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Non-native plants erode the stabilizing effects of biodiversity

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Title: Non-native plants erode the stabilizing effects of biodiversity

Running title: Plant invasion weakens biodiversity–stability relationships

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Abstract: Biodiversity is widely expected to stabilize ecosystem functioning [1-6], but the stabilizing effect likely depends on which species constitute biodiversity. The global proliferation of non-native species is fundamentally reshaping ecological communities worldwide [7-12], but whether these compositional changes undermine biodiversity's stabilizing role remains unresolved. Using plant community data from 142 terrestrial sites across the world and more than 11,000 local communities, we show that, compared with native plants, non-native plants weaken positive diversity–stability relationships across broad environmental gradients. Increasing non-native dominance shifts local plant communities from conservative toward more acquisitive resource-use strategies. This functional reorganization weakens the pathway through which diversity stabilizes constituent populations and thereby supports community stability, while leaving compensatory dynamics among species (species asynchrony) comparatively less affected. These findings show that native and non-native species are not functionally equivalent in their contributions to community stability, cautioning against treating non-native species as functional substitutes for native biodiversity. Our results highlight a previously underappreciated consequence of plant invasion: by altering community functional composition and disrupting the mechanisms through which diversity promotes stability, non-native species can undermine the stabilizing role of biodiversity. Limiting the spread and dominance of non-native species may therefore be critical not only for conserving native biodiversity, but also for safeguarding the capacity of plant communities to sustain ecosystem functioning under ongoing environmental change.

Keywords: biodiversity–stability relationship; plant invasion; functional traits; population stability; species asynchrony; temporal stability; Nutrient Network; NEON

Introduction

Decades of theoretical and empirical research have established that biodiversity can stabilize ecosystem functioning over time [1-6]. Yet the strength, and potentially even the direction, of this effect are contingent on community composition, depending not only on how many species are present but also on which species constitute the community [3,6,13-15]. Much evidence for biodiversity-mediated stability, however, comes from plant communities dominated by native species, or from studies that do not distinguish species by provenance status [1,2,5,15]. It is thus unclear whether native and non-native species affect ecosystem stability in the same way. As biological invasions escalate worldwide [7,16,17], this uncertainty is increasingly consequential: will biodiversity continue to stabilize ecosystem function when plant communities are increasingly dominated by non-native species?

The temporal stability of ecosystem functioning, commonly quantified as the temporal mean of ecosystem function divided by its temporal standard deviation [1,2,18], can arise through two complementary pathways: population stability and species asynchrony. Population stability reflects the degree to which constituent populations maintain stable dynamics through time, whereas species asynchrony captures the extent to which temporal declines in some species are compensated by increases in others [3,6,15,18-21]. Biodiversity can therefore stabilize aggregate ecosystem functioning by increasing population stability, by promoting compensatory dynamics among species, or both [6,15]. Functional traits provide a mechanistic link between community composition and these two pathways by shaping resource acquisition, niche differentiation and responses to environmental variation, thereby influencing both the temporal variability of individual populations and the covariance of fluctuations among species [22-25]. Species' functional strategies may therefore determine how

strongly biodiversity acts through population stability and species asynchrony [6,23].

It is well established that many non-native plants have fast trait syndromes associated with rapid resource acquisition, growth, dispersal and phenotypic plasticity [8-10,26]. Non-native plant establishment and accumulation can correspondingly shift invaded communities from conservative toward more acquisitive functional strategies [8-10]. This invasion-driven functional reorganization of communities could alter the relationship between community diversity and ecosystem stability by changing how biodiversity promotes population stability or species asynchrony. If non-native species contribute less than native species to population stability and species asynchrony, non-native invasion may weaken biodiversity's stabilizing effect on ecosystem functioning even if community richness remains the same. Disentangling these pathways is therefore essential for revealing how non-native plants alter the mechanisms through which biodiversity stabilizes ecosystem functioning.

Here, we address this knowledge gap by integrating time series from two vegetation monitoring networks: the U.S. National Ecological Observatory Network (NEON) and the global Nutrient Network (NutNet). For each network, we classified plant species as native or non-native using curated taxonomic sources and compiled species-level data for seven functional traits (Supplementary Table 1). Collectively, the two networks encompass 142 terrestrial sites and more than 11,000 local plant communities, each of which was surveyed for at least three years, enabling a coordinated test of how non-native plants modify biodiversity–stability relationships across broad environmental and biogeographic gradients (Fig. 1; Supplementary Tables 2 and 3). Applying the same analytical framework independently to each network, we ask whether non-native species weaken the stabilizing effect of biodiversity on ecosystem functioning and if so, whether this weakening can be traced

to shifts in community functional composition that alter biodiversity's contributions to population stability and species asynchrony (Fig. 1).

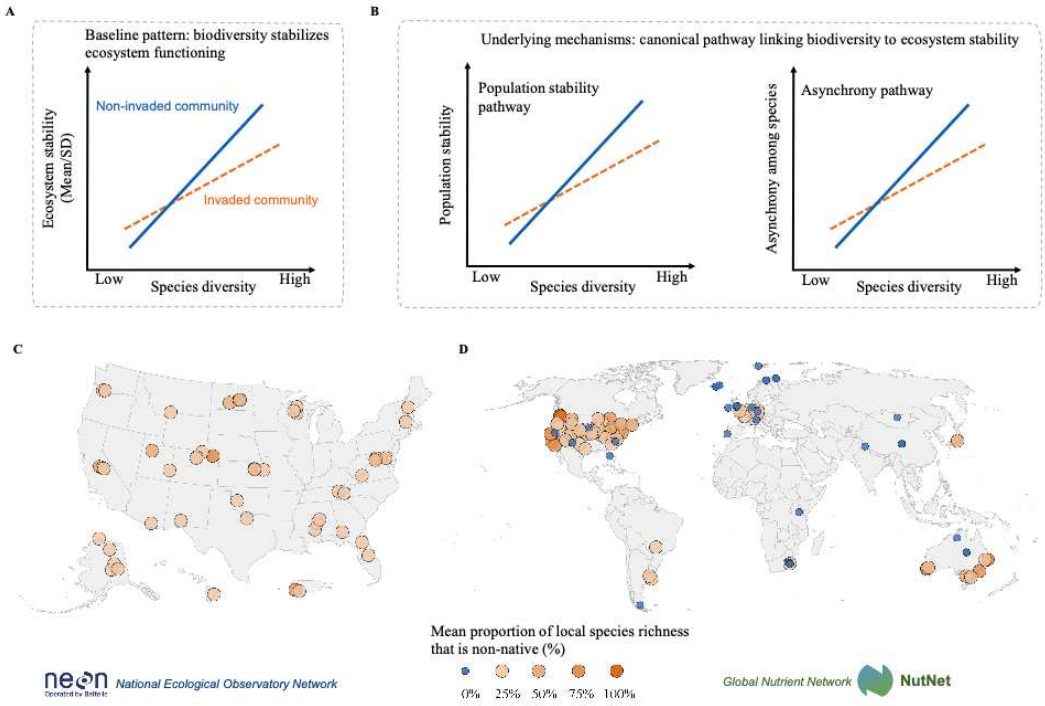


Figure 1. Conceptual framework for how non-native plants alter biodiversity–stability relationships and spatial distribution of study sites. (**A**) Hypothesized biodiversity–stability relationships in non-invaded and invaded plant communities. Temporal community stability is quantified as the temporal mean of aggregate community functioning divided by its temporal standard deviation (SD). The presence and increasing prevalence of non-native species are predicted to weaken the positive effect of biodiversity on community stability by altering the two mechanisms through which diversity stabilizes aggregate community functioning: population stability and species asynchrony. (**B**) Canonical pathways linking biodiversity to community stability. Biodiversity is expected to stabilize aggregate community functioning through two primary pathways: the population-stability pathway, whereby diversity increases the temporal stability of constituent populations, and the species-asynchrony pathway, whereby asynchronous fluctuations generate compensatory dynamics among species. (**C and D**) Spatial distribution of the 142 study sites in the U.S. National Ecological Observatory Network (NEON) and the global Nutrient Network (NutNet). Invasion status was defined at the site level: sites were classified as invaded if a non-native species was recorded in at least one sampled community during the study period, and otherwise as non-invaded. Multi-year plant

community records from the two networks were analyzed separately within a common analytical framework, providing independent tests across broad environmental gradients.

Results

In both datasets, the presence of non-native species significantly weakened the positive relationship between species diversity and the temporal stability of ecosystem functioning (Fig. 2; Supplementary Fig. S1; $P < 0.001$ for both datasets). This destabilizing effect was further confirmed by an independent slope-comparison analysis within invaded communities: diversity–stability slopes were significantly shallower when stability was calculated using all species than when it was calculated using native species only (Supplementary Fig. S2; $P < 0.001$ for both datasets). This pattern persisted after excluding all US sites from the NutNet dataset, leaving 199 local communities across 50 non-US sites (Supplementary Fig. S3).

To understand the basis of this weakening, we decomposed community-level stability into its temporal mean and temporal standard deviation (SD) components and estimated the effect of species diversity on each component separately. We then mapped these standardized effects into a two-dimensional mean–variability space. Native-only and invaded communities occupied distinct regions in this space (Fig. 2A, C), indicating that non-native species systematically altered how species diversity influenced the two basic components of stability. In invaded communities, diversity exhibited a reduced capacity to increase the temporal mean and/or dampen temporal variability, resulting in a weaker net stabilizing effect (Fig. 2; Supplementary Fig. S1). This destabilization scaled with invasion intensity: the stabilizing effect of species diversity declined progressively as the relative abundance of non-native species increased (Supplementary Fig. S4). These patterns were robust to alternative

minimum observation-length thresholds and held across both binary (i.e., presence/absence) and continuous (intensity) classifications of invasions (Supplementary Table 4).

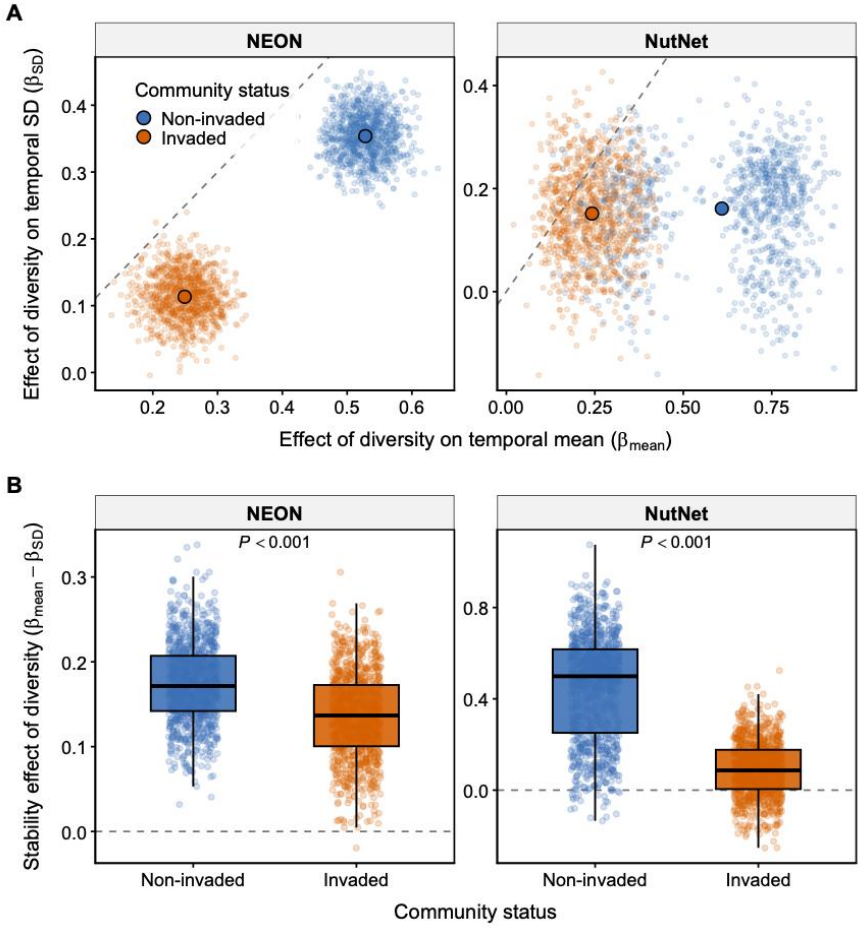


Figure 2. Non-native species weaken the stabilizing effect of species diversity on community temporal stability. Community temporal stability was defined as mean/SD, where mean is temporal mean productivity and SD is temporal standard deviation. Because stability was analyzed as log(mean/SD), the richness effect on stability can be decomposed into its effects on log(mean) and log(SD): $\beta_{stability} = \beta_{mean} - \beta_{SD}$, where β_{mean} and β_{SD} denote the standardized effects of species richness on log-transformed temporal mean and SD, respectively. For each bootstrap resample, we standardized species richness and each response variable, refitted the models for temporal mean and SD, and extracted the standardized slopes. **(A)** Two-dimensional mean–SD space. Each point represents one bootstrap estimate of β_{mean} and β_{SD}, estimated separately for non-invaded and invaded local communities in NEON and NutNet. Filled points with black outlines indicate group centroids. The

dashed line is the 1:1 line, where $\beta_{mean} = \beta_{SD}$ and thus $\beta_{mean/SD} = 0$. Points below the line indicate $\beta_{mean} > \beta_{SD}$, corresponding to a stabilizing effect of richness, whereas points above the line indicate $\beta_{mean} < \beta_{SD}$, corresponding to a destabilizing effect. Shifts toward the dashed line therefore indicate a weakened stabilizing effect of species richness. **(B)** Bootstrap distributions of the net stability effect of richness, calculated as $\beta_{mean} - \beta_{SD}$, for non-invaded and invaded communities in each dataset. Boxplots show medians, interquartile ranges and whiskers; points show individual bootstrap estimates. *P* values were obtained from paired Wilcoxon signed-rank tests comparing within-iteration differences in $\beta_{mean} - \beta_{SD}$ between invaded and non-invaded communities.

We next found that the increasing prevalence of non-native species was accompanied not only by changes in species numbers, but also by a directional shift in community functional composition (Fig. 3). Non-native species in our datasets predominantly exhibited acquisitive strategies, characterized by higher leaf nutrient concentrations and specific leaf area (SLA), lower leaf dry matter content (LDMC) and stem specific density (SSD), and lower species-level stability (Fig. 3; Supplementary Figs. S5, S6). Consistent with these species-level differences, community trait composition shifted toward the acquisitive end of the plant economics spectrum as non-native species became more prevalent, driving increases in SLA and nutrient concentrations and a parallel drop in structural tissues, including lower LDMC and SSD (Fig. 3C, D; Supplementary Fig. S6).

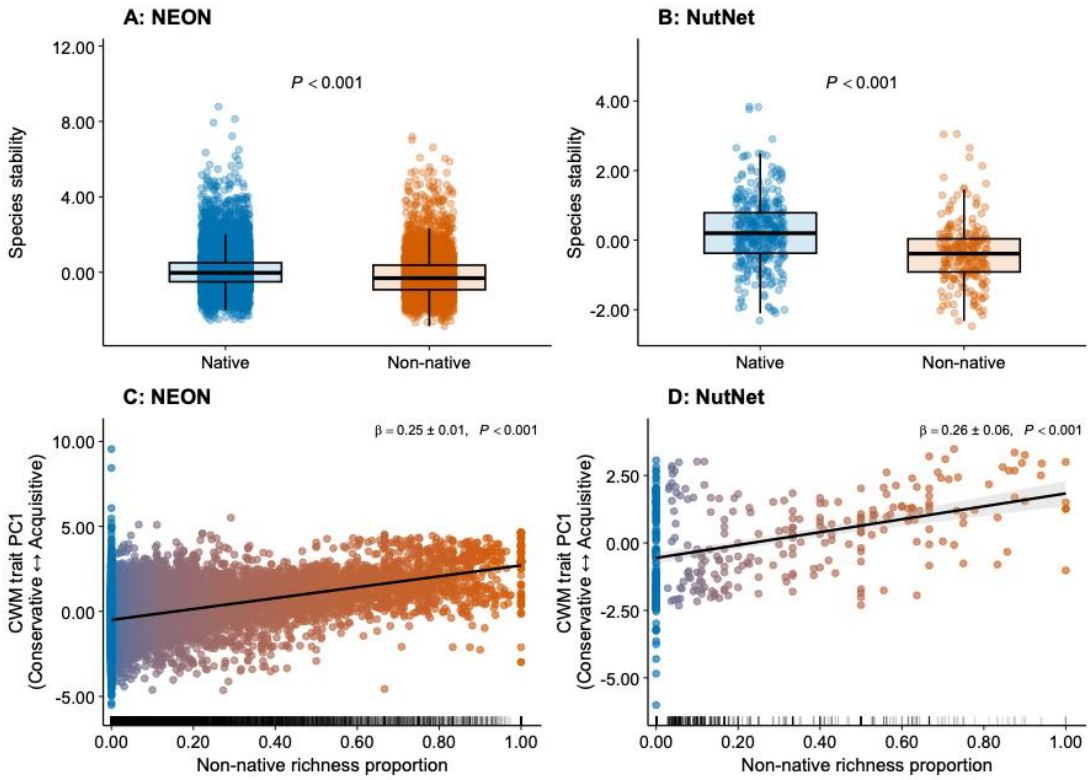


Figure 3. Non-native species are associated with lower species stability and shifts in community trait composition across NEON and NutNet. Panels **(A)** and **(B)** compare species stability between native and non-native species. Points represent individual observations, boxplots summarize the distributions, and *P*-values indicate differences between native and non-native species based on linear mixed-effects models. Panels **(C)** and **(D)** show the relationship between community trait composition and invasion intensity. Community trait composition is represented by the first principal component axis (CWM trait PC1), which captures a major gradient from conservative to acquisitive strategies. Each point represents one community and is colored by invasion intensity, quantified as the proportion of species richness contributed by non-native species. Solid lines and shaded bands show fitted relationships and their 95% confidence intervals. Model statistics are from linear mixed-effects models and are given as standardized effect estimates (β) and *P*-values. Together, these results indicate that non-native species are associated with reduced species stability and with shifts in community trait composition towards more acquisitive strategies in both monitoring networks.

Finally, we used piecewise structural equation modeling (SEM) to determine how this functional reorganization disrupted the specific mechanisms through which

diversity influences community stability. We found that species invasions weakened the links between species diversity and key stability drivers, particularly population stability (Fig. 4; Supplementary Fig. S7). In both datasets, the positive relationship between species diversity and population stability was substantially flattened–and in some cases inverted–in communities invaded by non-native species (Fig. 4; Supplementary Fig. S7; $P < 0.05$ for both datasets). By contrast, the relationship between species diversity and species asynchrony showed only modest weakening. Furthermore, the coupling between population stability and community stability was significantly weaker in communities containing non-native species, indicating that non-native occurrence reduced the extent to which greater population-level stability translated into greater community-level stability (Fig. 4; Supplementary Fig. S7; $P <$ 0.001 in both datasets). In contrast, the parallel pathway linking species diversity to community stability via species asynchrony remained largely intact, showing only modest changes (Fig. 4; Supplementary Fig. S7).

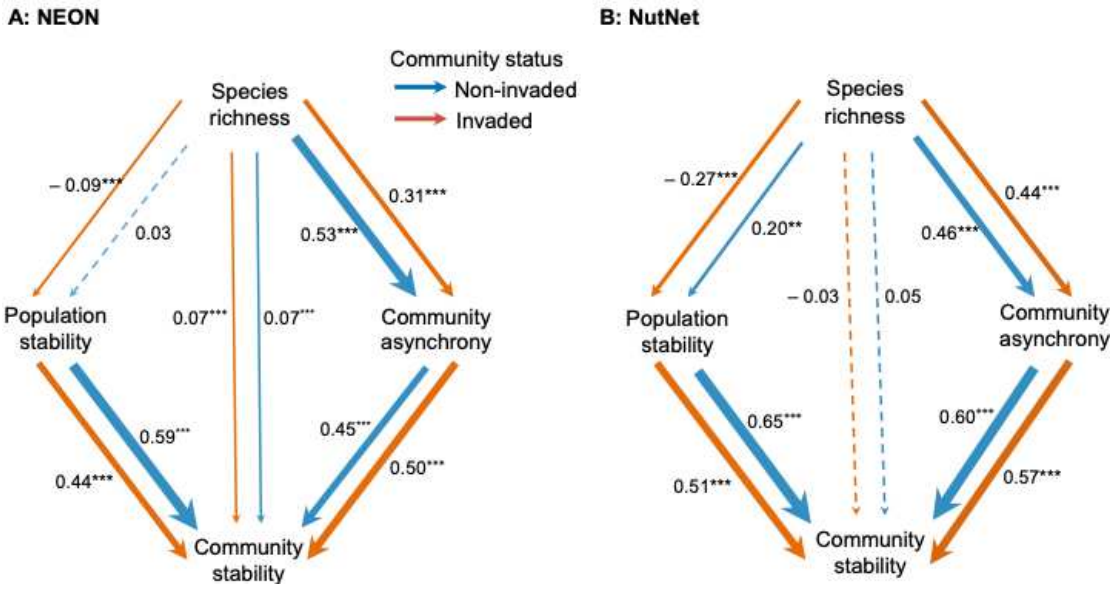


Figure 4. Piecewise structural equation models (SEM) linking diversity to community stability through population stability and community asynchrony in NEON (A) and NutNet (B). For each dataset, species richness, population stability, community asynchrony and community stability were

first residualized against climate principal-component axes and then re-standardized before model fitting. The same saturated piecewise SEM was fitted separately for native-only and invaded communities. The nested SEM layout shows native-only communities in the inner layer and invaded communities in the outer layer. Solid arrows denote significant paths ($P < 0.05$) and dashed arrows denote non-significant paths ($P \geq 0.05$); arrow width is proportional to the absolute standardized path coefficient, and values beside arrows are standardized path coefficients. Significance is indicated by superscript asterisks ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$; no asterisk, $P \geq 0.05$).

Discussion

Across two independent monitoring networks spanning 142 terrestrial sites and more than 11,000 local plant communities, we found that non-native plants consistently eroded the long-recognized capacity of biodiversity to stabilize plant community functioning. This erosion did not simply reflect species loss or changes in species richness. Instead, increasing non-native dominance was associated with a shift from conservative toward more acquisitive resource-use strategies. This disproportionately weakened the pathway through which diversity stabilizes constituent populations while leaving the species-asynchrony pathway comparatively less affected. Invasion therefore did not disrupt all stabilizing mechanisms equally, but primarily weakened the population-level foundation of biodiversity-mediated stability. These findings demonstrate that native and non-native species are not functionally equivalent contributors to community stability and that non-native species cannot be assumed to replace the stabilizing contributions of native biodiversity. Whereas previous studies have established that plant invasions alter resident biodiversity, ecosystem processes and community functional composition [8,10,27-30], our results reveal a previously underappreciated consequence: invasion also reorganizes the mechanisms through which biodiversity sustains ecosystem

functioning over time.

A likely contributor to this weakening was an invasion-associated shift in community functional composition toward more acquisitive resource-use strategies. Consistent with previous studies [8-10,26], non-native species in both the NEON and NutNet datasets tended to exhibit faster resource acquisition and reduced investment in structural tissues (e.g., lower LDMC and SSD). As such, communities dominated by non-native species may contain populations that are more temporally variable and less effectively buffered against environmental fluctuations. In this sense, non-native species do not simply add new trait values to an existing pool; they fundamentally alter the functional context in which biodiversity operates, thereby weakening biodiversity's stabilizing effect on community functioning. In addition, invasion-associated functional reorganization may also extend belowground. Recent evidence from NEON links invasive plants and their root traits to the homogenization of soil microbial communities [27], while plant resource-economic strategies can strongly regulate soil food-web multifunctionality [31]. Shifts toward acquisitive plant strategies may therefore alter belowground dynamics and potentially further weaken biodiversity-mediated stability.

We found that invasion-associated functional reorganization disrupted the pathways through which species diversity was translated into community-level stability. The clearest signal was a marked weakening of the positive relationship between species diversity and population stability, which in some cases even reversed in direction. This result indicates that, as non-native species accumulated, higher diversity no longer conferred the same stabilizing effect on constituent populations as it did in native-only communities. A likely explanation is that fast-growing and environmentally responsive non-native species closely track favorable environmental

conditions and consequently exhibit larger temporal fluctuations and lower population stability [23,32,33]. By contrast, the positive relationship between species diversity and species asynchrony weakened only modestly, suggesting that compensatory dynamics remained comparatively intact. This asymmetry identifies the population-stability pathway as the component of biodiversity-mediated stability most vulnerable to invasion. It may also help explain why invaded communities can retain aggregate temporal stability even as the mechanisms supporting it change [34]. Previous syntheses have often found that species diversity does not consistently enhance population stability in terrestrial ecosystems [15,35]. Yet these analyses rarely distinguish between invaded and uninvaded communities. Our results offer a potential explanation for this longstanding inconsistency: unrecognized variation in non-native prevalence may weaken or even reverse the expected positive relationship between species diversity and population stability.

Within invaded communities, native species richness was more strongly associated with community stability than total species richness, suggesting that non-native species did not contribute equivalently to stability. The diversity–stability relationship also weakened as native and non-native subcommunities diverged functionally (Supplementary Fig. S8), suggesting that invasion-associated shifts in trait composition contributed to this erosion. Yet invasion intensity was not significantly associated with aggregate community stability itself (Supplementary Fig. S9), despite clear changes in the pathways that sustained it. This decoupling is consistent with evidence that native- and exotic-dominated grasslands can exhibit similar aggregate stability through different mechanisms and that invasion can reduce diversity without reducing temporal stability [34,36]. Thus, invasion can leave aggregate stability largely unchanged while weakening the biodiversity-based mechanisms that

sustain it.

Overall, our results show that plant invasion can weaken biodiversity's capacity to stabilize ecosystem functioning. This weakening was closely associated with a shift toward fast, acquisitive resource-use strategies, consistent with patterns widely reported for non-native plants [8,10]. The convergence of these findings across two independent monitoring networks spanning continental to global scales suggests that the erosion of biodiversity–stability relationships may be widespread across invaded plant communities. By linking this broad-scale pattern to shifts in functional composition and stability pathways, our study strengthens the mechanistic basis for invasion management. Assessments of invasion impacts should therefore consider changes in the processes that sustain community stability. Our findings further underscore the need to prevent new invasions and reduce the ecological impacts of established ones. As climate change increases invasion risk across many regions [17], efforts to limit the spread and dominance of non-native plants will become increasingly important for protecting biodiversity and sustaining ecosystem functioning in a rapidly changing world.

Methods

Data sources

NEON plant community data

The National Ecological Observatory Network (NEON) provides standardized, quality-controlled plant community data across terrestrial sites in the United States [37,38]. NEON was designed as a continental-scale, long-term observatory to monitor ecological change over multiple decades, with plant community monitoring beginning at the first operational sites in 2013 and additional sites coming online progressively

through time. We used the NEON plant presence and percent cover data product (DP1.10058.001; RELEASE-2025), which records plant species presence, percent cover and associated taxonomic, nativity and location information from NEON plant diversity sampling. This dataset, download from R package neonDivData [38], was used to assess how non-native species modify diversity–stability relationships across 47 terrestrial sites.

NEON plant diversity sampling uses a nested, multiscale design within 400-m^2 plots [37,38]. Species presence and percent cover are recorded in 1-m^2 subplots, whereas larger 10-m^2 and 100-m^2 subplots provide presence–absence information that can be combined to characterize plot-scale species lists. Because our analyses required abundance information at fine spatial resolution, we restricted our analyses to the 1-m^2 percent-cover records. The NEON analytical subset included 10,713 quadrats from 1,467 plots across 47 terrestrial sites, spanning 2013–2023, with a mean temporal coverage of 6.45 years per quadrat (median = 6 years; range = 3–11 years).

To determine species origin in the NEON network, we combined record-level nativity information from NEON's taxonomic database and the Global Naturalized Alien Flora (GloNAF) database [39]. This integrated approach allowed us to rigorously classify taxa as native or non-native within each relevant sampling region. Across the NEON dataset, this procedure identified 5,057 native and 869 non-native plant species from 47 terrestrial sites.

Nutrient Network plant community data

The Nutrient Network (NutNet) is a globally distributed grassland research network designed to test how nutrient enrichment and consumer exclusion affect plant communities under standardized protocols [40,41]. NutNet began in the late 2000s as a coordinated, site-based experimental network, with the first sites contributing

vegetation data in 2007 and additional sites joining progressively under a common core protocol [41]. NutNet experiments are based on replicated 5 m × 5 m plots, with plant community composition surveyed in permanently marked 1 m × 1 m subplots using repeated species-level percent-cover estimates.

We used NutNet vegetation composition data as an independent, standardized dataset to complement the NEON analyses. To avoid confounding effects of experimental treatments and to maximize comparability with the NEON quadrat-level analyses, we retained only control plots, defined as plots without nutrient addition or consumer exclusion. For all subsequent calculations of diversity, invasion status and stability components, we used species percent cover from permanent 1 m × 1 m subplots. Species origin was determined by site investigators [42] and cross-checked against national or regional floras and databases where available [43]. The NutNet analytical subset included 368 subplots from 95 sites, comprising 2,972 native and 417 non-native vascular plant species, and spanning 2007–2025, with a mean temporal coverage of 8.95 years per subplot (median = 8 years; range = 3–18 years).

Across both datasets, we retained only community time series with at least three years of repeated vegetation observations. Here, communities refer to quadrat-level time series in NEON and subplot-level time series in NutNet. This filtering criterion ensured sufficient temporal replication to estimate species diversity, population stability, species asynchrony and community stability, while preserving the independent sampling structure of each monitoring network.

Plant trait data

We compiled species-level data for seven functional traits that capture major axes of plant ecological strategy, including resource acquisition, structural investment and life-history variation [44-46]: specific leaf area (SLA; $m^2\ kg^{-1}$), leaf dry matter

content (LDMC; g g^{-1}), leaf nitrogen concentration (Leaf N; mg g^{-1}), leaf area (cm^2), plant height (m), seed or diaspore mass (mg), and stem specific density (SSD; g cm^{-3}). Together, these traits represent well-established dimensions of plant form and function linked to growth strategy and competitive ability, while also capturing the conservative–acquisitive spectrum of plant resource-use strategies, allowing us to assess whether the accumulation of non-native species shifts community functional composition in ways that affect biodiversity–stability relationships.

Trait values were compiled from a harmonized synthesis of three major plant trait resources: the TRY Plant Trait Database (**https://www.try-db.org**) [47], the Global Inventory of Floras and Traits (GIFT, **https://gift.uni-goettingen.de**) [48], and the Botanical Information and Ecology Network (BIEN, **https://bien.nceas.ucsb.edu/bien/**) [49]. TRY integrates plant trait records from hundreds of contributed datasets into a standardized format, whereas GIFT and BIEN provide complementary information on plant traits, floristic distributions and taxonomic records. Trait records were matched to species in the curated vegetation datasets using standardized taxonomic names according to the World Checklist of Vascular Plants (WCVP) database [50] to ensure consistency across data sources.

Because trait coverage is incomplete across large regional and global species pools, some species lacked one or more trait values after database matching. We filled these gaps using phylogenetically informed imputation with the phylopars function in the R package *Rphylopars* [51]. This approach estimates missing trait values by incorporating phylogenetic covariance among species and, when informative, covariance among traits, thereby helping preserve biologically meaningful trait structure in large comparative datasets. Across traits, database-measured values accounted for 9.5–58.7% of NEON trait records and 7.7–72.5% of NutNet trait

records, with the remaining records imputed (Supplementary Table 5). Sensitivity analyses conducted for NEON traits suggested that this phylogenetic imputation approach works well despite the relatively large amount of missing data [52]. These differences in measured coverage reflect known variation in trait availability across global plant trait databases [53], with routinely measured traits such as plant height and diaspore mass generally better represented than traits such as SSD. To support trait imputation, we assembled a study-specific phylogeny for all taxa included in the final vegetation dataset. We used the broadly inclusive, dated global seed plant phylogeny of Smith and Brown [54] as the backbone, grafting missing species onto this reference tree using the R package *rtrees* [55].

Climate data

Because climate can covary with biodiversity and influence ecosystem stability, we extracted temperature and precipitation data and quantified both mean climatic conditions and interannual climate variability. We used the Climatic Research Unit Time-Series dataset, CRU TS v4.09 (**https://crudata.uea.ac.uk/cru/data/hrg/**) [56], which provides monthly climate variables for global land areas excluding Antarctica on a 0.5° × 0.5° grid for 1901–2024.

Climate variables were extracted at the spatial resolution of the vegetation sampling coordinates available for each network. For NEON, we extracted climate data at the plot level using plot coordinates; for NutNet, we extracted climate data at the site level because all subplots within a site shared the same coordinates and climate values. We used 2001–2024 as a common recent climate baseline because it provides a sufficiently long period for estimating interannual variability, covers nearly all vegetation survey years used in the analyses, and avoids differences in climate covariates arising solely from the different observation windows of NEON and

NutNet.

For each NEON plot or NutNet site, we extracted monthly mean temperature and monthly precipitation, aggregated monthly values to annual mean temperature and annual total precipitation, and calculated long-term means across 2001–2024. Interannual variability was quantified as the coefficient of variation of annual values, calculated as CV = SD/mean for both temperature and precipitation. As a robustness check, NEON plot-level climate covariates calculated over 2001–2024 were strongly correlated with those calculated over 2013–2023, the NEON observation window, for mean temperature, precipitation and their interannual variability (Pearson's r = 0.94–1.00).

Diversity and stability calculations

We quantified community diversity using species richness as the primary metric, and also calculated Shannon diversity and inverse Simpson diversity as complementary diversity measures using the vegan R package [57]. We quantified functional diversity as functional dispersion (FD_{is}), calculated as the abundance-weighted mean distance of species to the community centroid in multidimensional trait space using the FD R package [58]. For each community time series, we used species percent cover to calculate community temporal stability, population stability and species asynchrony. We used cover-based time series as the primary basis for stability calculations because cover was available at the species level in both networks, allowing us to partition community stability into population stability and species asynchrony. Because NutNet biomass was available only at the community level, we used biomass-based temporal stability as a robustness check for community-level biodiversity–stability relationships, and found consistent results (Supplementary Fig. S10).

Community temporal stability was calculated as the inverse coefficient of variation of total community cover:

$$S_{comm} = \frac{\mu_c}{\sigma_c}$$

where S_{comm} is community temporal stability, and μ_c and σ_c are the temporal mean and standard deviation (SD) of total community cover across years, respectively.

Population stability was calculated as the abundance-weighted average of species-level temporal stability within each community:

$$S_{pop} = \sum_i w_i \frac{\mu_i}{\sigma_i}$$

where S_{pop} is population stability, w_i is the mean relative contribution of species i to total community cover across years, and μ_i and σ_i are the temporal mean and standard deviation of species i's cover across years, respectively. Species with zero temporal variance were excluded from this calculation.

Species asynchrony was calculated following Loreau and de Mazancourt [19] as:

$$\emptyset = \frac{\sigma_c^2}{(\sum_i \sigma_i)^2}, \; Asyn = 1 - \emptyset$$

where $\emptyset$ is species synchrony; σ_c^2 is the temporal variance of total community cover, $\sum_i \sigma_i$ is the sum of species-level temporal standard deviations; and $Asyn$ is species asynchrony [19]. In instances where fewer than two species exhibited non-zero temporal variation, species synchrony (ϕ) was set to 1, resulting in an asynchrony (*Asyn*) of 0.

To examine whether non-native species weakened diversity's stabilizing effect by altering temporal mean community cover, temporal variability, or both, we decomposed community temporal stability into its mean and variability components:

$$\log(S_{comm}) = \log(mean) - \log(SD)$$

where mean and SD denote the temporal mean and standard deviation of community cover, respectively, corresponding to μ_c and σ_c above. We therefore analyzed the relationships of species richness with $\log(S_{comm})$, $\log(mean)$, and $\log(SD)$ separately.

We also calculated species-level temporal stability to compare native and non-native species. This analysis was distinct from population stability, which represents an abundance-weighted community-level aggregate. Because species origin can vary geographically, with the same species classified as native in one region and non-native in another, we assigned origin status at the species-by-community level and then compared species stability between native and non-native across all species-by-community time series.

Defining invasion status and quantifying invasion intensity at the local-community level

We defined invasion status and quantified invasion intensity at the local-community level. Local communities corresponded to 1 m × 1 m quadrats in NEON and 1 m × 1 m subplot units in NutNet. We first classified all species as native or non-native according to their origin status. To obtain a binary classification of invasion status for each community, a local community was classified as invaded only when at least one non-native species was recorded in two or more census years. Communities in which non-native species were absent or recorded in only a single census year were classified as non-invaded. This criterion reduced the influence of transient or potentially incidental occurrences. After retaining local communities with at least three census years, 5,894 of 10,705 NEON quadrats (55.1%) and 230 of 368 NutNet

subplots (62.5%) were classified as invaded. At broader spatial grains, invasion occurred in 1,052 of 1,467 NEON plots (71.7%) and 46 of 47 NEON sites (97.9%), and in 63 of 95 NutNet sites (66.3%).

Because biological invasion varies in degree, we also quantified invasion intensity as the relative contribution of non-native species within each local community, allowing us to test whether community trait composition and biodiversity–stability relationships changed progressively along invasion gradients. Our primary metric was richness-based invasion intensity, calculated as the proportion of species richness contributed by non-native species and ranging from 0, when no non-native species were present, to 1, when all species with known origin were non-native. This metric was calculated annually and then averaged across census years to represent long-term mean invasion intensity. Across local communities, mean richness-based invasion intensity was 15.5% in NEON and 23.3% in NutNet; averaged at the site level, corresponding values were 16.7% and 22.9%, respectively. To assess whether results depended on the dimension of invasion measured, we also calculated cover-based and Shannon-based invasion intensity, defined as the proportional contributions of non-native species to total plant cover and community Shannon diversity, respectively. As a further robustness check, we compared biodiversity–stability relationships calculated using all species with those calculated after excluding non-native species within the same invaded communities and found that the results remained consistent (Supplementary Fig. S2).

Together, these complementary approaches provided a multi-pronged strategy for testing invasion effects across categorical, continuous and within-community contrasts. The binary classification of plant communities tested whether persistently invaded communities differed from non-invaded communities; the continuous

invasion-intensity metrics tested whether effects scaled with the relative contribution of non-native species, thereby avoiding reliance on any single invaded/non-invaded threshold; and the all-species versus native-only comparison isolated the compositional contribution of non-native species within the same invaded communities. By evaluating invasion effects across these different scenarios, we could determine whether they reflected a reproducible ecological signal rather than an artefact of any single invasion metric, threshold or analytical comparison.

Statistical analyses

We combined linear mixed-effects models, principal component analysis (PCA), group-balanced model-refitting bootstrap, and piecewise structural equation models (SEM) to determine whether, and through which mechanisms, invasion by non-native species altered biodiversity–stability relationships. The analyses addressed three sequential questions. First, we tested whether the presence and relative contribution of non-native species weakened biodiversity–stability relationships, considering both community stability and its component processes (population stability and species asynchrony). Second, we examined whether non-native species differed from native species in functional traits and species-level stability, and whether community functional composition shifted with increasing invasion intensity. Third, we evaluated how invasion altered the mechanistic pathways linking biodiversity to community stability through population stability and species asynchrony.

Testing whether invasion weakens biodiversity–stability relationships

We first used linear mixed-effects models, fitted with the R packages *lme4* [59] and *lmerTest* [60], to test whether invasion modified biodiversity–stability relationships. Biodiversity was represented primarily by species richness, with Shannon diversity and functional diversity used as complementary metrics. Response variables included

618 community temporal stability, population stability, and species asynchrony. We
619 included climatic covariates to reduce the possibility that broad-scale climate
620 gradients, rather than invasion *per se*, explained variation in biodiversity–stability
621 relationships. Specifically, we summarized mean temperature, mean precipitation and
622 their interannual variability using PCA to reduce collinearity among climate variables
623 [61], and retained the first two climate PC axes, which together explained more than
624 70% of the total climatic variation and had eigenvalues greater than one, as covariates
625 in all mixed-effects models unless otherwise stated. To account for the hierarchical
626 sampling design, NEON models included random intercepts for plots nested within
627 sites, whereas NutNet models included only site as a random intercept because the
628 number of available subplots within sites was limited. All continuous predictors were
629 standardized to have mean 0 and SD 1 before model fitting to facilitate comparison of
630 effect sizes and interpretation of interaction terms. Standardization also centered
631 continuous predictors at zero, reducing non-essential collinearity between main
632 effects and their product terms in interaction models. We assessed model assumptions
633 by inspecting residual distributions, residual–fitted relationships and quantile–quantile
634 plots, and assessed multicollinearity using variance inflation factors (VIFs). We also
635 checked residual spatial autocorrelation using Moran's I, and no significant spatial
636 autocorrelation was detected ($P > 0.05$).

637 We fitted two complementary model sets. First, biodiversity × invasion status
638 models tested whether biodiversity–stability relationships differed between non-
639 invaded and invaded communities after controlling for climate covariates and
640 sampling hierarchy. Second, biodiversity × invasion intensity models tested whether
641 these relationships changed continuously along gradients of species invasion intensity.
642 A negative interaction term indicates that the positive biodiversity–stability

643 relationship weakens as non-native species become more prevalent. This framework
644 allowed us to evaluate invasion effects both as a binary community state and as a
645 continuous ecological gradient.

646 **Mean–variability decomposition and balanced bootstrap**

647 Because community temporal stability is defined by the ratio between the
648 temporal mean and temporal variability of community cover [2], we decomposed
649 biodiversity effects into effects on these two components [62]. In both NEON and
650 NutNet, we separately modeled the temporal mean and temporal standard deviation of
651 total community cover as response variables and estimated standardized biodiversity
652 effects on each component, denoted β_{mean} and β_{SD}. This decomposition allowed us to
653 assess whether biodiversity–stability relationships were associated primarily with
654 changes in mean community cover, temporal variability, or both.

655 For each biodiversity metric, β_{mean} and β_{SD} were estimated separately for non-
656 invaded and invaded communities within the same modeling framework. The two-
657 dimensional β_{mean}-β_{SD} effect space was used to visualize how biodiversity effects on
658 the temporal mean and temporal variability of community cover differed between
659 invasion states. We further summarized these effects using the mean–variability
660 contrast, $\Delta v = \beta_{mean} - \beta_{SD}$. Larger values of Δv indicate that biodiversity had a
661 stronger positive effect on mean community cover relative to its effect on temporal
662 variability, implying a stronger net contribution to stability. Smaller values indicate
663 that biodiversity effects on temporal variability were relatively stronger and could
664 offset or weaken the stability gains associated with increased mean cover. As a
665 sensitivity analysis, we repeated the mean–variability decomposition using detrended
666 temporal variability, calculated after removing linear temporal trends from
667 community cover time series [2,20], and obtained consistent results (Supplementary Fig.

S11).

To quantify uncertainty and reduce the influence of sample-size imbalance within and between networks, we used a custom refitting-based balanced bootstrap implemented in R. Within each network, we sampled equal numbers of non-invaded and invaded communities in each bootstrap iteration, with sample sizes set separately for NEON and NutNet according to their respective data structures. For NEON, we performed 999 bootstrap iterations, each sampling 3,000 local communities from each invasion-status group, with replacement when the available sample size in a group was smaller than the target sample size. For NutNet, we performed 999 bootstrap iterations, each sampling 100 local communities from each invasion-status group. In each iteration, we refit the same mixed-effects model and obtained empirical distributions of β_{mean}, β_{SD}, and Δv. To test whether the mean–SD contrast differed between invasion states, we calculated the paired bootstrap difference $\Delta v_{Invaded} - \Delta v_{Non-invaded}$ within each iteration. We used this paired-difference distribution to estimate the mean group difference and 95% percentile interval, and tested whether the difference was centred on zero using paired *t*-tests and Wilcoxon signed-rank tests.

Trait differences and functional shifts along invasion gradients

We next assessed whether non-native species differed from native species in functional traits and whether community functional composition shifted along invasion gradients. To reduce trait dimensionality and identify the dominant axis of community functional strategy, we performed PCA on community-weighted mean (CWM) trait values. The first principal component (PC) was interpreted as the primary community functional strategy axis, representing a trade-off between conservative and acquisitive strategies (Supplementary Fig. S6).

We then used mixed-effects models to test whether the dominant functional strategy of plant communities shifted systematically with invasion intensity. Invasion intensity was represented primarily by the proportion of non-native species richness, with cover-based and Shannon-based invasion metrics used as complementary measures (Supplementary Fig. S12). In addition, we compared key trait values between native and non-native species, and also compared their species-level temporal stability, to determine whether non-native species differed from native species in both functional strategy and temporal stability.

Piecewise structural equation models of biodiversity–stability pathways

Finally, we used piecewise SEM implemented in the R package *piecewiseSEM* [63], with linear mixed-effects component models fitted using *lme4* [59], to evaluate whether invasion altered the pathways through which biodiversity affected community stability. We specified the SEM structure based on hypothesized biodiversity–stability pathways, informed by prior biodiversity–stability theory and empirical evidence [3,15,20,21,64,65]. The saturated model included both the direct path from biodiversity to community stability and two indirect paths mediated by population stability and species asynchrony [15,64]. Because all hypothesized paths were included, the model was saturated; therefore, tests of directed separation and Fisher's C were not required. We reported marginal and conditional R^2 for each component model and used standardized path coefficients to compare the relative strength of pathways. Collinearity diagnostics, conducted using the R package *performance* [66], showed that VIFs were below 3 for all component models, indicating no severe multicollinearity.

Because climate variables may jointly influence biodiversity and stability components, we adjusted SEM variables for climate before model fitting rather than

adding multiple climate covariates directly to each component model. Specifically, species richness, community stability, population stability and community asynchrony were each regressed against the leading climate PC axes. Residuals from these models were extracted and re-standardized, and these climate-adjusted variables were then used in group-specific piecewise SEMs. Component models retained the same random-effect structures as the preceding mixed-effects analyses, with plots nested within sites for NEON and site-level random intercepts for NutNet. All analyses were conducted in R version 4.5.2 (R Core Team, 2025) [67].

Data and Code Availability Statement

All datasets used in this study are publicly available from their original providers or accessible through established data-sharing frameworks. Plant trait data were compiled primarily from TRY (https://www.try-db.org/TryWeb/Data.php), GIFT (https://gift.uni-goettingen.de), and BIEN (https://bien.nceas.ucsb.edu/bien/biendata/). Climate data were derived from the CRU TS gridded dataset provided by the Climatic Research Unit at the University of East Anglia (https://crudata.uea.ac.uk/cru/data/hrg/). NEON vegetation survey data were provided by the National Ecological Observatory Network data portal, specifically the Plant presence and percent cover data product (https://data.neonscience.org/data-products/DP1.10058.001), and we used the standardized version from the R data package neonDivData (https://github.com/daijiang/neonDivData). NutNet data were obtained through the Nutrient Network's coordinated data-sharing framework and relevant project-level published data releases where applicable (https://nutnet.org/datadois). All analyses were conducted in R using the packages documented in the Methods.

Author contributions

P.Y. and D.L. developed the study design and analytical framework. P.Y. conceived the study, conducted the analyses and wrote the first draft of the manuscript. D.L. and J.A.C. contributed to data curation, interpretation of results and critical revision of the manuscript. Y.Y., M.N., C.T.C., N.N., Y.M., S.L., E.B., E.W.S. and I.S. contributed to data compilation, interpretation and manuscript development. E.B., E.W.S. and I.S. contributed to Nutrient Network data coordination, interpretation and authorship/publication guidance. J.A.C. contributed to manuscript framing, interpretation and critical revision. A.C.R., A.E., A.J., A.S.M., C.C., C.D., C.V., D.M., E.I.H.-G., E.T.P., H.M.M., H.O.V., I.D., I.S.J., J.A.C., J.D.B., J.L.M., J.M., J.M.H.K., J.P.M., K.A.B., K.D., K.P.K., K.Z., L.A.B., L.L., L.Lan., M.C.C., M.N.B., M.W.C., M.M., N.E., N.G.S., N.H., P.L.P., P.M., P.Z., R.M., R.N., R.V., S.A.P., S.E.K., S.H., T.W.C., X.R., Y.H., Y.L. and Z.R. contributed data and/or site-level expertise, discussed the results and commented on or revised the manuscript. All authors approved the final version of the manuscript. Detailed NutNet author contributions are provided in Supplementary Table 6.

Competing interests

The authors declare no competing interests.

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