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Combining local, landscape, and regional geographies to assess plant community vulnerability to invasion impact

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Abstract

Invasive species science has focused heavily on the invasive agent. However, management to protect native species also requires a proactive approach focused on resident communities and the features affecting their vulnerability to invasion impacts. Vulnerability is likely the result of factors acting across spatial scales, from local to regional, and it is the combined effects of these factors that will determine the magnitude of vulnerability. Here, we introduce an analytical framework that quantifies the scale-dependent impact of biological invasions on native richness from the shape of the native species–area relationship (SAR). We leveraged newly available, biogeographically extensive vegetation data from the U.S. National Ecological Observatory Network to assess plant community vulnerability to invasion impact as a function of factors acting across scales. We analyzed more than 1000 SARs widely distributed across the USA along environmental gradients and under different

levels of non-native plant cover. Decreases in native richness were consistently associated with non-native species cover, but native richness was compromised only at relatively high levels of non-native cover. After accounting for variation in baseline ecosystem diversity, net primary productivity, and human modification, ecoregions that were colder and wetter were most vulnerable to losses of native plant species at the local level, while warmer and wetter areas were most susceptible at the landscape level. We also document how the combined effects of cross-scale factors result in a heterogeneous spatial pattern of vulnerability. This pattern could not be predicted by analyses at any single scale, underscoring the importance of accounting for factors acting across scales. Simultaneously assessing differences in vulnerability between distinct plant communities at local, landscape, and regional scales provided outputs that can be used to inform policy and management aimed at reducing vulnerability to the impact of plant invasions.

INTRODUCTION

Biological invasions are one of the major threats to natural ecosystems, and there is mounting evidence showing declines in native species richness caused by invasions (Vilà et al., 2011). However, management to prevent biodiversity losses is challenged by uncertainty in predicting where biological invasions will have meaningful impacts. A renewed focus on understanding what makes a community vulnerable to invasion impact could serve as a complementary approach to protecting native species (Barney & Whitlow, 2008; Theoharides & Dukes, 2007). Plant community vulnerability to invasion is likely determined by a combination of factors acting across spatial scales, local to regional, and it is their combined effects that will dictate the magnitude of impacts. In this study, we leverage the availability of biogeographically extensive vegetation data from the National Ecological Observatory Network (NEON) to assess native plant community vulnerability to invasion impact as a function of factors acting across scales.

Vulnerability to invasion impact depends largely on features of the community affected, that is, biotic resistance, abiotic constraints, and native propagule availability (Ibáñez et al., 2021; Levine, 2001). As a result, the strongest impacts of plant invasions take place at the local scale, with impact weakening as larger areas are sampled (Crystal-Ornelas & Lockwood, 2020; Powell et al., 2013). Still, vulnerability is likely driven by processes interacting with invasive impacts at different scales. For example, at

the local scale, greater resource availability could increase impact from invasion since invasive species commonly outcompete native plants when resource availability is high (Davis et al., 2000). At the landscape scale, disturbances and invasive propagule pressure are the two most common factors associated with the threat of native communities becoming invaded (González-Moreno et al., 2014; MacDougall & Turkington, 2005; Shea & Chesson, 2002). At the regional scale, milder climates are associated with higher invasive species richness, while harsher environments usually have fewer invasive species (Allen & Bradley, 2016; Vila & Ibáñez, 2011). At the same time, native communities in more stressful environments could be more susceptible to invasion (Didham et al., 2007), making it unclear which climatic conditions could aggravate or ameliorate vulnerability to invasion impact. Given the range of local to regional processes contributing to plant invasions, comprehensive assessments of community vulnerability to invasion impacts need to simultaneously account for processes acting at different scales.

The starting functional composition of native communities and the species lost after invasion are key aspects of vulnerability (Bradley et al., 2019; Mollot et al., 2017; Pearse et al., 2019). Here again, the compound effects of local, landscape, and regional features could be associated with losses of diversity (Lomolino et al., 2016). At the local scale, features of a community, for example, microclimatic conditions and resource availability, affect plant richness (Bartels & Chen, 2010). At the landscape scale, land use and disturbances can affect native

richness via meta-population dynamics since isolation and lack of connectivity to source populations are often linked to native species losses (Ibáñez et al., 2014). At the regional scale, biodiversity varies along climatic gradients (Francis & Currie, 2003; Smith et al., 2020), and these different levels of diversity can influence regional levels of invasion since biotic resistance to introductions can be related to native species richness (Beaury, Finn, et al., 2020; although see Lonsdale, 1999; Sax & Gaines, 2006; Stohlgren et al., 1999). The presence and intensity of these cross-scale drivers of native species loss are likely linked to communities' vulnerability to invasion.

In this study, we introduce a framework for combining local, landscape, and regional geographies to understand the vulnerability of native communities to non-native plant impacts. We define vulnerability as declines in native plant richness with increasing cover of non-native species. Our work expands on Powell et al. (2013), who documented the scale-dependent effect of biological invasions via modifications in the native species–area relationships (SARs). The SAR is a fundamental pattern in ecology in which the number of native species (species richness) rises as the sample area increases, until it reaches an asymptote (Figure 1a). The SAR can be mathematically described in different ways (Scheiner, 2003). We followed Powell et al. (2013) and used a power curve to estimate native richness, R, as a function of area sampled, A ($R = cA^z$; Arrhenius, 1921). The two parameters in this equation represent the number of native species at one unit of area, c, and the rate of native species accumulation with increases in area, z. Analyzing species richness data at three locations, Powell et al. (2013) showed differences in SARs between uninvaded and invaded plots (Figure 1a, blue and red colors, respectively) and documented how the negative effect of invasion decays from the local level (lower c values in invaded plots) to broader spatial scales (higher z values in invaded plots). Here, we expand this analysis, invaded versus uninvaded, and use instead the gradient of invasion found at each NEON ecoregion (Figure 1a, blue to red colors) to estimate the relationship between degree of invasion and the SAR parameters (Figure 1b). We expect non-native cover to reduce local native species richness and therefore have a negative association with c (β_c local vulnerability, where impact is highest) and a positive association with z as the local losses of richness observed in smaller plots dissipate over larger areas (β_z landscape vulnerability; declining impact over space) (Figure 1b).

Furthermore, the use of SAR curves and newly available biogeographic vegetation data from NEON plant community surveys affords a unique opportunity to simultaneously measure how local, landscape, and regional processes influence vulnerability to invasion impact. NEON survey locations are distributed across ecoregions (Figure 1c), delineated based on climatic and ecological variability (Keller et al., 2008; Schimel et al., 2011). Within each of these ecoregions (Figure 1c) we were able to assess how parameters of SAR curves were affected by degree of invasion (Figure 1b) as a measure of local and landscape vulnerability, while further analyses of these parameters helped to account for regional drivers of vulnerability. By focusing on ecosystem vulnerability to the effects of invasion, our study addresses information gaps identified by managers and practitioners dealing with invaded communities (Beaury, Fusco, et al., 2020).

METHODS

We leveraged NEON's plant surveys to gather information on native species richness (number of native species) and levels of invasion (i.e., percent cover of non-native plants). Within each ecoregion, NEON has established between one and three sites. Each site contains ~30 plots, with distances between them ranging from 0.5 to 10 km, and plant surveys were conducted at each of these plots between 2016 and 2017 (Barnett, Adler, et al., 2019). We estimated a SAR for each plot; parameters from these curves (c, z; Figure 1) provided the basis for the analysis of plant community vulnerability across scales.

NEON data

Plant richness, number of species, and plant cover data (National Ecological Observatory Network [NEON], 2020) were downloaded from the NEON data portal application programming interface with the NEON Utilities package (Lunch et al., 2020). Within each plot, plant species are identified along a progression of nested subplots starting at 1 m^2 and ending at 400 m^2 (see Appendix S1: Figure S1 for site locations and detailed subplot layout). Plants that could not be resolved to species are reported to the lowest taxonomic rank possible. Taxonomy across all plots was reviewed, and origin—native, native to North America but introduced in some region, non-native, or unknown—was assigned according to the USDA Plants Database (United States Department of Agriculture, Natural Resources Conservation Service, 2020). Only plants classified as non-native were considered in the calculation of invasion cover, while all others (i.e., native, native introduced [8%], unknown [6%]) were included in the calculation of native richness. Species-specific plant cover is recorded in six or eight 1-m^2 subplots (Barnett, Duffy, et al., 2019); we used these cover data to estimate average
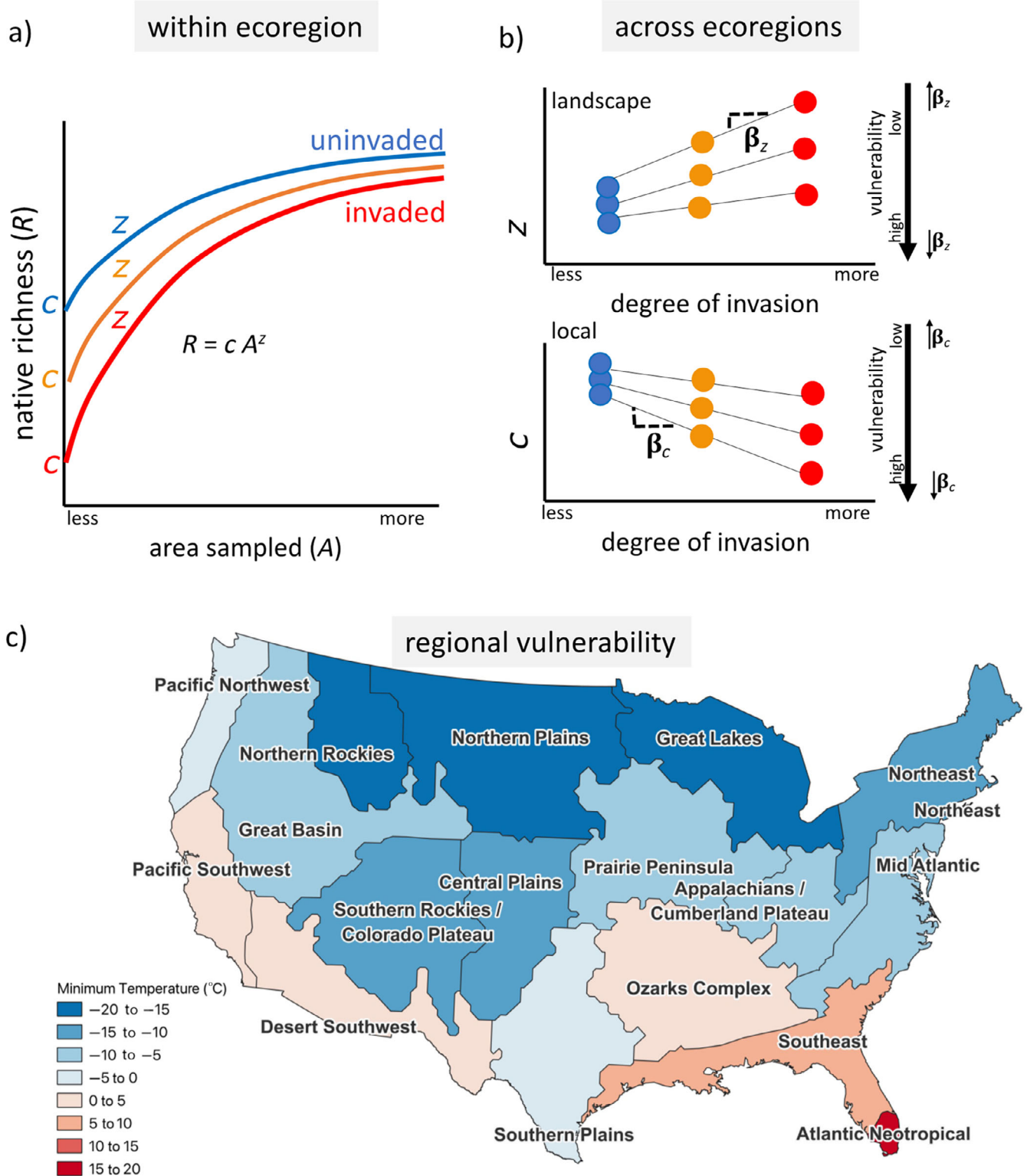
FIGURE 1 Analytical framework used to assess vulnerability to plant invasion impact across scales. (a) Species–area relationships (SARs) in uninvaded (blue) and invaded (red) plots within a National Ecological Observatory Network (NEON) ecoregion. (b) Expected differences in curve parameters (c and z) as a function of degree of invasion (color scale) are described by ecoregion-level landscape (β_z) and local (β_c) vulnerability parameters. The three sets of connected points show how expectations for the curves would change across ecoregions, with the lower sets of points illustrating most vulnerable regions. (c) NEON ecoregions in contiguous United States, color-coded by minimum average temperature in coldest month to show regional differences.

non-native plants' percent cover per plot. Tree basal area and shrub cover are also recorded, but values for non-native species (i.e., basal area and cover percentages) were too low to be included in the analyses.

Environmental data

We focused on environmental predictors known to influence native plant richness and, therefore, likely to alter vulnerability to invasion impact (Beaury, Finn, et al., 2020; Dong et al., 2015). We used remotely sensed net primary productivity (NPP) estimates as a proxy for resource availability and vegetation structure and, ultimately, intrinsic plant community features that could determine richness (e.g., Naeem et al., 1996; Tilman et al., 2001), with the expectation that, on average, communities with higher NPP would have higher native richness. NPP (gC m^{-2} year^{-1}) for each plot was obtained in May 2020, at 250-m resolution, from http://files.ntsg.umt.edu/data/NTSG_Products/MOD17/MODIS_250/modis-250-npp/. We also used the global Human Modification map as a proxy for landscape patterns associated with human-caused disturbance and landscape change, both variables that could affect native richness (Chase et al., 2020; Seabloom et al., 2002). The Human Modification Index (HMI) provides a cumulative measure of human modification of terrestrial lands across the globe at a 1-km resolution. It is a continuous 0–1 metric that reflects the proportion of a landscape modified based on modeling the physical extents of 13 anthropogenic stressors and their estimated impacts using spatially explicit global data sets with a median year of 2016. It was obtained in May 2020 from Kennedy et al. (2018) at https://doi.org/10.6084/m9.figshare.7283087.v1. Here, our expectation was that higher HMI would be associated with lower numbers of native species. While NPP and HMI could also affect the impact of non-native species on native plants, our data set, 1035 curves, did not include enough variability for us to simultaneously assess both the direct and indirect (via invasion) effects of these variables on native richness. We opted for the most parsimonious approach and only included the direct association of NPP and HMI with native richness (see *Analysis* in what follows).

To address how climatic conditions could drive vulnerability to invasions, we retrieved a series of climatic variables (temperature and precipitation) at 30 arc-sec resolution (~1 km), associated with each of the data plots from the WorldClim data set, https://www.worldclim.org/data/monthlywth.html, in May 2020. Graphical representation of the environmental data can be found in Appendix S2: Figure S1.

Species–area relationships

We used the nested NEON data to construct SAR curves for each plot. To ensure robust estimation of SAR parameters and of their associations with other factors (see *Analysis*), we only included NEON sites with more than 20 plots and with at least three plots with nonzero non-native plant cover. Plots were included only if they had at least 10 subplots and a minimum of five native species. The resulting data set contained 1035 plots across 35 sites within 17 ecoregions (Figure 1c). We used the vegan package (version 2.4-2) in R (R Core Team, 2021) to construct SAR curves, using the "collector" method to fit the nested structure of the subplots, and subplots were added as a function of their size, small to large. Richness values along the SAR curve were then used to calculate parameters c and z (means and SDs) for each plot (see Appendix S2 for estimates: Figure S1).

Analysis

To assess vulnerability across scales, we developed a hierarchical model where local richness (parameter c; 1 m^2) and rate of accumulation of species on the landscape (parameter z; ~ 10 km^2) were analyzed as a function of non-native species cover to estimate local and landscape vulnerability (parameters β_* in Figure 1b; Sofaer et al., 2018; Bradley et al., 2019). We included NPP, a proxy for intrinsic ecosystem features associated with richness, and the HMI, a proxy for disturbance and landscape change effects on richness. Both variables were standardized within each ecoregion. The effect of all three covariates (non-native cover, NPP, and HMI) on SAR parameters was estimated at the ecoregion level to reflect geographic variability across regions. For the analysis of z we also included predicted local native richness, $\ln(C)$, as a covariate to account for the negative correlation between these two parameters (Catano et al., 2021; Powell et al., 2013). For plot, p, at site, s, and ecoregion, E, SAR parameters c and z likelihoods and process models were as follows:

$$c_{p,s,E} \sim \text{Normal}\left(C_{p,s,E}, \sigma c_{p,s,E}^2\right) \text{ limited to} \geq 0$$

$$C_{p,s,E} = \theta_s + \beta c_E \text{Non-native Cover}_{p,s,E} + \gamma 1_E \text{NPP}_{p,s,E} + \gamma 2_d \text{HMI}_{p,s,E}$$

and

$$z_{p,s,E} \sim \text{Normal}\left(z_{p,s,E}, \sigma z_{p,s,E}\right) \text{ limited to} \geq 0 \text{ and} \leq 1$$

$$Z_{p,s,E} = \delta_E + \beta z_E \text{Non-native Cover}_{p,s,E} + \mu 1_E \text{NPP}_{p,s,E} + \mu 2_E \text{HMI}_{p,s,E} + \mu 3_E \ln\left(C_{p,s,E}\right).$$

Means and SD of the parameters (c, z, σ_*^2) are estimates from the SAR curves; likelihood for c (number of species at 1 m^2) was limited to positive values, and z (rate of species accumulation) was limited to a range between 0 and 1 (the largest 97.5 percentile value estimated was 0.77; Rosenzweig, 1995). To accommodate the hierarchical structure of the analysis, we followed a Bayesian approach. We used slightly informative hyperparameters for some coefficients and uninformative priors for most. The site-level number of species at 1 m^2, θ, was estimated as a function of the maximum richness (MR) found among plots at that site, $\theta_s \sim$ Normal(MR$_s$,10), reflecting maximum local richness and indirectly accounting for spatial associations between plots not covered by the covariates. The base rate of species accumulation, δ_E, was estimated at the ecoregion level, $\delta_E \sim$ Normal(0.25,1) (Rosenzweig, 1995). The effects of NPP, HMI, and, for z, local richness (ln[C]) were estimated as $\gamma_*,\mu_* \sim$ Normal(0,10) for each ecoregion.

On a second level analysis, local and landscape vulnerability to non-native plant impact, β_* parameters, was analyzed as a function of regional-level climatic variables (standardized). We did not include climate in the previous analysis because climatic variables varied little within plots in an ecoregion, but they varied across regions (Appendix S2: Figure S1). Furthermore, this ecoregion-level analysis allowed us to investigate the regional impact of climate on vulnerability. We carried out extensive exploratory data analyses to find the climatic variables that better explained variability in these parameters. These were average minimum temperature of the coldest month (Temp) and precipitation during the driest month (Precip). These two variables had the highest correlation (Pearson) with the β_* parameters. Ecoregion-level parameters were estimated as

$$\beta c_E = \alpha c_0 + \alpha c_1 \text{Temp}_E + \alpha c_2 \text{Precip}_E,$$

$$\beta z_E = \alpha z_0 + \alpha z_1 \text{Temp}_E + \alpha z_2 \text{Precip}_E,$$

where αc_* and αz_* are estimated from noninformative priors, αc_*, $\alpha z_* \sim$ Normal(0,1000).

Outputs from the analysis of the SAR parameters, that is, posterior means, variances, and covariances, were used to calculate SAR parameters (c and z) across the contiguous USA and then used to estimate native richness at 1 m^2 and at 400 m^2, the extent of our curves. To better assess the impact of non-native plants on native richness, we estimated richness under three scenarios of non-native cover: none (0% cover), low (10% cover), and high (50% cover); we ran 10,000 simulations. We used climate, NPP, and HMI averages for 1- and 10-km^2 grid cells and report results at these scales, 10 km^2 for continental-scale predictions and 1 km^2 for landscape-level

predictions, which are useful for management. To better assess vulnerability to invasion impact across regions with large differences in richness, we estimated an effect size of vulnerability, ES. For each grid cell, ES = ln(number of native species with non-native cover/number of native species without non-native cover). Analyses and predictions were run in JAGS (Plummer, 2021) using the rjags package in R (R Core Team, 2021). Maps were generated using QGIS (QGIS Development Team, 2021).

RESULTS

Given our inclusion criteria, data from 17 ecoregions, 35 sites, and 1035 plots (i.e., 1035 curves) were used in the analyses. At the plot level, native plant richness varied between five and 133 species. Non-native species were present in 723 plots. Percent cover of herbaceous non-native plants varied from zero to 100% (mean 8.26%, median 1.66%). All parameter values (means, SDs, and 95% CIs) can be found in Appendix S3: Table S1. Goodness of fit (predicted vs. observed R^2) was 0.89 for c and 0.93 for z.

Impact of non-native cover on native species richness (c)—Local vulnerability (β_c; 1 m^2)

As expected, the impact of non-native species on local richness was negative, and significant, for all NEON ecoregions except one, Atlantic Neotropical (Figure 2a). Local vulnerability was greatest in northern and eastern ecoregions (Figure 2b) and had little correlation with other ecoregion level variables, that is, maximum number of species across plots, average number of native species at 1 m^2, and maximum non-native species cover (<0.3; Pearson correlation, not shown). The overall effect of non-native plant cover on local richness (αc_0) was negative, with impact decreasing (less negative) with higher minimum temperatures (αc_1) and increasing (more negative) with increasing precipitation in the driest month (αc_2) (Figure 2c).

Impact of non-native cover on native species accumulation rate (z)—Landscape vulnerability (β_z; ~10 km^2)

For this parameter the expectation was a positive association with non-native species cover, reflecting higher non-native impact at local scales (lower c) and resulting in faster accumulation of species with increasing area. A slower accumulation of species (z) would then suggest greater
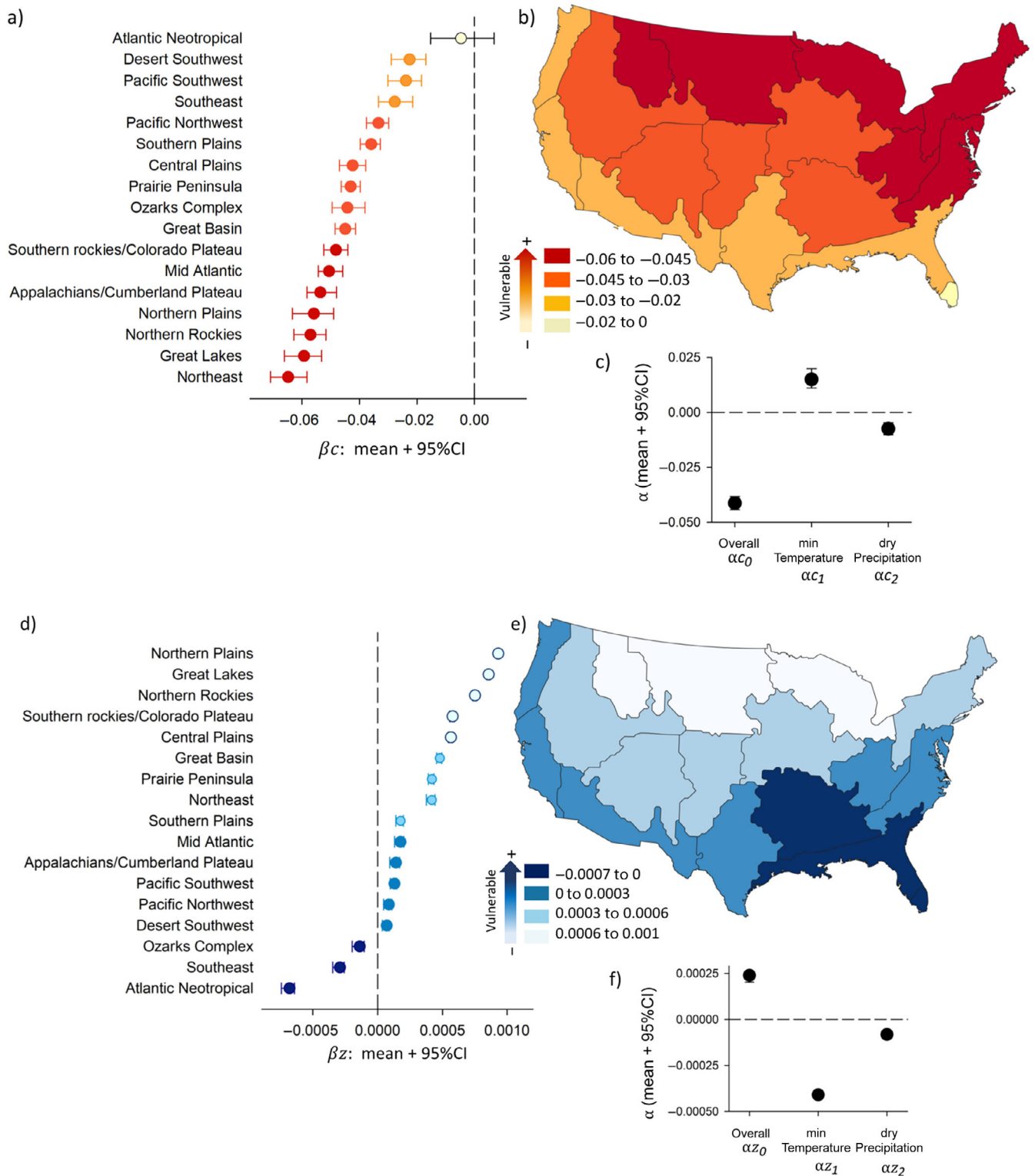
FIGURE 2 Impact of non-native plant cover on local (a–c) and landscape (d–f) vulnerability. (a, d) Estimates of β_c (expected negative) and β_z (expected positive) parameters for each of the National Ecological Observatory Network (NEON) ecoregions included in the analysis. (b, e) Map of NEON ecoregions showing mean values of β_c and β_z. (c, f) Results of analysis of non-native plant cover impact coefficients (β_c and β_z), as a function of an overall effect (α_{*0}), and of average minimum temperature in coldest month (α_{*1}) and precipitation in driest month (α_{*2}). Coefficients with 95% CIs that do not cross zero are considered statistically significant.

landscape vulnerability. All NEON ecoregions except three showed the expected positive association (Figure 2d). Landscapes in southern and western ecoregions were most vulnerable, that is, lower rates of species accumulations in plots with non-native species (Figure 2e). Landscape vulnerability (β_z) had little correlation (<0.2 Pearson r; not shown) with other ecoregion-level variables, that is, maximum number of species in plots, average number of native species at 1 m^2, maximum non-native species cover. Correlation between local vulnerability (β_c) and landscape vulnerability (β_z) was high (−0.77, Pearson r), even after including local richness, ln(C), in the analysis of z. Landscape vulnerability (lower β_z) increased with higher minimum temperatures (αz_1) and with increasing precipitation in the driest month (αz_2) (Figure 2f).

Impact of NPP on local native species richness and species accumulation rate

We expected NPP to be positively associated with the parameters of the SAR curve, that is, higher local richness and higher species accumulation in areas of higher NPP. Instead, we found that the relationship between NPP and local native richness (c) varied across NEON ecoregions, being significant for most and ranging from negative (11 ecoregions) to positive (five ecoregions) in a heterogeneous geographic pattern (Figure 3a,b). Similarly, the association between NPP and rate of species accumulation (z), which also varied geographically, was statistically significant for 10 of the 17 ecoregions, and values ranged between positive (five ecoregions) and negative (five ecoregions) (Figure 3c,d).

Impact of HMI on local native species richness and species accumulation rate

As a proxy for human-related disturbance and landscape change, we expected HMI to have a negative relationship with the two SAR parameters. Here again, for both local native richness, (c), and species accumulation rate, (z), we found an idiosyncratic response that varied from negative to positive, 15 ecoregions showed a significant association between c and HMI (Figure 4a,b), and nine out of the 17 ecoregions had a significant association between z and HMI (Figure 4c,d).

Regional patterns of vulnerability to invasion

Simulated vulnerability to invasions, expressed as effect size (ES), reflects ecoregion responses to local levels of invasion, NPP and HMI, and continental responses to climate. Negative values (pink to red colors; Figure 5) indicate a reduction in native species richness under non-native species cover. Inserts in Figure 5 also illustrate the large heterogeneity in predictions at the 1-km^2 scale. The Great Basin, parts of the Southern Plains, and the Appalachians had the largest estimates of vulnerability (biggest predicted difference in native richness between no invasion and high invasion). As expected, impacts were higher at the smallest scale (1 m^2; Figure 5a,c), than when calculated for a larger area (400 m^2; Figure 5b,d). Throughout most of the United States, impacts were only statistically significant when simulating richness under 50% invasion cover (Figure 5c,d, small maps).

DISCUSSION

Leveraging multiscale data on native and non-native plant species, we quantified differences in SARs to assess the compound effects of local, landscape, and regional drivers of vulnerability to the impact of invasion on native communities. Our simulations showed that high levels of non-native cover compromised native richness, and do so consistently, across all ecoregions. Results also showed that communities in colder areas were more vulnerable to local-scale losses in native species, whereas in warmer regions, vulnerability is greatest at landscape scales, that is, these areas have lower rates of species accumulation, implying that local non-native impact (1 m^2) carries over at larger scales (up to 10 km^2). We documented how the compound effects of cross-scale factors resulted in a heterogeneous spatial pattern of vulnerability that cannot be predicted by analyses at any single scale. By identifying geographic variation in vulnerability to invasion impact across scales (from 1 km^2, 10 km^2, regional), our results are more suitable to local, landscape, and regional decision-making.

It is well known that the impacts of invasive species are context-specific and can vary as a function of environmental conditions and features of the affected community (Helsen et al., 2018; Levine, 2001), but we have yet to understand what underlies this variation (Crystal-Ornelas & Lockwood, 2020; Ricciardi et al., 2021). Results from our analyses shed some light on how vulnerability to non-native plants cover varies regionally as a function of temperature and precipitation (Figure 2) and how this influence manifests geographically as it interacts with other factors acting at landscape and local scales (Figure 5). After accounting for levels of local richness, productivity (NPP), and human modification (HMI), colder and wetter ecoregions seem to be most vulnerable to losses of native plant species at the local level
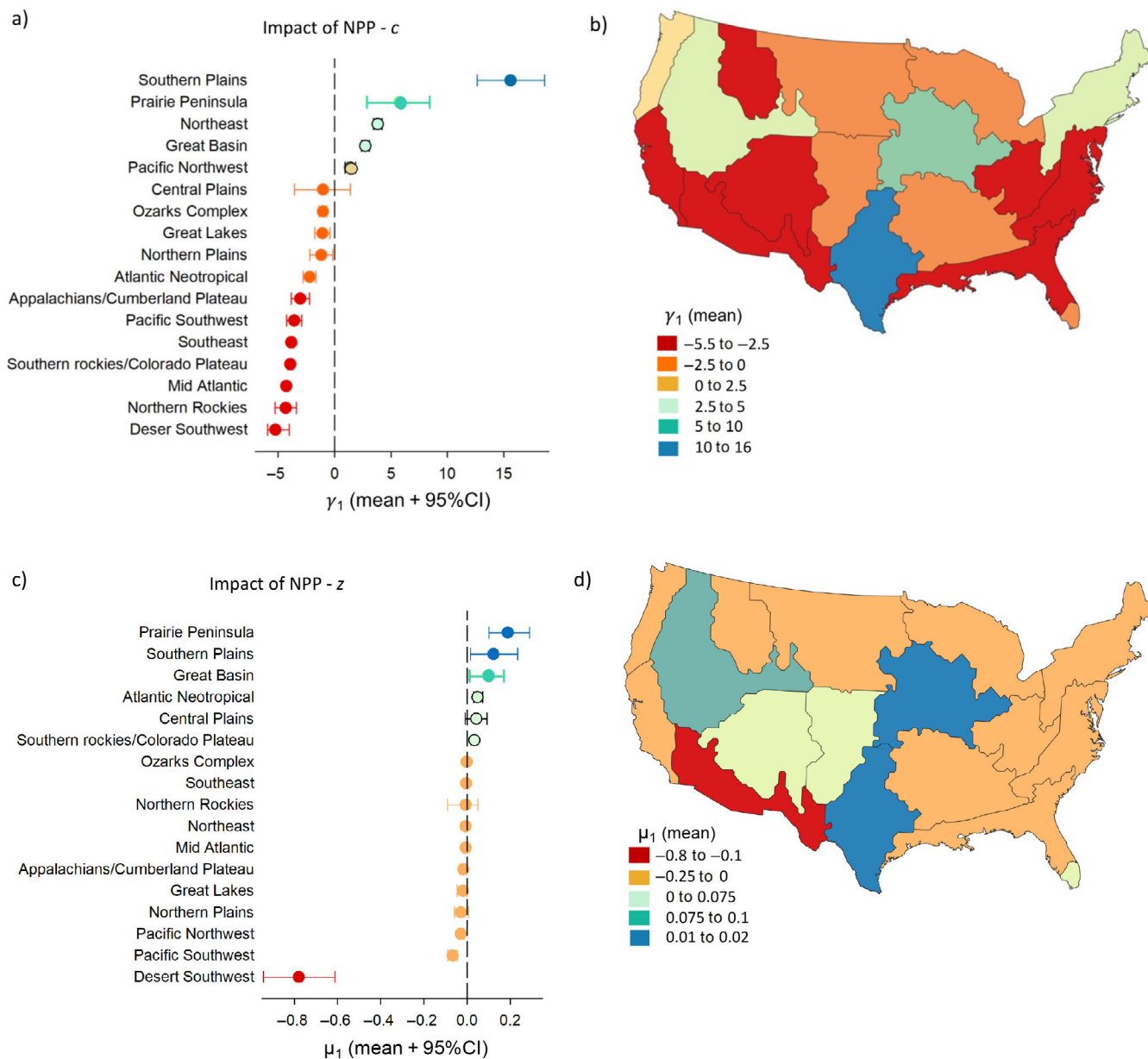
FIGURE 3 Association between net primary productivity (NPP) and local native richness, c, and rate of species accumulation, z. (a, b) Effects of NPP on c for each National Ecological Observatory Network (NEON) ecoregion (graphs) and spatial distribution (maps showing mean values). (c, d) Effects of NPP on z for each NEON ecoregion (graphs) and spatial distribution (maps; mean values). Coefficients were considered statistically significant if their 95% CI did not overlap with zero.

(Figure 2a–c), while warmer and wetter areas seem most susceptible at the landscape level (Figure 2d–f). Although our analysis does not demonstrate causality, we hypothesize on the likely drivers behind these patterns. At the local level, the higher vulnerability we found in colder regions could be associated with the shorter growing seasons. In these areas, many invasive plants have shown extended phenology, that is, earlier leaf-out and later leaf senescence, in comparison with the native community, giving them a competitive advantage that could lead to greater impacts (Fridley, 2012). With respect to the effect of

precipitation during the driest quarter, here we only see this effect in cold to cool areas (Figure 2b) as the negative effect of temperature is of greater magnitude (Figure 2c). This increase in vulnerability with precipitation could be related to higher non-native than native performance under optimal growing conditions (Sorte et al., 2012). Indeed, many invasive species show traits associated with fast growth rates, which can be sustained only under higher resource availability (Richardson & Pyšek, 2008).

The regional patterns associated with landscape vulnerability (Figure 2c–f) are more difficult to explain,
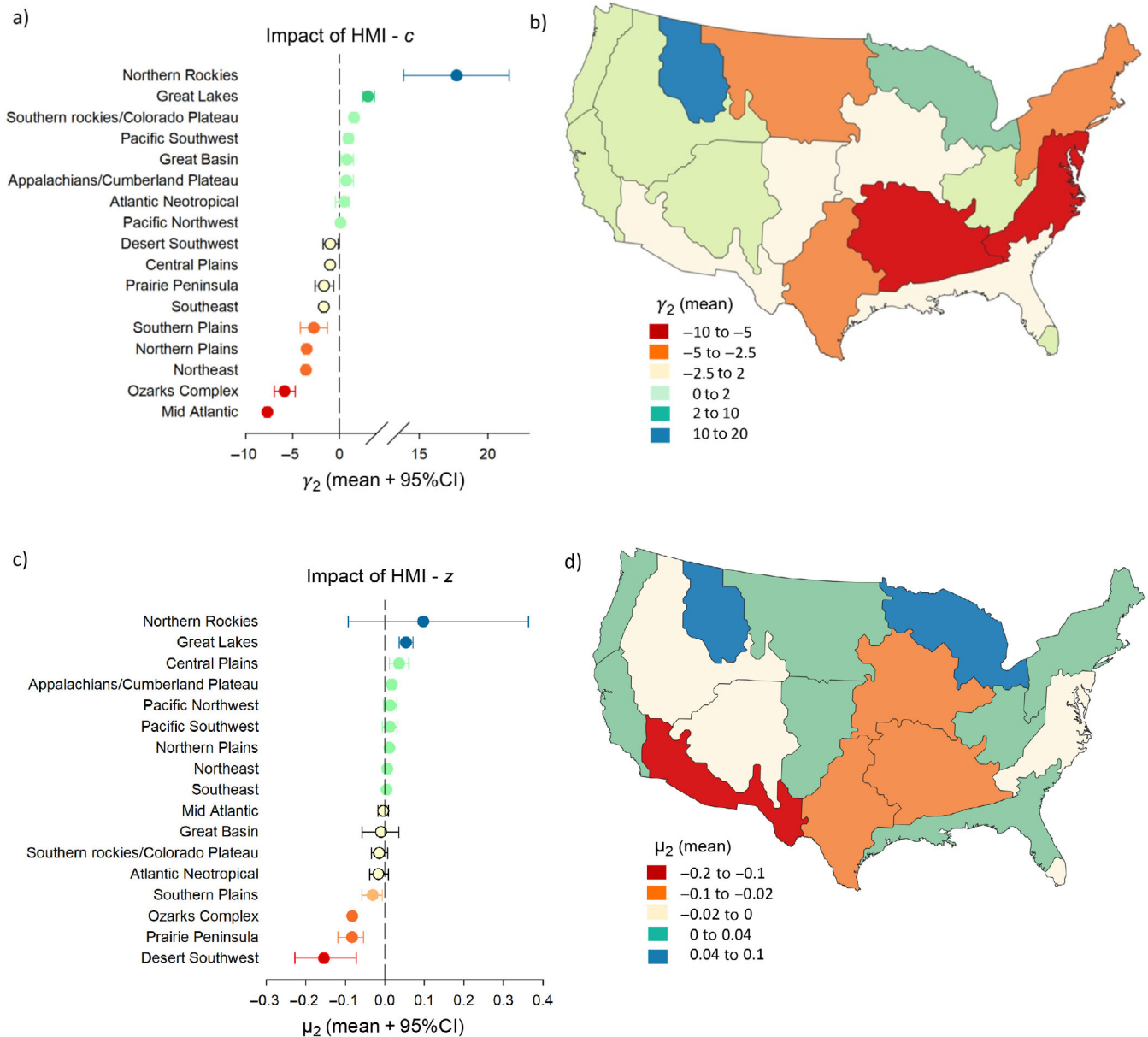
FIGURE 4 Association between Human Modification Index (HMI) and local native richness, c, and rate of species accumulation, z. (a, b) Effects of HMI on c for each National Ecological Observatory Network (NEON) ecoregion (graphs) and spatial distribution (maps; mean values). (c, d) Effects of HMI on z for each NEON ecoregion (graphs) and spatial distribution (maps; mean values). Coefficients were considered statistically significant if their 95% CI did not overlap zero.

although they appear mostly driven by average minimum temperature (Figure 2e,f) and roughly conform to previous work showing a negative relationship between the rate of species accumulation and ecosystem productivity (Chase et al., 2015). When analyzing the species accumulation rate parameter, z, we accounted for intrinsic features of these communities, local diversity and NPP, and landscape features via HMI and estimated the relationship for each ecoregion. Thus, the bioclimatic factors we observed at the continental level are likely related to regional drivers of vulnerability. The higher levels of

species richness in the most vulnerable regions (Kartesz, 2015) could have something to do with these patterns; with higher richness, dominant native species are likely to be less abundant (Gray & Wilsey, 2001) and, thus, less probable to appear in SAR surveys. This agrees with the interpretation by Powell et al. (2013) that the disproportional impact of invasion falls on more common species; but if an area is inherently species-rich without great dominance, increases in z under invasion might be of lower magnitude. The varying impact of non-native cover along environmental gradients and
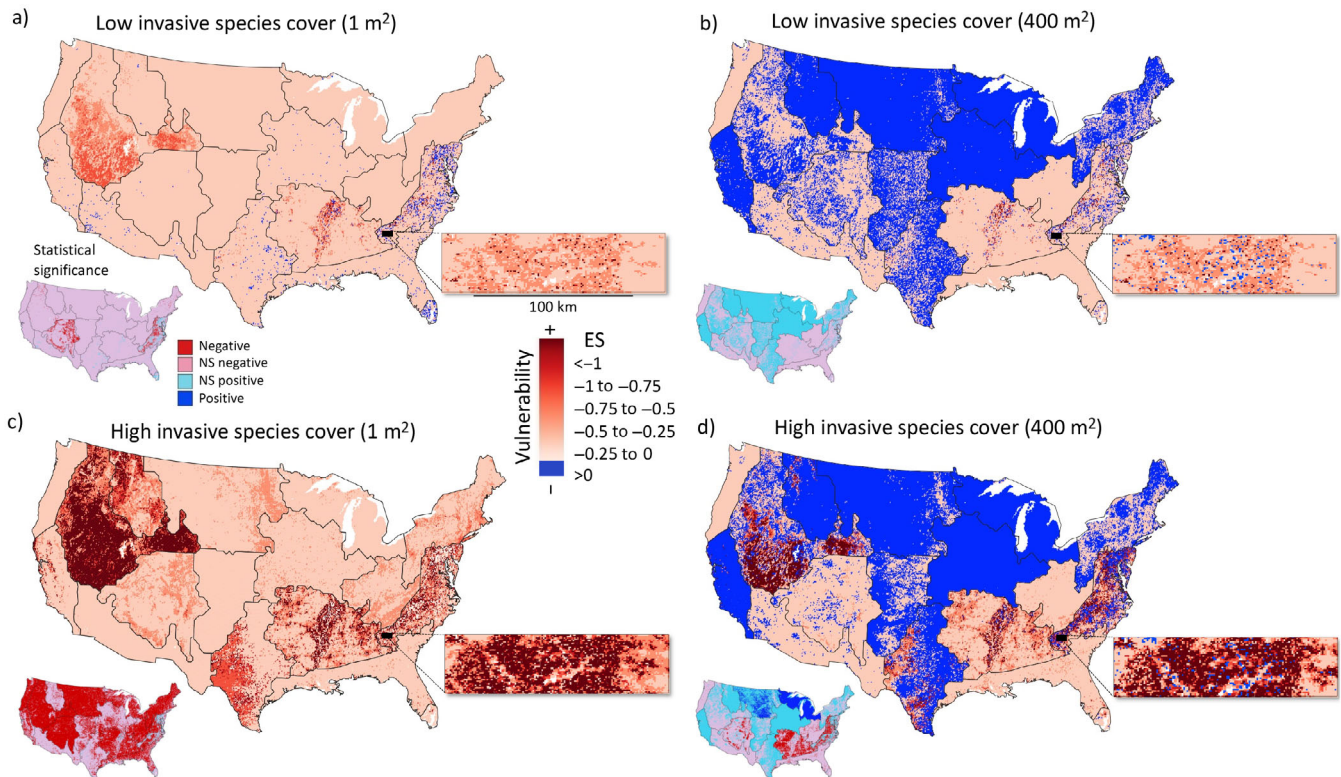
FIGURE 5 Vulnerability to non-native species cover expressed as effect size (ES). (a, b) Vulnerability at low non-native plant cover (10%) estimated at 1 and 400 m^2. (c, d) Vulnerability at high non-native plant cover (50%) estimated at 1 m^2 and 400 m^2. Large maps show 10 km^2 mean ES estimates, smaller maps reflect statistical significance defined as follows: Negative (ES mean negative, 95% CI does not overlap zero), NS negative (ES mean negative, 95% CI overlaps zero, non-significant [NS]), NS positive (ES mean positive, 95% CI overlaps zero, NS), and Positive (ES mean positive, 95% CI does not overlap zero). Rectangular inserts show 1 km^2 ES averages for a representative area. Note that predictions are based on National Ecological Observatory Network data and extrapolated to other locations using net primary productivity and Human Modification Index.

across scales is likely the result of many interacting factors. While we accounted for some of these factors and quantified their combined impacts, further field studies could help identify additional drivers of impact at different scales.

To better quantify the impact of non-native species on native richness, we accounted for as much of the underlying variability in species richness as possible by including other factors associated with richness, that is, NPP and HMI. NPP has been frequently associated with plant richness, with higher NPP at more diverse locations due to either complementarity among co-occurring species or to higher chances of including highly productive species (Al-Mufti et al., 1977; Grace et al., 2007; but see Adler et al., 2011). Higher levels of HMI are usually associated with losses in native species via disturbance, isolation, and habitat loss (Ehrlich, 1988; Ibáñez et al., 2014; Shea & Chesson, 2002). However, our estimated effects of NPP and HMI at the ecoregion level were not always as expected. Within most ecoregions the associations between NPP and local native richness and species

accumulation rate were negative (Figure 3), and some of the associations with HMI were positive (Figure 4), both contrary to expectations. It would require further analysis to learn whether the negative relationship between NPP and richness is due to the dominance of highly productive species or to any other feature of the plant communities in the region. Similarly, within some ecoregions, human activities might have been concentrated in areas of higher species richness (Araújo, 2003), concealing any potential negative effects. For this reason, it is important to be cautious about making generalized predictions based on geographically limited data.

Our analyses allowed us to predict geographic variation in native species richness that incorporated local (β_c), landscape (β_z), and regional (α_{*0}) vulnerability to invasion. Impacts were only significant at high non-native cover and, as predicted by Powell et al. (2013), higher at smaller spatial scales (Figure 5). These simulations of vulnerability under invasion did not reflect the geographic patterns we found with respect to climate (Figure 2). The difference was that our simulations

accounted for compounding factors acting across local, landscape, and regional scales, underscoring the importance of accounting for cross-scale effects. Predictions also showed sharp contrasts among ecoregions, reflecting estimated ecoregion-level parameters (Figures 2–4). NEON data collection has greatly improved the availability of continent-wide standardized data, but within-ecoregion environmental and invasion gradients are not fully represented (i.e., most sites had low levels of invasion).

Still, existing NEON vegetation data allowed us to examine vulnerability to plant invasion. Our results analyzing the compound effects of local, landscape, and regional drivers of vulnerability to invasion contradict a meta-analysis by Vellend et al. (2013) that found no net change in local-scale plant biodiversity over time under invasion. Unlike the data from an assortment of studies that feed into meta-analyses, NEON provides standardized vegetation survey data collected across the 17 main ecoregions in North America. Even with relatively low levels of invasion in most plots, we were able to quantify a significant effect, likely due to the information-rich data from the NEON survey design.

The science and management of invasive species are currently heavily geared toward invasive agents. Recognition is growing that this invader-focused approach is, in many cases, ineffective and unsustainable and that there is a need for research and practice to inform alternatives (Barney & Tekiela, 2020; McGeoch et al., 2016). In contrast, vulnerability to invasion impact depends largely on features of the community affected, that is, biotic resistance, abiotic constraints, and native propagule availability (Ibáñez et al., 2021; Levine, 2001). By considering invasion from the perspective of community vulnerability, we could address invasion in a proactive rather than reactive manner, with a focus on prevention (Mack et al., 2000), and practitioners could use vulnerability predictions to identify which, within their management units, are the most vulnerable communities to plant invasions; such information could help prioritize limited resources for early detection, monitoring, and/or control of invasions. SAR curves derived from NEON data allowed us to simultaneously assess differences in vulnerability between distinct plant communities at local, landscape, and regional scales. An advantage of this approach is that our analysis did not depend on predicting invasive species presence, a highly ad hoc process (Aikio et al., 2012; Lockwood et al., 2005; Martinez-Ghersa & Ghersa, 2006), or on differentiating whether invasive species were drivers or passengers of change (MacDougall & Turkington, 2005). Considering compounding factors acting across scales provided a better understanding about how these drivers interact in ways not predicted by the analysis of single factors.

Furthermore, by assessing vulnerability across scales, we were able to quantify heterogeneity in the magnitude of community-level vulnerability associated with non-native plants' impact, providing the analytical infrastructure to produce outputs at scales (1 km^2 to regional). These predictions could be used to identify areas likely to be susceptible to non-native species impacts, areas that can then be prioritized for monitoring and management.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data (Ibáñez, 2022a) are available in Dryad at https://doi.org/10.5061/dryad.z612jm6dx. Code (Ibáñez, 2022b) is available in Zenodo at https://doi.org/10.5281/zenodo.6477962. Plant richness, number of species, and plant cover data (NEON, 2020) were downloaded from the NEON data portal application programming interface with the NEON Utilities package (Lunch et al., 2020). Net primary productivity (NPP) for each plot were downloaded from http://files.ntsg.umt.edu/data/NTSG_Products/MOD17/MODIS_250/modis-250-npp/. The HMIs were obtained from Kennedy et al. (2018) at https://doi.org/10.6084/m9.figshare.7283087.v1. Climate data were downloaded from https://www.worldclim.org/data/monthlywth.html (CRU-TS 4.03 [Harris et al., 2014] downscaled with WorldClim 2.1 [Fick & Hijmans, 2017]). All data sets were accessed in May 2020.

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SUPPORTING INFORMATION

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

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