deserts, and Great Plains (Fig. 6, Same vs Typical traits), suggesting that it contributes to abundance differences observed in models not including traits (Fig. 4a). Benefits from higher leaf N were small, however, relative to overall differences in abundance.

Hypothesis 1 is based on the idea that non-native species' traits, which have been influenced by humans, help them to thrive in human-modified environments (Davis *et al.*, 2000; MacDougall *et al.*, 2018). It is derived from observations that non-native species often come from native ranges with long histories of human agriculture (Kalusová *et al.*, 2017; Fristoe *et al.*, 2023), have fast economic traits (Pyšek & Richardson, 2007; Ordonez *et al.*, 2010), and respond positively to disturbance (Hobbs & Huenneke, 1992; Chytrý *et al.*, 2008; Moles *et al.*, 2012). Our results show that fast resource strategies among non-native species are very common, can contribute to high abundance, but are often insufficient to explain differences in abundance between native and non-native species.

Hypothesis 2 – biogeographic origin

After accounting for trait–abundance relationships, native and non-native species still differed in abundance (Figs 4b, 6). These differences support H2 in the Great Plains and Deserts, where non-native species were usually more abundant than functionally similar native species, but not in forested ecoregions where the opposite pattern was observed. The process of introduction can create advantages, such as release from natural enemies, as well as disadvantages, such as little time for local adaptation (Maron & Vila, 2001; Catford *et al.*, 2009). In addition, postintroduction spread and establishment take time (Dietz & Edwards, 2006). In North America, non-native plant species' residence times range from *c.* 50–500 yr (Mitchell *et al.*, 2010), and estimates of range infilling based on climate envelope models suggest that much of their potential ranges remains unoccupied (Bradley *et al.*, 2015; Häkkinen *et al.*, 2023). If abundance is still increasing at the plot scale, our point-in-time measurements may underestimate potential non-native species abundance. For example, it has been argued that North American forests are not inherently resistant to invasion but rather slow to be invaded, due to low species turnover, small pools of shade-tolerant invaders, and lower fecundity and recruitment of shade-tolerant species (Martin *et al.*, 2009). These processes may explain why non-native species were often less abundant than similar native species in forested ecoregions.

Viewed in this temporal context, it is surprising that non-native species, including both invasive and noninvasive species, are already more abundant than functionally similar native species in the Great Plains and Deserts. This may indicate that their biogeographic origin provides non-native species with ecological advantages (Catford *et al.*, 2009; Saul & Jeschke, 2015). It may also reflect the importance of human interventions beyond introduction *per se* (Buckley & Catford, 2016; Carboni *et al.*, 2016). In the Great Plains, some of the most prevalent non-native species, such as *Poa pratensis* L., *Melilotus officinalis* (L.) Lam., and *Bromus inermis* Leyss., have been bred for forage or turf production, potentially providing competitive advantages (Driscoll *et al.*, 2014), and are widely planted, increasing propagule pressure. In the Deserts, a different pattern emerges, with the most prevalent non-native species being annuals and the most prevalent native species being perennials. Altered

disturbance regimes, with heavier grazing and more frequent fire (Mack & Thompson, 1982), likely contribute to the success of fast growing non-native annuals, but do not explain why they are more abundant than native species with similar economic traits (Figs 4b, 6). A possible explanation is that the non-native species have other, novel characteristics, such as adaptations to fire (e.g. *Bromus tectorum* L.) or tolerance of grazing (e.g. *Alyssum desertorum* Stapf), that native species lack (Mack & Thompson, 1982).

Hypothesis 3 – biogeographic origin among fast species

Relative to native species, non-native species typically had greater abundance advantages (Deserts and Great Plains) or smaller abundance disadvantages (Eastern and Northwest Forests) when considering species with high leaf N (dashed lines in Fig. 6). This provides partial support for H3, that fast non-native species will be more abundant than fast native species. Similarly, among extracontinental non-native species in Europe, those with fast economic traits are most abundant (Fristoe *et al.*, 2021). Non-native species may be particularly good at being fast, for example, by having high resource use efficiency (Pyšek & Richardson, 2007). Selection by humans, or evolution in association with humans, could have left non-native species with combinations of traits that help them thrive in human-modified environments (Driscoll *et al.*, 2014; MacDougall *et al.*, 2018). Non-native species could also benefit more from being fast, for example, if fast traits are associated with greater enemy release (Blumenthal *et al.*, 2009).

Non-native species abundance across plots with different CWM traits

With increasing CWM leaf N, non-native species usually became more abundant, even relative to native species with similar leaf N values. This pattern was observed in all ecoregions except for Northern Forests, and for species with both low and medium leaf N (Figs 4b, 5, 6). To the degree that high CWM leaf N values reflect resource-rich environments (Bruehlheide *et al.*, 2018), non-native species appear to benefit more from such environments than do functionally similar native species. Furthermore, given that some of our data sources focused on relatively pristine areas, our results may underestimate the effects of resource-rich habitats on non-native species abundance. It has long been observed that many non-native plants thrive in disturbed, resource-rich environments (Hobbs & Huenneke, 1992; Davis *et al.*, 2000; Chytrý *et al.*, 2008; Seabloom *et al.*, 2015). Our results fit with these patterns, but show that they do not apply solely to non-native species with fast traits (Fig. 5), suggesting the importance of colonization opportunities for expanding populations of non-native species (Davis *et al.*, 2000; Häkkinen *et al.*, 2023).

In conclusion, a combination of continental-scale datasets allowed us to test hypotheses that have long been debated in invasion biology. In the United States, non-native species have consistently fast traits and are most abundant in fast CWM plots, reinforcing the importance of limiting disturbance and associated colonization opportunities for managing non-native species.

However, non-native species' fast traits are insufficient to explain their high abundance. The fact that non-native species are often more abundant than similar native species, despite limited residence time in the United States, suggests that they are novel in ways that promote their abundance. The ongoing task of understanding how novel characteristics and interactions cause non-native species to become invasive will therefore be critical for effective management.

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Competing interests

None declared.

Author contributions

DMB, JD, HRS, IP and CJBS designed the study with contributions from DB, EMB, BAB, JDC, JSD, RE, II, DCL, LP and MV. HRS, IP and LP led the dataset development and organization. JD analyzed the data with HRS, DMB and IP. DMB wrote the manuscript with contributions from JD, HRS, IP, CJBS, DB, EMB, BAB, JDC, JSD, RE, II, DCL, LP and MV.

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Data availability

This manuscript relies primarily on data previously published by the authors (Petri *et al.*, 2023). Additional data used in the preparation of the manuscript are available in Dryad: doi: [10.5061/dryad.rjdfn2zpq](https://doi.org/10.5061/dryad.rjdfn2zpq). The code used in association with those datasets is available on GitHub: <https://github.com/DiezJ/PAINLES-repository>.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Rank-abundance curves for native species and invasive species by ecoregion.

Fig. S2 Parameter estimates from the leaf N Bayesian relative abundance regression models.

Fig. S3 Parameter estimates from the leaf N Bayesian relative abundance regression models, including growth form effects.

Fig. S4 Focal species relative cover as a function of the three-way interaction between species origin, species leaf dry matter content (LDMC), and the CWM LDMC of other species within the same plot.

Fig. S5 Predicted differences in abundance between non-native species and co-occurring native species as a function of CWM leaf dry matter content.

Fig. S6 Differences in predicted abundance between non-native species and co-occurring native species, and the sensitivity of these differences to observed differences in leaf dry matter content.

Fig. S7 Parameter estimates from the leaf dry matter content Bayesian relative abundance regression models.

Fig. S8 Parameter estimates from the leaf dry matter content Bayesian relative abundance regression models, including growth form effects.

Fig. S9 Focal species relative cover as a function of the three-way interaction between species origin, species specific leaf area (SLA), and the CWM SLA of other species within the same plot.

Fig. S10 Predicted differences in abundance between non-native species and co-occurring native species as a function of CWM specific leaf area.

Fig. S11 Differences in predicted abundance between non-native species and co-occurring native species, and the sensitivity of these differences to observed differences in specific leaf area.

Fig. S12 Parameter estimates from the specific leaf area Bayesian relative abundance regression models.

Fig. S13 Parameter estimates from the specific leaf area Bayesian relative abundance regression models, including growth form effects.

Table S1 Effects of species origin, ecoregion, and growth form on leaf economic traits at the ecoregion level.

Table S2 Effects of species origin, ecoregion, and growth form on leaf economic traits at the plot scale.

Table S3 Effects of species origin, ecoregion, and growth form on relative cover at the plot scale.

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