



Naturalized species drive functional trait shifts in plant communities

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Despite decades of research documenting the consequences of naturalized and invasive plant species on ecosystem functions, our understanding of the functional underpinnings of these changes remains rudimentary. This is partially due to ineffective scaling of trait differences between native and naturalized species to whole plant communities. Working with data from over 75,000 plots and over 5,500 species from across the United States, we show that changes in the functional composition of communities associated with increasing abundance of naturalized species mirror the differences in traits between native and naturalized plants. We find that communities with greater abundance of naturalized species are more resource acquisitive aboveground and belowground, shorter, more shallowly rooted, and increasingly aligned with an independent strategy for belowground resource acquisition via thin fine roots with high specific root length. We observe shifts toward herbaceous-dominated communities but shifts within both woody and herbaceous functional groups follow community-level patterns for most traits. Patterns are remarkably similar across desert, grassland, and forest ecosystems. Our results demonstrate that the establishment and spread of naturalized species, likely in combination with underlying environmental shifts, leads to predictable and consistent changes in community-level traits that can alter ecosystem functions.

invasive plants | functional traits | invasive species impacts | community-weighted mean traits

Over 13,000 plant species, nearly 4% of the world's flora, have naturalized beyond their native ranges (1), and projections indicate novel species introductions will continue for decades (2). In many cases, the naturalization of introduced plant species leads to invasions that alter ecosystem functioning (3) and impact ecological, economic, and social systems (4, 5). Plant traits (i.e., morphological, phenological, or physiological characteristics of plants) influence the rates at which nutrients, water, and carbon are cycled and stored within ecosystems (6, 7). Therefore, changes in ecosystem functioning resulting from the establishment and spread of naturalized plants are likely driven by trait differences between native and naturalized species. However, linking naturalized species to community-level trait shifts and subsequent changes in ecosystem function has been challenging because we do not know whether naturalized species drive predictable and consistent changes in the functional composition of plant communities.

Plant functional strategies can be characterized by a species' position along four key gradients of trait variation: 1) the aboveground and belowground conservation gradient, which contrasts fast-growing and resource-acquisitive leaves and roots with those that are slow-growing and long-lived; 2) the belowground collaboration gradient, which contrasts plants that acquire soil resources independently via thin roots with high specific root length (SRL) with those that outsource resource acquisition to mycorrhizal symbionts; and two independent size gradients, 3) one for maximum plant height and 4) one for maximum rooting depth (8). Native and naturalized species exhibit considerable differences in traits associated with several of these axes (9, 10). Numerous studies have documented higher specific leaf area (SLA) and leaf nutrient concentrations and lower leaf dry matter content (LDMC) of naturalized compared to native species (9–11). These differences position naturalized species on the fast, or acquisitive, end of the leaf economics spectrum (8, 12). Findings related to the belowground conservation gradient remain inconclusive: Studies have found higher (13, 14), similar (15), and lower (16, 17) root N and higher (17), similar (16, 18), and lower (14) root tissue density (RTD) in naturalized compared to native species. Despite these mixed results, general trends for higher nutrient uptake in naturalized compared to native species (18, 19) and coordination between aboveground and belowground resource acquisition traits (8, 20, 21) suggest that

Significance

The establishment of naturalized plant species often leads to invasions that change ecosystem functioning and associated ecosystem services. The traits of native and naturalized species differ, but how these differences shift the functional composition of whole plant communities remains unknown. Our research shows that across deserts, grasslands, and forests, plant communities with higher abundance of naturalized species are more acquisitive above and belowground, shorter, more shallowly rooted, and less dependent on mycorrhizal symbionts for resource acquisition. These functional shifts likely drive observed changes in carbon storage, litter decomposition, and nutrient and water cycling in invaded ecosystems. This mechanistic understanding of functional community change is a crucial step toward predicting and mitigating impacts of naturalized and invasive species.

The authors declare no competing interest.

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naturalized species align with the acquisitive end of the belowground conservation gradient. Naturalized plant species also tend to have higher SRL and thinner root diameters (16, 17, 19, 22, 23) than natives, placing naturalized species on the do-it-yourself (i.e., less reliance on mycorrhizae) end of the belowground collaboration gradient (8). How naturalized species compare to native species in terms maximum height and maximum rooting depth also remains uncertain, with results that vary by region. For example, invasive species across European grasslands and forests tend to be taller than co-occurring natives (24), and some naturalized species in Mediterranean systems of California have deeper roots than co-occurring natives (25). However, short, shallow-rooted, annual species are common invaders across many western United States ecosystems that were historically dominated by taller, deeper-rooted, perennial grasses and shrubs (26, 27), and short understory plants often invade US forest ecosystems (28). These conflicting results may arise because most studies compare size traits of native and naturalized species from similar functional groups or among closely related taxa (9, 10). This helps control for the influence of phylogenetic similarities among species but may minimize realistic and relevant differences in size traits that likely contribute to invasions and their impacts.

Invasion ecologists have also started to ask how functional traits of nonnative species drive ecosystem changes observed in communities undergoing colonization and invasion by introduced plants (17, 29, 30). Among other impacts, naturalized species have been shown to alter nutrient (31–33), carbon (34, 35), and water (32, 36, 37) cycles, change ecosystem productivity (4, 5), and modify decomposition patterns (38, 39). Such ecosystem impacts are likely underpinned by changes in the functional composition of plant communities resulting from the colonization and proliferation of naturalized species. Several studies have demonstrated predictable changes in functional composition along gradients of introduced species abundance (40–44). However, because these studies have focused on individual species and sites, it remains unclear to what extent trait differences between naturalized and native species scale up to the community-level, and whether changes in functional composition are consistent across habitats.

Here, we combined large datasets of plant abundance and functional traits to provide a general picture of how naturalized species alter trait distributions of plant communities in six distinct ecoregions in the United States: Eastern Temperate Forests, Great Plains, Mediterranean California, North American Deserts, Northern Forests, and Northwestern Forested Mountains (45). We developed several overarching predictions about how community functional composition would change in relation to naturalized species abundance based on documented differences between native and naturalized species. Where previous studies conflicted, we specify lower confidence in those predictions. Specifically, we predicted that communities with greater abundance of naturalized species would be associated with the fast end of the aboveground (higher confidence) and belowground (lower confidence) conservation gradient, the do-it-yourself end of the root collaboration gradient (higher confidence), and the short/shallow ends of the height and rooting depth gradients (lower confidence; Fig. 1).

To test these predictions, we integrated compositional data from over 75,000 vegetation monitoring plots across the continental US from the Standardized Plant Community with Introduced Status database (SPCIS hereafter; ref. 46) with species-level trait data to determine how naturalized species alter the functional composition of plant communities. The SPCIS database includes plots that span a gradient of no or low invasion to high or complete dominance by naturalized plants from areas with varied degrees of disturbance which could affect naturalized species abundance (46, 47). We used leaf, root, and size trait data from several databases (*Methods* for details) and published literature to estimate species-level trait values, community weighted mean (i.e., CWM) trait values for each plot, and abundance-weighted trait values of native and naturalized species in plots where both occurred.

Another open question is the degree to which trait shifts depend on changes in functional group composition. Invasions in some ecosystems are characterized by shifts in dominance of functional groups, whereas in other ecosystems, key invaders belong to the same functional group as dominant natives. For instance, herbaceous grass and forb species commonly invade shrubland ecosystems throughout the western US (26) while woody trees and

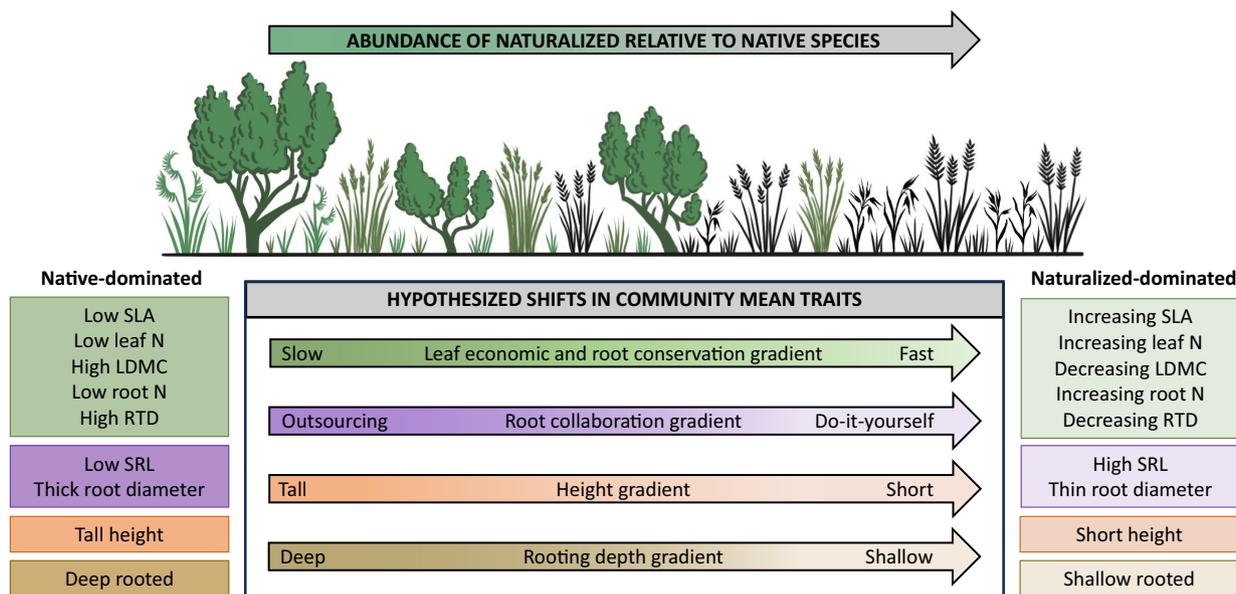


Fig. 1. Expectations for community-level shifts in traits associated with dominant axes of plant functional variation. We expect that increasing abundance of naturalized species will shift community functional composition toward the fast end of the aboveground and belowground conservation gradient, the do-it-yourself end of the collaboration gradient, and the short/shallow ends of the height and rooting depth gradients. Native species are shown in shades of green, whereas naturalized species are shown in black.

shrubs are common invaders in eastern US forests (28). We assessed how abundance and traits of herbaceous and woody species change along gradients of naturalized species abundance to help clarify to what extent trait shifts at the community-level are caused by shifts in functional group composition or by shifts in traits within functional groups.

Environmental conditions resulting from disturbance or other perturbations can promote the proliferation of species with specific traits, regardless of whether the species are native or not (48, 49). Because of this, environmental effects on overall functional composition may result from compositional changes in both native and naturalized species (47, 50). To disentangle the effects of naturalized species themselves and underlying environmental conditions on overall changes in functional composition, we examined differences between abundance-weighted traits of co-occurring naturalized and native species in the same sites. These analyses provide insight into whether trait differences between co-occurring native and nonnative species could account for community-level trait shifts. In addition, we assessed how abundance-weighted trait means of native and naturalized species change in relation to naturalized species abundance to determine whether traits of the two groups respond similarly to underlying environmental gradients.

Our data integration efforts resulted in over 50% of all species in SPCIS having available trait data (i.e., 5,757 of 11,258 species had associated data for at least one trait). However, global patterns of bias in trait availability were apparent in our dataset with high coverage of vegetative height (i.e., 3,958 species) and leaf economic traits (e.g., 3,513 species had SLA values) and considerably lower coverage of root traits (e.g., 1,409 species had rooting depth values). Because of these differences, only plots that had trait data available for species comprising at least 80% of the plot's abundance were included in analyses (51) (*SI Appendix, Figs. S1 and S2*). Our core analyses assessed how CWM traits of whole communities (i.e., including both native and naturalized species) changed along gradients of naturalized species abundance. In addition, we analyzed differences between abundance-weighted traits of co-occurring naturalized and native species within communities and trait shifts within native and naturalized species along gradients of naturalized species abundance. We also assessed how the proportion of herbaceous and woody species changed in relation to naturalized species abundance and how the abundance-weighted trait means of these two functional groups changed along gradients of naturalized species abundance.

Results

Shifts in Functional Composition. Across six distinct ecoregions spanning deserts, grasslands, and forests, plant communities with higher abundance of naturalized species were more acquisitive above and belowground, shorter, more shallowly rooted, and aligned with a do-it-yourself strategy for belowground resource acquisition (Figs. 2 and 3 and *SI Appendix, Table S1*). Differences between abundance-weighted traits of naturalized and native species within communities where they co-occurred were similar to patterns found along gradients of abundance; compared to co-occurring native species, naturalized species had more acquisitive leaf traits, were shorter and more shallowly rooted, and had higher SRL (Figs. 2 and 3 and *SI Appendix, Table S2*). Most abundance-weighted traits of naturalized and native species exhibited different mean values (Figs. 2 *G–L* and 3 *E–H*) and divergent relationships with naturalized species abundance (*SI Appendix, Fig. S3*). Further, increasing abundance of naturalized species was associated with greater proportions of herbaceous species (Fig. 4*A*). However, the abundance-weighted trait means of both woody and herbaceous species changed in similar directions to whole community shifts

along gradients of naturalized species abundance for most traits (Fig. 4 *B–G* and *SI Appendix, Fig. S4*).

Naturalized Species Lead to More Acquisitive Communities.

Consistent with our predictions, communities with higher abundance of naturalized species exhibited higher CWM SLA (Fig. 2*A*), leaf N (Fig. 2*C*), and lower LDMC (Fig. 2*B*). This general shift toward the acquisitive and fast end of the aboveground conservation gradient was also found within co-occurring native and naturalized species (SLA: Fig. 2*G*; LDMC: Fig. 2*H*; leaf N: Fig. 2*I* and *SI Appendix, Table S2*) and was remarkably consistent across ecoregions (*SI Appendix, Tables S1 and S2*), and within both woody and herbaceous functional groups (Fig. 4 *B* and *C* and *SI Appendix, Fig. S4A*). Patterns were similar in direction but nonsignificant for leaf P (Figs. 2*D* and 3*J* and *SI Appendix, Fig. S4B*). Mirroring aboveground patterns, communities with higher abundances of naturalized species exhibited higher CWM root N (Fig. 2*E*) and lower RTD (Fig. 2*F*), shifting functional community composition toward the acquisitive end of the root conservation gradient. However, these patterns were not consistent within communities or within woody and herbaceous functional groups. No differences between co-occurring native and naturalized species root N and RTD were observed (Fig. 2 *K* and *L*). Root N increased within both woody and herbaceous functional groups (Fig. 4*D*), but RTD decreased only within herbaceous species (*SI Appendix, Fig. S4C*) with increasing naturalized species abundance.

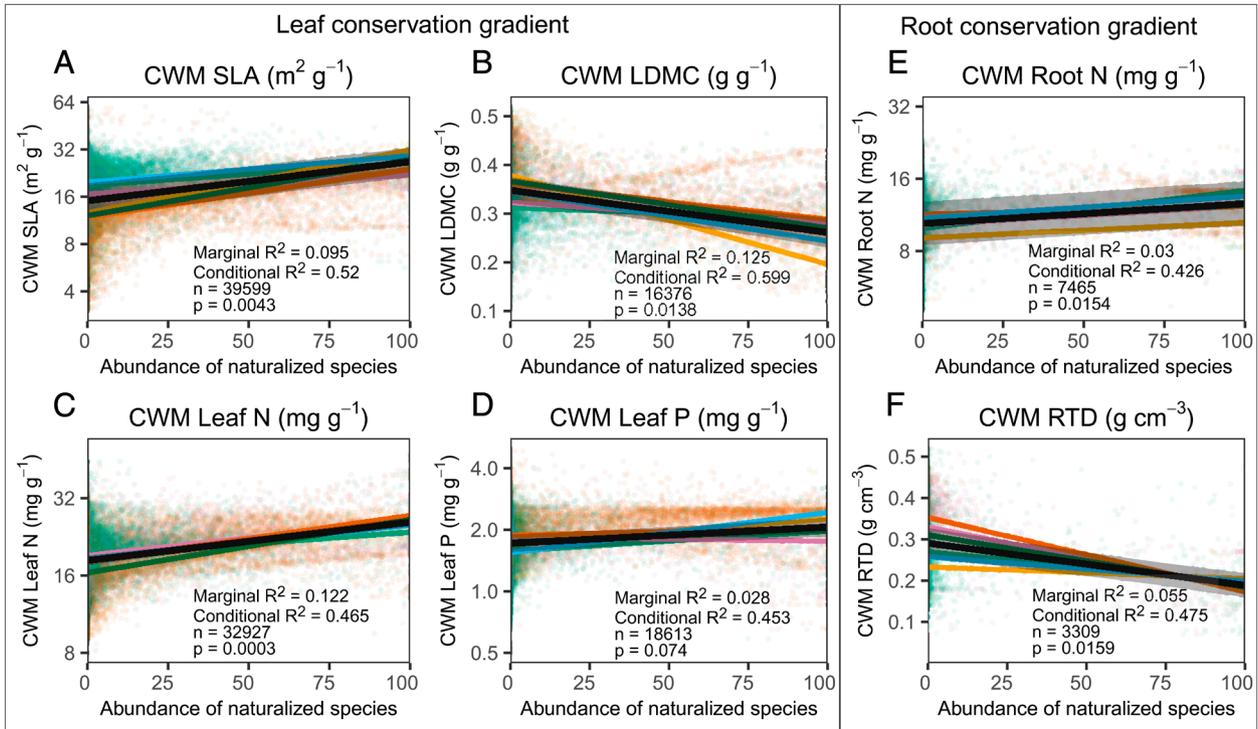
Naturalized Species Lead to Communities that are Shorter, Shallower, and Aligned with an Independent Strategy for Belowground Resource Acquisition.

Communities with higher abundance of naturalized species exhibited higher SRL (Fig. 3*A*) and lower root diameter (Fig. 3*B*). Within communities, naturalized species had higher abundance-weighted SRL than co-occurring natives (Fig. 3*E*) but did not differ in root diameter (Fig. 3*F*). SRL of both woody and herbaceous species increased with naturalized species abundance (Fig. 4*E*), but root diameter only decreased among herbaceous species (*SI Appendix, Fig. S4D*). We found that as the abundance of naturalized species increased, communities had shorter maximum height (Fig. 3*C*) and shallower maximum rooting depth (Fig. 3*D*). Similar patterns were present within communities: Compared to co-occurring natives, naturalized species were shorter (Fig. 3*G*) and more shallowly rooted (Fig. 3*H*) on average. Woody and herbaceous species showed opposite patterns in relation to aboveground and belowground size gradients; maximum height and rooting depth of woody species decreased whereas maximum height and rooting depth of herbaceous species increased with increasing abundance of naturalized species (Fig. 4 *F* and *G*).

Discussion

Our results demonstrate that differences between traits of native and naturalized species lead to predictable and consistent functional trait shifts in plant communities. Changes in environmental conditions caused by disturbances likely set the stage for altered community composition (52), but two key findings indicate that naturalized species drive changes in community-level functional traits: 1) substantial differences in abundance-weighted trait means of co-occurring naturalized and native species, and 2) unique changes in abundance-weighted trait means of native and naturalized species along gradients of naturalized species abundance. These shifts may underpin many of the impacts naturalized species have on ecosystem functions (3).

TRAIT SHIFTS ALONG GRADIENTS OF NATURALIZED SPECIES ABUNDANCE



TRAIT DIFFERENCES BETWEEN CO-OCCURRING NATURALIZED AND NATIVE SPECIES

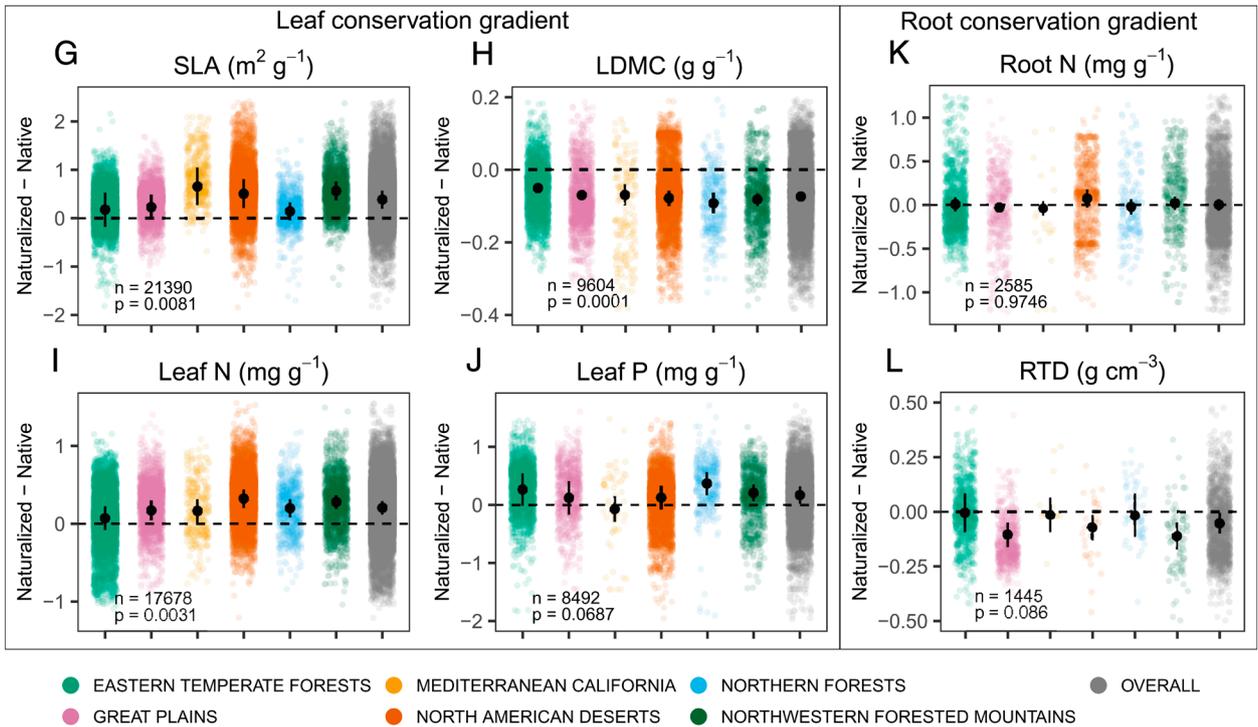
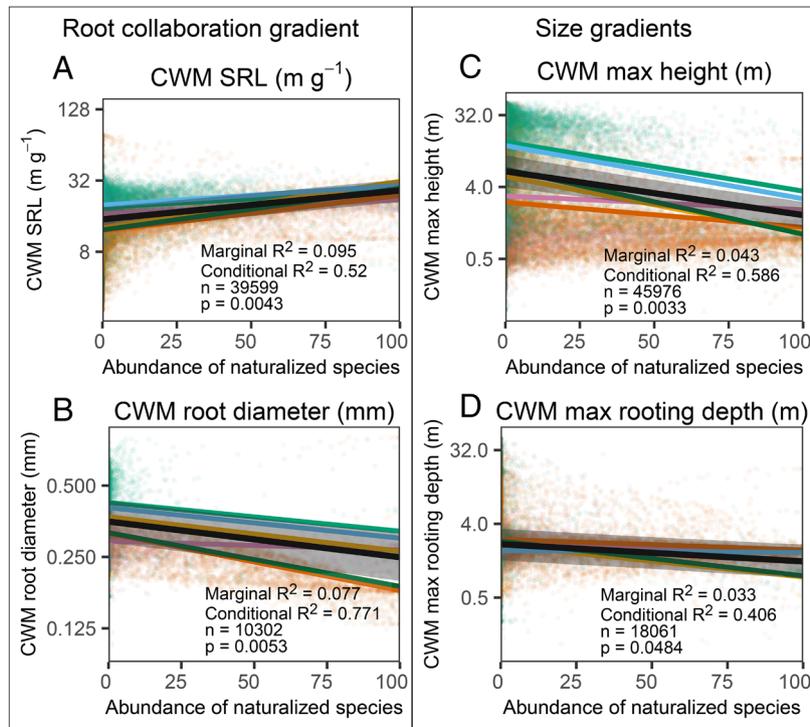


Fig. 2. Communities become more acquisitive as the abundance of naturalized species increases. Panels (A–F): In plots (points) with greater relative abundance of naturalized species, CWM traits shift toward the fast and acquisitive end of the leaf and root conservation gradients (colored lines show model predictions for EPA Level 1 ecoregions, black lines show model predictions across all ecoregions, and gray ribbons show prediction intervals for the overall relationship across all ecoregions). In plots where they cooccur, naturalized species have more acquisitive abundance-weighted leaf and root traits than native species (panels G–L). Small points show within-plot differences between abundance-weighted traits of naturalized and native species, large black points show the mean difference between the groups (± 2 SD).

Like patterns found at individual sites (40–44), we show that the establishment and proliferation of naturalized species with acquisitive leaf and root traits results in communities that align with the fast end of the aboveground and belowground conservation gradient. These

results fit with previous observations of acquisitive traits among naturalized species (9–11, 20) and may arise from biases in the types of species that people tend to introduce, such as those associated with agriculture or other human-modified landscapes (53). The



TRAIT DIFFERENCES BETWEEN CO-OCCURRING NATURALIZED AND NATIVE SPECIES

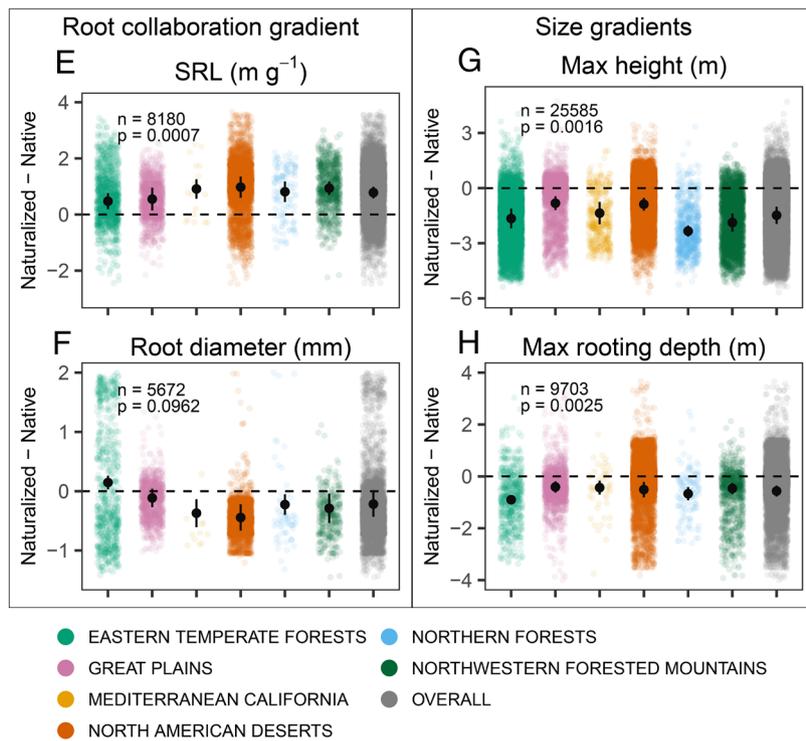


Fig. 3. Communities become shorter, more shallowly rooted, and aligned with the do-it-yourself end of the root collaboration gradient as the abundance of naturalized species increases. Panels (A–D): In plots (points) with greater relative abundance of naturalized species, CWM traits shift toward the do-it-yourself end of the root collaboration gradient and the short/shallow ends of the height and rooting depth gradients (colored lines show model predictions for EPA Level 1 ecoregions, black lines show model predictions across all ecoregions, and gray ribbons show prediction intervals for the overall relationship across all ecoregions). In plots where they cooccur, naturalized species have higher SRL, are shorter, and more shallowly rooted than native species (panels E–H). Small points show within-plot differences between abundance-weighted traits of naturalized and native species, large black points show the mean difference between the groups (± 2 SD).

replacement of native species that have long-lived conservative leaves by naturalized species that have short-lived acquisitive leaves likely contributes to observed trends of increased nutrient cycling, litter

decomposition, and aboveground net primary production in communities dominated by naturalized plant species (29, 33, 34, 39). Although research on root traits is more scarce, similar dynamics may

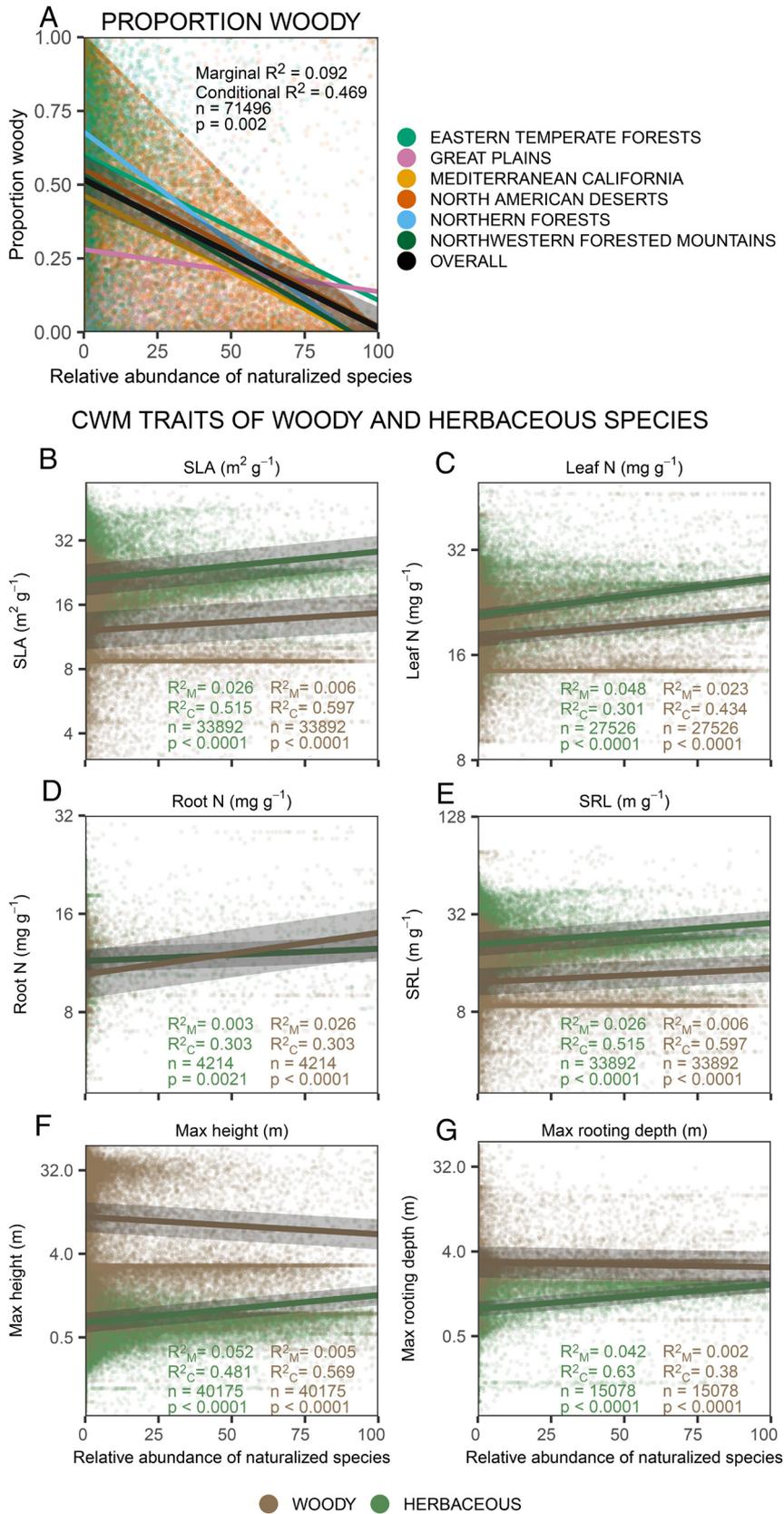


Fig. 4. With increasing abundance of naturalized species, communities become increasingly dominated by herbaceous plants and traits of both woody and herbaceous species shift, often in similar directions. Panel (A): In plots (points) with greater abundance of naturalized species, herbaceous species become more dominant (colored lines show model predictions for EPA Level 1 ecoregions, black lines show model predictions across all ecoregions, and gray ribbons show prediction intervals for the overall relationship across all ecoregions). Panels (B–E): Abundance-weighted means traits of woody species (brown points) and herbaceous species (green points) respond similarly to gradients of naturalized species abundance for (A) specific leaf area, (B) leaf nitrogen concentration, (C) root nitrogen concentration, and (D) specific root length. Panels (F and G): As the abundance of naturalized species increases, woody species (brown points) become shorter and more shallowly rooted whereas herbaceous species (green points) become taller and more deeply rooted.

occur belowground: naturalized plants with high root nitrogen concentrations and low root tissue densities likely promote rapid nutrient cycling and decomposition (54).

Our work supports emerging evidence that naturalized species, and the communities they dominate, are positioned toward the do-it-yourself end of the root collaboration gradient. Trait values associated with this independent strategy of resource acquisition have been documented for naturalized species established in desert (19, 22), grassland (23, 55, 56), and forest (16, 17, 57) communities across the continental United States. Where community-level functional composition has been assessed, researchers have found increased CWM SRL and reduced CWM root diameter with increasing abundance of naturalized species (58). Further, experimental and synthesis research has found that invasive species often benefit less from mycorrhizal symbionts than natives (57, 59). Our findings provide additional support for the notion that differences in root collaboration traits between native and naturalized species scale to the community level and may result in plant assemblages with reduced dependency on mycorrhizal symbionts. These community-level shifts may help explain the myriad effects naturalized species have on the diversity of soil biota (60) and associated soil processes (54).

Higher proportions of herbaceous species likely contribute to the trend of highly invaded communities being shorter and more shallowly rooted than communities with low abundance of naturalized species (see additional discussion below). Short, shallowly rooted invasive species commonly invade deserts and shrubland ecosystems (26, 27, 57) and understory grasses, forbs, and shrubs that are shorter and more shallowly rooted than dominant trees, are common invaders in eastern forests (28). Given that nutrient, water, and carbon cycling are influenced by numerous belowground traits (54), shifts in belowground functional composition may lead to myriad widespread impacts. For instance, increased establishment of short, shallow-rooted naturalized species likely contributes to reductions in carbon storage documented in invaded systems throughout western US rangelands (35) and eastern US forests (61) and may drive observed trends of increased water utilization in upper soil layers (36) and reduced nutrient utilization in deep soil layers (32) in grassland systems.

Trait differences between native and naturalized species likely account for much of the shift in community-level traits, but environmental gradients that select for specific functional strategies in both native and naturalized species pools likely also contribute to community-level changes in functional composition. For example, acquisitive leaf traits underpin abundance increases of both native and naturalized species responding to nutrient enrichment (49). Our results suggest that naturalized species can both drive and respond to ecological change (47). Naturalized species appear to drive shifts in community-level leaf traits including SLA, LDMC, leaf N, and leaf P (*SI Appendix, Fig. S3 A–D*) but underlying environmental gradients appear to select for similar root N and RTD in both native and naturalized species (*SI Appendix, Fig. S3 E–F*). As in other continental scale analyses (50, 62), we could not fully account for the role of local disturbances and environmental conditions. Data on human disturbance (63) and changing environmental conditions (64) at local scales are essential to more accurately quantify the interactive effects of invasive species and environmental conditions on changing plant communities and ecosystems.

Trends in functional composition also appear to be influenced by two mechanisms: 1) a general shift toward herbaceous-dominated communities (52) and 2) trait shifts within woody and herbaceous functional groups. Many of the naturalized species documented in SPCIS are herbaceous (46). For example, nonnative annual

grasses are ubiquitous invaders in arid and semiarid shrublands of the western US (26). Other common herbaceous species in the database include *Alliaria petiolata* (i.e., garlic mustard) and *Microstegium vimineum* (stiltgrass), which are highly abundant in forests in the eastern US (65). These and other key invaders drive general shifts toward herbaceous-dominated communities, which contributes to changes in functional community composition and shifts the structure of the ecosystems toward lower-stature vegetation. However, trait shifts within woody and herbaceous functional groups also contributed to functional composition at the community level. For example, increases in root N were observed within both herbaceous and woody species, suggesting that community-level shifts can be attributed primarily to trait shifts within functional groups. Our results indicate that both mechanisms drive community-level functional change but their importance varies by trait.

Clarifying the consequences of species introductions on community-level traits is a critical first step toward linking changes in community composition to changes in ecosystem function. Our results demonstrate that shifts in functional composition stemming from trait differences between native and naturalized species are widespread and consistent across several ecosystem types. As a consequence of these trait shifts, changes to ecosystem functions are likely also widespread. Being able to identify such shifts in community composition may provide new and efficient means for anticipating whether invasion by specific species will lead to associated changes in ecosystem function. Detecting these shifts in community functional composition from local to regional scales would advance our ability to conserve and manage communities and ecosystem functions threatened by naturalized and invasive species.

Methods

The SPCIS database (46) combines and harmonizes compositional data from over 80,000 vegetation monitoring plots from the United States and Puerto Rico. It integrates the National Ecological Observatory Network (66–68) data, Bureau of Land Management Assessment and Monitoring data, the Forest Inventory and Analyses data along with other smaller datasets. In addition to comparable information on occurrence and abundance, the database also provides native status of species; 10,227 species are listed as native and 1,235 species are listed as introduced/naturalized. We chose to work with plots from the following six well-represented, EPA Ecoregions (i.e., Eastern Temperate Forests, Great Plains, Mediterranean California, North American Deserts, Northern Forests, and Northwestern Forested Mountains) and excluded plots from Puerto Rico and Alaska. This resulted in 75,287 plots for which we gathered associated species-level trait data.

We integrated SPCIS community compositional data with leaf, root, and size traits from several databases (69–71). We obtained observation-level values for SLA, LDMC, leaf N, leaf P, and height from TRY (69). Species-level root diameter, root N, RTD, and SRL data were obtained from the Global Root Trait (GRooT) database (70), and data for rooting depth were obtained from GRooT and the Root Systems of Individual Plants Database (RSIP) (71). For all trait values obtained from the TRY database besides maximum plant height, we first calculated study-level means for each species and then calculated species-level means using study-level means. Maximum height and maximum rooting depth were estimated as the 97.5% quantile of all available values in the databases for each species to avoid the effects of outliers. For species that occurred in over 5,000 plots but had less than three associated values for a specific trait available in databases, we extracted additional values from published literature, which resulted in the addition of 72 trait values for 28 species to our dataset.

To quantify shifts in functional composition with increasing abundance of naturalized species, we calculated CWM traits for plots that had trait data available for species comprising at least 80% of the plot's abundance (51). CWM traits for each plot were calculated as the mean species-level trait value weighted by species' relative abundances. For plots with greater than 80% but less than 100% trait coverage, we

relativized CWM to include only those species for which trait data were available. This resulted in different numbers of plots used for specific trait analyses. Nearly 46,000 plots were included in analyses of maximum height but only 3,300 plots were included in analyses for root tissue density. The number of plots included in each analysis are provided in all figures, supplementary maps (SI Appendix, Figs. S1 and S2) and in supplementary tables (SI Appendix, Tables S1 and S2). We used linear mixed-effects models to assess relationships between naturalized species abundance and CWM traits. In these models, CWM traits were included as response variables, the scaled proportion of naturalized species was included as a fixed effect, EPA Level 1 ecoregions (n = 6) were included as random effects with varying intercepts and slopes, and EPA Level 4 ecoregions (n = 748) were included as random intercepts. We included these smaller EPA Level 4 ecoregions in our models to account for variation arising from differences in ecosystem type.

To compare the average traits of co-occurring native and naturalized species, we calculated abundance-weighted traits for native and naturalized species from within the same communities. We did this by weighting species-level trait values by species' relative abundances for each of the two groups. The difference in these values was used as the response variable in mixed effects models that included native status as a fixed effect, and a random effect of EPA Level 4 ecoregions nested within EPA Level 1 ecoregion (SI Appendix, Table S2). We used linear mixed effects models to assess relationships between naturalized species abundance and abundance-weighted means of woody and herbaceous species, and abundance-weighted means of native and naturalized species. Only plots with both native and naturalized species or both woody and herbaceous species present were included in these analyses. In these models, abundance-weighted means of specific groups (i.e., woody or herbaceous species, native or naturalized species) were included as response variables, the scaled proportion of naturalized species was included as a fixed effect, and EPA Level 1 ecoregions and EPA Level 4 ecoregions were included as random effects.

CWM values and abundance-weighted traits for SLA, leaf N, leaf P, maximum height, maximum rooting depth, root diameter, SRL, and root N concentration were log-transformed prior to all analyses. All data integration, statistical analyses, and data visualization were performed using R (72) v. 4.0.0 and the following

1. M. van Kleunen *et al.*, Global exchange and accumulation of non-native plants. *Nature* **525**, 100–103 (2015).
2. H. Seebens *et al.*, No saturation in the accumulation of alien species worldwide. *Nat. Commun.* **8**, 14435 (2017).
3. J. G. Ehrenfeld, Ecosystem consequences of biological invasions. *Annu. Rev. Ecol. Syst.* **41**, 59–80 (2010).
4. M. Vilà *et al.*, Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* **14**, 702–708 (2011).
5. P. Pyšek *et al.*, A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biol.* **18**, 1725–1737 (2012).
6. S. Lavorel, E. Garnier, Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Funct. Ecol.* **16**, 545–556 (2002).
7. K. N. Suding *et al.*, Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biol.* **14**, 1125–1140 (2008).
8. A. Weigelt *et al.*, An integrated framework of plant form and function: The belowground perspective. *New Phytol.* **232**, 42–59 (2021).
9. M. V. Kleunen, E. Weber, M. Fischer, A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.* **13**, 235–245 (2010).
10. A. Ordoñez, I. J. Wright, H. Olff, Functional differences between native and alien species: A global-scale comparison. *Funct. Ecol.* **24**, 1353–1361 (2010).
11. M. R. Leishman, T. Haslehurst, A. Ares, Z. Baruch, Leaf trait relationships of native and invasive plants: Community- and global-scale comparisons. *New Phytol.* **176**, 635–643 (2007).
12. I. J. Wright, P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, The worldwide leaf economics spectrum. *Nature* **428**, 821–827 (2004).
13. M. S. Smith, J. D. Fridley, M. Goebel, T. L. Bauerle, Links between belowground and aboveground resource-related traits reveal species growth strategies that promote invasive advantages. *Plos One* **9**, e104189 (2014).
14. H. Liu *et al.*, Root plasticity benefits a global invasive species in eutrophic coastal wetlands. *Funct. Ecol.* **38**, 165–178 (2024), 10.1111/1365-2435.14452.
15. A. J. Leffler, J. J. James, T. A. Monaco, Temperature and functional traits influence differences in nitrogen uptake capacity between native and invasive grasses. *Oecologia* **171**, 51–60 (2012).
16. J. S. Caplan, S. J. Meiners, H. Flores-Moreno, M. L. McCormack, Fine-root traits are linked to species dynamics in a successional plant community. *Ecology* **100**, e02588 (2019).
17. I. Jo, J. D. Fridley, D. A. Frank, Linking above- and belowground resource use strategies for native and invasive species of temperate deciduous forests. *Biol. Invasions* **17**, 1545–1554 (2015).
18. J. S. Caplan *et al.*, Nutrient foraging strategies are associated with productivity and population growth in forest shrubs. *Ann. Botany* **119**, 977–988 (2017).
19. A. J. Leffler, J. J. James, T. A. Monaco, R. L. Shelley, A new perspective on trait differences between native and invasive exotic plants. *Ecology* **95**, 298–305 (2014).

R packages: TNRS (73), lme4 (74), lmerTest (75), MuMIN (76), merTools (77), ggplot (78), and cowplot (79). All data and code used for analyses can be found in the associated Figshare repository (80).

Data, Materials, and Software Availability. Data have been deposited in Figshare (10.6084/m9.figshare.25215338) (80). Previously published data were used for this work (46, 69–71).

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20. J. G. Díaz, M. Vilà, I. M. Parker, E. G. Riva, Functional assembly of grassland plant species in native communities in Spain and recipient communities in California. *J. Ecol.* **111**, 214–226 (2023).
21. P. B. Reich, The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *J. Ecol.* **102**, 275–301 (2014).
22. J. T. Arredondo, D. A. Johnson, Root architecture and biomass allocation of three range grasses in response to nonuniform supply of nutrients and shoot defoliation. *New Phytol.* **143**, 373–385 (1999).
23. J. L. Funk, A. A. Wolf, Testing the trait-based community framework: Do functional traits predict competitive outcomes? *Ecology* **97**, 2206–2211 (2016).
24. J. Divišek *et al.*, Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. *Nat. Commun.* **9**, 4631 (2018).
25. S. L. Young, G. B. Kyser, J. N. Barney, V. P. Claassen, J. M. DiTomaso, Spatio-temporal relationship between water depletion and root distribution patterns of centaurea solstitialis and two native perennials. *Restoration Ecol.* **18**, 323–333 (2010).
26. M. J. Germino, J. Belpap, J. M. Stark, E. B. Allen, B. M. Rau "Ecosystem impacts of exotic annual invaders in the genus bromus" in *Exotic Bromo-Grasses in Arid and Semiarid Ecosystems of the Western US* (2016), pp. 61–95.
27. J. L. Funk, R. J. Standish, W. D. Stock, F. Valladares, Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. *Ecology* **97**, 75–83 (2016).
28. J. D. Fridley, Of Asian forests and european fields: eastern U.S. plant invasions in a global floristic context. *PLoS ONE* **3**, e3630 (2008).
29. M. R. Lee *et al.*, Invasive species' leaf traits and dissimilarity from natives shape their impact on nitrogen cycling: A meta-analysis. *New Phytol.* **213**, 128–139 (2017).
30. V. G. Balogianni, S. D. Wilson, R. E. Farrell, A. S. MacDougall, Rapid root decomposition decouples root length from increased soil C following grassland invasion. *Ecosystems* **18**, 1307–1318 (2015).
31. J. Ehrenfeld, Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6**, 503–513 (2003).
32. E. W. Seabloom, W. S. Harpole, O. J. Reichman, D. Tilman, Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl. Acad. Sci. U.S.A.* **100**, 13384–13389 (2003).
33. P. Castro-Diez, O. Godoy, A. Alonso, A. Gallardo, A. Saldaña, What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. *Ecol. Lett.* **17**, 1–12 (2014).
34. C. Liao *et al.*, Altered ecosystem carbon and nitrogen cycles by plant invasion: A meta-analysis. *New Phytol.* **177**, 706–714 (2008).
35. R. C. Nagy *et al.*, A synthesis of the effects of cheatgrass invasion on US Great Basin carbon storage. *J. Appl. Ecol.* **58**, 327–337 (2021).
36. M. Garbowski, D. B. Johnston, D. V. Baker, C. S. Brown, Invasive annual grass interacts with drought to influence plant communities and soil moisture in dryland restoration. *Ecosphere* **12**, e03417 (2021).
37. M. Vasquez-Valderrama, M.R. González, R. López-Camacho, M.P. Baptiste, B. Salgado-Negret, Impact of invasive species on soil hydraulic properties: Importance of functional traits. *Biol. Invasions* **22**, 1849–1863 (2020).

38. O. Godoy, P. Castro-Díez, R. S. P. Van Logtestijn, J. H. C. Cornelissen, F. Valladares, Leaf litter traits of invasive species slow down decomposition compared to Spanish natives: A broad phylogenetic comparison. *Oecologia* **162**, 781–790 (2010).
39. K. Helsen *et al.*, Impact of an invasive alien plant on litter decomposition along a latitudinal gradient. *Ecosphere* **9**, e02097 (2018).
40. G. Fried, M. Carboni, L. Mahaut, C. Violle, Functional traits modulate plant community responses to alien plant invasion. *J. PPEES Sources* **37**, 53–63 (2019).
41. D. S. Sodhi, S. W. Livingstone, M. Carboni, M. W. Cadotte, Plant invasion alters trait composition and diversity across habitats. *Ecol. Evol.* **67**, 1–12 (2019).
42. R. D. Fernandez, P. Castro-Díez, R. Aragón, N. Pérez-Harguindeguy, Changes in community functional structure and ecosystem properties along an invasion gradient of *Ligustrum lucidum*. *J. Vegetation Sci.* **32**, e13098 (2021).
43. C. Liu *et al.*, Effects of the invasive leafy spurge (*Euphorbia esula* L.) on plant community structure are altered by management history. *NeoBiota* **81**, 157–182 (2023).
44. E. Forey *et al.*, Alien palm invasion leads to selective biotic filtering of resident plant communities towards competitive functional traits. *Biol. Invasions* **25**, 1489–1508 (2023).
45. J. M. Omerik, G. E. Griffith, Ecoregions of the conterminous United States: Evolution of a hierarchical spatial framework. *Environ. Management* **54**, 1249–1266 (2014).
46. L. Petri *et al.*, SPCIS: Standardized plant community with introduced status database. *Ecology* **104**, e3947 (2023).
47. A. MacDougall, R. Turkington, Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* **86**, 42–55 (2016).
48. W. Dawson, M. Fischer, M. van Kleunen, Common and rare plant species respond differently to fertilization and competition, whether they are alien or native. *Ecol. Lett.* **15**, 873–880 (2012).
49. A. A. Broadbent *et al.*, Dominant native and non-native graminoids differ in key leaf traits irrespective of nutrient availability. *Global Ecol. Biogeography* **29**, 1126–1138 (2020).
50. E. M. Beaury *et al.*, Macroscale analyses suggest invasive plant impacts depend more on the composition of invading plants than on environmental context. *Global Ecol. Biogeography* **32**, 1964–1976 (2023).
51. R. J. Pakeman, H. M. Quested, Sampling plant functional traits: What proportion of the species need to be measured? *Appl. Vegetation Sci.* **10**, 91–96 (2007).
52. I. Jo *et al.*, Disturbance-mediated community characteristics and anthropogenic pressure intensify understory plant invasions in natural forests. *J. Ecol.* **112**, 1856–1871 (2024).
53. A. S. MacDougall *et al.*, The neolithic plant invasion hypothesis: The role of preadaptation and disturbance in grassland invasion. *New Phytol.* **220**, 94–103 (2018).
54. R. D. Bardgett, L. Mommer, F. T. D. Vries, Going underground: Root traits as drivers of ecosystem processes. *Trends in Ecol. Evol.* **29**, 692–699 (2014).
55. J. E. Larson, J. L. Funk, Seedling root responses to soil moisture and the identification of a belowground trait spectrum across three growth forms. *New Phytol.* **210**, 827–838 (2016).
56. T. H. Holmes, K. Rice, Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. *Ann. Bot.* **78**, 233–243 (1996).
57. A. R. Ebert, D. A. Frank, J. D. Fridley, Contrasting mycorrhizal growth responses in native and invasive woody species are associated with distinct root trait syndromes. *Funct. Ecol.* **37**, 2312–2324 (2023).
58. C. Liu *et al.*, Effects of the invasive leafy spurge (*Euphorbia esula* L.) on plant community structure are altered by management history. *NeoBiota* **81**, 157–182 (2023).
59. R. A. Bunn, P. W. Ramsey, Y. Lekberg, Do native and invasive plants differ in their interactions with arbuscular mycorrhizal fungi? A meta-analysis. *J. Ecol.* **103**, 1547–1556 (2015).
60. P. Zhang, B. Li, J. Wu, S. Hu, Invasive plants differentially affect soil biota through litter and rhizosphere pathways: A meta-analysis. *Ecol. Lett.* **22**, 200–210 (2019).
61. M. S. Strickland, J. L. Devore, J. C. Maerz, M. A. Bradford, Grass invasion of a hardwood forest is associated with declines in belowground carbon pools. *Global Change Biol.* **16**, 1338–1350 (2010).
62. H. Bruelheide *et al.*, Global trait-environment relationships of plant communities. *Nat. Ecol. Evol.* **2**, 1906–1917 (2018).
63. D. M. Theobald *et al.*, Earth transformed: Detailed mapping of global human modification from 1990 to 2017. *Earth System Sci. Data* **12**, 1953–1972 (2020).
64. F. J. Dentener, Global Maps of Atmospheric Nitrogen Deposition, 1860, 1993, and 2050 (ORNL DAAC, Oak Ridge, Tennessee, USA, 2006).
65. V. L. Rogers *et al.*, Where is garlic mustard? Understanding the ecological context for invasions of *Alliaria petiolata*. *BioScience* **72**, 521–537 (2022).
66. NEON (National Ecological Observatory Network). Plant presence and percent cover (DP1.10058.001), PROVISIONAL (2020a). <https://data.neonscience.org/data-products/DP1.10058.001>. Accessed 1 May 2020. Data archived at [10.1002/ecy.3947].
67. NEON (National Ecological Observatory Network). Non-herbaceous perennial vegetation structure (DP1.10045.001), PROVISIONAL (2020b). <https://data.neonscience.org/data-products/DP1.10045.001>. Accessed 1 May 2020. Data archived at [10.1002/ecy.3947].
68. NEON (National Ecological Observatory Network). Vegetation structure (DP1.10098.001), PROVISIONAL (2020c). <https://data.neonscience.org/data-products/DP1.10098.001>. Accessed 1 May 2020. Data archived at [10.1002/ecy.3947].
69. J. Kattge *et al.*, TRY plant trait database – enhanced coverage and open access. *Global Change Biol.* **26**, 119–188 (2020).
70. N. R. Guerrero-Ramírez *et al.*, Global root traits (GRooT) database. *Global Ecol. Biogeogr.* **30**, 25–37 (2021).
71. S. J. Tumber-Dávila, H. J. Schenk, E. Du, R. B. Jackson, Plant sizes and shapes above and belowground and their interactions with climate. *New Phytol.* **235**, 1032–1056 (2022).
72. R Core Team. R: A language and environment for statistical computing. (R Foundation for Statistical Computing, Vienna, Austria, 2019) URL <https://R-project.org/>
73. B. Maitner, B. Boyle, TNRS: Taxonomic name resolution service (R package version 0.3.4 2023).
74. D. Bates, M. Maechler, B. Bolker, S. Walker, Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
75. A. Kuznetsova, P. B. Brockhoff, R. H. B. Christensen, lmerTest Package: Tests in linear mixed effects models. *J. Stat. Softw.* **82**, 1–26 (2017).
76. K. Barton, MuMIn: Multi-Model Inference (R package version 1.48.4 2023). <https://cran.r-project.org/web/packages/MuMIn/index.html>. Accessed 11 August 2024.
77. J. E. Knowles, C. Frederick, merTools: Tools for analyzing mixed effect regression models (R package version 0.6.2 2023). <https://cran.r-project.org/web/packages/merTools/index.html>. Accessed 11 August 2024.
78. H. Wickham, *ggplot2: Elegant Graphics for Data Analysis* (Springer-Verlag, New York, 2016).
79. C. Wilke, cowplot: Streamlined plot theme and plot annotations for 'ggplot2' (R package version 1.1.3 2020). <https://cran.r-project.org/web/packages/cowplot/index.html>. Accessed 11 August 2024.
80. M. Garbowski, Data associated with the manuscript "Naturalized species drive functional trait shifts in plant communities". Figshare. <https://doi.org/10.6084/m9.figshare.25215338>. Deposited 11 August 2024.