Above- and below-ground effects of plant diversity depend on species origin: an experimental test with multiple invaders

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Summary
• Although many plant communities are invaded by multiple nonnative species, we have limited information on how a species’ origin affects ecosystem function. We tested how differences in species richness and origin affect productivity and seedling establishment.
• We created phylogenetically paired native and nonnative plant communities in a glasshouse experiment to test diversity–productivity relationships and responsible mechanisms (i.e. selection or complementarity effects). Additionally, we tested how productivity and associated mechanisms influenced seedling establishment. We used diversity-interaction models to describe how species’ interactions influenced diversity–productivity relationships.
• Communities with more species had higher total biomass than did monoculture communities, but native and nonnative communities diverged in root: shoot ratios and the mechanism responsible for increased productivity: positive selection effect in nonnative communities and positive complementarity effect in native communities. Seedling establishment was 46% lower in nonnative than in native communities and was correlated with the average selection effect. Interspecific interactions contributed to productivity patterns, but the specific types of interactions differed between native and nonnative communities.
• These results reinforce findings that the diversity–productivity mechanisms in native and nonnative communities differ and are the first to show that these mechanisms can influence seedling establishment and that different types of interactions influence diversity–productivity relationships.

Introduction
Anthropogenic global change is leading to widespread changes in species distributions (Wardle et al., 2011), altering community composition and associated species interactions (Tylianakis et al., 2008) and modifying ecosystem functions (Hooper et al., 2005; Wardle et al., 2011; Strayer, 2012). The addition of single nonnative species strikingly transforms community composition and ecosystem function (Vilà et al., 2011; Pyšek et al., 2012; Strayer, 2012), but considering how a single nonnative species alters ecosystems captures only a piece of how invasion impacts ecosystems, because many ecosystems now contain multiple nonnative species (Chytrý et al., 2008; Catford et al., 2012; Strayer, 2012; Kuebbing et al., 2013; Jackson, 2015).

Communities dominated by nonnative species can function differently from those dominated by native species. For example, native and nonnative plant communities increase in productivity with increasing species richness (Hooper et al., 2005; Wilsey et al., 2009; Isbell & Wilsey, 2011b; Cook-Patton & Agrawal, 2014), but these positive diversity–productivity relationships are frequently attributed to ‘complementary effects’ in native communities and to ‘selection effects’ in nonnative communities (Wilsey et al., 2009; Isbell & Wilsey, 2011b). Complementarity effects arise when species partition resources based on their ability to access resources, species facilitate one another, or interspecific interactions among species enhance their total productivity (Hooper et al., 2005). By contrast, selection effects arise when communities contain a species that is highly productive in monoculture and that outyields in mixture (Hooper et al., 2005). Indeed, evidence to date suggests that plant communities comprising native species are more likely than plant communities comprising nonnative species to have complementary interactions – such as partitioning resources based on their ability to access resources (i.e. difference in root length) or facilitating one another (i.e. nitrogen-fixing species increasing total available nitrogen) – that promote their coexistence and lead to positive complementary effects (Tilman et al., 1996; Loreau & Hector, 2001; Hooper et al., 2005; Wilsey et al., 2009; Isbell & Wilsey, 2011a; Martin et al., 2014).

Differences in diversity–productivity relationships and strength of complementarity and selection effects between nonnative and native communities could have long-term effects on
species recruitment into communities. The establishment of new species in communities can be regulated by productivity (Grime, 1998) and associated diversity–productivity mechanisms (Fargione & Tilman, 2005), and seedling establishment should decrease in communities with larger positive selection effects, like nonnative communities, owing to the presence of a strong competitor (Fargione & Tilman, 2005). If diversity–productivity relationships in nonnative communities are attributed to positive selection effects then we should expect lower seedling establishment in nonnative communities, which could explain why many nonnative-dominated communities resist plant compositional changes through time (Kulmatiski, 2006; Cramer et al., 2008).

Why native and nonnative communities might differ in the strength and sign of complementarity and selection effects is unknown. The strength and direction of interactions between nonnative species may differ from interactions between native species (Wilsey et al., 2009; Isbell & Wilsey, 2011a; Martin et al., 2014), but this hypothesis has never been explicitly tested. New methods that extend earlier diversity effects models (Loreau & Hector, 2001) can now define the contributions of both individual species and interspecific interactions between species to diversity–productivity relationships (Kirwan et al., 2009; Connolly et al., 2013). Comparisons between these diversity-interaction (DI) models allow for testing hypotheses about how specific types of interspecific interactions contribute to overall diversity effects and provide a way to test whether interactions between native and nonnative species differ. Our work expands upon previous research (Wilsey et al., 2009; Isbell & Wilsey, 2011a; Cook-Patton & Agrawal, 2014; Martin et al., 2014) by employing DI models to test how interactions between species pairs within communities influence diversity–productivity relationships.

Here, we use old-field ecosystems in the southeastern USA to test how changes in species richness influence primary productivity, associated diversity–productivity mechanisms (i.e. selection and complementarity effects), and seedling establishment in a glasshouse experiment. We focus on differences in productivity between roots and shoots, because how biomass is allocated in communities is critical for assessing total primary productivity (Wilsey & Polley, 2006; Bessler et al., 2009), and few studies have considered differences in root-to-shoot ratios between native and nonnative species (but see Wilsey & Polley, 2006). Old-field communities are dominated by herbaceous and graminoid plants (Souza et al., 2011a). But under minimal anthropogenic management (i.e. mowing or burning), such ecosystems revert to wooded shrub or forested communities (Kuebbing et al., 2014). This natural conversion from forb-dominated to woody-dominated provides an opportunity to test how woody seedling establishment may differ between native and nonnative communities. Furthermore, because woody nonnative shrubs can persist in old-field ecosystems and cause ‘arrested succession’ (Cramer et al., 2008), we compare differences in native and nonnative woody species establishment in our experimental communities.

In this study, we ask four interrelated questions. How do changes in species richness affect above- and below-ground biomass production in native and nonnative plant communities? Is the same mechanism (i.e. complementarity or selection effect) responsible for the net biodiversity effect in native and nonnative communities? How do the diversity–productivity effect and its associated mechanisms (i.e. complementarity or selection effect) limit woody seedling establishment in native and nonnative plant communities? Are the same types of pairwise interactions responsible for changes in above-ground biomass production in native and nonnative communities?

Materials and Methods

Plant communities

We used old-field ecosystems to examine differences in the response of native and nonnative communities because they have been widely studied in tests on impacts of changing species richness and invasion (Wilsey & Potvin, 2000; Sanders et al., 2007; Wilsey et al., 2009), contain high native and nonnative species richness (Souza et al., 2011a; Kuebbing et al., 2014), and are becoming more common, especially in parts of the eastern United States as agricultural land abandonment continues (Cramer et al., 2008). We selected four native and four nonnative plant species that were phylogenetically paired and are commonly found in old fields in eastern Tennessee and provide a representative suite of native and nonnative species pairs for this particular ecosystem (Table 1; Wofford & Kral, 1993; Souza et al., 2011b). We selected species pairs based on the following criteria: species are locally common in old fields; species had a closely related native/nonnative match at the family or genus level; and we were able to obtain viable seeds. Here, we use the term ‘native’ to refer to a species that has evolved in a given area or that arrived there by natural means without intentional or accidental intervention of humans from an area where it is native. By contrast, we use the term ‘nonnative’ to refer to a species whose presence in a region is attributable to human actions that enabled the species to over- come fundamental biogeographical barriers (Richardson et al., 2011). In this experiment, we distinguish between native and nonnative species by considering whether the plant species evolved in eastern Tennessee and, in particular, with the soil biota common to old-field communities.

We constructed plant communities that varied in species origin (native or nonnative) and species richness (one to four species; Table 1) in a nearly full factorial design. Owing to a limited number of seedlings of the native mint Pycnanthemum virginianum and the nonnative grass Phleum pratense, we did not plant the following three species mixtures: Lepidoea capitata Sorghastrum nutans Pycnanthemum virginianum and Lepidoea cuneata Phleum pratense Leucanthemum vulgare. All other possible species combinations within either the native or nonnative groups were replicated 20 times and each community contained 12 individual seedlings in a 3 x 4 grid, with random species placement in mixed species pots. We planted a total of 560 pots (14 total species combinations x two community types x 20 replicates = 560 pots) and 6720 individual plants.

We germinated seedlings in trays of twice-autoclaved sand (Qui-krete Hardscapes Play Sand, Danielson, CT, USA; item No. 212779) in growth chambers (12 : 12 h, 18 : 22°C, day : night light
Table 1 Eight phylogenetically paired old-field plant species used in a test of how interactions between native and nonnative species affect diversity–productivity relationships and woody seedling establishment

<table>
<thead>
<tr>
<th>Family</th>
<th>Native species</th>
<th>Functional group</th>
<th>Nonnative species</th>
<th>Functional group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asteraceae</td>
<td>Achillea millefolium L.</td>
<td>Forb</td>
<td>Leucanthemum vulgare Lam.</td>
<td>Forb</td>
</tr>
<tr>
<td>Fabaceae</td>
<td>Pycnanthemum virginianum Schrad.</td>
<td>Forb</td>
<td>Prunella vulgaris L. var. vulgaris</td>
<td>Forb</td>
</tr>
<tr>
<td>Lamiaceae</td>
<td>Sorgastrum nutans (L.) Nash</td>
<td>Graminoid</td>
<td>Phleum pratense L.</td>
<td>Graminoid</td>
</tr>
<tr>
<td>Poaceae</td>
<td>Forb</td>
<td>Nitrogen-fixer</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

regime) and planted 1-wk-old seedlings in 21 square pots (Belden Jumbo Senior Square pots, 13.34 cm width × 13.34 cm length × 16.51 cm height; Belden Plastics, St Paul, MN, USA). We staggered seed planting dates so that seedling emergence was within a day for all seedlings. We collected seeds from local populations or purchased seeds from suppliers (Ernst Conservation Seed LP, Meadville, PA, USA; Roundstone Native Seed LLC, Upton, KY, USA; Prairie Moon Nursery, Winona, MN, USA; B&T World Seeds, Aigues Vives, France). To improve water filtration and permeability, we filled pots with a 1 : 1 volumetric ratio of autoclaved sand (Quickrite Hardscapes Play Sand, item no. 212779) and field soil, which we collected from the upper 15 cm of mineral soils from five old fields in Oak Ridge National Environmental Research Park (35°54′12″N, 84°20′22″W), in Oak Ridge, TN, USA. The soil classification is Captina silt loam with moderate-to-medium granular structure and medium internal drainage. Before 2002, the fields were managed for fescue production and now the old fields are maintained to support wildlife habitat through regular mowing (Souza et al., 2011b). We homogenized and sieved the soils (10 mm) before mixing with sand.

After 1 wk of planting, we replaced dead individuals, which we assume died from transplant stress. We randomly arranged pots on benches in a glasshouse at the University of Tennessee, Knoxville, TN, USA, and watered them biweekly, or more frequently if pots showed signs of overdrying (i.e. if soils began to pull away from the sides of the pot). At days 50 and 100, we fertilized plants with a 20 : 20 : 20 (nitrogen : phosphorus : potassium, N : P : K) water-soluble fertilizer at the recommended application rate of 0.49 mg cm⁻² (Southern Agricultural Insecticides Inc., Palmetto, FL, USA).

How do changes in species richness affect above- and below-ground biomass production in native and nonnative plant communities?

After 112 d of growth, we randomly selected half of the pots (10 pots per treatment combination for 280 total pots) for biomass removal. Above-ground biomass was clipped, sorted, and dried in a forced-air oven at 60°C for at least 48 h before weighing. To remove below-ground coarse root biomass, we sieved soil from each pot through a 5 mm wire sieve. We did not separate root biomass by species in the mixed species pots because we could not distinguish individual species roots visually. Roots were rinsed, dried in a forced-air oven at 60°C for c. 72 h, and weighed.

To test for differences in productivity between native and nonnative communities and among richness treatments, we used permutational ANOVAs with nonsequential sums of squares. Permutational tests are appropriate when data do not meet assumptions of traditional parametric tests (e.g. model residuals are normally distributed) but still test the null hypothesis that imposed treatments (here, plant community origin and richness) do not affect response variables (Anderson, 2001). In models of the community biomass response variables (above-ground, below-ground, total, and above : below-ground ratio) we tested for the main effects of origin (native or nonnative), richness (one to four species), and composition (phylogenetic composition, e.g. familial taxonomic group: ‘Fabaceae’ or ‘Fabaceae-Poaceae’ pair) and the interactions between origin and richness and origin and composition. The ‘composition’ term accounts for the phylogenetic pairing of native and nonnative species while the origin × composition interaction tests how origin effects vary between paired native and nonnative communities (Wilsey et al., 2009).

Is the same mechanism (i.e. complementarity or selection effect) responsible for the net biodiversity effect in native and nonnative communities?

We used the above-ground biomass data to calculate the net biodiversity effect (NBE) and its two additive components, the complementarity (CE) and selection effects (SE), which describe the overyielding behavior of species in mixture compared with monoculture (Loreau & Hector, 2001). We calculated the components as follows: SE = N × cov(ARY, M) and CE = N × ∆RY × M, where N is the species richness, ARY is the change in the relative yield of a species and is calculated as the yield of a species in mixture divided by the yield of the species in monoculture less the proportion of the species (i.e. proportion of individuals) planted in mixture, M is a species’ average monoculture biomass, ∆RY is the mean change in relative yield for each species mixture, and M is the mean monoculture biomass for each species in mixture (Loreau & Hector, 2001). We analyzed the significance of the biodiversity effects using permutational ANOVAs as described previously.

How do the diversity–productivity effect and its associated mechanisms (i.e. complementarity or selection effect) limit woody seedling establishment in native and nonnative plant communities?

We added native and nonnative woody plant seeds to native and nonnative plant communities. We added three seeds from three additional native (Celastrus scandens L., Sambucus nigra L. and
*Fraxinus americana* L.) and three nonnative (*Celastrus orbiculatus* Thunb., *Lonicer a maackii* (Rupr.) Herder, and *Ligustrum sinense* Lour.) woody plant species to pots with biomass remaining at day 115. We selected woody species that were phylogenetically paired at the family taxonomic level and are common early successional species found invading old fields in the southeastern USA.

After 100 d, we counted, clipped, and weighed the established seedlings. Because the native woody species had negligible seedling establishment (on average, less than one native woody seedling established per pot), we aggregated seedling establishment data for all species. Thus, instead of comparing seedling establishment for each woody species individually, we compared variation in total number of seedlings established and average seedling biomass across species. Seedlings were dried in a forced-air oven at 60°C for 48 h before weighing.

We analyzed seedling establishment and growth data using the same methods as in the first experiment. Because selection and complementarity effects influence establishment of species in some communities (Fargione & Tilman, 2005), we tested for relationships between the average diversity effect and the average number of seedlings and seedling mass for each unique community composition with Pearson’s correlation test (Wilsey et al., 2009). For all permutational ANOVAs, we used the R package lmPerm (Wheeler, 2010) and we performed all data analysis in R v.3.0.0 (R Development Core Team, 2013).

Are the same types of pairwise interactions responsible for changes in above-ground biomass production in native and nonnative communities?

We used hierarchical linear DI models that allowed us to test alternative hypotheses about the contribution of individual species and interactions of species pairs to changes in productivity in plant communities (Table 2; Connolly et al., 2013; Kirwan et al., 2009). By comparing the goodness-of-fit of models (using the corrected Akaike information criterion procedure, AICc), we can assess which species or pairwise species interactions are most important for explaining biodiversity–productivity patterns in native and nonnative communities (Kirwan et al., 2009). The models were as follows:

| Null model (M0) | $y = \beta + \epsilon$ |
| Species identity model (M1) | $y = \sum_{i=1}^{4} P_i + \epsilon$ |
| Average pairwise interactions model (M2) | $y = \sum_{i=1}^{4} P_i + \delta_{\text{avg}} \sum_{i<j} P_i P_j + \epsilon$ |
| All pairwise interactions model (M3) | $y = \sum_{i=1}^{4} P_i + \sum_{i<j} \delta_i (P_i P_j) + \epsilon$ |
| Additive species-specific pairwise interactions model (M4) | $y = \sum_{i=1}^{4} P_i + \lambda_i (P_i(1-P_i)) + \epsilon$ |
| Species functional group model (M5) | $y = \sum_{i=1}^{4} P_i + \delta_{\text{NF}} \sum_{i<j} (P_i P_j) + \delta_{\text{NF}} \sum_{i<j} (P_i P_j) + \epsilon$ |
| Reference model (MR) | $y = \lambda_{\text{m}} + \epsilon$ |

The identity effect of each species $i$ ($\beta_i P_i$) is a function of the production of each species in monoculture ($P_i$) weighted by its proportion ($P_i$) in the community, and interactions between two species ($i$ and $j$) are modeled as the product of their proportions ($P_i P_j$). The species identity model (M1) tests how the effects of each species individually, but not its interactions, contribute to changes in productivity. Each successive model tests how the addition of differing pairwise interactions improves model fit for predicting changes in productivity through the addition of species interaction coefficient estimates. The interaction coefficients estimate the following: the average interaction effect across all species pairs ($\delta_{\text{avg}}$; model 2), the individual interaction effect for each species pair ($\delta_{ij}$; model 3), or the contribution of a single species in an interaction, independently of its neighbor’s identity ($\lambda_i$; model 4). Because nitrogen-fixing species can alter plant interactions (Kuebbing & Núñez, 2015), we include a functional group model that tested how interactions between species pairs that included a nitrogen-fixing species ($\delta_{\text{NF}}$; model 5) or did not contain a nitrogen-fixing species ($\delta_{\text{NF}}$; model 5) influenced community productivity. Finally, we include a reference model that estimates the contribution of each plant community individually ($\lambda_{\text{m}}$; model R), which accounts for all structural effects arising from community composition and serves as a baseline for testing how well other models capture these structural effects (Connolly et al., 2013). We compared DI models (Kirwan et al., 2009) to updated generalized DI (GDI) models, which can improve DI model performance through the inclusion of a coefficient ($\theta$) that allows for variation in the total contribution of species pairwise interactions (Connolly et al., 2013). When $\theta = 1$, results from GDI models are equivalent to DI models. Because we found no indication that $\theta \neq 1$, or that GDI models provided a better fit to our data (log-likelihood test, $P > 0.05$; Connolly et al., 2013), we present results from DI models. We compared the performance of models with the corrected AICc, and

<table>
<thead>
<tr>
<th>Diversity-interaction hypothesis</th>
<th>Model comparison</th>
<th>$\Delta$AICc native</th>
<th>$\Delta$AICc nonnative</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species differ in their individual monoculture performance</td>
<td>M1 to M0</td>
<td>-208.89</td>
<td>-101.56</td>
</tr>
<tr>
<td>There is a diversity effect on ecosystem functioning</td>
<td>M2 to M1</td>
<td>-25.96</td>
<td>-34.63</td>
</tr>
<tr>
<td>Separate pairwise interactions differ</td>
<td>M3 to M2</td>
<td>-11.94</td>
<td>3.04</td>
</tr>
<tr>
<td>Species contribute equally in pairwise interactions, regardless of neighbor identity</td>
<td>M4 to M3</td>
<td>-0.31</td>
<td>-2.14</td>
</tr>
<tr>
<td>Patterns in species interactions can be described by whether the species pair contains a nitrogen-fixing species</td>
<td>M5 to M3</td>
<td>-4.23</td>
<td>-1.78</td>
</tr>
</tbody>
</table>

We compared models using corrected Akaike information criteria (AICc), and AICc differences in bold support acceptance of a diversity-interaction hypothesis.
differences in AICc (> 2) indicated that the model was a better fit to the data than other models (Burnham & Anderson, 2002). We used R statistical software v.3.0.0 (R Development Core Team, 2013) for all modeling and model comparisons.

Results

How do changes in species richness affect above- and below-ground biomass production in native and nonnative plant communities?

Native and nonnative communities differed in their overall biomass allocation patterns. Nonnative communities had 52% higher ratios of above-ground to below-ground biomass than did native communities (nonnative, 3.3 ± 0.15; native, 2.15 ± 0.20; Supporting Information Table S1). Across all potted communities, nonnative communities produced 27% more above-ground biomass and 29% less below-ground biomass than did native communities (Fig. 1a,c; Table S1). We found transgressive overyielding (i.e. biomass in mixtures was greater than that of the most productive monoculture) for below-ground biomass only in the native Lespedeza-Sorghastrum plant community, which had 18% more below-ground biomass (0.40 ± 0.04 g cm⁻²) than the most productive native monoculture (L. capitata, 0.34 ± 0.03 g cm⁻²; Table S2).

Both native and nonnative communities showed a positive diversity–productivity relationship for above-ground biomass production, but only native communities had a positive diversity–productivity relationship for below-ground biomass production (significant origin × richness interaction; Table S1). Native communities with four species had 51% more above-ground and 67% more below-ground biomass than monoculture native communities (Fig. 1b), whereas nonnative communities with four species had only 34% more above-ground biomass than did monoculture nonnative communities (Fig. 1d).

Community composition, which accounted for phylogenetic pairing of species within communities, always significantly predicted community response to changes in species richness (Table S1). The variation in above- and below-ground biomass production in monoculture and mixture pots varied widely among species pairs (Fig. S1). The nitrogen-fixing Fabaceae species, L. cuneata (nonnative) and L. capitata (native), typified the differences in behavior of closely related native and nonnative species. While both species produced the highest monoculture biomass in terms of above-ground (L. cuneata, 0.79 ± 0.05 g cm⁻²; L. capitata, 0.52 ± 0.02 g cm⁻²; Table S2) and below-ground biomass (L. cuneata, 0.35 ± 0.02 g cm⁻²; L. capitata, 0.34 ± 0.03 g cm⁻²; Table S2), they had opposite responses in mixed-species pots. Polyculture pots containing Fabaceae species (Fig. S1) had greater differences in above-ground biomass between native and nonnative plant species than polyculture pots lacking Fabaceae species (Fig. S1), which shows that the nonnative Lespedeza was primarily responsible for the overyielding behavior of nonnative plant communities in mixture and thus the positive selection and net biodiversity effect (Table S3).

Is the same mechanism (i.e. complementarity or selection effect) responsible for the net biodiversity effect in native and nonnative communities?

Native and nonnative communities differed in the sign and magnitude of the selection effect (Fig. 2). On average native communities had a negative selection effect (−0.22 ± 0.09) and nonnative communities had a positive selection effect (0.37 ± 0.09), and these differed significantly by community origin (P < 0.05 for origin and origin × richness; Fig. 2). This difference arose because native species with lower monoculture yields and nonnative species with higher monoculture yields tended to overyield in mixture (Fig. 2; Table S2).

Native communities had slightly higher positive complementarity effects (1.47 ± 0.14) than nonnative communities (0.83 ± 0.10), but this difference was not significant. Both native and nonnative communities had a positive net biodiversity effect (native, 1.24 ± 0.12; nonnative, 1.20 ± 0.14) that did not differ.
across richness treatments or by community origin. The direction and magnitude of all biodiversity effects were similar across two-, three-, and four-species mixtures ($P > 0.05$ for richness terms; Fig. 2).

How do the diversity–productivity effect and its associated mechanisms (i.e. complementarity or selection effect) limit woody seedling establishment in native and nonnative plant communities?

Native and nonnative communities differed in seedling recruitment and growth ($P < 0.05$, community origin; Fig. 3; Table S1). The number of seedlings was 61% lower in nonnative pots than in native pots ($P < 0.05$ community origin; Fig. 3; Table S1). The average seedling biomass in nonnative communities was 46% lower than that in native communities.

The average selection effect for a plant community was significantly related to woody seedling establishment in native and nonnative plant communities.

Are the same types of pairwise interactions responsible for changes in above-ground biomass production in native and nonnative communities?

Different types of pairwise interactions best explained the positive diversity–productivity relationships in native and nonnative communities (Table 2). In native communities, we found no indication that pairwise interactions between native species differed (e.g. a single interaction coefficient adequately described all native pairwise interactions, M2 and M3 comparison; Table 2), suggesting that interspecific interactions among all four native species had equivalent effects on the diversity–productivity relationship. Instead, patterns in species interactions were best described by whether or not the species pair contained a nitrogen-fixing species (M3 and M5 comparison, Table 2). Full model results can be found in Methods S1 and S2.

**Discussion**

Native and nonnative communities did not respond in the same way to changes in species richness. Although both native and nonnative communities had positive diversity–productivity relationships, the mechanism driving the increased productivity differed: there was a positive selection effect in nonnative communities and a positive complementarity effect in native communities. Seedling establishment and growth were stunted in nonnative communities, and this was attributable to a strong positive selection effect. Finally, while interspecific interactions contributed to the positive diversity–productivity relationship,
the specific types of interactions differed between native and non-native communities.

Native plant communities diverged widely from nonnative plant communities in their biomass allocation strategy. Native communities produced more below-ground biomass and less above-ground biomass than did nonnative communities. Comparisons between native and nonnative species typically show that nonnatives produce more above-ground biomass than do native species (Ehrenfeld, 2010; Vilà et al., 2011). To our knowledge, no research has extensively reviewed the differences between native and nonnative below-ground biomass production or above-ground to below-ground biomass ratios (i.e. root: shoot ratios) across ecosystem types, although studies of grassland species have found results similar to those reported here (Wilsey & Polley, 2006; but see Isbell & Wilsey, 2011a).

Positive selection effects are important mechanisms for explaining the dominance of nonnative species in invaded communities (Wilsey et al., 2009; Vilà et al., 2011) and were responsible for the increase in productivity in the experimental nonnative communities. We found that the positive selection effect on nonnative communities was significantly and oppositely related to the response of that plant community to seedling establishment. Previous studies show negative relationships between selection effects and community richness (Wilsey et al., 2009) and between selection effects and community invasibility (Fargione & Tilman, 2005). Positive selection effects signal that productive monoculture species are overyielding in species mixture. Overyielding of the nonnative *Lespedeza* caused the positive selection effect in nonnative communities, while the underyielding of the native *Lespedeza* influenced the negative selection effect in native communities. Nonnative *Lespedeza* is known to suppress woody seedling establishment through shading (Brandon et al., 2004), whereas native *Lespedeza* is associated with increased yielding of many grassland species (Hille Ris Lambers et al., 2004). The different impacts of the dominant congenic legumes in our study align with previous studies finding differences in growth and impact of native and nonnative congeners (Morrison & Mauck, 2007; Feng & Fu, 2008; Burghardt & Tallamy, 2013).

The native and nonnative *Lespedeza* species did not have parallel functions in their respective communities. DI models showed that interspecific interactions between nonnative species pairs containing *Lespedeza* were significantly more important for explaining above-ground biomass production than interactions between species pairs that did not contain *Lespedeza*. By contrast, in native communities, we found that pairwise interactions between species were best described by a single interaction term, indicating that interactions among all native species were equally important for promoting the positive diversity–productivity relationship, regardless of the presence of the native *Lespedeza*. The variation in interaction influence between the native and nonnative *Lespedeza* species may be because they differ in nitrogen-fixing ability and subsequent influences on soil nitrogen and that, for these species, phylogeny is a poor proxy for trait similarity. A second potential cause for the difference in interspecific interactions for the congeners could arise from the history of interactions among species within each plant community. The nonnative *Lespedeza* was the only species whose native range did not overlap with any other species in the nonnative community; thus, the interspecific interactions between the Asian *Lespedeza* and the three European species it grew alongside could be considered to be novel. Novel interactions between native and nonnative species are invoked as explanations of why nonnative species can outcompete or outperform native species (e.g. missed mutualism, enemy escape, and novel weapons hypotheses; Catford et al., 2009). Novel interactions between nonnative species could be equally important for understanding dynamics in co-invaded communities.

Differences in the yielding behavior between one species pair, native and nonnative *Lespedeza*, drove differences in the mechanism responsible for native and nonnative community productivity patterns and potentially seedling establishment. One might question whether our results are widely applicable to other plant communities. We think they are relevant to other invaded plant communities for two reasons. First, many plant communities contain two distinct categories of nonnative species: ‘dominant’ or ‘strong’ nonnatives, as determined by the relative biomass of the species within the community, such as the nonnative *Lespedeza*, and ‘subdominant’ or ‘weak’ nonnatives (Ortega & Pearson, 2005; Peltzer et al., 2009). We argue that there is a high likelihood that any community containing a dominant nonnative species would overyield in mixture and cause a positive selection effect (Wilsey et al., 2009; Vilà et al., 2011), as in the behavior of the nonnative *Lespedeza* in our communities. Second, we constrained our selection of nonnative species to those that had closely related native species in old-field communities. This criterion excluded selection of seven nonnative species, including four
nonnatives recorded as having impacts on native plant communities in Tennessee (TN EPPC, 2009), which represented six unique plant families. Theory and experimental evidence indicates that nonnative species that are less closely related to native species will be more likely to invade and cause impacts (Strauss et al., 2006; Funk et al., 2008; but see Dietz et al., 2008). Thus our experiment, which excluded these phylogenetically unrelated nonnatives, was a conservative test of the differences between native and nonnative communities.

Our work joins a growing body of evidence indicating that species origin is a relevant biological trait when considering the ecological impact (or potential impact) of a species (Simberloff et al., 2012; Burghardt & Tallamy, 2013; Paolucci et al., 2013; Hassan & Ricciardi, 2014). Furthermore, the origin of species within a community should be considered in studies examining links between biodiversity and ecosystem function (Wilsey et al., 2009; Isbell & Wilsey, 2011a). Proponents of ignoring species origin as a relevant biological characteristic argue that we should focus only on ‘problematic’ species, based on their singular community impact (Davis et al., 2011). In the experiments described here, we nearly always found significant interactions between community origin and community composition; thus, our results suggest that origin is important for considering how groups of nonnative species interact with one another. The consideration of species origin and the evolutionary history of co-occurring nonnatives is important if we are to understand and predict the ecosystem response of communities with new combinations of native and nonnative species.

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