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

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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/. Human modification index (HMI) 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 and Hijmans, 2017]). All data sets were accessed May 2020.

Abstract Invasive species science has heavily focused 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 1,000 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 heterogenous 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.

Keywords hierarchical analysis, impact, invasive, NEON, richness, vulnerability

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 toward understanding what makes a community vulnerable to invasion impact could be a complementary approach to protecting native species (Theoharides and Dukes 2007; Barney and Whitlow 2008). 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 highly depends on features of the community affected, i.e., biotic resistance, abiotic constraints, and native propagule availability (Levine 2001, Ibáñez et al. 2021). As a result, the strongest impacts of plant invasions take place at the local scale, with impact weakening as larger areas are sampled (Powell et al. 2013, Crystal-Ornelas & Lockwood 2020). 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 resources are 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 (Shea & Chesson 2002, MacDougall & Turkington 2005, González-Moreno et al. 2014).

At the regional scale, milder climates are associated with higher invasive species richness, while harsher environments usually have fewer invasive species (Vilà & Ibáñez 2011, Allen & Bradley 2016). At the same time, native communities under 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 (Mollot et al. 2017, Pearse et al. 2019; Bradley et al. 2019). Here again, the compound effects of local, landscape and local features could be associated with losses of diversity (Lomolino et al. 2017). At the local scale, features of a community, e.g., microclimatic conditions and resource availability, affect plant richness (Bartels and 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 et al. 2020a; although see Lonsdale 1999, Stohlgren et al. 1999, Sax & Gaines 2006). 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 (SAR). 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 (Fig. 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 SAR between un-invaded and invaded plots (Fig. 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 *vs* uninvaded, and use instead the gradient of invasion found at each NEON ecoregion (Fig. 1a, blue to red colors) to estimate the relationship between degree of invasion and the SAR parameters (Fig. 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) (Fig. 1b).

Furthermore, the use of SAR curves and newly available biogeographic vegetation data from NEON plant community surveys afford a unique opportunity to simultaneously measure how local, landscape, and regional processes influence vulnerability to invasion impact. NEON survey locations are distributed across ecoregions (Fig. 1c), delineated based on climatic and ecological variability (Keller et al. 2008, Schimel et al. 2011). Within each of these ecoregions (Fig. 1c) we were able to assess how parameters of SAR curves are affected by degree of invasion (Fig. 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 et al. 2020b).

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 to three sites. Each site contains ~30 plots, with distances between them ranging from 0.5 to 10 km, plant surveys were conducted at each of these plots between 2016 and 2017 (Barnett et al. 2019a). We estimated a SAR for each plot; parameters from these curves (c, z; Fig. 1) provided the basis for the analysis of plant community vulnerability across scales.

NEON data - 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). 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 Fig. 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 USDA Plants Database (USDA & NRCS 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 et al. 2019b); we used these cover data to estimate average 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 focus on environmental predictors known to influence native plant richness, and therefore likely to alter vulnerability to invasion impact (Dong et al. 2015, Beaury et al. 2020a). We used remotely sensed net primary productivity estimates (NPP) 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 have higher native richness. NPP (gC m^{-2} y^{-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 (Seabloom et al. 2002, Chase et al. 2020). 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 datasets 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 is that higher HMI is 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, 1,035 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 below).

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 Fig. S1.

Species area relationships (SAR) –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 non-zero non-native plant cover. Plots were only included if they had at least 10 subplots and a minimum of five native species. The resulting dataset contained 1,035 plots across 35 sites within 17 ecoregions (Fig. 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, subplots were added as a function of their size, small to large. Richness values along the SAR were then used to calculate parameters c and z (means and SDs) for each plot (see Appendix S2 for estimates, Fig. 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 Fig. 1b; Sofaer et al. 2018; Bradley et al. 2019). We included net primary productivity (NPP; a proxy for intrinsic ecosystem features associated with richness) and human modification index (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 (Powell et al. 2013, Catano et al. 2021). For plot, p, at site, s, and ecoregion, E, SAR parameters c and z likelihoods and process models were:

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

$$C_{p,s,E} = \theta_s + \beta c_E Non - native\ Cover_{p,s,E} + \gamma 1_E NPP_{p,s,E} + \gamma 2_d HMI_{p,s,E}$$

and

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

$$Z_{p,s,E} = \delta_E + \beta z_E Non - native\ Cover_{p,s,E} + \mu 1_E NPP_{p,s,E} + \mu 2_E HMI_{p,s,E} + \mu 3_E \ln(C_{p,s,E})$$

Means and SD of the parameters (c, z, σ_*^2) are estimates from 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 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 in that site, $\theta_s \sim Normal(\mathrm{MR}_s, 10)$, reflecting maximum local richness and indirectly accounting for spatial associations between plots not covered by the covariates. Base rate of species accumulation, δ_E, was estimated at the ecoregion level, $\delta_E \sim$ *Normal*(0.25,1) (Rosenzweig 1995). The effect of NPP, HMI and, for *z,* of local richness (*ln[C]*) were estimated as γ_*, μ_* *Normal*(0,10) for each ecoregion.

On a second level analysis, local and landscape vulnerability to non-native plant impact, β_* parameters, were 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 (see Appendix S2 Fig. S1). Furthermore, this ecoregion level analysis allowed us to investigate 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*:*

$$\beta c_E = \alpha c_0 + \alpha c_1 Temp_E + \alpha c_2 Precip_E$$

$$\beta z_E = \alpha z_0 + \alpha z_1 Temp_E + \alpha z_2 Precip_E$$

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

Outputs from the analysis of the SAR parameters, i.e., 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 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*(no. native species with non-native cover/no. 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 1,035 plots (i.e., 1,035 curves) were used in the analyses. At the plot level, native plant richness varied between 5 and 133 species. There were non-native species present in 723 plots. Percent cover of herbaceous non-native plants varied from zero to 100% (mean 8.26% and median 1.66%). All parameter values (means, SDs and 95% confidence intervals) 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* (βc; 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 (Fig. 2a). Local vulnerability was greatest in northern and eastern ecoregions (Fig. 2b); and had little correlation with other ecoregion level variables, i.e., 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) (Fig. 2c).

Impact of non-native cover on native species accumulation rate (*z*) *– Landscape vulnerability* (βz; ~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 landscape vulnerability. All NEON ecoregions except three showed the expected positive association (Fig. 2d). Landscapes in southern and western ecoregions were most vulnerable, i.e., lower rates of species accumulations in plots with non-native species (Fig. 2e). Landscape vulnerability (βz) had little correlation (< 0.2 Pearson r; not shown) with other ecoregion level variables, i.e., maximum number of species in plots, average number of native species at 1 m^2, maximum non-native species cover. Correlation between local vulnerability(βc) and landscape vulnerability (βz) was high (-0.77, Pearson r), even after including local richness, *ln(C)*, in the analysis of *z*. Landscape vulnerability (lower βz) increased with higher minimum temperatures (αz_1) and with increasing precipitation in the driest month (αz_2) (Fig. 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, i.e., 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 (Fig. 3a,b). Similarly, the association between NPP and rate of species accumulation (*z*), also varied geographically, was statistically significant for 10 of the 17 ecoregions, and values ranged between positive (five ecoregions) and negative (five ecoregions) (Fig. 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 (Fig. 4a,b), and nine out of the 17 ecoregions had a significant association between *z* and HMI (Fig. 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; Fig. 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; Fig. 5a, c), than when calculated for a larger area (400 m^2; Fig. 5b, d). Throughout most of the U.S., impacts were only statistically significant when simulating richness under 50% invasion cover (Fig. 5c, d, small maps).

Discussion

Leveraging multi-scale data on native and non-native plant species, we quantified differences in SAR to assess the compound effects of local, landscape and regional drivers of vulnerability to the impact of invasion on native communities. Our simulations show high levels of non-native cover compromise native richness, and do so consistently, across all ecoregions. Results also show that communities in colder areas are more vulnerable to local-scale losses in native species, whereas in warmer regions vulnerability is greatest at landscape scales, i.e., these areas have lower rates of species accumulation implying local non-native impact (1 m^2) carries over at larger scales (up to 10 km^2). We document how the compound effects of cross-scale factors result in a heterogenous 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 (Levine 2001, Helse et al. 2018), 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 into how vulnerability to non-native plants cover varies regionally as a function of temperature and precipitation (Fig. 2), and how this influence manifests geographically as it interacts with other factors acting at landscape and local scales (Fig. 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 (Fig. 2a-c), while warmer and wetter areas seem most susceptible at the landscape level (Fig. 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, i.e., 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 (Fig. 2b), as the negative effect of temperature is of higher magnitude (Fig. 2c). This increase in vulnerability with precipitation could be related to higher non-native than native performance under optimal growing conditions (Sorte et al. 2013). Indeed, many invasive species show traits associated with fast growth rates which can only be sustained under higher resource availability (Pyšek & Richardson 2008).

The regional patterns associated with landscape vulnerability (Fig. 2c-f) are more difficult to explain, although they appear mostly driven by average minimum temperature (Fig. 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 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 underlaying variability in species richness as possible by including other factors associated with richness, i.e., 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 Alder et al. 2011). Higher levels of HMI are usually associated with losses in native species via disturbance, isolation, and habitat loss (Ehrlich 1988, Shea & Chesson 2002, Ibáñez et al. 2014). 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 (Fig. 3), and some of the associations with HMI were positive (Fig. 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 (Araujo 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 (βc), landscape (βz) 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 (Fig. 5). These simulations of vulnerability under invasion did not reflect the geographic patterns we found with respect to climate (Fig. 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 (Fig. 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 of 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.

Invasive species science and their management are currently heavily geared toward the invasive agent. 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 (McGeoch et al. 2016, Barney & Tekiela 2020). Contrastingly, vulnerability to invasion impact highly depends on features of the community affected, i.e., biotic resistance, abiotic constraints, and native propagule availability (Levine 2001, Ibáñez et al. 2021). 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); practitioners can use vulnerability predictions to identify which, within their management units, are the most vulnerable communities to plant invasions; information that can 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 does not depend on predicting invasive species presence, a highly ad-hoc process (Aikio et al. 2012, Martínez-Ghersa and Ghersa 2006, Lockwood et al. 2005), or on differentiating whether invasive species are drivers or passengers of change (MacDougall and 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.

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Figure 1. Analytical framework used to assess vulnerability to plant invasion impact across scales. (a) Species-area-relationships (SAR) in un-invaded (blue) and invaded (red) plots within a 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 (βz) and local (βc) 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 the contiguous USA, color-coded by minimum average temperature in the coldest month to show regional differences.

Figure 2. Impact of non-native plant cover on local (a-c) and landscape (d-f) vulnerability. a, d) Estimates of βc (expected negative) and βz (expected positive) parameters for each of the NEON ecoregions included in the analysis; b, e) map of NEON ecoregions showing mean values of βc and βz. c, f) Results of the analysis of non-native plant cover impact coefficients (βc and βz), as a function of an overall effect (α_{*0}), and of average minimum temperature in the coldest month (α_{*1}) and precipitation in the driest month (α_{*2}). Coefficients with 95%CIs that do not cross zero are considered statistically significant.

Figure 3. Association between net primary productivity (NPP) and local native richness, c, and rate of species accumulation, z. (a-b) The effects of NPP on c for each NEON ecoregion (graphs) and spatial distribution (maps showing mean values). (c-d) The 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 4. Association between Human Modification Index (HMI) and local native richness, c, and rate of species accumulation, z. (a-b) The effects of HMI on c for each NEON ecoregion (graphs) and spatial distribution (maps; mean values). (c-d) The 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.

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: 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, non-significant), 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 NEON data and extrapolated to other locations using NPP and HMI.

Figure 1.

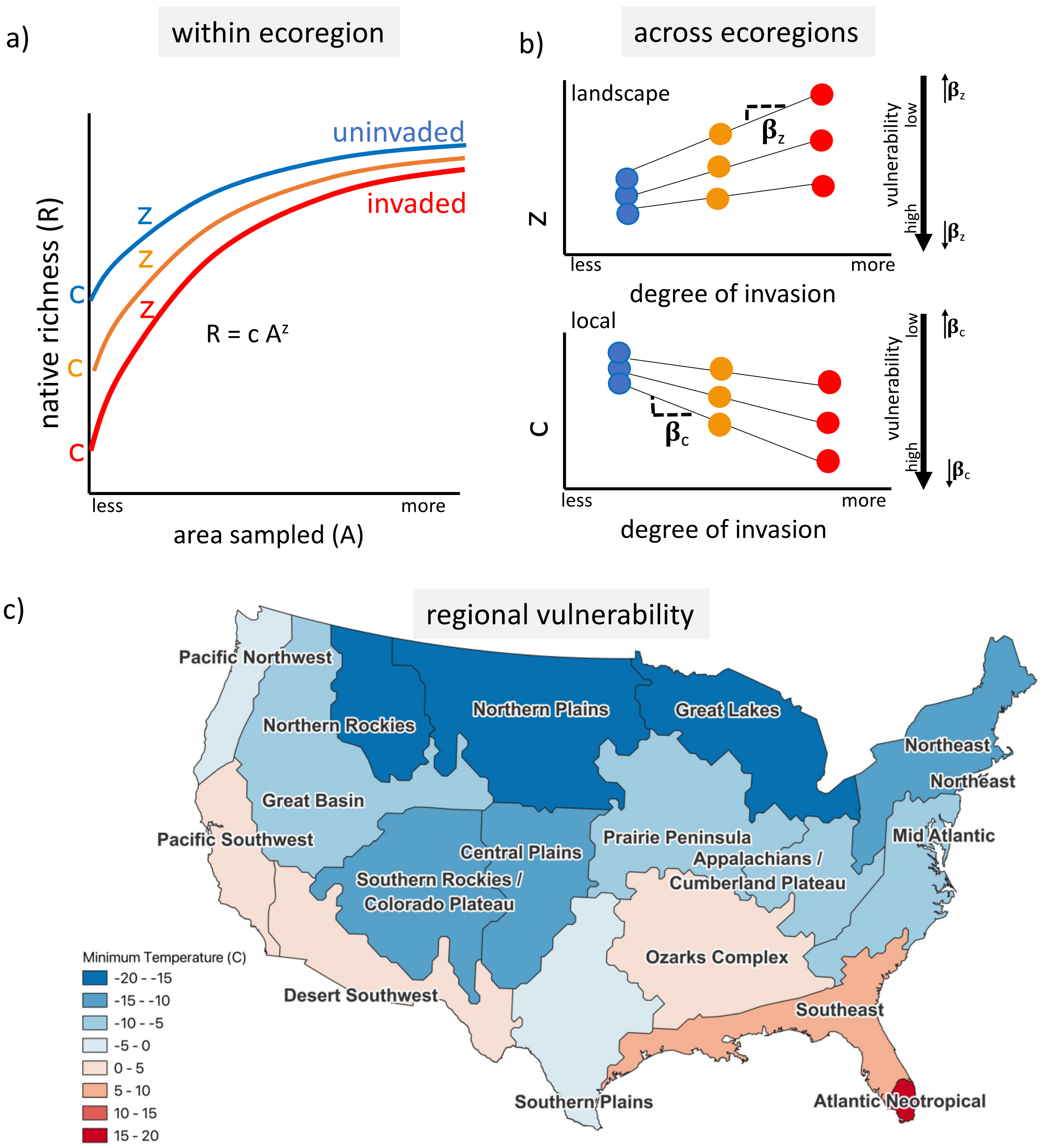

a)
within ecoregion
native richness (R)
uninvaded
invaded
z
z
z
c
c
c
R = c A^z
less
more
area sampled (A)
b)
across ecoregions
landscape
z
β_z
less
more
degree of invasion
vulnerability
low
high
β_z
β_z
local
c
β_c
less
more
degree of invasion
vulnerability
low
high
β_c
β_c
c)
regional vulnerability
Pacific Northwest
Northern Rockies
Northern Plains
Great Lakes
Northeast
Northeast
Great Basin
Pacific Southwest
Central Plains
Prairie Peninsula
Appalachians / Cumberland Plateau
Mid Atlantic
Southern Rockies / Colorado Plateau
Ozarks Complex
Desert Southwest
Southeast
Southern Plains
Atlantic Neotropical
Minimum Temperature (C)
-20 - -15
-15 - -10
-10 - -5
-5 - 0
0 - 5
5 - 10
10 - 15
15 - 20

Figure 2.

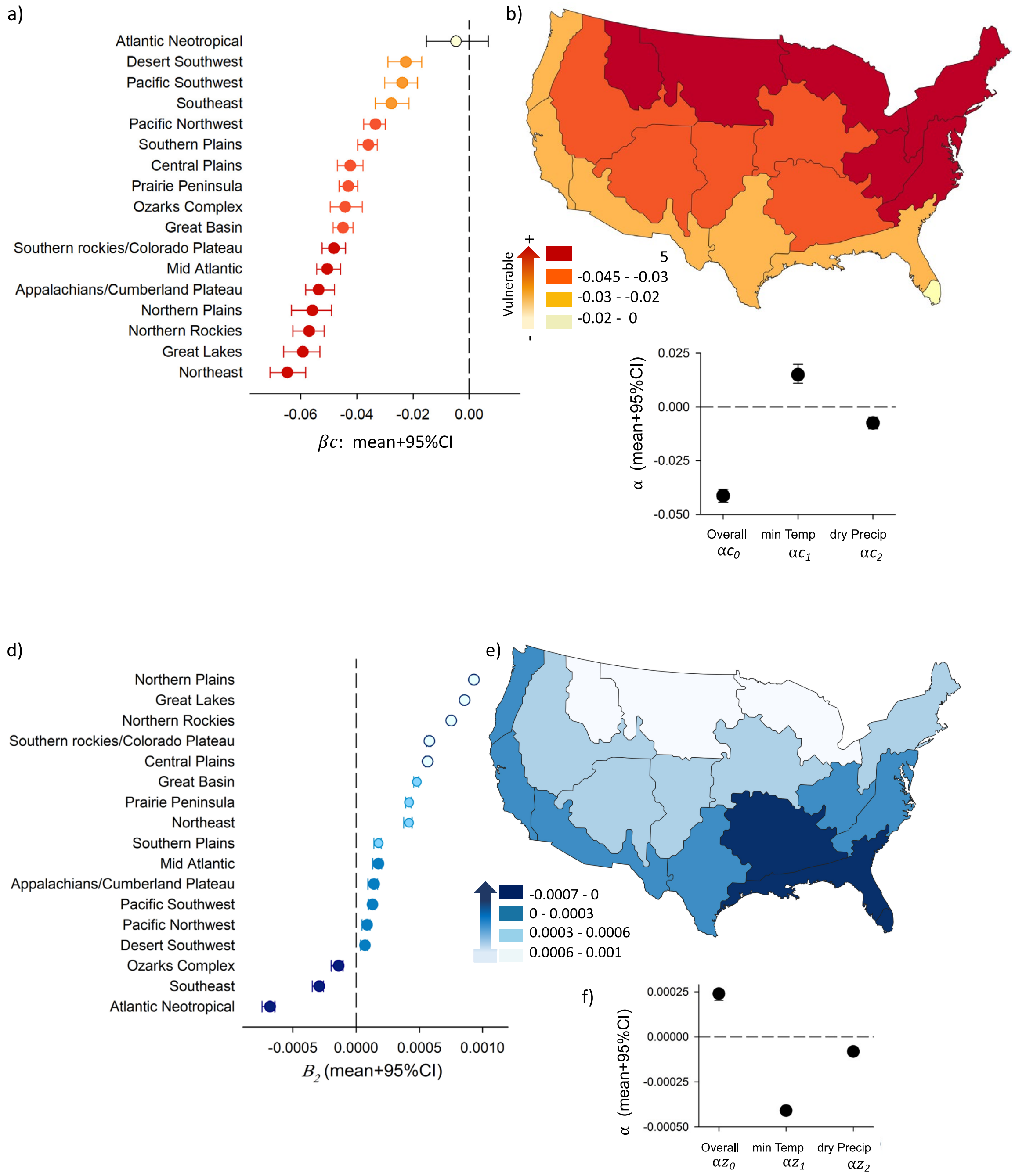

a)
Atlantic Neotropical
Desert Southwest
Pacific Southwest
Southeast
Pacific Northwest
Southern Plains
Central Plains
Prairie Peninsula
Ozarks Complex
Great Basin
Southern rockies/Colorado Plateau
Mid Atlantic
Appalachians/Cumberland Plateau
Northern Plains
Northern Rockies
Great Lakes
Northeast
-0.06
-0.04
-0.02
0.00
βc: mean+95%CI
b)
Vulnerable
+
-
5
-0.045 - -0.03
-0.03 - -0.02
-0.02 - 0
0.025
0.000
-0.025
-0.050
α (mean+95%CI)
Overall
αc_0
min Temp
αc_1
dry Precip
αc_2
d)
Northern Plains
Great Lakes
Northern Rockies
Southern rockies/Colorado Plateau
Central Plains
Great Basin
Prairie Peninsula
Northeast
Southern Plains
Mid Atlantic
Appalachians/Cumberland Plateau
Pacific Southwest
Pacific Northwest
Desert Southwest
Ozarks Complex
Southeast
Atlantic Neotropical
-0.0005
0.0000
0.0005
0.0010
B_2 (mean+95%CI)
e)
-0.0007 - 0
0 - 0.0003
0.0003 - 0.0006
0.0006 - 0.001
f)
0.00025
0.00000
-0.00025
-0.00050
α (mean+95%CI)
Overall
αz_0
min Temp
αz_1
dry Precip
αz_2

Figure 3.

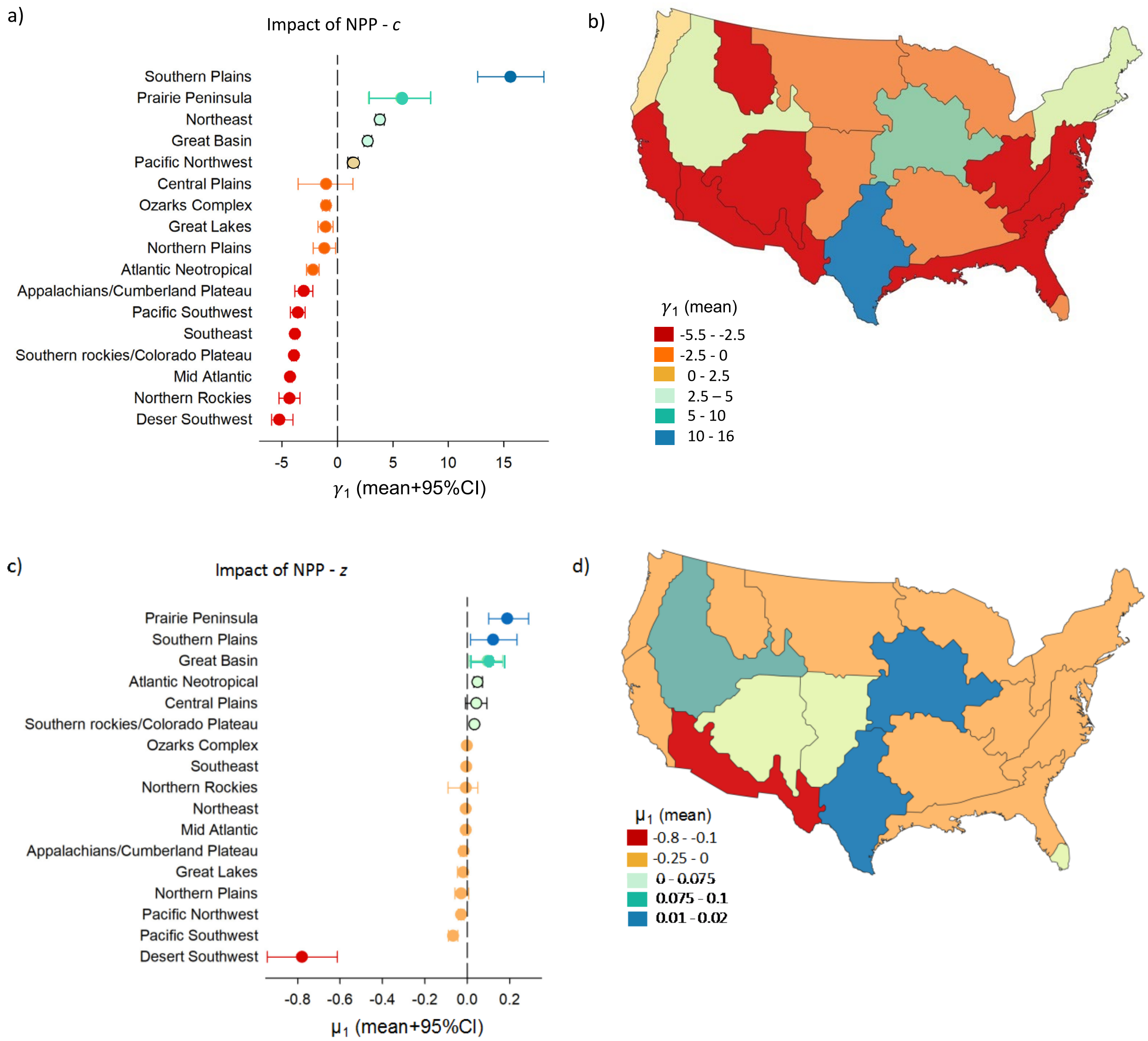

a)
Impact of NPP - *c*
Southern Plains
Prairie Peninsula
Northeast
Great Basin
Pacific Northwest
Central Plains
Ozarks Complex
Great Lakes
Northern Plains
Atlantic Neotropical
Appalachians/Cumberland Plateau
Pacific Southwest
Southeast
Southern rockies/Colorado Plateau
Mid Atlantic
Northern Rockies
Deser Southwest
-5
0
5
10
15
γ_1 (mean+95%CI)
b)
γ_1 (mean)
-5.5 - -2.5
-2.5 - 0
0 - 2.5
2.5 – 5
5 - 10
10 - 16
c)
Impact of NPP - *z*
Prairie Peninsula
Southern Plains
Great Basin
Atlantic Neotropical
Central Plains
Southern rockies/Colorado Plateau
Ozarks Complex
Southeast
Northern Rockies
Northeast
Mid Atlantic
Appalachians/Cumberland Plateau
Great Lakes
Northern Plains
Pacific Northwest
Pacific Southwest
Desert Southwest
-0.8
-0.6
-0.4
-0.2
0.0
0.2
μ_1 (mean+95%CI)
d)
μ_1 (mean)
-0.8 - -0.1
-0.25 - 0
0 - 0.075
0.075 - 0.1
0.01 - 0.02

Figure 4.

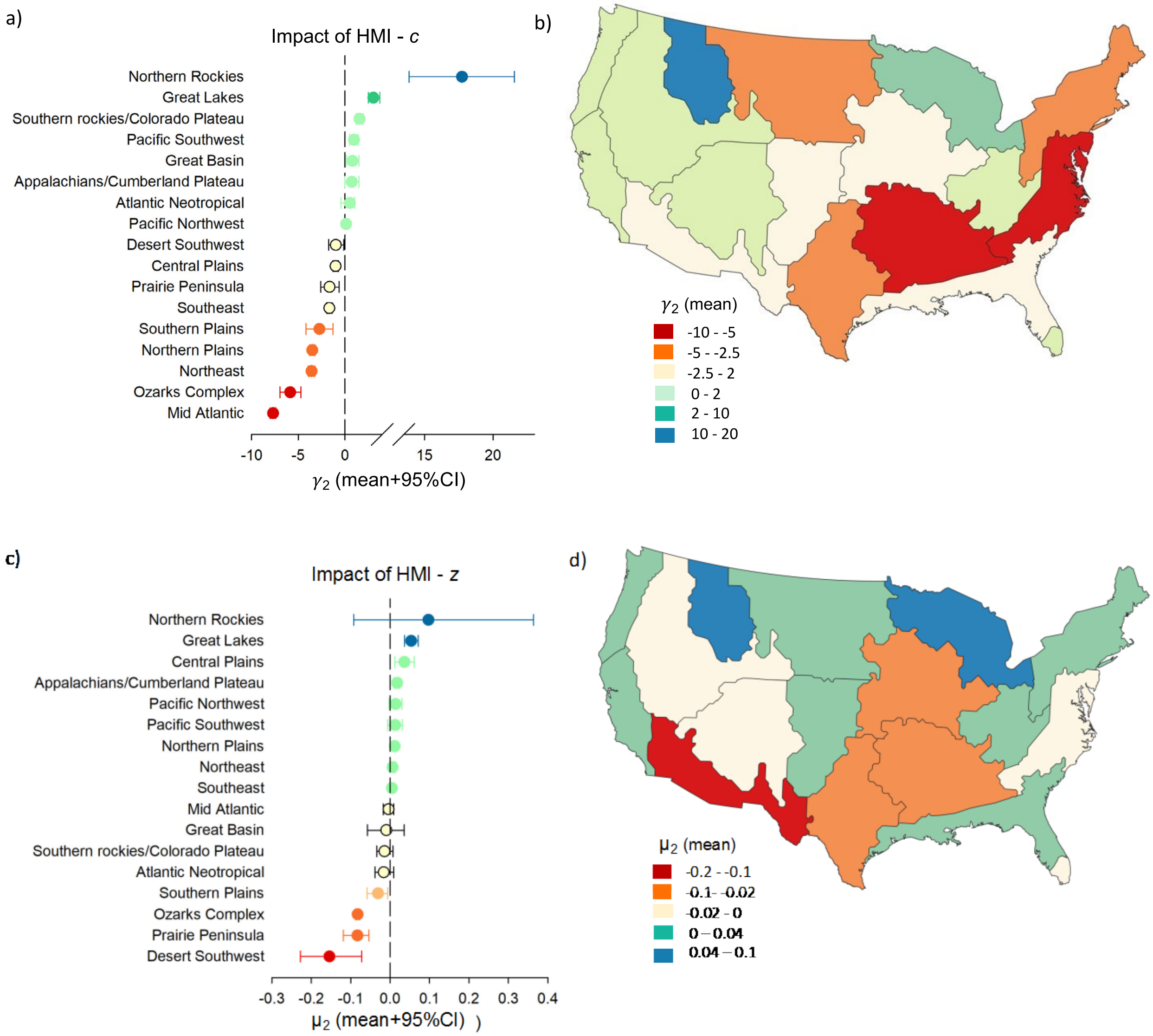
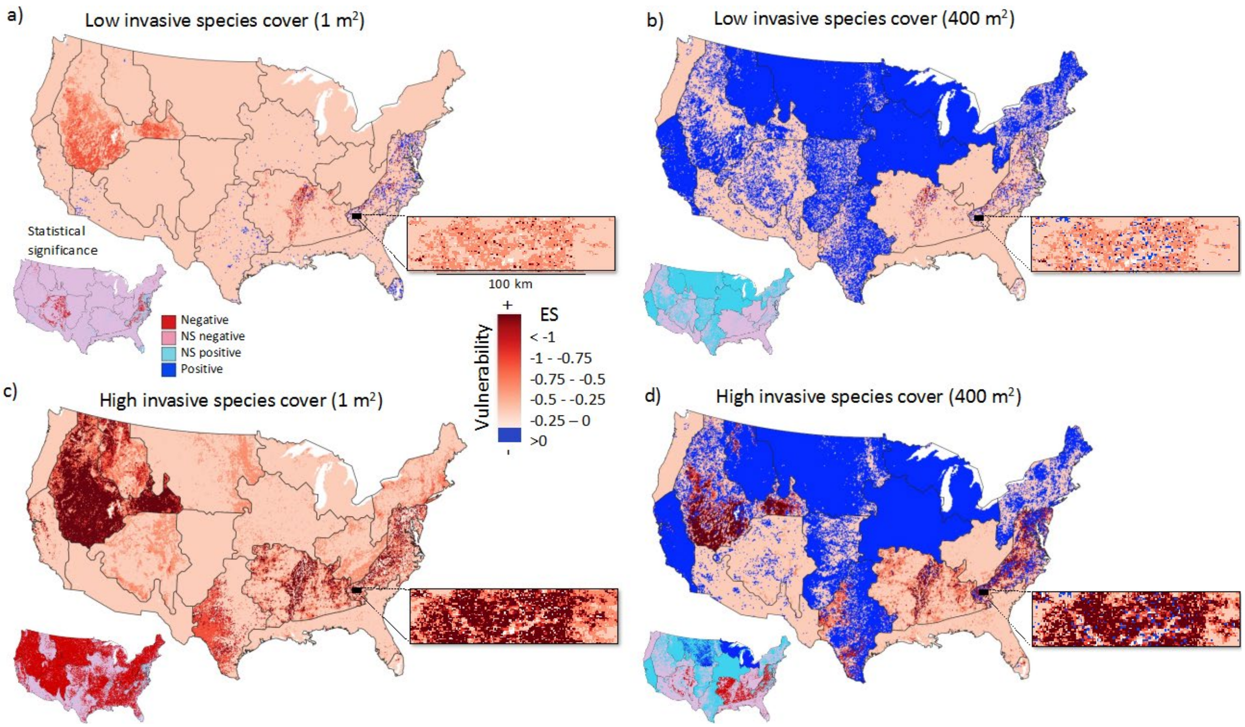

a)
Impact of HMI - *c*
Northern Rockies
Great Lakes
Southern rockies/Colorado Plateau
Pacific Southwest
Great Basin
Appalachians/Cumberland Plateau
Atlantic Neotropical
Pacific Northwest
Desert Southwest
Central Plains
Prairie Peninsula
Southeast
Southern Plains
Northern Plains
Northeast
Ozarks Complex
Mid Atlantic
-10
-5
0
15
20
γ_2 (mean+95%CI)
b)
γ_2 (mean)
-10 - -5
-5 - -2.5
-2.5 - 2
0 - 2
2 - 10
10 - 20
c)
Impact of HMI - *z*
Northern Rockies
Great Lakes
Central Plains
Appalachians/Cumberland Plateau
Pacific Northwest
Pacific Southwest
Northern Plains
Northeast
Southeast
Mid Atlantic
Great Basin
Southern rockies/Colorado Plateau
Atlantic Neotropical
Southern Plains
Ozarks Complex
Prairie Peninsula
Desert Southwest
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
μ_2 (mean+95%CI))
d)
μ_2 (mean)
-0.2 - -0.1
-0.1- -0.02
-0.02 - 0
0 – 0.04
0.04 – 0.1

Figure 5.


a)
Low invasive species cover (1 m^2)
b)
Low invasive species cover (400 m^2)
Statistical significance
100 km
Negative
NS negative
NS positive
Positive
+
Vulnerability
-
ES
< -1
-1 - -0.75
-0.75 - -0.5
-0.5 - -0.25
-0.25 – 0
>0
c)
High invasive species cover (1 m^2)
d)
High invasive species cover (400 m^2)