Richness, phylogenetic diversity, and abundance all have positive effects on invader performance in an arid ecosystem

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Abstract. In search of generalities in biological invasions, it is sometimes forgotten that invader success can be a function of both the diversity of the invaded community and the relatedness of the invader relative to community residents. Both qualities are likely to be especially important in stressful ecosystems, and identifying the species and community attributes that influence biological invasions can help direct management efforts in a sensitive ecosystem like those in arid regions. Pink Morning Glory, *Ipomoea carnea* Jaq. (Family: Convolvulaceae), is an annual vine native to Central and South America and is invasive in Egypt. We examined the performance of *I. carnea* at different densities in assembled communities of Egyptian annual native species. The native plant communities were manipulated to represent gradients of species richness and phylogenetic diversity and relatedness to *I. carnea*. We quantified the performance of *I. carnea* in these communities and examined the contribution of resident species richness, phylogenetic diversity, and phylogenetic relatedness to invader resistance. Our findings revealed that there was a positive relationship between invader performance and its mean phylogenetic distance to the resident species. Furthermore, species-rich communities with more distantly related species positively contributed to invader performance in contrast to the classic biotic resistance hypothesis. Beyond these positive relationships, a positive density-dependent effect of *I. carnea* on its performance was observed. We conclude that facilitative interactions are potentially important drivers promoting the successful invasion of the nonnative species *I. carnea* in water-limited and harsh ecosystems. These results suggest that perhaps contrary to understanding from temperate systems, communities with a higher diversity of species could be more likely to be invaded by arid-adapted species that are distantly related to natives. Thus, policy and management in arid regions should carefully consider reviewing the importation of nonnative species that are phylogenetically distinct and adapted to arid conditions and prioritizing their control once they are established.

Key words: biotic resistance; density-dependent effect; facilitative interactions; invasive species; *Ipomoea carnea*; morning glory; phylogenetic diversity; phylogenetic relatedness.

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INTRODUCTION

The invasion of habitats by nonnative species is a major management priority all over the world (Pysek et al. 2010, Suetsugu et al. 2012). Determining the factors that control the invasion success of nonnative species has considerable applied significance in habitat restoration and environmental management. The impact of invasive species on native species is thought to depend on the performance of invaders (often construed as fitness) relative to the resident community, where high-performing invaders likely outcompete residents if they are competing for similar resources (MacDougall et al. 2009, Bennett et al. 2014). Thus, understanding the mechanisms by which the invasion success of a nonnative species is influenced by, as well as impacts, a resident community is critical for interpreting and managing the processes and outcomes of species invasion.

One of the major factors believed to affect invader performance is the biotic resistance of the resident community (Elton 1958, Levine and D'Antonio 1999, Prieur-Richard et al. 2000, Fridley et al. 2007), which refers to the propensity of resident species in a particular assemblage to limit the invasion success of nonnative species (Levine et al. 2004, Catford et al. 2009). The biotic resistance hypothesis has its basis in competition theory (Case 1990, Shea and Chesson 2002, MacDougall et al. 2009) and has been supported by small-scale experiments, particularly those from plant communities (Kennedy et al. 2002, Levine et al. 2004, Mwangi et al. 2007). However, a literature review found that biotic resistance to invasion was supported in less than 30% of more than 100 studies (Jeschke et al. 2012), which does not necessarily undermine biotic resistance as a mechanism influencing invasion, but rather signals that there are other factors that also influence invader success.

Biotic resistance occurs when members of a resident community occupy the niche of the invader, reducing its survival and fitness. Therefore, higher species diversity can reduce the likelihood of successful invasion (Levine et al. 2004, Vilà et al. 2011) by complementing niche space with diverse resident species that collectively efficiently utilize local resources (Elton 1958, Case 1990, Kennedy et al. 2002). It might also lead to a sampling effect, in which there is a greater probability of species-rich communities including residents with strong competitive effects that repel invader success (Fargione and Tilman 2005, Hooper and Dukes 2010, Oakley and Knox 2013). Despite the logic underpinning biotic resistance, the opposite pattern revealing a positive relationship between residents and invader species richness has also been recorded (Robinson et al. 1995, Palmer and Maurer 1997). Such a pattern could be attributed to covarying climatic changes or environmental perturbations (Tilman 1993, McIntyre and Lavorel 1994, Burke and Grime 1996, Stohlgren et al. 1999, Naeem et al. 2000), or perhaps appointed to the probability of facilitative interactions that increases with increasing species diversity.

While species richness does explain some of the effects of biotic resistance, other mechanisms need to be accounted for as well. The fact is that invaders are not actually affected by the number of species per se, but rather by ecological mechanisms modulating their coexistence with residents such as niche complementary and competitive interactions. For example, invader similarity or dissimilarity to the resident species should be subsequently better measures of the biotic resistance of the community to the invader (Laughlin 2014). However, measures of species similarity or dissimilarity are usually predicated on indirect measures using species traits (McGill et al. 2006, Brym et al. 2011), phylogenetic distances (Li et al. 2015a, Cadotte et al. 2018), or a combination of the two (Cadotte et al. 2013), of recipient communities relative to the invading species.

Resistance to invasion could be a function of the relatedness of the invader to the community or the phylogenetic diversity (measured as the total amount of evolutionary time or phylogenetic branches represented by an assemblage) of the invaded community. Darwin's naturalization hypothesis (DNH; Procheş et al. 2008, Li et al. 2015b, Cadotte et al. 2018) states that resident species that are closely related to the invader occupy similar niches, reducing the availability of the resources required for invader establishment and population growth. In addition, resi-

dent communities with high phylogenetic diversity are thought to decrease invader success because niche complementarity among residents is already high and resource use is more complete (Strauss et al. 2006, Diez et al. 2008, Gerhold et al. 2011), which is analogous to the hypothesis that biotic resistance is higher in communities with greater species richness, except that a phylogeny might provide a more direct measure of niche diversity than the number of species.

Invasion studies have often documented negative relationships between the number of native species and the number of nonnative species at fine scales (e.g., from experimental studies <5 m^2; Hodgson et al. 2002, Fridley et al. 2004, Hulme 2008). However, broadscale studies (e.g., observational studies or natural surveys) have observed the opposite pattern, namely a positive correlation between native species richness and nonnative species richness (Stohlgren et al. 1999, 2006, Brooks et al. 2013, Peng et al. 2019). These contradicting findings constitute what is often referred to as an "invasion paradox" (Shea and Chesson 2002, Byers and Noonburg 2003, Fridley et al. 2004, Davies et al. 2005). Beyond these contradicting invasion patterns, a suite of ecological mechanisms that are believed to determine invasibility have been shown to be context-dependent and lack generality. For example, experimental studies often test or infer that niche partitioning is driving local invasions (Knops et al. 1999, Hector et al. 2001, Levine et al. 2004, Fargione and Tilman 2005), which should be particularly relevant for areas where disturbance rates are low, shaded, non-successional uplands or nutrient-poor ecosystems (Cronk and Fuller 1995, Davis et al. 2000, Wardle 2001). By contrast, Brown and Peet (2003, see too: Davis et al. 2000, Levine 2000) suggested that positive native/nonnative richness relationships are expected in dispersal- or immigration-driven communities. Additionally, facilitation among native and nonnative richness might occur in stressful or highly disturbed areas such as roadsides or agrarian landscapes and should cause positive native/nonnative richness correlations.

In parallel, the performance of an invader might also depend on its own density, relying on the assumption that there are strong density-dependent effects on plant population performance (Wills et al. 1997, Li et al. 2015a, 2015b). In other words, intraspecific plant density might be important for the success of the colonization process for invasive populations and should be considered to be an indicator for invader performance (Bazzaz 1986) since large numbers of plant propagules must be introduced to a new site before a population becomes established (Martins and Jain 1979). Growing evidence reveals that the probability of establishment of invasive population seems to be conditioned with whether the invader tends to be more or less abundant (Bazzaz 1986, Meekins and McCarthy 2002).

In this study, we experimentally introduce the Pink Morning Glory, *Ipomoea carnea* Jaq. (Family: Convolvulaceae), an annual vine native to Central and South America, into communities assembled from a species pool of native Egyptian annuals where *I. carnea* is invasive. The communities were assembled by manipulating species richness, phylogenetic diversity, and phylogenetic relatedness of the residents to *I. carnea*. We also manipulated invader density. We focused on four response traits (plant height, aboveground biomass, root biomass, and the stomatal conductance that was used as a proxy of the photosynthetic rate of individual invader plants transplanted into manipulated communities) that capture different aspects of the invader performance (Primack and Kang 1989). We tested whether the higher performance of the invader occurs in assemblages with (1) lower resident richness, (2) lower phylogenetic diversity of resident communities, (3) more distant phylogenetic relatedness between the invader and the resident species, and (4) lower invader density.

MATERIALS AND METHODS

Study site and species

This experimental study mimicked Egyptian natural arid systems and was run in the greenhouse at the University of Toronto Scarborough in Ontario, Canada, from fall 2015 to winter 2016. Temperature and relative humidity (30°C to 35°C, 36%, respectively) were adapted to simulate arid conditions. A total of 240 seedlings from 16 Egyptian native species belonging to 13 families were transplanted into 24 pots, each pot had a surface area of 30 × 30 cm and a soil depth of 30 cm.

The Egyptian native species used in this experiment were relatively analogous in size and biomass productivity. These native species were as follows: *Trifolium resupinatum* L. (Fabaceae), *Melilotus indicus* (L.) All. (Fabaceae), *Chenopodium album* L. (Chenopodiaceae), *Chenopodium ficifolium* Sm. (Chenopodiaceae), *Beta vulgaris* L. supsp. *maritima* (L.) Arcang (Chenopodiaceae), *Spergularia marina* (L.) Bessler (Caryophyllaceae), *Emex spinosa* (L.) Compd. (Polygonaceae), *Rumex dentatus* L. (Polygonaceae), *Urospermum picroides* (L.) F.W. Schmidt (Asteraceae), *Pluchea dioscoridis* (L.) DC (Asteraceae), *Centaurea calcitrapa* L. (Asteraceae), *Apium graveolens* L. (Apiaceae), *Epilobium hirsutum* L. (Onagraceae), *Juncus subulatus* Forssk. (Juncaceae), *Polypogon monspeliensis* (L.) Desf. (Poaceae), and *Cenchrus echinatus* L. (Poaceae).

Phylogenetic data

We constructed a phylogeny of the 16 plant species using four commonly sequenced genes available in GenBank (Benson et al. 2006): rbcL, matK, ITS1, and 5.8s (Appendix S1: Table S1). Of the 16 species, 15 had at least one gene represented in GenBank, except for *J. subulatus*, and so we used genetic sequences from the congeneric relative, *Juncus acutus* L., as a proxy. We also included the genetic sequences of *Amborella trichopoda* Baill. (a species that diverged early in angiosperm evolution) to serve as an outgroup species. Sequences were aligned for each region independently using FASconCAT v1.0 (Kück and Meusemann 2010) and combined into a single supermatrix. We then selected best-fit maximum-likelihood (ML) models of nucleotide substitution for each gene sequence using jModeltest (Posada 2008). The ML phylogeny was generated using the PhyML algorithm with a BIONJ starting tree (Guindon and Gascuel 2003, Anisimova and Gascuel 2006) to estimate the phylogeny. Nodal support was estimated using approximate likelihood-ratio test scores, which have been shown to correlate with ML bootstrap scores but require much less computational time (Guindon and Gascuel 2003). We then used a semiparametric rate-smoothing method (Sanderson 2002) to transform the phylogeny to an ultrametric tree using the R package "ape" (Paradis et al. 2004). We iterated these functions across a suite of rate-smoothing parameters and found that the parameter value that maximized the likelihood was $\Lambda = 1$. The final ultrametric phylogenetic tree including 15 native species and the invader is provided (Fig. 1). This tree was used to quantify phylogenetic patterns in each treatment pot.

Experimental treatments

Ten individual seedlings were transplanted into each pot to control for plant density, and to make all pots have equal density before the invasion regardless of treatment. In total, 24 pots were treated as invaded polycultures. All pots were randomly assigned to four treatments: Treatment A had low species richness with low phylogenetic distances; treatment B had low species richness with high phylogenetic distances; treatment C had high species richness with low phylogenetic distances; and treatment D had high species richness with high phylogenetic distances. For each treatment, there were three unique combinations of two or five species fully crossed with low level or high level of resident phylogenetic distance drawn randomly from the species pool. For each unique combination, there were two levels of invader density: high density (two stems of *I. carnea*) and low density (one stem of *I. carnea*; Appendix S1: Table S2).

Phylogenetic analysis

We calculated Faith's phylogenetic diversity (PD) of all resident species in each pot (not including the invader) using function PD in R package "Picante" (version 1.8; Kembel et al. 2010). Phylogenetic relatedness between the invader and the residents in each recipient community was calculated using the mean pairwise phylogenetic distance (MPD) between the invader and all resident species in each recipient community as the average of the mean pairwise distance between the invader and each resident species using the cophenetic tree and the MPD function in Picante (Kembel et al. 2010).

Measuring Ipomoea carnea *performance*

Starting January 2016, *I. carnea* individuals were monitored in all invaded pots. We assessed invader performance using height from the soil surface (cm), the number of leaves, and the stomatal conductance (mmol of water/($m^2 \cdot$s)) which we measured using an SC-1 Leaf Porometer (Decagon Devices, Pullman, Washington, USA). These performance traits were measured directly
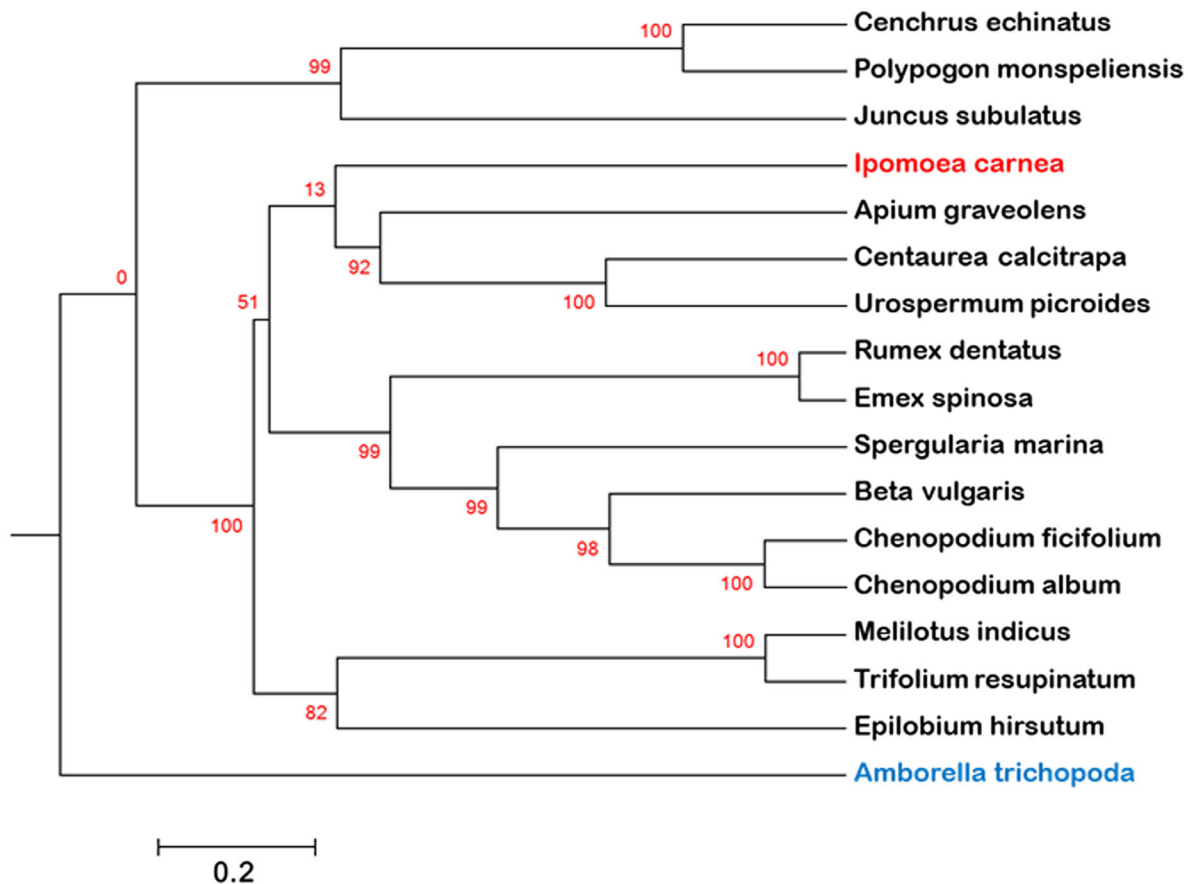
Fig. 1. The rooted ultrametric phylogenetic tree including the pool of 15 native species, one outgroup species (in blue), and the target studied invasive plant species (*Ipomoea carnea*, in red).

from the treated pots. All performance measurements were carried out every 15 d until May 2016.

We set additional pots (hereafter biomass pots) of isolated individuals of *I. carnea* to calibrate predictive models of the aboveground and belowground biomass (in grams). In these pots, we recorded the same performance measures that we collected directly from the treatment pots and harvested 16 plants to measure the above- and belowground biomass every 15 d. We ended the experiment in May 2016, when the vegetation reached peak standing biomass, and we counted the number of *I. carnea* stems in each pot. All *I. carnea* stems were removed from each pot and biomass sorted into living aboveground plant biomass (leaves and stem) and belowground biomass (all rooting material). All samples were dried in a drying oven (VWR International,

Radnor, Pennsylvania, USA) at 50°C for three days until constant dry weight was reached, and then weighed using a Mettler Toledo ML Series precision balance (XE Analytical Balance; Mettler Toledo, Columbus, Ohio, USA).

Invader performance of *I. carnea* was measured using the five performance traits: height, number of leaves, photosynthetic rate, and the aboveground and belowground biomass. First, we built predictive models to estimate the above- and belowground biomass using the measured traits of *I. carnea* individuals from the destructively sampled biomass pots. For this purpose, we built several multiple linear regression models of aboveground biomass regressed against height, stem diameter, number of leaves, and the photosynthetic rate as response variables. We compared these models using Akaike information criterion (AIC) and Akaike weights (AW) in

addition to diagnosis plots to infer the best regression models. We repeated the analysis for belowground biomass. We used the best model in each case to predict the above- and belowground biomass of *I. carnea* individuals in the pot treatments.

Statistical analysis

We constructed a series of mixed linear effect models including invader performance measures as response variables. The fixed effects were resident richness, phylogenetic diversity (PD), the MPD, and invader abundance interacted with measurement times (early, middle, late). We also included pot identity as a random effect using the "lme4" package (version 1.1-20; Bates et al. 2015) to capture the ontogenetic changes in the performance measures of the invader and plant community. All models were compared using AIC and AW to infer which model was the best fit to identify the optimal model that explains invader growth performance, among a set of candidate models (Johnson and Omland 2004). We checked diagnostic plots (e.g., residual vs. fitted plots and observed vs. fitted plots) for potential outliers, and the residuals were plotted against fitted values to identify violation of homogeneity indicated by differences in spread. To overcome the large spread of fitted values, phylogenetic measures were log-transformed in order to improve the normality of the error distribution (as determined by inspection of the Q-Q plot), and also we verified normality using Shapiro–Wilk test (Shapiro and Wilk 1965). All explanatory variables that characterize the recipient community included in the model structure (resident richness, phylogenetic measures, and invader abundance) were only weakly correlated with each other (Pearson's correlations all <0.6), and so multicollinearity was not an issue. All analyses were completed using R v.3.3.1 (R Core Team 2018).

RESULTS

We assessed the influence of species richness and phylogenetic measures of the resident community and invader abundance on the growth performance of the invasive species, *I. carnea*. Our measures of invader performance included height, leaf production, biomass, and photosynthetic rate were all significantly influenced by at least one measure of community diversity (Tables 1, 2, Fig. 2). Below, we detail the effects of specific diversity measures integrated with invader abundance on the invader performance measures.

Effect of phylogenetic measures on invader performance

Contrary to our expectation of negative effects of diversity on invader performance, we found significant positive relationships between the invader performance measures and PD as well as the MPD between the invader and residents across measurement times. First, invader biomass production increased significantly in high phylogenetically diverse (high PD) treatments for aboveground biomass ($X^2 = 10.54$; $P < 0.01$) and for belowground biomass ($X^2 = 10.65$; $P < 0.01$) as evidenced by top biomass models (AIC = −91.61, AW = 0.52, $R^2 = 0.81$; AIC = −73.76, AW = 0.46, $R^2 = 0.63$) for above- and belowground biomass, respectively (Tables 1, 2).

Second, invader height increased significantly with increasing MPD ($X^2 = 10.58$; $P < 0.01$) as evidenced by top height model (AIC = 94.34; AW = 0.72, $R^2 = 0.57$). The number of leaves produced by the invader was explained by MPD ($X^2 = 19.19$; $P < 0.0001$) and significantly increased with greater MPD as evidenced by the leaf production model (AIC = 1224.2, AW = 0.58, $R^2 = 0.55$). Likewise, photosynthetic rate was better explained and increased marginally significantly with MPD ($X^2 = 6.76$; $P < 0.07$) as evidenced by the top photosynthetic rate model (AIC = 1271.71, AW = 0.55, $R^2 = 0.47$). Therefore, *I. carnea* exhibited higher performance in pots that had higher phylogenetic diversity and where *I. carnea* was more dissimilar to residents.

Effect of resident richness on invader performance

Top models of invader performance revealed positive significant relationships ($P < 0.01$) between resident richness and invader height as well as leaf production in all inoculated pots (Table 1, Fig. 2). Higher values of height and leaf production were significantly explained by resident richness ($X^2 = 9.28$, $P < 0.01$; $X^2 = 7.33$,

Table 1. Results of linear mixed models testing the significance of the effects of resident phylogenetic diversity (PD), mean pairwise phylogenetic distance (MPD), and invader abundance on the performance measures (height–leaf production–aboveground biomass–belowground biomass) of the target species *Ipomoea carnea*.

Fixed effect by response variable	df	χ^2	P
Height (cm)			
Resident richness	8	9.278	**0.0258**
Mean pairwise phylogenetic distance (MPD)	8	10.58	**0.0142**
Aboveground biomass (g)			
Resident phylogenetic diversity (PD)	8	10.5448	**0.0145**
Invader abundance	8	2.75361	0.4312
Leaf production			
Resident richness	8	7.3349	**0.062**
Mean pairwise phylogenetic distance (MPD)	8	19.1948	**<0.0001**
Belowground biomass (g)			
Resident phylogenetic diversity (PD)	8	10.6588	**0.013**
Invader abundance	8	1.1071	0.775
Photosynthetic rate (mmol/(m^2·s))			
Invader abundance	8	12.41	**<0.006**
Mean pairwise phylogenetic distance (MPD)	8	6.762	**0.07**

Note: Significant effects ($P < 0.05$) are in bold.

Table 2. Comparison of linear mixed models for the parameters studied (values for random effects are expressed as variance/SD).

Model parameters	Response variables				
	Height (cm)	Aboveground biomass (g)	Leaf production	Belowground biomass (g)	Photosynthetic rate (mmol/(m^2·s))
Marginal R^2	0.324735	0.7783425	0.2845274	0.6041792	0.470697
Conditional R^2	0.5789917	0.8163409	0.5625022	0.6255974	0.470697
Random effect					
Pot identity	0.04215/ 0.2053	0.01668/0.08166	8.252/2.873	0.002145/0.04631	0
Residuals	0.06979/ 0.2642	0.032227/0.17952	12.988/3.604	0.037489/0.19362	0.0002

$P < 0.01$, respectively) across all measurements. Therefore, an increase in resident richness led to an increase in performance measures of the invasive *I. carnea*.

Effect of invader abundance on its performance

Top invader biomass models exhibited positive but nonsignificant relationships between biomass and invader abundance in all inoculated pots ($P < 0.4$). In these models, we found that the aboveground biomass and belowground biomass were nonsignificantly correlated with invader abundance ($X^2 = 2.75$, $P < 0.4$; $X^2 = 1.77$, $P < 0.7$, respectively) across all measurements. However, the photosynthetic rate model revealed a positive and highly significant effect

of invader abundance ($X^2 = 12.41$, $P < 0.006$) on its photosynthetic rate as evidenced by top model selection (AIC = 1271.71, AW = 0.55, $R^2 = 0.47$; Fig. 2).

DISCUSSION

The results of this study did not support the classic biotic resistance hypothesis, which states that increasing resident diversity decreases the success of invasive species (Elton 1958). As a general pattern, we found that the richness of resident species had a positive impact on invader performance and facilitated its establishment within the community. Furthermore, our five measures of performance (height, shoot biomass,
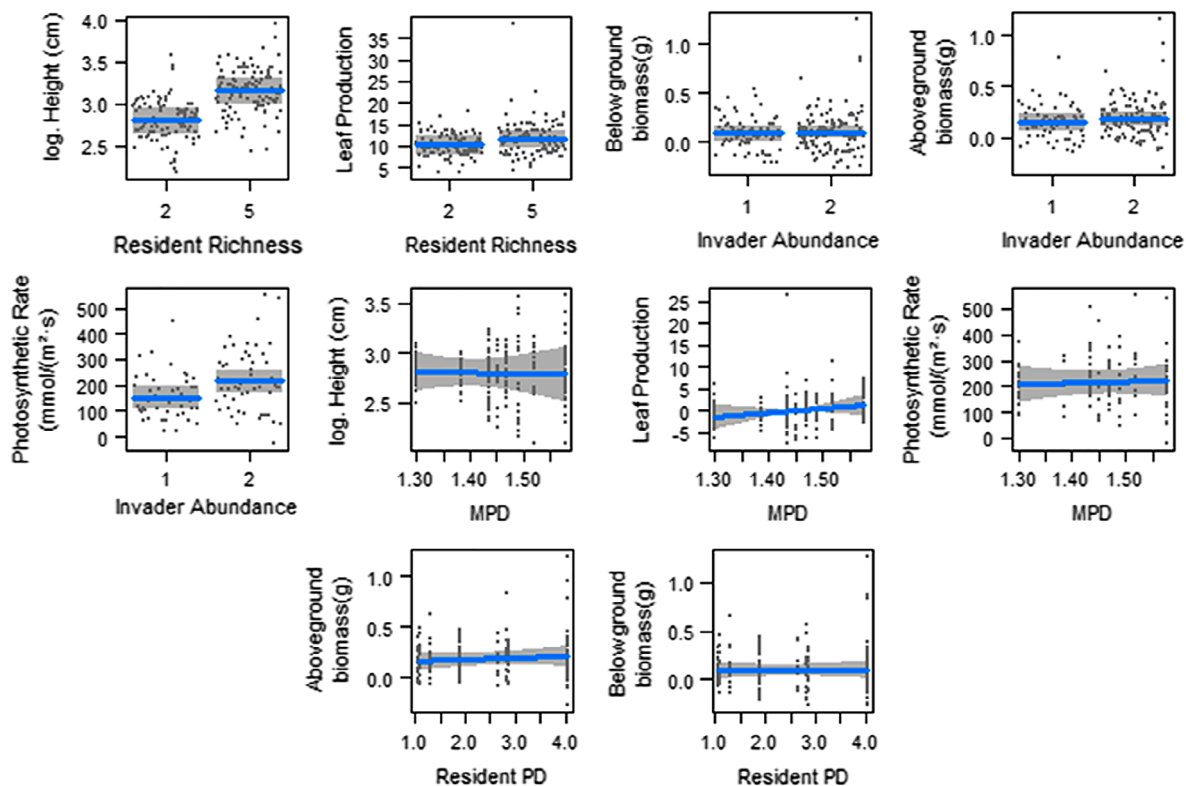
Fig. 2. Showing the response of invader performance measures (height [cm], belowground biomass [g], aboveground biomass [g], photosynthetic rate [mmol/(m²·s)], leaf production) to diversity measures (resident phylogenetic diversity [PD], mean pairwise phylogenetic distance [MPD] between the invader and resident natives, resident richness). Regression lines are fitted for each diversity measure and invader abundance, and shaded areas around regression lines indicate upper and lower 95% confidence intervals expected by the model. Black points show the observed data points.

root biomass, leaf production, and photosynthetic rate) increased with increasing resident richness, resident phylogenetic diversity of the recipient community, and the mean phylogenetic distance between the invader and the resident species. Our results provide clear evidence that invaders at high densities exhibit greater performance, at least at the scale of this study.

The observation that *I. carnea* tends to exhibit high performance in more phylogenetically diverse communities could be driven either by the lower niche overlap in the presence of distantly related species or by the displacement of competitively inferior native species that are closely related to the invader *I. carnea* (MacDougall et al. 2009, Sol et al. 2014, Cadotte et al. 2018). Alternatively, this could be evidence that distantly related residents in a community facilitate invaders (Hooper et al. 2005, Jeschke et al. 2012, Valiente-Banuet and Verdú 2013), at least in water-limited, arid systems such as ours. Several studies have reported that invaders with high performance tend to be more distantly related to native residents (Strauss et al. 2006, Li et al. 2015b). Consistent with these previous findings, our results provide an evidence for the negative effect of closely related resident species on invader performance, a pattern consistent with DNH (Daehler 2001, Cadotte et al. 2018), even though these classic theories do not include facilitation as a potential mechanism.

Indeed, facilitation is more likely to occur among distantly related species, increasing survival as well as growth rate (Hierro and Cock 2013) and enhancing the coexistence of nonnative species within native assemblages (Palmer and

Maurer 1997, Richardson et al. 2000, MacDougall and Turkington 2005, Hacker and Dethier 2006, Wolkovich et al. 2009, Altieri et al. 2010), a pattern that is consistent with our findings. Likewise, facilitation could be a reflection of several mechanisms including creation of favorable environmental conditions such as elevated soil moisture caused by shading, the promotion of increased nutrient utilization, or improving soil properties (Filazzola and Lortie 2014, McIntire and Fajardo 2014). As a result of these conditions, facilitation benefits promote higher diversity and results in more phylogenetically diverse communities (Valiente-Banuet and Verdú 2007, 2013) which might further facilitate the invasibility of diverse plant communities.

In our experiment, the potential mechanisms linking phylogenetic diversity to invader success are likely complicated, but we can see a candidate mechanism, which requires additional experimentation. Namely, our experiment mimics a water-limited system, and an assemblage of distantly related species could result in a greater utilization of local resources and enhance coexistence and biomass production (Flynn et al. 2011, Cadotte 2013, 2017). Greater coexistence and biomass production would result in greater light interception (Hautier et al. 2009) and thus greater shading. In water-limited, arid environments, this higher shading is likely to result in higher soil moisture, and this additional water availability for plants could enhance reproduction, survival, growth, and performance of the invader within the recipient community (Harrington 1991, Li and Wilson 1998). Thus, even though competition occurs in our system, these negative interactions are outweighed by the positive effects of greater soil moisture in high diversity assemblages. As a result, our findings are consistent with current literature suggesting that facilitative interactions increase with increasing the stressful conditions in harsh environments (Holmgren and Scheffer 2010, Pistón et al. 2016, Al-Namazi et al. 2017).

Beyond the effect of higher phylogenetic diversity on invader performance, we also observed a positive density-dependent effect of *I. carnea* on its own performance. It is commonly assumed that the likelihood that the invader is successful increases proportionally as invader density increases (Yokomizo et al. 2009, Elgersma and Ehrenfeld 2011). There is some evidence indicating that positive density dependence increases species survival and reproduction (Wills et al. 1997). This positive density dependence can occur because individuals of the same species might influence local environmental conditions that favor its own kind, and could result in competitive superiority over resident species under a range of environmental conditions (Powell and Knight 2009, Molina-Montenegro et al. 2012, Franzese and Ghermandi 2014, Cuda et al. 2015). This positive density dependence could be also attributed to the shape of the density dependence curve, assuming that successful invasive population have more scramble type of density dependence (Aikio et al. 2008). Even though negative density dependence is frequently observed (Augspurger 1984, Connell et al. 1984, Condit et al. 1994, Wills et al. 1997), we believe more work on invasions in arid environments would support the observation of positive density dependence.

Overall, our findings demonstrate the value of integrating species richness, phylogeny, and density-dependent effects, which might be used for developing an action plan to manage invasion in arid ecosystems. Further studies are needed to evaluate whether natural arid systems are more or less susceptible to be invaded by a nonnative species distantly related to native communities. Moreover, observational studies on invaded communities of various successional stages and across a range of environmental conditions could go a long way toward determining the generality of our findings. It is crucial to monitor the invasion stages for each nonnative species, so we can see at which stage the invader reveals high performance.

Finally, current invasion theory and applied nonnative species risk assessment focus on the threat and negative impact from nonnatives that are either closely related to resident species (MacDougall et al. 2009) or other successful invaders (Cadotte and Jin 2014). While such assumptions would likely prove true in many contexts, we believe practitioners that assess invasion risk in arid environments should explicitly consider distantly related (though correctly preadapted) species in their diagnoses. It may be that arid environments tend to be relatively simple and so any adequately adapted species could pose a

threat. More research is needed that is focused on understanding the potentially greater impacts of invasion in arid environments in light of globalization and the movement of nonnative plant species.

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Supporting Information