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Biological invasion hotspots: a trait-based perspective reveals new sub-continental patterns

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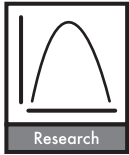
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Biological invasion hotspots: a trait-based perspective reveals new sub-continental patterns

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Invader traits (including plant growth form) may play an important, and perhaps overlooked, role in determining macroscale patterns of biological invasions and therefore warrant greater consideration in future investigations aimed at understanding these patterns. To assess this need, we used empirical data from a national-level survey of forest in the contiguous 48 states of the USA to identify geographic hotspots of forest plant invasion for three distinct invasion characteristics: invasive species richness, trait richness (defined as the number of the five following plant growth forms represented by the invasive plants present at a given location: forbs, grasses, shrubs, trees, and vines), and species richness within each growth form. Three key findings emerged. 1) The hotspots identified encompassed from 9 to 23% of the total area of our study region, thereby revealing many forests to be not only invaded, but highly invaded. 2) Substantial spatial disagreement among hotspots of invasive species richness, invasive trait richness, and species richness of invasive plants within each growth form revealed many locations to be hotspots for invader traits, or for particular growth forms of invasive plants, rather than for invasive plants in general. 3) Despite eastern forests exhibiting higher levels of plant invasion than western forests, species richness for invasive forbs and grasses in the west were respectively greater than and equivalent to levels found in the east. Contrasting patterns between eastern and western forests in the number of invasive species detected for each growth form combined with the spatial disagreement found among hotspot types suggests trait-based variability in invasion drivers. Our findings reveal invader traits to be an important contributor to macroscale invasion patterns.

Biological invasions are well-established as a leading component of global environmental change (Lodge 1993, Vitousek et al. 1997, Ricciardi 2007, Simberloff et al. 2013, Fei et al. 2014). Studying biological invasions using a macroecological framework, i.e. across large geographic areas and multiple taxa (Brown 1999), has produced many useful insights. Examples include a greater understanding of how propagule pressure and human disturbance contribute to the spread of invaders from multiple taxonomic groups (Gavier-Pizarro et al. 2010, Pyšek et al. 2010, Guo et al. 2012, Liebhold et al. 2013, Iannone et al. 2015). Investigating invasions at large scales have also revealed the scale-dependence of relationships between native and non-native diversity (Shea and Chesson 2002). Macroecological investigation can further prevent biases caused by studying too few species or too small of spatial scales (Jeschke et al. 2012, Hulme et al. 2013).

Similarly, considering how the functional traits of species (sensu McGill et al. 2006, Petchey and Gaston 2006) relate to invasion success has yielded valuable insights. Literature reviews and analysis of databases have revealed traits related to seed size, growth rate, numerous aspects of reproduction

(e.g. frequency, timing, types, etc.), attractiveness to humans, and physiological performance can all contribute to a species' ability to successfully invade (Rejmanek and Richardson 1996, Pyšek and Richardson 2007, van Kleunen et al. 2010, Sol et al. 2012). Field-based investigations ranging from the plot to the global level have further revealed that the functional distinctness of non-native species, relative to native species, contributes greatly to invasion success (Fargione et al. 2003, Ordonez 2013). This particular insight has even been applied to preventing the establishment of invasive plants in re-assembling communities of restored ecosystems (Pokorny et al. 2005, Funk et al. 2008).

Given these insights, it seems plausible that considering invader traits under the macroecology framework may provide better understanding of patterns of biological invasions. Macroscale investigations of invasion patterns tend to rely on measures of species richness estimated across very broadly defined taxa, e.g. all invasive plants or forest insect pests (e.g. Guo et al. 2012, Liebhold et al. 2013). Important within taxon variability, or nuances, may be overlooked by not considering invader traits. Meanwhile, investigations into the

contribution of functional traits to invasion success often consider many species from across large geographic areas, but they are typically not spatially explicit (e.g. Rejmanek and Richardson 1996, van Kleunen et al. 2010, Sol et al. 2012, Ordóñez 2013). Macroscale investigations considering invader traits, in addition to invader richness, are limited (e.g. Thuiller et al. 2006).

Here we investigate whether invader traits play an important role in explaining macroscale invasion patterns using a systematic, spatially-referenced dataset pertaining to forest plant invasions across the contiguous 48 states of the United States of America (USA) (Oswalt et al. 2015) in conjunction with an analytical framework capable of identifying where invasion occurrence is greater than expected by random chance (Potter et al. 2015). We used three distinct characteristics of plant invasions: overall invasive species richness; trait richness, approximated as the number of plant growth forms represented by the invasive plants present at a given location (i.e. forbs, grasses, trees, shrubs, and vines); and species richness within each growth form to answer the following questions: 1) are the hotspots of invasive species richness and trait richness geographically distinct, 2) are the hotspots of invasive plants of individual growth forms geographically distinct, and 3) are there substantial areas of non-overlap between growth form-specific hotspots and invasive species richness hotspots? Answering ‘yes’ to any of these questions would reveal the need to consider invader traits when investigating macroscale invasions.

The use of growth form as a surrogate for invader traits does not imply a complex of shared functional traits, or that species having the same growth form function similarly, as functional variability within growth forms can be considerable (Lavorel et al. 2007). Instead, it is intended as a first step in understanding the degree to which traits, even simple ones, contribute to macroscale invasion patterns. Many traits, both aboveground and belowground, reflect how plants respond to and affect environmental variability, i.e. their functionality (Lavorel et al. 2007). Compiling data on these traits for the large set of species currently invading most geographic areas, however, is logistically challenging. Identifying trait-based spatial variability related to a simple trait such as growth form would justify such efforts.

Material and methods

Data acquisition and preparation

Invasive plant data were collected as part of the United States Dept of Agriculture Forest Service Forest Inventory and Analysis Program’s (FIA) 2012 invasive plant inventory (Oswalt et al. 2015). FIA defines invasive plants in terms of USA Executive Order 13112 of 3 February 1999 as ‘an alien [plant] species whose introduction does or is likely to cause economic or environmental harm or harm to human health’ (Ries et al. 2004). FIA monitors forest conditions across the nation on both public and private lands at an intensity of one plot (0.40-ha) for every 2428 ha of forested land, resulting in about 120 000 to 130 000 plots for the contiguous 48 states (Bechtold and Patterson 2005). The amount of plots varies due to temporal trends in both forest

distribution and plot accessibility. FIA defines forests as areas at least 37 m wide and 0.40 ha in size that are currently, or were historically, covered at least 10% by trees of any size, and that are not slated for non-forest use. The proportion of FIA plots monitored for invasive plants varies by FIA Region (Supplementary material Appendix 1, Fig. A1), as does the number, and specific species, of invaders recorded (Oswalt et al. 2015). Nevertheless, these differences have little impact on macroscale invasion patterns (Iannone et al. 2015). Furthermore, adjacent FIA Regions have considerable overlap in the species they record, thus accounting for cross-FIA-Region invasions. (See Supplementary material Appendix 1, Table A2 for a list of the ~ 200 species monitored by one or more FIA Region.)

We divided our study area (i.e. the contiguous 48 states of the USA) into 12 577 40-km² hexagons, developed through intensification of the Environmental Monitoring and Assessment Program (EMAP) North American hexagon coordinates (White et al. 1992). Doing so created both equally-sized sub-divisions and directional uniformity in distances among the sub-division centroids (i.e. isotropy) (Shima et al. 2010). These properties, which are highly desirable for spatial analyses, are not possessed by politically- or naturally-defined spatial units (e.g. counties, states, watersheds). Of these hexagons, we selected 7904 which contained at least one FIA plot where invasive plants were monitored (Supplementary material Appendix 1, Fig. A3). We used plant growth form as a surrogate for invader traits which is justifiable. Morphological trait variation such as that exhibited among plant growth forms has long been recognized to convey ecological functionality (Gatz 1979, James 1982, Tilman et al. 1997), and with regard to invasive plants relates to variability in key invasion drivers, range size, and invasion success (Herron et al. 2007, Ricklefs et al. 2008, Bucharova and Van Kleunen 2009). For each hexagon, invasive species richness and the number of species belonging to each of the five following growth forms: forbs, grasses, shrubs, trees, and vines was tabulated. We also tabulated trait richness, quantified as the number of growth forms in a given hexagon. Species that exhibit multiple growth forms (e.g. trees/shrubs) were classified as the form most commonly exhibited under forested conditions. (See Supplementary material Appendix 1, Table A2 for a list of how monitored species were classified.)

Detecting and visualization of hotspots

To identify macroscale-level hotspots for invasive species richness, trait richness, and invasive species richness within each growth form, we utilized the Getis-Ord G_i^* statistic (Getis and Ord 1992) in ArcMap 10.1 (ESRI, Redlands, CA). This statistic determines if the value of an attribute at a specific location (hexagon) given the location’s neighborhood (defined below) is higher than would be expected at random relative to the mean for that attribute across an entire study region.

We conducted separate hotspot analyses for eastern and western forests (eastern sampled hexagons = 4841; western sampled hexagons = 3063; Supplementary material Appendix 1, Fig. A3). This separation was based on the limited number of forested hexagons occurring in the center

of the USA, i.e. the spatial isolation between most eastern and western forests, and on differences between these forests in numerous factors that could impact invasion patterns. These factors include the degree to which many socioeconomic and ecological factors affect forest plant invasions (Iannone et al. 2015), a wide range of abiotic and biotic conditions (Cleland et al. 2007, McNab et al. 2007), and patterns in ownership (most western forests are publicly owned and most eastern forests are privately owned) that affect management priorities and practices (Smith et al. 2002). Finally, the proportional representation of growth forms among species sampled varied much more between the eastern and western FIA Regions managing these forests than it did between the FIA Regions within each half of the country (Table 1). Hotspot analyses were not conducted for invasive trees or vines in the west, as invasive trees and vines only occurred in five and 25 western hexagons, respectively.

The Getis-Ord G_i^* statistic requires the specification of a distance at which values are to be determined higher than random, i.e. the neighborhood distance. We determined neighborhood distances for each analyzed characteristic in each half of the country by identifying the distance at which spatial autocorrelation most influenced each characteristic. To do so, we calculated Moran's I for incremental 5-km distances from 20 to 165 km. These preliminary analyses revealed that spatial autocorrelation was strongest at neighborhood distances of no more than one hexagon for all invasion characteristics in both halves of the USA (30 km in the west and from 30 to 45 km in the east). Therefore, the neighborhood for our analyses was defined as a given hexagon and its six bordering hexagons. This pattern of localized spatial autocorrelation agrees with the finding that the spatial autoregressive processes contributing to macroscale invasion patterns occur at more localized scales (Guo et al. 2012, Iannone et al. 2015).

To visually assess the results, we mapped the hexagons determined to be statistically significant hotspots ($p < 0.05$), i.e. where the values of invasive species richness, trait richness, or the number of species belonging to a particular growth form were greater than would be expected at random. To determine the extent to which hotspots of invasive species richness coincided with hotspots of trait richness and individual growth forms, we estimated and mapped the extent to which these areas overlapped. Additionally, we compared and contrasted the extent of each kind of invasion

hotspot (i.e. the percentage of hexagons surveyed that were hotspots) between each half of the country, as well as patterns within hotspots of invasive species richness, trait richness, and the number of species belonging to each growth form. We first constructed a contingency table for each east-west comparison. Given the high replication in our dataset, contingency analyses (G tests) always revealed statistically significant differences between the east and west, regardless of their ecological importance. We therefore opted to report on the strength of these differences, and did so by computing a Cramér's V statistic for each contingency table (Cramér 1946, Acock and Stavig 1979). These comparisons aided in revealing how national-level patterns of invasive richness were affected when considering all invasive plant species combined vs trait richness or individual growth forms.

Results

Hotspot locations/overlap

Depending on the invasion characteristic analyzed, from 9 to 23% of the hexagons surveyed were identified as invasion hotspots (Table 2; Fig. 1–2). Each type of hotspot exhibited unique spatial patterns, with some distinctions being more pronounced than others. Hotspots for invasive species and trait richness were quite similar with regards to geographic locations, although some notable spatial disagreement occurred (Fig. 1). In the east, both were largely concentrated in southeastern forests, with smaller, isolated hotspots for invasive species richness occurring further north and in both Louisiana and the southeast; larger, isolated hotspots for trait richness occurred in Arkansas and Oklahoma (see Supplementary material Appendix 1, Fig. A1 for state locations). In the west, both hotspot types occurred along the Pacific coast, in the interiors of California, Oregon, and Washington, in the Rocky Mountains of Idaho and Colorado, and in a small pocket in Nebraska. A small hotspot of invasive trait richness was also detected along the Wyoming–South Dakota border and an extensive hotspot for invasive species richness not coinciding with trait richness hotspots occurred in Montana and northern Idaho (Fig. 1). The extent to which trait richness hotspots spatially coincided with those of invasive species richness was 14% lower in the east than in the west (Fig. 1).

Hotspots for individual growth forms were often quite distinct from one another and from those of invasive species richness (Fig. 2A–E). In the east, hotspots for invasive forbs were scattered throughout much of the region. Of these hotspots, 44% did not overlap with hotspots of invasive species richness. Non-overlapping hotspots occurred in the northeast, the upper midwest, and in a large area within Oklahoma and Arkansas. In the west, invasive forb hotspots occurred mostly in large clusters in California, Oregon, Washington, Idaho, Montana, and Colorado, with some smaller, isolated ones occurring in Utah and South Dakota (Fig. 2A). In contrast to the east, most of these hotspots (75%) overlapped hotspots of invasive species richness. Those that did not occurred in Utah, Colorado, South Dakota, and in isolated locations of Montana.

Table 1. Proportion of invasive species monitored in each FIA Region belonging to each plant growth form. Note the greater variability in growth form proportions between eastern and western FIA Regions than between the FIA Regions within the eastern and western halves of the USA. NRS = Northern Research Station (i.e. FIA Region), SRS = Southern Research Station, PNW = Pacific Northwest Research Station, RMS = Rocky Mountain Research Station.

Growth Form	Eastern FIA Regions		Western FIA Regions	
	NRS	SRS	PNW	RMS
Forbs	0.30	0.15	0.54	0.75
Grasses	0.08	0.12	0.17	0.16
Shrubs	0.28	0.29	0.29	0.05
Trees	0.23	0.22	0.00	0.01
Vines	0.13	0.23	0.00	0.03

Table 2. Comparisons of patterns in relative extent of hotspots (i.e. percentage of investigated hexagons invaded), and in mean and total within-hotspot species richness between eastern and western forests. Differences between the east and the west intensify as values of Cramér's V increase from 0 to 1.

Hotspot type	Hotspot extent (%)			Mean \pm SE within hotspot richness (total species/growth form detected)		
	East	West	V	East	West	V
Species richness	20	17	0.05	7.47 \pm 0.07 (54)	3.10 \pm 0.07 (56)	0.77
Trait richness	23	19	0.05	4.25 \pm 0.02 (5)	1.68 \pm 0.03 (5)	0.91
Forb	14	12	0.02	1.58 \pm 0.03 (13)	2.33 \pm 0.07 (39)	0.44
Grass	15	17	0.03	1.35 \pm 0.02 (7)	1.20 \pm 0.03 (5)	0.13
Shrub	14	9	0.09	3.17 \pm 0.05 (15)	1.56 \pm 0.07 (10)	0.54
Trees*	20	<1	NA	1.48 \pm 0.02 (13)	1.00 \pm 0.00 (2)	NA
Vines*	21	<1	NA	1.94 \pm 0.04 (12)	1.00 \pm 0.00 (4)	NA

*Hotspot analyses for invasive trees and vines were not conducted in the west as these growth forms were present in too few hexagons, which would have caused all hexagons for which they were present to be identified as statistically significant hotspots. Values shown for these growth forms were calculated from the hexagons where these growth forms were present. Similarly, Cramér's V was not calculated for these growth forms.

Hotspots for invasive grasses in both halves of the country were largely aggregated (Fig. 2B). In the east, one large hotspot occurred in southeastern forests, with smaller satellite hotspots occurring in Mississippi, Oklahoma, and the upper midwest, of which, 80% overlapped with hotspots of invasive species richness. Non-overlapping hotspots occurred on the periphery of invasive species richness hotspots and in the upper midwest. In the west, invasive grass hotspots occurred in California, Oregon, Washington, Idaho, and Colorado. Most (59%) did not overlap with hotspots of invasive species richness (Fig. 2B). Non-overlapping hotspots often extended from invasive species richness hotspots into different ecosystems (e.g. coastal to the Cascade Mountains), with some occurring in isolated locations of southern California.

Hotspots for invasive shrubs were scattered throughout the east; in the west, they were mostly contained along the California, Oregon, and Washington coasts (excluding small hotspots within interior California; Fig. 2C). Spatial disagreement between invasive shrub and invasive species richness hotspots were larger in the west than in the east (37 vs 30%, respectively; Fig. 2C). In the east, non-overlapping hotspots formed large areas in both the northeast

and the upper midwest. In the west, non-overlapping hotspots occurred along the northern coast of California and within the Olympic Peninsula (Fig. 2C).

In the east, hotspots of invasive trees occurred in southeastern forests, extending north, west, and south into southern Florida (Fig. 2D). Hotspots for invasive vines exhibited similar patterns, but were less prevalent in Florida (Fig. 2E). The extent to which these hotspots did not overlap with those of invasive species richness was considerable (49 and 43% for invasive trees and vines, respectively; Fig. 2D–E). Non-overlapping hotspots mostly occurred in the southeast, extending down into southern Florida for invasive trees and westward into Louisiana and Texas for both invasive trees and vines. Invasive trees and vines only occurred in five and 25 western hexagons, respectively.

Regional comparisons

Values of Cramér's V revealed that hotspot extents (i.e. the percentage of hexagons surveyed identified as hotspots) differed much less between eastern and western forests than did within hotspot richness (Table 2). Hotspot extents for all invasion characteristics, excluding invasive grasses, were greater in the east than in the west (Table 2). Regarding within hotspot richness, even though the total number of species and growth forms detected across all corresponding hotspots were similar between the east and west, mean within hotspot richness for these hotspot types were more than doubled in the east (Table 2; Fig. 3A–B). For invasive forb hotspots, mean within hotspot richness was 41% higher, and three times more total species were detected, in the west than in the east (Table 2; Fig. 4A). Regarding invasive grasses, mean within hotspot richness and the total number of species detected were similar between the east and west (Table 2; Fig. 4B). For invasive shrubs, the east had five more detected species and a mean within hotspot richness more than double that in the west (Table 2; Fig. 4C). Finally, most tree and vine invasions occurred in the east, where the mean within hotspot species richness tended to be greater than one (Table 2; Fig. 4D–E); no hotspot analyses were conducted for these growth forms in the west because they were rarely detected.

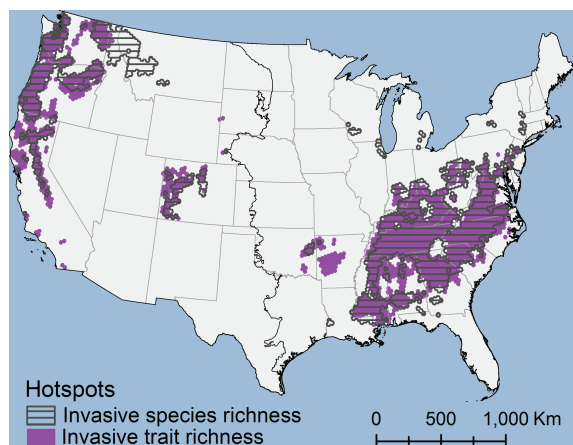


Figure 1. Geographic patterns and overlap between hotspots for invasive species richness and trait richness. The percentage of trait richness hotspots not overlapping those of species richness were 23 and 37% in the east and the west, respectively.

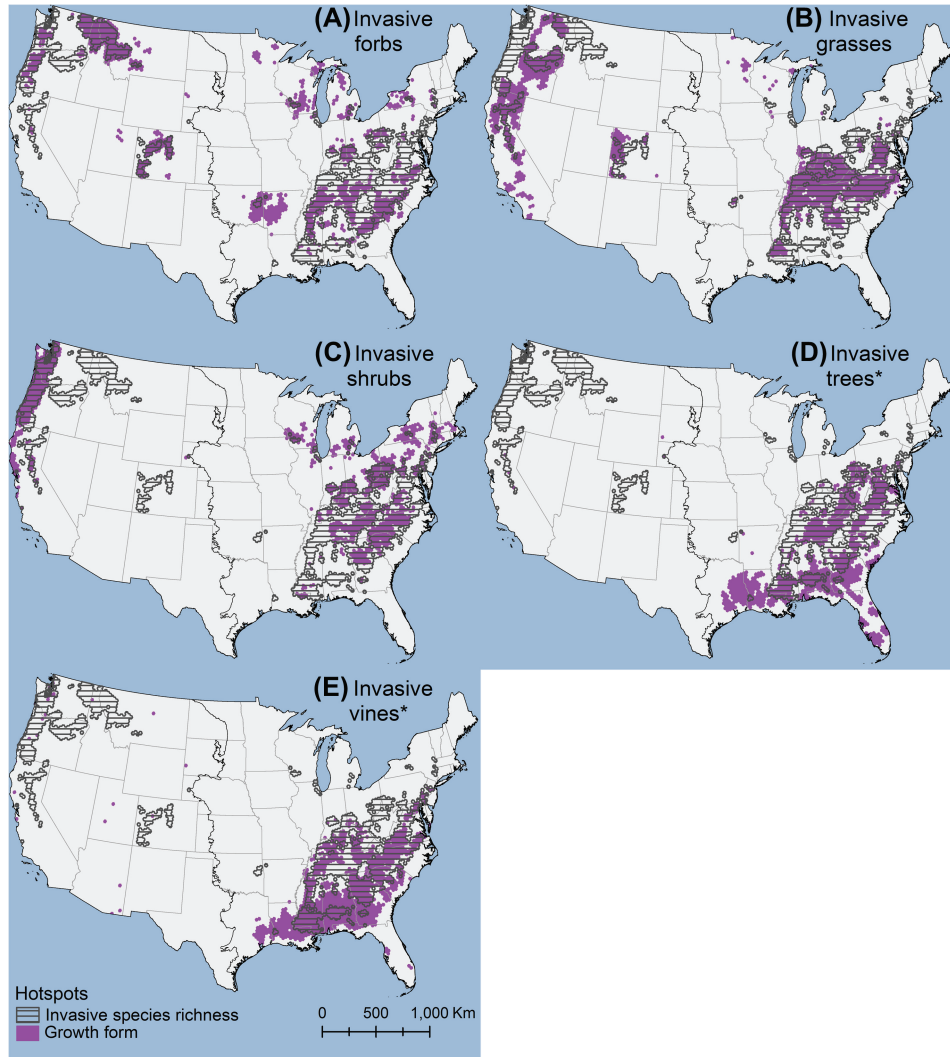


Figure 2. Hotspots of forest plant invaders belonging to different plant growth forms and their overlap with hotspots for invasive species richness. *Invasive trees and vines occurred in too few hexagons in the west to conduct formal hotspot analyses. These panels instead show the hexagons in the west where these growth forms were detected. In the east, the percentage of growth form hotspots not overlapping those of invasive species richness were 44, 20, 30, 49, and 43% for forbs, grasses, shrubs, trees, and vines, respectively. In the west, these percentages were 25, 59, and 37% for forbs, grasses, and shrubs.

Discussion

This study demonstrates that considering invader traits under a macroecology framework is critical for better

understanding of biological invasions patterns. Specifically, the results indicate that invader traits comprise an important component of these broad-scale patterns. First, although hotspots for invasive species richness and trait

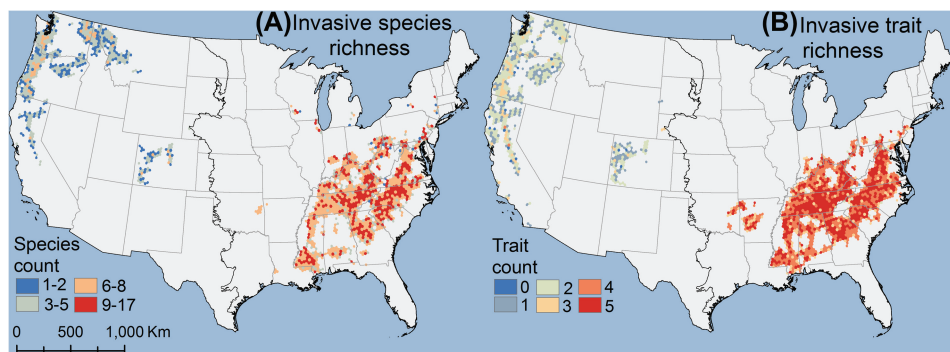


Figure 3. Comparisons of hotspot extent and within-hotspot richness patterns between the east and the west for invasive species richness and invasive trait richness.

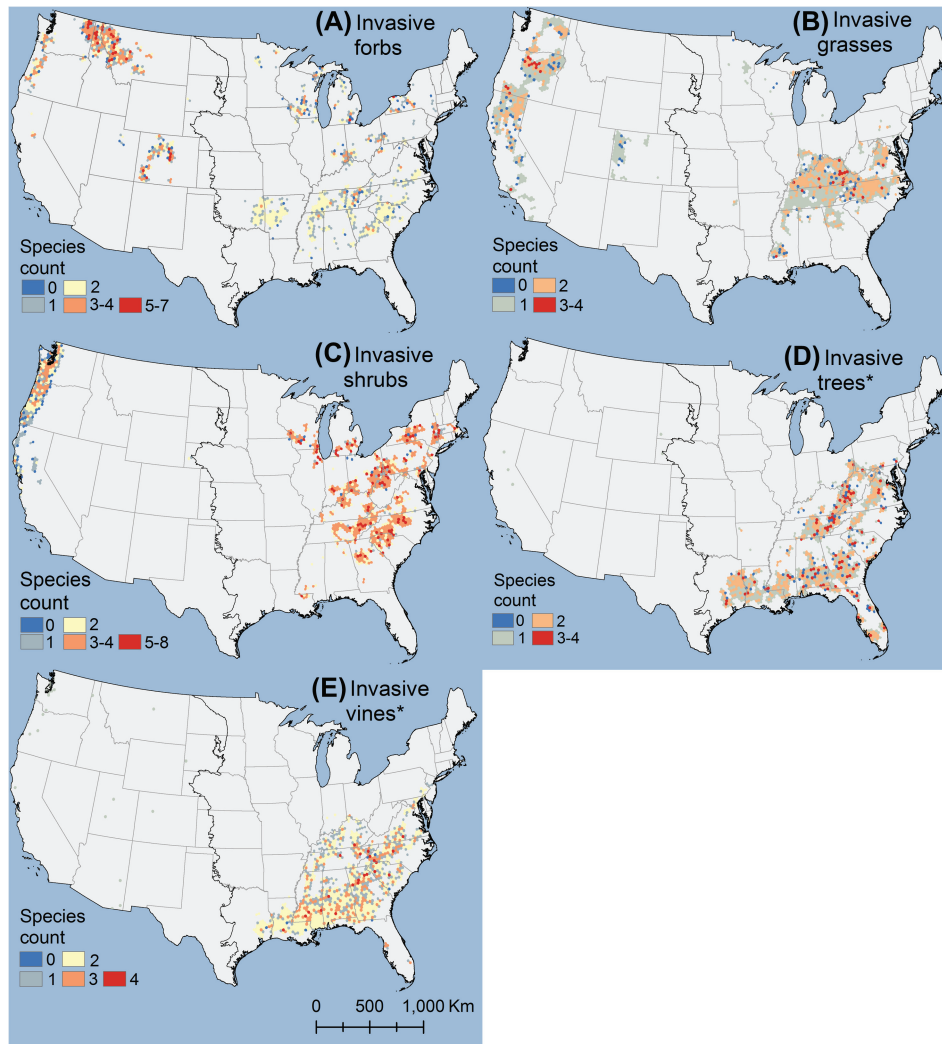


Figure 4. Comparisons of hotspot extent and within-hotspot richness patterns between the east and the west for forest plant invaders belonging to different plant growth forms. *Invasive trees and vines occurred in too few hexagons in the west to conduct formal hotspot analyses. These panels instead show the hexagons in the west where these growth forms were detected.

richness had considerable overlap, there were notable spatial disagreements between the two. Second, invasive plants having different growth forms exhibited unique spatial patterns in where their hotspots occurred. Third, the amount of spatial disagreement between growth form-specific and invasive species richness hotspots was often substantial. Importantly, these patterns spanned the borders of FIA Regions (Supplementary material Appendix 1, Fig. A1), suggesting the existence of regional patterns that were not biased by variability in sampling intensity and monitored species lists. The differences in location and extent associated with the various hotspot types make sense when considering that relationships between species richness and trait richness are inconsistent and that species having different traits tend to vary in environmental needs (Díaz and Cabido 2001, Petchey and Gaston 2002, Cadotte et al. 2011). Our findings also reaffirm the ecological insights gained by considering functional traits (McGill et al. 2006, Petchey and Gaston 2006) and reveal important new questions and insights regarding the understanding of biological invasions at macroscales.

Large portions (from 9 to 23%) of our study regions (i.e. eastern and western USA) were identified as hotspots for one or more invasion characteristic. Although these percentages seem reasonable given the likely invasibility of all ecological communities (Crawley 1987, Williamson 1996), the fact that these hexagons were identified as statistically significant invasion hotspots, rather than as simply having invasive plants, suggests many forests may not only be invasible, but highly invasible. This conjecture is supported by the previously noted expansiveness of forest plant invasions in the USA (Iannone et al. 2015, Oswalt et al. 2015) and by the increased recognition of forest susceptibility to invasions by non-native plants in general (Martin et al. 2009). This finding also suggests the need to account for invader traits when evaluating the spatial extent and degree of invadedness for other invasive taxa and/or ecosystem types.

The spatial variability detected among invasion hotspot types would have gone undetected if traits were not considered, causing some areas to not be identified as invasion hotspots. To illustrate, invasion hotspots were revealed in Florida, Louisiana, eastern Texas, and parts of Arkansas for

invasive trait richness, invasive trees, and/or invasive vines, but not for all invasive plants in general, i.e. invasive species richness. These findings reaffirm the important contribution of growth form to macroscale patterns of plant invasion (Ricklefs et al. 2008, Bucharova and Van Kleunen 2009) and confirm the utility of using this trait in our investigation. Searching for variation among invasive plants having different growth forms in the degree to which known drivers of macroscale invasion patterns (e.g. propagule pressure, human-induced disturbance, etc.) affect their distributions will be a logical first step in understanding the causes of the geographic variability in hotspots we identified. Knowledge of the factors that contribute to trait-based range variability for plants in general (e.g. Woodward and Williams 1987, Box 1996, Ordoñez et al. 2009) will likely be informative given that native and non-native species having similar traits can exhibit similar environmental needs at large spatial scales (Diez et al. 2008). Identifying the drivers of this trait-based variability will help to determine whether or not uninvaded locations within hotspots are vulnerable or resistant to invasions.

At the same time, unexpected patterns revealed by east–west comparisons indicate the potential for a more-targeted consideration. Generally, eastern hotspots were more expansive and contained more invasive species than western hotspots. Greater invasion of eastern than western forests has been observed in other national-level investigations and may reflect a longer legacy of settlement and therefore human-induced disturbance in eastern forests (Iannone et al. 2015, Oswalt et al. 2015), a well-established invasion driver (Gavier-Pizarro et al. 2010, Pyšek et al. 2010, Guo et al. 2012). The contrast in the regional patterns of invasive grass and forb hotspots was unexpected, however. Hotspots for these growth forms had either a similar or greater number of species in western than eastern forests. These contrasting patterns, coupled with the longer legacy of settlement and human-induced disturbance in eastern than in western forests, suggest the need for further consideration of the extent to which the effects of human-induced disturbance on invasive plant establishment vary among plant growth forms. East–west comparisons in the frequency, intensity, and types of human-induced disturbance occurring within each hotspot type could help address this consideration, as could smaller-scale manipulative experiments.

The identification of trait-based variability among invasion hotspots can also help to inform large-scale invasive species management and policy. For example, we found eastern forests to be susceptible to invasions by each of the five growth forms whereas western forests were much less susceptible to invasive trees and vines. Assuming these patterns reflect habitat suitability, they can help to assess the regional appropriateness of species for horticultural trade, a leading vector of plant invasions (Reichard and White 2001, Maki and Galatowitsch 2004, Bradley et al. 2011). Additionally, given that invasion drivers, environmental impacts, and the effectiveness of potential control strategies often vary considerably among invasive plant species having different growth forms (Gordon 1998, Iannone et al. 2008, 2013, Bucharova and Van Kleunen 2009), identifying trait-based variability among invasion hotspots can help managers to determine the types of invaders most suited for the regions

they manage, thereby informing them on how to better limit and mitigate against the negative impacts of these invaders. With this in mind, hotspots of trait richness may present particular challenges, as they are likely to represent areas having a greater diversity of invader impacts and that similarly require a greater diversity of control strategies.

Future study on the following aspects may further improve our understanding of how invader traits contribute to macroscale patterns of biological invasions. First, although considering plant growth form revealed important insights, considering other traits, or groups of traits, may prove even more useful. Investigating traits known to distinguish native from invasive species of the same growth form may be particularly insightful [e.g. earlier leaf emergence in invasive shrubs (Harrington et al. 1989)]. Such traits likely vary among growth forms (Herron et al. 2007) and across locations (Thompson et al. 1995). Even investigations using other easy-to-assess traits besides growth form (e.g. longevity, photosynthetic pathway, whether or not the species fixes nitrogen, etc.) may reveal important insights. Such investigations only require information on the absence/presence of species in given locations and the traits of those species. Although not essential, national-level, empirically collected datasets, such as those used here, can enhance these efforts, especially with regards to spatial and temporal progressions of invasions (Oswalt et al. 2015). Second, we compared simple measures of species and trait richness, and thus only identified hotspots of invader establishment. Future studies may benefit from using measures more indicative of invader impacts such as abundance, prevalence, or dominance (Hillebrand et al. 2008). Finally, an important next step will be determining what drives the variability in hotspot locations found among the invaders having different growth forms, trait richness, and invasive species richness.

Conclusions

Our investigation illustrates the impact of invader traits on macroscale invasion patterns, and the large spatial extent of forest vulnerability to non-native plant invasions. By considering the simple trait of plant growth form, we found previously undetected hotspots for individual growth forms of invasive plants and for multiple invader traits (as indicated by growth forms) that did not coincide spatially with hotspots for invasive plants in general (i.e. invasive species richness); thus, we found invasion hotspots to be trait-specific. Our results also revealed regional variability in the commonality (i.e. species richness) of invasive plant species possessing particular growth forms. The detection of such trait-based patterns is important for generating new questions and insights regarding the understanding of biological invasions at macroscales.

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Supplementary material (Appendix ECOG-01973 at <www.ecography.org/appendix/ecog-01973>). Appendix 1.