

Phylogenetic relatedness and leaf functional traits, not introduced status, influence community assembly

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Abstract. Considerable debate focuses on whether invasive species establish and become abundant by being functionally and phylogenetically distinct from native species, leading to a host of invasion-specific hypotheses of community assembly. Few studies, however, have quantitatively assessed whether similar patterns of phylogenetic and functional similarity explain local abundance of both native and introduced species, which would suggest similar assembly mechanisms regardless of origin. Using a chronosequence of invaded temperate forest stands, we tested whether the occurrence and abundance of both introduced and native species were predicted by phylogenetic relatedness, functional overlap, and key environmental characteristics including forest age. Environmental filtering against functionally and phylogenetically distinct species strongly dictated the occurrence and abundance of both introduced and native species, with slight modifications of these patterns according to forest age. Thus, once functional and evolutionary novelty were quantified, introduced status provided little information about species' presence or abundance, indicating largely similar sorting mechanisms for both native and introduced species.

Key words: Bayesian hierarchical model; Darwin's naturalization hypothesis; environmental filtering; functional traits; invasive species; phylogeny; seed mass; specific leaf area, SLA.

INTRODUCTION

Most hypotheses in invasion biology implicitly assume that introduced species differ either functionally or evolutionarily from native species (Callaway and Ridenour 2004, van Kleunen et al. 2010). This topic has a long and unresolved history (Jeschke et al. 2012). In part, this ambiguity has led to recent debate over whether invaders are fundamentally different from native species, therefore requiring their own subfield of invasion-specific hypotheses (Davis et al. 2011, Simberloff and Vitale 2014). Many hypotheses in invasion biology assume that native and introduced species follow different rules, yet one of the key unanswered questions is whether abundant native and introduced species share traits and evolutionary histories that distinguish them from rare native and introduced species (Cadotte et al. 2010, Lind and Parker 2010). For example, Darwin's naturalization hypothesis (DNH) predicts that distantly related invaders will occur in communities more frequently than closely related

invaders because shared ancestry would lead to greater functional overlap and therefore stronger biotic resistance by native species (Strauss et al. 2006, Park and Potter 2013). Darwin also hypothesized that shared ancestry could provide pre-adaptation to local environments, resulting in greater probability of occurrence for closely related introduced species (Duncan and Williams 2002). These conflicting hypotheses, referred to as Darwin's conundrum (Diez et al. 2008), essentially predict either niche partitioning or environmental filtering, respectively, as driving forces of community assembly.

Traditionally, mechanisms of community assembly and DNH have been tested using null models comparing observed patterns of phylogenetic or functional dispersion to those of randomly generated communities. Overdispersion might arise from niche partitioning, while clustering may be indicative of environmental filtering. To date, null-model tests of introduced species' occurrences are equivocal. Over regional scales, introduced species can be either phylogenetically distinct from native species (Strauss et al. 2006) or closely related (Duncan and Williams 2002, Diez et al. 2008, Ordóñez 2014). Within-habitat patterns are similarly equivocal, as evolutionary distinct invaders are both selected for (Davies et al. 2011, Parker et al. 2012), and against (Diez et al. 2008, Ricotta et al. 2010).

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However, we posit that null-model tests can be significantly improved with new statistical approaches incorporating information about functional traits, environmental context, and species' local abundances. For example, although different forces may govern a species' occurrence and abundance (Boulangeat et al. 2012), most null-model tests use lists of species occurring in a given area (e.g., Strauss et al. 2006, Schaefer et al. 2011), ignoring local abundance once established. Thus, in the absence of local abundance data, null-model tests give equal weight to rare and common species (e.g., Diez et al. 2008, Davies et al. 2011) despite observations that abundant species influence local processes more strongly than rare species (Vázquez et al. 2007). Null-model tests also typically examine patterns of phylogenetic relatedness and assume phylogenetic conservation of functionally important traits. However, complementing phylogenetic tests with tests of functional trait similarities can provide a more comprehensive test of community assembly mechanisms, particularly when traits are not conserved (e.g., Kraft and Ackerly 2010). Finally, most null-model tests ignore quantitative variation in environmental context. These limitations are especially important because if the local abundance of a species can be predicted using a quantitative framework incorporating functional and evolutionary dispersion within a given environment, then assembly rules for both introduced and native species can be merged into a unified theory of community assembly.

We asked three main questions: (1) How do trait and phylogenetic similarity influence the occurrence and abundance of native species? (2) Do trait and phylogenetic similarity affect introduced species differently than native species? And, (3) do community assembly mechanisms vary along environmental gradients? We developed a novel Bayesian hierarchical mixture model that simultaneously determines assembly patterns of both colonization (presence/absence) and abundance of both native and introduced species at local scales. This model also analyzes the effects of environmental variation on assembly. To date, this is the first study we know of to quantitatively partition the effects of phylogeny, phenotype, and environment on occurrence and abundance of co-occurring native and introduced species.

METHODS

Study sites

During the summer of 2012, we surveyed understory composition of 25 forest stands of varying age, size, and species composition near the Smithsonian Environmental Research Center in Edgewater, Maryland, USA (SERC; 38°53' N, 76°33' W; see Plate 1). Information on each stand can be found in Appendix C: Table C1. Age determination and species composition of our surveyed stands has been previously described (McMahon et al. 2010). In these forests, most introduced species are herbaceous or woody shrubs common to the eastern United States, including *Berberis thunbergii*, *Lonicera*

japonica, *Microstegium vimineum*, *Rosa multiflora*, and *Rubus phoenicolasius*, among others. All 18 introduced species in this study are considered "invasive" by state or federal agencies.

Understory surveys

A single rectangular plot (20 × 50 m) was established in the center of each forest stand using a handheld GPS. Within each plot, we placed 9–10 1-m² quadrats randomly along two intersecting transects ($n = 18$ –20 per forest plot). Within each quadrat, we estimated cover of each species relative to quadrat area to the nearest one percent. Prior to analyses, we removed all species not present in both phylogeny and trait data sets. These species were relatively rare, accounting for <13% of the total cover across all plots. As quadrats often contained fewer than five species, we summed species cover across all quadrats within a forest stand and calculated relative cover for each species by dividing species cover by total cover. This placed relative cover and presence/absence on the same spatial scale; species were only determined to be absent from a forest stand if they were not observed in any quadrat. Furthermore, using relative cover enabled us to compare species' performances among sites that vary in productivity, species composition, or sample size (Colautti et al. 2014).

In each quadrat, we also measured photosynthetically available light, soil volumetric water content (VWC), and litter depth. Light was measured in cloudless conditions using two readings from an AccuPAR LP-80 PAR/LAI light meter (Decagon Devices, Pullman, Washington, USA) placed diagonally across each quadrat at ~1.0 m height. We also took similar measurements at roughly the same time in full sunlight environments. We then standardized light data as light transmittance (e.g., light within the forest divided by full sunlight). For soil moisture, we took the mean of two VWC readings in each quadrat using a FieldScout TDR 300 moisture meter with 12-cm probes (Spectrum Technologies, Aurora, Illinois, USA). Litter depth was estimated in each quadrat by taking a ruler measurement in the center of each quadrat. We averaged light transmittance, soil VWC, and litter depth across quadrats within each forest stand.

Plant traits

To estimate ecological similarity among species, we quantified plant traits for 71 of the 116 species encountered, comprising 87% of the total cover. We measured three traits: specific leaf area (SLA), leaf toughness, and seed mass. SLA correlates with photosynthetic efficiency, leaf longevity, and growth rate (Westoby et al. 2002). Toughness represents anti-herbivore defense investment, and seed dispersal contrasts maternal investment strategies (i.e., high dispersal, low survival vs. low dispersal, high survival; Westoby et al. 2002). These traits are frequently used to describe functional similarity among species as differentiation of

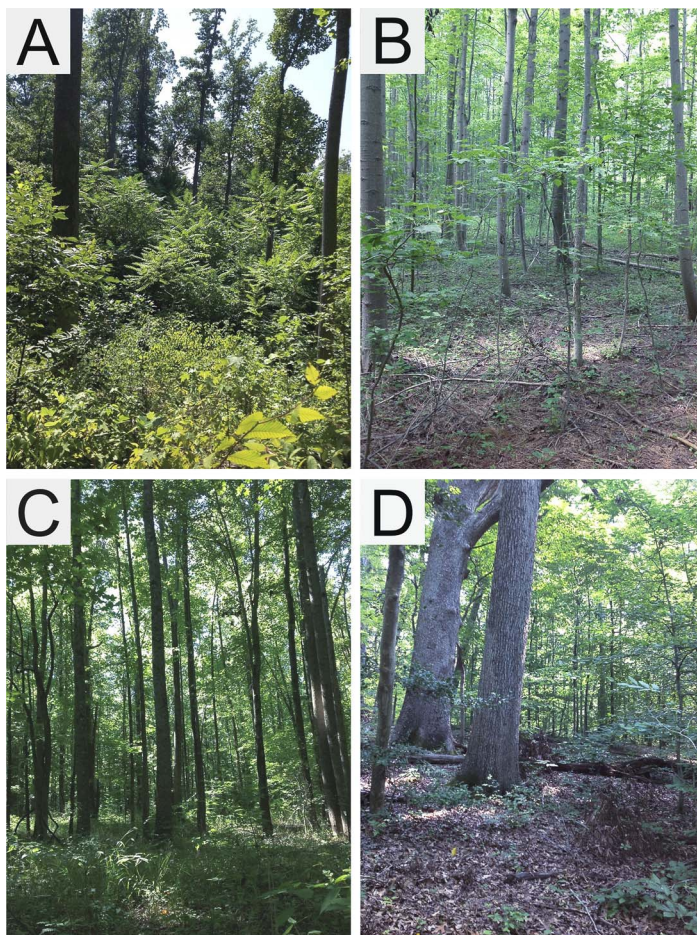


PLATE 1. Forest stands of varying age near the Smithsonian Environmental Research Center, Maryland, USA. (A) A 5-year-old forest, (B) a 22-year-old forest, (C) a 75-year-old forest, and (D) a 175-year-old forest. Photo credits: J. Shue.

these traits often relates to community assembly processes (Kraft et al. 2008, Kunstler et al. 2012). Furthermore, introduced species generally possess higher SLA and lower seed mass than native species (Ordonez et al. 2010, van Kleunen et al. 2010).

We collected 3–5 apical shade leaves for each species, where each leaf was acquired from different individuals. SLA (cm^2/g dry mass) was determined by measuring leaf area using a LI 3000C portable area meter (Li-Cor, Lincoln, Nebraska, USA) and recording leaf dry mass. Leaf toughness was measured using a Mecmesin BFG 500N force penetrometer (Mecmesin, Slinfold, West Sussex, UK). Seed mass was taken from the Kew Seed Information Database (*available online*),⁶ except for *R. phoenicolasius*, which was provided by the National Clonal Germplasm Repository (S. Wada, *personal communication*).

Phylogeny

We generated a highly resolved phylogeny constructed from a single molecular megatree of all plants in the study. Using three independently aligned loci for a large

set of taxa (1705 species), we constructed an aligned matrix that spanned 6944 base pairs for all taxa. Details of the phylogenetic reconstruction and dating of nodes for the molecular megatree can be found in Erickson et al. (2014). The dated chromatogram, which included all 1705 taxa, was rooted with a clade of ferns, and then had the SERC community pruned out from the larger phylogeny (Appendix B: Fig. B1).

Trait analyses

We determined whether introduced species differed substantially from native species in measured traits using non-metric multidimensional scaling (nMDS) on three variables: SLA, toughness, and seed mass (Appendix B: Fig. B2). Trait data were scaled by standard deviation across the entire species pool, but not centered, prior to analysis because nMDS based on Bray-Curtis dissimilarity coefficients does not function with negative values. We tested the phylogenetic structure of each plant trait (i.e., whether related species exhibited similar trait values) using Blomberg's *K* (Kraft and Ackerly 2010). We calculated the significance of the phylogenetic signal by comparing the variances of phylogenetically independent contrasts in our observed data with those from

⁶ <http://data.kew.org/sid/>

trees where the tips were randomly relabeled (999 permutations).

Species-level tests of community assembly

Mean phylogenetic distance (MPD) for each species in a forest stand was calculated as the mean pairwise phylogenetic distance to all other co-occurring species. Similarly, mean trait distance (MTD) for each species in a forest stand was calculated as the mean Euclidean distance in trait-space to all other co-occurring species. Phylogenetic and trait distances were both weighted by plant relative abundance, resulting in more abundant species having larger impacts on MTD and MPD than rare species. This resulted in 1775 unique observations, with 71 observations per forest stand.

Species absences dominated the relative cover data. When present, most species were extremely rare, such that occurrence data were approximately gamma distributed. We therefore developed a hierarchical hurdle model using a Bayesian framework. This model allowed us to simultaneously assess the influence of MPD, MTD, and introduced status on both the probability of species occurrence and relative cover in each forest stand while quantifying the extent to which environmental variables drove these relationships. This method thus asks whether trait similarity drives species' abundance and occurrence and does not assume a direct relationship between traits and performance per se. The likelihood function and model details can be found in Appendix A; fully annotated Python code, including STAN code for the Bayesian hurdle model, can be found in the Supplement.

We used R v.3.0.2 for tests of phylogenetic signals (R Development Core Team 2013). Blomberg's *K* analyses used the *picante* package (Kembel et al. 2010). Ordinations were conducted in Python v.2.7 (*available online*).⁷ Bayesian models were written in STAN and run using PYSTAN v.2.3.0 (Stan Development Team 2013).

RESULTS

Plant traits

Non-metric multidimensional scaling (nMDS) revealed no significant differences in trait syndromes between native and introduced species (PERMANOVA, $P = 0.363$; Appendix B: Fig. B3). SLA and leaf toughness loaded most heavily along the first trait axes and were negatively correlated (Appendix B: Figs. B2 and B3). The second trait axis described seed mass. Only SLA showed near-significant phylogenetic signal, but the trend was weak ($K=0.137$, $P=0.065$). Seed mass did not vary considerably among species and contributed relatively little to the overall ordination, and SLA and toughness were negatively correlated ($r = -0.53$). Therefore, calculations of MTD primarily reflect differ-

ences in leaf economic spectrum as represented by SLA/leaf toughness, rather than seed mass.

When pooled across all forest stands, neither native nor introduced species were, on average, phylogenetically or phenotypically different from the overall species pool. Neither MTD nor MPD varied significantly between native and introduced species (Appendix C: Table C3). However, keeping the introduced status parameter in our model allows it to account for trait differences among native vs. introduced species that we did not measure, including important predictors of abundance like growth rate or fecundity (van Kleunen et al. 2010).

Species presence/absence

Area under the curve (AUC) of the presence/absence portion of the model suggested that our model accurately predicted occurrence (AUC = 0.66). Phylogenetic relatedness had relatively little influence on species' occurrence patterns among forest stands (Fig. 1A). Indeed, only four forest stands showed even marginally significant patterns of decreased probability of occurrence for phylogenetically dissimilar species (Fig. 1A; Appendix B: Fig. B4). In contrast, phenotypically similar species were more likely to occur in a given forest stand than phenotypically dissimilar species, suggesting that trait matching to the environment is an important determinant of colonization (Fig. 1B; Appendix B: B5). Importantly, the effects of MPD and MTD on introduced species occurrences were rarely different from native species (Fig. 1D, E). Thus, the strongest effect of trait and phylogenetic distance on presence/absence patterns was that stands were more likely to contain species with similar SLA/leaf toughness, and effects were similar for both native and introduced species in almost all forest stands.

Species abundances

The abundance portion of the model also had an accurate fit to the data, as there was a high correlation between observed and predicted relative cover (Pearson $r = 0.77$). In nearly all forest stands, functional and phylogenetic dissimilarity led to reduced relative cover, such that the most abundant species in all forest stands were closely related species possessing a relatively narrow range of leaf trait values (Fig. 1F, G; Appendix B: Figs. B6 and B7). For example, in one typical forest (TEACH2), SLA of rare species ranged from 104.3 to 1029.4, whereas SLA of abundant species ranged from 296.0 to 417.1 (Appendix B: Fig. B7). Similar funnel clouds indicating environmental filtering of leaf traits could be found in numerous forest stands (e.g., Appendix B: Fig. B7).

Introduced species were marginally more abundant than native species in nine forest stands and significantly more abundant than natives in the four youngest forest stands (Fig. 1H). However, introduced species' abundances were largely determined by similar factors, given

⁷ <http://www.python.org>

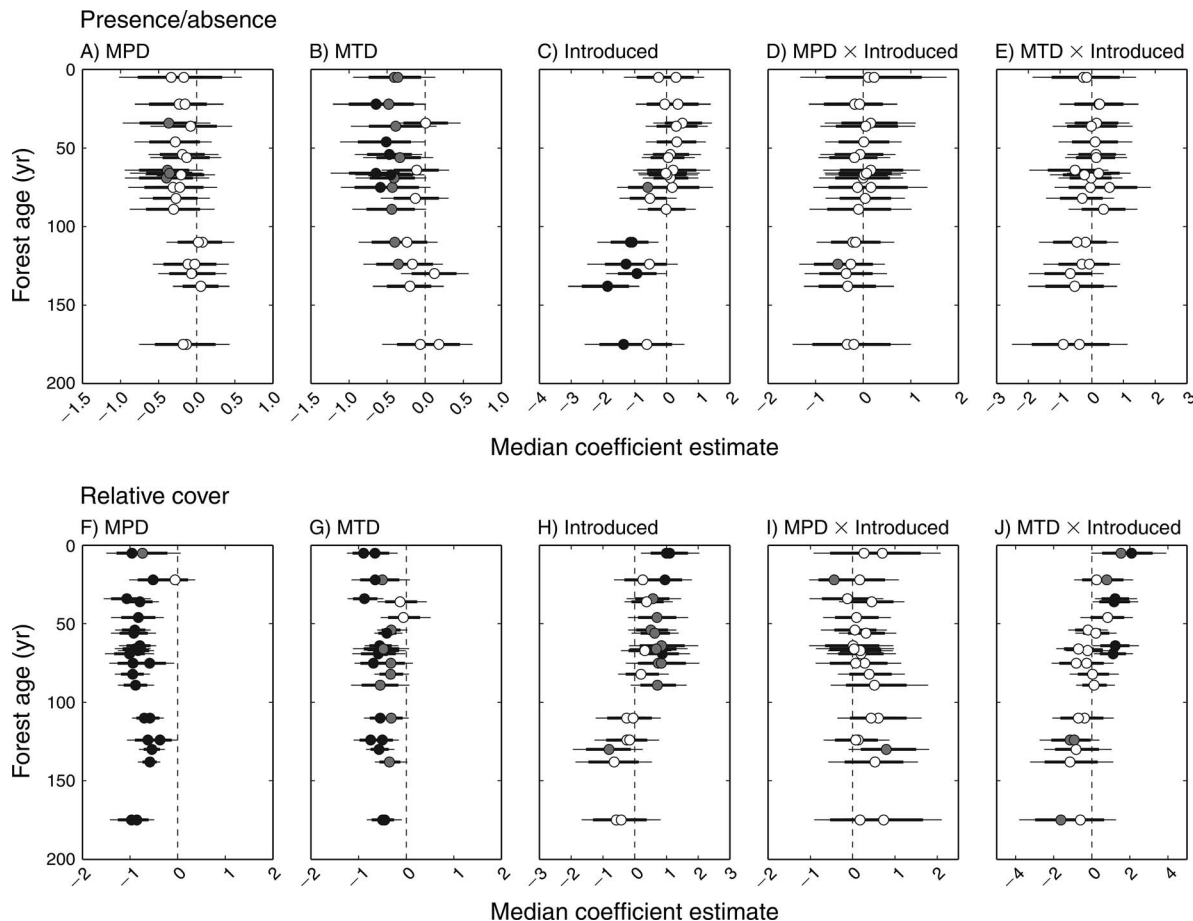


FIG. 1. Phylogenetically dissimilarity resulted in lower abundance in most forest stands. Ecologically dissimilar species were less likely to occur and less abundant within most forest stands. The figure shows coefficients for each parameter in each forest stand. Black circles indicate statistically significant coefficients (i.e., 95% CI excludes zero). Gray circles indicate marginally significant coefficients (i.e., 80% CI excludes zero). White circles indicate nonsignificant coefficients. (A) Mean phylogenetic distance (MPD) had no effect on native species' occurrences in most forest stands. (B) Functionally dissimilar native species were less likely to occur in younger forests (mean trait distance, MTD). (C) Introduced species were less likely than natives to occur in many older forests. (D and E) Effects of MPD and MTD on introduced species presences' did not significantly differ from those of native species in any forest stand. (F) Phylogenetically and (G) functionally dissimilar natives species had reduced cover in almost all forest stands. (H) Introduced species exhibited higher relative cover than natives in many younger forest stands. (I) The effect of MPD on relative cover was identical for both native and introduced species. (J) MTD exerted weaker effects on introduced species' cover in young forest, and slightly stronger effects on introduced species' cover in older forests.

only five significant interactions between MPD or MTD and introduced status (Fig. 1I, J). Environmental filtering of introduced species was weaker than that of natives in seven younger forest stands and slightly stronger than that of natives in three older forest stands (Fig. 1J; Appendix B: B8). In the seven young forest stands with significant interaction coefficients, introduced species abundance was independent of trait similarity to co-occurring species (Appendix B: Fig. B8).

Abiotic variables

Litter depth was the strongest predictor of introduced species occurrences in our data (Appendix B: Fig. B9). Introduced species were less likely to occur than native species in forest stands with deeper litter layers (Fig. 2A), and more abundant than natives in young forests

(Fig. 2B) with wet soils (Fig. 2C). Although the 80% confidence intervals (CI) of both parameters narrowly included zero (Appendix B: Fig. B9H), the bulk of the posterior distribution lay above or below zero, indicative of a high probability that these parameters are important ($\text{Pr}(\text{VWC} > 0) = 0.89$, $\text{Pr}(\text{Age} < 0) = 0.87$). Introduced species experienced moderately or significantly weaker filtering than native species in seven forest stands and moderately stronger filtering in three forest stands (Fig. 1J). The different filtering effects on native and introduced species were explained by light transmittance and forest age (Appendix B: Fig. B9J). Introduced species had no relationship between abundance and MTD in young forests with high light transmittance.

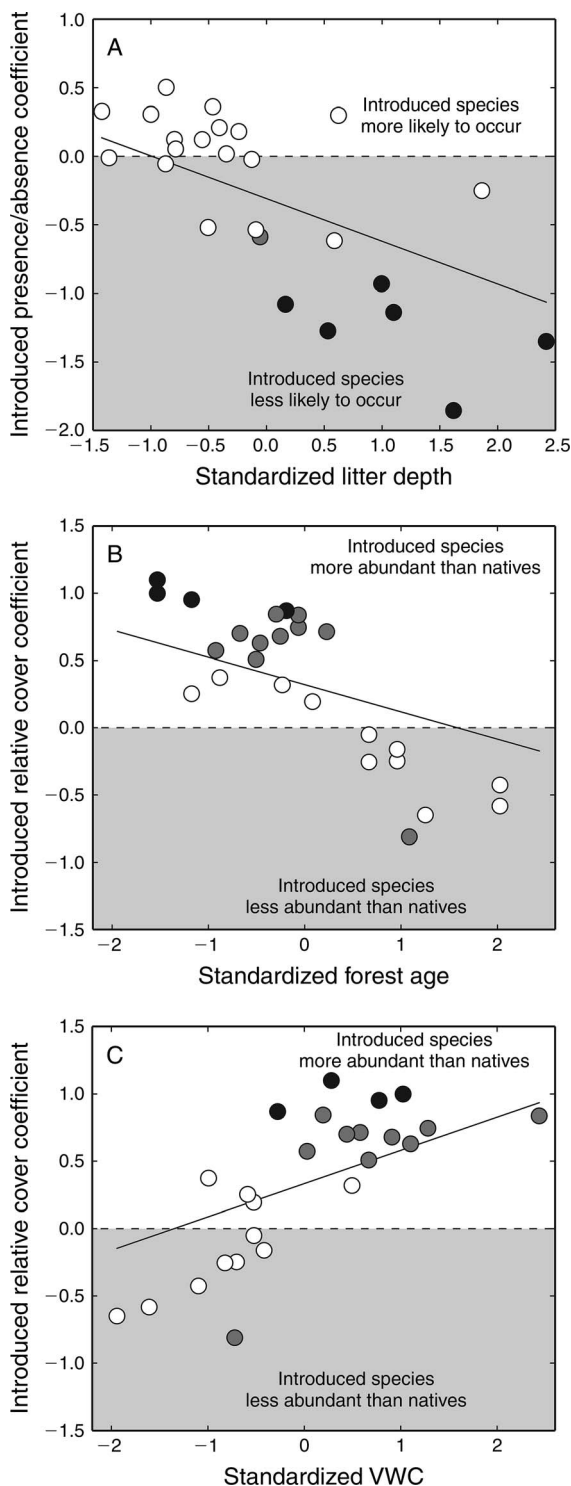


FIG. 2. (A) The probability of introduced species occurring in a plot was negatively correlated with litter depth. Additionally, introduced species were more abundant than natives in (B) young forests with (C) high soil moisture content. Points are the median coefficient estimates for the introduced parameter for each forest stand on the y-axis and standardized litter depth, age, and soil moisture of each forest on the x-axis. Points are color coded for significance as in Fig. 1.

DISCUSSION

Previous studies have shown that invasive species are phylogenetically distinct from native species at both regional (Strauss et al. 2006, Schaefer et al. 2011) and local scales (Jiang et al. 2010, Parker et al. 2012), leading to speculation that introduced plants become invasive by escaping herbivores (Ness et al. 2011) or competing less with existing natives (Violle et al. 2011). In contrast, we found that increasing phylogenetic and phenotypic dissimilarity led to fewer occurrences and reduced abundances of both native and introduced species in nearly all forest stands (Fig. 1). Given that our calculations of phenotypic dissimilarity primarily reflect differences in leaf economics, our results support previous research documenting the prevalence of habitat filtering for leaf functional traits as a driving force of community assembly (Kraft and Ackerly 2010, Paine et al. 2012), but extends this premise to both native and introduced species. Phylogenetic novelty provided no advantage for introduced species in our study sites, supporting the notion that trait matching to environmental drivers is a more important determinant of community structure.

The discrepancy between our results and some previous studies might arise for two reasons. First, we examined DNH across local communities, treating each community as the unit of observation. Many previous studies have focused on regional patterns where species may not co-occur within a local community (Strauss et al. 2006, Diez et al. 2008, Schaefer et al. 2011), or test DNH at multiple scales within a single community (Davies et al. 2011). Second, most previous tests use only presence/absence information and categorical assessments of invasiveness (Strauss et al. 2006, Diez et al. 2008, Schaefer et al. 2011), rather than incorporating information on local abundance. When we repeated our analyses with phylogenetic and trait distances unweighted by local abundances, we found the opposite pattern: Phylogenetically novel introduced species were more likely to occur, consistent with earlier observations (Appendix B: Fig. B10). Thus, the decision to weight phylogenetic and functional distances by species abundances is critical as it can potentially lead to opposite predictions and interpretations. Given that common and rare species contribute equally to MPD or MTD in unweighted analyses, we speculate that weighting by abundance more accurately reflects the stronger impacts of abundant species on processes important to community assembly (Vázquez et al. 2007).

The strong environmental filtering we found for introduced species is consistent with the hypothesis that highly dissimilar introduced species often fail to establish in a novel environment (Maitner et al. 2012). Similarly, Cadotte et al. (2010) also found that introduced species undergo environmental filtering. Filtering of leaf traits for introduced species in younger forests with higher light availability was relatively weak, however, suggesting some differences in assembly

mechanisms for introduced vs. native species based on forest age. These differences probably reflect source pool bias. The introduced species in our study are mostly disturbance-adapted species like *Microstegium vimineum*, *Lonicera japonica*, and *Rosa multiflora*; there were no late successional, introduced species to filter out in younger forests. In contrast, native species were a larger, more diverse pool of both early and late successional species, potentially leading to stronger environmental filtering of native species in younger forests. In addition, although we found strong environmental filtering for both introduced and native species, Cadotte et al. (2010) found niche partitioning for native species. Niche partitioning may operate at the smallest spatial scales (i.e., the 1.0–25 m² quadrat level; Kraft et al. 2008, Cadotte et al. 2010, Kraft and Ackerly 2010) that we were unable to analyze with our data, thus we cannot conclusively rule out niche partitioning. Nevertheless, phylogenetic and functional overdispersion has been detected in plot sizes identical to ours (Cavender-Bares et al. 2004, Valiente-Banuet and Verdú 2007, Verdú and Pausas 2007), suggesting that we would have been able to detect these patterns if present. Community assembly mechanisms may also operate differently for different traits (Kraft and Ackerly 2010), such that the inclusion of additional trait variables beyond leaf traits and seed mass may have detected niche partitioning. Thus, we cannot conclusively reject niche partitioning as an important process in our study system, particularly at small spatial scales.

Here, species with similar SLA and leaf toughness to other species in the community were more likely to establish and succeed within a forest stand, suggesting selection for species with similar leaf economic characteristics regardless of introduced status. However, these traits lacked a phylogenetic signal ($K \ll 1$ for all traits), thus the phylogenetic clustering that we observed must result from unmeasured traits that are conserved. For example, root morphology or mycorrhizal fungal associations are generally clustered phylogenetically (Reinhart et al. 2012, Chen et al. 2013). Indeed, increased abundance of introduced plants in younger forests is often attributed to belowground interactions that might reflect such traits. Specifically, exotic earthworms are often disproportionately abundant in younger forests at our study site, reducing litter depth and altering belowground microbial processes (Szlavec et al. 2011). In broader surveys, the abundance of earthworms is correlated with increased cover of introduced plants (Nuzzo et al. 2009). Both results are consistent with our finding of increased introduced species abundance in younger forests with decreased litter depth (Appendix B: Fig. B9), highlighting the potential role of belowground interactions in facilitating introduced species.

Many hypotheses in invasion biology implicitly rely on evolutionary context. For example, DNH suggests that closely related invaders should struggle to colonize

a community due to niche packing, while enemy release assumes that phylogenetic novelty allows introduced species to escape herbivores (Maron and Vilà 2001). Our statistical approach provided a rigorous method of quantifying phylogenetic relatedness relative to the recipient community, and we found similar sorting mechanisms governed the abundance of both native and introduced species. The few observed differences we found reflected forest age, which may be due to some underlying mechanism facilitating introduced species in younger forests or, more likely, an inherent bias in the source pool of introduced species. Importantly, the quantitative framework presented here provides a statistically rigorous framework incorporating the role of phylogenetic relatedness, phenotypic differences, and environmental context in driving local organism occurrence and abundance. This framework can be applied across both native and introduced species, providing an objective test of whether introduced species are operating by fundamentally different rules relative to native species.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C and the Supplement are available online: <http://dx.doi.org/10.1890/14-1883.1.sm>