





LETTER

Biotic resistance to invasion is ubiquitous across ecosystems of the United States

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Abstract

The biotic resistance hypothesis predicts that diverse native communities are more resistant to invasion. However, past studies vary in their support for this hypothesis due to an apparent contradiction between experimental studies, which support biotic resistance, and observational studies, which find that native and non-native species richness are positively related at broad scales (small-scale studies are more variable). Here, we present a novel analysis of the biotic resistance hypothesis using 24 456 observations of plant richness spanning four community types and seven ecoregions of the United States. Non-native plant occurrence was negatively related to native plant richness across all community types and ecoregions, although the strength of biotic resistance varied across different ecological, anthropogenic and climatic contexts. Our results strongly support the biotic resistance hypothesis, thus reconciling differences between experimental and observational studies and providing evidence for the shared benefits between invasive species management and native biodiversity conservation.

Keywords

biodiversity, biogeography, biotic resistance, conservation, diversity-invasibility hypothesis, invasive species, non-native species, plant ecology.

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INTRODUCTION

In the past hundred years, the abundance and diversity of native species have dramatically declined across the globe (IPBES 2019). Along with climate change, land use and pollution, non-native species invasions have been cited as one of the leading drivers of the current biodiversity crisis (IPBES 2019). Not only are invasions *driving* biodiversity loss but, for decades, ecologists have hypothesised that one of the many *consequences* to biodiversity loss is a further increase in the establishment and spread of invasive species (Elton 1958; Fridley *et al.* 2007). The resulting biotic resistance hypothesis (also known as the diversity-invasibility relationship) predicts that species-rich native communities limit the niche space available to other species, and thus more diverse communities have greater biotic resistance to incoming non-native species. Evidence in favor of this hypothesis would suggest that promoting native biodiversity is an effective strategy to limit non-native species establishment, ultimately reducing the number of invasions.

However, inconsistent support for the biotic resistance hypothesis raises the question as to whether efforts to target native biodiversity have any effect on non-native species invasions, particularly in plant communities (Fridley *et al.* 2007; Jeschke *et al.* 2012). Experimental studies provide substantial evidence that higher native species richness results in lower invasion (Levine *et al.* 2004; Fridley *et al.* 2007; Byun *et al.* 2013; Peng *et al.* 2019; Smith & Côté 2019). Observational studies at the site level vary, but in the few observational studies that

extend beyond a local scale to include multiple sites (e.g. Stohlgren *et al.* 2006; Iannone *et al.* 2016), all find that higher native richness relates to higher numbers of non-native species (Fridley *et al.* 2007; Peng *et al.* 2019; Smith & Côté 2019).

The lack of consensus among studies was previously thought to be an artefact of spatial scale: habitat quality and habitat heterogeneity drive diversity across broad spatial extents, whereas biotic interactions drive diversity within the smaller scale plant neighbourhood (Levine 2000; Shea & Chesson 2002; Davies *et al.* 2007; Sandel & Corbin 2010; Von Holle 2013). However, two recent meta-analyses suggest that the contradiction may be driven by differences in experimental vs. observational studies (Peng *et al.* 2019; Smith & Côté 2019). While observational studies have the power of describing variation across broad spatial extents, these studies have limited control over extrinsic environmental or anthropogenic variables that affect native and non-native plant richness (Rejmanek 2003; Nunez-Mir *et al.* 2017). These extrinsic variables are often controlled for in experiments, but may confound our understanding of biotic resistance in observational analyses. Thus, evidence in support of biotic resistance has been limited to manipulated systems confined to local scales, and we lack broad-scale evidence for biotic resistance across a diversity of habitats.

Despite inconsistent evidence for biotic resistance, natural resource managers have adopted the approach of conserving and restoring native plant diversity in hopes of reducing invasions (Funk *et al.* 2008; Nimmo *et al.* 2015; Guo *et al.* 2018).

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This strategy aims to prevent invasions during the establishment stage – before some non-native species spread (Blackburn *et al.* 2011) and eradication becomes less likely. Nonetheless, natural resource managers consistently report that they are losing ground against invasions (Beaury *et al.* 2019) and invasive plant management continues to absorb time and resources (Pimentel *et al.* 2005). As these invasions advance the global decline in native biodiversity (IPBES 2019), we must identify and validate resource-effective conservation and restoration strategies that limit the success of non-native species during all stages of the invasion process.

Although past observational studies have not supported biotic resistance, new statistical techniques and the use of big data in ecology could alter those conclusions. An important component of broad-scale analysis (Iannone *et al.* 2016), and a potential flaw in past observational studies of biotic resistance (Rejmanek 2003; Nunez-Mir *et al.* 2017), are confounded interactions between species pools and other drivers of diversity. For example habitat characteristics correlated with species richness—such as resource availability, community type, or disturbance regime—affect the nature of the biotic resistance relationship (Stohlgren *et al.* 2006; Davies *et al.* 2007; Sandel & Corbin 2010; Von Holle 2013). Over large areas, heterogeneity in these factors may drive covariation between native and non-native richness even when biotic resistance is in effect (Levine 2000; Shea & Chesson 2002; Levine 2004). As large, standardised data sets become available and methods for analysing these data advance, we have an opportunity to retest foundational ecological and invasion hypotheses underlying conservation decision making (Guo *et al.* 2012; Nunez-Mir *et al.* 2017; Smith & Côté 2019).

To provide clarity to our understanding of biotic resistance, we used a novel statistical approach with 24 456 observational field surveys from the U.S. National Park Service to quantify the relationship between native and non-native plant richness across ecosystems of the U.S. The National Park Service data are unique in that they were collected at a fine spatial grain (most plots $\leq 400 \text{ m}^2$), but span a vast spatial extent and a diversity of habitats. Using these data, we addressed the following questions: (1) Do more species-rich native plant communities reduce the probability of non-native occurrence?; and (2) How does the relationship between native and non-native richness vary with different drivers of species diversity such as (i) habitat, (ii) proximity to human activity and (iii) climate? We hypothesised that accounting for these multiple drivers of diversity would lead to a consistent negative relationship between native and non-native plant richness – thereby reconciling the contrasting findings that have thus far characterised broad-scale observational studies of biotic resistance.

MATERIALS AND METHODS

Plant survey data

Plant survey data were obtained through the U.S. National Park Service (NPS) Vegetation Inventory Plot Data (Fig. 1, Table S1). Each park or monument ($n = 153$) was considered a site and was included in the analysis if located in the lower 48 states and if the vegetation sampling protocol followed the

methods described in the U.S. Geological Survey's Field Methods for Vegetation Mapping (1994). Plot size varied from 25 m^2 to 5400 m^2 depending on community type (i.e. plots were larger in forests where sampling effort must be greater to capture species richness of larger growth forms), although most plots were 400 m^2 or smaller (Fig. S3). Each plot ($n = 24\,456$) included a list of all observed plant species, the dominant vegetation type and geolocation. We used the United States Department of Agriculture PLANTS Database to identify the origin of each plant species as either native or non-native to the continental U.S. (The PLANTS Database 2018). For each plot, we calculated native and non-native plant richness as the number of unique species of that respective designation. Non-native richness serves as an estimate of the number of niches occupied by non-native species in a community.

Environmental characteristics

The number of non-native plants in a community depends on niche availability, which varies with habitat (Shea & Chesson 2002; Long *et al.* 2009). To analyse variation in biotic resistance between habitats, we included two measures of habitat for each plot: community type (e.g. forest, herbaceous), which describes the structure of the vegetation in each plot, and ecoregion (e.g. Eastern Temperate Forest, Great Plains), which describes the ecosystem characteristics specific to different regions of the U.S. The NPS categorised community type as one of the following: forest, woodland, shrubland or herbaceous (we excluded sparsely vegetated, disturbed or mixed community types due to uneven sampling across ecoregions). We used the Environmental Protection Agency's spatial layer of Level I Ecoregions (Omernik 1987) to assign each plot to one of seven ecoregions (Fig. 1) based on its location. NPS sites often sampled across community types and in several cases spanned ecoregions (Table S2).

Human activity and resulting landscape disturbance are primary sources of non-native propagules (Lonsdale 1999; Bartomeus *et al.* 2012) and cause periodic niche vacancies in plant communities (Shea & Chesson 2002; Brown & Peet 2003). These factors are thus likely to affect plot-level non-native richness. To estimate each plot's proximity to human activity as a proxy for propagule pressure and disturbance, we used GIS to calculate the Euclidean distance between each plot and the nearest urban/developed or agricultural land. Land cover data were downloaded from the National Land Cover Database 2001 and 2011 spatial layers (Homer *et al.* 2012). We selected these years to straddle the time period over which the NPS sampled. We also measured the distance between each plot and the nearest road as an alternative measure of distance to human activity, but model comparison using Akaike Information Criterion (AIC) showed that the model using distance to land cover types was a better fit than the model using distance to roads (Appendix S1).

Finally, climate drives the distribution of both native (Lomolino *et al.* 2010) and non-native plant species (Sax 2001). To account for the effects of temperature on plant richness, we used GIS to assign each plot a USDA hardiness zone (PRISM Climate Group 2018). Hardiness zones divide the

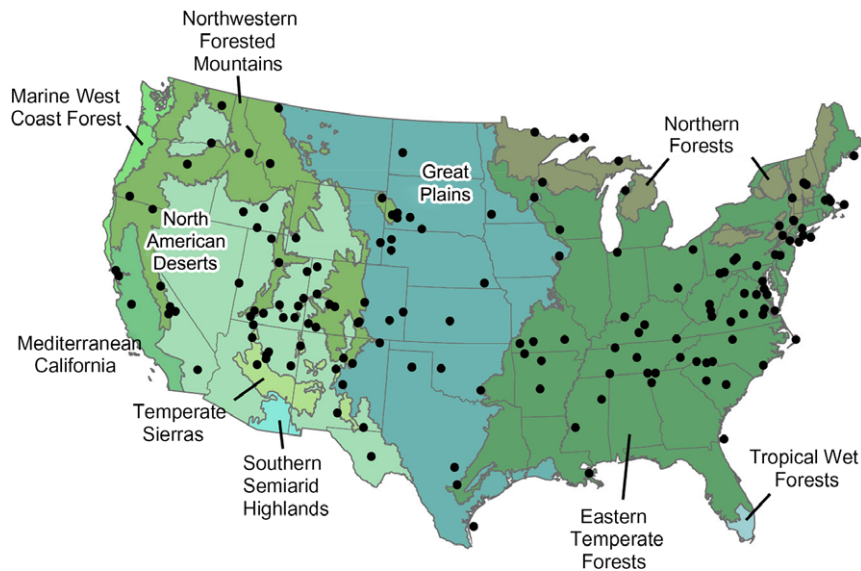


Figure 1 National Park Service site locations ($n = 153$) for plant surveys encompass a range of community types and ecoregions

U.S. into regions based on average minimum winter temperature, which is commonly used to describe the climates within which plants are likely to successfully grow. Additional climatic variables were excluded to avoid collinearity (Appendix S1).

Statistical approach

The data set included 12 359 plots with zero non-native species. To account for plots without non-native species, we used a zero-inflated model from the glmmTMB package in R (Zuur *et al.* 2009; Brooks *et al.* 2017). Total species richness varied from 1 to 163 species per plot. To account for variation in plot diversity, we used the binomial distribution (Zuur *et al.* 2013) to predict non-native species occurrence rather than non-native species richness.

This approach is different than previous analyses of plant richness data that more commonly use Poisson or negative binomial regression models to predict patterns in non-native richness. However, these models assume an unbounded upper limit to the number of ecological niches in a system (i.e., no competition for niche space), which is both unlikely to be true (Shea & Chesson 2002) and fails to control for variation in richness across ecosystems (Moore *et al.* 2001; Rejmanek 2003). For example, maximum species richness varies greatly between resource poor (e.g. desert) and resource rich ecosystems (e.g. forest), and thus 'high' native richness is relative to the community at hand. As native and non-native richness covary across habitats, studies may spuriously attribute this covariation to a lack of biotic resistance. In other words, resource abundant communities may have more native and non-native species because of habitat quality, not because of a lack of biotic resistance (Levine 2000; Shea & Chesson 2002; Levine *et al.* 2004).

Using the binomial distribution, we assume that each community has a fixed number of available niches (trial size, estimated as total species richness per plot) and non-native species occupy a certain percentage of these niches (binomial

probability, predicted as non-native species occurrence). This allows us to use the relative role of non-native species in a community to understand the likelihood of non-native occurrence and how this occurrence varies across ecosystems of different levels of diversity, vegetation structure, anthropogenic influence and climate. In other words, using the binomial distribution, we analysed the relationship between native and non-native richness in addition to, not in spite of, covarying habitat characteristics (i.e. biotic resistance may still occur in communities with high non-native richness, see Levine 2000 and Levine *et al.* 2004). Additional details are provided in Appendix S1.

We included the following fixed effects: native richness, community type, ecoregion, distance to human activity as a proxy for propagule pressure and disturbance and hardiness zone as a measure of climate. Sites spanned a gradient of each of these variables, so we included site as a random effect to account for spatio-temporal autocorrelation between plots. The two measures of habitat were included as additive effects and in an interaction with native richness (Appendix S1). We compared fitted non-native richness across community types and ecoregions using a Tukey test for pairwise comparisons. To assess the relative effects of each variable, we used a Z score transformation so that all numeric variables (native richness, distance to human activity and hardiness zone) fell on the same scale. We used simulation to predict the binomial probability of non-native plant occurrence and uncertainty around this probability (Appendix S1). All analyses were performed in R v. 3.5.1 (R Development Core Team 2018).

RESULTS

We found a negative relationship between native richness and non-native occurrence across all community types and ecoregions ($Z = -22.53$, $P < 0.0001$, $SE = 0.02$). Although consistently negative, the strength of biotic resistance varied by habitat with more variation occurring among ecoregions than among community types (Figs 2 & 3).

For all community types, non-native occurrence was significantly higher in the Great Plains, Mediterranean California, and the Northwestern Forested Mountains when compared to the North American Deserts (Table S3). Mediterranean California also had significantly greater non-native occurrence when compared with Temperate Sierras regardless of community type (Table S3). On average, Mediterranean California and the Great Plains had the highest probability of non-native occurrence (0.14 and 0.12 respectively). Within each ecoregion, forests consistently had the lowest likelihood of non-native occurrence while herbaceous communities had the highest (Table S4). Shrublands and woodlands did not significantly differ in biotic resistance.

The negative slope of biotic resistance occurred in all habitats regardless of distance to urban/developed or agricultural land (Fig. 4, Fig. S1 in Appendix S1), although plots near human activity had significantly more non-native species, and thus higher likelihood of non-native occurrence ($Z = -18.74$, $P < 0.0001$, $SE = 0.009$). Hardiness zone had a significant positive effect on non-native occurrence ($Z = 13.62$, $P < 0.0001$, $SE = 0.009$), indicating that more non-native species occurred in warmer climates. Native richness had a greater effect on non-native occurrence ($b = -0.49$, $SE = 0.02$) than either distance to human activity ($b = -0.17$, $SE = 0.009$) or hardiness zone ($b = 0.33$, $SE = 0.02$). Deviance explained by the full model was 13%.

DISCUSSION

Higher native plant richness significantly reduced the probability of non-native plant occurrence across all community types and ecoregions sampled by the National Park Service. These highly valued ecosystems are some of the most iconic in

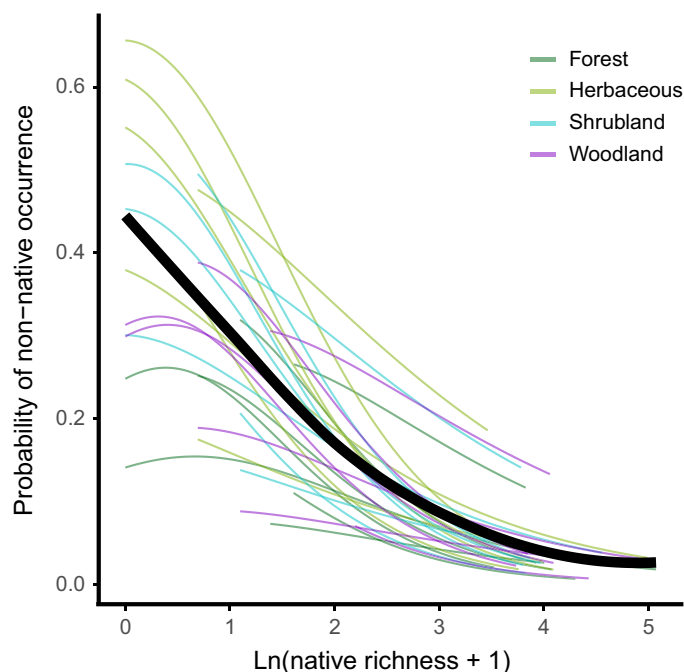


Figure 3 The overall negative relationship between native richness and non-native occurrence composed of unique curves of biotic resistance for each of the 28 combinations of community type (colours) and ecoregion (not labeled)

the United States and span a diverse range of anthropogenic influence, habitat and species diversity. Although non-native species readily occurred in many areas, we found universal support for the biotic resistance hypothesis. This widespread evidence of biotic resistance provides support for conservation

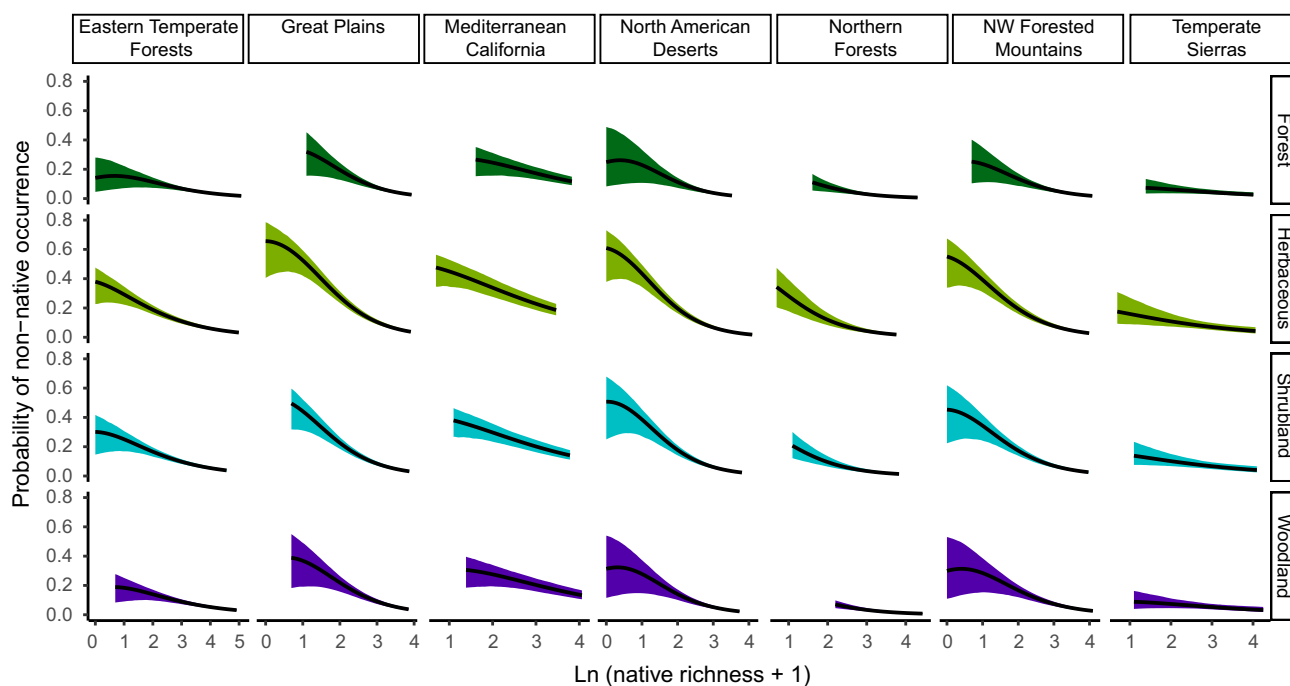


Figure 2 Predicted decline in non-native occurrence with increasing native richness across four community types (rows) and seven ecoregions (columns). Shaded polygons represent 95% credible intervals

and restoration activities that promote native biodiversity to reduce non-native species establishment, thereby reducing the pool of potentially invasive plants.

Our results contrast with findings of previous broad-scale observational studies of biotic resistance, which often found a positive relationship between native and non-native species richness (Fridley *et al.* 2007; Peng *et al.* 2019; Smith & Côté 2019). Because our approach controlled for factors that covary with species richness (Moore *et al.* 2001; Rejmanek 2003; Iannone *et al.* 2016), our analysis characterised biotic resistance independent of the effects of habitat, distance to human activity and climate on plant richness. Environmental heterogeneity is less of a barrier for observational studies at small scales where within site variation is often limited. However, these studies remain difficult to compare due to differences in spatial grain (Peng *et al.* 2019), spatial extent (Smith & Côté 2019), statistical approach (Nunez-Mir *et al.* 2017) and how they measure invader success (e.g. the majority of broad-scale studies use richness data, whereas small-scale studies may use richness, cover, survival, etc., see Fridley *et al.* 2007). The quality and quantity of the National Park Service data allowed us to both account for environmental heterogeneity and compare fine-scale data across sites. By doing so, we demonstrate consistency in biotic resistance between many observational analyses, field experiments (Levine *et al.* 2004; Peng *et al.* 2019; Smith & Côté 2019), and analyses of both types that found variation in biotic resistance depending on site-specific characteristics (Stohlgren *et al.* 2006; Davies *et al.* 2007; Sandel & Corbin 2010; Von Holle 2013).

One limitation to using observational data is that we cannot establish directionality in the relationship between native

richness and non-native occurrence. For example, the spread and impact of non-native species can significantly reduce native richness (Bradley *et al.* 2019). It could thus be possible that low native richness in this data set results from the increasing abundance/invasion of non-native species, which enables additional non-natives to establish via invasional meltdown (Simberloff & Von Holle 1999). However, ecosystems can absorb non-native species without a concomitant decline in native richness (Sax & Gaines 2003), and in this data set, native richness varied across ecosystems even in the absence of non-native species (i.e. low native richness was not always associated with high non-native occurrence). Furthermore, our analysis included proximity to human activity, which is often strongly correlated to non-native species abundance (Lonsdale 1999; Shea & Chesson 2002; Brown & Peet 2003; Bartomeus *et al.* 2012; Seabloom *et al.* 2013). If biotic resistance was not in effect, we would expect areas of high human impact to have high non-native occurrence regardless of native diversity. Rather, non-native occurrence declined with native richness even in areas with high likelihood of invasion (Fig. 4), which suggests that the pattern observed here is more likely attributable to biotic resistance than to non-native species impacts.

System-specific variation in biotic resistance suggests that a combination of local, landscape and regional factors influence the occurrence of non-native species (Figs 2 & 3). For example herbaceous communities, which can be more seasonally dynamic than other community types (Shea & Chesson 2002; Clark & Johnson 2011), had the highest probability of non-native occurrence. Forests, which have less seasonal turnover and thus may provide fewer opportunities for non-native species to establish (Bartomeus *et al.* 2012; Nunez-Mir *et al.* 2017), had the lowest. At the ecoregion level, low richness areas of Mediterranean California (Baldwin *et al.* 2017) and the Great Plains are particularly vulnerable to incoming non-native species. In general, systems with low native diversity were more likely to have a positive trend between native richness and non-native occurrence (Fig. 3). In these cases, niche availability could allow both native and non-native plants to establish and coexist (Stohlgren *et al.* 2006; Davies *et al.* 2007).

Proximity to urban development and agricultural lands, which are related to propagule pressure and disturbance (Lonsdale 1999; Bartomeus *et al.* 2012), increased the likelihood of non-native occurrence across all habitats (Fig. 4). This effect may explain why Mediterranean California and the Great Plains were particularly vulnerable to incoming non-native species. Sites in Mediterranean California – Point Reyes National Seashore and Golden Gate National Recreation Area – are part of the highly developed San Francisco Bay Area. This proximity to urban landscapes, coupled with the extensive history of intense land-use in California, has likely resulted in high propagule pressure and regular disturbances promoting invasions in the habitats sampled in this analysis (Corbin & D'Antonio 2004). This is in stark contrast to the Temperate Sierras, which is a relatively remote, forest-dominated ecoregion with few incidences of non-native species (Table S2). In the Great Plains, sites have low native diversity (Table S2) and neighbor large swaths of agricultural lands,

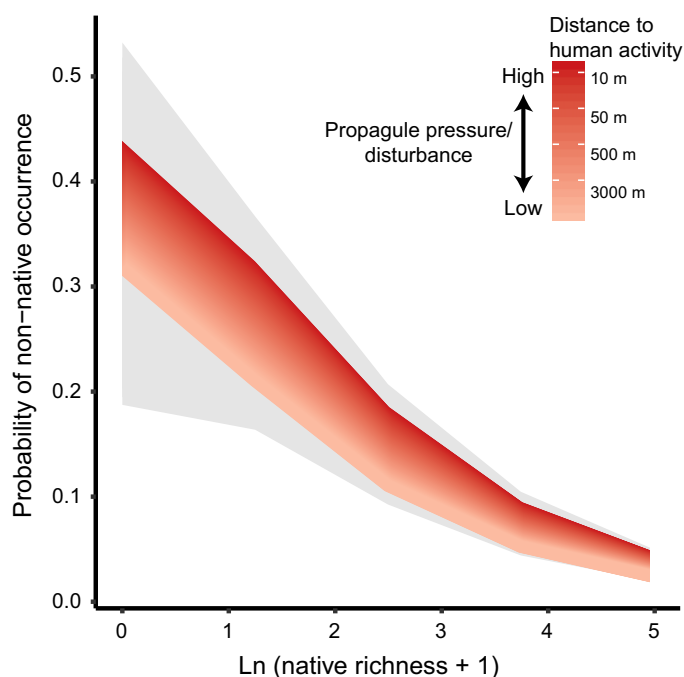


Figure 4 Predicted effect of proximity to human activity as a proxy for the effect of propagule pressure and disturbance on biotic resistance. Predictions and 95% credible intervals are for herbaceous communities in Eastern Temperate Forests

resulting in low biotic resistance, high propagule pressure and regular disturbance in surrounding areas, which may cause the high probability of non-native occurrence we observed. Managing post-disturbance is a well-supported recommendation for reducing invasions (Hobbs & Huenneke 1992; Guo *et al.* 2018), and our study confirms that anthropogenically affected areas require more management of incoming non-native species with the potential to become invasive.

Our analysis also supports the hypothesis that species diversity follows a climatic gradient (Lomolino *et al.* 2010) such that warmer climates contain more species, including higher diversity of non-native plants. As the climate changes, warming areas with low native diversity could be increasingly vulnerable to invasion as non-native species shift poleward (Allen & Bradley 2016) or increase in abundance as temperatures become more suitable (Hulme 2017).

While assessing ecological vulnerability based on different anthropogenic and climatic contexts is informative, high native diversity was the strongest indicator of low non-native species occurrence. As a result, there is a potential positive feedback between managing native biodiversity to reduce invasions and reducing invasions to benefit native biodiversity (IPBES 2019). Our analysis provides support for biotic resistance during the earliest stages of the invasion process, when non-native species are first establishing (Blackburn *et al.* 2011). It remains unknown from these occurrence data whether species are indeed naturalised or simply casual non-natives (*sensu* Richardson *et al.* 2000), but the strength of the relationship (Figure 3) suggests that both types of non-natives are likely suppressed by high native diversity. It is also unknown whether high native diversity can prevent the spread of one or more non-natives that do occur. Future broad-scale analyses could explicitly test diversity-invasibility by incorporating non-native abundance as a proxy for invasive plant impact (Bradley *et al.* 2019). Lastly, diverse communities are still often invaded (e.g., Stohlgren *et al.* 2006). Although conserving native plant diversity decreases the likelihood of non-native occurrence, more work is needed to understand the broad-scale anthropogenic and environmental factors that drive ecosystem vulnerability to non-native establishment and ultimately to invasion.

AUTHORSHIP

E.M.B., J.T.F., J.D.C. and B.A.B. generated hypotheses. J.D.C. organised National Park Service data and ran pilot statistical analyses. E.M.B. and V.B. managed the data set. E.M.B. and B.A.B. led writing. E.M.B. and J.T.F. performed statistical analyses. All authors contributed to framing the manuscript, interpreting the results, editing and approving the final draft.

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DATA AVAILABILITY STATEMENT

Data and R code used for analysis is now available on FigShare. Plant surveys were sourced from the U.S. National Park Service Vegetation Inventory Plot Data, currently available from: <https://irma.nps.gov/DataStore/Collection/Profile/7>.

Guide to files/metadata: <https://doi.org/10.6084/m9.figshare.10316717.v1>. Dataset: <https://doi.org/10.6084/m9.figshare.10316720.v1>. R Code: <https://doi.org/10.6084/m9.figshare.10316732.v2>; <https://doi.org/10.6084/m9.figshare.10316729.v1>; <https://doi.org/10.6084/m9.figshare.10316741.v1>

REFERENCES

- Allen, J.M. & Bradley, B.A. (2016). Out of the weeds? Reduced plant invasion risk with climate change in the continental United States. *Biol. Cons.*, 203, 306–312.
- Baldwin, B.G., Thornhill, A.H., Freyman, W.A., Ackerly, D.D., Kling, M.M., Morueta-Holme, N. *et al.* (2017). Species richness and endemism in the native flora of California. *Am. J. Bot.*, 104, 487–501.
- Bartomeus, I., Sol, D., Pino, J., Vicente, P. & Font, X. (2012). Deconstructing the native–exotic richness relationship in plants. *Glob. Ecol. Biogeogr.*, 21, 524–533.
- Beaury, E.M., Fusco, E.J., Jackson, M.R., Laginhas, B.B., Morelli, T.L., Allen, J.M. *et al.* (2019). Incorporating climate change into invasive species management: insights from managers. *Biol. Invasions*, 1–20. <https://doi.org/10.1007/s10530-019-02087-6>.
- Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V. *et al.* (2011). A proposed unified framework for biological invasions. *Trends Ecol. Evol.*, 26, 333–339.
- Bradley, B.A., Laginhas, B.B., Whitlock, R., Allen, J.M., Bates, A.E., Bernatchez, G. *et al.* (2019). Disentangling the abundance–impact relationship for invasive species. *PNAS*, 116, 9919–9924.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. *et al.* (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal*, 9, 378–400.
- Brown, R.L. & Peet, R.K. (2003). Diversity and invasibility of Southern Appalachian plant communities. *Ecology*, 84, 32–39.
- Byun, C., de Blois, S. & Brissson, J. (2013). Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *J. Ecol.*, 101, 128–139.
- Clark, G.F. & Johnston, E.L. (2011). Temporal change in the diversity–invasibility relationship in the presence of a disturbance regime. *Ecol. Lett.*, 14, 52–57.
- Corbin, J.D. & D'Antonio, C.M. (2004). Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology*, 85, 1273–1283.
- Davies, K.F., Harrison, S., Safford, H.D. & Viers, J.H. (2007). Productivity alters the scale dependence of the diversity–invasibility relationship. *Ecology*, 88, 1940–1947.
- Elton, C.S. (1958). *The Ecology of Invasions by Plants and Animals*. Methuen, London.
- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D. *et al.* (2007). The invasion paradox: reconciling pattern and process in species invasions. *Ecology*, 88, 3–17.

- Funk, J.L., Cleland, E.E., Suding, K.N. & Zavaleta, E.S. (2008). Restoration through reassembly: plant traits and invasion resistance. *Trends Ecol. Evol.*, 23, 695–703.
- Guo, Q., Rejmánek, M. & Wen, J. (2012). Geographical, socioeconomic, and ecological determinants of exotic plant naturalization in the United States: insights and updates from improved data. *NeoBiota*, 12, 41–55.
- Guo, Q., Brockway, D.G., Larson, D.L., Wang, D. & Ren, H. (2018). Improving ecological restoration to curb biotic invasion—a practical guide. *Invasive Plant Science and Management*, 11, 163–174.
- Hobbs, R.J. & Huenneke, L.F. (1992). Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.*, 6, 324–337.
- Homer, C.H., Fry, J.A. & Barnes, C.A. (2012). The National Land Cover Database. U.S. Geological Survey.
- Hulme, P.E. (2017). Climate change and biological invasions: evidence, expectations, and response options: Alien species and climate change in Great Britain. *Biol. Rev.*, 92, 1297–1313.
- Iannone, B.V., Potter, K.M., Hamil, K.-A.D., Huang, W., Zhang, H., Guo, Q. *et al.* (2016). Evidence of biotic resistance to invasions in forests of the Eastern USA. *Landscape Ecol.*, 31, 85–99.
- IPBES (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science–Policy Platform on Biodiversity and Ecosystem Services. Available at: www.ipbes.net Last accessed 09 September 2019.
- Jeschke, J.M., Aparicio, L.G., Haider, S., Heger, T., Lortie, C.J., Pyšek, P. *et al.* (2012). Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota*, 14, 1–20.
- Levine, J.M. (2000). Species diversity and biological invasions: relating local process to community pattern. *Science*, 288, 852–854.
- Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.*, 7, 975–989.
- Lomolino, M.V., Riddle, B.R., Whittaker, R.J. & Brown, J.H. (2010). Ecological geography of continental and oceanic biotas. In: *Biogeography*, 4th edn. Sinauer Associates Inc., Sunderland, MA, pp. 657–693.
- Long, J.D., Trussell, G.C. & Elliman, T. (2009). Linking invasions and biogeography: Isolation differentially affects exotic and native plant diversity. *Ecology*, 90, 863–868.
- Lonsdale, W.M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology*, 80, 1522–1536.
- Moore, J.L., Mouquet, N., Lawton, J.H. & Loreau, M. (2001). Coexistence, saturation and invasion resistance in simulated plant assemblages. *Oikos*, 94, 303–314.
- Nimmo, D.G., Mac Nally, R., Cunningham, S.C., Haslem, A. & Bennett, A.F. (2015). Vive la résistance: reviving resistance for 21st century conservation. *Trends Ecol. Evol.*, 30, 516–523.
- Nunez-Mir, G.C., Liebhold, A.M., Guo, Q., Brockerhoff, E.G., Jo, I., Ordonez, K. *et al.* (2017). Biotic resistance to exotic invasions: its role in forest ecosystems, confounding artifacts, and future directions. *Biol. Invasions*, 19, 3287–3299.
- Omerik, J.M. (1987). Ecoregions of the conterminous United States. *Ann. Assoc. Am. Geogr.*, 77, 118–125.
- Peng, S., Kinlock, N.L., Gurevitch, J. & Peng, S. (2019). Correlation of native and exotic species richness: a global meta-analysis finds no invasion paradox across scales. *Ecology*, 100, e02552.
- Pimentel, D., Zuniga, R. & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.*, 52, 273–288.
- PRISM Climate Group (2018). USDA Plant Hardiness Zone Maps. Oregon State University.
- R Development Core Team (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org/>.
- Rejmánek, M. (2003). The rich get richer – responses. *Front. Ecol. Environ.*, 1, 123–123.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib.*, 6, 93–107.
- Sandel, B. & Corbin, J.D. (2010). Scale, disturbance and productivity control the native-exotic richness relationship. *Oikos*, 119, 1281–1290.
- Sax, D.F. (2001). Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *J. Biogeogr.*, 28, 139–150.
- Sax, D.F. & Gaines, S.D. (2003). Species diversity: from global decreases to local increases. *Trends Ecol. Evol.*, 18, 561–566.
- Seabloom, E.W., Borer, E.T., Buckley, Y., Cleland, E.E., Davies, K., Firn, J. *et al.* (2013). Predicting invasion in grassland ecosystems: is exotic dominance the real embarrassment of richness? *Glob. Change Biol.*, 19, 3677–3687.
- Shea, K. & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.*, 17, 170–176.
- Simberloff, D. & Von Holle, B. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions*, 1, 21–32.
- Smith, N.S. & Côté, I.M. (2019). Multiple drivers of contrasting diversity–invasibility relationships at fine spatial grains. *Ecology*, 100, e02573.
- Stohlgren, T.J., Jarnevich, C., Chong, G.W. & Evangelista, P.H. (2006). Scale and plant invasions: a theory of biotic acceptance. *Preslia*, 78, 405–426.
- The PLANTS Database (2018). United States Department of Agriculture National Plant Data Team. Greensboro, NC.
- United States Geological Survey – National Parks Service Vegetation Mapping Program (1994). *Field Methods for Vegetation Mapping*. The Nature Conservancy and Environmental Systems Research Institute, Arlington.
- Von Holle, B. (2013). Environmental stress alters native–nonnative relationships at the community scale. *Biol. Invasions*, 15, 417–427.
- Zuur, A.F., Ieno, E.N., Walker, N., Savilev, A.A. & Smith, G.M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media, NY, pp. 245–293.
- Zuur, A.F., Hilbe, J.M. & Ieno, E.N. (2013). Binomial, beta-binomial, and beta glmm applied to cheetah data. In: *A Beginner's Guide to GLM and GLMM with R: A Frequentist and Bayesian Perspective for Ecologists*. Highland Statistics Limited, Newburgh, UK, pp. 207–246.

SUPPORTING INFORMATION

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

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