

# Environmental harshness drives spatial heterogeneity in biotic resistance

Basil V. Iannone III<sup>1,2</sup>, Kevin M. Potter<sup>3</sup>, Qinfeng Guo<sup>4</sup>, Insu Jo<sup>2</sup>,  
Christopher M. Oswalt<sup>5</sup>, Songlin Fei<sup>2</sup>

**1** School of Forest Resources and Conservation, University of Florida, Gainesville, FL, USA **2** Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA **3** Department of Forestry and Environmental Resources, North Carolina State University, Research Triangle Park, NC, USA **4** USDA Forest Service Southern Research Station, Research Triangle Park, NC, USA **5** USDA Forest Service Southern Research Station, Knoxville, TN, USA

Corresponding author: *Songlin Fei* ([sfei@purdue.edu](mailto:sfei@purdue.edu))

---

Academic editor: *José Hierro* | Received 22 July 2018 | Accepted 7 November 2018 | Published 4 December 2018

**Citation:** Iannone BV III, Potter KM, Guo Q, Jo I, Oswalt CM, Fei S (2018) Environmental harshness drives spatial heterogeneity in biotic resistance. *NeoBiota* 40: 87–105. <https://doi.org/10.3897/neobiota.40.28558>

---

## Abstract

Ecological communities often exhibit greater resistance to biological invasions when these communities consist of species that are not closely related. The effective size of this resistance, however, varies geographically. Here we investigate the drivers of this heterogeneity in the context of known contributions of native trees to the resistance of forests in the eastern United States of America to plant invasions. Using 42,626 spatially referenced forest community observations, we quantified spatial heterogeneity in relationships between evolutionary relatedness amongst native trees and both invasive plant species richness and cover. We then modelled the variability amongst the 91 ecological sections of our study area in the slopes of these relationships in response to three factors known to affect invasion and evolutionary relationships – environmental harshness (as estimated via tree height), relative tree density and environmental variability. Invasive species richness and cover declined in plots having less evolutionarily related native trees. The degree to which they did, however, varied considerably amongst ecological sections. This variability was explained by an ecological section's mean maximum tree height and, to a lesser degree, SD in maximum tree height ( $R^2_{GLMM} = 0.47$  to 0.63). In general, less evolutionarily related native tree communities better resisted overall plant invasions in less harsh forests and in forests where the degree of harshness was more homogenous. These findings can guide future investigations aimed at identifying the mechanisms by which evolutionary relatedness of native species affects exotic species invasions and the environmental conditions under which these effects are most pronounced.

## Keywords

Environmental harshness, environmental variability, evolutionary divergence, forests, invasive plants, phylogeny, relative tree density

## Introduction

Observations across large geographic areas reveal considerable spatial heterogeneity in the degree to which ecological communities are invaded by non-native species (Stohlgren et al. 2006, Liebhold et al. 2013, Iannone et al. 2015). Spatial variability in the degree to which various ecological factors affect invasions partially explains this heterogeneity (e.g. Riitters et al. 2018). Identifying what drives this heterogeneity is of importance to both basic ecological understanding and land management aimed at controlling invasive species. Analyses of increasingly available large-scale forest data have revealed that forests exhibit large-scale spatial heterogeneity in both the number and dominance of invasive plant species that are present within them (Iannone et al. 2015, Oswalt et al. 2016). Understanding what causes this heterogeneity will improve basic understanding of forest plant invasions and help to protect the many ecosystem services that forests provide from threats posed by invasive plants (Gonzalez et al. 2005, Martin et al. 2009, Pejchar and Mooney 2009).

Analyses of the same large-scale forest data have also revealed evidence that native tree communities contribute to the ability of forests to resist plant invasions in general, i.e. regardless of invader growth form, and that these contributions vary spatially (Guo et al. 2015, Iannone et al. 2016). The characteristics of native tree communities most negatively related to plant invasions (i.e. invasive plant species richness and dominance) include aboveground native tree biomass and the degree to which native tree species are evolutionarily related (Iannone et al. 2016). The detected contribution of native tree biomass to invasion resistance likely reflects the fact that trees are a leading component of forest biomass, primary productivity and resource uptake (Muller 2003). The contribution of evolutionary relatedness of native trees to invasion resistance likely reflects the assumption that communities containing less evolutionarily related species exhibit greater diversity in both measurable functional traits and unidentified phenotypic traits and, thus, a greater breadth in niche usage (Faith 1992, Webb et al. 2002, Lososová et al. 2015, Tan et al. 2015, but see Gerhold et al. 2015).

The objective of this investigation was to determine the degree to which environmental characteristics of forests drive spatial heterogeneity in the effects that native tree evolutionary relatedness has on overall forest plant invasions. This investigation was conducted in the forests of the eastern United States of America (USA). We pursue this objective in the context of three separate characteristics of evolutionary relatedness: how divergent (*sensu* Tucker et al. 2017) species are relative to one another across a phylogenetic tree (i.e. phylogenetic species clustering [PSC] and phylogenetic species variability [PSV]; [Helmus et al. 2007]), the amount of evolutionary history contained

within these phylogenetic relationships (i.e. phylogenetic diversity [PD]; [Faith 1992]) and the evenness in abundance at which species occur across a phylogenetic tree (i.e. phylogenetic species evenness [PSE]; [Helmus et al. 2007]). Regarding environmental characteristics, we investigate environmental harshness, as defined by Marks et al. (2016) and relative tree density, both of which can affect the establishment and growth of invasive plants (Theoharides and Dukes 2007, Guo et al. 2015). We also investigate the role of environmental variability, as it can accelerate evolutionary radiation amongst native species via allopatric speciation (Qian and Ricklefs 2000) and can reflect niche availability for invasions (Davies et al. 2005).

## Methods

### Evolutionary relatedness and biotic resistance

Evolutionary relatedness is typically defined within the context of phylogenetic relatedness or the locations of species relative to one another across a phylogenetic tree that describes the hypothesised evolutionary relationships amongst species. Many studies investigating the effects of phylogenetic relatedness on invasion have done so in the context of the evolutionary relatedness between invasive and native species, i.e. within the context of “Darwin’s naturalisation hypothesis” that species from novel genera may have an advantage when invading new locations because they are less likely to compete with closely related species or share natural enemies with them (e.g. Diez et al. 2008, Lososová et al. 2015). Nevertheless, we are unlikely to know ahead of time the particular species that will invade a given community. For this reason, knowing how the phylogenetic relatedness amongst native species in a given community affects invasion in general is likely of greater utility in understanding spatial heterogeneity in the degree to which native ecosystems resist plant invasions. Ecological communities consisting of species that are more divergent relative to one another across the phylogenetic tree of life can exhibit greater resistance to invasion (Gerhold et al. 2011, Lososová et al. 2015), although the degree of resistance varies considerably across large spatial scales (Iannone et al. 2016). This geographic variability suggests that the effect of evolutionary relatedness of native communities on exotic invasions is itself affected by other factors.

### Data compilation

To meet our objective, we first obtained native tree and invasive plant data from 42,626 forested plots from the United States Department of Agriculture’s Forest Inventory and Analysis programme (FIA) located within the two ecological domains (*sensu* Cleland et al. 1997) of the eastern USA (Suppl. material 1, fig. S1.1). The location of these data, as well as all other data used for subsequent analyses in this paper can be found below in the paper’s Data accessibility section. FIA monitors spatiotemporal patterns of for-

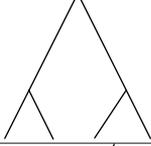
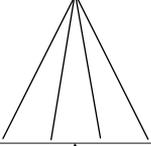
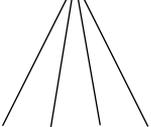
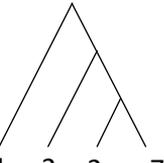
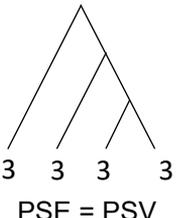
est conditions at the national-level using a fixed grid of permanent plots occurring at an approximate intensity of one plot for every 2,428 ha of forests; all plots are 0.40 ha in size and are defined using a consistent plot design (Bechtold and Patterson 2005). Forests are defined as areas at least 36.6 m wide and 0.40 ha in size that historically or currently have at least 10% tree cover (for trees of any size).

We used four metrics (Table 1) to estimate three characteristics of evolutionary relatedness amongst the native trees in each plot. First, we constructed a phylogenetic supertree of 397 native angiosperm and gymnosperm tree species occurring in the FIA plots of the contiguous 48 states (Potter 2018). This reference phylogeny, with branch lengths measured in millions of years, was constructed based on a review of 189 molecular systematics and paleobotanical studies. Using this phylogenetic tree and the R package Picante (Kembel et al. 2010), we quantified two different aspects of phylogenetic divergence, following Helmus et al. (2007) —phylogenetic species variability (PSV) and phylogenetic species clustering (PSC). PSV quantifies variability amongst species in a hypothetical random (non-selected) trait, thus quantifying how divergent species are relative to one another across an entire phylogenetic tree and the extent to which the phylogenetic arrangement of these species represents a star phylogeny, as illustrated in Table 1. PSC quantifies the degree to which the phylogenetic branch tips for species in a given community are divergent, or clustered, relative to one another. From the same phylogenetic tree, we also estimated the amount of evolutionary history within each plot using the metric phylogenetic diversity (PD) proposed by Faith (1992). PD is estimated by summing the lengths of the phylogenetic branches for the tree species found within a given plot. By definition, PD increases with species richness. The utility of PD in describing the amount of evolutionary history within a given community was also confirmed by Tucker et al. (2017). Lastly, we calculated the phylogenetic species evenness (PSE) metric proposed by Helmus et al. (2007). This metric is an indicator of phylogenetic divergence that accounts for the relative abundances of species within the investigated community. PSE equals PSV when all species are equally abundant in a community and declines as they are decreasingly so.

A benefit of using PSV, PSC and PSE is that these metrics of phylogenetic divergence do not require prior knowledge of the regional species pool from which species could populate a plot (Helmus et al. 2007). An initial correlation analysis revealed PD to be strongly related to and, thus, dependent on, the number of native tree species in each plot ( $r_{PD} = 0.82$ ). The three other phylogenetic metrics, however, exhibited weaker relationships with native tree species richness ( $r_{PSV} = -0.31$ ,  $r_{PSC} = 0.49$  and  $r_{PSE} = 0.09$ ) and, thus, reflected more independent characteristics.

We assessed overall plant invasion in each plot by compiling data on invasive plant richness and cover data, following Iannone et al. (2016). Invasive richness is the number of invasive plant species found and invasive cover is the summed total cover of these species (which can exceed 100% of the area of a plot because of overlap by individual plants). Invasive richness and cover serve as indicators of invasive species establishment and dominance, respectively. FIA defines invasive plants in accordance with USA Executive Order 13112 as non-native plant species likely to cause economic

**Table 1.** Explanation of the four investigated metrics of evolutionary relatedness. PD is defined by Faith (1992) and PSE, PSV and PSC are defined by Helmus et al. (2007).

Metric	Definition of metrics & notes	Lower	Higher
Phylogenetic species clustering (PSC)	Quantifies the degree to which phylogenetic branch tips are divergent or clustered relative to one another. Ranges from 0 (low divergence) to 1 (high divergence)		
Phylogenetic species variability (PSV)	Quantifies variability amongst species in a hypothetical neutral trait and thus divergence across the branch lengths of a phylogeny. Ranges from 0 (low) to 1 (high, star phylogeny)		
Phylogenetic diversity (PD)	Summed lengths of phylogenetic branches. Values increase with species richness. Positive value has no upper limit. Increases with greater values		
Phylogenetic species evenness (PSE)	Hypothesised to reflect evenness in traits and phenotypic variation. PSE = PSV when all species are equally abundant and declines with greater differences in abundance. NOTE: Numbers at branch tips on the right signify number of individuals		

or environmental harm (Ries et al. 2004). The list of monitored invasive plants in the eastern USA includes approximately 76 different species; some species were merged into single groups to accommodate field identification. These species include 18 forbs, 9 grasses, 21 shrubs, 14 trees and 14 vines (Suppl. material 2, table S2.1). Although invasive plant sampling protocols, including the specific species monitored, vary between the Northern and Southern FIA Administrative Regions (described in Suppl. material 2, text S2.1), this variability has little effect on macroscale invasion patterns (Iannone et al. 2015). Furthermore, most of the invasive plants monitored are of concern to large portions of each and, in some cases both, of the administrative regions, alleviating concerns about spatial variability in invasive plant species pools.

### Confirming/quantifying spatial variability in invasion resistance

Using a mixed-effects modelling framework developed by Dixon Hamil et al. (2016), we modelled invasive richness and cover in response to the four phylogenetic metrics (PSC, PSV, PSE and PD), allowing for independent (i.e. random) intercept and slope estimates for each of the 91 ecological sections (*sensu* Cleland et al. 1997) nested within our study region (Suppl. material 1, fig. S1.2). Phylogenetic metrics were stand-

ardised  $[x - \text{mean}(x)/\text{SD}(x)]$ , allowing for cross-variable comparison (Schielzeth 2010). Inspection of variance inflation factors (Legendre and Legendre 2012) revealed no evidence of complications due to collinearity. We assessed model fit using the coefficient of determination for generalised mixed-effect models, i.e.  $R^2_{GLMM}$  (Johnson 2014). To assess statistical significance, we resampled section-level slope estimates (i.e. conditional plus fixed estimates) 10,000 times allowing for replacement and calculated the bias corrected, accelerated 95% confidence interval (CI) of each bootstrapped distribution (Efron and Tibshirani 1986). We assumed the phylogenetic metric to be a statistically significant indicator of biotic resistance across our study region when its 95% CI encompassed values less than zero. Likewise, we assumed a phylogenetic metric to be an indicator of invasion success when its 95% CI encompassed values greater than zero. We relied on bootstrapped rather than actual distributions to estimate 95% CIs because actual distributions were non-normal (Suppl. material 3, fig. S3.1).

### Identifying drivers of spatial heterogeneity in invasion resistance

We compiled data from the FIA database on plot-level maximum tree height (m) and relative tree density. Maximum tree height was used as an inverse indicator of environmental harshness. Marks et al. (2016) found maximum tree height to be negatively correlated to multiple environmental indicators of environmental harshness across forests of both the eastern and western USA. Relative tree density was calculated as described by Potter and Woodall (2014). This standardised metric quantifies the number of trees per unit area currently in a given FIA plot and divides that value by the maximum number of trees that could grow in that plot. We then calculated means and SD for each of these metrics at the ecological section level (Suppl. material 1, fig. S1.2; Suppl. material 1, table S1.1). Means estimated overall section-level environmental harshness and relative tree density, while SD of these metrics served as section-level indicators of the environmental (abiotic and biotic) variability experienced by invading plants. As an additional, indirect metric of environmental variability, we calculated the mean Jaccard's distance (based on absence/presences of native tree species) amongst plots within each of the 91 ecological sections. Ecological sections having greater mean Jaccard's distances in native tree species composition were assumed to be more environmentally variable.

We conducted preliminary regression analyses to assess the degree to which maximum tree height, relative tree density and SD in these variables predicted forest age. We did so to rule out the possibility of our findings reflecting nothing more than forest successional stages, i.e. variation between young and old forests in the degree of invasion. Both maximum tree height and relative tree density explained relatively small proportions of variability in FIA estimates of forest stand age at both the individual plot and ecological section levels (range in  $R^2 = 0.04$  to  $0.24$ ). SD of maximum tree height and relative density also explained relatively small proportions of forest stand age ( $R^2 = 0.25$  and  $0.04$ , respectively). These low  $R^2$  values revealed that mean and SD

of maximum tree height and relative density were largely indicative of environmental conditions other than forest successional stages.

We modelled slope estimates for relationships between phylogenetic metrics indicative of biotic resistance and invasive richness and cover in each of the 91 ecological sections (determined as described above) in response to the section-level mean and SD of maximum tree height and relative tree density, as well as section-level estimates of mean Jaccard's distance (model shown in Table 2). We used these statistical models to assess whether environmental harshness, relative tree density and/or environmental variability drive spatial heterogeneity in the degree to which evolutionary relatedness contributes to invasion resistance. We assessed model fit using the conditional estimate for the coefficient of determination for generalised mixed-effect models, i.e.  $R^2_{GLMM}$  (Johnson 2014).

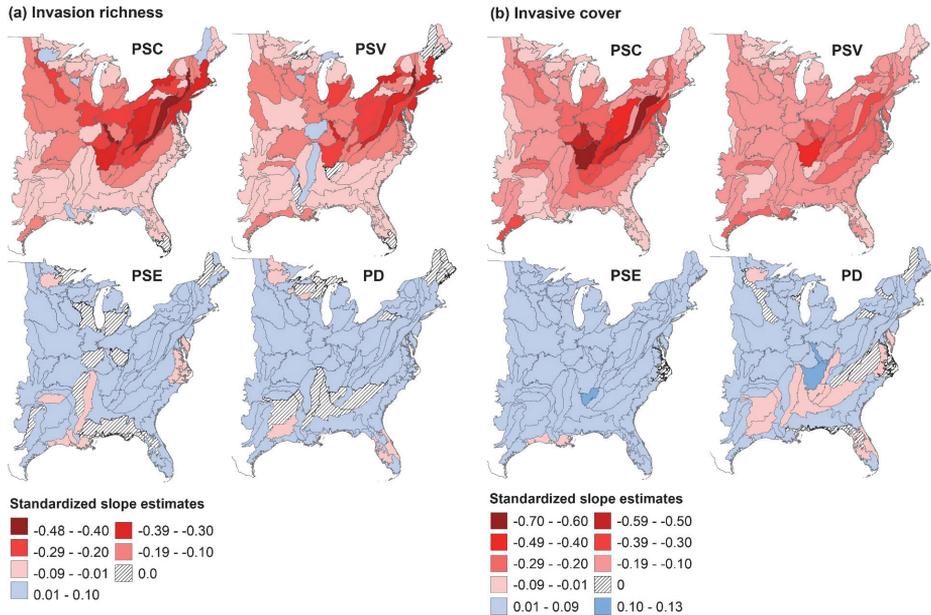
Prior to analysis, we standardised explanatory variables [ $x - \text{mean}(x)/\text{SD}(x)$ ], allowing us to assess the relative contribution of each to this spatial heterogeneity (Schiegg 2010). To account for possible spatial autocorrelation amongst more closely located ecological sections, we incorporated the ecological province (Suppl. material 1, fig. S1.3), i.e. the larger ecoregion scale in which each ecological section was nested, into statistical models as a random effect. The distribution of slope estimates for relationships between invasion and phylogenetic metrics were left-skewed (Suppl. material 3, fig. S3.1). To address this, we transposed slope estimates to positive values greater than 1 and transformed the data using a power transformation [ $(x + \text{abs}(\min(x)) + 1)^7$ ] to help meet the assumption of normality. Inspection of variance inflation factors (Legendre and Legendre 2012) revealed no evidence of complications due to collinearity.

Statistical analyses were conducted in R v 3.0.1 (R Core Team 2014) using the nlme package (Pinheiro et al. 2017) to construct linear mixed-effects models, the MuMIn package (Bartoń 2014) to estimate coefficients of determination and the bootstrap package (Tibshirani and Leisch 2013) to conduct bootstrap analyses.

## Results

### Spatial heterogeneity in invasion resistance

Mapping the section level slope estimates determined via mixed-effects modelling confirmed spatial variability in relationships between phylogenetic (PSC, PSV, PD and PSE) and invasion (richness and cover) metrics (Fig. 1). Slope values for PSC and PSV were largely negative across ecological sections, while those for PD and PSE were largely positive. The 95% confidence intervals (CI) of the bootstrapped distributions of section-level slope estimates revealed these trends to be statistically significant, i.e. 95% CIs did not encompass zero (Suppl. material 3, fig. S3.2). Slope values for PSC and PSV also exhibited greater spatial variability and magnitudes in their relationships with invasive richness and cover than did PD and PSE (Fig. 1;



**Figure 1.** Standardised relationships between four metrics of evolutionary relatedness and invasive (a) richness and (b) cover.

Suppl. material 3, fig. S3.2). (See Suppl. material 3, table S3.1 for values of section level slope estimates.) Given that PD and PSE were not indicative of biotic resistance to invasion, we did not investigate the drivers of spatial heterogeneity in relationships between these metrics and invasion metrics.

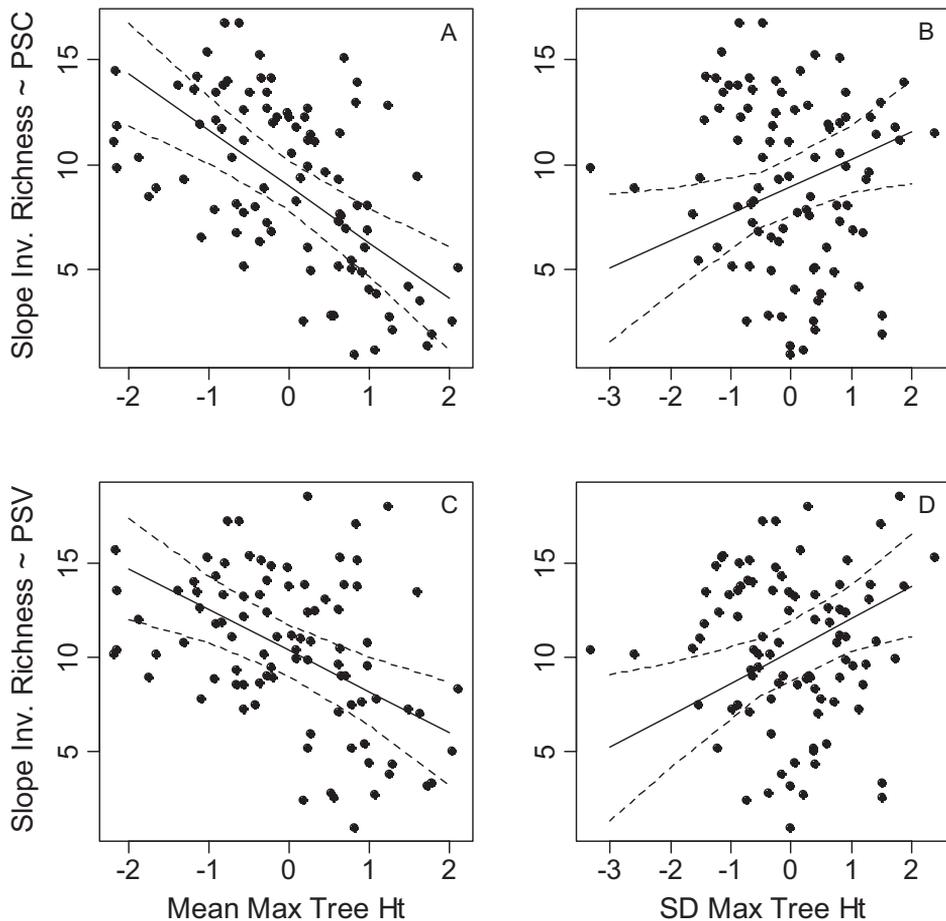
### Drivers of spatial heterogeneity in biotic resistance to invader establishment (i.e. invasive richness)

Spatial variability in the degree to which both PSC and PSV were related to invasive richness was largely explained by mean and SD maximum tree height (Table 2;  $R^2_{GLMM}$  of statistical models = 0.55 and 0.47, respectively). Slopes of all other model terms were not statistically significant from zero ( $p$ -values = 0.15 to 0.57). Slopes for mean maximum tree height were negative (Table 2), revealing both PSC and PSV to be more negatively related to invasive richness in ecological sections having greater maximum tree heights (Figs 2a, c). In contrast, slopes for SD maximum tree height were positive (Table 2). This reveals both PSC and PSV to be less negatively related to invasive richness in ecological sections having more variable maximum tree heights (Figs 2b, d). Standardised slope estimates revealed mean maximum tree height to have more than twice the effect as SD on this spatial variability for PSC and a 27% greater effect than

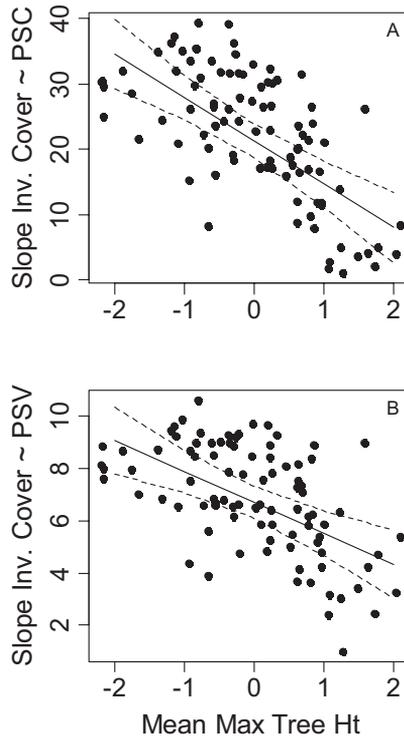
**Table 2.** Results of linear mixed-effects models. These models were used to determine the relative contribution of mean and SD of maximum tree height and relative tree density, as well as mean Jaccard's distance, to spatial heterogeneity in relationships between metrics of phylogenetic divergence (PSC and PSV) and invasion (invasive richness and cover). Models contained ecological provinces as a random effect.

Dependent variable	Explanatory variables					$R^2_{GLMM}$
	Mean Max tree ht.	SD Max tree ht.	Mean Rel. density	SD Rel. density	Mean Jaccard's dist.	
Invasive richness ~ PSC	$-2.66 \pm 0.54^{****}$	$1.29 \pm 0.55^*$	$0.83 \pm 0.60$	$-0.24 \pm 0.42$	$-0.73 \pm 0.50$	0.55
Invasive richness ~ PSV	$-2.18 \pm 0.59^{***}$	$1.71 \pm 0.60^{**}$	$0.86 \pm 0.66$	$-0.55 \pm 0.46$	$-0.75 \pm 0.55$	0.47
Invasive cover ~ PSC	$-6.64 \pm 1.17^{****}$	$0.07 \pm 1.19$	$1.94 \pm 1.31$	$0.62 \pm 0.91$	$-0.21 \pm 1.09$	0.63
Invasive cover ~ PSV	$-1.18 \pm 0.29^{***}$	$0.16 \pm 0.29$	$0.37 \pm 0.32$	$0.04 \pm 0.22$	$-0.08 \pm 0.27$	0.49

\* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; \*\*\*\* $p < 0.0001$



**Figure 2.** Effects of mean and SD maximum tree height in 91 ecological sections on the degree to which PSC (A, B) and PSV (C, D) affect invasive species richness (i.e. slope values for these relationships). Note that values on x and y axes were transformed (z-transformed and  $[(x + \text{abs}(\min(x)) + 1)^2]$ , respectively) prior to analysis. Untransformed values for slopes were largely negative (Fig. 1; Suppl. material 3, fig. S3.1).

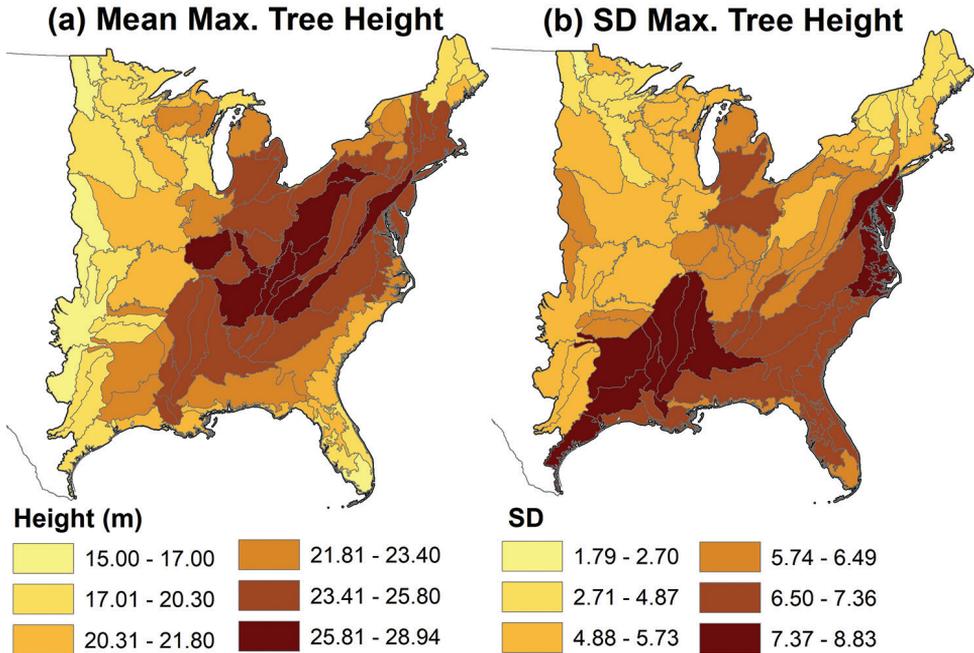


**Figure 3.** Effects of mean maximum tree height in 91 ecological sections on the degree to which PSC (A) and PSV (B) affect invasive species cover (i.e. slope values for these relationships). Note that values on x and y axes were transformed (z-transformed and  $[(x + \text{abs}(\min(x)) + 1)^7]$ , respectively) prior to analysis. Untransformed values for slopes were largely negative (Fig. 1; Suppl. material 3, fig. S3.1)

SD for PSV (Table 2). Slopes for mean maximum tree height had smaller  $p$ -values (Table 2) and smaller 95% CIs relative to their slopes (Fig. 2), than those for SD maximum tree height, suggesting a more consistent impact on spatial heterogeneity in relationships between invasion richness and both PSC and PSV.

### Drivers of spatial heterogeneity in biotic resistance to invader dominance (i.e. invasive cover)

Spatial variability in the degree to which both PSC and PSV were related to invasive cover was explained solely by mean maximum tree height (Table 2;  $R^2_{GLMM}$  of statistical models = 0.63 and 0.49, respectively). Slopes of all other model terms were not statistically significant from zero ( $p$ -values = 0.26 to 0.95). Slopes for mean maximum tree height were negative (Table 2), revealing both PSC and PSV to be more negatively related to invasive cover in ecological sections having greater overall maximum tree heights (Figs 3a, b).



**Figure 4.** Section level means (a) and SD (b) for maximum tree height (i.e. an inverse metric of environmental harshness).

### Spatial context

Follow-up mapping of section-level estimates of statistically significant explanatory variables shown in Table 2, i.e. mean and SD of maximum tree height, revealed spatial patterns contributing to our current findings. The greatest values for mean maximum tree height occurred in and around the Appalachian Mountains (Fig. 4a) where both PSC and PSV exhibited stronger negative associations with invasive richness and cover (Fig. 1). This pattern contributed to the strong negative slope values exhibited by maximum tree height in all statistical models (Table 2). The greatest values for SD of maximum tree height occurred in the southern portion of our study region (Fig. 4b) where PSC and PSV both tended to exhibit weaker and sometimes positive relationships with invasive richness (Fig. 1). This pattern contributed to the positive slope values for SD maximum tree height in statistical models for relationships between invasive richness and both PSC and PSV (Table 2).

### Discussion

We found evidence that environmental harshness and, to a lesser degree, variability in environmental harshness drive spatial heterogeneity in the contribution of phylogenetic divergence (PSC and PSV) of native trees to biotic resistance to overall plant

invasions in eastern USA forests. While spatial heterogeneity in the contribution of native trees to biotic resistance to forest plant invasions was previously noted (Iannone et al. 2016), this investigation is the first to our knowledge that identifies potential drivers of this large-scale heterogeneity. This detected contribution of phylogenetic divergence to invasion resistance illustrates how variation in localised processes by which evolutionary relatedness is hypothesised to limit invasions, e.g. niche overlap/competitive exclusion (Procheş et al. 2008, Thuiller et al. 2010), can contribute to complex large-scale invasion patterns. In addition, the spatial heterogeneity revealed also illustrates the utility of applying a community-level framework when investigating large-scale invasion patterns (Shea and Chesson 2002). Finally, our findings support the value of considering biotic and environmental filters to invasion in unison in order to understand overall invasion patterns (Pearson et al. 2018).

In contrast to phylogenetic divergence, we found no evidence that the amount of evolutionary history (i.e. PD) or the evenness at which these native tree species occur across a given community's phylogenetic tree (i.e. PSE) contribute to biotic resistance across macroscales. The consistently positive associations that PD and PSE shared with both invasive richness and cover suggests these metrics to be more indicative of niche availability than biotic resistance, at least at the spatial scale of our investigation. The weak magnitudes of these associations also revealed them to be of little value in predicting macroscale invasion patterns. The positive association between PD and invasion was not surprising, as this metric is strongly related to native species richness, which itself is positively related to invasive richness and cover at large spatial scales (Stohlgren et al. 2006, Fridley et al. 2007, Iannone et al. 2016). Causes of the positive association between phylogenetic species evenness (PSE) and invasion are less clear. Even though species evenness can contribute to biotic resistance at small spatial scales in grasslands (Wilsey and Polley 2002), this tells us little about how species evenness affects large-scale invasions in forests. Thus, studies to determine how variability in spatial scale and ecosystem type affects the contribution of species evenness to biotic resistance are needed.

By revealing factors that affect the strength of relationships between phylogenetic divergence and invasion, our study revealed conditions under which phylogenetic divergence of native tree communities likely contributes most to invasion resistance in forest ecosystems. Standardised slope estimates revealed that mean maximum tree height was the explanatory variable having the greatest effect. This factor was negatively correlated with slope values for relationships between both PSC and PSV and both invasion richness and cover. Given that maximum tree height is an inverse measure of environmental harshness (Marks et al. 2016), these negative relationships reveal a greater potential for more phylogenetically divergent tree communities to limit invader establishment and dominance under less harsh environmental conditions. This effect may reflect the long-recognised decline in the ecological importance of competition in more harsh environments (Bertness and Callaway 1994). That is, an invader's ability to deal with stress may be more important than its ability to deal with competition

when invading harsher environments, regardless of the niche space occupied by the native community. Determining the component(s) of environmental harshness that most affect relationships between phylogenetic relatedness and invasion will increase our understanding of the causes of the patterns revealed here. Investigating factors both related to tree height and that directly affect plant growth, e.g. soil productivity, drought, cold etc. (Marks et al. 2016), may be fruitful.

Increased environmental variability across large geographic areas can increase species richness (Qian and Ricklefs 2000), which, in some situations, is positively related to certain metrics of evolutionary relatedness (Potter and Woodall 2014). Increased environmental variability is also positively associated with invasions (Davies et al. 2005). For these reasons, we expected factors indicative of environmental variability to affect the magnitude of relationships between metrics of phylogenetic divergence and invasion. We found such evidence for the SD of maximum tree height, but not for SD of relative tree density or mean Jaccard's distances. The positive correlation of SD of maximum tree height to slope values for relationships between invasive richness and both PSC and PSV reveals phylogenetically divergent tree communities to limit invader establishment more in ecological sections that are less variable regarding environmental harshness. However, smaller slope and larger  $p$ -value estimates for SD vs. mean maximum tree height reveal overall environmental harshness to be more influential.

The decline in the effects of phylogenetic divergence on invasion in ecological sections having more variable maximum tree height may reflect an increased number of locations having more harsh environments. That is, it indicates an increase in the number of locations where phylogenetic divergence affects invader establishment less. An increase in the number of locations experiencing canopy disturbance (natural or human) may also contribute to our finding regarding SD in maximum tree height given that increased light facilitates forest plant invasions (Eschtruth and Battles 2009, Iannone et al. 2013). However, given that SD in maximum tree height and mean stand age are only weakly related, it is likely that increased SD in maximum tree height reflects more than increased rates of canopy disturbance. Declines in the effects of phylogenetic divergence on invasion in ecological sections having more variable maximum tree height may also reflect the previously noted positive associations between invasion and environmental variability (Davies et al. 2005). Considering components of forest plant communities other than, or in addition to, native trees, e.g. native understorey plants, soils etc., is likely to improve understanding of how environmental variability affects large-scale forest plant invasions.

We utilised two different measures of invasion — invasive species richness and cover — as both provide different perspectives on invasion patterns. Invasive richness is an indicator of invader establishment and invasive cover is an indicator of invader dominance. Prior theoretical and empirical investigations reveal the deeper understanding that can be gained by considering multiple invasion metrics simultaneously within the same investigation (Kennedy et al. 2002, Stohlgren et al. 2003, Guo and Symstad 2008, Catford et al. 2012, Iannone et al. 2015). For instance, we found evi-

dence that the effects of phylogenetic divergence on both invader establishment and dominance (i.e. richness and cover, respectively) declines with increased environmental harshness. In contrast, variability in environmental harshness only influenced the ability of phylogenetic divergence to affect invasive plant establishment and not invasive plant dominance. Based on our findings, we would predict that, even if phylogenetic divergence does not prevent invader establishment in a given area due to that area exhibiting greater spatial variability in environmental harshness, it might still limit invader dominance so long as the overall/mean environmental harshness of the area is low. This insight is of practical importance given that invasive cover may reflect invader impacts more than invasive species richness, potentially making it of greater relevance to invasive plant management (Guo and Symstad 2008, Hillebrand et al. 2008).

Identifying the factors that affect the ability of PSC and PSV to contribute to invasion resistance may also help to reveal how characteristics of evolutionary relationships (e.g. divergence, branch lengths and species evenness) emerge under different environmental conditions. For instance, both PSC and PSV limit invader establishment (as estimated by invasive richness) to greater degrees in forests that are less harsh. Therefore, the levels of environmental harshness found in a forest, by indirectly affecting invader establishment, have the potential to affect future PSC and PSV values for that forest. Therefore, our findings illustrate how knowing the phylogenetic relationships within an ecological community can help to understand the conditions from which these relationships emerge, i.e. the “phylogenetic-patterns-as-results utility” of known phylogenetic relationships (Gerhold et al. 2015).

## **Conclusions**

We found evidence that environmental harshness and, to a lesser degree, spatial variability in environmental harshness, affect the ability of more phylogenetically divergent native tree communities to limit the establishment and dominance of invasive plants. Therefore, through indirect pathways, these factors may affect short-term invasion patterns and community-level change and, in so doing, affect the long-term characteristics of evolutionary relationships. Nevertheless, these factors did not explain all variability in phylogenetic-invasion relationships. Therefore, future investigations are needed. Considering how other known drivers of invasion patterns, such as propagule pressure and plant functional traits, as well as understorey native plant communities and forest soils, contribute to variability in the degree to which phylogenetic divergence of native trees contributes to invasion resistance, will likely be beneficial. Also needed is the determination of the component(s) of environmental harshness most contributing to our findings and the mechanisms by which phylogenetic divergence amongst native trees affects overall plant invasion. Controlled experiments replicated across our study region would greatly help in this regard. Such considerations will increase our understanding of how the evolutionary relatedness amongst species in a given community affects invasions and community change.

## Data accessibility

Iannone BV III, Potter KM, Guo Q, Jo I, Oswalt CM, Fei S (2018) Data on native tree diversity (species richness and phylogenetic), biomass, relative density, tree height and invasive plants in forests of the eastern USA. Purdue University Research Repository. <https://purr.purdue.edu/publications/3072/1> doi: 10.4231/R7GX48TW.

## Acknowledgements

Thanks to the many Forest Inventory and Analysis workers who collected the data used in this study and to Beth Schulz, Andrew Gray and Chris Witt for helping to compile data. This study was supported by National Science Foundation Macrosystems Biology grants #1241932 and #1638702 and by Cost Share Agreement 14-CS-11330110-042 between the United States Department of Agriculture Forest Service and North Carolina State University.

## References

- Bartoń K (2014) MuM. In: multi-model inference. R package version 1.10.0. <http://cran.r-project.org/package=MuMIn>.
- 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.
- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends in Ecology & Evolution* 9: 191–193. [https://doi.org/10.1016/0169-5347\(94\)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4)
- Catford JA, Vesik PA, Richardson DM, Pyšek P (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invulnerable ecosystems. *Global Change Biology* 18: 44–62. <https://doi.org/10.1111/j.1365-2486.2011.02549.x>
- 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, 181–200.
- Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ (2005) Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* 86: 1602–1610. <https://doi.org/10.1890/04-1196>
- Diez JM, Sullivan JJ, Hulme PE, Edwards G, Duncan RP (2008) Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. *Ecology Letters* 11: 674–681. <https://doi.org/10.1111/j.1461-0248.2008.01178.x>
- Dixon Hamil K, Iannone BV III, Huang W, Fei S, Zhang H (2016) Cross-scale contradictions in ecological relationships. *Landscape Ecology* 31: 7–18. <https://doi.org/10.1007/s10980-015-0288-z>

- Efron B, Tibshirani R (1986) Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Statistical Science* 1: 54–75. <https://doi.org/10.1214/ss/1177013815>
- Eschtruth AK, Battles JJ (2009) Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecological Monographs* 79: 265–280. <https://doi.org/10.1890/08-0221.1>
- Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61: 1–10. [https://doi.org/10.1016/0006-3207\(92\)91201-3](https://doi.org/10.1016/0006-3207(92)91201-3)
- 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: 3–17. [https://doi.org/10.1890/0012-9658\(2007\)88\[3:TIPRPA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2)
- Gerhold P, Cahill Jr JF, Winter M, Bartish IV, Prinzing A (2015) Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology* 29: 600–614. <https://doi.org/10.1111/1365-2435.12425>
- Gerhold P, Partel M, Tackenberg O, Hennekens SM, Bartish I, Schaminee JHJ, Fergus AJF, Ozinga WA, Prinzing A (2011) Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *The American Naturalist* 177: 668–680. <https://doi.org/10.1086/659059>
- Gonzalez P, Hasson R, Lakyda P, McCallum I, Nilsson S, Pulhin J, van Rosenberg B, Scholes B, Shvidenko A, Barber CV, Persson R (2005) Forest and woodland systems. In: Hassan R, Scholes R, Ash N (Eds) *Millennium Ecosystem Assessment: Ecosystems and Human Well-being: Current State & Trends Assessment*. Island Press, Washington, DC, 585–621.
- Guo Q, Fei S, Dukes JS, Oswald C, Iannone BV III, Potter KM (2015) A unified approach for quantifying invasibility and degree of invasion. *Ecology* 96: 2613–2621. <https://doi.org/10.1890/14-2172.1>
- Guo Q, Symstad A (2008) A two-part measure of degree of invasion for cross-community comparisons. *Conservation Biology* 22: 666–672. <https://doi.org/10.1111/j.1523-1739.2008.00915.x>
- Helmus MR, Bland TJ, Williams CK, Ives AR (2007) Phylogenetic measures of biodiversity. *The American Naturalist* 169: E68–E83. <https://doi.org/10.1086/511334>
- Hillebrand H, Bennett DM, Cadotte MW (2008) Consequences of dominance: a review of evenness effects of local and regional ecosystem processes. *Ecology* 89: 1510–1520. <https://doi.org/10.1890/07-1053.1>
- Iannone BV III, Oswald CM, Liebhold AM, Guo Q, Potter KM, Nunez-Mir GC, Oswald, SN, Pijanowski BC, Fei S (2015) Region-specific patterns and drivers of macro-scale forest plant invasions. *Diversity and Distributions* 21: 1181–1192. <https://doi.org/10.1111/ddi.12354>
- Iannone BV III, Potter KM, Dixon Hamil K, Huang W, Zhang H, Guo Q, Oswald CM, Woodall CW, Fei S (2016) Evidence of biotic resistance to invasions in forests of the Eastern USA. *Landscape Ecology* 31: 85–99. <https://doi.org/10.1007/s10980-015-0280-7>
- Iannone BV III, Zellner ML, Wise DH (2013) Modeling the impacts of life-history traits, canopy gaps, and establishment location on woodland shrub invasions. *Ecological Applications* 24: 467–483. <https://doi.org/10.1890/13-0833.1>

- Johnson PCD (2014) Extension of Nakagawa & Schielzeth's  $R^2$ GLMM to random slopes models. *Methods in Ecology and Evolution* 5: 944–946. <https://doi.org/10.1111/2041-210X.12225>
- Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. *Nature* 417: 636–638. <https://doi.org/10.1038/nature00776>
- Legendre P, Legendre L (2012) *Numerical Ecology*. Elsevier Science B.V., Amsterdam.
- Liebholt 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. *Diversity and Distributions* 19: 1208–1216. <https://doi.org/10.1111/ddi.12112>
- 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. *Global Ecology and Biogeography* 24: 786–794. <https://doi.org/10.1111/geb.12317>
- Marks CO, Muller-Landau HC, Tilman D (2016) Tree diversity, tree height and environmental harshness in eastern and western North America. *Ecology Letters* 19: 743–751. <https://doi.org/10.1111/ele.12608>
- 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. *Frontiers in Ecology and the Environment* 7: 142–149. <https://doi.org/10.1890/070096>
- 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, 15–37.
- Oswalt CM, Fei S, Guo QF, Iannone BV III, Oswalt SN, Pijanowski BC, Potter KM (2016) A subcontinental view of forest plant invasions. *Neobiota* 31: 105–106. <https://doi.org/10.3897/neobiota.31.8785>
- Pearson DE, Ortega YK, Eren O, Hierro JL (2018) Community assembly theory as a framework for biological invasions. *Trends in Ecology & Evolution* 33: 313–325. <https://doi.org/10.1016/j.tree.2018.03.002>
- Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution* 24: 497–504. <https://doi.org/10.1016/j.tree.2009.03.016>
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2017) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3. <https://CRAN.R-project.org/package=nlme>
- Potter KM (2018) Do United States protected areas effectively conserve forest tree rarity and evolutionary distinctiveness? *Biological Conservation* 224: 34–46. <https://doi.org/10.1016/j.biocon.2018.05.007>
- 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. *Forest Ecology and Management* 321: 117–129. <https://doi.org/10.1016/j.foreco.2013.06.026>
- Procheş Ş, Wilson JRU, Richardson DM, Rejmánek M (2008) Searching for phylogenetic pattern in biological invasions. *Global Ecology and Biogeography* 17: 5–10.

- Qian H, Ricklefs RE (2000) Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature* 407: 180–182. <https://doi.org/10.1038/35025052>
- R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- 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 K, Potter K, Iannone BV III, Oswalt CM, Fei S, Guo Q (2018) Landscape correlates of forest plant invasions: A high-resolution analysis across the eastern United States. *Diversity and Distributions* 24: 274–284. <https://doi.org/10.1111/ddi.12680>
- Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1: 103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17: 170–176. [https://doi.org/10.1016/S0169-5347\(02\)02495-3](https://doi.org/10.1016/S0169-5347(02)02495-3)
- Stohlgren T, Barnett D, Flather C, Fuller P, Peterjohn B, Kartesz J, Master L (2006) Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biological Invasions* 8: 427–447. <https://doi.org/10.1007/s10530-005-6422-0>
- Stohlgren TJ, Barnett DT, Kartesz JT (2003) The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment* 1: 11–14. [https://doi.org/10.1890/1540-9295\(2003\)001\[0011:TRGRPO\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0011:TRGRPO]2.0.CO;2)
- Tan J, Pu Z, Ryberg WA, Jiang L (2015) Resident-invader phylogenetic relatedness, not resident phylogenetic diversity, controls community invasibility. *The American Naturalist* 186: 59–71. <https://doi.org/10.1086/681584>
- Theoharides K, Dukes J (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist* 176: 256–273. <https://doi.org/10.1111/j.1469-8137.2007.02207.x>
- Thuiller W, Gallien L, Boulangeat I, De Bello F, Münkemüller T, Roquet C, Lavergne S (2010) Resolving Darwin's naturalization conundrum: a quest for evidence. *Diversity and Distributions* 16: 461–475. <https://doi.org/10.1111/j.1472-4642.2010.00645.x>
- Tibshirani R, Leisch, F (2013) Bootstrap: Functions for the Book “An Introduction to the Bootstrap”. R package version. <http://CRAN.R-project.org/package=bootstrap> [2012.04-1]
- Tucker CM, Cadotte MW, Carvalho SB, Davies TJ, Ferrier S, Fritz SA, Grenyer R, Helmus MR, Jin LS, Mooers AO, Pavoine S, Purschke O, Redding DW, Rosauer DF, Winter M, Mazel F (2017) A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews* 92: 698–715. <https://doi.org/10.1111/brv.12252>
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>
- Wilsey BJ, Polley HW (2002) Reductions in grassland species evenness increase dicot seedling invasion and spittle bug infestation. *Ecology Letters* 5: 676–684. <https://doi.org/10.1046/j.1461-0248.2002.00372.x>

### **Supplementary material 1**

#### **Locations of Northern and Southern FIA Regions and of the ecological domains, provinces and sections in which study plots were located**

Authors: Basil V. Iannone III, Kevin M. Potter, Qinfeng Guo, Insu Jo, Christopher M. Oswalt, Songlin Fei

Data type: occurrence

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.40.28558.suppl1>

### **Supplementary material 2**

#### **Description of differences between Northern and Southern FIA Regions in invasive plant species monitoring protocols**

Authors: Basil V. Iannone III, Kevin M. Potter, Qinfeng Guo, Insu Jo, Christopher M. Oswalt, Songlin Fei

Data type: protocols

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.40.28558.suppl2>

### **Supplementary material 3**

#### **Section-level standardised slope estimates for the 91 ecological sections from initial models of invasive richness and cover in response to four metrics of evolutionary relatedness—PSC, PSV, PD and PSE**

Authors: Basil V. Iannone III, Kevin M. Potter, Qinfeng Guo, Insu Jo, Christopher M. Oswalt, Songlin Fei

Data type: supporting data

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.40.28558.suppl3>