BIODIVERSITY RESEARCH

Phylogenetic isolation increases plant success despite increasing susceptibility to generalist herbivores

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ABSTRACT

Aim Theory suggests that introduced species that are phylogenetically distant from their recipient communities should be more successful than closely related introduced species because they can exploit open niches and escape enemies in their new range, i.e. Darwin's Naturalization Hypothesis. Alternatively, it has also been hypothesized that closely related invaders might be more successful than novel invaders because they are pre-adapted to conditions in their new range; a paradox coined Darwin's Naturalization Conundrum. To date, these hypotheses have been tested primarily at the regional scale, not within local plant communities where introduced species colonize, compete and encounter herbivores.

Location Global.

Methods and Results We used community phylogenetics to analyse data from 49 published experiments to examine the importance of phylogenetic relatedness and generalist herbivory on native and exotic plant success at the community level. Plants that were categorized as 'invasive' were indeed less related to the recipient community than 'non-pest' exotic plants. Distantly related exotic plants were also more abundant than closely related species. Phylogenetic relatedness predicted herbivore impact, but in a way that was opposite to predictions, as herbivores had stronger, not lesser, impacts on distantly related plants. Importantly, these same patterns generally held for native plants, as distantly related native plants were more abundant and more susceptible to herbivores than closely related species, ultimately resulting in herbivores suppressing community-level phylogenetic diversity.

Main conclusions Distantly related plants were more locally successful despite experiencing stronger control by generalist herbivores, a finding that was robust across native and exotic species. To our knowledge, this is the first evidence that phylogenetic matching influences the local success of both native and exotic species and that herbivores can influence community phylodiversity. Phylogenetic relatedness explained a relatively small portion of the variance in the data even after taking herbivory into account, however, suggesting that phylogenetic matching works in combination with other factors to influence community assembly.

Keywords
Biological invasions, biotic resistance, Darwin's Naturalization Hypothesis, enemy release hypothesis, herbivory, phylogenetic relatedness.

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INTRODUCTION

Exotic species are invading new ecosystems faster than has ever occurred via natural processes (Mack *et al.*, 2000), homogenizing the world's biota and leading to significant ecological and economic impacts (Wilcove *et al.*, 1998; Pimentel *et al.*, 2005). It has long been hypothesized that invasions are biased towards introduced species that are unrelated to the recipient community. Darwin's Naturalization Hypothesis (DNH, Darwin, 1859), for example, posits that more distantly related

species will be more successful invaders than closely related species because they can exploit unfilled niches in the recipient community (Rejmánek, 1996). The same pattern, however, could result from two other mechanisms, including differential enemy attack whereby pathogens and herbivores have weaker impacts on distantly related plants because they possess more novel anti-herbivore defences (Maron & Vila, 2001; Keane & Crawley, 2002; Callaway & Ridenour, 2004; Cappuccino & Arnason, 2006; Webb *et al.*, 2006), or from mutualism and facilitation among 'nurse plants' and distantly related bene-factors (Valiente-Banuet & Verdú, 2007). In contrast, Darwin also recognized the potential for closely related species to be more successful invaders. Under this scenario, invaders that are closely related to native species might have a better chance of thriving because they share traits with native species that pre-adapt them to local environmental conditions, including defence and tolerance of shared enemies (Cavender-Bares *et al.*, 2009; Lind & Parker, 2010; Thuiller *et al.*, 2010). Thus, there are opposing hypotheses predicting that successful invaders are either closely or distantly related to native species; a paradox coined Darwin's Naturalization Conundrum (Diez *et al.*, 2008).

To date, tests of the Naturalization Hypothesis have received mixed support, in part because studies have examined different spatial scales and used disparate metrics of phylogenetic relatedness (Procheş *et al.*, 2008; Thuiller *et al.*, 2010). Studies conducted at continental and regional scales, for example, generally use a taxonomic framework to test whether success-fully introduced species belong to genera or families common to the species pool of the introduced range, finding a wide range of evidence both for and against DNH (Rejmánek, 1996; Daehler, 2001; Duncan & Williams, 2002; Ricciardi & Atkin-son, 2004; Lambdon & Hulme, 2006; Ricciardi & Mottiar, 2006; Diez *et al.*, 2008, 2009). Strauss *et al.* (2006) expanded on these studies by using community phylogenetics, a relatively new method that produces a quantitative estimate of related-ness based on phylogenetic information, to show that evolu-tionarily distant grasses in California were more likely to be considered noxious or invasive species than closely related grasses, in support of the DNH.

However, many of the mechanisms that determine invasion success, such as colonization, competition and herbivory, occur at the local scale. At these scales, communities are often subsets of the regional or continental species pool; thus, shared taxonomy at the regional scale is an insufficient metric for asking whether phylogeny influences processes at the local scale (Cavender-Bares *et al.*, 2009). To our knowledge, no studies have used community phylogenetics to examine whether patterns of invasions at the local scale have a phylogenetic signature, but there is some evidence for local patterns of herbivory on non-native species to be driven by phylogeny. Pearse & Hipp (2009) showed that insect herbivory on non-native oaks decreased with increasing phylogenetic distance from a native oak in a common botanical garden. Similarly, Hill & Kotanen (2009) found a negative but weak relationship between phylogenetic distance and insect leaf damage in a

broad group of co-occurring native and exotic plants, but no relationship when examined specifically among 20 native and 15 exotic Asteraceae (Hill & Kotanen, 2010). Thus, the prevailing pattern to date is that phylogenetic distance can be predictive of increased invasiveness at the regional scale and decreased insect herbivory at the local scale, but to our knowledge, no studies have explicitly linked both processes at the local scale where organisms interact.

Theory and empirical evidence suggest that the outcome of evolutionarily novel plant–herbivore interactions may depend on the quantitative degree of relatedness among plants and herbivores (Verhoeven *et al.*, 2009). In Parker *et al.* (2006), for example, native herbivores had stronger negative impacts on exotic plants than native plants, and exotic herbivores had stronger negative impacts on native plants, a pattern indicating that each type of herbivore had stronger impacts on the plants that were an evolutionary mismatch. Moreover, in the case of native herbivores, impacts were even stronger on exotic plants that did not have a native congener in the recipient flora (Ricciardi & Ward, 2006), suggesting that more distantly related plants were more strongly impacted by herbivores, in contrast to predictions of DNH. However, the latter analysis was based on regional taxonomic lists and made no attempt to determine whether this pattern held at the local scale. Moreover, there was no corresponding test of whether exotic herbivores had differential impacts on more distantly related native plants, the corollary to an evolutionary mismatch between native herbivores and exotic plants.

Herbivore escape via phylogenetic isolation is often cited as a key component of the naturalization and Enemy Release Hypotheses, but to date, there have been no experimental studies examining the interrelationship between plant related-ness, herbivory and invasion success. Here, we analyse data from 49 published manipulative experiments examining the impact of generalist herbivores on local communities to test the importance of relatedness on herbivory and exotic plant success. Using a phylogenetic supertree with divergence times for 362 species, we asked whether (1) invasive exotic plant species were more phylogenetically distinct relative to the local community than non-pest exotic plant species; (2) locally abundant plants were more phylogenetically distinct regardless of plant origin; (3) phylogenetic distinctiveness resulted in diminished top-down control by herbivores; (4) the effect of plant distinctiveness on herbivory differed if the community was under pressure from native versus exotic herbivores; and (5) herbivores altered community-level phylogenetic diversity.

METHODS

We used the data set from Parker *et al.* (2006), a meta-analysis that examined the impacts of generalist herbivores on exotic plant success in 68 manipulative field studies, plus two additional studies published since then (Webster *et al.*, 2005; Parker *et al.*, 2007, Appendix S1). All studies excluded herbivores and had control sites with herbivores, conducted the experiment in a field setting and reported plant community

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response in terms of plant cover or biomass per area. To examine the role of community phylogeny in determining invasive plant success via escape from herbivory, we narrowed the original data set to include only studies that published species-level abundance data for the majority of the total plant community (mean ± SE of 93.8 ± 1.4% of the total community), resulting in a final data set of 49 experiments from 26 publications. Studies reported that they excluded either native ($N = 24$) or exotic herbivores ($N = 25$). Across all studies, exotic plants comprised 31.5 ± 3.9% of the total plant community, whereas native plants comprised 62.3 ± 3.8%, indicating that these studies examined sites that were highly invaded although natives generally comprised the bulk of the community.

To test the hypothesis that evolutionary relatedness to the local community influences invasion success and herbivory, we standardized both the response variable (impact of herbivory) and the phylogenetic framework across all experiments. For each experiment, we standardized the impact of herbivory by transforming measured variables (biomass or percent cover) for each plant species into the unweighted log response ratio (RR) with the form $\ln(X_{+H}/X_{-H})$ where X_{+H} is the measured plant variable in the presence of herbivores and X_{-H} is the variable with herbivores excluded (Parker et al., 2006). Prior to transformation, we added a 1 to each variable to allow for calculations when plant abundance was zero. Thus, RR describes the impact of herbivory on each plant species in its local community, with values >0 indicating facilitation by herbivores and values <0 indicating suppression.

To standardize the metric of phylogenetic distance between plants in a local community, we constructed a phylogenetic 'supertree' incorporating each of the plant species found in the data set of published experiments (or genus for plants not identified to species in the original study). Our hypothesized relationship among all species ($N = 362$) was ultrametric with the positioning of major nodes based on published estimates of divergence times. Estimates of phylogenetic relatedness and divergence times among species were drawn from multiple sources. The estimated divergence time between charophytes and green land plants (ca. 1060 Mya) was based on Sanderson et al. (2004) and the divergence between bryophytes and vascular plants (ca. 580 Mya) on Douzery et al. (2004). The phylogenetic relationships and dating of nodes of major angiosperm clades were based on Wikstrom et al. (2001). Wikstrom et al. (2001) reported multiple estimates for divergence times of nodes; we thus pooled all estimates. The estimated divergence times among genera and species lacking phylogenetic information were standardized to 5 and 1 Mya, respectively. Divergence times between and within families are not always equivalent (Shaw et al., 2005), but these conservative estimates of divergence represented the minimum time that included all families in the supertree and assumed that taxonomic rank provides some information on the temporal order of divergence (e.g. family > genus > species divergence). As a check on these methods, we also calculated relatedness values using Pagel's (1992) approach of assuming that generic

divergence times are half the branch length distance from the family, and species' divergence times are half the branch length distance from the genus. These calculations did not change our conclusions and thus were not retained.

To estimate relatedness, we used an approach similar to Webb's (2000) indices of community phylogenetic relatedness but with three main differences. First, we used information on branch lengths rather than nodal counts to gauge phylogenetic distance. This was necessary because nodes between distantly related taxa in a small community would not reflect evolutionary distance as accurately as an explicit date-calibrated branch length. Second, because resampling procedures across the entire supertree would also be from a global (cross-continental) pool of species, generating communities with species composition that are unlikely in nature, we did not standardize our relatedness metrics using a resampling method (see Webb, 2000). Instead, we standardized our means by dividing distance estimates by the total branch length distance from root to tip of the entire phylogeny (1060.59 Mya). This standardization resulted in metrics tending towards zero when the community is more closely related (i.e. phylogenetically clustered) and towards one when they are more distantly related (i.e. overdispersed). Third, we calculated phylogenetic distance per species (relatedness; e.g. Strauss et al., 2006) rather than an overall community metric (dispersion). This allowed for species-level regressions between estimates of phylogenetic distance, abundance and herbivore impact.

Using our phylogenetic supertree, we calculated two metrics of evolutionary relatedness for each species relative to its local (experimental) community: mean phylogenetic distance (PD) and nearest neighbour distance (NND). PD was calculated as the sum of branch lengths between the focal species and each species in the rest of the local community (i.e. all species found in both the presence and the absence of herbivores for a given study) divided by one less than the number of species in the local community. NND is the smallest branch length distance from the focal species to any other member of the local community. Both PD and NND were calculated for each focal species with respect to the community as a whole, including both native and exotic species (designated PD_c and NND_c), and with respect to only the native species in the community (PD_n and NND_n). Distance to nearest neighbour is generally assumed to reflect interactions with the most phenotypically similar species, as originally proposed by Darwin, whereas mean phylogenetic distance (PD) is assumed to reflect interactions with the entire recipient community (Strauss et al., 2006).

We tested the influence of phylogenetic distinctiveness on exotic plant success using logistic regression. Exotic plants were classified as 'invasive' if they were found in the Global Invasive Species Database (http://www.issg.org) or as 'non-pest' if they were not. Invasive and non-pest designations were used as the response variable, with each of the phylogenetic metrics tested separately as an explanatory variable in a logistic regression. Thus, we used estimates of evolutionary distance from the local community to predict the likelihood of a plant being declared

'invasive'. Neither of the relatedness metrics using only the native species in the recipient community significantly predicted invasiveness (Table 1). We thus focused the rest of our analyses on plant relatedness relative to the entire recipient community.

We used ANCOVA to test the influence of phylogenetic relatedness and plant origin on plant abundance. We constructed separate tests for communities in the absence versus presence of herbivores, with plant origin as a fixed effect, either PD_c or NND_c as a covariate and the interaction term (plant origin × relatedness). Phylogenetic metrics were log-transformed to meet the assumptions of the model. This design allowed us to test whether local plant abundance differed by plant origin (native versus exotic) as moderated by phylogenetic relatedness, with a significant interaction term (e.g. plant origin × relatedness) indicative of invasion success being influenced by phylogenetic distance. We did not separate introduced plants by invasive versus non-pest status because initial ANOVAs showed no difference in the abundance of invasive versus non-pest plants across studies (see Results).

We used ANCOVA to test the influence of phylogenetic relatedness and plant origin on generalist herbivory. We constructed separate tests for native versus exotic herbivores, with plant origin included as a fixed effect and either PD_c or NND_c included as a covariate. Phylogenetic metrics were log-transformed to meet the assumptions of the model. This design allowed us to test whether plant response to herbivory differed by plant origin (native versus exotic) as moderated by phylogenetic relatedness separately for both native and non-native herbivores, with a significant interaction term (e.g. plant origin × relatedness), indicating that herbivore impact differed by the degree of the putative evolutionary mismatch.

We also tested whether herbivores influenced community-level phylogenetic diversity. From the assembled and dated phylogenetic tree, we calculated the pairwise distance matrix of branch lengths between all species using packages 'picante' and 'ape' in R 2.12 (R Development Core Team 2010) and then weighted each species by its relative abundance in the absence and presence of herbivores. Mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD) for each study were then calculated using the distance matrix weighted by species abundance using the picante functions 'mpd' and 'mntd' in R (Webb *et al.*, 2002). Two studies (one from each herbivore origin category) were excluded from this analysis because only a single plant species dominated the community in one of the herbivory treatments, rending the distance among species within a treatment incalculable. Paired *t*-tests were then used to compare MPD and MNTD between +H and −H treatments separately for native and exotic herbivore studies.

RESULTS

Phylogenetic relatedness predicted plant invasiveness (Table 1). Specifically, invasive plants were significantly more distant than non-pest species ($P = 0.035$) from their nearest relative in the entire community (NND_c). There was also a trend for invasive plants to be more phylogenetically distant from the entire community (PD_c, $P = 0.082$). Neither of the relatedness metrics using only the native species in the recipient community predicted invasiveness (Table 1). Although invasive plants were more phylogenetically distant than non-pests, there was no difference in local abundance between invasive and non-pest plant populations, either in communities with or without herbivores, although both were more abundant than the mean native plant population (Table 2).

Relatedness predicted plant success at the local level in both the presence and absence of herbivores, and the effect appeared largely consistent between native and exotic plants. In the absence of herbivores, increasingly phylogenetically distant native and exotic plant populations had higher relative abundance than species that were more closely related to the recipient community (Fig. 1a,b). The effect of phylogenetic isolation on abundance, however, was stronger for exotic species for both relatedness metrics (Fig. 1a,b; Plant

Table 1 Results from logistic regressions using predicting 'invasiveness' of introduced plants as a function of four phylogenetic relatedness metrics: PD_c (phylogenetic distance of each introduced species to the whole experimental community), NND_c (phylogenetic distance of each introduced species to the nearest neighbour in the whole experimental community), PD_n (phylogenetic distance of each introduced species to only the native species in the experimental community) and NND_n (phylogenetic distance of each introduced species to the nearest native plant in the experimental community). The positive relationship for NND_c suggests that 'invasive' plants were more distantly related to the nearest neighbour in the plant community than were 'non-pest' exotic plants. Bold values are significant at $P < 0.05$.

Metric	Estimate	SE	χ^2	$Pr(\geq|\chi^2|)$
PD_c	0.006	0.004	3.04	0.082
NND_c	**0.044**	**0.021**	**4.46**	**0.035**
PD_n	0.003	0.003	0.87	0.352
NND_n	0.007	0.013	0.26	0.610

Table 2 Invasive and non-pest exotic plant populations were both more locally abundant than native plant populations. Data are least-square mean percentage abundance of native plant populations, invasive plant populations and non-pest plant populations relative to total plant abundance in each community generated from separate ANOVAs in the absence of herbivores versus the presence of herbivores, with pest status as fixed factor and community as a random factor. (Model results: −herbivores: Plant Type$_{2,795}$: $F = 4.22$, $P = 0.015$; +herbivores: Plant Type$_{2,818}$: $F = 4.82$, $P = 0.008$). Levels not connected by the same letter are significantly different (Student's *t*-test).

Population	−herbivores Mean ± SE	+herbivores Mean ± SE
Native	7.85 ± 0.93a	6.67 ± 0.80a
Invasive	11.05 ± 1.58b	10.56 ± 1.76b
Non-Pest	10.26 ± 1.28b	9.98 ± 1.34b

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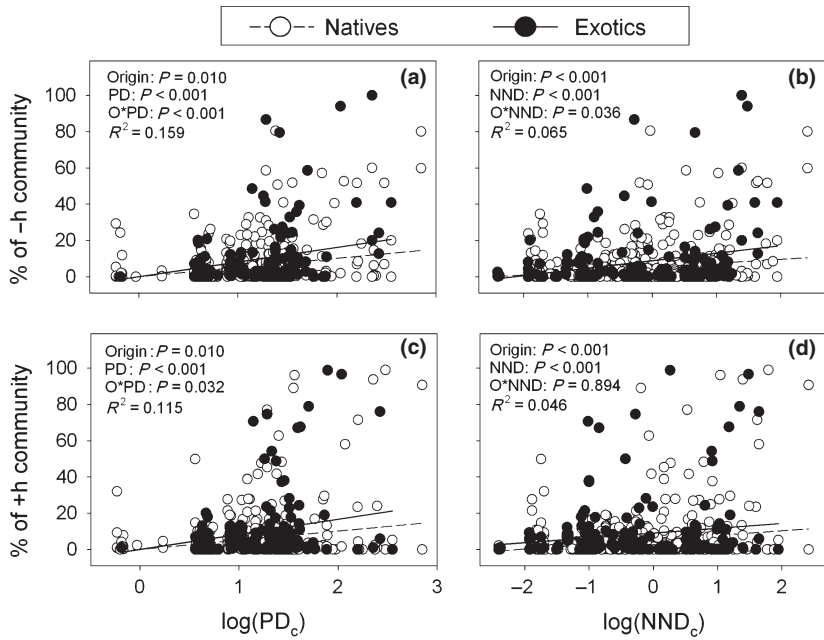
Figure 1 More distantly related native and exotic plant populations had higher relative abundance in their local communities, both in the absence of herbivores (a,b) and in the presence of herbivores (c,d).

Origin × PD_c/NND_c, $P \leq 0.036$). In the presence of herbivores, increasingly distant native and exotic plants were still more abundant than closely related plants (Fig. 1c,d), but the positive effect of relatedness was stronger for exotics only when calculated as distance to the entire recipient community (Fig. 1c; Plant Origin × PD_c, $P = 0.032$), not when calculated as distance to the nearest neighbour (Fig. 1d; Plant Origin × NND_c, $P = 0.894$).

Relatedness also had significant effects on herbivory, but the strength of the effect depended on particular plant–herbivore mismatches. Specifically, native herbivores had stronger impacts on more distantly related plants when relatedness was calculated relative to the entire community, and the effect was stronger for exotic plants (Fig. 2a; Plant Origin × PD_c, $P = 0.006$). Native herbivores also had increasingly negative impacts on distant plants when relatedness was estimated as distance to the nearest neighbour, with a trend for this effect to be stronger for exotic plants (Fig. 2b; Plant Origin × NND_c, $P = 0.066$). In contrast, exotic herbivores had stronger impacts on both native and exotic plants that were more phylogenetically distant from the local community, but there were no interactions between phylogenetic distance and plant origin (Fig. 2c,d).

Herbivores also altered community phylodiversity. Specifically, there was a strong trend for native herbivores to compress MPD within plant communities ($P = 0.057$, Fig. 3a), but not mean nearest taxon distance ($P = 0.960$, Fig. 3b). In contrast, exotic herbivores had no impact on MPD ($P = 0.267$, Fig. 3c) or on mean nearest taxon distance within communities ($P = 0.375$, Fig. 3d).

DISCUSSION

Our quantitative phylogenetic analysis of plant invasions in 49 herbivore exclusion experiments yielded support both for

and against Darwin's Naturalization Hypothesis (DNH). Increasing phylogenetic distinctiveness, for example, was generally predictive of an exotic plant being declared 'invasive'. This phylogenetic signal persisted across the idiosyncrasies of diverse local plant communities from a variety of habitats across several continents, suggesting a robust pattern similar to that previously shown at the regional scale among invasive grasses in California (Strauss *et al.*, 2006). These results are consistent with Darwin's general hypothesis that more distantly related species may be more successful invaders (Darwin, 1859). However, in contrast to DNH, increasing phylogenetic distance from the local plant community translated into more, not less, intense herbivory by both native and exotic generalist herbivores. Distantly related plants were thus more locally successful despite experiencing stronger herbivory, ultimately resulting in less phylogenetically diverse communities in the presence of native herbivores.

A significant difference between our calculations of relatedness and those of previous studies (Strauss *et al.*, 2006) is that we include both native and exotic plants in calculations of relatedness, rather than limiting relatedness metrics to include only the native plants. The omission of exotic plants is not ecologically realistic and can give spurious results. For example, we found effects of relatedness on plant invasiveness or herbivory only when relatedness was calculated relative to the entire recipient community, not when relatedness was restricted to only native species (Table 1). This pattern is ecologically significant given that communities are commonly invaded by multiple non-native species (Simberloff & Von Holle, 1999; Mack *et al.*, 2000), and these non-native species compete with one another, with natives, and all of them potentially share herbivores. Thus, estimates of community phylogeny based only on natives will not capture the entire

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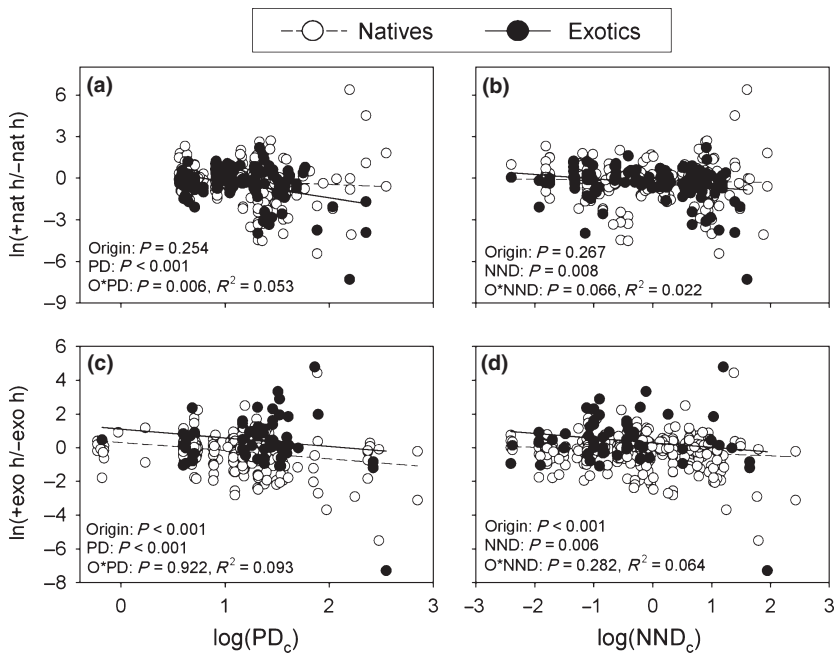
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Figure 2 Plants more distantly related to their local community were more susceptible to generalist herbivores. The response ratio (RR) of plant performance in the presence of a native herbivores relative to performance without native herbivores declines with mean phylogenetic distance (PD_c) from the entire local community (a) and from the nearest relative (NND_c) in the local community (b). The significant interaction term in (a), and nearly significant interaction term in (b), indicates that the effect of relatedness on herbivory was stronger for exotic than native plants. In panels (c) and (d), exotic herbivores had stronger impacts on both native and exotic plants that were increasingly phylogenetically distant from the local community.
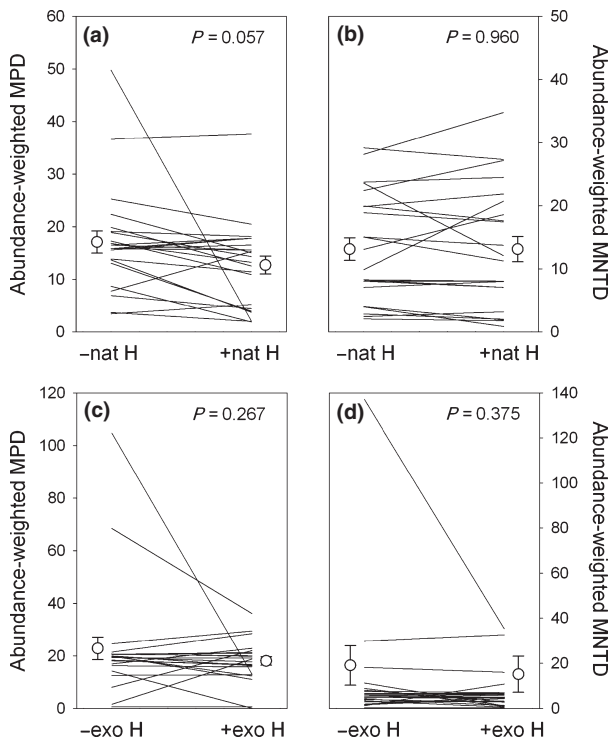

Figure 3 Native herbivores strongly trended towards suppressing mean phylogenetic distance among species within a community (a), but had no effect on mean nearest taxon distance (b). Exotic herbivores had no effect on either relatedness metric (c,d).

phylogenetic spectrum or the entirety of ecological interactions in a local community.

We also found a significant relationship between invasiveness and phylogeny only when relatedness was calculated relative to the nearest neighbour in community, not when relatedness was calculated relative to the entire recipient community (Table 1). If distance to the nearest neighbour reflects distance to the most phenotypically similar species in a community, an unknown assumption in our study, then this result suggests that limiting similarity among closely related species influences invasion success. However, there was still a trend for distance to the entire community to be predictive of invasion success (Table 1), and there were significant effects of PD on plant abundance and herbivore impact (Figs 1 and 2). These results suggest that invasion success is also the net result of diverse interactions among a diverse group of species, as others have suggested (Strauss *et al.*, 2006). Given that PD addresses deep-level phylogenetic clustering and that NND addresses terminal-level clustering (Webb *et al.*, 2002), significant results at both ends of the relatedness spectrum indicate that numerous aspects of the phylogenetic neighbourhood influence invasion success. More work is needed, however, to determine the relative importance of different mechanisms across this dichotomy.

Invasive plants are considered more problematic than non-pest exotic plants, and invasive plants were more distant from the local communities than non-pest exotics, implying that evolutionarily distant invaders in these studies were more ecologically successful. However, there was no difference in local abundance between invasive and non-pest exotic plants. This finding raises uncertainty about the ecological significance of species-level classifications of invasiveness, particularly when ecological impact is a function of local population density (Sakai *et al.*, 2001). It is possible that the local populations of invasive species in our studies may not have been the most invasive genotypes or populations of these species or that invasive and non-pest plants could have dissimilar ecological or economic impacts despite similar local abundance. The data

to make these distinctions rarely exist for most populations of introduced species (Wilcove *et al.*, 1998), however, despite their need (Davis, 2009).

One of the most striking patterns in our results was the similar way that phylogenetic dissimilarity predicted both native and exotic plant success despite increasingly strong top-down impact (Figs 1 and 2). The generality of this pattern across both native and exotic plants from a variety of habitats indicates that our findings have broad relevance to questions regarding the role of evolutionary history in community assembly. Increasing success of phylogenetically dissimilar species has generally been attributed to three factors, including one that we specifically examined. First, community assembly could proceed via 'niche filling' of distantly related species. This mechanism implies that more closely related species fared poorly because of limiting similarity, arguing against the role of niche conservatism in local community assembly, and is supported by studies implicating competition as a mechanism for phylogenetic overdispersion at the community scale (reviewed in Cavender-Bares *et al.*, 2009). Second, more distantly related species may be more likely to benefit from positive interspecific interactions with members of the recipient community (Valiente-Banuet & Verdú, 2007; Verdú *et al.*, 2009), consistent with the notion that facilitative interactions in the recipient community can promote invasions (Simberloff & Von Holle, 1999). We did not address either causal mechanism explicitly, but our findings are consistent with these predictions and with recent studies showing a distinct phylogenetic signature of overdispersion at the local scale (Verdú *et al.*, 2009; Letcher, 2010).

Third, intense herbivore pressure from generalists is predicted to cause either phylogenetic overdispersion or clustering (Cavender-Bares *et al.*, 2009), and our study did explicitly examine the effect of herbivory on community phylogeny. Our results are broadly consistent with the prediction that generalists will cause phylogenetic clustering. Native generalist herbivores suppressed community phylodiversity (Fig. 3a) by having stronger effects on plants that were more distantly related to the recipient community (Fig. 2a,b), a pattern that was conserved for both native and exotic herbivores on both native and exotic plant species (Fig. 2c,d). These patterns are opposite to predictions from the Enemy Release and Novel Weapons Hypotheses and empirical results with more specialized insect herbivores (Hill & Kotanen, 2009, 2010; Pearse & Hipp, 2009; Ness *et al.*, 2011), pointing to the growing recognition that generalist and specialist herbivores have fundamentally different interactions with native and non-native plants (Joshi & Vrieling, 2005). Specialists, for example, generally consume, at most, a few closely related plant species and thus are likely not pre-adapted to feeding on taxonomically novel, unrelated plants. This provides a relatively straightforward explanation for why phylogenetic isolation can provide plants with release from specialist enemies, leading to the prediction that specialists are less likely than generalist herbivores to cause phylogenetic clustering (Cavender-Bares *et al.*, 2009).

Generalists, in contrast, consume a wide variety of often unrelated plants, and there is no a priori reason why they would not be pre-adapted for feeding on taxonomically novel plants (Keane & Crawley, 2002; Lind & Parker, 2010). In fact, evolutionary logic suggests that the opposite pattern may be likely; generalists could preferentially consume distantly related plants because they are less likely to contain defences similar to the native community (Hokkanen & Pimentel, 1989; Parker & Hay, 2005; Morrison & Hay, 2011). Alternatively, the same pattern of phylogenetic clustering could result if generalist herbivores fed preferentially on the most abundant plants in a community, which in these studies were the most phylogenetically distinct species, possibly as a result of facilitative interactions or release from competition. Thus, the stronger impact of herbivores on distantly related species in these studies could have resulted from an evolutionary mismatch between plants and generalist herbivores or from proportional feeding on abundant plants, but both mechanisms ultimately result in herbivores suppressing community phylodiversity.

The pattern that phylogenetically distant exotic plants were more abundant but impacted more strongly by generalist herbivores suggests a potential interaction between competition, herbivory and phylogeny in driving species invasions. For example, one way to interpret our findings is that the positive effects of being phylogenetically distinct on competition outweighed the negative effects of increasing generalist herbivory. One important piece of data that we cannot evaluate that would strengthen this argument is the relative intensity of herbivory and competition across these studies. It could be that phylogenetically distinct exotic plants experienced relatively greater release from competition when herbivore intensity is low and community interactions are dominated by competition.

Phylogenetic tools and the increasing availability of genetic data now permit incorporation of explicit evolutionary relatedness metrics into most ecological studies conducted at the community scale (Cavender-Bares *et al.*, 2009). By incorporating a standardized metric of phylogenetic relatedness into our meta-analysis of the impact of herbivores on plant invasions, we explicitly showed that distantly related exotics were more successful than closely related exotics despite experiencing greater impacts by generalist herbivores. These findings support some but not all elements of Darwin's Naturalization Hypothesis. To our knowledge, our study is the first to show that herbivores can influence community phylogenetic structure, and the first to show a local pattern of plant success via phylogenetic release across both native and exotic species, suggesting that evolutionary history influences community assembly. Ultimately, however, phylogenetic relatedness alone explained a relatively small portion of the variability in the data set, suggesting that models incorporating phylogeny in conjunction with other important factors, including plant abundance, plant phenotypic traits and the intensity of herbivory, could substantially improve the predictive power of community phylogenetics.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Studies in analyses.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCH

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Authors contributions: J.D.P. and D.E.B. conceived the ideas and collected the data; J.D.P., D.E.B., M.J.L. and E.M.L. analysed and interpreted the data; J.D.P. led the writing.

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Appendix S1. Studies in analyses.

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