

# Evidence of biotic resistance to invasions in forests of the Eastern USA

Basil V. Iannone III · Kevin M. Potter · Kelly-Ann Dixon Hamil ·  
Whitney Huang · Hao Zhang · Qinfeng Guo · Christopher M. Oswalt ·  
Christopher W. Woodall · Songlin Fei

Received: 31 March 2015 / Accepted: 12 September 2015 / Published online: 23 October 2015  
© Springer Science+Business Media Dordrecht 2015

## Abstract

**Context** Detecting biotic resistance to biological invasions across large geographic areas may require acknowledging multiple metrics of niche usage and potential spatial heterogeneity in associations between invasive and native species diversity and dominance.

**Objectives** Determine (1) if native communities are resistant to biological invasions at macroscales; (2) the metrics that best quantify biotic resistance at these

scales; and (3) the degree to which the direction and magnitude of invader-native associations vary with scale and/or location.

**Methods** Using a mixed-effects modeling framework to account for potential sub-regional and cross-scale variability in invader-native associations, we modeled the species richness and cover of invasive plants in 42,626 plots located throughout Eastern USA forests in relationship to plot-level estimates of native tree biomass, species richness, and evolutionary diversity.

**Results** We found (1) native tree biomass and evolutionary diversity, but not species richness, to be negatively associated with invader establishment and dominance, and thus indicative of biotic resistance; (2) evidence that evolutionary diversity limits invader dominance more than it does invader establishment;

---

Special issue: Macrosystems ecology: Novel methods and new understanding of multi-scale patterns and processes.

---

Guest Editors: S. Fei, Q. Guo, and K. Potter.

---

**Electronic supplementary material** The online version of this article (doi:[10.1007/s10980-015-0280-7](https://doi.org/10.1007/s10980-015-0280-7)) contains supplementary material, which is available to authorized users.

---

B. V. Iannone III (✉) · S. Fei  
Department of Forestry and Natural Resources, Purdue  
University, West Lafayette, IN, USA  
e-mail: biannone@purdue.edu

S. Fei  
e-mail: sfei@purdue.edu

K. M. Potter  
Department of Forestry and Environmental Resources,  
North Carolina State University, Research Triangle Park,  
NC, USA

K.-A. D. Hamil · W. Huang · H. Zhang  
Department of Statistics, Purdue University,  
West Lafayette, IN, USA

Q. Guo  
USDA Forest Service Southern Research Station,  
Research Triangle Park, NC, USA

C. M. Oswalt  
USDA Forest Service Southern Research Station,  
Knoxville, TN, USA

C. W. Woodall  
USDA Forest Service Northern Research Station,  
Saint Paul, MN, USA

(3) evidence of greater invasion resistance in parts of the agriculturally-dominated Midwest and in and around the more-contiguous forests of the Appalachian Mountains; and (4) the magnitude to which native tree biomass and evolutionary diversity limit invasion varies across the ranges of these metrics.

**Conclusions** These findings illustrate the improved understanding of biotic resistance to invasions that is gained by accounting for sub-regional variability in ecological processes, and underscores the need to determine the factors leading to spatial heterogeneity in biotic resistance.

**Keywords** Big data · Biomass · FIA Program · Invasive plants · Macrosystems · Niche · Evolutionary diversity · Taxonomic diversity

## Introduction

Biological invasions and their impacts will likely increase with the continuing expansion of global commerce (Jenkins 1996; Lodge et al. 2006; Hulme 2009), making the need to identify the factors affecting invasion perhaps greater than ever. One of the most enduring hypotheses for explaining why some ecosystems are more invulnerable than others is the “biotic resistance hypothesis”, which postulates that communities having greater biodiversity are less invulnerable, due to having fewer unfilled niches (Elton 1958; Levine and D’Antonio 1999; Fridley et al. 2007). This hypothesis not only offers a mechanistic explanation of invasions, but also provides insight into system stability (McCann 2000; Ives and Carpenter 2007). Nevertheless, studies testing this hypothesis have produced inconsistent results both within and across spatial scales (Fridley et al. 2007) with empirical support for this hypothesis generally declining over time (Jeschke et al. 2012). A more thorough evaluation of this hypothesis using improved information from spatially referenced, national-level datasets (i.e. “big data”) may help to better understand if and how communities resist invasions.

Both native diversity and biomass need to be considered when testing for biotic resistance to invasions (Guo et al. 2015). Most studies, especially those at macroscales, define diversity as species richness. However, native species richness may be a

poor indicator of niche usage across large spatial scales, as it has been found to be positively related to invader richness at such scales (Stohlgren et al. 2003). Other metrics may better quantify niche usage at large spatial scale. For instance, metrics of evolutionary diversity hypothesized to be positively related to diversity in both known functional (Faith 1992, 2002) and unknown phenotypic traits (Lososová et al. 2015; Tan et al. 2015) may better reflect niche usage. Negative associations between native phylogenetic diversity and the number and proportion of non-native species at the national level (Lososová et al. 2015) support this conjecture. Regarding native biomass, not accounting for it may lead to failure in identifying open niches in highly diverse communities during early stages of succession or those caused by temporal population fluctuations or disturbance (Shurin and Srivastava 2005; Clark and Johnston 2011). In these circumstances, resident species may not have yet attained maximum biomass, increasing resource availability (Davis et al. 2000; Guo et al. 2015). Overall, a more robust evaluation of biotic resistance may be gained by moving beyond species richness to additional indicators of niche usage, including both metrics of native biodiversity and estimates of native biomass.

As with biodiversity, invasions can be defined/measured in multiple ways, each conveying different information. For example, invasion richness indicates the number of successful invasions while measures of invasive species biomass or cover quantify invader dominance. Study outcomes can vary depending on the measure of invasion used (Guo and Symstad 2008; Catford et al. 2012). This reasoning, along with the deeper understanding that can be gained from utilizing multiple invasion measures (Guo and Symstad 2008; Catford et al. 2012; Iannone et al. 2015), necessitates the consideration of multiple invasion measures when investigating biotic resistance.

Finally, testing the biotic resistance hypothesis across large spatial scales requires accounting for scale dependencies and spatial heterogeneity in ecological processes, both of which are key components and research priorities in macrosystems and landscape ecology (Wu and Hobbs 2002; Heffernan et al. 2014; Soranno et al. 2014). The scale dependency of ecological associations is well established (Turner 1989; Wiens 1989; Crawley and Harral 2001), particularly for associations between invasive and native species (Fridley et al. 2007). Cross-scale contradictions in

association directions can emerge from the type of statistical model used, from the absence of important explanatory variables in these statistical models, and from variation among explanatory variables in the scale at which they are most influential (Dixon Hamil et al. 2015). Less studied is the contribution of spatial heterogeneity in invader-native associations to large-scale invasion patterns. Large geographic areas encompass great environmental variability, and therefore considerable spatial heterogeneity in ecological processes. Given that this spatial heterogeneity can result in the emergence of complex large-scale patterns (Peters et al. 2007), large-scale tests of biotic resistance may benefit by accounting for spatial variability in associations between invasive and native species. As the causes of this heterogeneity may be unknown and vary among locations, such tests will further benefit from statistical approaches not requiring such information (Dixon Hamil et al. 2015).

Here we report on an investigation into macroscale patterns of biotic resistance within the context of forest plant invasions in the Eastern United States of America (USA). We used a high number of data observations recorded as part of the United States Forest Service's (USFS) Forest Inventory and Analysis Program (FIA) (Oswalt et al. 2015) to test for associations between native trees and invasive plants that would suggest biotic resistance. FIA data, being collected across all USA forests using consistent sampling protocols and a spatially systematic design (Bechtold and Patterson 2005), are well-suited for investigating cross-scale variability in species interactions (Araújo and Rozenfeld 2014). In forests, trees comprise the majority of biomass and primary production (Muller 2003), and thus resource uptake, making them important contributors to biotic resistance (Davis et al. 2000; Guo et al. 2015).

Specifically, we wanted to determine: (1) if native communities are resistant to biological invasions at macroscales; (2) the metrics that best quantify biotic resistance to biological invasions at these spatial scales; and (3) the degree to which the direction and magnitude of invader-native associations suggesting biotic resistance vary with spatial scale and/or location. We asked these questions in the context of two separate measures of invasion—invader richness and invasion cover (defined below). This allowed us to assess the extent to which answers vary relative to how invasion is quantified. As forests and the services they

provide are increasingly harmed by invasive plants (Martin et al. 2009; Pejchar and Mooney 2009; Fei et al. 2014), particularly in our study region (Oswalt et al. 2015), the findings of this investigation will have implications for invasive species management and policy.

## Methods

### Data acquisition and preparation

We obtained measures of biotic resistance and plant invasion for 42,626 FIA plots located across the forests of the Eastern USA. We defined this region as all areas within either the Humid Temperate or Humid Tropical Domains (Cleland et al. 2007). The Humid Temperate domain encompasses most of the Eastern USA, while the Humid Tropical Domain encompasses the southern tip of Florida (Appendix A1 in supplementary material). The FIA program is a national-level effort to monitor spatiotemporal patterns associated with forest resources (Bechtold and Patterson 2005). Monitoring occurs across a grid of 0.40-ha permanent plots located at an approximate intensity of one plot for every 2428 ha regardless of land use (~130,000 partially and/or fully forested FIA plots are located in the contiguous 48 states and southern coastal Alaska). FIA plots in the eastern USA are sampled on a 5-year rotation with 20 % of plots being sampled annually. Our dataset contained the most recent estimates for each plot. FIA defines forests as areas at least 36.6 m wide and 0.40 ha in size, having at least 10 % cover of trees (historic or current) of any size, and that are not slated for non-forest use. FIA defines invasive plants in accordance with USA Executive Order 13112 as exotic plant species likely to cause economic or environmental harm (Ries et al. 2004).

To account for the multiple factors potentially contributing to biotic resistance, we gathered data for all plots on aboveground live biomass of native trees (hereafter *biomass*) and on three measures of native tree diversity. Biomass was determined as detailed in Woodall et al. (2011) and applied in Potter and Woodall (2014). Briefly, individual tree sound volumes were estimated based on regional volume equations then converted to bole oven-dry biomass using species-specific wood density values. Bole

oven-dry biomass estimates were then utilized to estimate total tree oven-dry biomass across all tree components using the Component Ratio Method (Woodall et al. 2011).

For native diversity, we estimated *native species richness*, i.e. the number of native tree species occurring in a given plot, and two measures of evolutionary diversity—*phylogenetic species variability* and *phylogenetic species clustering* (Helmus et al. 2007). Evolutionary diversity measures were estimated using a phylogenetic supertree of the 397 native tree species occurring throughout the contiguous 48 states. As described by Potter and Woodall (2012), this tree was constructed using surveys of recent molecular systematic and paleobotanical studies. Phylogenetic species variability (PSV) is an index of phylogenetic clustering quantifying divergence from a star phylogeny with species becoming less evolutionarily related, i.e. approaching a star phylogeny, as values increase from 0 to 1. This metric assumes that phylogeny branch lengths are proportional to the variance in neutral, unselected traits, and therefore requires only information on phylogenetic relatedness, and not on actual traits, to calculate. Phylogenetic species clustering (PSC) quantifies the extent to which species are clustered at the branch tips of the phylogenetic supertree, with clustering decreasing (and phylogenetic evenness increasing) as values increase from 0 to 1. We chose these measures over others (e.g. Faith 1992; Helmus et al. 2007), because variance inflation factors of linear models revealed no evidence of complications due to collinearity (Legendre and Legendre 2012). Additionally, like native species richness, these metrics weight species equally, making their comparisons to species richness more meaningful.

To account for the fact that invasions can be measured in multiple ways and that invader-native relationships suggesting biotic resistance may vary among these measurements, we estimated two separate invasion measures. *Invasion richness*, i.e. the number of invasive plant species found in a plot, estimates the number of species to successfully invade. *Invasion cover*, i.e. the summed total cover of all invasive plants found in a plot, estimates invader dominance. This last measure can therefore be greater than 100. The moderate degree to which both measures were correlated ( $r = 0.64$ ) did not deter the utility of analyzing each separately.

We then determined the ecological division and section in which each plot was located (sensu Cleland et al. 1997, 2007). As described below, this information was used in our statistical analyses to accommodate for potential spatial heterogeneity in invader-native associations. These geographic classifications are used by the USFS to assist in ecosystem delineation and regional management efforts, and are based on climate, potentially dominant vegetation, topography, geology, and soils. This classification system is hierarchical in that the 91 ecological sections within in our study region are each nested within one of five larger ecological divisions, all of which are nested within either the Humid Temperate or Humid Tropical Domains. For this classification, the importance of climate increases with scale, while that of other factors decreases (Cleland et al. 1997). By accounting for a wide range of biotic and abiotic variables, this classification ensures that the plots within a given region are more similar with regards to this variability than to plots in other regions. Descriptions of ecological sections can be found in McNab et al. (2007). The location and name of each ecological division and section within our study region can be found in supplementary material Appendix A1. The fact that these regions are nested and based on ecologically meaningful characteristics limits potential complications associated with arbitrarily deciding cutoffs of spatial scales (Shurin and Srivastava 2005; Dark and Bram 2007).

A law aimed at protecting the privacy of forest landowners limits the ability of researchers to attain the exact coordinates of FIA plots. Instead, coordinate values are spatially perturbed so that plots appear within the same county, but within 0.8–1.6 km of the actual location. This perturbation is unlikely to result in a misclassification of plot location, as its spatial extent is very small relative to the sizes of the ecological sections, which are thousands of square km in area. The high number of plots typically occurring within ecological sections helps to ensure that the interpretation of our statistical analyses is not affected by unlikely misclassifications (98 % of the ecological sections had data from 25 or more FIA plots, with most having considerably more; range in plot counts per ecological section = 10 to 3573).

The Northern and Southern FIA Regions (Appendix A1 in supplementary material) vary in how they monitor invasive plants; however, this variability

has very little effect on macroscale invasion patterns (Iannone et al. 2015) and, as described below, is accounted for in our statistical analysis. First, as the invasive species of concern vary by region, so too does the number and identity of monitored species. However, there was considerable overlap between regions in the lists of species monitored, thereby accounting for cross-regional invasions (Table A2 in supplementary material). Second, the Southern Region monitored all FIA plots for invasive plants, while the Northern Region only monitored 18 %. Nevertheless, summary statistics calculated for all southern plots and for a random selection of 18 % of these plots (i.e. sampling intensity equivalent to the Northern Region) differed little, revealing varying sampling intensities to be of little concern. To illustrate estimates for the full and randomly-selected data, respectively, were: invasion richness (mean  $\pm$  SD) =  $1.16 \pm 1.29$  and  $1.14 \pm 1.28$ ; invasion cover =  $17 \pm 29$  % and  $16 \pm 29$  %; and invasive species detected = 49 and 44. The five species not detected in the randomly-selected dataset occurred in four or fewer plots in the full dataset. Finally, the Northern FIA Region surveys for invasive plants during the growing season due to obvious snow depth obstructions (Woodall et al. 2013), while the Southern FIA Region surveys all year.

#### Data analysis

We used a mixed-effects modeling framework for our analysis, as it possessed three needed characteristics. First, it accounted for potential spatial heterogeneity in invader-native associations without having to know the cause, or causes, of this heterogeneity (Dixon Hamil et al. 2015). Second, it was able to control for differences between the Northern and Southern FIA Regions in sampling details. Third, it was able to deal with statistical complications arising from extremely large datasets. For example, the many observations in our dataset ( $N = 42,626$ ) can lead to the statistical significance of independent variables (e.g. native biomass, species richness, PSV, and PSC) despite scatter plots demonstrating weak, and potentially ecologically unimportant, relationships (Anderson et al. 2000; Woodall and Westfall 2010; Spanos 2014). The exact manner in which this framework addressed these issues is explained below.

For both invasion measures, we constructed a statistical model containing all four biotic resistance measures as fixed effects and nested sub-regions as random effects, each having independent intercept and slope estimates. By doing so, we accommodated for potential spatial heterogeneity in invader-native associations. Models were run both at the ecological division level ( $n = 5$  random effects) and at the ecological section level ( $n = 91$  random effects). Assuming independence among ecological sections/divisions was reasonable, as plots within a given section/division are more similar to one another with regards to a wide range of abiotic and biotic conditions than to plots within other sections/divisions (Cleland et al. 1997), and because spatial autocorrelative processes contributing to macroscale invasion patterns likely occur at distances smaller than the sizes of ecological sections and divisions (Guo et al. 2012; Iannone et al. 2015). Calculating slopes estimates separately for each ecological section also controlled for variability among ecological sections with regards to the timing of invasive plant data collection.

To determine if forests exhibit biotic resistance to biological invasions (Question 1), and the metrics that best quantify biotic resistance (Question 2), we resampled (i.e. bootstrapped) from the slope estimates of the 91 ecological sections (as determined by summing conditional and fixed slope estimates) for each biotic resistance measure 10,000 times, allowing for repetition, and then calculated the bias corrected, accelerated 95 % confidence interval (CI) of each generated distribution (Efron and Tibshirani 1986). We used 95 % CIs of bootstrapped distributions rather than of the actual distributions, as the latter deviated slightly from normality. We assumed a metric to be reflective of biotic resistance when its 95 % CI encompassed values less than zero. Given our large sample size ( $N = 42,626$ ), 95 % CIs provided a more conservative test of statistical significance than did the  $P$ -values of fixed model effects. We assumed biotic resistance measures differ from one another in magnitude, i.e. effect size, when the absolute values of their 95 % CIs did not overlap. We assumed spatial variability of magnitudes to increase with increased ranges of 95 % CIs. As we utilized 95 % CIs of bootstrapped distributions rather than standard errors of fixed effects to assess statistical significance, differences between the Southern and Northern FIA



Regions in sampling efforts were unlikely to affect ecological inferences.

To determine if the direction and magnitude of invader-native associations suggesting biotic resistance vary with either scale or location (Question 3), we mapped slope estimates for each ecological section and division. Comparing these maps allowed us to assess the degree to which association direction and magnitude varied between ecological sections and division, i.e. between smaller and larger spatial scales. Mapping slope estimates for models containing ecological sections as random effects also enabled us to detect spatial patterns related to association direction and magnitude (e.g. aggregations of slopes having similar directions or estimates) and to therefore assess the degree to which association direction and magnitude are location dependent.

We also used AIC values (Akaike 1973) to compare performance of models having random slope estimates for either ecological divisions or sections, with models containing biotic resistance measures as only fixed linear effects (i.e. having no random effects). As each model accounted for spatial heterogeneity in association directions and magnitudes to differing degrees, models having the lowest AIC value are likely to best represent invader-native associations for our study region given our dataset (Anderson et al. 2000).

In addition, we investigated potential biotic contributors to the spatial heterogeneity in invader-native associations that we detected by modeling section-level slope estimates for each biotic resistance measure in response to section-level means for same biotic resistance measure ( $n = 91$  sections). We confirmed that simple linear relationships were best to assess these relationships using a Davies test to detect potential changes in slope values (Davies 1987). A significant relationship for a given biotic resistance measure suggests the effects of that measure on invasion varies as the measure increases or decreases. No statistically significant relationship suggests that measure to be similarly associated to invasion across its entire numerical range.

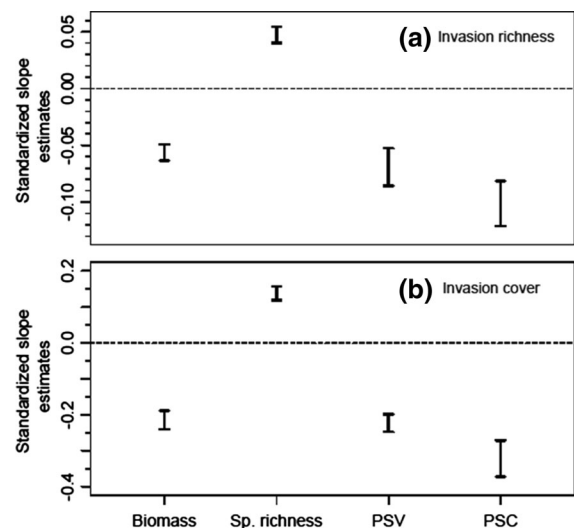
Statistical analyses were conducted in R v 3.0.1 (R Core Team 2013) using the lme4 package (Bates et al. 2014) to construct random mixed-effects models and the bootstrap package (Tibshirani and Leisch 2013) to conduct bootstrap analyses. Biotic resistance measures were standardized [ $x - \text{mean}(x)/\text{SD}(x)$ ] in order to determine their relative contribution to invasion

patterns (Schielzeth 2010). Prior to analysis, invasion richness and native tree biomass were both square root-transformed [ $\sqrt{x + 1}$ ], and invasion cover was log transformed [ $\log_{\text{natural}}(x + 1)$ ]. Maps were constructed in ArcMap 10.1 (ESRI, Redlands, CA).

## Results

### Variability among biotic resistance measures (Questions 1 and 2)

Comparing 95 % confidence intervals (CI) of the bootstrapped distributions of section-level slope estimates (i.e. conditional plus fixed slope estimates) revealed each biotic resistance measure to be significantly associated with both invasion measures, and the direction of these associations to vary (Fig. 1; See Table A3 in supplementary material for numerical values of 95 % CI). Native tree biomass, phylogenetic species variability (PSV), and phylogenetic species clustering (PSC) were all negatively associated with both invasion measures. In contrast, native species



**Fig. 1** Bootstrapped 95 % confidence intervals for section-level slope estimates (i.e. conditional plus fixed slope estimates) of biotic resistance measures for the 91 ecological sections in models for **a** invasion richness and **b** invasion cover across our entire study region. Biomass = native biomass, Sp. richness = native species richness, PSV = phylogenetic species variability, and PSC = phylogenetic species clustering. Increased interval size suggests greater spatial variability in slope estimates across the 91 ecological sections

richness was positively associated to both invasion measures.

The magnitude of these associations also varied among biotic resistance measures (Fig. 1). PSC was most strongly associated to both invasion measures, as its absolute 95 % CI interval only overlapped slightly with that of PSV in the invasion richness model. Biomass and PSV shared associations of similar magnitudes with both invasion measures, i.e. their 95 % CIs overlapped considerably. Native species richness was least associated with both invasion measures. Its absolute 95 % CI overlapped only slightly with that of biomass in the invasion richness model.

Differences in the extent to which association magnitudes varied among ecological sections (as estimated by 95 % CI ranges) also varied among biotic resistance measures (Fig. 1). For the invasion richness model, slope estimates varied among ecological sections most for PSV and PSC, as their 95 % CI ranges were more than double those for native biomass and species richness. For the invasion cover model, slope estimates varied most among ecological sections for PSC. Its 95 % CI range was up to two times greater than those of all other biotic resistance measures. For this same model, the extent to which slope estimates for biomass and PSV varied among ecological sections was similar and slightly larger than for species richness.

#### Variability across location and scale (Question 3)

Mapping slope estimates revealed association direction and magnitude to be affected by both scale and location, although location was most influential (Figs. 2, 3; see Appendix A4 in supplementary material for slope estimates). Increasing the scale of random effects from section to division caused only two associations to shift directions—the association between PSV and invasion richness shifted from positive to negative in the Savannah division (i.e. southern tip of Florida; Fig. 2c) and the association between native biomass and invasion cover shifted from negative to positive in the Prairie division (western portion of study region; Fig. 3a). When decreasing from division to section, most sections retained the association direction of the division in which they were nested. Notable exceptions include the switch from positive to negative associations

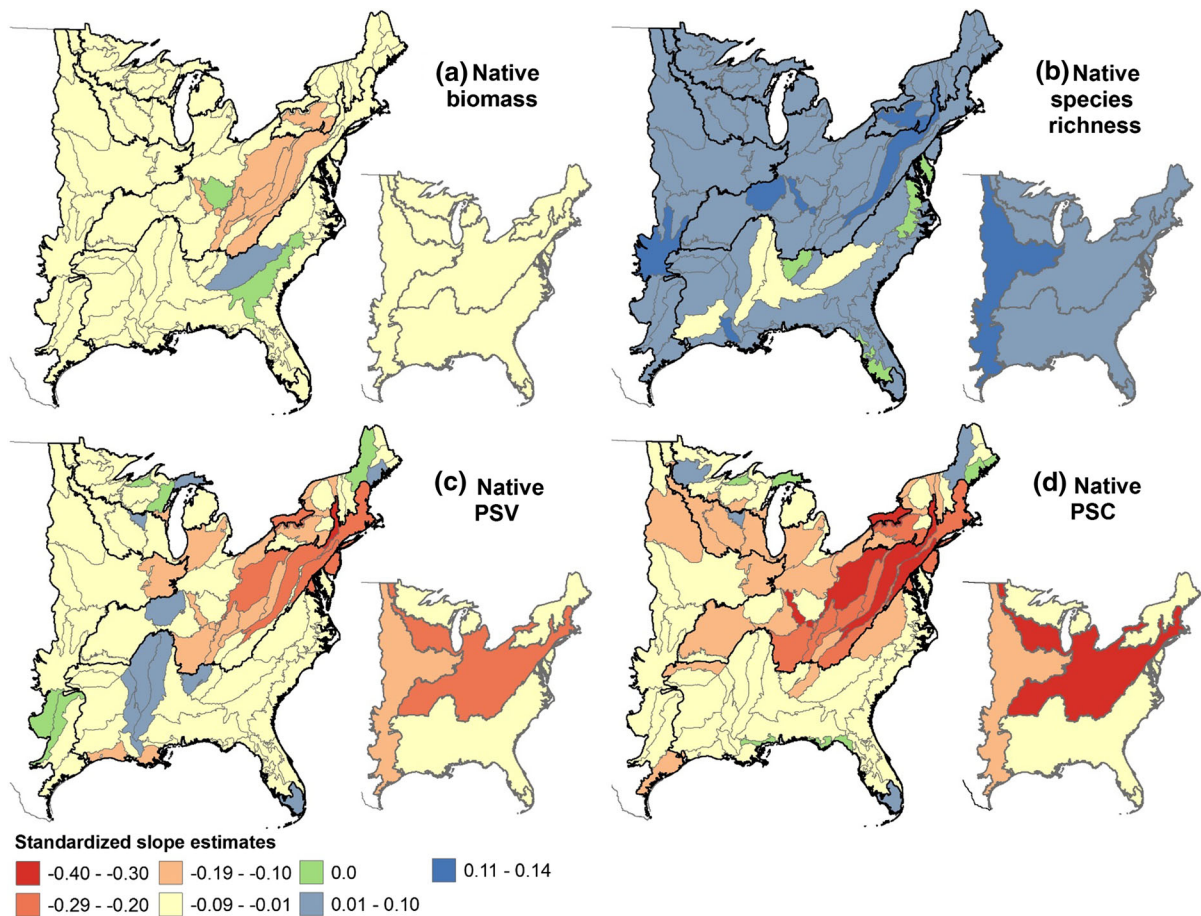
between native species richness and both invasion measures in the south central portion of study region (Figs. 2b, 3b) and the switch from negative to positive associations between PSV and invasion richness in sections along the Mississippi River (Fig. 2c). For both invasion richness and cover, association magnitudes for most sections were smaller than those of the division in which they were nested (Figs. 2, 3).

Mapping section-level slope estimates also revealed distinct spatial patterns. For example, the ecological sections in which native biomass, PSV, and PSC were most negatively associated with both invasion measures tended to be aggregated within or near the Appalachian Mountains (Figs. 2, 3). Stronger negative associations between PSC and invasion richness also occurred in a band throughout the Midwest (Fig. 2d). Aggregations of ecological sections in which native species richness associations were strongly positive occurred for invasion cover (Fig. 3b), but less so for invasion richness (Fig. 2b). Ecological sections in which native species richness was negatively associated with both invasion measures were aggregated in the south-central part of our study region, although these associations were weak (Figs. 2b, 3b). Finally, despite PSV and PSC exhibiting overall negative associations with invasion (Fig. 1), they were positively associated with invasion richness in some ecological sections (Fig. 2b, c). Contrasts in association direction occurred much less for biomass in the invasion richness model (Fig. 2a), and for all biotic resistance measures in the invasion cover model (Fig. 3).

Comparing AIC values among models revealed that accounting for greater spatial heterogeneity in invader-native associations improved model performance (Table 1). For invasion richness models, adding random slope estimates for ecological divisions and sections decreased AIC values by 4.8 and 23.3 %, respectively. Improvements, although less pronounced, were still substantial for invasion cover models; adding random slope estimates for ecological divisions and sections decreased AIC values by 1.7 and 6.9 %, respectively.

#### Biotic attributes of invasion associations

Slope estimates for associations between biotic resistance measures and invasion were often contingent upon the section-level means for these measures, and



**Fig. 2** Geographical patterns and cross-scale variation in associations between invasion richness and the four metrics of biotic resistance. Smaller and larger maps show associations at the division and section levels, respectively

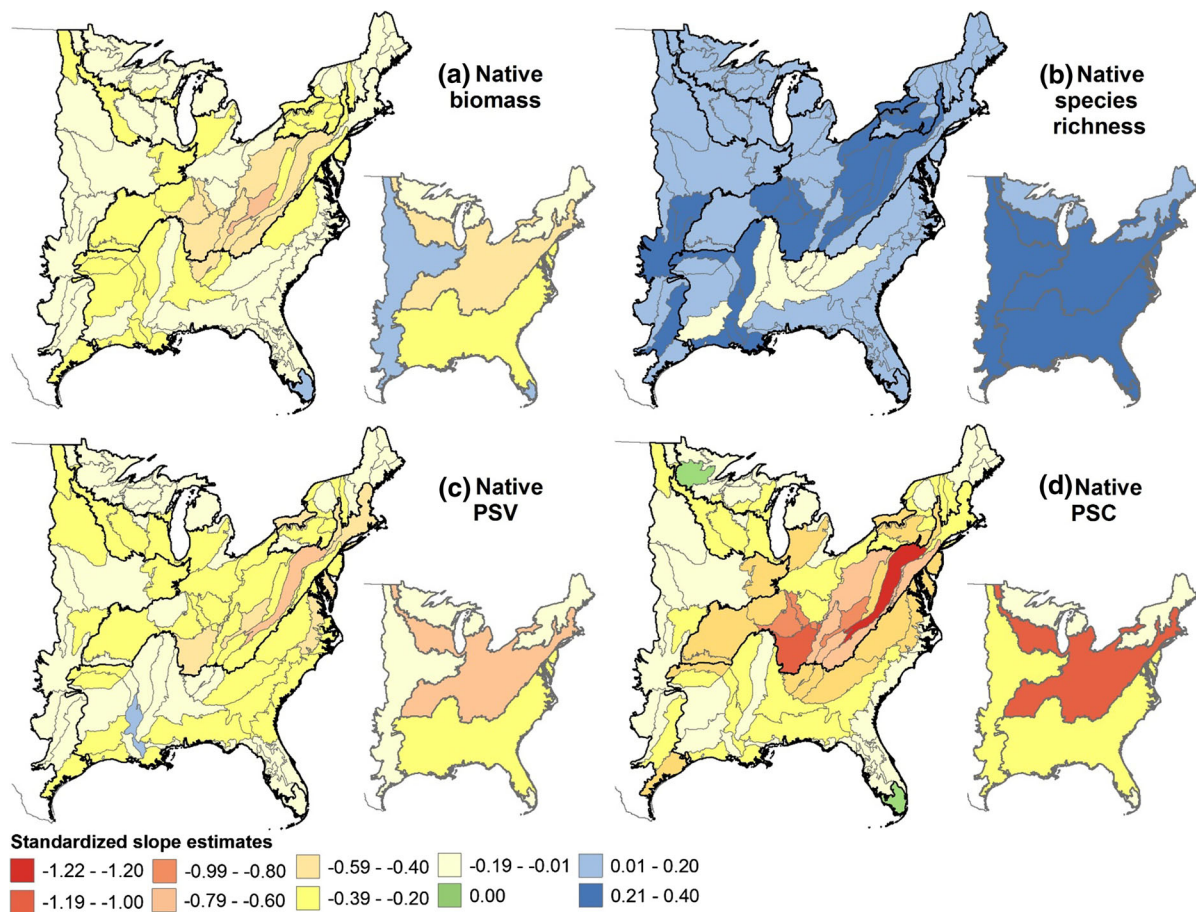
thus varied relative to biotic attributes. For example, the associations of both native biomass and PSC to invasion became more negative with increasing section-level means for these measures (Fig. 4a, d, e, h). This pattern was less pronounced for native biomass than for PSC. In contrast, associations between PSV and invasion became less negative, or more positive, with increasing section-level means for PSV, although these relationships were weak (Fig. 4c, g). Associations between native species richness and invasion remained constant across section-level means of native species richness (Fig. 4b, f). Note that conducting analyses without the two leftmost data points in Fig. 4d, h (i.e. potential outliers) did not affect findings; relationships only became more negative and the adjusted  $R^2$  values changed only slightly.

## Discussion

### Key findings

Our study revealed evidence of biotic resistance to invasive plant establishment and dominance across large geographic areas, with native tree biomass and evolutionary diversity as two best metrics in measuring biotic resistance. Furthermore, follow-up correlations revealed variable associations between native tree biomass and plot-level estimates of stand age and forest cover ( $r = 0.53$  and  $0.37$ , respectively), suggesting native biomass to be an indicator of invasion resistance across gradients of forest disturbance and successional stage. Regarding the negative associations between evolutionary diversity and invasion,





**Fig. 3** Geographical patterns and cross-scale variation in associations between invasion cover and the four metrics of biotic resistance. Smaller and larger maps show associations at the division and section levels, respectively

**Table 1** Changes in model performance through the addition of random slope estimates for ecological division and section

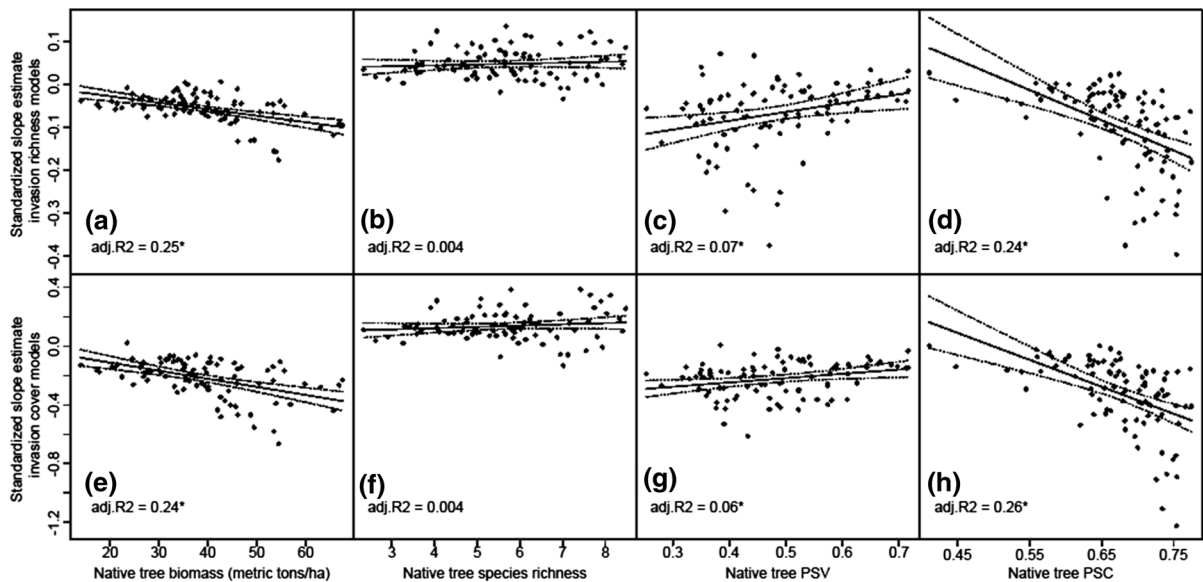
Model	Invasion richness		Invasion cover	
	AIC	$\Delta AIC^*$	AIC	$\Delta AIC^*$
Fixed	47,195	–	159,635	–
Random divisions	44,921	–2274	157,700	–2635
Random sections	36,211	–10,984	148,694	–10,941

\* Values of  $\Delta AIC$  are relative to the AIC values of fixed effects models

they agree with a prior investigation showing lower invader dominance and species richness in more evolutionarily diverse plant communities (Lososová et al. 2015). Follow-up correlations revealed both PSV and PSC to be only weakly related to stand age and

forest cover ( $|r| = 0.07$  to  $0.27$ ), suggesting evolutionary diversity, like biomass, is an indicator of invasion resistance across a range of forest conditions.

Like many other large-scale investigations (reviewed in Fridley et al. 2007), ours revealed native species richness to be positively associated with invasion and thus more indicative of niche availability than native niche usage at large spatial scales. Even in the ecological sections where native species richness was negatively associated with invasion, these associations were weak, suggesting native species richness is a poor indicator of biotic resistance at these larger scales. The negative invader-native species richness associations sometimes detected at small scales (Fridley et al. 2007), in combination with our finding of invasion being negatively associated with native tree biomass and evolutionary diversity at the sub-



**Fig. 4** Relationships between section-level slope estimates (i.e. conditional plus fixed slope estimates) for models of invasion richness (a–d) and invasion cover (e–h) and section-level averages for each biotic resistance measure. Significant relationships reveal that the potential effect of a biotic resistance

measure on invasion varies with the mean level of the same measure. Adj.  $R^2$  values followed by “\*” were statistically significant at the  $P \leq 0.01$  level. Relationships in b and f were non-significant ( $P \geq 0.23$ )

continental scale, suggests that indicators of niche usage, and thus biotic resistance, vary with spatial scales.

Mapping division- and section-level slope estimates revealed the direction of invader-native associations to be mostly robust across spatial scales, while magnitude of these associations varied across spatial scales. The direction of invader-native associations for a given ecological section typically mirrored those of the larger ecological division in which they were nested, although with some exceptions. These exceptions, in conjunction with the overall robustness of association direction, suggest geographic location to be more important than spatial scale in driving directional variability in associations between invasive and native species, at least for the measures of biotic resistance we investigated. Regarding association magnitudes, most ecological sections exhibited weaker invader-native associations than did the ecological divisions in which they were nested. Again, exceptions occurred, revealing location-specific contingencies. While scale-dependent changes in ecological associations (Turner 1989; Wiens 1989; Crawley and Harral 2001), including those for biological invasions (Fridley et al. 2007), are well documented, the contingency of these changes on location is

less so. We contend that our findings are not statistical anomalies as we used ecologically homogeneous sub-regions (Cleland et al. 1997) and not arbitrary spatial cutoffs to assess the effects of heterogeneity and scale (Shurin and Srivastava 2005; Dark and Bram 2007).

Mapping section-level slope estimates also revealed spatial heterogeneity in the magnitudes by which biotic resistance measures indicate resistance to biological invasions. The strongest negative associations for both invasion measures, and thus the greatest potential biotic resistance to invasions, occurred in forests within or near the Appalachian Mountains. Strong negative associations between PSC and invasion richness also occurred throughout the upper Midwest. These spatial patterns suggest these regions exhibit characteristics that allow native biomass and evolutionary diversity to more effectively prevent invader establishment and dominance.

At least some of this spatial heterogeneity is attributable to section-level variability in the values of the biotic resistance measures themselves. For example, for native biomass and PSC, section-level invasion slope estimates were negatively related with the section-level means of these metrics, suggesting the metrics contribute more to biotic resistance in

forests where their levels are elevated. A positive relationship between section-level slope estimates and means revealed the opposite for PSV. Given that biomass, PSV, and PSC vary relative to forest productivity (Potter and Woodall 2014), these relationships may reflect variation in, and among, the degree to which these metrics quantify biotic resistance to invasion across resource gradients. Regardless of the cause, differences in the direction and magnitude of the relationships between section-level slope estimates and means suggest each biotic resistance measure reflects different aspects of niche usage, further supporting the need for multiple measures when investigating biotic resistance. In contrast to biomass, PSV, and PSC, no relationships between section-level slope estimates and means were detected for native species richness, suggesting it to be a consistent indicator of niche availability.

Given that the strength of the relationships between section-level slopes and means for a given biotic resistance measure were weak ( $\text{adj. } R^2 \leq 0.26$ ), other factors likely drive the spatial heterogeneity in the abilities of biomass and evolutionary diversity to indicate the resistance to biological invasions. What these factors are is unclear. Determining the contributions of factors already known to affect macroscale invasion patterns such as propagule pressure, disturbance, and socioeconomic factors (Lockwood et al. 2005; Gavier-Pizarro et al. 2010; Pyšek et al. 2010; Guo et al. 2012; Liebhold et al. 2013; Iannone et al. 2015) will likely be beneficial. Furthermore, the potential for multiple factors to contribute to these patterns simultaneously must be considered. For instance, despite the forests of the Appalachian Mountains being less disturbed (Riitters et al. 2002), this characteristic alone cannot explain stronger biotic resistance in all regions. If it could, one would not expect strong negative associations between invasion and PSC in the Midwest given the extensive forest fragmentation throughout that region (Riitters et al. 2002; Masek et al. 2008). Regardless of the cause, these spatial patterns are an important starting point for investigating forest characteristics that promote biotic resistance. Knowledge of these spatial patterns can also help to develop more-targeted, region-specific management and policy.

Finally, although the results for invasion richness and cover often paralleled, the differences that did occur suggest that the same biotic resistance measure

can affect invader establishment and dominance differently. For example, there were fewer ecological sections in which PSV and PSC were negatively associated with invasion richness than with invasion cover. This difference suggests that evolutionary and functional diversity (Faith 1992, 2002) both limit invader dominance more than invader establishment. This pattern also suggests that evolutionary diversity is related to niche availability in specific sections. These insights illustrate the utility of investigating multiple invasion measures (Guo and Symstad 2008; Catford et al. 2012; Iannone et al. 2015) and of the national-level sampling efforts to collect these measures (Oswalt et al. 2015).

### Broader insights

Our investigation yielded insights into how to better analyze macrosystems data. Many statistical models often used to study large areas assume homogeneous relationships across a study region (e.g. constant slopes from ordinary least squares regression). Given the environmental heterogeneity inherent to large geographic areas (e.g. Cleland et al. 1997, 2007), the validity of this assumption likely declines greatly when increasing the spatial scale of investigations. Our investigation, by revealing improved model performance [i.e. declines in AIC values (Akaike 1973; Anderson et al. 2000)], variability in association directions and magnitudes contingent on geographic location, and insightful spatial patterns (e.g. aggregation of strong negative associations), clearly illustrates how using a statistical model that accounts for spatial heterogeneity in an ecological process can improve our understanding of said process at macroscales. This improvement in understanding is logical given the contribution of smaller-scale spatial variability in ecological processes to larger-scale ecological patterns (Peters et al. 2007). The extent to which decreasing the size of the unit of spatial heterogeneity no longer improves large-scale understanding is unknown. Identifying this threshold would likely benefit many macrosystem investigations.

Less reliance on *P*-values for ecological inference may also benefit macrosystem investigations. Given the often massive size of macrosystem datasets (Soranno and Schimel 2014), statistical power is sufficient to deem all fixed effects “statistically significant” even when their effect sizes are extremely

small, and thus ecologically unimportant (Anderson et al. 2000; Spanos 2014). Using existing model frameworks in novel ways, such as what we demonstrated in this study, is one option to detect ecologically meaningful relationships in “big datasets” without relying on *P*-values. One could also decrease statistical power by adding many more explanatory terms to statistical models. However, important explanatory terms may be unknown or unavailable for large geographic areas, while their addition may deter understanding by increasing model complexity.

Finally, our analysis revealed the potential contribution of native trees to invasion resistance in forests. This finding has both practical and ecological implications. Tree data for large geographic areas are likely easier to attain than are data for other components of forest communities (e.g. plant understories). Therefore, native tree-invasive plant associations suggest that easier-to-attain tree data will be of utility in determining the resistance of forests in other regions to plant invasions. Associations between native trees and invasive plants also suggest that species such as trees comprising the majority of biomass and primary production in a community (Muller 2003) (i.e. dominating resource consumption; Davis et al. 2000; Guo et al. 2015) can limit invasion despite potentially contributing little to overall community biodiversity. For example, while trees may be the leading interceptor of sunlight in forest ecosystems (hence a factor in negative native tree-invasive plant relationships), relative to organisms in the soil, leaf-litter layer, and understory plant community, they often contribute little to overall forest biodiversity (Wardle 2002; Moore et al. 2004; Gilliam 2007).

#### Future directions

Our investigation revealed ways to improve upon the understanding it generated. Identifying the factors that contribute to the spatial heterogeneity in invader-native association magnitude and direction is clearly needed. Again, investigating those factors already known to affect macroscale invasion patterns such as propagule pressure, disturbance, or socioeconomic factors (Lockwood et al. 2005; Gavier-Pizarro et al. 2010; Pyšek et al. 2010; Guo et al. 2012; Liebhold et al. 2013) may be of great utility. Future studies may benefit by incorporating smaller units of

heterogeneity, as doing so may help to detect more fine-scale patterns and the threshold of heterogeneity at which understanding is maximized. Given the strong associations between invasion and the phylogenetic diversity measures aimed at conveying functional trait diversity (Faith 1992, 2002), future investigations may benefit from modeling invasions in response to actual measures of functional trait diversity (e.g. Petchey and Gaston 2006; Laliberté and Legendre 2010). Furthermore, given the contribution of invader traits to invasion (Catford et al. 2009), future investigations may benefit by analyzing functionally distinct invaders separately. Finally, incorporating data on native plant species in forest understories (i.e. species more functionally similar to invaders) into future investigations may enhance our understanding of how the different biotic components of forests contribute to biotic resistance.

#### Conclusion

Our investigation revealed evidence that native biomass and evolutionary diversity are better measures of biotic resistance to invader establishment and dominance across large geographic areas than species richness. We also found evidence that evolutionary diversity limits invader dominance more than invader establishment. Finally, accounting for spatial heterogeneity in invader-native associations within our statistical models revealed geographic sub-regions where biotic resistance to invasions was most pronounced. Such insights not only illustrate the need to determine the factors that cause spatial heterogeneity in biotic resistance to invasions, but also the improved understanding of other ecological processes across large spatial scales that can be gained by accounting for the sub-regional variability in these processes.

**Acknowledgments** We would like to thank the many FIA workers who collected the data used in this investigation; Beth Schulz, Andrew Gray, and Chris Witt for helping to compile the data; Johanna Desprez and Jarrod Doucette for GIS-related advice; and two anonymous reviewers for their constructive criticisms and suggestions on how to improve this paper. This research was supported by NSF Macrosystems Biology Grant # 1241932 and by a Research Joint Venture Agreement 13-JV-11330110-043 and Cost Share Agreement 14-CS-11330110-042 between the USDA Forest Service and North Carolina State University.



## References

- Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Caski F (eds) Proceedings, 2nd International Symposium of Information Theory. Akademiai Kiado, Budapest, pp. 267–281
- Anderson DR, Burnham KP, Thompson WL (2000) Null hypothesis testing: problems, prevalence, and an alternative. *J Wildl Manag* 64(4):912–923
- Araújo MB, Rozenfeld A (2014) The geographic scaling of biotic interactions. *Ecography* 37(5):406–415
- Bates D, Maechler M, Bolker B, Walker S (2014) lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>
- Bechtold WA, Patterson PL (2005) The enhanced forest inventory and analysis program—national sampling design and estimation procedures. General Technical Report SRS-80. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville
- Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers Distrib* 15(1):22–40
- Catford JA, Vesk PA, Richardson DM, Pyšek P (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invulnerable ecosystems. *Glob Chang Biol* 18(1):44–62
- Clark GF, Johnston EL (2011) Temporal change in the diversity–invasibility relationship in the presence of a disturbance regime. *Ecol Lett* 14(1):52–57
- Cleland DT, Avers PE, McNab WH, Jensen ME, Bailey RG, King T, Russell WE (1997) National hierarchical framework of ecological units. In: Boyce MS, Haney A (eds) Ecosystem management applications for sustainable forest and wildlife resources. Yale University Press, New Haven, pp 181–200
- Cleland DT, Freeouf JA, Keys JE, Nowacki GJ, Carpenter CA, McNab WH (2007) Ecological subregions: sections and subsections for the conterminous United States. General Technical. Report WO-76. U.S. Department of Agriculture, Forest Service, Washington, D.C. Map, presentation scale 1:3,500,000; Albers equal area projection; colored
- Crawley MJ, Harral JE (2001) Scale dependence in plant biodiversity. *Science* 291(5505):864–868
- Dark SJ, Bram D (2007) The modifiable areal unit problem (MAUP) in physical geography. *Prog Phys Geogr* 31(5):471–479
- Davies RB (1987) Hypothesis testing when a nuisance parameter is present only under the alternative. *Biometrika* 74(1):33–43
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88(3):528–534
- Dixon Hamil K, Huang W, Iannone BV, III, Fei S, Zhang H (2015) Analysis of multiscale ecological data. *Landsc Ecol*. doi:10.1007/s10980-015-0288-z
- Efron B, Tibshirani R (1986) Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Stat Sci* 1(1):54–75
- Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London
- Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biol Conserv* 61(1):1–10
- Faith DP (2002) Quantifying biodiversity: a phylogenetic perspective. *Conserv Biol* 16(1):248–252
- Fei S, Phillips J, Shouse M (2014) Biogeomorphic impacts of invasive species. *Annu Rev Ecol Evol Syst* 45(1):69–87
- Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Holle BV (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88(1):3–17
- Gavier-Pizarro GI, Radeloff VC, Stewart SI, Huebner CD, Keuler NS (2010) Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecol Appl* 20(7):1913–1925
- Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience* 57(10):845–858
- Guo Q, Symstad A (2008) A two-part measure of degree of invasion for cross-community comparisons. *Conserv Biol* 22(3):666–672
- Guo Q, Rejmanek 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, Fei S, Dukes JS, Oswalt C, Iannone BV III, Potter KM (2015) A unified approach to quantify invasibility and degree of invasion. *Ecology* 96:2613–2621
- Heffernan JB, Soranno PA, Angilletta MJ, Buckley LB, Gruner DS, Keitt TH, Kellner JR, Kominoski JS, Rocha AV, Xiao J, Harms TK, Goring SJ, Koenig LE, McDowell WH, Powell H, Richardson AD, Stow CA, Vargas R, Weathers KC (2014) Macrosystems ecology: understanding ecological patterns and processes at continental scales. *Front Ecol Environ* 12(1):5–14
- Helmus MR, Bland TJ, Williams CK, Ives AR (2007) Phylogenetic measures of biodiversity. *Am Nat* 169(3):E68–E83
- Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *J Appl Ecol* 46(1):10–18
- Iannone BV III, Oswalt CM, Liebhold AM, Guo Q, Potter KM, Nunez-Mir GC, Oswalt SN, Pijanowski BC, Fei S (2015) Region-specific patterns and drivers of macroscale forest plant invasions. *Divers Distrib* 21(10): 1181–1192
- Ives AR, Carpenter SR (2007) Stability and diversity of ecosystems. *Science* 317(5834):58–62
- Jenkins PT (1996) Free trade and exotic species introductions. *Conserv Biol* 10(1):300–302
- Jeschke JM, Gómez Aparicio L, Haider S, Heger T, Lortie CJ, Pyšek P, Strayer DL (2012) Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota* 14:1–20
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91(1):299–305
- Legendre P, Legendre L (2012) Numerical ecology. Elsevier Science B.V., Amsterdam
- Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87(1):15–26
- Liebhold AM, McCullough DG, Blackburn LM, Frankel SJ, Von Holle B, Aukema JE (2013) A highly aggregated



- geographical distribution of forest pest invasions in the USA. *Divers Distrib* 19(9):1208–1216
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends Ecol Evol* 20(5):223–228
- Lodge DM, Williams S, MacIsaac HJ, Hayes KR, Leung B, Reichard S, Mack RN, Moyle PB, Smith M, Andow DA, Carlton JT, McMichael A (2006) Biological invasions: recommendations for U.S. policy and management. *Ecol Appl* 16(6):2035–2054
- Lososová Z, de Bello F, Chytrý M, Kühn I, Pyšek P, Sádlo J, Winter M, Zelený D (2015) Alien plants invade more phylogenetically clustered community types and cause even stronger clustering. *Glob Ecol Biogeogr* 24(7):786–794
- Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Front Ecol Environ* 7(3):142–149
- Masek JG, Huang C, Wolfe R, Cohen W, Hall F, Kutler J, Nelson P (2008) North American forest disturbance mapped from a decadal Landsat record. *Remote Sens Environ* 112(6):2914–2926
- McCann KS (2000) The diversity-stability debate. *Nature* 405(6783):228–233
- McNab WH, Cleland DT, Freeouf JA, Keys JE, Jr, Nowacki GJ, Carpenter CA (2007) Description of ecological subregions: sections of the conterminous United States [CD-ROM]. General Technical Report WO-76B. U.S. Department of Agriculture, Forest Service, Washington, DC
- Moore JC, Berlow EL, Coleman DC, de Ruiter PC, Dong Q, Hastings A, Johnson NC, McCann KS, Melville K, Morin PJ, Nadelhoffer K, Rosemond AD, Post DM, Sabo JL, Scow KM, Vanni MJ, Wall DH (2004) Detritus, trophic dynamics and biodiversity. *Ecol Lett* 7(7):584–600
- Muller RN (2003) Nutrient relations of the herbaceous layer in deciduous forest ecosystems. In: Gilliam FS, Roberts MR (eds) *The Herbaceous layer in Forests of Eastern North America*. Oxford University Press, New York, pp 15–37
- Oswalt C, Fei S, Guo Q, Iannone BV III, Oswalt S, Pijanowski B, Potter K (2015) A subcontinental view of forest plant invasions using national inventory data. *NeoBiota* 24:49–54
- Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. *Trends Ecol Evol* 24(9):497–504
- Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. *Ecol Lett* 9(6):741–758
- Peters DC, Bestelmeyer BT, Turner MG (2007) Cross-scale interactions and changing pattern–process relationships: consequences for system dynamics. *Ecosystems* 10(5):790–796
- Potter KM, Woodall CW (2012) Trends over time in tree and seedling phylogenetic diversity indicate regional differences in forest biodiversity change. *Ecol Appl* 22(2):517–531
- Potter KM, Woodall CW (2014) Does biodiversity make a difference? Relationships between species richness, evolutionary diversity, and aboveground live tree biomass across U.S. forests. *For Ecol Manag* 321:117–129
- Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau M-L, Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy DB, Shirley S, Solarz W, Vilà M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proc Natl Acad Sci* 107(27):12157–12162
- Ries P, Dix ME, Lelmini M, Thomas D (2004) National strategy and implementation plan for invasive species management. FS-805. U.S. Department of Agriculture, Forest Service, Washington, DC
- Riitters KH, Wickham JD, O'Neill RV, Jones KB, Smith ER, Coulston JW, Wade TG, Smith JH (2002) Fragmentation of continental United States forests. *Ecosystems* 5(8):0815–0822
- Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol* 1(2):103–113
- Shurin JB, Srivastava DS (2005) New perspectives on local and regional diversity: beyond saturation. In: Holyoak M, Liebold M, Holt RD (eds) *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, pp 399–417
- Soranno PA, Schimel DS (2014) Macrosystems ecology: big data, big ecology. *Front Ecol Environ* 12(1):3–3
- Soranno PA, Cheruvilil KS, Bissell EG, Bremigan MT, Downing JA, Fergus CE, Filstrup CT, Henry EN, Lottig NR, Stanley EH, Stow CA, Tan P-N, Wagner T, Webster KE (2014) Cross-scale interactions: quantifying multi-scaled cause–effect relationships in macrosystems. *Front Ecol Environ* 12(1):65–73
- Spanos A (2014) Recurring controversies about P values and confidence intervals revisited. *Ecology* 95(3):645–651
- Stohlgren TJ, Barnett DT, Kartesz JT (2003) The rich get richer: patterns of plant invasions in the United States. *Front Ecol Environ* 1(1):11–14
- Tan J, Pu Z, Ryberg WA, Jiang L (2015) Resident-invader phylogenetic relatedness, not resident phylogenetic diversity, controls community invasibility. *Am Nat* 186(1):59–71
- R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Tibshirani R, Leisch F (2013) Bootstrap: Functions for the Book “An introduction to the bootstrap”. R package version. 2012.04-1. <http://CRAN.R-project.org/package=bootstrap>
- Turner MG (1989) Landscape ecology: the effect of pattern on process. *Annu Rev Ecol Syst* 20:171–197
- Wardle DA (2002) *Communities and ecosystems: linking the aboveground and belowground components*. Princeton University Press, Princeton and Oxford
- Wiens JA (1989) Spatial scaling in ecology. *Funct Ecol* 3(4):385–397
- Woodall CW, Westfall JA (2010) Curious or spurious correlations within a national-scale forest inventory? In: McWilliams W, Roesch FA (eds), *Monitoring Across Borders: 2010 Joint Meeting of the Forest Inventory and Analysis (FIA) Symposium and the Southern Mensurationists*. e-General Technical Report SRS-157. U.S. Department of

- Agriculture, Forest Service, Southern Research Station, Asheville, pp. 39–43
- Woodall CW, Heath LS, Domke G, Nichols M (2011) Methods and equations for estimating volume, biomass, and carbon for trees in the U.S. forest inventory, 2010. US Forest Service General Technical Report NRS-GTR-88. USFS Northern Research Station, Newtown Square, pp. 30
- Woodall CW, Westfall JA, Zhu K, Johnson DJ (2013) Assessing the effect of snow/water obstructions on the measurement of tree seedlings in a large-scale temperate forest inventory. *Forestry* 86(4):421–427
- Wu J, Hobbs R (2002) Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. *Landscape Ecol* 17(4):355–365