Decoupling the dimensions of plant invasion success reveals divergent trait syndromes across invasion outcomes and growth forms

Gabriela C. Nunez-Mir,[1]* Bethany A. Bradley[2], Qinfeng Guo[3]

[1] Department of Biological Sciences, University of Illinois, Chicago, Chicago, IL 60607, USA.

[2] Department of Environmental Conservation, University of Massachusetts, Amherst, Amherst, MA 01003, USA.

[3] USDA FS - Eastern Forest Environmental Threat Assessment Center, Research Triangle Park, NC 27713, USA.

* Corresponding author: gnm@uic.edu

ABSTRACT

The number of invasive plant species and their impacts continue to increase globally, yet efforts to identify traits that reliably predict invasion success have produced inconsistent results. To address this challenge, we asked whether trait–invasion relationships vary across dimensions of invasion success and growth forms. Using 16 functional and niche traits for 622 invasive plant species across the continental United States, we tested the effects of traits on three dimensions of success: local abundance, habitat breadth, and invasive range size. Native range size and tolerance of stressful environments consistently predicted habitat breadth and invasive range size across growth forms. In contrast, the traits associated with local abundance differed markedly between woody and herbaceous invaders. Herbaceous species were associated with traits linked to competitive dominance, whereas woody species were associated with persistence, stress tolerance, and competitive tolerance. These findings reveal multiple pathways to invasion success and show that invasion dimension and growth form are critical considerations when predicting plant invasiveness.

INTRODUCTION

Invasive species harm ecosystems and cost global economies billions of dollars each year (Brondízio et al., 2019; Pyšek, Hulme, et al., 2020), prompting extensive scientific effort to understand why some introduced species become invasive while others do not. One major line of inquiry explores whether species traits are linked to invasion outcomes, based on the theory that traits can indirectly capture ecological mechanisms that underlie invasion success (Drenovsky et al., 2012; Van Kleunen et al., 2010). Species traits are measurable proxies for mechanisms involved in resource acquisition, dispersal, and reproduction, indicating how an organism interacts with others and its surrounding environment (Funk et al., 2017; Funk & Wolf, 2016). Furthermore, species traits represent a taxon-independent approach to generalizing patterns of ecological structure and function by connecting processes occurring at various biological scales (i.e., individual, population, community) and environmental gradients (Funk et al., 2017; Laughlin, 2014; McGill et al., 2006). For invasive plants, several trait-based conceptual models of invasion success have been proposed with varying levels of empirical support—such as the traditional "ideal weed" hypothesis, which emphasizes rapid growth, high fecundity, and vigorous vegetative reproduction (Baker, 1965; Pyšek & Richardson, 2007). Yet, empirical support remains inconsistent (Gioria et al., 2023; Palma et al., 2021) and a generalizable framework for predicting invasion success is still lacking (Pyšek, Bacher, et al., 2020).

Underlying these disparate trait-based hypotheses is a disagreement over which strategies most consistently promote invasion success. Strategies such as strong competitive ability (Kuebbing & Nuñez, 2016; Levine et al., 2004), broad environmental tolerance (Higgins & Richardson, 2014; Pfadenhauer et al., 2023), fast life history (K. Guo et al., 2024; Suda et al.,

2015) and asexual regeneration (Nunez-Mir et al., 2019; Wang et al., 2017) are each associated with distinct trait syndromes and evidence for their importance has accumulated largely in isolation drawn on different subsets of invasive species For example, the importance of competitive ability in achieving invasion success has been greatly emphasized in the invasive plant ecology literature, with studies frequently linking invasion success to functional traits such as taller height, larger seed mass, and larger leaf area (Y. Chen et al., 2024; Palma et al., 2021; Tecco et al., 2010). Yet, successful invasive plants have also been found to engage in conservative strategies that promote environmental generalism and resistance to edaphic and atmospheric stressors, displaying contrasting traits such as smaller leaf area, lower specific leaf area, and lower leaf nitrogen content (Fristoe et al., 2021; H. Liao et al., 2021). Because these competing invasion strategies and their associated traits have rarely been evaluated simultaneously, it remains unclear which are most consistently associated with invasion success and whether their importance shifts across spatial scales and growth forms.

Another source of inconsistency in trait–invasiveness research is that "invasion success" is often defined in binary terms (e.g., invasive vs. naturalized, invasive vs. native) despite wide variation in metrics used to assess invasiveness (Blackburn et al., 2011; Colautti & MacIsaac, 2004; Palma et al., 2021). Metrics such as local abundance, habitat breadth, and geographic range size are commonly used, individually or jointly, to characterize invasiveness (Carboni et al., 2016; Catford et al., 2016; Hui et al., 2023). Much like Rabinowitz's framework for native species rarity (Rabinowitz, 1981), these metrics capture distinct demographic aspects of a species' performance in its introduced range, emphasizing that invasion success is inherently multidimensional (Fristoe et al., 2021).

Individual dimensions of invasion success capture ecological processes operating at different spatial scales and therefore also reflect the scale dependence of invasiveness. For instance, reaching high levels of abundance locally reflects competitive dominance at the neighborhood-scale shaped by resource acquisition strategies and biotic interactions (Hejda et al., 2009; Levine et al., 2004; Maron & Vila, 2001). On the other hand, exhibiting broad habitat breadth reflects processes relevant at broader scales that promote environmental generalism and the ability to occupy diverse ecological settings (Higgins & Richardson, 2014; Pfadenhauer et al., 2023; Pyšek et al., 2015). Invasive range size (hereafter 'range size') may be seen as a bridge between local and broad-scale processes by capturing reproductive and dispersal capacity, invasive spread, and establishment across heterogeneous environments (Procheş et al., 2012; Pyšek et al., 2014; Theoharides & Dukes, 2007). This multidimensional, multi-scale framework has only recently been applied empirically in Australia, Europe, and the United States (Bradley et al., 2025; Fristoe et al., 2021; H. Liao et al., 2021; Palma et al., 2021).

Further complicating the search for generalizable invasive traits is the possibility that invaders of different primary growth forms leverage contrasting strategies to achieve invasion success. Although distinctions in the development, morphology, and physiology among plant growth forms are well established, how these differences translate into invasion strategies remains less understood. Recent studies find that plants of different growth forms employ distinct ecological strategies for adaptation to fine-scale environmental conditions (Cheng et al., 2021), resource use and acquisition (Luo et al., 2026; Rossatto & Franco, 2017), and interspecific competition (Abaturov, 2015), which are then reflected in corresponding trait syndromes. Given that environmental filtering, resource acquisition, and competition are

fundamental components of the invasion process, different plant growth forms may likewise rely on distinct trait syndromes to achieve invasion success.

Given these sources of variation, we argue that apparent contradictions in the trait–invasiveness literature may arise because studies frequently rely on binary metrics of invasiveness or singular dimensions of invasion success, pool distinct plant growth forms, and focus on traits associated with only a subset of the ecological mechanisms thought to promote invasion. Consequently, competing explanations of invasion success are rarely evaluated simultaneously within a unified framework. In this work, we advance the development of a generalizable trait-based framework for plant invasion success by addressing these gaps. We compiled a comprehensive dataset of 16 functional and niche traits associated with environmental tolerance, competitive ability, fast life history, and asexual regeneration for 622 non-native invasive plant species across the continental United States. We tested whether the importance of these traits varies across three dimensions of invasion success: local abundance, habitat breadth, and range size. We also assessed whether different plant life forms exhibit distinct trait syndromes associated with success in each dimension. By integrating multiple dimensions of invasion success across diverse life forms and a comprehensive suite of functional and niche traits, our study helps reconcile contrasting findings in the invasion literature, strengthens the theoretical foundation for invasion forecasting, and enhances the utility of trait-based approaches for invasive plant management and early detection and rapid response efforts.

MATERIALS AND METHODS

Metrics of invasion success

We used trait information to predict three metrics of invasion success: local abundance, habitat breadth, and range size. This information for the conterminous U.S. was obtained from (Bradley et al., 2025), which aggregated spatial occurrence and abundance data from 14 databases derived from field measurements and observations of invasive plants. In Bradley et al. (2025), abundance is defined as the number of observations with >10% invasive plant cover or a qualitative description of high abundance (e.g., monoculture); habitat breadth is defined as the number of Level III EPA ecoregions (Omernik & Griffith, 2014) occupied by the invasive plant (out of 86 in the conterminous U.S.); and range size is defined as the number of equal-area 50-km diameter hexagons occupied by the invasive plant (out of 5,117 in the conterminous U.S.). In our analyses, habitat breadth and range size were modeled as described above, and local abundance was modeled as the log-transformed rate of high-abundance records relative to the number of occupied hexagons (manual offset), thereby testing trait effects on abundance conditional on spatial establishment.

Trait predictors of invasion success

Following the invasion literature, we proposed four mechanisms by which invasive plants may achieve high local abundance, broad habitat breadth or large range sizes and identified 16 functional, morphological, and niche traits linked to these mechanisms (Table 1, Table S1 for more details).

Table 1. Hypothesized ecological strategies for plant invasion success and associated traits evaluated in this study.

Hypothesized strategy	Associated species traits
Environmental tolerance	Native range size, minimum elevation, maximum elevation, minimum soil pH, maximum soil pH, minimum hardiness zone, maximum hardiness zone, minimum precipitation, maximum precipitation
Competitive ability	Mean leaf length and width, maximum plant height, mean specific leaf area (SLA), mean seed weight
Adaptability and fast life history	Genome size
Asexual regeneration	Resprouting and regenerative capacity, clonal propagation

We compiled traits data for 962 invasive plants in the United States, identified from EDDMapS, a web-based national network that aggregates observation records and distribution data of invasive species and pests in the United States and Canada (Bargeron & Moorhead, 2007), and species classified as "Invasive (category D2)" or "Widespread invasive (category E)" in the United States Geological Survey (USGS) Register of Introduced and Invasive Species (Version 2.0) (Simpson et al., 2025). Traits data were collected from online factsheet databases, including the CABI Compendium: Invasive Species, the USDA Plants Database, the North Carolina State Extension Plant Toolbox, the UC-Berkeley Jepson Herbarium, the USFS-Fire Effects Information System, and University of Michigan's CLIMBERS (Al-Shayeb et al., *in press*). We also collected morphological, reproductive, and environmental tolerance data from the BIEN database version 4.2 (Enquist et al., 2016) using the 'R BIEN' R package (Maitner et al., 2018) and the TRY Plant Trait Database (Kattge et al., 2020). Using the 'TR8' R package (Bocci, 2015), we collected additional data from the LEDA Traitbase (Kleyer et al., 2008), the Ecological Flora of the British Isles (Fitter & Peat, 1994) and BROT (Tavşanoğlu & Pausas, 2018). In addition to the databases referenced above, we obtained clonality data from the

COMPADRE Plant Matrix Database (Salguero-Gómez et al., 2015) using the 'Rcompadre' R Package (Jones et al., 2022), seed mass data from the Seed Information Database (Society for Ecological Restoration et al., 2023), genome size data from the Plant DNA C-values Database release 7.1 (Pellicer & Leitch, 2020), and native range size data from the Royal Botanic Gardens Kew's Plants of the World Online (POWO) using the 'expowo' R package (Zuanny et al., 2024). The estimated year of introduction to the United States for each species was obtained from various sources, including databases referenced above, the earliest recorded occurrence in the continental United States in the Global Biodiversity Information Facility (GBIF) and (Bradley et al., 2025). This data was used to estimate minimum residence time for each species, a recognized driver of invasion success (Pyšek et al., 2009; Williamson et al., 2009).

Despite our data collection efforts, data availability varied by trait. The most data-rich trait in our dataset was maximum plant height, with measured data for almost 89% of the species in our dataset. For genome size, the most data-deficient trait, we were able to collect data for 51% of the species. To address trait data deficiencies, we performed phylogenetically informed data imputation sensu Nunez-Mir & McCary (2024) on 12 continuous traits expected to be phylogenetically conserved: minimum and maximum pH, hardiness zone, elevation and precipitation, maximum plant height, leaf width and length, and genome size. Imputation allows for the inclusion of more species that would otherwise need to be excluded from modeling due to incomplete data. Previous studies indicate that analyses using imputed trait datasets often produce more accurate estimates than those where only measured data were used (Johnson et al., 2021; Kim et al., 2018; Penone et al., 2014). Moreover, Palma et al. (2022) found that methodological decisions related to trait dataset construction, including imputation, had little influence on inferred trait–invasion relationships. We used the 'Rphylopars' R package, a tool to

impute missing trait data via the estimation of phylogenetic and trait covariance across species. We removed species for which we lacked data for the entire genus and species for which we only had data for 2 traits or fewer. We created a phylogenetic tree for all remaining species using the 'U.PhyloMaker' R package (Jin & Qian, 2023). For each trait, we excluded imputed values that extended beyond the original data range to keep the imputed dataset aligned with actual observations and limit potential bias. Our final dataset after imputation included complete data for 622 invasive species.

Statistical framework

Reducing dimensionality of the traits dataset

To address multicollinearity and to improve interpretation of findings, we reduced the high dimensionality of our traits dataset by performing two principal component analyses (PCA) for traits associated with "environmental tolerance" and with "competitive ability" strategies (Table 1). Prior to PCA, we performed Box-Cox transformations on all traits to satisfy assumptions of normality. From each PCA, we extracted the principal components that captured at least 65% of variance and interpreted the loadings of traits on each component (Fig. 1).

We extracted three principal components from the "environmental tolerances" PCA. PC1, hereafter named *warm-adaptation PC*, appeared to capture a gradient in temperature tolerances (i.e., maximum and minimum hardiness zone loading positively). PC2, hereafter named *soil moisture/pH niche PC*, mapped a gradient in precipitation on one side (i.e., minimum precipitation loading negatively), and maximum pH on the other, with positive values capturing

wet, acidic habitats and negative values capturing dry, alkaline habitats. PC3, hereafter named *montane affinity PC*, captured an elevation gradient with maximum elevation loading positively.

We extracted two principal components from the "competitive ability" PCA. PC1, hereafter named *pioneer-competitor PC*, separated species that are good at colonizing new areas (i.e., low maximum plant height, mean seed weight, leaf length and width) versus strong competitors at later stages (i.e., large maximum plant height, mean seed weight, leaf length and width). PC2, hereafter named *acquisitive-conservative PC*, captured the leaf economics spectrum, separating plants with acquisitive leaf traits (i.e., high SLA, large leaf width and length) versus conservative (i.e., low SLA, small leaf width and length).

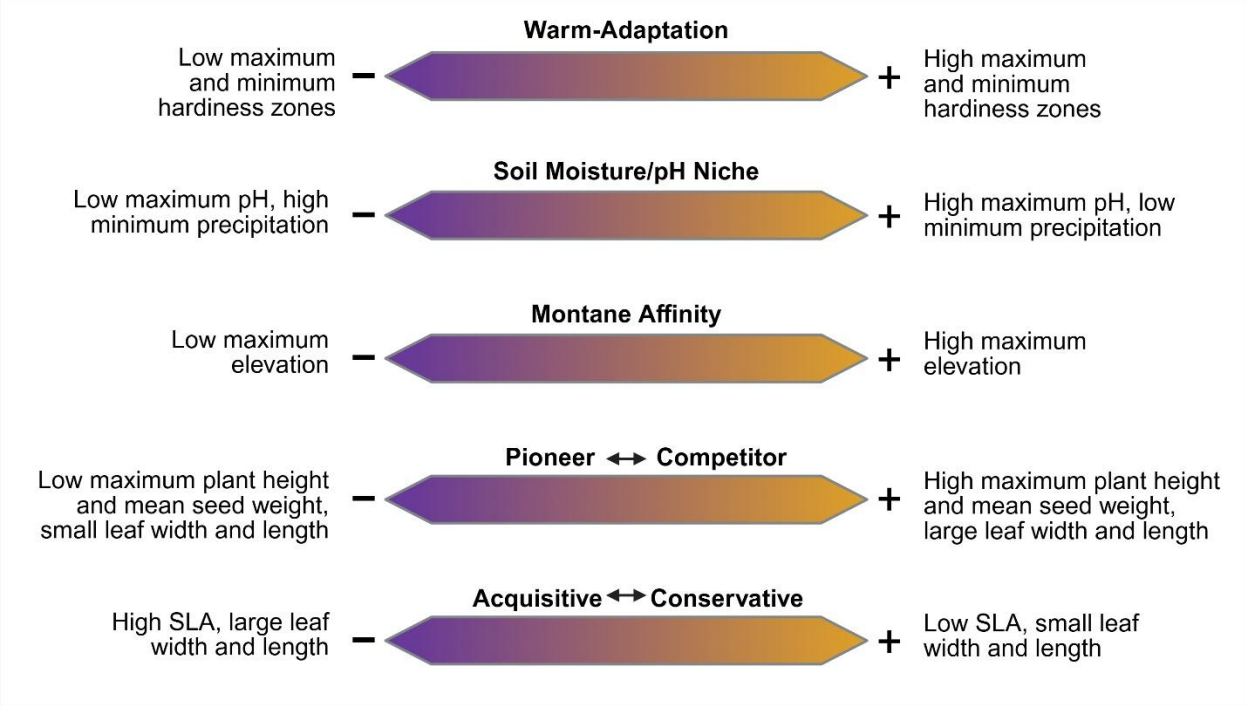

Fig. 1. Five principal components (PCs) derived from analyses of traits associated with environmental tolerance and competitive ability. Functional and niche traits contributing to each axis are shown, with gradients indicating the direction of trait loadings along each component.

Identifying traits linked to multidimensional invasion success

To assess the effects of the species traits (genome size, asexual regeneration), native range size, and the five environmental tolerance and competitive ability PCs on the three dimensions of invasion success, we performed a series of phylogenetic generalized least squares (PGLS) models that account for the non-independence of species due to phylogenetic relationships. We incorporated a phylogenetic correlation structure defined by Pagel's lambda into our models using the 'nlme' R package (Pinheiro et al., 2017). Residence time was also included in our PGLS models as a covariate to account for its effects on invasion success. We performed PGLS models for each dimension of invasion success as a response for all species and for woody and herbaceous species separately. Additional PGLS models were fit to compare trait effects across primary growth forms (i.e., graminoids, forbs, trees/shrubs, and vines) and between annual and perennial herbaceous plants. We computed pseudo-R2 values for each model using the 'performance' R package (Lüdecke et al., 2021). Prior to the PGLS analyses, all continuous numerical traits were Box–Cox transformed to improve normality and meet model assumptions. Model assumptions were subsequently evaluated through visual inspection of residual plots. As a sensitivity check, we repeated all analyses using only species with complete trait data before imputation (n = 231), which allowed us to assess whether imputation altered qualitative conclusions.

RESULTS

Traits linked to invasion success vary across dimensions

The strength and direction of trait effects on invasion outcomes differed among dimensions of success (Fig. 2, Tables S2–S10). For habitat breadth, montane affinity had the strongest effect among traits, positively associated with broader habitat use across all invasive plants. Tolerance of colder environments, indicated by a negative effect of the warm-adaptation PC, was also strongly associated with increased habitat breadth, in particular for trees/shrubs and perennial herbs. The soil moisture–pH niche PC also negatively affected habitat breadth, suggesting that tolerance of more alkaline and dry soil conditions promotes habitat generalism, especially for trees/shrubs. Native range size was positively associated with habitat breadth overall and for herbaceous species, but not for woody species. Residence time in the U.S. also had a strong positive effect on habitat breadth across all life forms.

Traits associated with range size were similar to those associated with habitat breadth. Montane affinity was strongly positively associated with range size across all life forms, excluding graminoids and annuals. The soil moisture–pH niche PC had a negative effect overall and for woody and annual species, but not for other herbaceous species. Warm-adapted annual species also displayed larger range sizes. Native range size was positively associated with invasive range size overall and for herbaceous species, but not for woody species. Residence time was positively associated with range size across life forms. Unlike habitat breadth, asexual regeneration had a positive effect on range size overall and for herbaceous species, particularly invasive forbs. Genome size had a negative effect on range size for invasive vines exclusively.

Trait associations with local abundance differed markedly from those for habitat breadth and range size, with traits related to competitive ability emerging as more important. Species positioned toward the competitor end of the pioneer–competitor gradient (i.e., larger seeds, larger leaves, and greater plant height) were more likely to achieve high local abundance. However, this pattern was not significant for woody invaders when modeled separately. Furthermore, species with leaves closer to the conservative side of the leaf economics spectrum (i.e., smaller, thicker leaves) were more likely to be abundant, although to a lesser extent and only in the overall model.

In contrast to the other invasion success dimensions, climatic and edaphic niche traits were strongly structural habit-dependent. Tolerance of warm climates was associated with higher local abundance primarily for woody invaders, indicated by a strong positive effect of the warm-adaptation PC, but also for invasive forbs and perennial herbaceous species. Similarly, tolerance of more alkaline and arid conditions was associated with higher local abundance for woody species, while herbaceous species tended to be more abundant in more acidic, wetter conditions, reflected in opposing effects of the soil moisture–pH niche PC between structural habits. This effect was also observed in the primary growth form models for trees and shrubs, but not for any herbaceous growth forms or vines. Perennial herbaceous species exhibited a negative relationship between asexual regeneration and local abundance. An affinity for montane environments was associated with lower abundance overall, but not for any specific growth forms. Native range size had a negative effect exclusively for woody species, suggesting that woody invaders with smaller native ranges tended to be more locally abundant. However, this effect was not observed for specific growth forms. Residence time was negatively associated with local abundance overall and for herbaceous species.

As a sensitivity check, we repeated all analyses using only the subset of species with complete, non-imputed trait data (n = 231 of 622 species in the full imputed dataset). Patterns of trait–invasion relationships were largely consistent between the two analyses, and the majority of significant associations in the imputed-data analysis remained directionally consistent in the complete-case analysis. Some effects that were significant in the full imputed dataset were no longer significant in the complete-case analysis (e.g., warm adaptation effect on local abundance in the overall model); given that the complete-case sample retained only 37% of species overall (and as little as 36% within some growth-form subsets, e.g., vines: n = 16 of 44), reduced statistical power is the most likely explanation for these differences rather than a change in the underlying relationship. A small number of additional significant effects emerged in specific growth-form subsets in the complete-case analysis (e.g., vines); because these subsets are much smaller, we treat these as unstable rather than as robust departures from the imputed-data results. Full complete-case results are provided in Fig. S1 and Tables S11–S13.

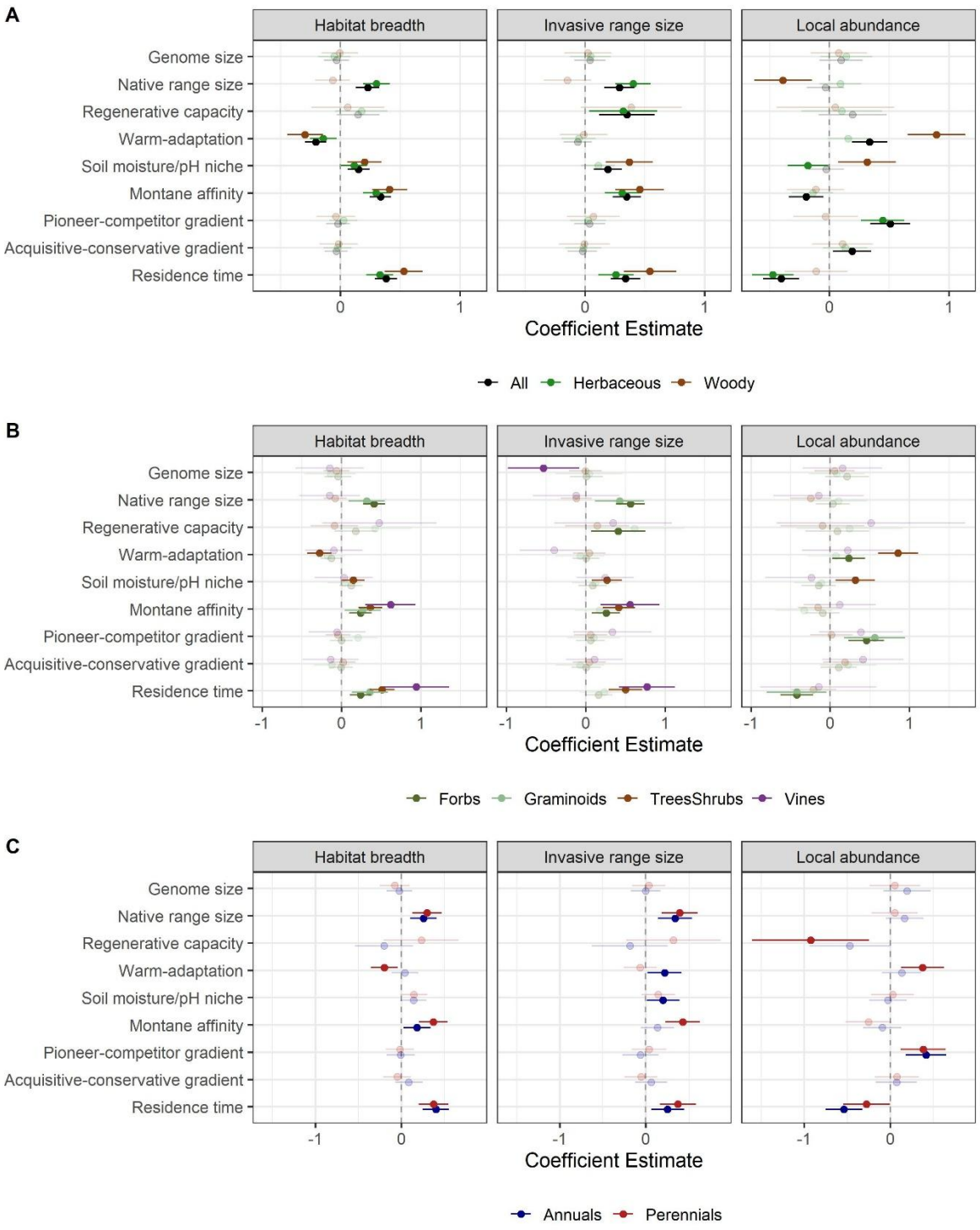

Fig. 2. Results from phylogenetic generalized least squares models assessing the effects of traits across three dimensions of invasion success (habitat breadth, range size, and local abundance. (A) Results for all (n = 622), herbaceous (n = 448) and woody (n = 174) invasive species. **(B)** Results for invasive plants across growth forms: graminoids (n = 99), forbs (n = 309), trees/shrubs (n = 170) and vines (n = 44). **(C)** Results for annual (n = 219) and perennial (n

= 205) herbaceous invasive plant species. Dots represent coefficient estimates; whiskers represent 95% confidence intervals. Solid colored symbols represent statistically significant effects ($p < 0.05$).

The magnitude of trait effects on invasion success differs across dimensions and life forms

Across all models, explained variance was highest for habitat breadth and lowest for local abundance (Tables 2 and 3). Modeling woody and herbaceous invasives separately substantially improved model performance for woody species, with woody models explaining a larger proportion of variation than herbaceous models across all invasion dimensions. In particular, models for woody species captured approximately 30–50% of the variation. Further stratifying species by primary growth form did not substantially improve model performance beyond the gains observed when separating structural habits, although the range size model for graminoids explained much less variation (6.5%) than the herbaceous model and the habitat breadth model for vines explained more variation (60%) than all other models. Separating annual and perennial herbaceous invaders also increased the explanatory power of our models for perennial species, but not for annuals, which performed similarly to the herbaceous model.

Table 2. Variance explained by phylogenetic generalized least squares models assessing the effects of traits across three dimensions of invasion success (habitat breadth, range size, and local abundance) for all (n = 622), herbaceous (n = 448) and woody (n = 174) invasive species.

Invasion success dimension	Structural habit	Pseudo-R^2
Habitat breadth	All	0.35
	Herbaceous	0.25
	Woody	0.52
Range size	All	0.23
	Herbaceous	0.19
	Woody	0.37
Local abundance	All	0.21
	Herbaceous	0.19
	Woody	0.34

Table 3. Variance explained by phylogenetic generalized least squares models assessing the effects of traits across three dimensions of invasion success (habitat breadth, range size, and local abundance) across growth forms: graminoids (n = 99), forbs (n = 309), trees/shrubs (n = 170) and vines (n = 44).

Invasion success dimension	Growth form	Pseudo-R^2
Habitat breadth	Forbs	0.22
	Graminoids	0.24
	Trees/Shrubs	0.49
	Vines	0.60
Range size	Forbs	0.22
	Graminoids	0.065
	Trees/Shrubs	0.31
	Vines	0.28
Local abundance	Forbs	0.20
	Graminoids	0.15
	Trees/Shrubs	0.29
	Vines	0.28

Table 4. Variance explained by phylogenetic generalized least squares models assessing the effects of traits across three dimensions of invasion success (habitat breadth, range size, and local abundance) for annual (n = 219) and perennial (n = 205) herbaceous invasive species.

Invasion success dimension	Lifespan	Pseudo-R^2
Habitat breadth	Annuals	0.24
	Perennials	0.39
Range size	Annuals	0.15
	Perennials	0.35
Local abundance	Annuals	0.22
	Perennials	0.21

DISCUSSION

The need for robust frameworks to characterize and predict invasiveness has been a major driver of trait-based invasion research in the last 30 years, but progress towards a unified framework has been limited by inconsistent and context-dependent results (Gioria et al., 2023; Pyšek, Bacher, et al., 2020). Here, we sought to integrate contrasting findings by leveraging a

macroecological approach using a dataset of 622 invasive plant species in the United States and 16 species traits related to environmental tolerance, competitive ability, fast life history, and asexual regeneration. Furthermore, we defined invasion success in a non-binary, nuanced manner, linking species traits to three distinct dimensions of invasiveness: local abundance, habitat breadth and range size. We find that the traits linked to invasion success, as well as the strength of these associations, vary across dimensions of invasiveness and life forms. In particular, our findings indicate that woody and herbaceous invaders follow distinct pathways to high local abundance, with woody species exhibiting trait syndromes that promote persistence and competitive tolerance, whereas herbaceous species exhibit trait syndromes associated with competitive suppression of neighbors.

Overall, invasive plant species with broad habitat breadths and large range sizes in the United States were characterized by large native ranges and higher tolerance to stressful edaphic and atmospheric conditions, specifically those posed by dry, alkaline soils and high elevations. Native range size is widely considered an indicator of effective dispersal, broad environmental tolerance, and higher introduction pressure, and is therefore often associated with successful establishment and large invasive ranges (Q. Guo et al., 2025; Lavoie et al., 2013; Procheş et al., 2012). Conversely, harsh habitats—such as those with low nutrient availability, saline, sodic or highly alkaline soils, low soil moisture or high elevations—are known to be generally less invaded (Alpert et al., 2000; Zefferman et al., 2015). Invasive plants capable of occupying such environments are therefore able to achieve larger invasive ranges and display broader habitat breadths. In addition to these traits, habitat breadth was associated with an affinity for temperate climates, likely reflecting the predominance of cooler climatic regimes across much of the United States. Additionally, asexual regeneration was associated with larger range sizes in the

United States. Asexual regeneration has been widely associated with invasion success for plants (Nunez-Mir et al., 2019; Razanajatovo et al., 2016; Reichard & Hamilton, 1997; Van Kleunen et al., 2015), with prolific resprouting promoting persistence/reinvasion and uniparental reproduction enabling rapid population growth and niche occupation.

On the other hand, highly abundant invasive plants overall tended to be lowland, warm-adapted plants aligned with competitive life-history strategies (i.e., taller, larger seeds, and larger leaves) and resource-conservative leaves. Studies focused on the relationship between species traits and local abundance emphasize the importance of competitive ability in achieving invasion success at the local scale, also showing that invasive species that are commonly highly abundant tend to have larger height, seed mass, and leaf area (Fristoe et al., 2021; Palma et al., 2021). Resource-conservative leaves (i.e., low SLA) may promote high abundance by improving heat and drought tolerance (Münchinger et al., 2023; Valliere et al., 2023) and by impacting native plant regeneration through ecosystem-level alterations caused by lower leaf decomposability and higher litter accumulation (B.-M. Chen et al., 2018; Mariotte et al., 2017; Stinson et al., 2006). However, separating growth forms revealed a more complex relationship between species traits, competition, and success in this dimension.

Herbaceous invasive plants of all growth forms and lifespans displayed a strong and consistent association between high local abundance and traits on the competitive side of the pioneer-competitor gradient PC, consistent with the patterns observed in the overall model. This trait syndrome has been frequently connected to aboveground competitive dominance of invasive herbaceous species (Y. Chen et al., 2024; Palma et al., 2021; Van Kleunen et al., 2010). In herbaceous communities, reaching the upper vegetation layer is understood to provide an asymmetric competitive advantage for light and space over shorter plants, contributing to higher

abundance (Gaudet & Keddy, 1988; Moravcová et al., 2015; Thiele et al., 2010). Similarly, larger leaves are correlated with competitiveness of herbaceous plants, presumably by facilitating faster resource acquisition (Keddy et al., 2002; Wingler & Sandel, 2023). Higher seed mass is also generally associated with strong competitive ability and persistence, as larger seeds are capable of storing larger energy reserves and often produce larger plant seedlings (Graebner et al., 2012; Palma et al., 2021).

On the other hand, for woody species, warm adaptation and tolerance of dry, alkaline soils were strongly associated with high local abundance—the latter being associated with success in all three invasion dimensions. The connection between elevated pH and forest invasions has been previously established in the literature, although the mechanisms underlying this pattern are not well-understood. Invasive woody plants—trees (Gómez-Aparicio & Canham, 2008), shrubs (Heneghan et al., 2006; Huebner et al., 2014; Kourtev et al., 2003), and lianas (Leicht-Young et al., 2009; Ward et al., 2020)—are associated with increased pH in soils, but it is unclear whether the higher soil pH observed in invaded forest habitats is due to underlying site conditions that promote invasibility by these species (e.g., anthropogenic disturbance) or to positive soil feedbacks induced by the invaders themselves. Elevated soil pH in forests is commonly associated with anthropogenic disturbance and urbanization, driven by nutrient inputs and runoff such as road salts, calcium-enriched irrigation water, and the weathering of concrete and other materials used in urban areas adjacent to forests (Craul, 1985; Jim, 1998; Pregitzer et al., 2016). On the other hand, higher soil pH can also arise from belowground invasive plant processes that alter nitrogen cycles (Ehrenfeld et al., 2001; C. Liao et al., 2008), which in turn can lead to higher competitive ability through increased biomass and productivity or positive soil feedbacks (Chang et al., 2025; Li et al., 2024).

Differences in the ecological strategies leveraged by woody and herbaceous invaders were also reflected in relationships between local abundance and other characteristics, including native range size and residence time. Although herbaceous species displayed patterns consistent with the overall model and broader literature, native range size in woody species was negatively correlated with local abundance and unrelated to either habitat breadth or invasive range size. Although positive abundance–range size relationships are extensively documented across non-plant taxa (Bock & Ricklefs, 1983; Gaston et al., 1998; Kotze et al., 2003), plants—and trees specifically—appear to be an exception to this trend, displaying weakly positive (Köckemann et al., 2009; Murphy et al., 2006), negative (Williams et al., 2010), or no relationships (Ren et al., 2013). Negative abundance–range size relationships observed in trees have been hypothesized to be driven by ecological specialization, particularly in unusual habitats or stressful edaphic conditions (Williams et al., 2010), potentially reflecting the greater importance of tolerance and persistence strategies among woody species. Consistent with this interpretation, Morin & Chuine (2006) found that late-successional tree species (superior competitors) were more likely to exhibit smaller ranges than pioneer species (poorer competitors). The divergence observed among plant life forms is also consistent with previous findings of weak or nonexistent associations between native and invasive range size in woody plants, a pattern attributed to ecological processes and evolutionary constraints specific to woody life forms (Q. Guo et al., 2025; Ricklefs & Latham, 1992).

Our findings also revealed that the effect of residence time on invasion success is more complex and growth-form-specific than generally recognized. We found residence time to be positively correlated with habitat breadth and range size across all growth forms but negatively correlated with local abundance in the overall model and for herbaceous growth forms (no effect

for trees/shrubs or vines). The relationship between residence time and abundance of invasive plants is poorly understood, but there is empirical evidence of invader abundance, impacts, and competitive performance decreasing at the community level over time (see Dostál et al., 2013; Sheppard & Schurr, 2019). Theoretically, negative residence time–abundance relationships for invasive plants may arise due to increased biotic resistance of native communities over time to novel invaders through accumulated eco-evolutionary experience—a process more often discussed regarding novel predator-prey interactions (Carthey & Banks, 2014; Saul & Jeschke, 2015). In the context of plant-plant competition, native genotypes with stronger competitive ability may be naturally selected for over time, leading to evolution-driven coexistence mechanisms that decrease invader dominance while shielding native species from local extirpation (Germain et al., 2020; Lankau, 2011; Oduor, 2013). For instance, Sheppard & Brendel (2021) found that the impact of competition from invasive neighbors on seed production of focal native species was reduced as coexistence time increased. Eco-evolutionary coexistence mechanisms may also involve adaptations that increase the tolerance of native plants to novel invasive weapons, such as allelopathy (Callaway et al., 2005; Huang et al., 2018), or increased negative impacts from interactions with other native communities, such as herbivores, pathogens, or soil microbes (Dostál et al., 2013).

Although our macroecological approach limits our ability to elucidate the mechanistic underpinnings of these patterns, these findings suggest that woody and herbaceous plants rely on distinct pathways to invasion success. The trait syndromes associated with woody invaders point to strategies that enhance persistence and tolerance of stressful conditions and competition from neighboring plants. Small native ranges of abundant woody invaders may be additional evidence of specialization to stressful or limiting conditions as a pathway to high abundance. In contrast,

herbaceous invaders are characterized by traits associated with strong competitive effects and the suppression of neighboring species, potentially making their local dominance more susceptible to evolution-driven shifts in native competitive ability over time and contributing to the observed decline in abundance with residence time. This distinction maps onto a framework long recognized in plant ecology—that of competitive response (tolerance) and competitive effect (suppression) (Goldberg, 1990; Goldberg & Landa, 1991; Jacquard, 1968). These complementary, non-mutually exclusive strategies reflect the ability to maintain performance under competition and stressful conditions, and the ability to suppress neighboring species, respectively. Consistent with our findings, a meta-analysis of 192 competition studies found that non-native plants generally outperform native species through greater competitive tolerance rather than stronger competitive suppression, and further reported that trees exhibited significantly weaker suppressive effects than other plant life forms (Golivets & Wallin, 2018). Together, these findings suggest that high local abundance may be achieved through alternative competitive strategies, with woody and herbaceous invasive species differing in the relative importance of competitive tolerance and suppression. This distinction may also help explain differences in the explanatory power of traits across growth forms. Trait-based models explained substantially more variation for woody species (pseudo-R^2 = 0.34–0.52), potentially indicating that persistence and competitive tolerance strategies are more tightly linked to intrinsic species traits than to external ecological processes (Kunstler et al., 2016; Pavanetto et al., 2024).

Beyond these key patterns, our analyses revealed some unexpected findings. For instance, in contrast with the prevailing evidence in the literature and the patterns observed here for trait associations with range size, the ability to reproduce asexually was associated with lower abundance for perennial herbaceous species. Palma and colleagues (2021) also found

490 reproductive flexibility to be negatively correlated with spread rate and habitat breadth,
491 suggesting that the role of sexual systems in invasion success may be more nuanced than
492 previously recognized. We were also surprised to see that smaller genome size, despite being
493 widely considered a unifying trait of invasiveness (K. Guo et al., 2024; Pandit et al., 2014;
494 Schmidt et al., 2017), was exclusively associated with the success of invasive vines and only in
495 the range size dimension. Genome size is correlated with various functional traits related to
496 adaptability to new environments, reproductive success, dispersal capacity and growth (Knight &
497 Beaulieu, 2008; Pyšek et al., 2023; Suda et al., 2015). Yet, these correlations are not always
498 linear or consistent across taxonomic groups and are often too complex to align neatly with
499 multidimensional invasion success (Pandit et al., 2014; Pyšek et al., 2023). It is possible that the
500 granularity of our invasion success metrics allowed the effects of functional traits correlated with
501 genome size and included in our analyses (e.g., seed size, plant height, specific leaf area) to
502 become partially disentangled from genome size itself.

503 The consistent explanatory power of functional and niche traits across all three invasion
504 dimensions, a notable finding given the inherent complexity of macroecological studies,
505 emphasizes the utility of a trait-based framework for predicting invasion success. Trait-based
506 models displayed greater explanatory power for habitat breadth and range size than for local
507 abundance. This finding, combined with the divergence of growth forms in strategies to reach
508 high local abundance and the influence of residence time discussed above, suggests that this
509 dimension of invasion success is more dynamic and context-dependent than the others. When
510 considering these dimensions as success at different spatial scales, achieving success locally by
511 reaching high abundance and community-level dominance is more likely to be influenced by
512 locally-varying factors not captured here, such as biotic interactions, propagule pressure, and

fine-scale abiotic context (Carr et al., 2019; Eschtruth & Battles, 2009). Indeed, the importance of accounting for context-dependence and invasion event-related factors when investigating drivers of invasion success has often been recognized (Gioria et al., 2023; Pyšek, Bacher, et al., 2020). Our findings add nuance to this framework by suggesting that context-dependent and invasion event-related processes may play a stronger role in shaping local abundance and dominance than broader-scale dimensions of invasion success such as range size and habitat breadth.

Our findings demonstrate that invasion success is not achieved in a singular manner, but rather through distinct trait syndromes with varying importance across dimensions of invasiveness and plant growth forms. A key insight emerging from our analyses is that herbaceous and woody invaders differ not only in the traits associated with achieving high local abundance, but also in how factors such as residence time and native range size relate to invasion success. These patterns suggest that the ecological processes underlying invasion success may differ more fundamentally among growth forms than is currently recognized. Future investigations of plant invasion success should focus on deriving mechanistic insights into this pattern. It is possible that the ecophysiological and evolutionary distinctions between woody and herbaceous plants drive ecological divergence, as adaptations of angiosperms at the tissue, physiological, and genomic levels underlie diverging responses to environmental stress between growth forms (Abaturov, 2015). Another promising avenue for future research is evaluating the role of introduction biases in shaping growth form-specific invasion syndromes. Differences in introduction pathways and propagule pressure may influence the traits associated with invasion success and contribute to the divergent patterns observed in this study.

Across all growth forms, habitat breadth and range size were more consistently and strongly predicted by species traits than local abundance, suggesting that local abundance is inherently more dynamic and context-dependent. This is a highly consequential finding of our study, as local abundance and community-level dominance are arguably the most relevant dimensions of invasion success for native species conservation and invasive plant management, given the empirically supported positive relationship between invader abundance and negative impacts on native communities (Bradley et al., 2019). Future research should therefore prioritize identifying drivers of local abundance and invasive dominance, with particular attention to the interplay between residence time and eco-evolutionary dynamics, as well as the role of propagule pressure and fine-scale environmental context. Advancing our understanding of invasion success will be critical for developing more effective and targeted proactive management strategies (e.g., risk assessments, early detection and rapid response), and will require embracing, rather than simplifying, the complexity of plant invasiveness revealed here.

Acknowledgements

We thank the developers and maintainers of the many public databases that made this work possible, including EDDMapS, the BIEN database, the TRY Plant Trait Database, the LEDA Traitbase, the Ecological Flora of the British Isles, BROT, the COMPADRE Plant Matrix Database, the Seed Information Database, the Plant DNA C-values Database, and the Royal Botanic Gardens Kew's Plants of the World Online. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

REFERENCES

Abaturov, B. D. (2015). Competitive separation of herbaceous and woody plant communities in steppe and forest zones. Biology Bulletin Reviews 2015 5:2, 5(2), 148–155. https://doi.org/10.1134/S2079086415020024

Alpert, P., Bone, E., & Holzapfel, C. (2000). Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology, Evolution and Systematics, 3(1), 52–66. https://doi.org/https://doi.org/10.1078/1433-8319-00004

Al-Shayeb, S. M. A., Aguilar, C., Yousefi, M., George, Z., Pfadenhauer, W. G., & Nunez-Mir, G. C. (in press). Invasive Flora Repository: Traits, environmental tolerances, and invasion history of invasive plant species in the U.S. Ecology.

Baker, H. G. (1965). Characteristics and modes of origin of weeds. Characteristics and Modes of Origin of Weeds., 147–172.

Bargeron, C. T., & Moorhead, D. J. (2007). EDDMapS—early detection and distribution mapping system for the southeast exotic pest plant council. Wildland Weeds, 10(4), 4–8.

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. Trends in Ecology & Evolution, 26(7), 333–339.

Bocci, G. (2015). TR8: an R package for easily retrieving plant species traits. Methods in Ecology and Evolution, 6(3), 347–350.

Bock, C. E., & Ricklefs, R. E. (1983). Range size and local abundance of some North American songbirds: a positive correlation. The American Naturalist, 122(2), 295–299.

Bradley, B. A., Evans, A. E., Sofaer, H. R., Vilà, M., Barnett, D. T., Beaury, E. M., Blumenthal, D. M., Corbin, J. D., Dukes, J. S., & Early, R. (2025a). A Quantitative Classification of the Geography of Non-Native Flora in the United States. Global Ecology and Biogeography, 34(4), e70041.

Bradley, B. A., Evans, A. E., Sofaer, H. R., Vilà, M., Barnett, D. T., Beaury, E. M., Blumenthal, D. M., Corbin, J. D., Dukes, J. S., & Early, R. (2025b). A Quantitative Classification of the Geography of Non-Native Flora in the United States. Global Ecology and Biogeography, 34(4), e70041.

Bradley, B. A., Evans, A. E., Sofaer, H. R., Vilà, M., Barnett, D. T., Beaury, E. M., Blumenthal, D. M., Corbin, J. D., Dukes, J. S., Early, R., Ibáñez, I., Pearse, I. S., Petri, L., & Sorte, C. J. B. (2025). A Quantitative Classification of the Geography of Non-Native Flora in the United States. Global Ecology and Biogeography, 34(4), e70041. https://doi.org/https://doi.org/10.1111/geb.70041

Bradley, B. A., Laginhas, B. B., Whitlock, R., Allen, J. M., Bates, A. E., Bernatchez, G., Diez, J. M., Early, R., Lenoir, J., Vilà, M., & Sorte, C. J. B. (2019). Disentangling the abundance–impact relationship for invasive species. Proceedings of the National Academy of Sciences, 116(20), 9919–9924. https://doi.org/10.1073/PNAS.1818081116

Brondízio, E. S., Settele, J., Diaz, S., & Ngo, H. T. (2019). Global assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services. IPBES.

Callaway, R. M., Ridenour, W. M., Laboski, T., Weir, T., & Vivanco, J. M. (2005). Natural Selection for Resistance to the Allelopathic Effects of Invasive Plants. Journal of Ecology, 93(3), 576–583. http://www.jstor.org/stable/3599423

Carboni, M., Münkemüller, T., Lavergne, S., Choler, P., Borgy, B., Violle, C., Essl, F., Roquet, C., Munoz, F., Consortium, D., & Thuiller, W. (2016). What it takes to invade grassland ecosystems: traits, introduction history and filtering processes. Ecology Letters, 19(3), 219–229. https://doi.org/https://doi.org/10.1111/ele.12556

Carr, A. N., Hooper, D. U., & Dukes, J. S. (2019). Long-term propagule pressure overwhelms initial community determination of invader success. Ecosphere, 10(8), e02826. https://doi.org/10.1002/ECS2.2826

Carthey, A. J. R., & Banks, P. B. (2014). Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. Biological Reviews, 89(4), 932–949. https://doi.org/10.1111/BRV.12087

Catford, J. A., Baumgartner, J. B., Vesk, P. A., White, M., Buckley, Y. M., & McCarthy, M. A. (2016). Disentangling the four demographic dimensions of species invasiveness. Journal of Ecology, 104(6), 1745–1758. https://doi.org/https://doi.org/10.1111/1365-2745.12627

Chang, X., Wang, W., & Zhou, H. (2025). Nitrogen Acquisition by Invasive Plants: Species Preferential N Uptake Matching with Soil N Dynamics Contribute to Its Fitness and Domination. In Plants (Vol. 14, Number 5, p. 748). https://doi.org/10.3390/plants14050748

Chen, B.-M., D'Antonio, C. M., Molinari, N., & Peng, S.-L. (2018). Mechanisms of influence of invasive grass litter on germination and growth of coexisting species in California. Biological Invasions, 20(7), 1881–1897.

Chen, Y., Xie, Y., Wei, C., Liu, S., Liang, X., Zhang, J., & Li, R. (2024). Invasive plant species demonstrate enhanced resource acquisition traits relative to native non-dominant species but not compared with native dominant species. Diversity, 16(6), 317.

Cheng, X., Ping, T., Li, Z., Wang, T., Han, H., & Epstein, H. E. (2021). Effects of environmental factors on plant functional traits across different plant life forms in a temperate forest ecosystem. New Forests 2021 53:1, 53(1), 125–142. https://doi.org/10.1007/S11056-021-09847-0

Colautti, R. I., & MacIsaac, H. J. (2004). A neutral terminology to define 'invasive' species. Diversity and Distributions, 10(2), 135–141. https://doi.org/https://doi.org/10.1111/j.1366-9516.2004.00061.x

Craul, P. J. (1985). A description of urban soils and their desired characteristics. Journal of Arboriculture, 11(11), 330–339.

Dostál, P., Müllerová, J., Pyšek, P., Pergl, J., & Klinerová, T. (2013). The impact of an invasive plant changes over time. Ecology Letters, 16(10), 1277–1284. https://doi.org/10.1111/ELE.12166

Drenovsky, R. E., Grewell, B. J., Dantonio, C. M., Funk, J. L., James, J. J., Molinari, N., Parker, I. M., & Richards, C. L. (2012). A functional trait perspective on plant invasion. Annals of Botany, 110(1), 141–153. https://doi.org/10.1093/AOB/MCS100

Ehrenfeld, J. G., Kourtev, P., & Huang, W. (2001). Changes in Soil Functions Following Invasions of Exotic Understory Plants in Deciduous Forests. Ecological Applications, 11(5), 1287–1300. https://doi.org/10.2307/3060920

Enquist, B. J., Condit, R., Peet, R. K., Schildhauer, M., & Thiers, B. M. (2016). Cyberinfrastructure for an integrated botanical information network to investigate the ecological impacts of global climate change on plant biodiversity. PeerJ Preprints.

Eschtruth, A. K., & Battles, J. J. (2009). Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. Ecological Monographs, 79(2), 265–280. https://doi.org/10.1890/08-0221.1

Fitter, A. H., & Peat, H. J. (1994). The ecological flora database. Journal of Ecology, 415–425.

Fristoe, T. S., Chytrý, M., Dawson, W., Essl, F., Heleno, R., Kreft, H., Maurel, N., Pergl, J., Pyšek, P., & Seebens, H. (2021). Dimensions of invasiveness: Links between local abundance, geographic range size, and habitat breadth in Europe's alien and native floras. Proceedings of the National Academy of Sciences, 118(22), e2021173118.

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., Laughlin, D. C., Sutton-Grier, A. E., Williams, L., & Wright, J. (2017). Revisiting the Holy Grail: using plant functional traits to understand ecological processes. Biological Reviews, 92(2), 1156–1173. https://doi.org/https://doi.org/10.1111/brv.12275

Funk, J. L., & Wolf, A. A. (2016). Testing the trait-based community framework: Do functional traits predict competitive outcomes? Ecology, 97(9), 2206–2211. https://doi.org/https://doi.org/10.1002/ecy.1484

Gaston, K. J., Blackburn, T. M., Gregory, R. D., & Greenwood, J. J. D. (1998). The anatomy of the interspecific abundance–range size relationship for the British avifauna: I. Spatial patterns. Ecology Letters, 1(1), 38–46.

Gaudet, C. L., & Keddy, P. A. (1988). A comparative approach to predicting competitive ability from plant traits. Nature, 334(6179), 242–243. https://doi.org/10.1038/334242a0

Germain, R. M., Srivastava, D., & Angert, A. L. (2020). Evolution of an inferior competitor increases resistance to biological invasion. Nature Ecology & Evolution 2020 4:3, 4(3), 419–425. https://doi.org/10.1038/s41559-020-1105-x

Gioria, M., Hulme, P. E., Richardson, D. M., & Pyšek, P. (2023). Why Are Invasive Plants Successful? Annual Review of Plant Biology, 74(1), 635–670. https://doi.org/10.1146/annurev-arplant-070522-071021

Goldberg, D. E. (1990). Components of resource competition in plants. In J. Grace & D. Tilman (Eds.), Perspectives on plant competition (pp. 357–364). Academic Press.

Goldberg, D. E., & Landa, K. (1991). Competitive Effect and Response: Hierarchies and Correlated Traits in the Early Stages of Competition. The Journal of Ecology, 79(4), 1013. https://doi.org/10.2307/2261095

Golivets, M., & Wallin, K. F. (2018). Neighbour tolerance, not suppression, provides competitive advantage to non-native plants. Ecology Letters, 21(5), 745–759. https://doi.org/10.1111/ELE.12934

Gómez-Aparicio, L., & Canham, C. D. (2008). Neighborhood models of the effects of invasive tree species on ecosystem processes. Ecological Monographs, 78(1), 69–86. https://doi.org/https://doi.org/10.1890/06-2036.1

Graebner, R. C., Callaway, R. M., & Montesinos, D. (2012). Invasive species grows faster, competes better, and shows greater evolution toward increased seed size and growth than exotic non-invasive congeners. Plant Ecology, 213(4), 545–553. https://doi.org/10.1007/s11258-012-0020-x

Guo, K., Pyšek, P., van Kleunen, M., Kinlock, N. L., Lučanová, M., Leitch, I. J., Pierce, S., Dawson, W., Essl, F., Kreft, H., Lenzner, B., Pergl, J., Weigelt, P., & Guo, W.-Y. (2024). Plant invasion and naturalization are influenced by genome size, ecology and economic use globally. Nature Communications, 15(1), 1330. https://doi.org/10.1038/s41467-024-45667-4

Guo, Q., Qian, H., & Qian, S. (2025). Climate space, traits, and the spread of nonnative plants in North America. Plant Diversity, 47(2), 255–263. https://doi.org/10.1016/J.PLD.2024.11.005

Hejda, M., Pyšek, P., & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. Journal of Ecology, 97(3), 393–403. https://doi.org/https://doi.org/10.1111/j.1365-2745.2009.01480.x

Heneghan, L., Fatemi, F., Umek, L., Grady, K., Fagen, K., & Workman, M. (2006). The invasive shrub European buckthorn (Rhamnus cathartica, L.) alters soil properties in Midwestern U.S. woodlands. Applied Soil Ecology, 32(1), 142–148. https://doi.org/https://doi.org/10.1016/j.apsoil.2005.03.009

Higgins, S. I., & Richardson, D. M. (2014). Invasive plants have broader physiological niches. Proceedings of the National Academy of Sciences of the United States of America, 111(29), 10610–10614. https://doi.org/10.1073/PNAS.1406075111

Huang, F., Lankau, R., & Peng, S. (2018). Coexistence via coevolution driven by reduced allelochemical effects and increased tolerance to competition between invasive and native plants. New Phytologist, 218(1), 357–369. https://doi.org/10.1111/NPH.14937

Huebner, C. D., Steinman, J., Hutchinson, T. F., Ristau, T. E., & Royo, A. A. (2014). The distribution of a non-native (Rosa multiflora) and native (Kalmia latifolia) shrub in mature closed-canopy forests across soil fertility gradients. Plant and Soil, 377(1), 259–276. https://doi.org/10.1007/s11104-013-2000-x

Hui, C., Pyšek, P., & Richardson, D. M. (2023). Disentangling the relationships among abundance, invasiveness and invasibility in trait space. Npj Biodiversity 2023 2:1, 2(1), 13-. https://doi.org/10.1038/s44185-023-00019-1

Jacquard, P. (1968). Manifestation et nature des relations sociales chez les végétaux supérieurs. Oecologia Plantarum, 3(13), 137–168.

Jim, C. Y. (1998). Physical and chemical properties of a Hong Kong roadside soil in relation to urban tree growth. Urban Ecosystems, 2(2), 171–181.

Jin, Y., & Qian, H. (2023). U. PhyloMaker: An R package that can generate large phylogenetic trees for plants and animals. Plant Diversity, 45(3), 347–352.

Johnson, T. F., Isaac, N. J. B., Paviolo, A., & González-Suárez, M. (2021). Handling missing values in trait data. Global Ecology and Biogeography, 30(1), 51–62.

Jones, O. R., Barks, P., Stott, I., James, T. D., Levin, S., Petry, W. K., Capdevila, P., Che-Castaldo, J., Jackson, J., & Römer, G. (2022). Rcompadre and rage—Two R packages to facilitate the use of the COMPADRE and COMADRE databases and calculation of life-history traits from matrix population models. Methods in Ecology and Evolution, 13(4), 770–781.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., & Abedi, M. (2020). TRY plant trait database–enhanced coverage and open access. Global Change Biology, 26(1), 119–188.

Keddy, P., Nielsen, K., Weiher, E., & Lawson, R. (2002). Relative competitive performance of 63 species of terrestrial herbaceous plants. Journal of Vegetation Science, 13(1), 5–16. https://doi.org/https://doi.org/10.1111/j.1654-1103.2002.tb02018.x

Kim, S. W., Blomberg, S. P., & Pandolfi, J. M. (2018). Transcending data gaps: a framework to reduce inferential errors in ecological analyses. Ecology Letters, 21(8), 1200–1210.

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J. M., Klimeš, L., & Klimešová, J. (2008). The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology, 96(6), 1266–1274.

Knight, C. A., & Beaulieu, J. M. (2008). Genome Size Scaling through Phenotype Space. Annals of Botany, 101(6), 759–766. https://doi.org/10.1093/aob/mcm321

Köckemann, B., Buschmann, H., & Leuschner, C. (2009). The relationships between abundance, range size and niche breadth in Central European tree species. Journal of Biogeography, 36(5), 854–864.

745 Kotze, D. J., Niemelä, J., O'Hara, R. B., & Turin, H. (2003). Testing abundance-range size
746 relationships in European carabid beetles (Coleoptera, Carabidae). Ecography, 26(5),
747 553–566.

748 Kourtev, P. S., Ehrenfeld, J. G., & Häggblom, M. (2003). Experimental analysis of the effect of
749 exotic and native plant species on the structure and function of soil microbial
750 communities. Soil Biology and Biochemistry, 35(7), 895–905.
751 https://doi.org/https://doi.org/10.1016/S0038-0717(03)00120-2

752 Kuebbing, S. E., & Nuñez, M. A. (2016). Invasive non-native plants have a greater effect on
753 neighbouring natives than other non-natives. Nature Plants 2016 2:10, 2(10), 16134-.
754 https://doi.org/10.1038/nplants.2016.134

755 Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., Poorter, L.,
756 Vanderwel, M., Vieilledent, G., Wright, S. J., Aiba, M., Baraloto, C., Caspersen, J.,
757 Cornelissen, J. H. C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J.,
758 Kurokawa, H., … Westoby, M. (2016). Plant functional traits have globally consistent
759 effects on competition. Nature, 529(7585), 204–207.
760 https://doi.org/10.1038/NATURE16476

761 Lankau, R. (2011). Rapid evolution and mechanisms of species coexistence. Annual Review of
762 Ecology, Evolution, and Systematics, 42(Volume 42, 2011), 335–354.
763 https://doi.org/10.1146/ANNUREV-ECOLSYS-102710-145100/CITE/REFWORKS

764 Laughlin, D. C. (2014). Applying trait-based models to achieve functional targets for theory-
765 driven ecological restoration. Ecology Letters, 17(7), 771–784.
766 https://doi.org/https://doi.org/10.1111/ele.12288

767 Lavoie, C., Shah, M. A., Bergeron, A., & Villeneuve, P. (2013). Explaining invasiveness from the
768 extent of native range: new insights from plant atlases and herbarium specimens.
769 Diversity and Distributions, 19(1), 98–105.
770 https://doi.org/https://doi.org/10.1111/ddi.12014

771 Leicht-Young, S. A., O'Donnell, H., Latimer, A. M., & Jr., J. A. S. (2009). Effects of an Invasive
772 Plant Species, Celastrus orbiculatus, on Soil Composition and Processes. The American
773 Midland Naturalist, 161(2), 219–231. https://doi.org/10.1674/0003-0031-161.2.219

774 Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic
775 plant invasions. Ecology Letters, 7(10), 975–989.

776 Li, J., He, J.-Z., Liu, M., Yan, Z.-Q., Xu, X.-L., & Kuzyakov, Y. (2024). Invasive plant
777 competitivity is mediated by nitrogen use strategies and rhizosphere microbiome. Soil
778 Biology and Biochemistry, 192, 109361.
779 https://doi.org/https://doi.org/10.1016/j.soilbio.2024.109361

780 Liao, C., Peng, R., Luo, Y., Zhou, X., Wu, X., Fang, C., Chen, J., & Li, B. (2008). Altered
781 ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New
782 Phytologist, 177(3), 706–714. https://doi.org/https://doi.org/10.1111/j.1469-
783 8137.2007.02290.x

784 Liao, H., Pal, R. W., Niinemets, Ü., Bahn, M., Cerabolini, B. E. L., & Peng, S. (2021). Different
785 functional characteristics can explain different dimensions of plant invasion success.
786 Journal of Ecology, 109(3), 1524–1536. https://doi.org/https://doi.org/10.1111/1365-
787 2745.13575

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. Journal of Open Source Software, 6(60).

Luo, J., Li, J., Sun, Y., Degen, A. A., Wang, X., Xiong, J., Aqeel, M., Xie, S., Tang, D., Li, F., Hu, W., Dong, L., Peng, J., Hou, Q., Deng, Y., Ran, J., & Deng, J. (2026). Differential resource acquisition strategies of herbaceous and woody plants in temperate forests. BMC Plant Biology 2026 26:1, 26(1), 196-. https://doi.org/10.1186/S12870-025-08026-Z

Maitner, B. S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S. M., Guaderrama, D., Hinchliff, C. E., Jørgensen, P. M., & Kraft, N. J. B. (2018). The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database. Methods in Ecology and Evolution, 9(2), 373–379.

Mariotte, P., Spotswood, E. N., Farrer, E. C., & Suding, K. N. (2017). Positive litter feedbacks of an introduced species reduce native diversity and promote invasion in Californian grasslands. Applied Vegetation Science, 20(1), 28–39.

Maron, J. L., & Vila, M. (2001). When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos, 95(3), 361–373.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. Trends in Ecology & Evolution, 21(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Moravcová, L., Pyšek, P., Jarošík, V., & Pergl, J. (2015). Getting the Right Traits: Reproductive and Dispersal Characteristics Predict the Invasiveness of Herbaceous Plant Species. PLOS ONE, 10(4), e0123634-. https://doi.org/10.1371/journal.pone.0123634

Morin, X., & Chuine, I. (2006). Niche breadth, competitive strength and range size of tree species: A trade-off based framework to understand species distribution. Ecology Letters, 9(2), 185–195. https://doi.org/10.1111/J.1461-0248.2005.00864.X

Münchinger, I. K., Hajek, P., Akdogan, B., Caicoya, A. T., & Kunert, N. (2023). Leaf thermal tolerance and sensitivity of temperate tree species are correlated with leaf physiological and functional drought resistance traits. Journal of Forestry Research 2023 34:1, 34(1), 63–76. https://doi.org/10.1007/S11676-022-01594-Y

Murphy, H. T., VanDerWal, J., & Lovett-Doust, J. (2006). Distribution of abundance across the range in eastern North American trees. Global Ecology and Biogeography, 15(1), 63–71.

Nunez-Mir, G. C., Guo, Q., Rejmánek, M., Iannone III, B. V, & Fei, S. (2019). Predicting invasiveness of exotic woody species using a traits-based framework. Ecology, 100(10), e02797. https://doi.org/10.1002/ecy.2797

Nunez-Mir, G. C., & McCary, M. A. (2024). Invasive plants and their root traits are linked to the homogenization of soil microbial communities across the United States. Proceedings of the National Academy of Sciences, 121(44), e2418632121.

Oduor, A. M. O. (2013). Evolutionary responses of native plant species to invasive plants: A review. New Phytologist, 200(4), 986–992. https://doi.org/10.1111/NPH.12429

Omernik, J. M., & Griffith, G. E. (2014). Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environmental Management, 54(6), 1249–1266.

Palma, E., Vesk, P. A., & Catford, J. A. (2022). Building trait datasets: effect of methodological choice on a study of invasion. Oecologia 2022 199:4, 199(4), 919–935. https://doi.org/10.1007/S00442-022-05230-8

Palma, E., Vesk, P. A., White, M., Baumgartner, J. B., & Catford, J. A. (2021). Plant functional traits reflect different dimensions of species invasiveness. Ecology, 102(5), e03317. https://doi.org/https://doi.org/10.1002/ecy.3317

Pandit, M. K., White, S. M., & Pocock, M. J. O. (2014). The contrasting effects of genome size, chromosome number and ploidy level on plant invasiveness: a global analysis. New Phytologist, 203(2), 697–703. https://doi.org/https://doi.org/10.1111/nph.12799

Pavanetto, N., Carmona, C. P., Laanisto, L., Niinemets, Ü., & Puglielli, G. (2024). Trait dimensions of abiotic stress tolerance in woody plants of the Northern Hemisphere. Global Ecology and Biogeography, 33(2), 272–285. https://doi.org/10.1111/GEB.13788

Pellicer, J., & Leitch, I. J. (2020). The Plant DNA C-values database (release 7.1). The New Phytologist, 226(2), 301–305.

Penone, C., Davidson, A. D., Shoemaker, K. T., Di Marco, M., Rondinini, C., Brooks, T. M., Young, B. E., Graham, C. H., & Costa, G. C. (2014). Imputation of missing data in life-history trait datasets: which approach performs the best? Methods in Ecology and Evolution, 5(9), 961–970.

Pfadenhauer, W. G., Nelson, M. F., Laginhas, B. B., & Bradley, B. A. (2023). Remember your roots: Biogeographic properties of plants' native habitats can inform invasive plant risk assessments. Diversity and Distributions, 29(1), 4–18. https://doi.org/10.1111/DDI.13639

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017). Package 'nlme.' Linear and Nonlinear Mixed Effects Models, Version, 3(1), 274.

Pregitzer, C. C., Sonti, N. F., & Hallett, R. A. (2016). Variability in Urban Soils Influences the Health and Growth of Native Tree Seedlings. Ecological Restoration, 34(2), 106 LP – 116. https://doi.org/10.3368/er.34.2.106

Procheş, Ş., Wilson, J. R. U., Richardson, D. M., & Rejmánek, M. (2012). Native and naturalized range size in Pinus: relative importance of biogeography, introduction effort and species traits. Global Ecology and Biogeography, 21(5), 513–523. https://doi.org/https://doi.org/10.1111/j.1466-8238.2011.00703.x

Pyšek, P., Bacher, S., Kühn, I., Novoa, A., Catford, J. A., Hulme, P. E., Pergl, J., Richardson, D. M., Wilson, J. R. U., & Blackburn, T. M. (2020). MAcroecological Framework for Invasive Aliens (MAFIA): disentangling large-scale context dependence in biological invasions. NeoBiota, 62, 407–461. https://doi.org/10.3897/neobiota.62.52787

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., … Richardson, D. M. (2020). Scientists' warning on invasive alien species. Biological Reviews, 95(6), 1511–1534. https://doi.org/10.1111/BRV.12627

Pyšek, P., Jarošík, V., Pergl, J., Moravcová, L., Chytrý, M., & Kühn, I. (2014). Temperate trees and shrubs as global invaders: the relationship between invasiveness and native distribution depends on biological traits. Biological Invasions, 16(3), 577–589.

873 Pyšek, P., Křivánek, M., & Jarošík, V. (2009). Planting intensity, residence time, and species
874 traits determine invasion success of alien woody species. Ecology, 90(10), 2734–2744.
875 https://doi.org/https://doi.org/10.1890/08-0857.1

876 Pyšek, P., Lučanová, M., Dawson, W., Essl, F., Kreft, H., Leitch, I. J., Lenzner, B., Meyerson, L.
877 A., Pergl, J., van Kleunen, M., Weigelt, P., Winter, M., & Guo, W.-Y. (2023). Small
878 genome size and variation in ploidy levels support the naturalization of vascular plants
879 but constrain their invasive spread. New Phytologist, 239(6), 2389–2403.
880 https://doi.org/https://doi.org/10.1111/nph.19135

881 Pyšek, P., Manceur, A. M., Alba, C., McGregor, K. F., Pergl, J., Štajerová, K., Chytrý, M.,
882 Danihelka, J., Kartesz, J., Klimešová, J., Lučanová, M., Moravcová, L., Nishino, M.,
883 Sádlo, J., Suda, J., Tichý, L., & Kühn, I. (2015). Naturalization of central European plants
884 in North America: species traits, habitats, propagule pressure, residence time. Ecology,
885 96(3), 762–774. https://doi.org/https://doi.org/10.1890/14-1005.1

886 Pyšek, P., & Richardson, D. M. (2007). Traits Associated with Invasiveness in Alien Plants:
887 Where Do we Stand? In W. Nentwig (Ed.), Biological Invasions (pp. 97–125). Springer
888 Berlin Heidelberg. https://doi.org/10.1007/978-3-540-36920-2_7

889 Rabinowitz, D. (1981). Seven forms of rarity. Biological Aspects of Rare Plant Conservation.

890 Razanajatovo, M., Maurel, N., Dawson, W., Essl, F., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P.,
891 Winter, M., & Van Kleunen, M. (2016). Plants capable of selfing are more likely to
892 become naturalized. Nature Communications, 7, 13313.

893 Reichard, S. H., & Hamilton, C. W. (1997). Predicting invasions of woody plants introduced into
894 North America. Conservation Biology, 11(1), 193–203.

Ren, H., Condit, R., Chen, B., Mi, X., Cao, M., Ye, W., Hao, Z., & Ma, K. (2013). Geographical Range and Local Abundance of Tree Species in China. PLOS ONE, 8(10), e76374-. https://doi.org/10.1371/journal.pone.0076374

Ricklefs, R. E., & Latham, R. E. (1992). Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. American Naturalist, 139(6), 1305–1321. https://doi.org/10.1086/285388

Rossatto, D. R., & Franco, A. C. (2017). Expanding our understanding of leaf functional syndromes in savanna systems: the role of plant growth form. Oecologia 2017 183:4, 183(4), 953–962. https://doi.org/10.1007/S00442-017-3815-6

Salguero-Gómez, R., Jones, O. R., Archer, C. R., Buckley, Y. M., Che-Castaldo, J., Caswell, H., Hodgson, D., Scheuerlein, A., Conde, D. A., & Brinks, E. (2015). The compadre P lant M atrix D atabase: an open online repository for plant demography. Journal of Ecology, 103(1), 202–218.

Saul, W. C., & Jeschke, J. M. (2015). Eco-evolutionary experience in novel species interactions. Ecology Letters, 18(3), 236–245. https://doi.org/10.1111/ELE.12408

Schmidt, J. P., Drake, J. M., & Stephens, P. (2017). Residence time, native range size, and genome size predict naturalization among angiosperms introduced to Australia. Ecology and Evolution, 7(23), 10289–10300. https://doi.org/https://doi.org/10.1002/ece3.3505

Sheppard, C. S., & Brendel, M. R. (2021). Competitive ability of native and alien plants: effects of residence time and invasion status. NeoBiota, 65, 47–69. https://doi.org/https://doi.org/10.3897/neobiota.65.63179

916 Sheppard, C. S., & Schurr, F. M. (2019). Biotic resistance or introduction bias? Immigrant plant
917 performance decreases with residence times over millennia. Global Ecology and
918 Biogeography, 28(2), 222–237. https://doi.org/https://doi.org/10.1111/geb.12844

919 Simpson, A., Wiltermuth, M. T., & Dorado, M. (2025). United States Register of Introduced and
920 Invasive Species. US Geological Survey.

921 Society for Ecological Restoration, International Network for Seed Based Restoration, & Royal
922 Botanic Gardens Kew. (2023). Seed Information Database (SID). https://ser-sid.org/

923 Stinson, K. A., Campbell, S. A., Powell, J. R., Wolfe, B. E., Callaway, R. M., Thelen, G. C.,
924 Hallett, S. G., Prati, D., & Klironomos, J. N. (2006). Invasive plant suppresses the growth
925 of native tree seedlings by disrupting belowground mutualisms. PLoS Biology, 4(5),
926 e140.

927 Suda, J., Meyerson, L. A., Leitch, I. J., & Pyšek, P. (2015). The hidden side of plant invasions:
928 the role of genome size. New Phytologist, 205(3), 994–1007.
929 https://doi.org/https://doi.org/10.1111/nph.13107

930 Tavşanoğlu, Ç., & Pausas, J. G. (2018). A functional trait database for Mediterranean Basin
931 plants. Scientific Data, 5(1), 1–18.

932 Tecco, P. A., Díaz, S., Cabido, M., & Urcelay, C. (2010). Functional traits of alien plants across
933 contrasting climatic and land-use regimes: do aliens join the locals or try harder than
934 them? Journal of Ecology, 98(1), 17–27. https://doi.org/https://doi.org/10.1111/j.1365-
935 2745.2009.01592.x

Theoharides, K. A., & Dukes, J. S. (2007). Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytologist, 176(2), 256–273.

Thiele, J., Isermann, M., Otte, A., & Kollmann, J. (2010). Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs. Journal of Vegetation Science, 21(2), 213–220.

Valliere, J. M., Nelson, K. C., & Martinez, M. C. (2023). Functional traits and drought strategy predict leaf thermal tolerance. Conservation Physiology, 11(1). https://doi.org/10.1093/CONPHYS/COAD085

Van Kleunen, M., Dawson, W., & Maurel, N. (2015). Characteristics of successful alien plants. Molecular Ecology, 24(9), 1954–1968.

Van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters, 13(2), 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

Wang, Y., Müller-Schärer, H., Kleunen, M., Cai, A., Zhang, P., Yan, R., Dong, B., & Yu, F. (2017). Invasive alien plants benefit more from clonal integration in heterogeneous environments than natives. New Phytologist.

Ward, E. B., Pregitzer, C. C., Kuebbing, S. E., & Bradford, M. A. (2020). Invasive lianas are drivers of and passengers to altered soil nutrient availability in urban forests. Biological Invasions, 22(3), 935–955. https://doi.org/10.1007/s10530-019-02134-2

Williams, J. N., Viers, J. H., & Schwartz, M. W. (2010). Tropical dry forest trees and the relationship between local abundance and geographic range. Journal of Biogeography, 37(5), 951–959.

Williamson, M., Dehnen-Schmutz, K., Kühn, I., Hill, M., Klotz, S., Milbau, A., Stout, J., & Pyšek, P. (2009). The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. Diversity and Distributions, 15(1), 158–166. https://doi.org/10.1111/J.1472-4642.2008.00528.X

Wingler, A., & Sandel, B. (2023). Relationships of the competitor, stress tolerator, ruderal functional strategies of grass species with lifespan, photosynthetic type, naturalization and climate. AoB PLANTS, 15(3), plad021. https://doi.org/10.1093/aobpla/plad021

Zefferman, E., Stevens, J. T., Charles, G. K., Dunbar-Irwin, M., Emam, T., Fick, S., Morales, L. V, Wolf, K. M., Young, D. J. N., & Young, T. P. (2015). Plant communities in harsh sites are less invaded: a summary of observations and proposed explanations. AoB PLANTS, 7, plv056. https://doi.org/10.1093/aobpla/plv056

Zuanny, D. C., Vilela, B., Moonlight, P. W., Särkinen, T. E., & Cardoso, D. (2024). expowo: An R package for mining global plant diversity and distribution data. Applications in Plant Sciences, 12(6), e11609.