

# Multiple dimensions of intraspecific diversity affect biomass of eelgrass and its associated community

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**Abstract.** Genetic diversity within key species can play an important role in the functioning of entire communities. However, the extent to which different dimensions of diversity (e.g., the number of genotypes vs. the extent of genetic differentiation among those genotypes) best predicts functioning is unknown and may yield clues into the different mechanisms underlying diversity effects. We explicitly test the relative influence of genotypic richness and genetic relatedness on eelgrass productivity, biomass, and the diversity of associated invertebrate grazers in a factorial field experiment using the seagrass species, *Zostera marina* (eelgrass). Genotypic richness had the strongest effect on eelgrass biomass accumulation, such that plots with more genotypes at the end of the experiment attained a higher biomass. Genotypic diversity (richness + evenness) was a stronger predictor of biomass than richness alone, and both genotype richness and diversity were positively correlated with trait diversity. The relatedness of genotypes in a plot reduced eelgrass biomass independently of richness. Plots containing eelgrass with greater trait diversity also had a higher abundance of invertebrate grazers, while the diversity and relatedness of eelgrass genotypes had little effect on invertebrate abundance or richness. Our work extends previous findings by explicitly relating genotypic diversity to trait diversity, thus mechanistically connecting genotypic diversity to plot-level yields. We also show that other dimensions of diversity, namely relatedness, influence eelgrass performance independent of trait differentiation. Ultimately, richness and relatedness captured fundamentally different components of intraspecific variation and should be treated as complementary rather than competing dimensions of biodiversity affecting ecosystem functioning.

**Key words:** biodiversity; community functioning; genetic diversity; genetic relatedness; genotypic richness; phenotypic diversity; trait diversity.

## INTRODUCTION

The number of genotypes in an assemblage (genotypic richness) can influence community productivity, resistance to disturbance, colonization and invasion success, and richness and abundance of associated species (Hughes and Stachowicz 2004, Reusch et al. 2005, Crutsinger et al. 2006, 2008, Johnson et al. 2006, De Meester et al. 2007, Crawford and Whitney 2010, Kotowska et al. 2010). Genetic diversity within key species may be of equal or greater importance than species diversity in determining ecosystem functioning (Cook-Patton et al. 2011, Latta et al. 2011). However, genotypic richness is just one measure of intraspecific diversity and more direct measures of genetic differentiation or functional diversity may be more mechanistically related to ecological outcomes. Yet, few studies have directly compared the influence of different intraspecific diversity metrics on community function.

Although the genotypic or species richness of an assemblage is often assumed to be a rough proxy for trait diversity, with greater trait diversity promoting resource partitioning and increased production, it is unlikely that each species or genotype is equally distinct. Direct measurements of functional trait dissimilarity can be a better predictor of diversity effects than species richness (Heemsbergen et al. 2004, Wojdak and Mittelbach 2007). However, measuring traits can be labor intensive, traits may be plastic, and choosing which traits matter to ecological processes a priori is often challenging and context dependent (Naeem and Wright 2003). Consequently, interest in using measures of genetic distance as proxies for functional diversity has increased (Felsenstein 1985, Harvey and Pagel 1991). Phylogenetic diversity of multi-species assemblages (e.g., total branch length in a phylogeny) is often a better predictor of assemblage productivity than the number of species or functional groups (Cadotte et al. 2008, 2009, Flynn et al. 2011). However, because not all traits that might influence ecosystem functions are evolutionarily conserved (Cavender-Bares et al. 2004, 2006, Moles et al. 2005, Silvertown et al. 2006, Best and Stachowicz 2013, Best et al. 2013), the relationship between overall phylogenetic distance

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and ecological processes can vary (Burns and Strauss 2011, Narwani et al. 2013, Godoy et al. 2014).

Analogously, genetic relatedness or allelic diversity within species could be more closely linked to trait diversity and assemblage performance than genotype richness (Massa et al. 2013, Stachowicz et al. 2013, Fischer et al. 2017). However there is considerable uncertainty in this relationship. For example, under strong selection trait differentiation can exceed (McKay and Latta 2002) or be less than (Petit et al. 2001) the amount predicted by overall genetic relatedness, resulting in little correlation between trait and genetic distance (Reed and Frankham 2001, McKay and Latta 2002; Abbott et al. unpublished manuscript). Genetic relatedness among individuals within a species could also have direct effects (independent of traits) on assemblage or individual performance due to inbreeding or outbreeding depression (e.g., Charlesworth and Charlesworth 1987, Ralls et al. 1988, Crnokrak and Roff 1999, Keller and Waller 2002) or kin recognition (Dudley and File 2007). Thus, the number of genotypes (richness) and their relatedness may have unique effects on performance such that the question is not as simple as, “which metric best captures overall trait diversity and predicts functioning?”

To assess the independent and interactive effects of these different dimensions of diversity, we factorially manipulated the genotypic richness and genetic relatedness of assemblages of the seagrass *Zostera marina* (eelgrass) in the field. Eelgrass provides critical habitat for fishes and invertebrates, while buffering shorelines from erosion and playing a key role in nutrient and carbon cycling (Williams and Heck 2001). Because many of these functions are correlated with standing plant biomass, we measured plant growth and biomass as response variables, as well as the abundance and diversity of epifaunal invertebrates. Eelgrass reproduces sexually and vegetatively, forming extensive monospecific meadows where genotypic richness varies at scales of meters (1–15 genotypes/m<sup>2</sup> in northern California; Hughes and Stachowicz 2009). Eelgrass genotypes differ in traits such as growth rate, nutrient uptake, photosynthetic efficiency, phenolic content, susceptibility to herbivores, and detrital production (Ehlers et al. 2008, Hughes et al. 2009, Tomas et al. 2011; Abbott et al., unpublished manuscript) that are thought to underlie the effects of genotypic richness (Hughes and Stachowicz 2004, 2011, Reusch et al. 2005, Massa et al. 2013). We previously measured these traits for all the genotypes used in our experiment, allowing us to explore the influence of trait diversity as an underlying mechanism driving the effects of different dimensions of genetic diversity on assemblage performance.

## METHODS

We used 41 unique genotypes to create a factorial field experiment, crossing genotypic richness (two or six genotypes) and relatedness (low, medium, and high, defined in *Selecting assemblages*). We used a large number of genotypes to minimize identity effects and create

assemblages that cover a wide range of relatedness. We collected the 41 genotypes across three tidal heights at five sites in Bodega Harbor, California, USA in May 2012 (Abbott et al., unpublished manuscript) and propagated them in outdoor tanks at the UC Davis Bodega Marine Laboratory to produce enough shoots for deployment in a field experiment in the summer of 2013. We estimated the relatedness of the 41 genotypes using 11 microsatellite loci selected from a pool of >30 loci designed specifically for *Zostera marina* (Reusch et al. 1999, Reusch 2000, Oetjen and Reusch 2007, Oetjen et al. 2010, Abbott and Stachowicz 2016). We determined the relatedness of all possible genotype pairs using a regression-based measure of the number of shared alleles, calibrated by the frequency of those alleles in the population (estimated using 220 unique genotypes collected at the same time as the 41) using the program STORM (Frasier 2008). We calculated the relatedness of eelgrass in the six-genotype treatments as the average relatedness of all pairwise combinations of the six genotypes.

### *Selecting assemblages*

Our treatments consisted of two levels of genotype richness, two or six genotypes, and three levels of relatedness within each richness level: less related than expected by chance (low), as related as expected by chance (mid), and more related than expected by chance (high). “By chance” here refers to expected values based on a random draw from the 41 genotypes. We selected genotype combinations for these treatments to minimize genotypic identity effects and standardize variation in relatedness among replicates within treatment (Table 1, see Appendix S1 for a list of all genotype combinations used).

We wanted to test explicitly the role of richness and relatedness in general, while minimizing identity effects, thus each replicate of a given treatment contained a different assemblage of genotypes. This required using a large number of genotypes, and as a result, our experiment did not contain monocultures of each genotype. We avoided confounding our richness and relatedness treatments with genotypic identity effects by minimizing the number of replicate genotypes within a treatment and maximizing the number of genotypes shared across treatments. For example, for the assemblages of six genotypes, within each relatedness level no genotype was present in more than six of the 12 plots and each assemblage differed by at least two genotypes. For the two-genotype plots, no genotype was present in more than two pairs for each relatedness level. Genotypes from different sites and tidal heights were represented in all treatments: all assemblages of six genotypes had genotypes from at least three different sites and two different tidal heights.

### *Field experiment*

In July 2013, we planted 12 replicates of each of the six treatments (two levels of richness crossed with three levels

TABLE 1. Range and variance of relatedness values for each level of richness  $\times$  relatedness.

	Distantly related	Intermediate relatedness	Closely related
Two-genotype plots			
Range	−0.69 to −0.38	−0.17 to 0.06	0.31 to 0.87
Mean	−0.51	−0.02	0.48
Variance	0.01	0.004	0.02
Six-genotype plots			
Range of means	−0.49 to −0.42	−0.045 to 0.071	0.38 to 0.45
Variance	<0.038	<0.032	<0.024

*Notes:* For the two-genotype plots we give the range of pairwise relatedness, mean relatedness, and variance in relatedness for the 12 pairs of genotypes at each relatedness level. For the six-genotype plots we give the range of mean pairwise relatedness and maximum variance in relatedness of all genotypes in the 12 replicate plots at each relatedness level.

of relatedness) in a randomized block design, with plots in a grid with 12 rows (each row is a block) and six columns, for a total of 72 plots. Although the slope of the shore was gradual at our location (<0.5 m difference between any plots) and the entire experiment was >20 m from the edge of a bed, these blocks paralleled the shore to account for effects of elevation/depth (Abbott and Stachowicz 2016). We randomly assigned each treatment to one of the six columns for each of the 12 rows. We established this grid within an existing eelgrass bed in Bodega Harbor, California by clearing 72 70  $\times$  60 cm plots of seagrass. We then inserted plastic containers (40.4 cm long  $\times$  32.7 cm wide  $\times$  15.2 cm deep) lined with 2 mm diameter mesh into the center of each plot and filled them within 3 cm of the top with homogenized, sieved, field-collected sediment. We planted 12 shoots in each plot: six of each genotype for the two-genotype plots and two of each genotype for the six-genotype plots. Prior to planting, we removed all epibionts from each shoot and standardized them to 30 cm of shoot and 2.5 cm of rhizome. We harvested the experiment 16 months later in October 2014 (after two growing seasons).

Prior to harvest, we assessed plant growth and mobile invertebrate community composition. Two weeks prior to the breakdown of the experiment we marked ten randomly selected shoots in each plot using the hole-punch method (Williams and Ruckelshaus 1993). After harvesting, growth was measured as leaf area produced (length that the hole-punch mark traveled from the base of the sheath  $\times$  shoot width). We estimated epifaunal community composition in each plot by collecting three eelgrass shoots from each plot and quickly depositing all three shoots directly into a plastic bag. In the lab, we removed all invertebrate grazers from the eelgrass and preserved them in 70% ethanol for later enumeration and identification to the lowest taxonomic level possible. For analyses we used two measures of invertebrate abundance: (1) we standardized abundance by the dry mass of the shoots of eelgrass from which the invertebrates were collected and (2) we estimated the total plot-level abundance of invertebrates by multiplying the abundance per gram of eelgrass sampled by the total mass of aboveground biomass from each plot at the end of the experiment. Because it is unlikely that richness scales linearly with the mass of eelgrass

either sampled or in the plot as a whole, we used cumulative richness from all three sampled shoots in analyses.

We next harvested all of the eelgrass from each container. Each physically connected section of eelgrass (group of ramets) was placed into individually labeled press seal bags and transported a short distance (~2.5 km) back to the laboratory, where they were stored in a refrigerator or frozen until processing. For each group of connected ramets we took a single leaf tissue sample for genetic analysis so that we could attribute biomass unambiguously to a genotype. We divided the final biomass of each ramet into shoots, roots, and rhizome, and weighed each after drying at 60°C for at least 48 h.

#### *Trait diversity*

We separately measured significant variation among these 41 genotypes for 17 traits when grown in a common garden (Abbott et al., unpublished manuscript). The 17 traits included: traits related to biomass accumulation (aboveground, belowground, and ratio of above- to belowground), growth rate (new shoots produced and leaf and rhizome growth rate), morphology (maximum root length, maximum leaf width and length, number of leaves, and rhizome diameter), nutrient uptake rate (nitrate uptake by the shoots and ammonium uptake by the roots), leaf phenolic content, and photosynthetic parameters based on rapid light curves measured using a Diving-PAM (Pulse Amplitude Modulated) fluorometer (Walz, Germany) (Hughes et al. 2009, Reynolds et al. 2016). Multivariate trait distance was uncorrelated with estimates of pairwise relatedness for these genotypes (Abbott et al., unpublished manuscript), allowing us to evaluate the effects of trait diversity on eelgrass performance, independent of relatedness. We measured trait diversity using standardized trait values both as the Euclidean distance between all possible genotype pairs, and as the distance among genotypes using the first two Principal Components from a Principal Components Analysis to account for correlations among traits; both indices were strongly correlated ( $r = 0.92$ ,  $P = <0.0001$ ) and the choice of index did not affect our results.

We quantified trait diversity for each assemblage of genotypes using Rao's quadratic entropy  $Q$  (Rao 1982,

Champely and Chessel 2002, Ricotta 2005), which is a measure of the sum of the pairwise trait differences among genotypes weighted by their relative abundance. We chose this metric because it represents the average divergence in traits among taxa (in this case, genotypes), and is therefore analogous to our measure of relatedness among eelgrass genotypes in each assemblage (Tucker et al. 2017). It also provides a measure of functional diversity that is not strongly influenced by the number of taxa present (richness), unlike other measures of functional diversity (e.g., Petchey and Gaston 2002), which sum differences among taxa (Botta-Dukát 2005, Mouchet et al. 2010, Schleuter et al. 2010, Clark et al. 2012). This allowed us to include trait diversity as a predictor in models of biomass accumulation along with genotypic richness and relatedness.

### *Re-genotyping*

In addition to the genotype samples we took at harvest, in November 2013 and May 2014 we collected 2 cm long pieces of leaf from each group of shoots we estimated to be part of the same physiologically connected ramet in the field in each plot in order to assess genotypic composition of the plots and how it changed over time. The tissue samples collected for genotyping were processed in the same manner as in the original genetic analysis. Each sample was identified as one of the original 41 genotypes or a new unique genotype. By the end of the experiment, new “invader” genotypes established in 16 of the 72 plots, but overall they composed less than 3% of the total eelgrass biomass. Within plots where invaders established, on average they composed less than 10% of total plot biomass. There were no effects of richness, relatedness, or trait diversity of eelgrass in a plot on the likelihood of an invader establishing (Appendix S2).

### *Statistical analysis*

Not all genotypes survived in plots in which they were planted, so we assessed whether there was any effect of the initial planted diversity (richness, relatedness, and trait diversity) on patterns of mortality and survival of genotypes. Because we detected no such effects (see Appendix S3), and because nearly two-thirds (44/68) of the genotypes that were lost during the experiment had already been lost from the plots by November 2013 (four months into the experiment), whereas all performance/functioning response variables were measured at the end of the experiment (October 2014), we used the final genotypic composition rather than initial composition to calculate plot-level realized diversity metrics. In addition to richness, relatedness, and trait diversity, we also included genotypic evenness as a realized diversity metric in our models to account for the differences in the relative abundance of genotypes in each plot at the end of the experiment. Because we included genotypic evenness separately in the model, we assumed an equal abundance

of all genotypes in each plot at the end of the experiment for our calculation of trait diversity. We did this to avoid systematic correlations between trait diversity and other parameters in the model. Some of the plots only had one genotype left at the end of the experiment; these plots all have a trait diversity and evenness of zero and richness and relatedness of one. We repeated our analyses with planted diversity metrics, but none of these was ever correlated with final performance (see *Results*).

We performed analyses using R 3.0.3 or R 3.3.3 (R Core Team 2014, 2017). We used logistic regression (glm function from the stats package in R; R Core Team 2014) to test the effects of planted genotypic richness, relatedness, and trait diversity on the likelihood that no shoots survive at the end of the experiment. For plots in which at least one genotype survived, we performed separate analyses of genotype survival for those planted with two genotypes and six genotypes. In two-genotype plots, we performed a logistic regression, testing the effects of planted genotypic richness, relatedness, and trait diversity on whether both genotypes survived. For the six-genotype plots, we used the proportion of surviving genotypes as a continuous response variable and used a generalized linear mixed model with the richness, relatedness, and trait diversity of planted genotypes as fixed effects, and block as a random effect, using a Bayesian approach in the MCMCglmm package in R (Hadfield 2010).

We used the same type of generalized linear mixed models (MCMCglmm package in R) to assess the effects of our realized diversity metrics on the performance and functioning of the eelgrass plots (eelgrass above and belowground biomass and leaf growth rate, and invertebrate grazer abundance and richness). For these models we specified a Gaussian distribution for the response variables and used priors that corresponded to an inverse-Gamma distribution, with shape and scale parameters equal to 0.001. We evaluated relative performance of our models using the model deviance information criterion (DIC). DIC is a Bayesian generalization of the Akaike information criterion (AIC) that is particularly suited to comparing models that use Markov chain Monte Carlo (MCMC) to obtain posterior distributions (Spiegelhalter et al. 2002). Similar to AIC, DIC measures model accuracy while penalizing excessive model complexity (additional parameters), with a lower DIC score indicating a preferred model. We tested univariate models for each diversity metric (realized richness, relatedness, trait diversity, and evenness), a full model that included all four metrics, and all possible two and three variable models. For simplicity only the best performing two and three variable models are presented in the results.

## RESULTS

### *Survivorship*

Eelgrass failed to establish permanently (complete mortality) in 22 of 72 plots. We found no effect of the initial



planted genotypic richness, average relatedness, or trait diversity of the genotypes in a plot on the likelihood of complete mortality (Appendix S3). Most of these plots never produced any new shoots and died within a few months of the initial planting, suggesting that complete mortality resulted from the failure of the transplants to establish, likely due to dislodgement by currents, burrowing organisms or floating algal mats, rather than interactions among shoots. Because complete mortality was independent of treatment, we excluded these plots from the rest of the analyses.

Within the plots in which eelgrass remained at the end of the experiment, neither the richness, relatedness, and trait diversity of planted genotypes, nor their interactions affected the proportion of genotypes surviving or any of our measures of plant performance or animal community diversity (Appendices S3 and S4). The lack of effect of planted diversity is probably because most (65%) of the genotypes that were lost from a plot in which they were planted were lost within the first 4 months of the experiment. Thus, for the vast majority of the duration of the experiment the genotypic composition in each plot was similar to that measured at the end of the experiment.

#### *Plant biomass and growth*

Realized richness and relatedness (calculated using observed genotypic composition at the end of the

experiment) independently influenced several measures of plant biomass. For example, the model that best explained variation in final belowground biomass included both richness, which was positively correlated with biomass, and relatedness, which was negatively correlated with biomass (Table 2A, Fig. 1). A model that also included evenness with richness and relatedness performed similarly ( $\Delta\text{DIC} = 0.56$ , Table 2A), suggesting that evenness also positively influenced belowground biomass (as seen in univariate analyses), but not enough to improve model performance while adding an additional variable. For aboveground biomass the best performing model included richness and evenness having a positive affect on biomass and relatedness having a negative affect, although a model that did not include relatedness performed essentially the same ( $\Delta\text{DIC} = 0.12$ , Table 2A, Fig. 2).

We included richness and evenness separately in our models to see how each contributed independently to eelgrass performance, and we found that both were included in our top models for explaining eelgrass biomass, although richness had a greater effect. In practice, richness and evenness are often combined to calculate the diversity (e.g., Shannon index) of an assemblage. Because genotypic Shannon diversity combines two measures of diversity that we found to be important, and it is a ubiquitous metric used to characterize the diversity of natural communities, we decided to run models that replaced the richness and evenness of eelgrass plots with their genotypic diversity. Unsurprisingly, by combining information

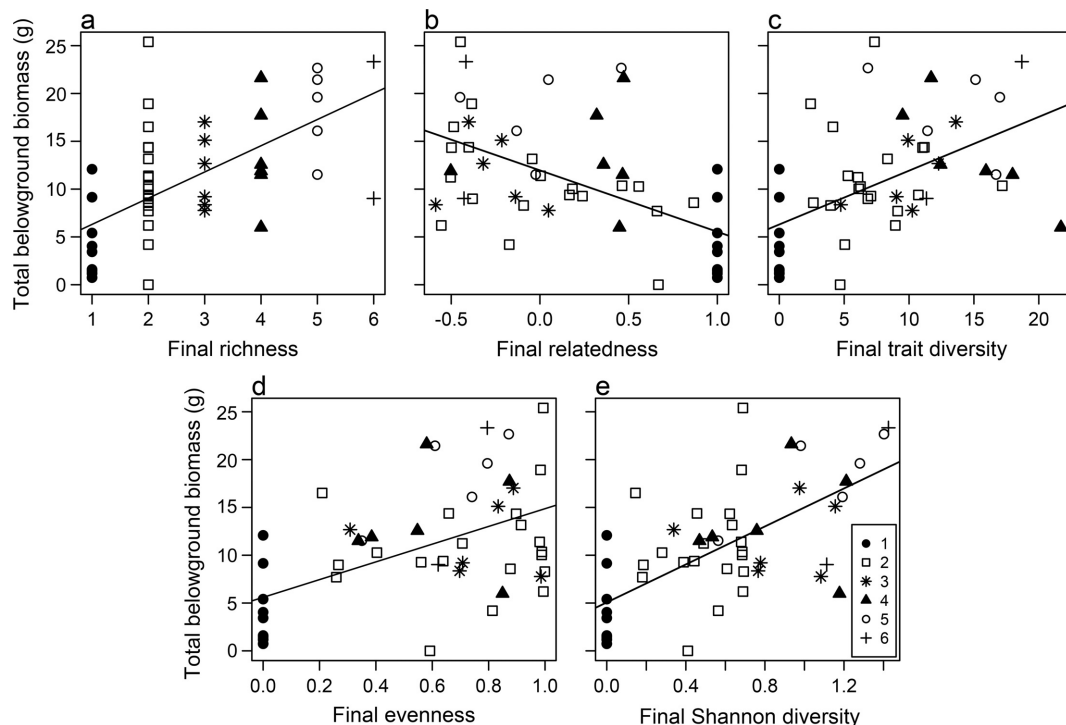


FIG. 1. Effects of realized (a) genotypic richness, (b) relatedness, (c) trait diversity, (d) evenness, and (e) Shannon diversity on belowground biomass. See Table 2 for statistical analysis. Different symbols are used to denote the richness of genotypes in each plot; the legend is in the bottom right corner of panel e.

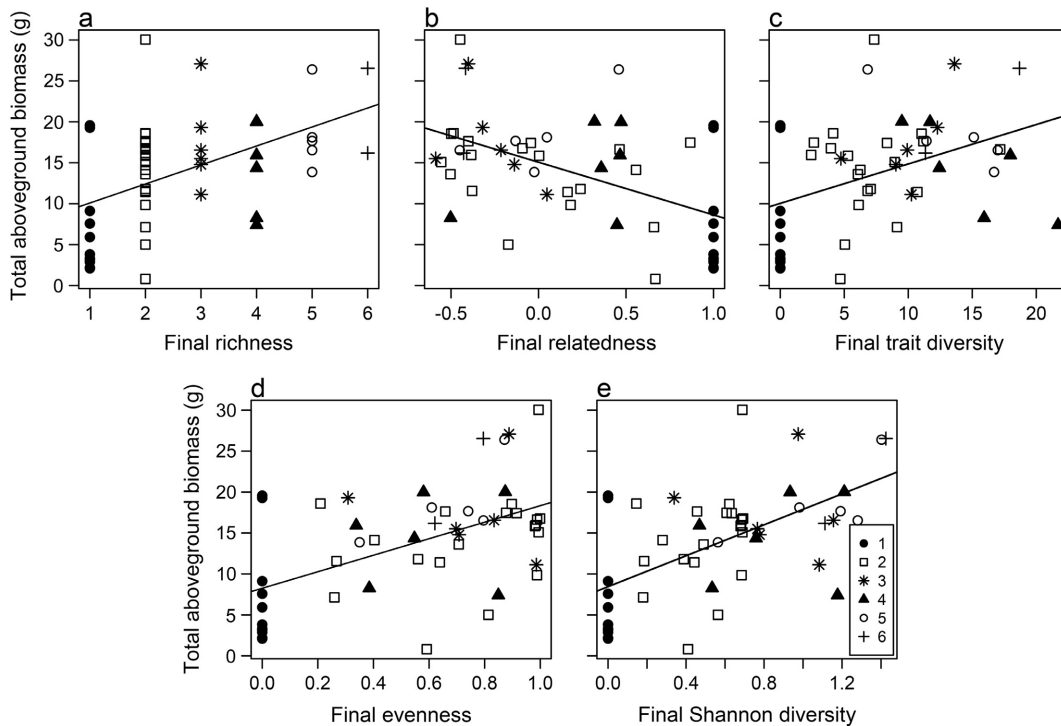


FIG. 2. Same as Fig. 1 but with aboveground biomass as the response variable.

about richness and evenness into a single metric and reducing the number of parameters, model performance increased when using genotypic diversity ( $\Delta\text{DIC} = 1.46$  for below and 2.84 for aboveground biomass when comparing the best performing models, Table 2B). Genotypic diversity proved to be the strongest predictor of eelgrass biomass, however relatedness was also included in the best performing models for both below- and aboveground biomass (Table 2B, Fig. 1 and 2).

A consistent positive correlation between trait diversity and diversity of genotypes, both for single traits and multivariate trait indices, suggests that trait diversity may mechanistically account for the effect of genotypic diversity on plant performance (Fig. 3). Trait diversity was not included in the best performing models for explaining eelgrass biomass, precisely because trait diversity was strongly correlated with richness ( $R^2 = 0.60$ , Fig. 3), and richness was a stronger predictor. Trait diversity was positively correlated with belowground and aboveground biomass in univariate analyses (Table 2, Fig. 1 and 2), and the performance of the full model, which included trait diversity, was not greatly reduced compared to the best performing model ( $\Delta\text{DIC} = 2.36$  for below and 1.57 for aboveground biomass).

In addition to using multivariate trait differentiation, we assessed the effect of each trait separately to see if the mean, variance, range, or extremes of trait values for genotypes in each plot had any influence on plant biomass or leaf growth. The range and variance of many traits were positively correlated with biomass; however, as

with our multivariate trait diversity metric, the strong correlation between trait and genotypic diversity meant that these factors dropped out of multi-factor models once Shannon genotypic diversity was included (Appendix S5).

Leaf growth over the last two weeks of the experiments was weakly positively affected by relatedness, but not by any other dimension of diversity (Appendix S6). The association of high relatedness with low aboveground biomass (Fig. 2) likely reduced self-shading and contributed to higher leaf growth rates in high-relatedness plots. Despite high leaf growth rates, standing biomass was lower in these plots, suggesting that turnover rates, leaf number, or herbivory rates vary with relatedness in such a way to reduce standing stock. The low belowground biomass in realized monocultures, combined with the high aboveground growth, resulted in a higher ratio of above to belowground biomass in plots with one genotype compared to plots with multiple genotypes (Fig. 4). By definition, realized monocultures have zero trait diversity or genotypic diversity, and a richness and relatedness of one. Therefore, we also ran models excluding all realized monocultures to determine whether this drove the effects we observed, which it did not (Appendix S7).

#### *Invertebrate community response*

Total estimated invertebrate abundance in an entire plot increased with eelgrass trait diversity (Table 3, Fig. 5A), even when only considering plots with >1 genotype (Appendix S7). The abundance of invertebrate grazers per

TABLE 2. Summary of generalized linear mixed model results for the effects of realized diversity metrics on below- and aboveground biomass of eelgrass.

Models 1–11 using final diversity metrics	Belowground biomass					Aboveground biomass				
	Posterior mean	Lower CI	Upper CI	pMCMC	DIC	Posterior mean	Lower CI	Upper CI	pMCMC	DIC
<b>A</b>										
<b>1) Richness + relatedness + trait diversity + evenness</b>					305.41					321.72
<i>Richness</i>	1.95	0.32	3.37	0.01		1.51	−0.28	3.42	0.11	
<i>Relatedness</i>	−3.01	−6.36	0.54	0.09		−3.06	−6.87	0.73	0.12	
<i>Trait diversity</i>	−0.06	−0.43	0.33	0.78		−0.12	−0.61	0.33	0.62	
<i>Evenness</i>	3.31	−2.24	8.10	0.19		5.47	−0.71	11.35	0.07	
<b>2) Richness + relatedness + evenness</b>					303.61					<b>320.15</b>
<i>Richness</i>	1.78	0.73	2.93	0.007		<b>1.18</b>	<b>−0.15</b>	<b>2.46</b>	<b>0.08</b>	
<i>Relatedness</i>	−2.94	−6.34	0.20	0.07		<b>−2.89</b>	<b>−6.67</b>	<b>0.96</b>	<b>0.14</b>	
<i>Evenness</i>	3.10	−1.97	7.78	0.23		<b>5.04</b>	<b>−1.06</b>	<b>10.65</b>	<b>0.10</b>	
<b>3) Richness + relatedness</b>					<b>303.05</b>					–
<i>Richness</i>	<b>1.89</b>	<b>0.97</b>	<b>3.05</b>	<b>&lt;0.001</b>		–	–	–	–	–
<i>Relatedness</i>	<b>−4.11</b>	<b>−6.43</b>	<b>−1.05</b>	<b>0.006</b>		–	–	–	–	–
<b>4) Richness + evenness</b>					–					320.27
<i>Richness</i>	–	–	–	–		1.50	0.27	2.78	0.02	
<i>Evenness</i>	–	–	–	–		7.50	2.74	12.33	0.001	
<b>5) Richness</b>					310.40					327.61
<i>Richness</i>	2.69	1.67	3.68	<0.001		2.25	1.03	3.49	<0.001	
<b>6) Relatedness</b>					311.89					323.72
<i>Relatedness</i>	−6.52	−9.21	−4.03	<0.001		−6.43	−9.79	−3.71	<0.001	
<b>7) Trait diversity</b>					316.71					330.96
<i>Trait diversity</i>	0.56	0.27	0.81	<0.001		0.48	0.21	0.84	0.004	
<b>8) Evenness</b>					317.19					324.01
<i>Evenness</i>	9.10	5.18	13.97	<0.001		10.06	5.56	15.03	<0.001	
<b>B</b>										
<b>9) Genotypic diversity + relatedness + trait diversity</b>					303.38					319.18
<i>Genotypic diversity</i>	6.69	2.25	11.86	0.009		7.06	1.84	12.55	0.01	
<i>Relatedness</i>	−3.19	−6.18	−0.19	0.05		−3.81	−7.34	−0.27	0.03	
<i>Trait diversity</i>	0.07	−0.25	0.38	0.66		−0.06	−0.42	0.37	0.74	
<b>10) Genotypic diversity + relatedness</b>					<b>301.59</b>					<b>317.31</b>
<i>Genotypic diversity</i>	<b>7.20</b>	<b>3.24</b>	<b>10.91</b>	<b>0.001</b>		<b>6.55</b>	<b>1.73</b>	<b>10.74</b>	<b>0.003</b>	
<i>Relatedness</i>	<b>−3.37</b>	<b>−6.30</b>	<b>−0.34</b>	<b>0.03</b>		<b>−3.64</b>	<b>−6.87</b>	<b>−0.015</b>	<b>0.04</b>	
<b>11) Genotypic diversity</b>					305.15					319.78
<i>Genotypic diversity</i>	9.79	6.20	12.78	<0.001		9.36	5.42	13.16	<0.001	

Notes: Block was included as a random effect in all models; but block effect results are omitted for brevity. Models are presented with posterior means (Bayes estimates), 95% credible intervals (CI; equivalent to 95% confidence intervals), deviance information criteria (DIC), and pMCMC values (probability of the estimate overlapping zero; Markov chain Monte Carlo methods). Section A (models 1–8) shows results for models including genotypic richness and evenness separately and section B (models 9–11) shows results including genotypic (Shannon) diversity in the place of richness and evenness. Results for the best performing models are shown in boldface type.

unit mass of eelgrass sampled increased with increasing relatedness, the only predictor showing any effect in univariate analyses (Table 3, Fig. 5B). However, adding trait diversity to the model including relatedness modestly improved model fit ( $\Delta AIC = 1.5$ ) largely due to the difference between single and multi-genotype plots (Appendix S7). The species richness of invertebrate grazers in the eelgrass samples from each plot was uncorrelated with any of the realized eelgrass diversity metrics (Appendices S7 and S8).

## DISCUSSION

Considerable current research examines the utility of different diversity measures for describing the species-diversity–ecosystem-functioning relationship (Cadotte et al. 2008, 2009, Flynn et al. 2011, Fischer et al. 2017). However, we show that different metrics of intraspecific diversity capture fundamentally different components of biodiversity and should be treated as complementary rather than competing dimensions of biodiversity that

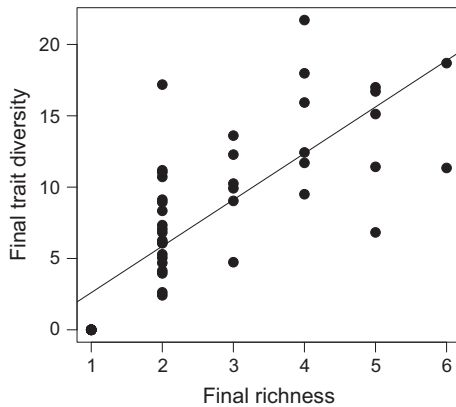


FIG. 3. Relationship between genotypic richness and trait diversity.

influence assemblage performance. Eelgrass assemblages with more genotypes and greater evenness of genotypes (genotypic diversity) attained higher plot-level biomass, whereas relatedness decreased biomass independently of genotypic and trait diversity. Furthermore, our use of multiple metrics clarified particular mechanisms underlying this relationship, as more genotypically diverse plots had higher trait diversity (Fig. 3), suggesting that niche differentiation among genotypes and more efficient use of available resources (e.g., Loreau et al. 2001) at the plot level leads to greater eelgrass biomass accumulation. Although our study focuses on intraspecific diversity in a key habitat-forming species, the same principles should apply to diversity at any level of biological organization.

Genotypic richness showed a strong positive relationship with eelgrass biomass, consistent with previous studies (Hughes and Stachowicz 2004, 2011, Reusch

et al. 2005). By statistically partitioning diversity effects, these studies highlighted the importance of complementarity (Reusch et al. 2005, Hughes and Stachowicz 2011), but never clearly revealed a trait-based mechanism. Our study showed that the evenness of eelgrass assemblages also positively influenced eelgrass biomass. Species evenness can affect community function (e.g., Wilsey and Potvin 2000, Polley et al. 2003, Mulder et al. 2004), but the influence of intraspecific genotypic evenness on function is less clear. Our finding that genotypic Shannon diversity, a measure that includes both richness and evenness, best predicted biomass accumulation implies that resource partitioning among genotypes promotes both coexistence at similar relative abundances (Chesson 2000) and higher assemblage performance (Tilman 1999).

Although eelgrass genotypic diversity explained greater variation in biomass than trait diversity, without knowing which traits are most important to intraspecific interactions, a multivariate measure of trait differentiation may not provide the best measure for how trait differences influence assemblage performance. Our multivariate trait index could be less correlated with eelgrass biomass than simple genotypic richness either because we failed to measure some relevant traits or because our index contains some irrelevant traits that weaken the correlation between differentiation and performance. Because we measured 17 different traits related to light and nutrient acquisition, biomass production above and below ground, rates of clonal spread, and resistance to herbivores, the failure to measure an unidentified trait seems an unlikely explanation. Unfortunately, the links between trait combinations and performance are likely to be complex, and different traits may be most relevant to predicting performance of different sets of genotypes. Furthermore, differentiation in some

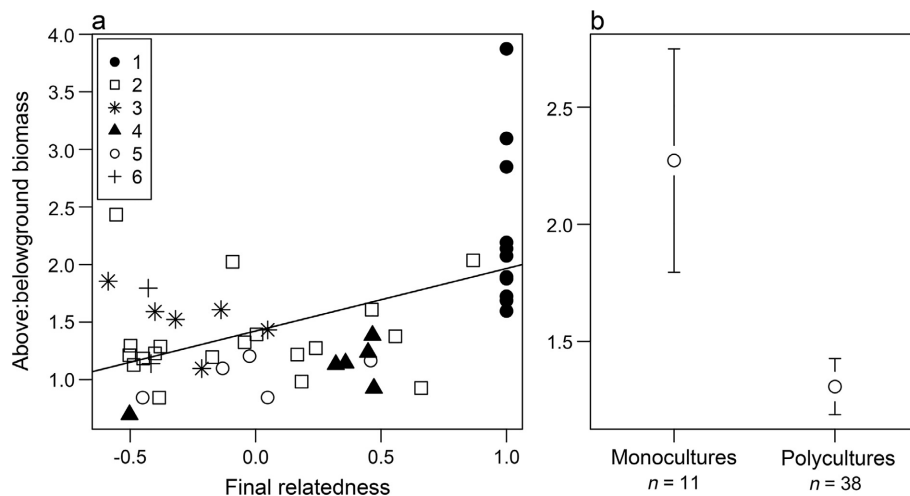


FIG. 4. (a) Relationship between the ratio of above- to belowground eelgrass biomass and the relatedness of eelgrass in each plot and (b) the mean ratio of above- to belowground biomass in plots with only one genotype (realized monocultures) compared to plots with multiple genotypes (realized polycultures) at the end of the experiment. Different symbols in panel a are used to denote the richness of genotypes in each plot. The error bars in panel b are 95% confidence intervals.



TABLE 3. Summary of generalized linear mixed model results for the effects of realized diversity metrics on invertebrate grazer abundance at the plot level and per unit eelgrass biomass.

Models 1–8 using final diversity metrics	Invertebrate abundance (no./plot)					Invertebrate abundance (no./g eelgrass)				
	Posterior mean	Lower CI	Upper CI	pMCMC	DIC	Posterior mean	Lower CI	Upper CI	pMCMC	DIC
<b>1) Richness + relatedness + trait diversity + evenness</b>					663.36					356.48
<i>Richness</i>	−12.74	−69.49	39.80	0.67		−2.25	−4.97	0.47	0.13	
<i>Relatedness</i>	−17.10	−134.9	109.3	0.79		5.79	−0.46	11.54	0.06	
<i>Trait diversity</i>	12.84	−1.78	25.53	0.07		0.87	0.22	1.58	0.01	
<i>Evenness</i>	−7.43	−193.1	169.9	0.95		−5.25	−13.78	4.69	0.26	
<b>2) Richness + relatedness + trait diversity</b>					661.32					<b>355.01</b>
<i>Richness</i>	−12.48	−63.90	45.41	0.66		<b>−2.07</b>	<b>−4.64</b>	<b>0.83</b>	<b>0.15</b>	
<i>Relatedness</i>	−13.18	−114.9	85.04	0.77		<b>7.48</b>	<b>2.41</b>	<b>12.27</b>	<b>&lt;0.001</b>	
<i>Trait diversity</i>	12.64	−0.88	26.57	0.08		<b>0.75</b>	<b>0.14</b>	<b>1.54</b>	<b>0.04</b>	
<b>3) Relatedness + trait diversity</b>					—					355.23
<i>Relatedness</i>	—	—	—	—		8.03	2.85	13.26	<0.001	
<i>Trait diversity</i>	—	—	—	—		0.38	−0.08	0.89	0.11	
<b>4) Richness + trait diversity</b>					659.24					—
<i>Richness</i>	−11.24	−64.76	40.30	0.66		—	—	—	—	
<i>Trait diversity</i>	13.26	1.01	26.22	0.03		—	—	—	—	
<b>5) Richness</b>					661.64					364.20
<i>Richness</i>	31.23	−3.47	65.50	0.08		−1.01	−2.92	0.83	0.30	
<b>6) Relatedness</b>					662.18					356.71
<i>Relatedness</i>	−73.12	−160.5	13.06	0.11		6.12	1.55	10.70	0.01	
<b>7) Trait diversity</b>					<b>657.48</b>					364.27
<i>Trait diversity</i>	<b>11.11</b>	<b>2.78</b>	<b>19.04</b>	<b>0.01</b>		−0.01	−0.46	0.47	0.94	
<b>8) Evenness</b>					662.98					361.03
<i>Evenness</i>	95.01	−34.53	244.2	0.18		−7.55	−14.38	−0.31	0.04	

Notes: Predictors and statistical testing as in Table 2. One point for invertebrate abundance (per gram eelgrass) was determined to be an outlier using the Grubbs test for single outliers ( $P = 0.002$ ; Grubbs 1950) and was removed from analyses. Results for the best performing models are shown in boldface type.

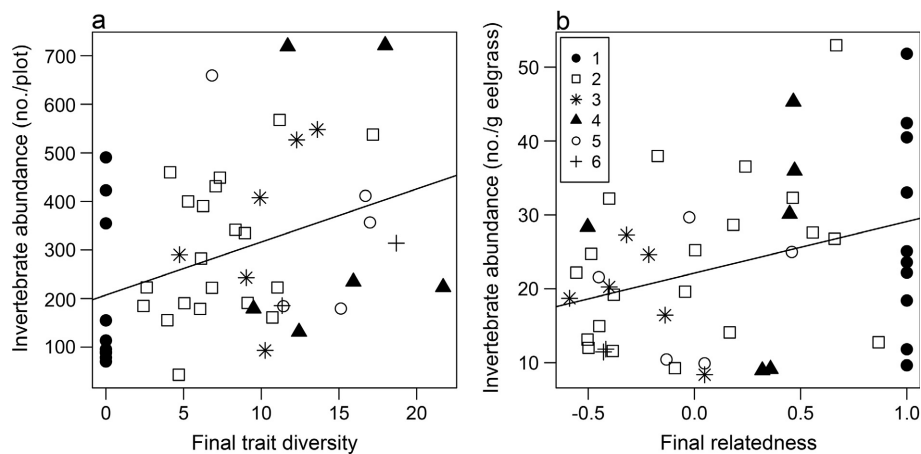


FIG. 5. Effects of (a) trait diversity on the abundance of invertebrate grazers per plot and of (b) relatedness on invertebrate abundance per gram of eelgrass sampled. See Table 3 for analyses. Different symbols are used to denote the richness of genotypes in each plot and the legend is in the upper left corner of panel b.

traits can lead to either complementarity or dominance, depending on heterogeneity in environmental conditions and the nature and magnitude of tradeoffs among traits (Mayfield and Levine 2010). Without tradeoffs, for example, genotypes with lower requirements for some limiting resource would likely outcompete others, and the greater the variation in traits, the greater the difference in competitive ability and the more likely competitive exclusion will occur (Abbott and Stachowicz 2016). Differences in certain traits and environmental conditions may be more likely to lead to trade-offs and thus only some subset of traits may influence how well trait diversity predicts performance (Kraft et al. 2015).

In contrast to the strong positive effects of genotypic richness and diversity, the relatedness of eelgrass genotypes reduced eelgrass biomass. Because relatedness and trait differences for the genotypes used in this study were uncorrelated (Abbott et al., unpublished manuscript), this effect cannot be attributed to low trait diversity in high relatedness plots. Relatedness could have direct effects on performance as some plants allocate fewer resources to root competition when in the presence of individuals of the same species (Mahall and Callaway 1991, 1996), genotype (Gersani et al. 2001, Falik et al. 2003, Gruntman and Novoplansky 2004), or close kin (Dudley and File 2007). Our finding that the ratio of above to belowground biomass was higher for plots that only had one genotype left at the end of experiment (realized monocultures) than those with multiple genotypes (Fig. 4) could be evidence of self vs. non-self recognition, with reduced allocation to intense belowground competition in the presence of closely related individuals.

Eelgrass trait diversity increased invertebrate grazer abundance at the plot scale, either because trait diversity leads to higher plant biomass and greater habitat volume (Borer et al. 2012, Best et al. 2014), or because different grazer taxa prefer different genotypes as food or habitat (Reynolds et al. 2017). Trait diversity did affect eelgrass biomass, although not as strongly as other variables that were uncorrelated with invertebrate abundance, suggesting that higher aboveground biomass is not the only mechanism involved. Several amphipods and isopods prefer different microhabitats within eelgrass beds at this site (Lürig et al. 2016), and the presence of genotypes with different heights, widths, or leaf traits may have influenced invertebrate biomass.

Our results, combined with those of previous studies, show a consistent pattern of genotypic richness/diversity enhancing the productivity of eelgrass assemblages (Hughes and Stachowicz 2004, 2011, Reusch et al. 2005, Stachowicz et al. 2013). Our study indicates that trait diversity among genotypes contributes to these effects and also influences the eelgrass-associated invertebrate community. The influence of relatedness on performance is more enigmatic. Previous studies of relatedness were confounded by a spurious positive correlation between relatedness and trait differentiation in a small sample of

genotypes (Stachowicz et al. 2013). In the present study, trait diversity and relatedness were uncorrelated, making the negative relationship between relatedness and biomass, and the positive relationship between relatedness and invertebrate grazer density more difficult to interpret. It is clear that the diversity metrics we tested influenced eelgrass performance in distinct ways; however, it remains unclear why relatedness influenced eelgrass and invertebrate grazers the way it did.

Understanding the relationship between biodiversity and ecosystem functioning is a major focus of modern ecology (e.g., Tilman 1999, Schmid 2002), and one of the main lines of inquiry has been the aspects of biodiversity (richness, genetic distance, functional diversity) that best predict ecosystem functioning (e.g., Flynn et al. 2011, Venail et al. 2015). While many studies have asked these questions about diversity among species, few have extended the approach to multiple dimensions of intraspecific variation, particularly within the marine realm. Each of our diversity metrics affected some community function, but the lack of correlation among certain metrics suggests they represent independent dimensions of biodiversity with unique effects on the eelgrass ecosystem. Genotypic diversity was the strongest predictor of eelgrass performance, likely driven by the strong relationship between genotypic and trait diversity. In contrast, relatedness had an independent negative effect on eelgrass biomass, and trait diversity alone best predicted invertebrate abundance. Thus three different dimensions of diversity influenced functioning in distinct ways (see also Cadotte et al. 2013). Considering potential complementarity among different aspects of diversity improves our understanding of diversity-function relationships and their underlying mechanisms.

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## SUPPORTING INFORMATION

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