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Macroscale analyses suggest invasive plant impacts depend more on the composition of invading plants than on environmental context

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Abstract

Aim: Native biodiversity is threatened by the spread of non-native invasive species. Many studies demonstrate that invasions reduce local biodiversity but we lack an understanding of how impacts vary across environments at the macroscale. Using ~11,500 vegetation surveys from ecosystems across the United States, we quantified how the relationship between non-native plant cover and native plant diversity varied across different compositions of invading plants (measured by non-native plant richness and evenness) and environmental contexts (measured by productivity and human activity).

Location: Continental United States.

Time Period: Surveys from 1990s-present.

Major Taxa Studied: Terrestrial plant communities.

Methods: We fit mixed effects models to understand how native plant richness, diversity and evenness varied with non-native cover. We tested how this relationship

varied when non-native cover interacted with non-native plant richness and evenness, and with productivity and human activity.

Results: Across the United States, communities with greater cover of non-native plants had lower native plant richness and diversity but higher evenness, suggesting rare native plants can be lost while dominant plants decline in abundance. The relationship between non-native cover and native community diversity varied with non-native plant richness and evenness but was not associated with productivity and human activity. Negative associations were strongest in areas with low non-native richness and evenness, characterizing plant communities that were invaded by a dominant non-native plant.

Main Conclusions: Non-native plant cover provides a first approximation of invasion impacts on native community diversity, but the magnitude of impact depended on non-native plant richness and evenness. Relationships between non-native cover and native diversity were consistent in strength across continental scale gradients of productivity and human activity. Therefore, at the macroscale, invasive plant impacts on native plant communities likely depend more on the characteristics of the invading plants, that is the presence of a dominant invader, than on the environmental context.

KEYWORDS

human activity, invasion impacts, invasive plants, macroecology, native plants, net primary productivity
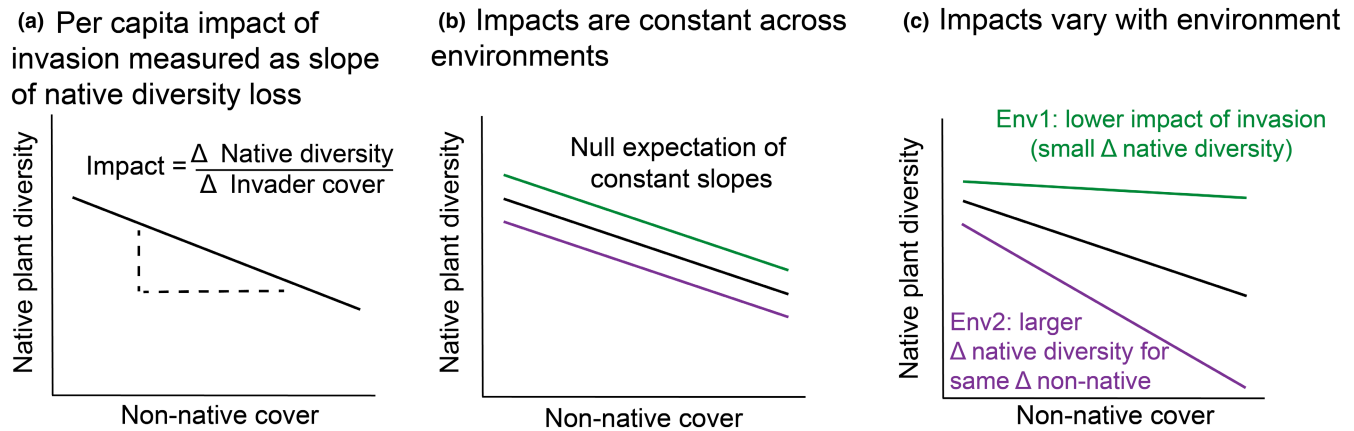
1 | INTRODUCTION

Predicting the ecological impacts of invasive plants remains an elusive goal in invasion ecology. Recent studies have shown that negative impacts experienced by native communities (e.g. diversity loss) are related to invader abundance (Bradley et al., 2019; Pearse et al., 2019), the identity of the invading species (Hejda et al., 2009; Pearse et al., 2019; Pearson et al., 2016) and the vulnerability of the native community (Catford et al., 2009). Most studies of invasion impact have been conducted at local scales and are thus poorly able to inform how impacts vary across environments. Macroecological studies are ideally suited to address this, but to date, such studies have largely focused on understanding variation in non-native plant establishment or abundance, with less attention on impacts (but see Pyšek et al., 2012). Consequently, few general patterns in invasion impacts have emerged (Crystal-Ornelas & Lockwood, 2020), and we lack an understanding of how the impacts of invasion vary across environmental gradients.

Understanding general patterns in invader impacts is challenged by variation in how impacts are quantified (Barney & Tekiela, 2020; Pyšek et al., 2012; Verbrugge, 2010) and the tendency of impact studies to focus on a few high-impact species or well-studied ecosystem types (Crystal-Ornelas & Lockwood, 2020; Hulme et al., 2013; Pyšek et al., 2008). These biases limit our capacity to identify patterns in invader impacts and to understand what conditions might

lead to variation in impact magnitude (Kumschick et al., 2015). For example, Brewer (2011) found that the impact of stiltgrass (*Microstegium vimineum*) invasion depended on spatial variation in light availability. In open areas, stiltgrass reached high abundance but native plant communities maintained diversity. In shaded areas, stiltgrass achieved lower abundance but because the native plant community was more vulnerable to competition for light, stiltgrass had a stronger negative effect on native species diversity. This example hints at a complex relationship between invader abundance and the environment that could lead to substantial variation in invasion impacts (Crystal-Ornelas & Lockwood, 2020; Ricciardi et al., 2021).

One way to understand how invasion impacts differ across environments is to characterize variation in the direction and strength of the relationship between non-native plant cover and native plant diversity (Figure 1). The slope of this association can be interpreted as the per capita impact of invasion—the magnitude of the decline in native diversity given each unit increase in invader cover (Parker et al., 1999; Sofaer et al., 2018). Previous work in plant communities has shown that non-native species have stronger per capita impacts than similarly dominant native species (Pearse et al., 2019), and the abundance-impact relationship is negative and linear (Bradley et al., 2019). Studies have also shown that the strength of this negative relationship (i.e. the slope in Figure 1) can vary across species (Hejda et al., 2009; Pearson et al., 2016) and across environments for the same species (Brewer, 2011), suggesting that the per capita

(a) Per capita impact of invasion measured as slope of native diversity loss

$$\text{Impact} = \frac{\Delta \text{ Native diversity}}{\Delta \text{ Invader cover}}$$

(b) Impacts are constant across environments

Null expectation of constant slopes

(c) Impacts vary with environment

Env1: lower impact of invasion (small Δ native diversity)

Env2: larger Δ native diversity for same Δ non-native

FIGURE 1 Conceptual figure showing how environmental context may alter the strength of the relationship between non-native cover and native diversity, representing the per capita impact of invasion. (a) Per capita impact is measured as the change in native diversity given a unit change of non-native cover (i.e. the slope of the relationship between native diversity and non-native cover). (b) The null expectation is that the change in native diversity is constant across environments, represented by different lines. In this example, environments differ in native diversity (intercepts), but not in the rate at which diversity declines with increasing non-native cover (constant slopes). (c) We hypothesize that the impact of invasion varies with environment. For the same increase of non-native cover, environments differ in the magnitude of diversity change, measured as the slope of each line.

impacts of invasion differ, even when the cover of invaders is comparable between environments (Figure 1c; Sofaer et al., 2019). To assess whether these patterns emerge at the macroscale, we asked how the strength of the presumed negative relationship between non-native cover and native diversity varies with key factors that could influence plant invasion patterns, such as the environmental context of the recipient plant community (e.g. ecosystem productivity, human activity). We also asked whether per capita impacts differed depending on the composition of the invading plant community, in which stronger per capita impacts could result from the presence of a dominant invader or from the cumulative effect of multiple non-native species (in which case, per capita impact could largely be the result of competition for space).

First, we hypothesized that an area's productivity could influence the relationship between non-native plant cover and native community diversity. Empirical studies have found that invaders have stronger impacts on recipient communities and their resource-dynamics in productive environments, even if these areas are less invasible (Goldstein & Suding, 2014; MacDougall et al., 2006). In other words, invading species can have stronger per capita impacts in areas with high productivity, potentially via competition for resources (Rees, 2013). How productivity relates to competition is a longstanding debate in ecology (Goldberg et al., 1999; Stotz et al., 2016; Tilman, 2020). But to the degree that low productivity can be associated with abiotic stress (e.g. water stress in plants), theoretical frameworks such as the Stress Gradient Hypothesis predict weaker competitive interactions or facilitation in resource poor, high stress environments (Maestre et al., 2009). We therefore expect weaker per capita impacts of invasion in areas with low productivity and stronger per capita impacts in areas with high productivity.

Second, the relationship between native community diversity and non-native cover may vary with the degree that human activity facilitates invasion and modifies a recipient community. It is

well-known in the invasion literature that human activity increases invasive species richness and abundance (Beaury et al., 2020; Lonsdale, 1999; Seabloom et al., 2006) by both increasing propagule pressure (e.g. introducing non-native plants through plant trade; Beaury et al., 2021) and creating disturbances that facilitate establishment and spread (Vilà & Ibáñez, 2011). There are also examples in which human activity at the local scale results in stronger negative impacts of invasion, beyond the direct effect of human activity on invader abundance (Didham et al., 2007). In these cases, human disturbance alters short-term resource pulses (i.e. fluctuating resources hypothesis; Davis et al., 2000), shifting competitive interactions to benefit invading species in a similar manner to how productivity might affect invasion impacts via resource competition. High human activity could therefore interact with invader abundance to result in greater negative impacts to native diversity when compared to areas with similar levels of invader cover but lower human activity.

Third, we hypothesized that plots with a greater number of co-occurring non-native plants could have more adverse impacts on native diversity. This could result from several mechanisms. First, different invasive species have different magnitudes of impact (Hejda et al., 2009; Pearson et al., 2016), so a larger non-native species pool could increase the likelihood that one of the invaders has a strong negative impact. Second, the presence of multiple non-native plant species could be a signature of one species altering the abiotic environment, creating niche space for subsequent invasions by more impactful invaders (i.e. invasional meltdown; Ricciardi et al., 2013; Simberloff & Von Holle, 1999). Third, invasive plants could amplify the impacts of one another if they compete with native species at different times and across space (Simberloff & Von Holle, 1999). Competition from multiple non-native species could therefore have a greater community level impact than would result from a smaller number of non-native species. For the first two mechanisms, we would expect greater negative impacts in areas with high richness

but low evenness of non-native plants, which would indicate the presence of multiple non-native species but one or a few focal invaders that dominate cover. For the third mechanism, we would expect greater negative impacts in areas with high richness and high evenness, indicating that cover is evenly distributed across the invading species.

Analysing changes to native community diversity as a function of non-native cover is a common way to assess community-level impacts associated with invasions (e.g. Bradley et al., 2019; Pearse et al., 2019). At local scales, analysis of these parameters reveals variation in per capita impacts with species' nativity (Pearse et al., 2019), identity (Pearson et al., 2016) and in some cases, environment (Brewer, 2011). At macroscales, existing vegetation surveys provide a means for using these parameters to quantify trends in impacts that can later be analysed to reveal the mechanistic underpinnings of variation in invasion impact, which would be a substantial step towards predicting and mitigating these impacts (Bradley et al., 2019; Ricciardi et al., 2021; Sofaer et al., 2018; Yokomizo et al., 2009). To our knowledge, we provide the first macroecological analysis identifying factors associated with variation in the relationship between non-native plant cover and native community diversity. We hypothesized that this relationship would vary with the environmental context, as measured by ecosystem productivity and human activity, and with the richness and evenness of the invading plants.

2 | MATERIALS AND METHODS

2.1 | Overview

We used a collated dataset of 11,578 vegetation surveys (a subset of Petri et al., 2023) to quantify how three native community response variables (native plant richness, diversity, and evenness) varied depending on four interaction terms: the interaction between absolute non-native plant cover and (1) productivity, (2) human activity, (3) the richness of non-native plants and (4) the evenness of non-native plants. We assessed the relationship between each response variable and the interaction terms using generalized linear mixed effects models ('glmmTMB' v. 1.0.2.1 R package), which were robust to a large sample size, multiple interaction terms and random effects to account for a complex spatial structure across datasets.

2.2 | Vegetation data

We used vegetation surveys collated and described by the Standardized Plant Community with Introduced Status Database (SPCIS) (Petri et al., 2023). Developers of the SPCIS dataset combined and standardized nine data sources that recorded the absolute percent cover of all plant species observed in plots and along transects distributed across the United States. SPCIS contains standardized taxonomy to the USDA PLANTS Database (https://plants.sc.egov.usda.gov/java/), with most taxa identified to the species level and remaining taxa identified to the level of genus or unidentified by data recorders. For each identified species or genus, SPCIS used the USDA PLANTS Database to assign nativity to the lower 48 United States, identifying taxa as native, non-native, or ambiguous nativity depending on the region within the United States. From the 43,867 invaded sampling units provided by SPCIS, we selected plots in the lower 48 United States that followed the most similar sampling protocols, which reduced the sample size to ~30,000 plots where plant cover was either sampled within canopy layers and then summed across layers to result in one absolute cover measure per species per plot, cover was not collected with canopy layers, or the canopy-specific cover measurements were integrated by the data source (Petri et al., 2023). For plots that had been resampled over time, we selected the most recent sampling date.

We further reduced the sample size to include only plots invaded by at least two non-native plants (needed to test hypotheses about non-native richness and evenness) and with <10% relative cover of species with unknown native status. The latter includes taxa associated with an estimated cover but with ambiguous nativity or unknown species level identity. This reduced the sample size to ~16,000 plots sampled by the Bureau of Land Management Assessment Inventory and Monitoring program (AIM), Carolina Vegetation Survey (CVS) (Peet et al., 2017), Forest Inventory & Analysis Phase 3 vegetation surveys (FIA), Illinois Critical Trends Assessment Program (IL_CTAP), National Ecological Observatory Network (NEON, 2019), National Park Service Inventory & Monitoring data (NPS), National Wetland Condition Assessment (NWCA), Virginia Natural Heritage Program (VNHP), and West Virginia Natural Heritage Program (WVNHP). Although several of these datasets focus sampling effort on less invaded areas (Petri et al., 2023), each dataset included multiple plots sampled at >50% relative cover of non-native plants, providing a robust sample size of plots across ecosystems that varied from low to high invasion (Figure 2).

Input datasets differed in the continuous cover value assigned to species present in a plot but at very low abundance (e.g. FIA assigned trace abundance a cover value of 0.0025% while NPS assigned a value of 0.5%), which resulted in an uneven distribution of plots across low values of percent cover. We used a change point analysis (Fong et al., 2017) to understand the potential influence of these plots. This analysis indicated that the effect of non-native cover on native community diversity differed between plots with less than and more than 2% non-native cover (Appendix S1), most likely because plots were clustered around certain cover values in this range. Plots with <2% non-native cover were therefore removed from analyses, reducing the sample size to ~13,000 plots. This also reduced differences among datasets and allowed us to focus on plots that were more likely to have an established population of non-native plants and thus more likely to experience measurable impacts on native communities.

Lastly, input datasets differed in whether plots were distributed across the United States (NEON and NPS data) or sampled a specific geographic region (CVS and AIM plots) or ecosystem type (FIA sampled forested ecosystems). Plot size was often adjusted
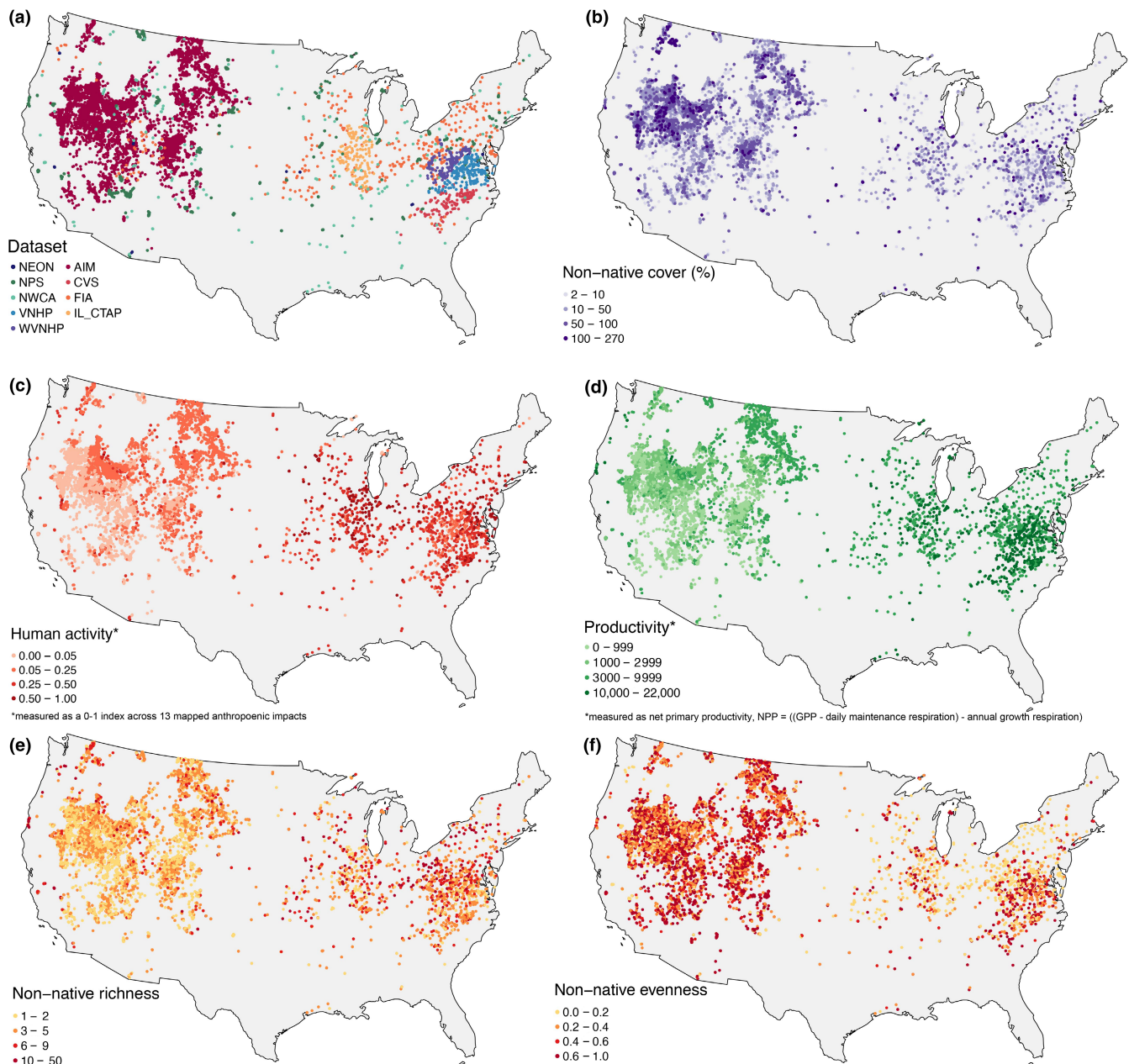
FIGURE 2 Predictor variables for plots included in the analysis by (a) data source, (b) absolute non-native cover (%), (c) human activity; higher values indicate more modified areas, (d) net primary productivity derived from remotely sensed data; higher values indicate more productive areas, (e) non-native plant richness and (f) non-native plant evenness.

in response to ecosystem type (e.g. smaller plots in herbaceous community types and larger plots in forests), and plot shape varied with dataset (Petri et al., 2023). To ensure these differences would not confound results, we conducted exploratory analyses on the covariance among variables (Figures S2–S13) and the effect of each variable on the association between native richness and non-native cover (Figures S14–S16). Most plot differences were associated with area sampled, data source, dominant vegetation type, and ecoregion, which together covaried with other sources of variation that could influence results (e.g. plot shape, sampling technique, canopy complexity). Area sampled, data source, dominant vegetation type and ecoregion were therefore included in

all models (discussed below), so as not to mistakenly attribute variation in each response variable to invasion impact. We only included level 4 ecoregions with five or more plots, which reduced the final sample size to 11,578 plots (26% of the invaded plots in SPCIS).

2.3 | Response variables

From the species level cover measurements provided by SPCIS, we calculated response variables of native plant richness, diversity and evenness per plot (Figure S11). We elected to use Simpson's diversity

and Evar evenness instead of Shannon's diversity and Pielou's evenness because the latter are more correlated with species richness (Camargo, 1995; Smith & Wilson, 1996). Native Simpson's diversity was calculated for plots with at least one native species and native evenness was calculated for plots with at least two native species, which reduced the sample size from 11,578 for native richness to 11,510 for the model of native diversity and 11,276 for the model of native evenness. The sample size for native diversity was further reduced to 11,508 because two plots were identified as outliers (diversity index >40, whereas the mean across plots was 5).

We fit a generalized linear mixed effects model to each response variable. The model of native richness was fit using a negative binomial distribution with quadratic parameterization to account for overdispersed count data. The models for native diversity and native evenness were both fit using a Gaussian distribution.

2.4 | Fixed effects

Fixed effects that measured productivity and human activity were extracted at each plot location from existing spatial datasets. Productivity was measured using net primary productivity (NPP) estimated with remotely sensed data at a 250-m resolution (NPP_{M250} from MODIS developed by Robinson et al., 2018). Because NPP may be affected by the abundance of non-native plants (Bradley & Mustard, 2006; Vilà & Ibáñez, 2011), we also associated plot locations with different measures of water availability, including soil water deficit (Trabucco & Zomer, 2019a), the Priestley-Taylor alpha coefficient (quantifies aridity stress on vegetation) (Trabucco & Zomer, 2019b), potential water deficit (Abatzoglou, 2013) and the global aridity index (Trabucco & Zomer, 2019a). Measures of productivity were highly correlated with one another (all correlation coefficients >0.8). We reported results of the best fit model given AIC, which used NPP.

Human activity was derived from the Global Human Modification Map at a 1 km resolution (GHM; Kennedy et al., 2018). This dataset provides an estimate of the anthropogenic effect on the earth based on spatial data quantifying the impact of 13 different factors (e.g. transportation corridors, human population density), several of which are directly associated with invasive plant propagule pressure (e.g. distance to roads). As a secondary measure of human activity, we calculated the Euclidean distance from each plot to the nearest parcel of land dominated by humans (developed and cultivated/planted land cover classes) based on land classifications in the National Land Cover Database (Homer et al., 2012). These variables were also correlated with one another. We reported results of the best fit model given AIC, which used the Global Human Modification Index.

For each plot, we calculated the absolute cover, richness, and evenness of non-native plants. Because the datasets recorded species percent cover within multiple canopy layers, the cover of an individual species never exceeded 100% per plot but absolute cover summed across non-native plants sometimes exceeded 100%, with a maximum value of 270% cover. However, 97% of the plots had <100% non-native cover, so we bound model predictions at 100%

(plots with cover >100% did not change model output and were retained for model fitting). We included non-native richness to test whether the effect of non-native cover was stronger in plots with multiple invading plant species (high richness), and we included non-native evenness to test whether this effect was driven by a dominant invader (low evenness) or the cumulative abundance of multiple non-native species (high evenness).

We included data source, longitude, and latitude as fixed effects to account for differences in sampling approach, vegetation type and spatial autocorrelation. Focal continuous predictor variables were rescaled to comparable values using different scaling factors depending on the range of the raw data (e.g. productivity varied between 100–20,000 whereas human modification varied between 0–1; see Supporting Code).

2.5 | Model structure and random effects

To determine a best fit model structure that accounted for spatial autocorrelation among plots, we first assessed the fit of several spatial and non-spatial models to the dataset, including autoregressive, generalized least squares, autocovariate and spatial eigenvector models (Dormann et al., 2007). However, spatially explicit models are rarely robust to non-random distributions of plots (i.e. variable neighbourhood distances) and few spatial model structures incorporate random effects (Dormann et al., 2007). Non-spatial models with built-in spatial covariance structures are an alternative, but these models can be extremely computationally intensive to fit with a large sample size because they often account for spatial structure by computing pairwise distances among plots. In contrast, generalized linear mixed effects models are well suited to large sample sizes and complex interaction terms. We found that including longitude, latitude and data source as fixed effects (broader spatial patterning), and vegetation type and ecoregion as random effects (finer grain spatial patterning), greatly reduced spatial autocorrelation in the residuals. We therefore continued with this approach, which we found to be the model structure best equipped to handle such a large sample size, multiple interaction terms and variation in sampling effort across datasets and geographies.

Random intercept effects of dominant vegetation type and ecoregion were included to reduce spatial autocorrelation and to account for as much extrinsic variation in vegetation types as possible, such that remaining variation in each response variable could be attributed to the focal predictor variables. Random effects included dominant vegetation type (National Land Cover Database; Homer et al., 2012), and level 4 ecoregion (Figure S1), which is the finest scale categorization of similar ecosystem types provided by the U.S. Environmental Protection Agency. Plots were sampled across eight vegetation types (Figure S5) and 253 ecoregions of the lower 48 United States (Figure S3). Including both variables as random effects on the intercept greatly reduced AIC compared to random slope effects (ΔAIC > 100) as well as matched patterns observed in the raw data (Figures S14–S16).

We also categorized and included area sampled as a random intercept effect. Across data sources, area sampled varied from 1 to

10,000 m². Area sampled did not have a strong directional effect on non-native plant cover measurements but did influence the response variables of native plant richness and evenness (Figure S13). The effect was predominantly on the intercept of each response variable and did not appear to strongly influence the shape of the association with non-native cover (Figures S14–S16). We therefore categorized area sampled based on logical breaks in the data and included this variable as a random intercept effect.

The final model for each response variable included fixed effects representing four interactions with non-native cover: (1) productivity, (2) human activity, (3) non-native richness and (4) non-native evenness. These variables were also included as direct fixed effects, with three additional direct fixed effects (dataset, longitude, latitude) and three random intercept effects (vegetation type, ecoregion, area sampled) included to account for spatial patterning. We used model selection based on AIC to determine this model structure. Each model was validated against a null model (see Appendix S1), which used the same probability distribution and random effects structure but lacked fixed effects. Model estimates, standard errors and *p*-values are reported in Table 1 and Table S1.

3 | RESULTS

Higher non-native plant cover was associated with lower native plant richness and diversity and higher native plant evenness (Figure 3). Non-native cover, non-native richness, and non-native evenness tended to have the largest effect sizes compared to the other predictor variables (Table 1), indicating strong and statistically significant ($p < 0.05$) associations with each response variable. The model estimates suggested

that on average, a 10% cover increase of non-native plants was associated with a decline in native richness of one species. There was some residual spatial autocorrelation among plots (Figures S17–S19) but Moran's *I* values were reduced compared to null models and were close to the recommended value of zero (richness: 0.24, diversity: 0.19, evenness: 0.09; Gittleman & Kot, 1990).

3.1 | Productivity

Native plant richness and diversity were higher in areas with higher NPP, whereas native plant evenness was lower. The association between each response variable and non-native cover was not altered by NPP (Figure 4a–c) (i.e. no statistically significant interactions between NPP and non-native cover).

3.2 | Human activity

Areas with higher human activity had significantly lower native richness, lower native diversity, and higher native evenness. Human activity did not significantly interact with non-native cover to influence any of the response variables (Figure 4d–f).
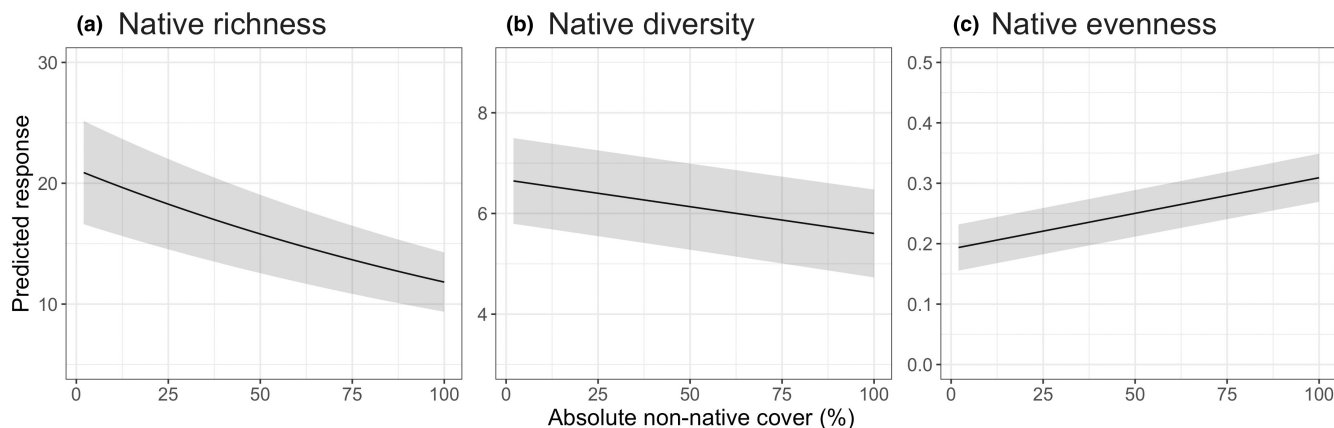
3.3 | Non-native richness

Non-native richness was significantly and positively associated with native plant richness, diversity, and evenness (Table 1). The

TABLE 1 Model estimates (B), standard errors (SE), and *p*-values (*p*) for best fit models of response variables native richness, diversity, and evenness.

Fixed effects	Response variable								
	Native richness ($n = 11{,}578$)			Native diversity ($n = 11{,}508$)			Native evenness ($n = 11{,}281$)		
	B	SE	*p*	B	SE	*p*	B	SE	*p*
Non-native cover	−0.91	0.06	<0.005**	−2.52	0.31	<0.005**	0.19	0.02	<0.005**
Productivity	0.05	0.01	<0.005**	0.30	0.08	<0.005**	−0.009	0.005	0.050*
Human activity	−0.07	0.01	<0.005**	−0.21	0.06	<0.005**	0.009	0.004	0.0175*
Log non-native richness	0.11	0.01	<0.005**	0.23	0.08	<0.005**	0.02	0.005	<0.005**
Non-native evenness	−0.11	0.02	<0.005**	−0.09	0.13	0.520	0.09	0.008	<0.005**
Non-native cover × NPP	−0.02	0.02	0.370	−0.16	0.12	0.177	−0.003	0.007	0.637
Non-native cover × GHM	0.005	0.02	0.797	0.15	0.12	0.183	−0.009	0.007	0.204
Non-native cover × log non-native richness	0.23	0.03	<0.005**	0.91	0.16	<0.005**	−0.03	0.01	<0.005**
Non-native cover × non-native evenness	0.12	0.07	0.065*	0.74	0.34	0.029**	−0.06	0.02	<0.005**
Longitude	0.02	0.002	<0.005**	0.06	0.007	<0.005**	−0.002	0.0004	<0.005**
Latitude	0.01	0.005	0.005**	−0.03	0.02	0.123	−0.009	0.001	<0.005**

Note: For simplicity, model estimates for the effect of dataset are reported in Table S1 and random effects are presented in Figures S20–S22. Focal predictor variables were rescaled to comparable values.

**p < 0.05; *p < 0.10 (marginally significant).

FIGURE 3 The mean relationship between absolute non-native plant cover and native plant (a) richness, (b) diversity and (c) evenness. Each relationship is predicted from the best fit model for each response variable, with all other predictor variables held at their mean. All relationships are statistically significant ($p < 0.05$). Shaded regions represent 95% CIs.

interaction between non-native plant richness and non-native cover was also significant for all three response variables: areas with low non-native richness showed steeper decreases to native richness and diversity, and a steeper increase in native evenness (Figure 4g–i).

3.4 | Non-native evenness

Non-native evenness was negatively associated with native richness, had no association with diversity ($p = 0.52$), and was positively associated with native evenness (Table 1). Non-native evenness altered the associations between all three response variables and non-native cover, although the effect on native richness was only marginally statistically significant ($p = 0.065$). The models predicted that when non-native evenness was low (cover was dominated by fewer species), declines were stronger in native richness and diversity and native evenness had a steeper increase as non-native cover increased (Figure 4j–l).

4 | DISCUSSION

In invasion ecology, it was unclear how invasive plant impacts vary across broad environmental gradients. In this study, we address this knowledge gap using newly available plant survey data (Petri et al., 2023) to identify factors that influence the association between non-native plant cover and native plant richness, diversity, and evenness. Across the continental United States, we found that greater cover of non-native plants was associated with lower native plant richness and diversity, and higher native plant evenness. The magnitude of change in each native response variable was primarily explained by the cover, richness and evenness of the invading plants, and their interactions. Native plant richness and diversity were lowest in plant communities with high non-native cover, low non-native richness and low non-native evenness, indicating the presence of one or a few dominant invaders. Contrary to our hypotheses, the association between native community

diversity and non-native cover was consistent across gradients of productivity and human activity. These findings indicate that at the macroscale, potential impacts on native diversity are more dependent on the composition of the invading community than on environmental factors.

Highly productive environments had higher native plant richness and diversity, but slightly lower native plant evenness. Productivity did not alter the association between any native species response variable and non-native plant cover, indicating that invasion impact is not sensitive to resource availability at broad scales. Regardless of productivity, communities nearing 100% absolute cover of non-native plants supported an average of 10 fewer native species compared to similar communities with low invader cover (Figures 3 and 4a). Many experiments and some observational studies have found that productive environments host species-rich native communities, which can exhibit biotic resistance to invasive plant establishment (Beaury et al., 2020; Levine et al., 2004, but see Stohlgren et al., 1999). However, our findings suggest that once invasive plants successfully establish and become abundant, species-rich native communities can be equally susceptible to losing that richness. In communities with few native species, the further loss of richness might have a particularly large negative effect on ecosystem functioning (i.e. loss of functional diversity).

Anthropogenic activities are well known to contribute to higher invasive plant establishment (Beaury et al., 2020) and spread (Vilà & Ibáñez, 2011). Here, we found that high human activity also was associated with lower native plant richness and diversity, but human activity did not significantly alter the strength of the interactions between native and non-native species. Our results therefore indicate that ecosystem types spanning gradients of productivity and human activity are similarly vulnerable to the impacts of invading plants. Interestingly, for all native response variables, the negative association with non-native cover was larger in magnitude than the direct negative effect of human activity or the positive association with productivity, supporting
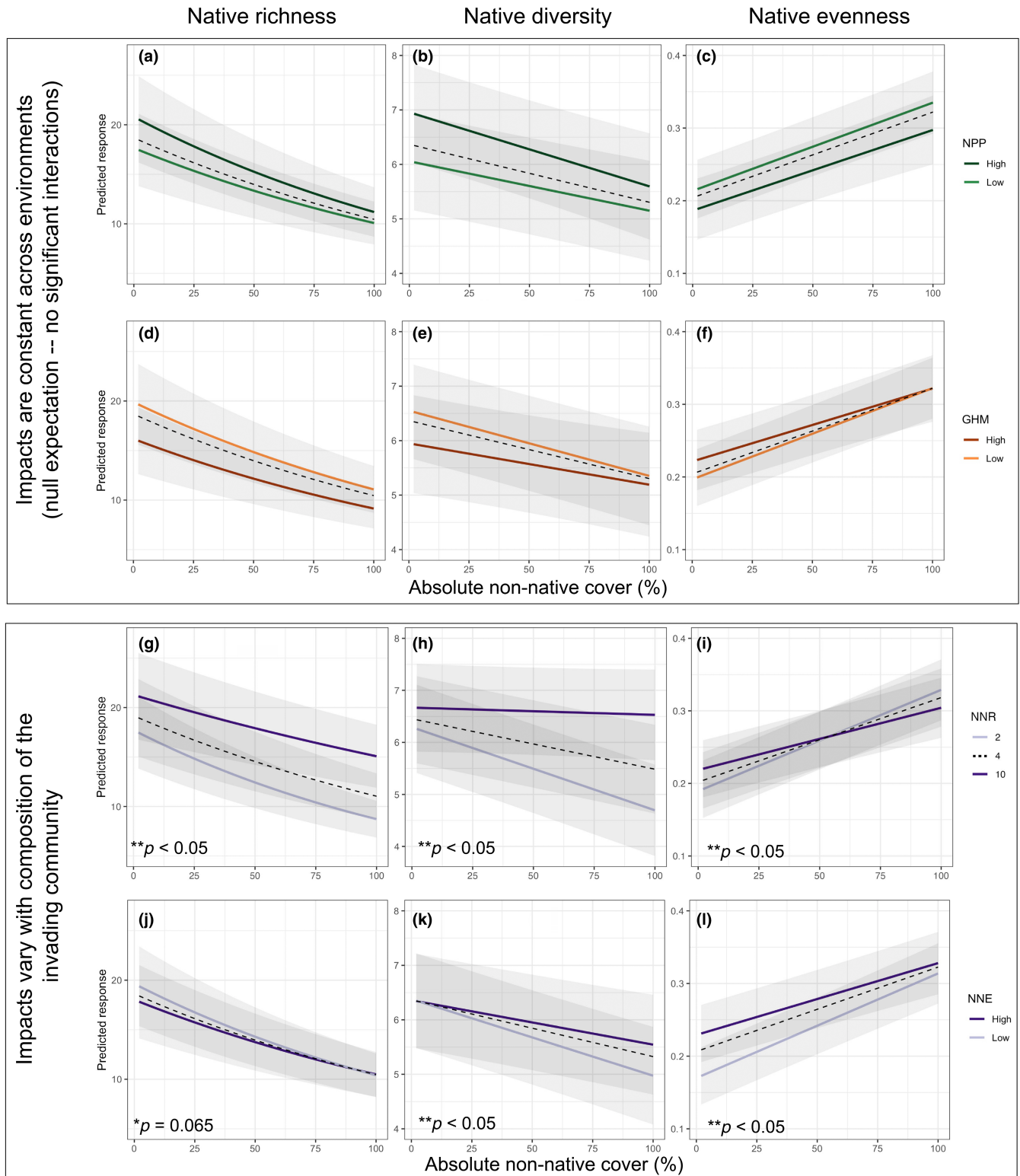
FIGURE 4 Relationships between non-native cover and native plant richness, diversity, and evenness across gradients of net primary productivity (NPP; a–c), human activity (measured as global human modification, GHM; d–f), non-native plant richness (NNR; g–i), and non-native plant evenness (NNE; j–l). All relationships were predicted from the global model fit to each response variable. Panels with statistically significant interactions (**$p < 0.05$ with one interaction *$p < 0.07$) are indicated. Dashed lines represent mean conditions, darker colour lines (high NPP, GHM, NNR, NNE) represent the mean plus two standard deviations of the mean, and lighter colour lines (low NPP GHM, NNR, NNE) represent the minimum value (predictor variables were right skewed, so the mean minus two standard deviations fell below the observed minimum value). Shaded regions are 95% CIs.

recent findings that, at the local scale, invasive species may have greater ecological impacts than other forms of anthropogenic global change (Lopez et al., 2022; Vilà et al., 2021). This could be influenced by the fact that most of the vegetation surveys we analysed were located in relatively pristine areas (e.g. National Parks) and the measure of human activity we used may not have captured local-scale disturbances. Detecting and classifying smaller disturbances remains a challenge for continental-scale analyses and warrants further investigation at both local and broad scales, including a need for more data collected in areas highly susceptible to invasions (i.e. in modified environments).

While productivity and human activity did not influence the relationship between non-native cover and native community diversity, the composition of the invading plant community significantly altered invasive plant impact. The steepest negative relationships between non-native cover and each native response variable occurred in plots with dominant invaders (high cover despite low non-native richness and evenness). This finding is consistent with the hypothesis that non-native species have different per capita effects (Pearson et al., 2016; Sofaer et al., 2018), with superior competitors resulting in greater negative impacts. This is also consistent with the hypothesis that most non-native plants will not reach high enough abundance to be considered invasive, but rather naturalize and behave functionally like native species (Simberloff et al., 2012). Stronger impacts at low non-native richness could also indicate that facilitation among non-native species, that is invasional meltdown (Simberloff & Von Holle, 1999), is more important during earlier stages of invasion but has less of an influence on community-level impacts.

On average, our results suggest that when a dominant invader is present and reaches high abundance, native communities could lose up to half their diversity. This negative effect was buffered in areas with high non-native richness, which also tended to have higher numbers of native species associated with high productivity (Table 1; Figure 3). It could be possible that high productivity/high resource availability facilitates the coexistence of high native and non-native richness, as well as reduces the magnitude of invasion impact (Godoy, 2019) but this was not supported across the productivity gradient. Other studies have proposed that a positive association between native and non-native richness indicates 'biotic acceptance' (Stohlgren et al., 1999) but more recent findings support that this positive association in observational data is more likely the result of native and non-native species responding to the same environmental cues (Beaury et al., 2020). We are not able to identify the relative role of impact, resistance and shared responses to environmental drivers but these associative tests do capture mean trends in invasion outcomes that are consistent across a broad set of ecosystems and that undoubtedly result from the interplay of multiple factors.

Across the dataset, plots with higher non-native plant cover had lower native plant richness and diversity but higher evenness. This suggests that heavily invaded communities had fewer rare species (e.g., McKinney, 2004) and/or dominant native species were less abundant

(Camargo, 1995; Smith & Wilson, 1996). While theoretical frameworks propose that the latter is more likely (Powell et al., 2011), it is unknown how frequently invasive plants impact rare versus common native species across ecosystems. However, the concomitant decrease in native species richness and increase in evenness suggests that rare native plants are being lost. In general, the strong associations between native plant diversity and the composition of the invading plants indicate that the geographic distribution of invasion levels can provide a first approximation of geographic variation in invasion impact. For example, areas with high invader cover, low native plant richness and high native evenness were predominantly located in the western United States but occurred across the geographic extent of the dataset (Figure 2; Figure S11). The raw data also showed higher non-native richness and productivity in the eastern United States, which could indicate that high native and non-native richness respond and (likely contribute) to high productivity (Table 1; Figure S11). Human activity also tended to be higher in the eastern and midwestern United States, which captures the history of human colonization, urbanization, and intensive agriculture characteristic of these regions, all of which have been previously associated with high levels of invasion (Beaury et al., 2020; Lonsdale, 1999; Seabloom et al., 2006; Vilà & Ibáñez, 2011).

5 | CONCLUSIONS & DATA LIMITATIONS

The geographic breadth and variation of the dataset provided a novel opportunity to look at associations between non-native cover and native diversity that informed our understanding of mean trends in invasion impacts. We found consistent evidence that non-native plant invasions were negatively associated with native plant community diversity, and the strength of the relationships was primarily a function of interactions between non-native plant cover and non-native species richness and evenness. Productivity and human activity have previously been linked to invasive species establishment and spread, but their lack of influence here indicates that these measures of environmental context may be less important in determining impact magnitude, that is the effects of a given increase in invader cover. Our data represent extreme differences across productivity and human activity gradients, but it is possible that macroscale measures of these variables were too coarse to explain plot-level variation in impact. Until better data become available, local scale studies could give more attention to how the environmental context shapes a native community's ability to maintain diversity. Future work could also compare the importance of invader community attributes and environmental context across global environmental gradients, including studies of areas with high invasion impacts, such as oceanic islands, or high native diversity, including many tropical regions. Such work would yield a more nuanced understanding of geographic and cross-biome vulnerability to high invasion impacts and the degree to which these can be approximated by invader abundance.

In general, observational surveys such as those examined here are somewhat limited in their measure of invasion impact because they represent a single snapshot in time (i.e. impacts may lag behind the level of

invader cover observed at any one point in time) are sensitive to plot-area effects (Ibáñez et al., 2023), and it is difficult to disentangle invasion impact from other environmental influences on native plant communities. Measuring how native diversity responds to invasion over time would address questions about invasion impacts, but these data are often geographically restricted (e.g., IL_CTAP) or do not yet span enough time to capture invasion impacts (e.g., NEON). These constraints limited our analysis to capturing mean, macroscale trends in community-level impacts that undoubtedly vary with more factors than we were able to account for here. Finally, the negative relationship between invader cover and native diversity could reflect two types of biotic interactions – invasion impact (high invader cover results in low native richness) and biotic resistance (high native richness results in low invader cover). Our work could not distinguish between these mechanisms, and it is likely that both influence invasion outcomes; understanding the mechanisms underlying these interactions is a priority of future studies.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government.

DATA AVAILABILITY STATEMENT

Data and code used for analyses are publicly available on FigShare: https://figshare.com/projects/Macroscale_associations_between_non-native_cover_and_native_diversity/157644. The data are subsetted from a larger project compiling vegetation surveys across North America: Petri, Laís, Beaury, Evelyn M., Corbin, Jeffrey, Peach, Kristen, Sofaer, Helen, Pearse, Ian S., Early, Regan, et al. 2023. "SPCIS: standardized plant community with introduced status database." *Ecology* e3947. 10.1002/ecy.3947. The subset of the data we used and the environmental variables associated with each plot location are also publicly available on FigShare: 10.6084/m9.figshare.21916842.

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REFERENCES

Abatzoglou, J. T. (2013). Development of gridded surface meteorological data for ecological applications and modelling. *International Journal of Climatology*, 33, 121–131.

Barney, J. N., & Tekiela, D. R. (2020). Framing the concept of invasive species "impact" within a management context. *Invasive Plant Science and Management*, 13, 37–40.

Beaury, E. M., Finn, J. T., Corbin, J. D., Barr, V., & Bradley, B. A. (2020). Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecology Letters*, 23, 476–482.

Beaury, E. M., Patrick, M., & Bradley, B. A. (2021). Invaders for sale: The ongoing spread of invasive species by the plant trade industry. *Frontiers in Ecology and the Environment*, 19, 550–556. https://doi.org/10.1002/fee.2392

Bradley, B. A., Laginhas, B. B., Whitlock, R., Allen, J. M., Bates, A. E., Bernatchez, G., Diez, J. M., Early, R., Lenoir, J., Vilà, M., & Sorte, C. J. B. (2019). Disentangling the abundance–impact relationship for invasive species. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 9919–9924.

Bradley, B. A., & Mustard, J. F. (2006). Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecological Applications*, 16, 1132–1147.

Brewer, J. S. (2011). Per capita community-level effects of an invasive grass, *Microstegium vimineum*, on vegetation in mesic forests in northern Mississippi (USA). *Biological Invasions*, 13, 701–715.

Camargo, J. A. (1995). On measuring species evenness and other associated parameters of community structure. *Oikos*, 74, 538–542.

Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, 15, 22–40.

Crystal-Ornelas, R., & Lockwood, J. L. (2020). The 'known unknowns' of invasive species impact measurement. *Biological Invasions*, 22, 1513–1525.

Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, 88(3), 528–534.

Didham, R. K., Tylianakis, J. M., Gemmell, N. J., Rand, T. A., & Ewers, R. M. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution*, 22, 489–496.

Dormann, C. F., McPherson, J. M., Araújo, M. B., Bivand, R., Bolliger, J., Carl, G., Davies, R. G., Hirzel, A., Jetz, W., Kissling, W. D., Kühn, I., Ohlemüller, R., Peres-Neto, P. R., Reineking, B., Schröder, B., Schurr, F. M., & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, 30(5), 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x

Fong, Y., Huang, Y., Gilbert, P. B., & Permar, S. R. (2017). chngpt: Threshold regression model estimation and inference. *BMC Bioinformatics*, 18, 454.

Gittleman, J. L., & Kot, M. (1990). Adaptation: Statistics and a null model for estimating phylogenetic effects. *Systematic Biology*, 39, 227–241.

Godoy, O. (2019). Coexistence theory as a tool to understand biological invasions in species interaction networks: Implications for the study of novel ecosystems. *Functional Ecology*, 33(7), 1190–1201.

Goldberg, D. E., Rajaniemi, T., Gurevitch, J., & Stewart-Oaten, A. (1999). Empirical approaches to quantifying interaction intensity:

Competition and facilitation along productivity gradients. *Ecology*, 80, 1118–1131.

Goldstein, L. J., & Suding, K. N. (2014). Applying competition theory to invasion: Resource impacts indicate invasion mechanisms in California shrublands. *Biological Invasions*, 16, 191–203.

Hejda, M., Pyšek, P., & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, 97, 393–403.

Homer, C. H., Fry, J. A., & Barnes, C. A. (2012). The National Land Cover Database. U.S. Geological Survey Fact Sheet 2012–3020. https://doi.org/10.3133/fs20123020

Hulme, P. E., Pyšek, P., Jarošík, V., Pergl, J., Schaffner, U., & Vilà, M. (2013). Bias and error in understanding plant invasion impacts. *Trends in Ecology & Evolution*, 28, 212–218.

Ibáñez, I., Petri, L., Barnett, D. T., Beaury, E. B., Blumenthal, D. M., Corbin, J. D., Diez, J., Dukes, J. S., Early, R., Pearse, I. S., Sorte, C. J. B., Vilà, M., & Bradley, B. (2023). Combining local, landscape, and regional geographies to assess plant community vulnerability to invasion impact. *Ecological Applications*, 33, e2821.

Kennedy, C. M., Oakleaf, J., Theobald, D. M., Baruch-Mordo, S., & Kiesecker, J. (2018). Global human modification. figshare. Dataset. https://doi.org/10.6084/m9.figshare.7283087.v1

Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J. M., Pyšek, P., Ricciardi, A., Bacher, S., Blackburn, T. M., Dick, J. T. A., Evans, T., Hulme, P. E., Kühn, I., Mrugała, A., Pergl, J., Rabitsch, W., Richardson, D. M., Sendek, A., & Winter, M. (2015). Ecological impacts of alien species: Quantification, scope, caveats, and recommendations. *Bioscience*, 65, 55–63. https://doi.org/10.1093/biosci/biu193

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

Lonsdale, W. M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology*, 80, 1522–1536.

Lopez, B., Allen, J. M., Dukes, J. S., Lenoir, J., Vilà, M., Blumenthal, D. M., Beaury, E. M., Fusco, E. J., Laginhas, B. B., Morelli, T. L., & O'Neill, M. W. (2022). Biological invasions interact with global environmental change to create ecological surprises. *Proceedings of the National Academy of Sciences of the United States of America*, 119(22), e2117389119.

MacDougall, A. S., Boucher, J., Turkington, R., & Bradfield, G. E. (2006). Patterns of plant invasion along an environmental stress gradient. *Journal of Vegetation Science*, 17, 47–56.

Maestre, F. T., Callaway, R. M., Valladares, F., & Lortie, C. J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, 97(2), 199–205.

McKinney, M. L. (2004). Do exotics homogenize or differentiate communities? Roles of sampling and exotic species richness. *Biological Invasions*, 6, 495–504.

NEON (2019). National ecological observatory network plant presence and percent cover (DP1.10058.001) and vegetation structure (DP1.10098.001) data. Accessed May, 2020.

Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., Williamson, M. H., von Holle, B., Moyle, P. B., Byers, J. E., & Goldwasser, L. (1999). Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, 1, 3–19.

Pearse, I. S., Sofaer, H. R., Zaya, D. N., & Spyreas, G. (2019). Non-native plants have greater impacts because of differing per-capita effects and nonlinear abundance–impact curves. *Ecology Letters*, 22, 1214–1220.

Pearson, D. E., Ortega, Y. K., Eren, Ö., & Hierro, J. L. (2016). Quantifying "apparent" impact and distinguishing impact from invasiveness in multispecies plant invasions. *Ecological Applications*, 26, 162–173.

Peet, R., Palmquist, K., Schafale, M., Weakley, A., & Lee, M. (2017). Carolina Vegetation Survey: An initiative to improve regional implementation of the U.S. National Vegetation Classification. *Phytocoenologia*, 48, 171–179.

Petri, L., Beaury, E. M., Corbin, J., Peach, K., Sofaer, H., Pearse, I. S., Early, R., Barnett, D. T., Ibáñez, I., Peet, R. K., Schafale, M., Wentworth, T. R., Vanderhorst, J. P., Zaya, D. N., Spyreas, G., & Bradley, B. A. (2023).

SPCIS: Standardized plant community with introduced status database. *Ecology*, 104(3), e3947. https://doi.org/10.1002/ecy.3947

Powell, K. I., Chase, J. M., & Knight, T. M. (2011). A synthesis of plant invasion effects on biodiversity across spatial scales. *American Journal of Botany*, 98, 539–548.

Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). 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 Biology*, 18, 1725–1737.

Pyšek, P., Richardson, D. M., Pergl, J., Jarošík, V., Sixtová, Z., & Weber, E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution*, 23, 237–244.

Rees, M. (2013). Competition on productivity gradients – What do we expect? *Ecology Letters*, 16, 291–298.

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs*, 83, 263–282.

Ricciardi, A., Iacarella, J. C., Aldridge, D. C., Blackburn, T. M., Carlton, J. T., Catford, J. A., Dick, J. T. A., Hulme, P. E., Jeschke, J. M., Liebhold, A. M., Lockwood, J. L., MacIsaac, H. J., Meyerson, L. A., Pyšek, P., Richardson, D. M., Ruiz, G. M., Simberloff, D., Vilà, M., & Wardle, D. A. (2021). Four priority areas to advance invasion science in the face of rapid environmental change. *Environmental Reviews*, 29, 119–141.

Robinson, N. P., Allred, B. W., Smith, W. K., Jones, M. O., Moreno, A., Erickson, T. A., Naugle, D. E., & Running, S. W. (2018). Terrestrial primary production for the conterminous United States derived from Landsat 30 m and MODIS 250 m. *Remote Sensing in Ecology and Conservation*, 4, 264–280.

Seabloom, E. W., Williams, J. W., Slayback, D., Stoms, D. M., Viers, J. H., & Dobson, A. P. (2006). Human impacts, plant invasion, and imperiled plant species in California. *Ecological Applications*, 16, 1338–1350.

Simberloff, D., Souza, L., Nuñez, M. A., Barrios-Garcia, M. N., & Bunn, W. (2012). The natives are restless, but not often and mostly when disturbed. *Ecology*, 93, 598–607.

Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions*, 1, 21–32.

Smith, B., & Wilson, J. B. (1996). A Consumer's guide to evenness indices. *Oikos*, 76, 70–82.

Sofaer, H. R., Jarnevich, C. S., & Pearse, I. S. (2018). The relationship between invader abundance and impact. *Ecosphere*, 9, e02415.

Sofaer, H. R., Jarnevich, C. S., Pearse, I. S., Smyth, R. L., Auer, S., Cook, G. L., Edwards, T. C. Jr, Guala, G. F., Howard, T. G., Morisette, J. T., & Hamilton, H. (2019). Development and delivery of species distribution models to inform decision-making. *BioScience*, 69(7), 544–557.

Stohlgren, T. J., Binkley, D., Chong, G. W., Kalkhan, M. A., Schell, L. D., Bull, K. A., Otsuki, Y., Newman, G., Bashkin, M., & Son, Y. (1999). Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, 69, 25–46.

Stotz, G. C., Pec, G. J., & Cahill, J. F. (2016). Is biotic resistance to invaders dependent upon local environmental conditions or primary productivity? A meta-analysis. *Basic and Applied Ecology*, 17, 377–387.

Tilman, D. (2020). *Plant strategies and the dynamics and structure of plant communities. (MPB-26)* (Vol. 26). Princeton University Press.

Trabucco, A., & Zomer, R. (2019a). Global high-resolution soil-water balance. figshare. Dataset. https://doi.org/10.6084/m9.figshare.7707605.v3

Trabucco, A., & Zomer, R. (2019b). Global aridity index and potential evapotranspiration (ET0) climate database v2. figshare. Dataset. https://doi.org/10.6084/m9.figshare.7504448.v3

Verbrugge, L. N. H. (2010). Evaluation of international risk assessment protocols for exotic species. 59.

Vilà, M., Beaury, E. M., Blumenthal, D. M., Bradley, B. A., Early, R., Laginhas, B. B., Trillo, A., Dukes, J. S., Sorte, C. J. B., & Ibáñez, I. (2021). Understanding the combined impacts of weeds and climate change on crops. *Environmental Research Letters*, 16, 034043.

Vilà, M., & Ibáñez, I. (2011). Plant invasions in the landscape. *Landscape Ecology*, *26*, 461–472.

Yokomizo, H., Possingham, H. P., Thomas, M. B., & Buckley, Y. M. (2009). Managing the impact of invasive species: The value of knowing the density–impact curve. *Ecological Applications*, *19*, 376–386.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

BIOSKETCH

The authors are part of a larger research group interested in invasive species and global change. Several participating members have collaborated for 10+ years, pursuing a diversity of research questions and funding opportunities. Their work is ongoing, with increasing interest in understanding interactions between invasive species and climate change, predicting vulnerability to invasive species impacts and understanding trait dynamics.