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LETTER

Trait vs. phylogenetic diversity as predictors of competition and community composition in herbivorous marine amphipods

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Abstract

Field studies of community assembly patterns increasingly use phylogenetic relatedness as a surrogate for traits. Recent experiments appear to validate this approach by showing effects of correlated trait and phylogenetic distances on coexistence. However, traits governing resource use in animals are often labile. To test whether feeding trait or phylogenetic diversity can predict competition and production in communities of grazing amphipods, we manipulated both types of diversity independently in mesocosms. We found that increasing the feeding trait diversity of the community increased the number of species coexisting, reduced dominance and changed food availability. In contrast, phylogenetic diversity had no effect, suggesting that whatever additional ecological information it represents was not relevant in this context. Although community phylogenetic structure in the field may result from multiple traits with potential for phylogenetic signal, phylogenetic effects on species interactions in controlled experiments may depend on the lability of fewer key traits.

Keywords

Coexistence, community phylogenetics, dominance, experiment, feeding, marine, Mean Nearest Taxon Distance, mesocosm, resource competition, seagrass.

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INTRODUCTION

Ecologists have long sought to understand if and why some combinations of species are more likely to coexist than others. There is a strong theoretical and empirical foundation for the idea that niche separation reduces competition and promotes coexistence (Macarthur & Levins 1967; Titman 1976), but scaling up from a limited number of species interactions to the assembly of whole communities remains challenging. In the last several years, however, the search for rigorous ways of testing for community-wide evidence of resource partitioning vs. environmental filtering has yielded a new set of tools.

Although early work dealt primarily with matrices of species presence and absence in community samples (Diamond 1975; Connor & Simberloff 1979), current approaches use evolutionary relationships (Webb *et al.* 2002; Cavender-Bares *et al.* 2009) and/or trait data (Weiher & Keddy 1995; McGill *et al.* 2006) to quantify differences between species that do and do not coexist. Based on the idea that phylogenetic distance between species could stand as a proxy for overall ecological differentiation, phylogenetic distance between community members that is greater than expected by chance has been suggested as potential evidence of competitive exclusion (Webb *et al.* 2002), but this approach assumes trait conservatism or at least phylogenetic signal for key traits (Losos 2008).

Partly to address this assumption, there is currently a focus on direct tests of the mechanisms linking phylogenetic relationships to community assembly. Although community phylogenetics was originally proposed to examine coexistence among species for which experimental approaches were intractable (such as tropical trees, Webb *et al.* 2002), the field is quickly expanding to systems with faster dynamics and smaller spatial scales. A handful of recent studies have manipulated the phylogenetic distance between interacting species pairs of plants (Burns & Strauss 2011), protists (Violle *et al.* 2011) or fungi (Maherali & Klironomos 2007; Peay *et al.* 2011) and looked for effects on competitive interactions. Most of these studies have also measured some kind of trait difference between species over the course of the study, and found some degree of correlation between trait and phylogenetic distance.

However, not all ecologically relevant traits show phylogenetic signal (Losos 2008), and in fact, there is good reason to suspect that traits related to resource acquisition in animals might differ among closely related species (Bohning-Gaese & Oberrath 1999; Johnson *et al.* 2008), perhaps as a means of reducing competition via habitat segregation (Losos 1995). When specific traits or groups of traits lack phylogenetic signal, it should be possible to separate the relative importance of particular traits vs. overall phylogenetic relatedness as predictors of ecological outcomes. In our investigation of a system of herbivorous marine crustaceans (amphipods and isopods), we have found little evidence of phylogenetic signal in the fundamental food niche (Best 2012), which we hypothesise should be important in determining competitive outcomes. In seagrass systems, most amphipods can feed on epiphytic microalgae growing on seagrass blades, but they vary in their access to alternative resources such as seagrass tissue, detritus or macroalgae (Duffy & Harvilicz 2001; Best & Stachowicz 2012). Exclusive access to alternative food resources via differences in fundamental feeding niche could thus have strong effects on resource competition. On the other hand, phylogenetic data may capture a more comprehensive and unbiased index of similarity that integrates over multiple niche dimensions (Cadotte *et al.* 2008; Burns & Strauss 2011), and may therefore predict additional variation in species outcomes that results from other important traits, such as interference competition, net reproductive rate or habitat use, some of which do show phylogenetic signal (Best 2012).

To assess the relative predictive power of these two types of data, we designed a mesocosm experiment in which species combinations varied independently in their feeding trait diversity and phylogenetic diversity. We replicated 18 different combinations of three species of amphipods (drawn from a pool of nine species), and tested for effects of feeding trait and phylogenetic diversity on competitive outcomes and community-wide production. Specifically, we tested the hypotheses that higher phylogenetic and/or trait diversity

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should (1) reduce the potential for competitive exclusion, resulting in more even abundances among competing species, (2) reduce the success of invading species due to more complete occupation of niche space and (3) ultimately increase overall secondary production and decrease primary producer biomass due to complementary resource use. Across these responses, we found effects of trait diversity at multiple levels, but no effects of phylogenetic diversity. This suggests that controlled experiments on the effects of phylogenetic relationships may be even more dependent on the lability of particular traits than the field studies they are designed to interpret.

METHODS

Study system

We selected species combinations from a pool of nine species of herbivorous marine amphipods, all commonly found in habitats dominated by eelgrass (*Zostera marina*) and macroalgae (*Ulva*. spp) in Bodega Bay, California (38°19.110′ N 123°04.294′ W). To isolate the effects of trait and phylogenetic diversity from the effects of species richness, we held species richness constant at three species per 30 cm diameter mesocosm. This is within the range observed in the field (0–9 species per equivalent area) yet low enough to allow interpretation of species interactions. For each of the 84 possible combinations of three species, we calculated phylogenetic and feeding trait diversity. We then selected 18 different species combinations for replication in outdoor flow-through mesocosms stocked with the full range of naturally available food sources.

Phylogeny

As detailed in Best (2012), we used Bayesian phylogenetic analysis in BEAST (Drummond & Rambaut 2007) to obtain a posterior distribution of ultrametric community phylogenies for the species in our system based on three genes: COI, 16S mitochondrial rRNA and 18S nuclear rRNA. The consensus phylogeny is given in Fig. 1a, but we incorporated uncertainty in topology and branch lengths by performing each analysis on 100 trees randomly drawn from the posterior distribution. Using each tree, we measured the phylogenetic diversity of each species combination as the Mean Nearest Taxon Distance (MNTD, Webb *et al.* 2002), hereafter phylogenetic MNTD. We also calculated the average value of this metric for each species combination over a sample of 1000 trees. We present the results obtained for the average phylogenetic MNTD, as well as the number of trees for which the results differed from the average. Finally, to ensure our results were not sensitive to metric, we also calculated the average Mean Pairwise Distance (MPD, Webb *et al.* 2002) and the average total community branch length (PD, Faith 1992) for each combination. We calculated all metrics using the Picante package (Kembel *et al.* 2010) in R (R Core Team 2012).

Feeding traits

The feeding trait data for these species were obtained using no-choice feeding trials, as described in Best & Stachowicz (2012). Briefly, for each combination of nine grazer species and four foods [eelgrass, eelgrass detritus (hereafter 'detritus'), macroalgae (*Ulva* spp.) or epiphytic microalgae], we measured consumption over 48 h in 250-mL cups filled with seawater. We measured feeding rates (consumption per individual per day) in terms of wet weight (for eelgrass, detritus and macroalgae), or chlorophyll *a* (for epiphytic microalgae). Species were considered capable of eating a food if their feeding rate on that food was significantly greater than zero. Based on these data, all nine species used in our experiment consume epiphytic microalgae, and smaller numbers consume macroalgae, detritus and/or fresh eelgrass (Fig. 1a). To determine the feeding trait diversity of a species combination, we calculated a feeding trait MNTD index in parallel to the phylogenetic MNTD described above, using a binary distance matrix. Given a pair of species, the binary feeding distance between them is the number of

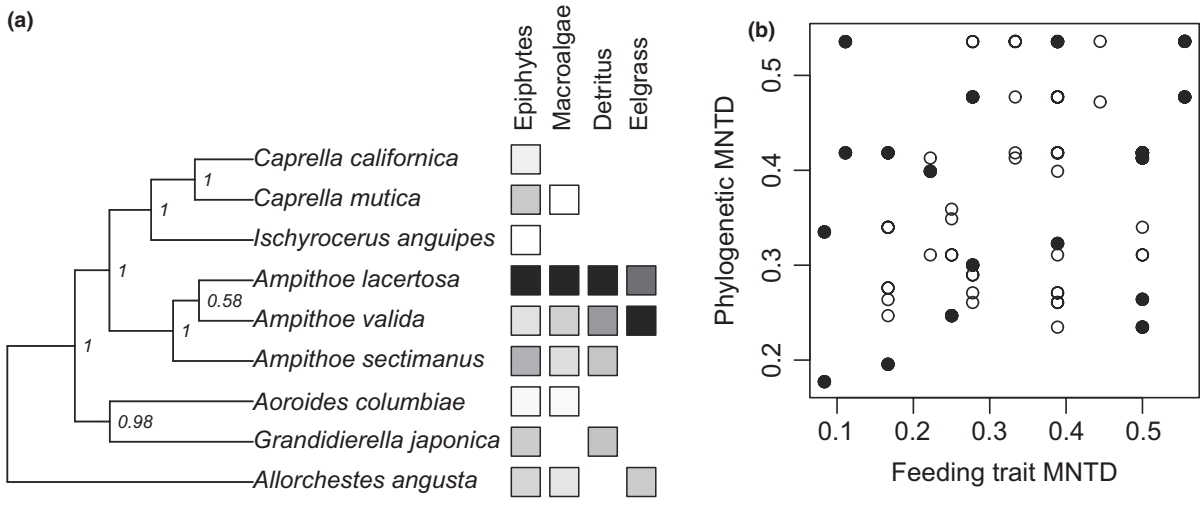

Figure 1 Phylogeny and feeding traits. In panel (a) the phylogeny is the maximum clade credibility consensus tree from three independent BEAST runs and is ultrametric with uncalibrated branch lengths relative to time. Filled boxes indicate that species showed significant consumption of that food in feeding trials. Within each food, darker shades represent higher feeding rates. Species are *Allorchestes angusta* Dana, 1856; *Ampithoe lacertosa* Bate, 1858; *A. sectimanus* Conlan and Bousfield, 1982; *A. valida* S. I. Smith, 1873; *Aoroides columbiae* Walker, 1898; *Caprella californica* Stimpson, 1857; *C. mutica* Schurin, 1935; *Grandidierella japonica* Stephense, 1938; *Ischyrocerus anguipes* Krøyer, 1838. Panel (b) shows both types of diversity for each species combination. Open circles represent all 84 possible combinations of three grazers out of the nine grazer pool. Closed circles represent the 18 combinations selected for inclusion in the experiment.

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foods that only one species eats, divided by the number of foods that at least one species eats. As such it represents the degree of overlap in potential feeding niche, but is not correlated with the presence/absence of particular species. This would not be the case if we used distances based on continuous feeding rates, as the largest feeding trait distances would then only be possible in the presence of the species with the highest feeding rates. As for phylogenetic diversity, we also calculated the trait MPD and Petchey and Gaston's Functional Diversity (FD, 2002) for each combination. We conducted the analyses for this study using the MNTD metrics, the MPD metrics and PD vs. FD, but obtained very similar results in each case, and present only the MNTD results.

Experimental mesocosms

We randomly selected 18 combinations out of 84 possibilities with the following constraints. To realistically represent the pool of individuals assembled into communities in the field, we made common species more prevalent than rare species. We also ensured that the full range of MNTD values were represented, that neither diversity metric was correlated with the presence of particular species, and that there was no correlation between phylogenetic MNTD and feeding trait MNTD in the sample ($r = 0.22$, $P = 0.37$, Fig. 1b). This lack of correlation was representative of our system rather than exceptional: repeating 10 000 random draws of 18 combinations, the median value of r was 0.30 and the median P-value 0.22 (see Fig. S1 in Supporting Information). For a list of combinations with their calculated diversity metrics see Table S1. We used three replicates per combination, along with six controls (no grazers added), for a total of 60 mesocosms. All species combinations should be possible natural communities, but we did not rule out combinations that are rarely observed in the field because community composition may be affected by the species interactions we wanted to test (Colwell & Winkler 1984).

We set up our experiment in June 2011 at the Bodega Marine Laboratory, using an array of 24.6 L outdoor flow-through mesocosms with 500-μm screens to prevent escape of juvenile amphipods. Mesocosms in the array were plumbed in groups of four per tank, with the tanks distributed across a known light gradient set up by shade from nearby buildings. To ensure even distribution of diversity gradients over the light gradient, we randomly assigned species combinations to tanks with the constraint that each tank contained all combinations of high and low phylogenetic and trait diversity. On the basis of daily observations, we also characterised the light gradient over the array using an index from 1 to 6 representing longest to shortest period of daily direct sun exposure.

In each mesocosm, we planted seven eelgrass shoots of equal shoot and rhizome length (30 and 2.5 cm respectively) in 8 cm of sieved mud from Bodega Harbor and allowed 8 days for epiphyte accumulation. We then added 40 g wet weight of macroalgae to each mesocosm. Initial eelgrass and macroalgal densities were within the range observed naturally in our system (Best & Stachowicz 2012), and all plant material was soaked for 5 min in fresh water to kill any attached animals. Finally, we added the grazers, using five adult males and five brooding females of each species to ensure the possibility of population growth. As the initial supply of macroalgae was completely consumed in several mesocosms within the first month, we added equal amounts of additional macroalgae to every mesocosm in weeks 5, 7 and 9. This further addition (a total of 70 g per mesocosm) was necessary to prevent population crashes early in the experiment, and mimics the ongoing input of drift algae from surrounding mudflats in the field, where macroalgae does not decline until late fall.

At the end of 10 weeks, we counted juvenile and adult amphipods of each species per mesocosm, and collected and separated all plant material. Epiphytic microalgae was cleaned from both the eelgrass shoots and the sides of the mesocosms, and both grazers and primary producers were placed in a 60 °C drying oven to obtain final dry weight. We also separately dried 10 replicate individuals of each species, collected from the field, to estimate the mean dry weight for each species and the initial dry biomass for each species combination.

Analysis

We tested for the effects of phylogenetic and feeding trait diversity on competitive outcomes by comparing the population growth of the species within each mesocosm. Within each mesocosm, we ordered the three species in the combination by their final population size, and coded these as high, middle and low performance levels. The least successful of the three species was frequently one of two species that failed to thrive in any mesocosms regardless of their species combination (see Fig. S2). As such, the relative abundance of the low level was negligible, and impossible to fit to parametric models, so we excluded it from the analysis. In contrast, a substantial fraction of the final abundance in our mesocosms was comprised of a single invading species. One of the species used in our experiment, *Aoroides columbiae*, invaded mesocosms where it was not originally stocked and reached abundances equal to or exceeding the abundance of the stocked species. As this species clearly played a role in species interactions, we included it in our analysis as a third performance level (invader). This performance level is only represented in mesocosms where *A. columbiae* was not originally stocked, but these are distributed along the full range of both diversity gradients. We then tested for interactions between performance level (high, middle and invader), and the phylogenetic and feeding trait diversity of the species combination. If increased diversity decreases competitive overlap and prevents dominance by a strong competitor, then the abundance of the highest performers should decrease relative to the abundance of lesser performers as diversity increases. Additionally, we expected that invader abundance would decrease with increasing diversity of the resident species.

To test for this interaction (and for all further analyses in this study), we used a mixed model framework. With final abundance as the response variable, the fixed effects were performance level, phylogenetic MNTD, feeding trait MNTD and two-way interactions between each of the diversity metrics and performance level. We also included the light gradient in the mesocosm array as a fixed effect for its potential to limit primary production and thus resource availability. Random intercept effects were tank, mesocosm, species combination and grazer species. This allowed us to account for substantial among-species variation in size and fecundity, and for non-independence of multiple observations per mesocosm. We also used random slope effects to allow for variation in grazer responses (grazer*light gradient, grazer*phylogenetic MNTD and grazer*feeding trait MNTD random effects). Finally, to investigate the success of invaders beyond the single most abundant species, we tested for effects of trait and phylogenetic diversity on final species richness.

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We used phylogenetic MNTD, feeding trait MNTD, and the light gradient as the fixed effects, and tank and species combination as the random effects.

We also examined how each species responded individually to variation in the trait and phylogenetic diversity of the assemblage. We used abundance of each species as the response variable, with grazer species, feeding trait MNTD, and their interaction as fixed effects, and tank, species combination, and mesocosm as the random effects. We repeated this test using phylogenetic MNTD. Using the slopes and intercepts fit for each grazer species in these models, we then calculated the effect size for each species as the change in abundance over the full length of the diversity gradient. We did not attempt to determine the significance of each species' response, as this would be somewhat biased by their relative abundances, and would have low power if multiple comparison adjustments were made.

Scaling up from community composition to overall system function, we tested for effects of trait and phylogenetic diversity on total grazer biomass and primary producer biomass. For grazer biomass, we used phylogenetic MNTD, feeding trait MNTD, the light gradient and initial grazer biomass as the fixed effects, and tank and species combination as the random effects. Initial grazer biomass was included because the mesocosms were initiated with equal grazer abundance but variable biomass depending on the included species. For the primary producers, we added producer (eelgrass, detritus, macroalgae or epiphytes) as a fixed effect and included two-way interactions between producer and all other fixed effects. We also included mesocosm as a random effect to account for multiple producers per mesocosm.

We conducted these analyses in SAS (SAS Institute Inc 2008) using the MIXED Procedure with the REML fitting method and the Kenward Rogers method for estimating denominator degrees of freedom (Littell *et al.* 1996). To test the significance of random effects, we used likelihood-ratio tests. For all models, we examined residuals for equal variance, normality and nonlinearity, and log-transformed response variables when necessary.

Finally, to aid in interpreting the effects of feeding trait and phylogenetic diversity, we tested for phylogenetic signal in both feeding rate on epiphytes (the universal resource), and total feeding rate on all alternate resources (eelgrass, macroalgae and detritus). We used Blomberg's K (Blomberg *et al.* 2003), implemented in the Phytools package in R (Revell 2011), obtaining both an estimate of K and a test for non-random correspondence between trait and phylogeny. We also assessed phylogenetic signal in species' relative performance by coding the performance levels as 1 (low), 2 (middle) or 3 (high), and calculating the average level for each species across all mesocosms in which it was found.

RESULTS

Effects of phylogenetic and trait diversity on competitive dynamics within mesocosms

We found that the relative abundances of component species were affected by feeding trait diversity, but not phylogenetic diversity. Under higher feeding trait diversity, high performers were less dominant, and middle performers increased. This converging of abundance at high trait diversity is shown by the opposing slopes of the trait diversity vs. abundance regressions (Fig. 2a, Table 1). In contrast, phylogenetic diversity had no effect on the relative abundance of performance levels; neither the phylogenetic MNTD term nor its interaction with performance level was significant. The random among-grazer variation in responses to the light gradient was significant, and there was a weak effect of tank (Table 1). The significance of all fixed effects in this analysis and those following was almost entirely unaffected by uncertainty in phylogenetic topology and branch lengths (Table 1).

Contrary to our predictions, the invading *A. columbiae* also increased in abundance with the trait diversity of the stocked assemblage (Fig. 2a). In combinations with higher trait diversity, the decrease in abundance of high performers therefore corresponded to increases in both the lesser competitors stocked in the mesocosms and an invading species. Although the high and middle performers and the invading *A. columbiae* accounted for an average of 95% of the total abundance in each mesocosm (range: 77–100%), higher feeding trait diversity also allowed a greater number of low-abundance invaders to enter the mesocosms, resulting in higher species richness (Fig. 2c). These additional invaders accounted for no more than 1% of total mesocosm abundance, but in several cases included brooding adults, which could have led to increased population sizes over a longer time period. Some of the invaders may have arrived in the mesocosms via the seawater system, and some were likely introduced as juveniles on the primary producers, despite efforts to minimise such contamination. However, there is no reason why introduction pressure would have varied across species combinations in any systematic way.

Although most species showed some variation in their relative performance, some were more often successful than others (see Fig. S2). There was little evidence for significant phylogenetic signal in average performance level ($K = 0.61$, $P = 0.53$), but two species consistently failed to produce population growth. *Grandidierella japonica* and *Ischyrocerus anguipes*, which are neither particularly similar to each other nor different from the other species (Fig. 1a), were almost always in the excluded low performance level and accounted for only 0–7 and 0–0.4% of total mesocosm abundance respectively. As they provided too little data to work with, we excluded them from subsequent analysis.

Differences in the way high and middle competitors responded to increased trait diversity may be partly due to variation among grazer species. We found that some species increased in abundance along the trait diversity gradient, and others decreased [significant interaction between grazer species and feeding trait MNTD (but not phylogenetic MNTD) Fig. 3, Table 1]. This difference in response was correlated with the species' feeding rates on epiphytic algae, the one resource which all species can consume (Fig. 4a), with a similar but weaker trend for total feeding rate on other foods (Fig. 4b). This suggests that species with slower consumption rates benefitted the most from higher trait diversity, where they were more likely to have exclusive access to a resource. Neither of the feeding rates showed significant phylogenetic signal (feeding on epiphytic algae: $K = 0.51$, $P = 0.64$; feeding on macrophytes: $K = 0.64$, $P = 0.42$).

Effects of phylogenetic and trait diversity on community-level outcomes

Despite significant changes in the relative abundances of component species over the feeding trait diversity gradient, total grazer biomass was unaffected (Table 1). Decreasing light availability had some negative effect, presumably via primary production, but the

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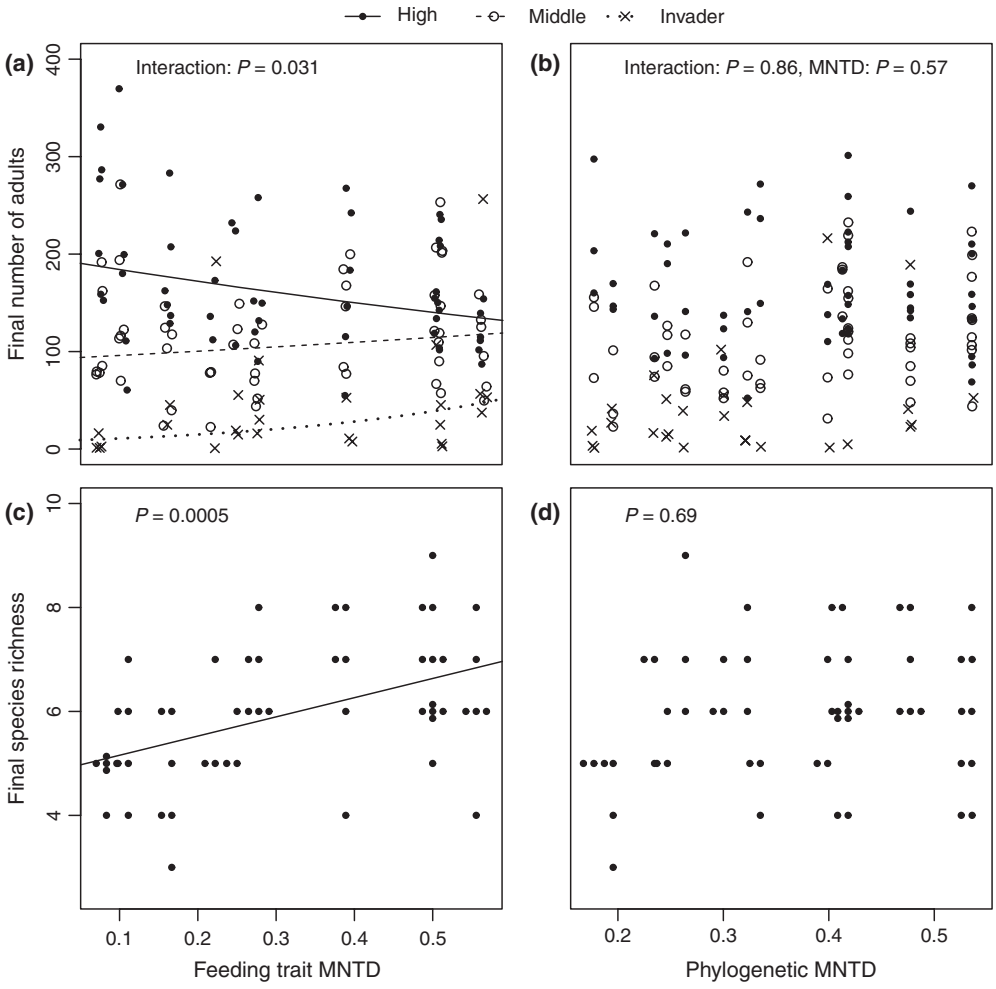

Figure 2 Effects of feeding trait and phylogenetic diversity on abundance of competitors and total species richness. Panels (a) and (b) show interactions between performance level and feeding trait and phylogenetic Mean Nearest Taxon Distance respectively. Abundance was log-transformed for analysis, estimated random effects were removed, and points and fitted lines were then back transformed to enable comparison with initial abundance (10 individuals per species). For panels (c) and (d), initial species richness was 3. In all four panels, the *x*-variables are slightly offset to avoid overlap of identical data points.

largest determinant of final grazer biomass was starting biomass (Table 1, see Fig. S3b), which varied between species combinations because some species are much larger than others. Similarly, initial grazer biomass was the main determinant of primary producer biomass, having a particularly negative effect on macroalgae and detritus (Table 1, see Fig. S3d). Accounting for this large identity effect, we also found that increasing feeding trait diversity differentially affected the primary producers, leading to increased epiphytic microalgae and decreased macroalgae [Fig. 5a, slope for epiphytes significantly different from zero ($P = 0.011$); macroalgae ($P = 0.064$); detritus and eelgrass, ($P > 0.25$)]. Thus, under higher trait diversity the universal resource increased, and a major alternative resource decreased. Grazer phylogenetic diversity did not affect primary producer biomass (Table 1, Fig. 5b).

DISCUSSION

We found consistent effects of feeding trait diversity on competitive outcomes and species richness, but no effect of phylogenetic diversity. This is in contrast to a handful of recent studies that appeared to provide the foundation for an emerging consensus that increasing phylogenetic distance between competitors decreases the intensity of competition (Burns & Strauss 2011; Peay *et al.* 2011; Violle *et al.* 2011). First, we discuss the potential mechanisms underlying the observed effects of trait diversity in our system. Next, we discuss possible reasons why phylogeny was not important in our system in comparison to others, including the type and number of traits involved in the interaction and the type of outcome investigated.

Feeding trait diversity: effects on competitive outcomes and community biomass

The major effect of increasing trait diversity was on the relative abundance of competing species. Neither total grazer abundance nor biomass varied across the feeding trait diversity gradient, but the abundances of the component species equalised (Fig. 2a) and additional species were able to invade (Fig. 2c), when trait diversity was high. In addition, the differential response of high and middle performers was underlain by variation among species in their responses to trait diversity (Fig. 3). Species with faster overall feeding rates on the universal resource (epiphytic algae) were negatively affected by increasing trait diversity, whereas species with slower

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Table 1 Statistical results for all models. *P*-values < 0.05 are interpreted as significant and given in bold. Conclusions about the significance of fixed effects were identical for all 100 trees sampled from the posterior distribution, with two exceptions (see footnotes)

Response variable	Fixed effects	df	*F*	*P*	Random effects	*P*
ln (Abundance by group)	Light gradient	1, 7.69	3.25	0.11	Tank	0.061
	Performance level	2, 42.2	7.44	**0.0017**	Mesocosm	1
	Phylo. MNTD	1, 17.1	0.33	0.57	Species combination	0.25
	Trait MNTD	1, 16.5	2.1	0.17	Grazer	0.65
	Performance level*Phylo. MNTD	2, 70.9	0.15	0.86	Grazer*Light gradient	**0.008**
	Performance level*Trait MNTD	2, 98.5	3.59	**0.031***	Grazer*Phylo. MNTD	1
					Grazer*Trait MNTD	1
Species richness	Light gradient	1, 50	3.41	0.071	Tank	1
	Phylo. MNTD	1, 50	0.05	0.69	Species combination	1
	Trait MNTD	1, 50	14.36	**0.0005**		
ln (Abundance by grazer)	Grazer	8, 135	15.4	**<0.0001**	Tank	**0.001**
	Trait MNTD	1, 135	0.22	0.51	Species combination	1
	Grazer*Trait MNTD	8, 136	2.67	**0.01**	Mesocosm	1
ln (Abundance by grazer)	Grazer	8, 135	5.84	**<0.0001**	Tank	**0.002**
	Phylo. MNTD	1, 138	1.09	0.3	Species combination	1
	Grazer*Phylo. MNTD	8, 135	1.47	0.17	Mesocosm	1
ln (Total grazer biomass)	Light gradient	1, 13.7	4.82	**0.046**	Tank	0.09
	Initial grazer biomass	1, 13.5	97.6	**<0.0001**	Species combination	**0.003**
	Phylo. MNTD	1, 12.7	1.73	0.21		
	Trait MNTD	1, 12.8	0.01	0.94		
ln (Producer biomass)	Producer	3, 181	55.12	**<0.0001**	Tank	1
	Light gradient	1, 7.81	0.07	0.8	Species combination	0.24
	Initial grazer biomass	1, 14.7	111.49	**<0.0001**	Mesocosm	0.37
	Phylo. MNTD	1, 14.3	0.62	0.44		
	Trait MNTD	1, 14.4	0.15	0.71		
	Producer*Light gradient	3, 181	3.37	**0.02**		
	Producer*Initial grazer biomass	3, 181	87.33	**<0.0001**		
	Producer*Phylo. MNTD	3, 181	0.97	0.41		
	Producer*Trait MNTD	3, 181	2.89	**0.037**†		

MNTD, Mean Nearest Taxon Distance.
*For 8/100 trees, the *P*-value for this effect fell between 0.05 and 0.12. Note that the random sampling of trees from the posterior distribution weights topologies and branch lengths according to their probability, but does not exclude any relatively unlikely topologies or branch lengths. As such, the consistency in results over 92% of the sampled trees indicates that the result is robust to all probable parameters of the phylogeny.
†For 1/100 of trees, the *P*-value for this effect fell between 0.05 and 0.06.

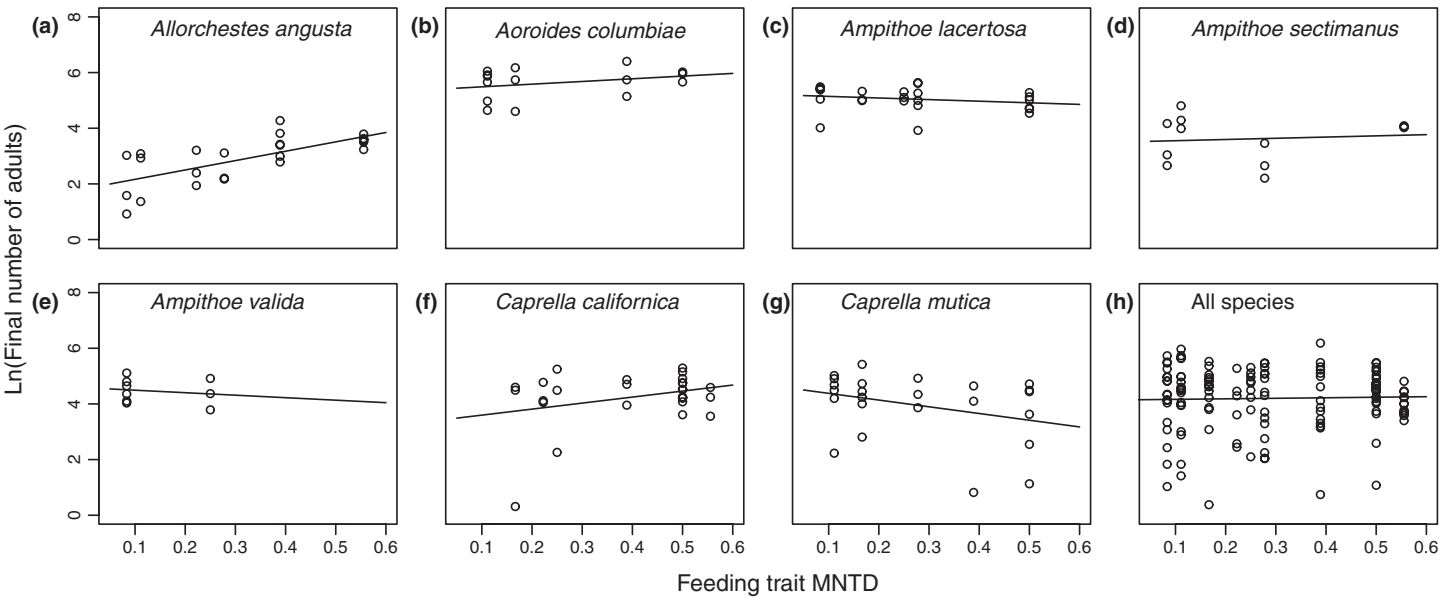

Figure 3 Grazer-level effects of feeding trait diversity. Panels (a) to (g) show responses for the seven species with non-negligible abundance. Panel (h) shows the overall pattern for the seven species combined. Abundance was log-transformed to meet the assumption of equal variance. To measure effect size over the gradient in terms of numbers of individuals, we used the fitted slopes and intercepts to calculate the expected abundance at each end of the feeding trait Mean Nearest Taxon Distance gradient, back-transformed these values and calculated the difference.

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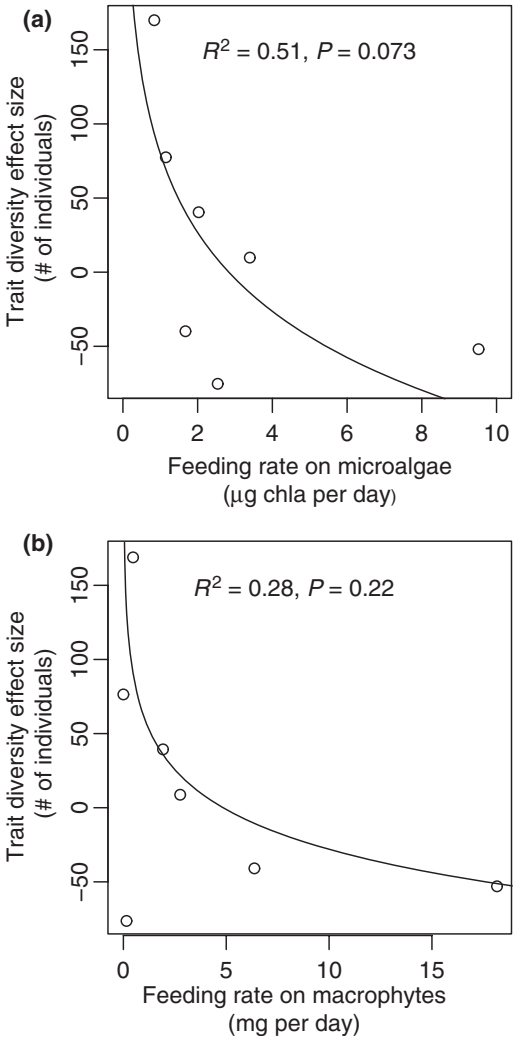

Figure 4 Effects of individual species' feeding niche on their response to trait diversity. Panel (a) shows the effect of feeding rates on epiphytic microalgae, the universal resource, and panel (b) shows the effect of the summed feeding rates on macrophytes (eelgrass, macroalgae and detritus, whichever are consumed by the species). The total number of foods that a species can eat had a weaker effect on the response to trait diversity (P = 0.25).

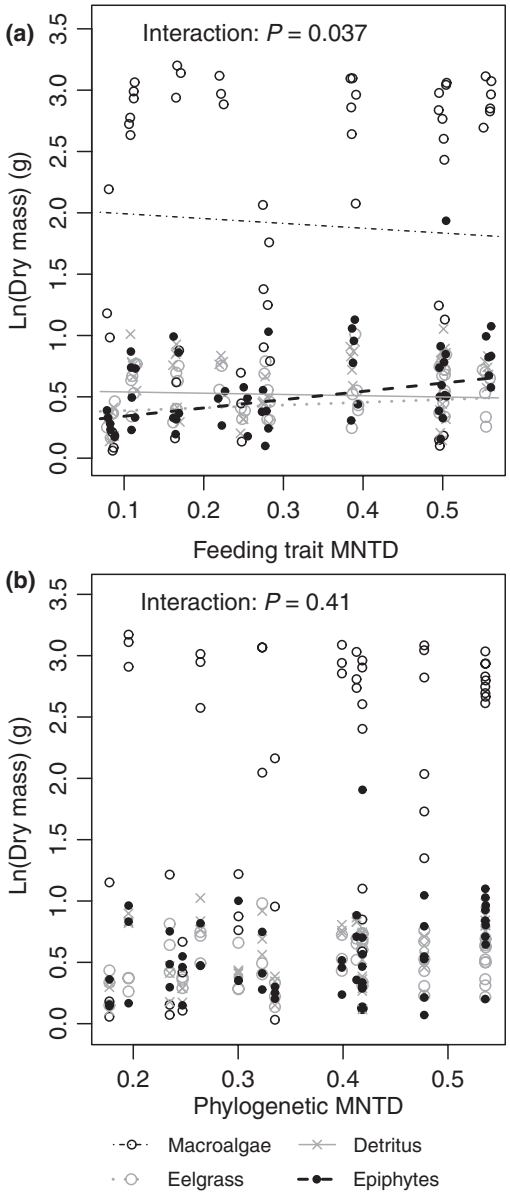

Figure 5 Effects of feeding trait and phylogenetic diversity on the biomass of all primary producers. Interactions are between the primary producer type and the feeding trait or phylogenetic Mean Nearest Taxon Distance respectively. Biomass was log-transformed for analysis and estimated random effects were removed. The x-variables are slightly offset to avoid overlap of identical data points. A large amount of the variation in macroalgal biomass is explained by the initial grazer biomass, which was determined by grazer identity (grazer species vary in size; see Fig. S3).

feeding rates benefitted (Fig. 4a). Overall, these results suggest that both the availability of a single common resource and the complementarity of alternative resources at high trait diversity may affect grazer diversity in this system. This situation could apply widely in marine systems, because most herbivores consume microalgae but differ in their ability to consume different macrophytes, but may also apply to grasslands or other terrestrial systems in which a broad range of herbivores consume seedlings of the same plants (Hulme 1994).

We can interpret the effects of species variation in feeding niche in terms of stabilising and equalising coexistence mechanisms (Chesson 2000; Mayfield & Levine 2010). At low trait diversity, there is high resource use overlap and no stabilising effects of exclusive resources. Thus, coexistence depends on equalising mechanisms that minimise fitness differences between competitors, slowing any one species' rise to dominance. In our experiment, this mechanism was weak: species differed in their feeding rates (Fig. 4) and fecundity (Best 2012), leading to greater dominance by single species under low trait diversity (Fig. 2a). In contrast, at high feeding trait diversity, stabilising effects appeared to dominate, as more species had exclusive access to a resource. This created opportunity for consumers that feed and reproduce more slowly to establish populations.

In addition to a more even distribution of abundance among competitors, increased feeding trait diversity also resulted in a greater number of invading species and more individuals of a single invading species (*A. columbiae*). This initially appears to be counter-intuitive, as greater occupation of resource niches is hypothesised to prevent successful establishment (Stachowicz & Tilman 2005). However, most of the invaders were grazers of epiphytes, and

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competition for epiphytes would be reduced in most high trait diversity assemblages, where species with complementary alternative resources had exclusive access to those resources. In contrast, low trait diversity communities were composed of either all generalists or all epiphyte specialists, both of which could cause intense competition for epiphytes. This is reflected in the positive relationship between trait diversity and epiphyte standing stock (Fig. 5a), and suggests that higher ecological diversity can actually increase the species richness at saturation if the community has access to a broader range of resource space over time. This is consistent with an earlier study in which higher phylogenetic diversity resulted in greater realised species richness (Maherali & Klironomos 2007).

Importantly, the changes in primary producer abundance along the feeding trait diversity gradient were small compared with the effect of initial grazer biomass, which was determined by the size of the included species. This is in keeping with previous findings that species identity is often more important than species richness to the functioning of seagrass-grazer systems (Duffy *et al.* 2001; Hughes *et al.* 2010), but it extends that finding. Recent approaches have shown that phylogenetic and/or trait data can account for substantial variation within levels of species richness and potentially uncover effects between levels (Connolly *et al.* 2011). In contrast, our result suggests that even with detailed information about species' trait or phylogenetic similarities, the presence or absence of particular species (in this case the largest species, *Ampithoe lacertosa*) is still the primary determinant of overall biomass.

Although grazer size had large effects on final plant biomass, it did not predict the identity of the grazer's alternative resources, and diversity in body mass was therefore not correlated with diversity in feeding niche. Similarly, while mouthpart morphology in amphipods can sometimes be linked to specialised diets (Mekhanikova 2010), mouthparts in our species do not have obvious morphological differences that might determine which types of macrophytes can be consumed. To accurately assess the effects of feeding trait diversity, there may not be an easy morphological substitute for the direct measurement of feeding rates.

Phylogenetic diversity: when is it a useful proxy?

In our experiment, feeding rates had important impacts on species interactions, but showed little phylogenetic signal. In contrast, competitive exclusion in protists was strongly predicted by both phylogenetic distance and a highly correlated difference in morphology (mouth size, Violle *et al.* 2011). The kind of trait involved in competitive interactions may be important, with morphological traits generally less labile than those associated with behaviour (Blomberg *et al.* 2003), foraging mode (Johnson *et al.* 2008) or habitat choices (Bohning-Gaese & Oberrath 1999). In addition, phylogeny may be a better predictor of species interactions that depend on a broad suite of traits (Kraft *et al.* 2007). The more traits involved in the interaction, the greater chance that some of them might have phylogenetic signal. In our experiment, however, competitive outcomes were driven by feeding niche (and potentially by other traits that also lack phylogenetic signal), but not by whatever ecological similarity is captured by the phylogeny. Cahill *et al.* (2008) found similar results in a meta-analysis of plant competition studies: interaction intensity was driven by variation in a key trait (size), rather than by phylogenetic relatedness (but see Burns & Strauss 2011 for an opposite finding).

If a larger suite of underlying traits increases the value of the phylogeny as a proxy for ecological similarity, then phylogenetic relatedness may be a better predictor of outcomes that integrate over a greater number of ecological dimensions. In our system, for example, community assembly patterns in the field may reflect grazer variation in responses to environmental gradients, phenology and predation susceptibility as well as resource use. If phylogenetic relatedness in amphipods integrates over these diverse trait axes, then phylogeny may be more predictive of community assembly or ecosystem function outcomes in the field. Non-random phylogenetic patterns in community assembly have been reported in a number of systems, including plants, animals and microbes (Cavender-Bares *et al.* 2004; Ackerly *et al.* 2006; Horner-Devine & Bohannan 2006; Vamosi & Vamosi 2007; Cooper *et al.* 2008; Rabosky *et al.* 2011), and some recent studies have found a strong predictive effect of phylogenetic diversity on total plant biomass or productivity in the field (Cadotte *et al.* 2008; Flynn *et al.* 2011).

Ultimately, the choice between trait and phylogenetic approaches depends on our objective: phylogenetic information may become more useful as the mechanism becomes less specific. If verified for a particular system, phylogenetic relationships may serve as an easily reproducible and one-dimensional predictor of particular patterns or outcomes. When it comes to understanding the processes underlying that pattern, however, using experimental tests to verify the cause of field patterns may be difficult. When phylogeny is very closely correlated with a measured trait (e.g. Violle *et al.* 2011), it is difficult to assess the causal importance of that trait relative to other conserved traits. If, on the other hand, phylogeny explains something independent of measured traits (Flynn *et al.* 2011; Peay *et al.* 2011; Verdú *et al.* 2012), we can choose to interpret phylogeny as a useful overall indicator, or we can look for new traits that show stronger phylogenetic signal. Using controlled experiments to explore the specific species interactions affected by phylogenetic relationships may produce highly variable outcomes, depending on how many and what kinds of traits underlie those interactions.

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AUTHORSHIP

RB initiated design, analysis and writing with substantial input from NC and JS at all stages. RB and NC carried out the experiment.

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