LETTER

Species pools, community completeness and invasion: disentangling diversity effects on the establishment of native and alien species

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Abstract

Invasion should decline with species richness, yet the relationship is inconsistent. Species richness, however, is a product of species pool size and biotic filtering. Invasion may increase with richness if large species pools represent weaker environmental filters. Measuring species pool size and the proportion realised locally (completeness) may clarify diversity-invasion relationships by separating environmental and biotic effects, especially if species' life-history stage and origin are accounted for. To test these relationships, we added seeds and transplants of 15 native and alien species into 29 grasslands. Species pool size and completeness explained more variation in invasion than richness alone. Although results varied between native and alien species, seed establishment and biotic resistance to transplants increased with species pool size, whereas transplant growth and biotic resistance to seeds increased with completeness. Consequently, species pools and completeness represent multiple independent processes affecting invasion; accounting for these processes improves our understanding of invasion.

Keywords

Alpha diversity, biotic resistance, competition, dark diversity, disturbance, exotic species, gamma diversity, invasibility, regional processes, structural equation modelling.

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INTRODUCTION

An enduring hypothesis in ecology is that species rich communities should be less susceptible to invasion (Elton 1958); fewer available resources and fewer unoccupied niches should result in more intense competition between invaders and the resident community (Tilman 2004; MacDougall *et al.* 2009). However, the evidence has been decidedly mixed (Levine *et al.* 2004; Fridley *et al.* 2007). One potential reason for these mixed relationships is that local richness is determined by multiple processes, including both the number of species found within the region capable of colonising that site (the site-specific species pool) and the effect of local processes (e.g. biotic interactions) on that species pool (Cornell & Harrison 2014; Laliberté *et al.* 2014; Pärtel *et al.* 2016). These divergent influences may confound any relationship between species richness and invasion (Shea & Chesson 2002).

Although evolutionary history, climate and dispersal may determine the species found in the region, local environmental factors determine which species within the region form the site-specific species pool (hereafter species pool; Cornell & Harrison 2014; Pärtel *et al.* 2016). This species pool then constrains local richness by determining the number of species that can colonise the site (Fig. 1). Large species pools result from benign and heterogeneous conditions, as there are fewer abiotic limitations to establishment and a greater diversity of

niches; however, such conditions are also suitable for a greater number of invading species (Fig. 1; Richardson *et al.* 2012). Thus, comparisons among sites varying in species pool size can result in positive richness-invasion relationships irrespective of any biotic resistance (Levine 2000; Shea & Chesson 2002; Fridley *et al.* 2007).

As species richness and invasion success both increase with species pool size, isolating the biotic effects of richness on invasion requires making richness relative to the species pool (Shea & Chesson 2002; Perelman *et al.* 2007). Community completeness (Pärtel *et al.* 2013) measures observed richness relative to the number of species from the species pool absent from the site (dark diversity; Pärtel *et al.* 2011). Consequently, completeness represents the effects of local biotic interactions on the species pool and is analogous to community saturation (Cornell & Lawton 1992). By comparison, species pool size represents potential species richness and is calculated as the sum of observed and dark diversity, making the two measures independent. Consequently, biotic resistance should increase with completeness (Morton & Law 1997; Moore *et al.* 2001; Fukami 2004) independent of species pool size (Fig. 1; but see Herben 2005). Moreover, by isolating the effects of species pool size, and hence the effects of environmental conditions on richness, we can isolate the effects of the local community on invasion from any confounding influence of the environment. However, information on the environment may still

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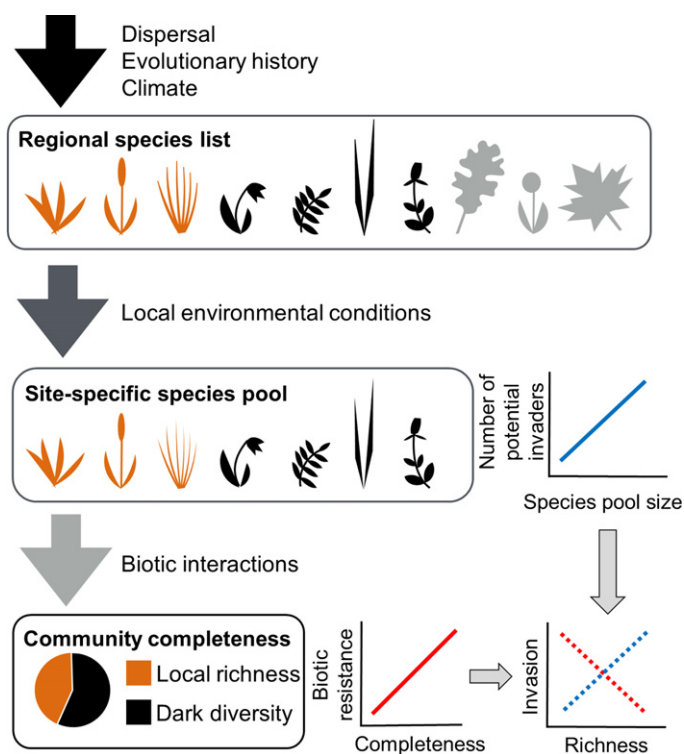*Correspondence: E-mail: jon.a.bennett@gmail.com*

Figure 1 The hypothesised relationships between the different aspects of plant diversity and invasion. The size of the site-specific species pool is determined by environmental filters and is representative of the number of potential niches and thus potential invaders. Local species richness is determined both by species pool size and the action of biotic filters. As such, its relationship with invasion can be positive or negative depending on the relative influence of the species pool and biotic filters. Community completeness, a standardised measure of local richness relative to the number of species from the site-specific pool that were excluded (dark diversity) should increase biotic resistance (i.e. reduces invasion). Observed species are shown in orange, biotically excluded species (dark diversity) in black, and environmentally excluded species in grey.

complement species pool size and completeness as there is no definitive answer as to which environmental factors determine species pools, species richness or invasion success, despite recent progress (Laliberté *et al.* 2014; Grace *et al.* 2016; Sardans *et al.* 2016).

For plants, the factors affecting invasion are likely to change across life stages, as regeneration and adult niches are frequently distinct (Grubb 1977). Both environmental and biotic filters can limit the establishment and growth of invaders (Foster *et al.* 2004; Levine *et al.* 2004; Richardson *et al.* 2012); however, environmental suitability is predicted to be more limiting to establishment from seed, whereas competition more limits growth (Theoharides & Dukes 2007). As such, biotic resistance associated with species richness or completeness may affect invader growth more than establishment (Levine *et al.* 2004); although, other biotic processes not directly related to local plant diversity (e.g. herbivory) may still suppress seed establishment (Maron *et al.* 2014). However, as noted earlier, larger species pools reflect more broadly favourable conditions and may reduce abiotic limitation of seed establishment. As such, species richness could have

converse effects among life-history stages, resulting in limited net effects on invasion (White & Shurin 2007). Accounting for species pool size and completeness may be critical to isolating the effects of diversity on invasion across life-history stages.

The relationship between completeness, species pools and invasion may also depend on the origin of the invading species. Although native and alien species can have similar establishment (Lemoine *et al.* 2015) and competitive abilities (Dawson *et al.* 2012), these aspects of their ecology can also differ (Buckley & Catford 2016), potentially altering diversity-invasion relationships (Sun *et al.* 2015). Consequently, understanding the diversity-invasion relationship may require separate consideration of native and alien species.

To test the relationships between richness, species pool size, completeness and invasion across life-history stages for alien and native species, we conducted a seed and transplant addition experiment. We sowed seed and transplanted individuals of native and alien species into plots of intact and cleared vegetation in 29 grassland sites naturally varying in species pool size and completeness. For each species and life-history stage, we measured invader success and the biotic effects on invasion (i.e. biotic acceptance or resistance). We then used model selection and structural equation models (SEM) to test:

(1) Does partitioning richness into species pool size and community completeness, and thus separating environmental and biotic effects, increase our understanding of invasion processes?
(2) Do more seeds establish in sites with larger species pools and is biotic resistance greater in more complete communities, especially resistance to invader growth?
(3) Are alien and native invaders affected by the same aspects of the plant community and environment?

MATERIALS AND METHODS

We selected 29 sites south of Tartu, Estonia (58.07–58.35°N; 26.14–26.97°E), representing a range of productivity. All sites were open habitats composed mostly of perennial species typical of semi-natural grasslands. In May 2014, we created a pair of plots (1.5 × 2.5 m) within each site, with each plot surrounded by a 0.5 m buffer zone. As we were interested in isolating the biotic effects of the plant community on invasion, we removed all vegetation from one plot per site by applying glyphosate herbicide (Round-Up®, Monsanto Europe, Brussels, Belgium) at manufacturer recommended rates (0.36 g glyphosate/m^2). Plant communities were allowed to recover after initial removal.

Each of the larger plots was subdivided into fifteen 0.5 × 0.5 m subplots. In early June 2014, we added one transplant to each subplot, representing one of 15 species. We also added 100 seeds of each species to an additional smaller plot (0.2 × 0.8 m) within the larger plot. The 15 species represented five pairs of native and alien congeners and five species functionally distinct from the congeneric pairs. The congeneric pairs were selected by identifying alien species present in local semi-natural grasslands, then finding a congeneric native species common in these habitats. Initially, we screened 16 species pairs, selecting the five pairs with the highest germination.

From the unselected species, we selected a further three forbs, one grass, and one legume, irrespective of their origin. Each species had high germination and were functionally distinct from the other species in the experiment (see Bennett *et al.* 2016).

We harvested the experiment in early August 2015 after two growing seasons. For the seed addition, we counted all individuals belonging to the 15 focal species (hereafter recruits), excluding large established plants. For surviving transplants, we harvested all aboveground biomass. Collected biomass was dried then weighed (see Appendix S1 for details).

As our hypotheses focused on site properties that influence invasion, we calculated two site-level metrics of invasion: invasion success and biotic effects on invasion (i.e. biotic resistance or acceptance). These metrics were calculated separately for recruits and transplants. To compare among total, native and alien species invasion, we calculated these metrics for three groups of species: all 15 species, the five native congeners, and the five alien congeners. Invasion success used data from intact vegetation and was calculated as the number of recruits or biomass of transplants summed across all species in that group. Biotic effects were calculated as the log ratio of summed recruits or transplant biomass in intact vegetation over the same measures in the cleared plot [ln(intact/cleared)]. Here, biotic effects represent the effect of the intact plant community on invasion, but ignore the effects of herbivores and pathogens. These calculations resulted in estimates of establishment and biotic effects for seeds and transplants within each species group.

To characterise each site, we measured a number of environmental variables and plant productivity. From the environmental variables, we used principal components analysis to extract three axes representing 1) soil texture and extractable potassium, 2) soil depth, acidity and extractable phosphorus and 3) soil carbon and nitrogen (see Table S1). We also estimated fine-scale environmental heterogeneity as the average of the coefficients of variation for soil depth, soil moisture and light availability. To measure disturbance effects on resource availability, we collected environmental data from a subset of the herbicide treated plots and tested for herbicide effects on the environment using mixed models. As mean soil moisture and light availability were measured over a 2-week period across sites, over which they varied with weather and plant growth, we use these means only to compare treatment effects within sites. Site productivity was estimated as shoot, root and leaf litter biomass from two 0.1 × 1.0 m plots bordering the plots at each site (see Appendix S1 for details).

For each site, we estimated three measures of diversity: species richness; species pool size; and community completeness. To calculate these measures, we used a combination of small- and large-scale surveys. At small-scales, community composition was estimated for each subplot (870 subplots) in late June and early July 2015. At larger-scales, a regional species list was developed for each site by surveying all vascular plants within a 10 ha area surrounding the plot, irrespective of habitat type. To calculate site-level species richness, we totalled the number of unique species found in subplots with intact vegetation for that site (15 per site). Species pools and community completeness estimates required that we first estimate dark diversity (the portion of the species pool excluded through biotic interactions), which we did by analysing the probability that species will co-occur using the 435 subplots with vegetation intact (see Appendix S1; Lewis *et al.* 2016). Site-level dark diversity was calculated as the sum of dark diversity across the subplots from a site after excluding species found in any of the intact subplots at the site. We also included species found only in disturbed plots at a site in dark diversity as such species may be found following small scale disturbances (e.g. digging by animals). To account for dispersal limitation in our species pool estimates, we filtered dark diversity by the regional species list for each site. Species pool size was calculated as the sum of dark and observed diversity and completeness as the ratio of observed to dark diversity [ln(observed/dark diversity); Pärtel *et al.* 2013]. Although both measures use observed and dark diversity, they represent distinct information and are typically uncorrelated (Pärtel *et al.* 2016).

Data analysis

We tested whether the success of seeds and transplants varied as a function of disturbance and species origin using four mixed models. The first two models included only treatment as a fixed effect with recruit counts or transplant biomass as response variables. The third and fourth models included treatment crossed with origin as fixed effects and used only the congeneric pairs. All models included site as a random factor.

To test which diversity aspects (richness, completeness or species pool size) best described invasion success and biotic effects on invasion, we first used model selection and multimodel inference. We ran all possible combinations of the three predictors in linear regressions with invasion as the response variable, analysing each of the twelve invasion measurements separately. From these model sets, we selected the model with the lowest AIC score as the most parsimonious model. We also calculated variable weights for each combination of diversity and invasion measure by summing the AIC weights across all models including the variable of interest (Burnham & Anderson 2002).

To test the relationships between each aspect of diversity and invasion after accounting for variation in the environment, we developed two sets of structural equation models (SEM): one focusing on species richness and the other on species pool size and community completeness. For each model set, we first modelled the relationship among the abiotic environment, productivity and diversity. We hypothesised that each environmental factor could influence each biomass measure and included direct paths between these measurements. We included a direct path between shoot and litter biomass, as litter was dead shoots. We also included correlative relationships between shoot-root and root-litter biomasses to represent unmeasured links related to site productivity. For each diversity measure, we included direct paths between the environmental and productivity variables. To simplify the models, we removed paths in a backward stepwise fashion to minimise AIC (Grace 2006), retaining all parameters that increased AIC by less than one.

Using the above models (Fig. 2) as starting points, we constructed four SEM using richness and four using completeness and species pools. These SEM tested which of the factors within the previous models determined invasion outcomes measured as: (1) total invasion success; (2) total biotic effects on invasion; (3) native vs. alien success and (4) biotic effects on natives vs. aliens. Each model included both seed recruitment and transplant growth. Biotic effect models used the log ratios comparing establishment in intact vs. disturbed vegetation. Total models included all 15 focal species. Native vs. alien models included only data from the congeneric pairs, with the invasion outcomes of native and alien species included as separate variables. For all SEM, we initially assumed that each abiotic, productivity and diversity variable could directly influence invasion outcomes (Levine *et al.* 2004; Eskelinen & Harrison 2014). To represent our hypothesis that native and alien species respond similarly, we also included correlated error terms between alien and native responses where appropriate. From these models, we repeated the backwards removal of terms based on AIC. For the final models,
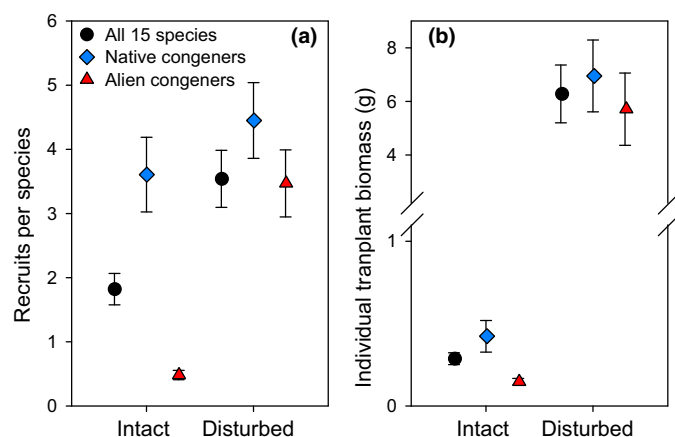

Figure 3 The average number of recruits from seed (a) and final transplant biomass (b) in intact and disturbed vegetation plots across 29 sites. There were five pairs of native and alien congeners. Error bars represent standard errors among sites.
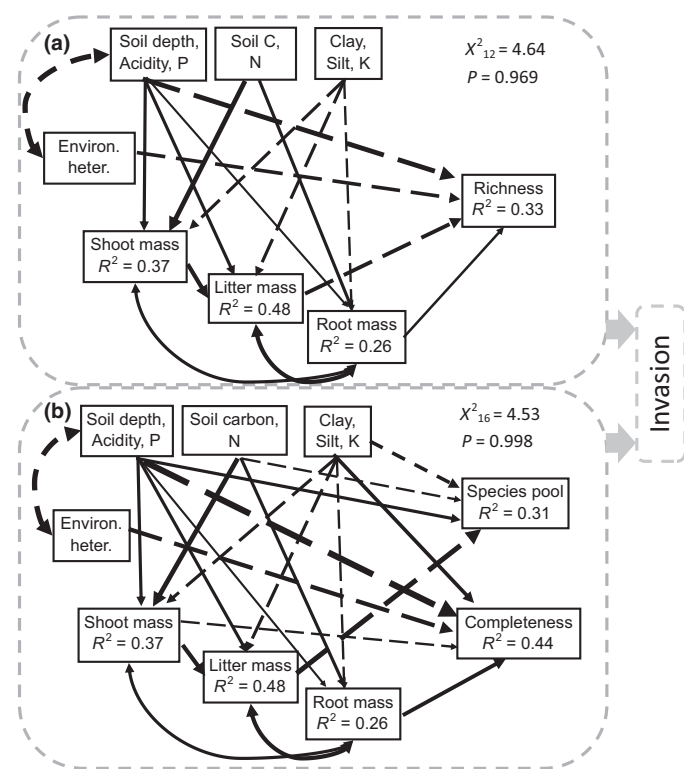
we assessed model fit using multiple indices and bootstrapped estimates of parameter significance. All analyses were conducted using SPSS with AMOS (v. 21.0, IBM SPSS, Chicago, Illinois, USA). Further details can be found in Appendix S1.

RESULTS

Across all 15 species, seedling establishment and transplant growth was reduced in intact vegetation relative to disturbed plots (Fig. 3; see Table S2). Light, soil moisture and carbon were also reduced in intact vegetation (see Tables S2 and S3), consistent with plant growth reducing resource availability and increasing competition. However, despite biotic resistance, 28% of the species established in intact vegetation from seed and 79% of transplants survived on average.

Species richness vs. species pools and completeness

In absence of any other factors, species pool size, completeness or the combination of the two variables outperformed species richness in describing invasion success and biotic resistance (Table 1). Only when none of the variables adequately predict invasion was species richness more heavily weighted than either completeness or species pool size (2 of 12 invasion measures). Species pools and completeness also outperformed richness when using SEM, although model fit was significant for all models (Table 2 and Table S4). Species richness had no effect on invasion that was not mirrored by either completeness or species pool size; whereas completeness or species pool size were frequently related to invasion in ways not captured by species richness (Fig. 4). Consequently, when averaged across all models, species pools and completeness increased the variation in invasion explained by 9% relative to richness, with increases of up to 27% for some models (Table 2). These results strongly suggest that partitioning richness into species pool size and completeness enhances our understanding of the relationship between diversity and invasion.

Figure 2 Structural equation models showing the relationships between the environment, productivity and diversity across 29 sites in southern Estonia. The three environmental variables represent axes from principal components analysis (Table S1). In one set of models, diversity is represented as species richness (a) and in the other richness was partitioned into species pool size and community completeness (b). The variation explained in endogenous variables is shown within the boxes. Arrow widths are proportional to the size of standardised effect, with solid arrows representing positive relationships and dashed arrows negative relationships. The full results can be found in Table S5. These models were used as the base of subsequent SEM models, where each variable from these models was related to the experimental invasion results (Fig. 4).

Table 1 The aspects of diversity that best explain invasion as shown through model selection and multi-model inference

Species group	Life stage	Most parsimonious model					Model averaged variable weights		
		Rich	Comp	Pool	AIC weight	R^2	Rich	Comp	Pool
All 15 species	Seeds	–	–	–	0.39	–	0.28	0.26	0.25
	Transplants	–	0.34	0.67	0.41	0.57	0.55	0.69	0.97
	Biotic effects – seeds	–	–	–	0.27	–	0.30	0.35	0.40
	Biotic effects – transplants	–	–	0.40	0.39	0.16	0.33	0.34	0.72
Native congeners	Seeds	–	–	–	0.43	–	0.25	0.25	0.23
	Transplants	–	0.39	0.66	0.45	0.59	0.54	0.67	0.94
	Biotic effects – seeds	–	–	–	0.24	–	0.40	0.31	0.34
	Biotic effects – transplants	–	–	0.51	0.50	0.26	0.32	0.31	0.84
Alien congeners	Seeds	–	0.28	–	0.24	0.08	0.39	0.41	0.25
	Transplants	–	–	0.51	0.42	0.26	0.37	0.35	0.92
	Biotic effects – seeds	–	–	−0.35	0.36	0.12	0.29	0.27	0.63
	Biotic effects – transplants	–	−0.66	–	0.50	0.43	0.35	0.84	0.28

For each measured aspect of invasion, we show the most parsimonious model and the AIC weights for each diversity measure averaged across all possible models. For the most parsimonious model, values indicate the standardised parameter estimate for that diversity aspect and dashes indicate that the parameter was not included in the model. If all diversity measures are dashes, the intercept only model had the lowest AIC score. Here, species richness is abbreviated as Rich, community completeness as Comp and species pool size as Pool.

Table 2 Model fit for structural equation models and the variation explained (R^2) in each aspect of invasion

Invasion model	Species group	Life stage	Richness		Species pool/ completeness		
			Model fit	R^2	Model fit	R^2	Difference in R^2
Overall invasion success	All 15 species	Seeds	$X^2_{20} = 6.37$	0.69	$X^2_{25} = 8.70$	0.80	0.10
		Transplants	$P = 0.998$	0.31	$P = 0.999$	0.24	−0.08
Overall biotic effects	All 15 species	Seeds	$X^2_{23} = 8.50$	0.27	$X^2_{24} = 8.17$	0.33	0.06
		Transplants	$P = 0.997$	0.21	$P = 0.999$	0.48	0.27
Native vs. alien invasion success	Native congeners	Seeds	$X^2_{30} = 17.07$	0.72	$X^2_{39} = 18.66$	0.82	0.10
		Transplants	$P = 0.972$	0.28	$P = 0.998$	0.27	0.00
	Alien congeners	Seeds		0.30		0.38	0.08
		Transplants		0.38		0.45	0.07
Biotic effects on native vs. alien species	Native congeners	Seeds	$X^2_{35} = 23.85$	0.30	$X^2_{40} = 27.21$	0.49	0.19
		Transplants	$P = 0.923$	0.11	$P = 0.938$	0.18	0.07
	Alien congeners	Seeds		0.65		0.65	0.00
		Transplants		0.17		0.38	0.21

SEMs describe diversity as species richness or partition species richness into species pool size and community completeness. Degrees of freedom from the chi-squared tests are shown as subscripts. Model fit is considered adequate if $P > 0.05$ (see Appendix S1 for more fit indices). Also shown are the differences in R^2 across different invasion aspects.

The differences among species pool size, completeness and species richness extended to their relationship with the environment (Fig. 2). Although each relationship between richness and the environment (Fig. 2a) was also represented in the completeness/species pool model (Fig. 2b), there were additional relationships between the environment and completeness or species pool size. For example soil texture and depth had opposing effects on completeness and species pools (Fig. 2b), resulting in reduced or absent relationships with richness (Fig. 2a). Similarly, the various productivity measures affected either completeness or species pool size, but never both, with limited effect on richness. Consequently, the various indirect pathways between the environment and invasion differed between the two models (see Table S6). Regardless, the environment and productivity only explained a minority of the variation in species pool size (31%), completeness (44%) and richness (33%).

Species pools, community completeness and invasion

Although many aspects of the environment had significant effects on invasion, including these paths in our models did not diminish the importance of species pools and completeness (Fig. 4, Table S5). Failing to account for species pool size and completeness did, however, reduce the variation explained in the different measures of invasion (Table S7). Comparing the parameter estimates between the most parsimonious model (Table 1) and those from the SEM (Fig. 4), we see that including the environmental variables changed the relationship between seedling establishment and completeness from positive to negative. This highlights the importance of accounting for environmental variation alongside species pools and completeness when testing for diversity effects on invasion.

We had hypothesised species pool size to be positively related to seed establishment and community completeness to
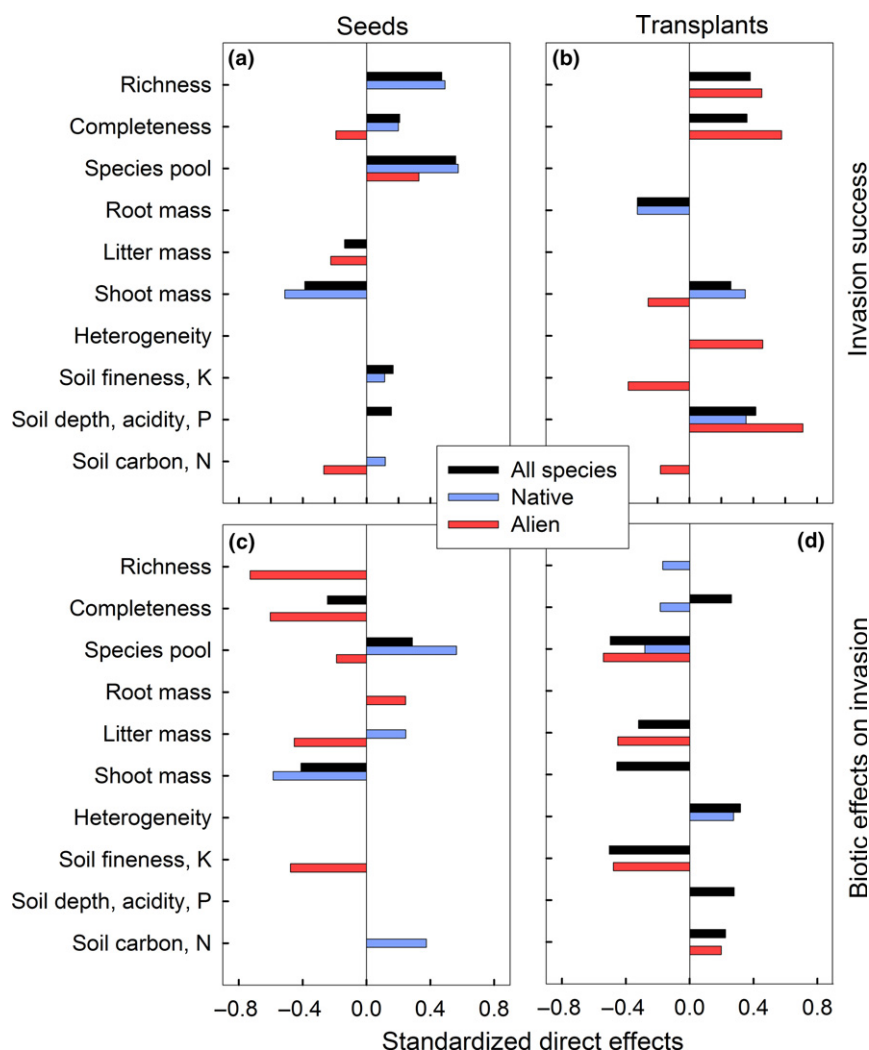
Figure 4 Standardised direct effects of diversity (richness, completeness and species pool size), productivity and the environment on invasion across the 29 sites taken from structural equation models (SEMs). Bars represent the standardised parameter estimate of the relationship between that variable and invasion. Only variables retained after SEM simplification are shown. Results from models using all 15 species are in black, with results from the five pairs of native and alien congeners in blue and red respectively. Invasion was measured as establishment in intact vegetation of (a) sown seed and (b) transplanted seedlings, and as the biotic effect on establishment [ln(intact/disturbed); negative values denote increasing resistance] for (c) seed and (d) transplants. Separate SEMs were used to generate the results for species richness (based on Fig. 2a) and for community completeness/species pool effects (based on Fig. 2b), with effects for productivity and environmental variables taken from the latter. Full results, including unstandardised direct effects, standardised total and indirect effects and bootstrapped significance estimates can be found in Tables S5 and S6.

increase biotic resistance to transplants. Across species, seed establishment increased (Fig. 4a) and biotic effects became less negative with species pool size, i.e. reduced resistance (Figs 4c; Table S5), supporting this aspect of our hypothesis. Completeness was positively related to seed establishment (Fig. 4a), but negatively related to biotic effects on seeds (Fig. 4c). This was the only evidence that biotic resistance increased with completeness, as transplant success and biotic effects on transplants were positively related to completeness (Fig. 4b and d). However, biotic effects on transplants became more negative with increasing species pool size (Fig. 4d).

Independent of species pools and completeness, several environmental variables had strong effects on invasion. Productive environments (high litter and shoot biomass) generally had negative biotic effects on invasion (Fig. 4c and d) and inhibited seed establishment (Fig. 4a), although transplant growth

increased in sites with high shoot and low root mass (Fig. 4b). Transplants were also directly associated with several aspects of the abiotic environment, whereas seeds were not. Specifically, transplant growth increased in deeper acidic soils (Fig. 4b) and biotic resistance (negative biotic effects) was greater in homogeneous environments with low nutrients and shallow soils with fine particle size (Fig. 4d).

Native vs. alien species

Alien species were unsuccessful within intact vegetation relative to native species as both seed and transplants (Fig. 3). However, there were no significant differences in establishment in disturbed areas (Fig. 3; origin by disturbance interaction: seed $P < 0.001$; transplants $P = 0.036$; Table S2), indicating that alien species experience greater biotic resistance.

Alien and native species responded similarly to some aspects of the community, but differed in others. Consistent with the overall invasion models, both alien and native species better established from seed in sites with large species pools, but experienced increased biotic resistance to transplant growth in these sites (Fig. 4a and d; Table S5). However, the relationship between species pool size and biotic effects on seed establishment varied (Fig. 4c). Biotic effects on native seeds were positive in sites with large species pools, but slightly negative for alien seeds (Fig. 4c). Native and alien invaders also differed in how they responded to community completeness. Native species were relatively weakly associated with completeness, with increased seed establishment and increased resistance to transplants in complete communities (Fig. 4a and d; Table S5). Conversely, alien seed establishment decreased and biotic effects on seeds became strongly negative with community completeness (Fig. 4a and c); however, alien transplants fared better in such communities (Fig. 4b).

There were also similarities and differences between alien and native species in their responses to the environment. Both native and alien seeds were generally less successful in more productive sites (Fig. 4a and c). However, native transplants exhibited greater growth in productive sites, whereas alien transplants grew less and experienced greater biotic resistance (Fig. 4b and d). Both native and alien transplants were more successful in deeper, acidic soils with high phosphorus. Alien transplants were also more successful in heterogeneous sites (Fig. 4b), although alien species generally fared poorly in finer soils, due to increased biotic resistance to both seeds and transplants (Fig. 4). Biotic effects were less negative for native seeds in fertile soils and in heterogeneous environments for native transplants (Fig. 4c and d). The remaining effects were weak (Fig. 4, see Table S5).

DISCUSSION

Our study suggests that diversity can be strongly related to invasion even after accounting for environmental variation, yet measuring only species richness is unlikely to reveal these relationships. Species richness is a product of the species pool and local processes (Cornell & Harrison 2014; Pärtel et al. 2016; Zobel 2016), which can have contrasting effects on invasion (Shea & Chesson 2002). Our results are consistent with this principle, yet the relationships differ from predictions (Shea & Chesson 2002; Fridley et al. 2007). Sites with larger species pools sometimes offered greater biotic resistance and completeness was sometimes positively related to invasion. In all cases, the relationship between species pool size or community completeness and invasion was dependent on the life-history stage of the invader as well as its origin. Consequently, a universal relationship between invasion and diversity seems unlikely.

Species richness vs. species pools and completeness

Invasion had variable, and occasionally opposing, relationships with species pool size and completeness. As a product of these two measures, species richness had reduced importance during model selection and lower R^2 values in the SEM relative to species pool size and completeness. This supports the assertion that environmental and biotic processes have differing effects on invasion (Shea & Chesson 2002; Fridley et al. 2007), although the precise relationships varied among life-history stages and by species origin. The differences between species pool size and completeness were also reflected in their relationship with the environment, with many relationships between the environment and these diversity aspects that were unobserved when using richness alone. Consequently, the indirect effects of the environment on invasion are also obscured when measuring richness alone. Not considering species pools and completeness thereby greatly limits our understanding of the processes driving invasion.

Species pools, community completeness and invasion

Invasion rates are expected to be higher in sites with large species pools as such sites represent environments where the conditions are favourable for a greater diversity of species (Morton & Law 1997; Shea & Chesson 2002; Fukami 2004). The limited empirical evidence is consistent with this hypothesis (Smith & Knapp 2001; Perelman et al. 2007), as were our results for seed establishment. However, biotic resistance to transplants was highest in sites with large species pools. By containing more species, larger species pools have a higher probability to contain strongly competitive species and exert greater biotic resistance (Herben 2005), which may explain this result. Our species pool estimates were only partially explained by the environment. They also contained only species found within the 10 ha surrounding the site. Many of the sites were isolated from similar habitats, which could limit species pool size by limiting dispersal of suitable species to that site (Butaye et al. 2002; Pärtel et al. 2013; Damschen et al. 2014). Moreover, strong competitors may have limited dispersal abilities (Kneitel & Chase 2004), potentially reinforcing the negative relationship between species pool size and biotic resistance. Nevertheless, these results suggest that sites with larger species pools represent broadly favourable habitats that increase initial establishment, but that at later life stages these same habitats become more competitive, largely through sampling effects, reducing expansion of the invading species.

More complete communities should exert greater biotic resistance as they are more saturated and have greater depletion of resources (Morton & Law 1997; Moore et al. 2001; Shea & Chesson 2002; Fukami 2004). However, across the 15 species, establishment and growth increased with completeness. Biotic resistance only increased with completeness for seeds, in contrast with our hypothesis. This suggests that these communities, like most others (Stohlgren et al. 2008), remain unsaturated and that increased completeness is representative of increased invasibility (Davis et al. 2005). Why resistance increased with completeness for seeds, but not transplants remains unclear. However, the seedling stage is more susceptible to the effects of competitors and antagonists than larger plants (Fenner 1987). Species with similar niches or those that share pathogens and herbivores may

limit seed establishment, but be unable to suppress larger plants.

Site productivity and the abiotic environment can be important determinants of invasion (Foster *et al.* 2004; Gerhardt & Collinge 2007; Eskelinen & Harrison 2014). Here, site productivity (shoot and litter biomass) was an important factor limiting seed establishment and increasing biotic resistance to seeds and transplants, consistent with productivity increasing competition and reducing propagule limitation (Foster *et al.* 2004). In contrast with previous hypotheses (Theoharides & Dukes 2007), the direct effect of the abiotic environment was typically limited for seeds, but strong for transplants. However, indirect abiotic effects on seed establishment, through species pool size, remained relatively strong (see Table S6), suggesting that the important aspects of the abiotic environment for seed establishment were captured by species pool size. Nevertheless, the divergent relationships seen for seeds and transplants highlight the importance of considering both regeneration and adult niches for invasion ecology (Grubb 1977).

Native vs. alien species

Many studies have suggested that there are limited ecological differences between alien and native species (Dawson *et al.* 2012; Lemoine *et al.* 2015). By choosing closely related native and alien species, we minimised potential trait differences among them. Still, differences in interactions with the resident community increased biotic resistance to alien species (Knapp & Kühn 2012; Sun *et al.* 2015). Higher biotic resistance for alien species runs contrary to most hypotheses (Buckley & Catford 2016), yet it is not without precedent (Sun *et al.* 2015). Importantly, establishment and the biotic effects on establishment were related to different aspects of the community and environment for native and alien species, suggesting important functional differences between these species groups despite close phylogenetic relationships.

Invasion by native and alien species differed in how they were related to species pool size and completeness. For native species, larger species pools allowed for increased establishment and less biotic resistance to seeds, but native transplants experienced greater resistance in sites with larger species pools and higher completeness. Previous work has shown species pool membership to be a good predictor of establishment (Breitschwerdt *et al.* 2015) and the larger species pools usually contained more of the native species (Fig. S1), suggesting that habitat suitability may allow for increased establishment and less resistance for seeds. For larger plants, increased resource requirements may result in greater biotic resistance, especially if there are strong competitors and more complete resource use (Fargione & Tilman 2005; Herben 2005). Alien transplants also experienced greater resistance in sites with larger species pools, but were better able to establish in sites with higher completeness. Conversely, alien seeds established better in sites with larger species pools and experienced greater resistance in more complete communities. This suggests that resistance to growth of alien species is greater in the presence of a strong competitor, but that resistance to alien establishment increases with resource use and niche occupancy. However, despite the increased resistance, sites with larger species pools and greater community completeness may represent a greater potential for establishment and coexistence of alien species, due to their potential to support a greater diversity of species and the potential for increased coexistence (Shea & Chesson 2002; Davis *et al.* 2005).

Site productivity had variable effects between native and alien species. More productive sites generally reduced invasion success and exerted greater biotic resistance on alien species, consistent with many studies (e.g. Perelman *et al.* 2007; Richardson *et al.* 2012). However, for native species, only seeds experienced greater biotic resistance in productive sites, suggesting that productivity limits microsite availability (Foster *et al.* 2004). If native species establish they take advantage of the beneficial conditions and expand rapidly. Both species groups were affected by soil characteristics, suggesting that resource availability may play a role in determining invasion (Eskelinen & Harrison 2014), yet the precise soil characteristics differed between alien and native species. However, these differences were largely idiosyncratic and likely dependent on the identity of the species.

CONCLUSIONS

The relationship between species richness and invasion is inconsistent among studies (Fridley *et al.* 2007). We suggest that this inconsistency occurs because species richness is a product of both the species pool and local processes, confounding its relationship with the mechanisms that regulate the establishment and growth of invading species. Species pool size indicates a greater variety of available niches (Shea & Chesson 2002), but also represents a greater probability that strong competitors will be present (Herben 2005), likely owing to the influence of dispersal limitation. Completeness, on the other hand, represents both the potential for coexistence among species (Davis *et al.* 2005) and the extent to which niches are filled and resources used within the community (Moore *et al.* 2001; Fukami 2004). Despite clear theoretical predictions, relationships between species pools, completeness and invasion remain highly dependent on plant life-history stage and whether establishment or biotic effects are considered. Seeds establish better and experience less resistance in sites with larger species pools, depending on site productivity. Plant growth increases in more complete communities and productive habitats, but experiences greater resistance in productive sites with larger species pools. If we consider only alien invaders, biotic resistance increases with completeness and species pool size, but so does invasion success, with the precise relationships differing between seeds and transplants. This suggests that invasion by alien species is affected by different processes at different life stages and that these processes are unlikely to be detected by measuring richness alone. Measuring species pools and completeness partitions the various processes affecting community assembly, thereby improving our understanding of invasion.

STATEMENT OF AUTHORSHIP

JAB and MP designed the study, JAB, KR, EK, UR, RT and CGB conducted the research. JAB conducted analyses and wrote the manuscript. All authors edited the manuscript and contributed to revisions.

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