

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

Sara E. Kuebbing<sup>1,4</sup>, Aimée T. Classen<sup>1,2</sup>, Nathan J. Sanders<sup>1,3</sup> and Daniel Simberloff<sup>1</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996-1610, USA; <sup>2</sup>Natural History Museum of Denmark, University of Copenhagen, DK-2100, Copenhagen, Denmark; <sup>3</sup>Center for Macroecology, Evolution and Climate, University of Copenhagen, DK-2100, Copenhagen, Denmark; <sup>4</sup> Present address: Yale School of Forestry and Environmental Studies, Yale University, 195 Prospect Street, New Haven, CT 06511, USA

## 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.

Author for correspondence:  
Sara E. Kuebbing  
Tel: +1 203 432 5100  
Email: sara.kuebbing@yale.edu

Received: 4 March 2015  
Accepted: 27 April 2015

*New Phytologist* (2015) **208**: 727–735  
doi: 10.1111/nph.13488

**Key words:** below-ground productivity, biodiversity–ecosystem function, co-occurring nonnatives, invasion impact, old field, selection effect.

## 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 overyields 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 overcome 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: *Lespedeza capitata* *Sorghastrum nutans* *Pycnanthemum virginianum* and *Lespedeza 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 × 4 grid, with random species placement in mixed species pots. We planted a total of 560 pots (14 total species combinations × two community types × 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

Family	Native species	Functional group	Nonnative species	Functional group
Asteraceae	<i>Achillea millefolium</i> L.	Forb	<i>Leucanthemum vulgare</i> Lam.	Forb
Fabaceae	<i>Lespedeza capitata</i> Michx. Hornem.	Nitrogen- fixer	<i>Lespedeza cuneata</i> (Dum. Cours.) G. Don	Nitrogen- fixer
Lamiaceae	<i>Pycnanthemum virginianum</i> Schrad.	Forb	<i>Prunella vulgaris</i> L. var. <i>vulgaris</i>	Forb
Poaceae	<i>Sorghastrum nutans</i> (L.) Nash	Graminoid	<i>Phleum pratense</i> L.	Graminoid

regime) and planted 1-wk-old seedlings in 2 l 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<sup>-2</sup> (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:  $SE = N \times \text{cov}(\Delta RY, M)$  and  $CE = N \times \overline{\Delta RY} \times \overline{M}$ , where  $N$  is the species richness,  $\Delta RY$  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,  $\overline{\Delta RY}$  is the mean change in relative yield for each species mixture, and  $\overline{M}$  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., *Lonicera maaackii* (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 lmpm (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)	$y = \beta + \varepsilon$
Species identity model (M1)	$y = \sum_{i=1}^4 \beta_i P_i + \varepsilon$
Average pairwise interactions model (M2)	$y = \sum_{i=1}^4 \beta_i P_i + \delta_{\text{avg}} \sum_{i<j}^4 P_i P_j + \varepsilon$
All pairwise interactions model (M3)	$y = \sum_{i=1}^4 \beta_i P_i + \sum_{i<j}^4 \delta_{ij} (P_i P_j) + \varepsilon$
Additive species-specific pairwise interactions model (M4)	$y = \sum_{i=1}^4 \beta_i P_i + \sum_{i=1}^4 \lambda_i (P_i (1 - P_i)) + \varepsilon$
Species functional group model (M5)	$y = \sum_{i=1}^4 \beta_i P_i + \delta_{\text{NF}} \sum_{i<j}^4 (P_i P_j) + \delta_{\text{NMF}} \sum_{i<j}^4 (P_i P_j) + \varepsilon$
Reference model (MR)	$y = \lambda_m + \varepsilon$

**Table 2** Comparisons between hierarchical diversity–interaction models test specific hypotheses about how individual species and pairwise interactions between species contribute to changes in above-ground productivity in native and nonnative plant communities

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

We compared models using corrected Akaike information criteria (AICc), and AICc differences in bold support acceptance of a diversity–interaction hypothesis.

The identity effect of each species  $i$  ( $\beta_i P_i$ ) is a function of the production of each species in monoculture ( $\beta_i$ ) 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 & Nuñez, 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 ( $\delta_{\text{NMF}}$ ; model 5) influenced community productivity. Finally, we include a reference model that estimates the contribution of each plant community individually ( $\lambda_m$ ; 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



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,  $3.3 \pm 0.15$  (SE); native,  $2.15 \pm 0.20$ ; 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 ( $0.40 \pm 0.04 \text{ g cm}^{-2}$ ) than the most productive native monoculture (*L. capitata*,  $0.34 \pm 0.03 \text{ g cm}^{-2}$ ; 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  $\times$  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).

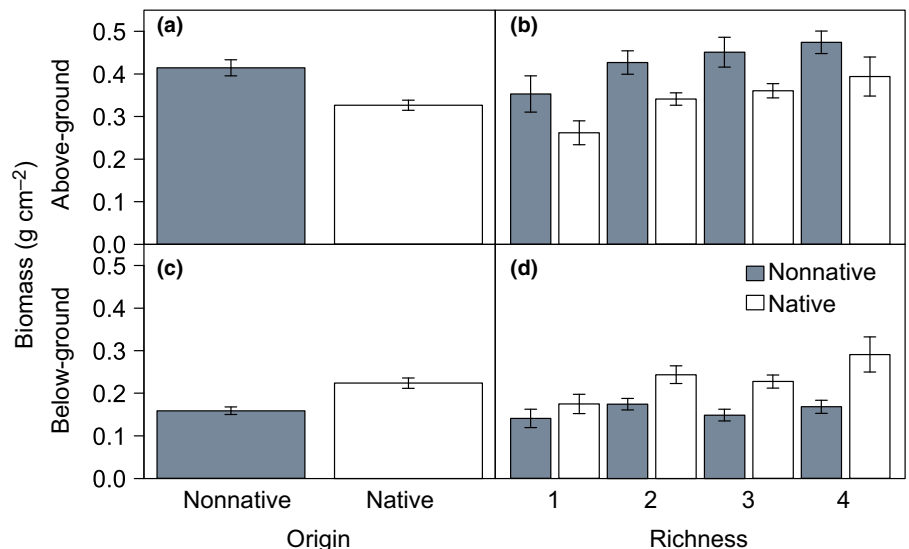
Community composition, which accounted for phylogenetic pairing of species within communities, always significantly

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*,  $0.79 \pm 0.05 \text{ g cm}^{-2}$ ; *L. capitata*,  $0.52 \pm 0.02 \text{ g cm}^{-2}$ ; Table S2) and below-ground biomass (*L. cuneata*,  $0.35 \pm 0.02 \text{ g cm}^{-2}$ ; *L. capitata*,  $0.34 \pm 0.03 \text{ g cm}^{-2}$ ; 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).

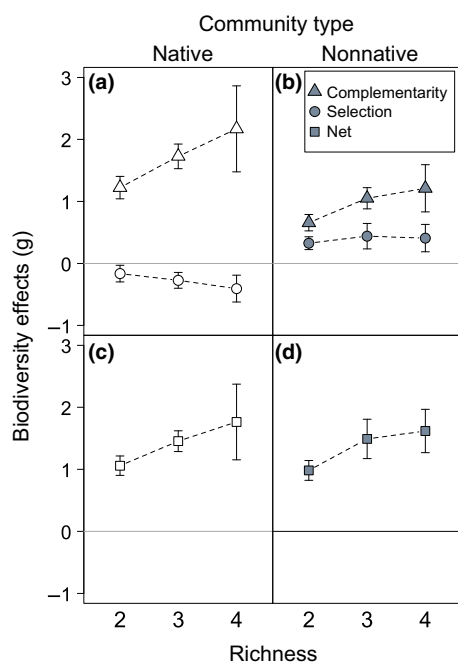
Is the same mechanism (i.e. complementarity or selection effect) responsible for the net biodiversity effect in native and nonnative communities?

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 ( $-0.22 \pm 0.09$ ) and nonnative communities had a positive selection effect ( $0.37 \pm 0.09$ ), and these differed significantly by community origin ( $P < 0.05$  for origin and origin  $\times$  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 ( $1.47 \pm 0.14$ ) than nonnative communities ( $0.83 \pm 0.10$ ), but this difference was not significant. Both native and nonnative communities had a positive net biodiversity effect (native,  $1.24 \pm 0.12$ ; nonnative,  $1.20 \pm 0.14$ ) that did not differ



**Fig. 1** In a test of differences in the biodiversity–productivity relationship, native and nonnative plant communities differed in their total above-ground (a) and below-ground (c) biomass production. These patterns were consistent across pot richness levels, where pots with higher plant species richness also had higher above-ground (b) and below-ground (d) biomass. Here, biomass values represent the dry plant mass per soil surface area ( $\text{g cm}^{-2}$ ) and richness represents the number of plant species in each potted community. Error bars represent  $\pm$  SE of the mean.



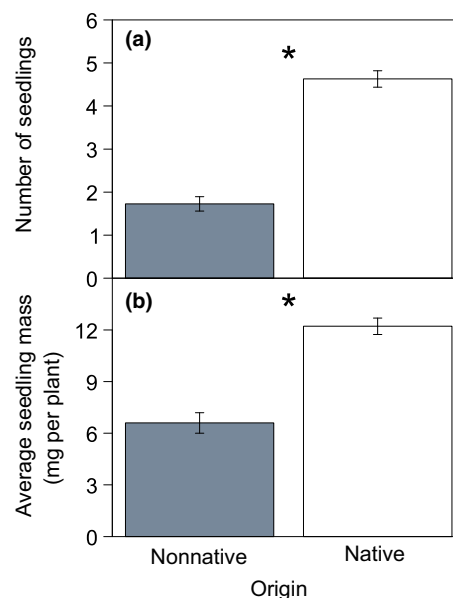
**Fig. 2** Phylogenetically paired native and nonnative plant communities diverged in the magnitude and sign of selection and complementarity effects (a, b), but had positive biodiversity–productivity relationships as indicated by the positive net biodiversity effect for both community types (c, d). Positive selection effects indicate that high biomass species were overyielding in mixture, while positive complementarity effects indicate that low biomass species were overyielding in mixture. Error bars represent  $\pm$  SE of the mean.

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 and growth in native and nonnative plant communities, although the direction of this relationship differed by community origin. Increasingly positive selection effects were related to decreasing number of established seedlings in nonnative plant communities (seedling number,  $r = -0.69$ ,  $P = 0.03$ ; seedling mass,  $r = -0.57$ ,  $P = 0.08$ ; Fig. 4) but to an increasing number of established seedlings and total seedling mass in native plant communities (seedling number,  $r = 0.71$ ,  $P = 0.02$ ; seedling mass,  $r = 0.75$ ,  $P = 0.01$ ; Fig. 4).



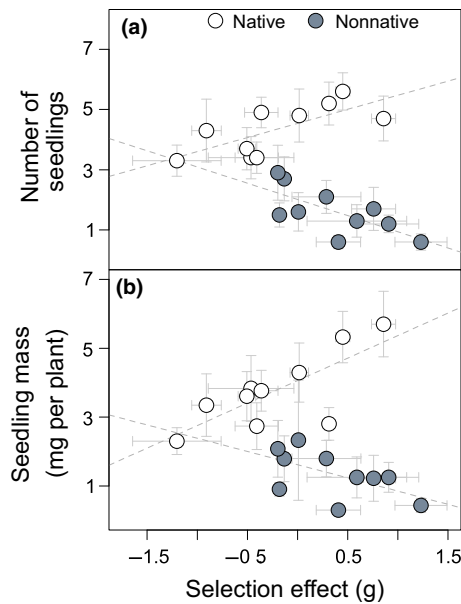
**Fig. 3** Plant community origin altered the establishment (a) and average biomass (b) of introduced seedlings in a glasshouse experiment. Error bars represent  $\pm$  SE of the mean and asterisks (\*) represent significance difference at  $P < 0.05$ .

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. However, in nonnative communities, we found that pairwise interactions among species pairs did not contribute equally to the positive 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,



**Fig. 4** Plant community selection effects were related to the number of plant seedlings established (a) and the average seedling biomass (b) for native and nonnative plant communities, although the direction of the relationships differed by community type. Selection effect measures the overyielding behavior of species in mixture, where a positive selection effect indicates that the most productive species in monoculture is overyielding in mixture. Error bars represent  $\pm$  SE of the mean.

the specific types of interactions differed between native and nonnative 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 in 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 congeneric 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 Diez *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.

## Acknowledgements

Lara Souza and Martin Nuñez provided valuable suggestions on our experimental design and helpful comments on the manuscript. Jaime Call, Michael Dehart, Josh Galperin, Katie Stuble, and Rafael Zenni assisted with field and glasshouse work. Finally, we give a special thanks to Dr Ken McFarland and his staff for their indispensable help in the glasshouse. S.E.K. was supported through the University of Tennessee Yates Dissertation Writing Fellowship and the Department of Ecology and Evolutionary Biology.

## References

- Anderson MJ. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 626–639.
- Bessler H, Temperton VM, Roscher C, Buchmann N, Schmid B, Schulze E, Weisser WW, Engels C. 2009. Aboveground overyielding in grassland mixtures is associated with reduced biomass partitioning to belowground organs. *Ecology* **90**: 1520–1530.
- Brandon AL, Gibson DJ, Middleton BA. 2004. Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. *Biological Invasions* **6**: 483–493.
- Burghardt KT, Tallamy DW. 2013. Plant origin asymmetrically impacts feeding guilds and life stages driving community structure of herbivorous arthropods. *Diversity and Distributions* **19**: 1553–1565.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY, USA: Springer.
- Catford JA, Jansson R, Nilsson C. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* **15**: 22–40.
- Catford JA, Vesk PA, Richardson DM, Pyšek P. 2012. Quantifying levels of biological invasion: towards the objective classification of invaded and invulnerable ecosystems. *Global Change Biology* **18**: 44–62.
- Chytrý M, Maskell L, Pino J, Pyšek P, Vilà M, Font X, Smart SM. 2008. Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology* **45**: 448–458.
- Connolly J, Bell T, Bolger T, Brophy C, Carnus T, Finn JA, Kirwan L, Isbell F, Levine J, Lüscher A *et al.* 2013. An improved model to predict the effects of changing biodiversity levels on ecosystem function. *Journal of Ecology* **101**: 344–355.
- Cook-Patton SC, Agrawal AA. 2014. Exotic plants contribute positively to biodiversity functions but reduce native seed production and arthropod richness. *Ecology* **95**: 1642–1650.
- Cramer VA, Hobbs RJ, Standish RJ. 2008. What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution* **23**: 104–112.
- Davis M, Chew MK, Hobbs RJ, Lugo AE, Ewel JJ, Vermeij GJ, Brown JH, Rosenzweig ML, Gardener MR, Carroll SP *et al.* 2011. Don't judge species on their origins. *Nature* **474**: 153–154.
- 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.
- Ehrenfeld JG. 2010. Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics* **41**: 59–80.
- Fargione JE, Tilman D. 2005. Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters* **8**: 604–611.
- Feng YL, Fu GL. 2008. Nitrogen allocation, partitioning and use efficiency in three invasive plant species in comparison with their native congeners. *Biological Invasions* **10**: 891–902.
- Funk JL, Cleland EE, Suding KN, Zavaleta ES. 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology & Evolution* **23**: 695–703.
- Grime JP. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* **86**: 902–910.
- Hassan A, Ricciardi A. 2014. Are non-native species more likely to become pests? Influence of biogeographic origin on the impacts of freshwater organisms. *Frontiers in Ecology and the Environment* **12**: 218–223.
- Hille Ris Lambers J, Harpole WS, Tilman D, Knops J, Reich PB. 2004. Mechanisms responsible for the positive diversity–productivity relationship in Minnesota grasslands. *Ecology Letters* **7**: 661–668.
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S *et al.* 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**: 3–35.
- Isbell FI, Wilsey BJ. 2011a. Increasing native, but not exotic, biodiversity increases aboveground productivity in ungrazed and intensely grazed grasslands. *Oecologia* **165**: 771–781.
- Isbell FI, Wilsey BJ. 2011b. Rapid biodiversity declines in both ungrazed and intensely grazed exotic grasslands. *Plant Ecology* **212**: 1663–1674.
- Jackson M. 2015. Interactions among multiple invasive animals. *Ecology*. doi:10.1890/15-0171.1.
- Kirwan L, Connolly J, Finn J, Brophy C, Lüscher A, Nyfeler D, Sebastia M. 2009. Diversity–interaction modeling: estimating contributions of species identities and interactions to ecosystem function. *Ecology* **90**: 2032–2038.
- Kuebbing SE, Nuñez MA. 2015. Negative, neutral, and positive interactions among nonnative plants: patterns, processes, and management implications. *Global Change Biology* **21**: 926–934.
- Kuebbing SE, Nuñez MA, Simberloff D. 2013. Current mismatch between research and conservation efforts: the need to study co-occurring invasive plant species. *Biological Conservation* **160**: 121–129.
- Kuebbing SE, Souza L, Sanders NJ. 2014. Effects of co-occurring non-native invasive plant species on old-field succession. *Forest Ecology and Management* **324**: 196–204.



- Kulmatiski A. 2006. Exotic plants establish persistent communities. *Plant Ecology* 187: 261–275.
- Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412: 72–76.
- Martin LM, Polley HW, Daneshgar PP, Harris MA, Wilsey BJ. 2014. Biodiversity, photosynthetic mode, and ecosystem services differ between native and novel ecosystems. *Oecologia* 175: 687–697.
- Morrison JA, Mauck K. 2007. Experimental field comparison of native and non-native maple seedlings: natural enemies, ecophysiology, growth and survival. *Journal of Ecology* 95: 1036–1049.
- Ortega YK, Pearson DE. 2005. Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. *Ecological Applications* 15: 651–661.
- Paolucci EM, MacIsaac HJ, Ricciardi A. 2013. Origin matters: alien consumers inflict greater damage on prey populations than do native consumers. *Diversity and Distributions* 19: 988–995.
- Peltzer DA, Bellingham PJ, Kurokawa H, Walker LR, Wardle DA, Yeates GW. 2009. Punching above their weight: low-biomass non-native plant species alter soil properties during primary succession. *Oikos* 118: 1001–1014.
- Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology* 18: 1725–1737.
- R Development Core Team. 2013. *R: a language and environment for statistical computing, v.3.0.0*. Vienna, Austria: R Foundation for Statistical Computing.
- Richardson DM, Pyšek P, Carlton JT. 2011. Essential concepts and terminology in invasion ecology. In: Richardson DM, ed. *Fifty years of invasive ecology: the legacy of Charles Elton*. Chichester, UK: Wiley-Blackwell, 409–420.
- Sanders NJ, Weltzin JF, Crutsinger GM, Fitzpatrick MC, Nuñez MA, Oswalt CM, Lane KE. 2007. Insects mediate the effects of propagule supply and resource availability on a plant invasion. *Ecology* 88: 2383–2391.
- Simberloff D, Souza L, Nuñez MA, Barrios-García MN, Bunn W. 2012. The natives are restless, but not often and mostly when disturbed. *Ecology* 93: 598–607.
- Souza L, Bunn WA, Simberloff D, Lawton RM, Sanders NJ. 2011a. Biotic and abiotic influences on native and exotic richness relationship across spatial scales: favourable environments for native species are highly invulnerable. *Functional Ecology* 25: 1106–1112.
- Souza L, Bunn WA, Weltzin JF, Sanders NJ. 2011b. Similar biotic factors affect early establishment and abundance of an invasive plant species across spatial scales. *Biological Invasions* 13: 255–267.
- Strauss SY, Webb CO, Salamin N. 2006. Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences, USA* 103: 5841–5845.
- Strayer DL. 2012. Eight questions about invasions and ecosystem functioning. *Ecology Letters* 15: 1199–1210.
- Tennessee Exotic Pest Plant Council (TN EPPC). 2009. *Invasive exotic pest plants in Tennessee*. [WWW document] URL [http://http://www.tneppc.org/invasive\\_plants](http://http://www.tneppc.org/invasive_plants) [accessed 5 February 2015].
- Tilman D, Wedin D, Knops J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379: 718–720.
- Tylianakis JM, Didham RK, Bascompte J, Wardle DA. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11: 1351–1363.
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708.
- Wardle DA, Bardgett RD, Callaway RM, Van der Putten WH. 2011. Terrestrial ecosystem responses to species gains and losses. *Science* 332: 1273–1277.
- Wheeler B. 2010. *lmPerm: permutation tests for linear models*. R package version 1.1-0. Vienna, Austria: R Foundation for Statistical Computing.
- Wilsey BJ, Daneshgar PP, Polley HW. 2011. Biodiversity, phenology and temporal niche differences between native- and novel exotic-dominated grasslands. *Perspectives in Plant Ecology, Evolution, and Systematics* 13: 265–276.
- Wilsey BJ, Potvin C. 2000. Biodiversity and ecosystem functioning: importance of species evenness in an old field. *Ecology* 81: 887–892.
- Wilsey BJ, Teaschner TB, Daneshgar PP, Isbell FI, Polley HW. 2009. Biodiversity maintenance mechanisms differ between native and novel exotic-dominated communities. *Ecology Letters* 12: 432–442.
- Wofford BE, Kral R. 1993. *Checklist of the vascular plants of Tennessee*. Fort Worth, TX, USA: BRIT Press.

## Supporting Information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Absolute differences in above- and below-ground biomass production for potted plant communities.

**Table S1** Full ANOVA table from permutational ANOVAS

**Table S2** Average above- and below-ground biomass for phylogenetically paired native and nonnative communities

**Table S3** Aboveground biomass of eight old-field species grown in monoculture and mixtures in potted plant communities

**Methods S1** Full results for diversity-interaction models comparing influence of interspecific interactions on diversity–productivity patterns in potted plant communities.

**Methods S2** R-Code for permutational ANOVA models and diversity-interaction models.

Please note: Wiley Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.