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

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1	Running title: Dimensions of intraspecific diversity
2	Multiple dimensions of intraspecific diversity affect biomass of eelgrass and its associated
3	community
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24 Abstract

25 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 26 27 of genotypes vs. the extent of genetic differentiation among those genotypes) best predicts 28 functioning is unknown and may yield clues into the different mechanisms underlying diversity 29 effects. We explicitly test the relative influence of genotypic richness and genetic relatedness on 30 eelgrass productivity, biomass, and the diversity of associated invertebrate grazers in a factorial 31 field experiment using the seagrass species, Zostera marina (eelgrass). Genotypic richness had 32 the strongest effect on eelgrass biomass accumulation, such that plots with more genotypes at the 33 end of the experiment attained a higher biomass. Genotypic diversity (richness + evenness) was a 34 stronger predictor of biomass than richness alone, and both genotype richness and diversity were 35 positively correlated with trait diversity. The relatedness of genotypes in a plot reduced eelgrass 36 biomass independently of richness. Plots containing eelgrass with greater trait diversity also had 37 a higher abundance of invertebrate grazers, while the diversity and relatedness of eelgrass 38 genotypes had little effect on invertebrate abundance or richness. Our work extends previous 39 findings by explicitly relating genotypic diversity to trait diversity, thus mechanistically 40 connecting genotypic diversity to plot-level yields. We also show that other dimensions of 41 diversity, namely relatedness, influence eelgrass performance independent of trait differentiation. 42 Ultimately, richness and relatedness captured fundamentally different components of 43 intraspecific variation and should be treated as complementary rather than competing dimensions of biodiversity affecting ecosystem functioning. 44 45 **Key words:** genetic relatedness, trait diversity, genetic diversity, genotypic richness, community

46 functioning

47 Introduction

48 The number of genotypes in an assemblage (genotypic richness) can influence community 49 productivity, resistance to disturbance, colonization and invasion success, and richness and 50 abundance of associated species (Hughes and Stachowicz 2004; Reusch et al. 2005; Crutsinger et 51 al. 2006, 2008; Johnson et al. 2006; De Meester et al. 2007; Crawford and Whitney 2010; 52 Kotowska et al 2010). Genetic diversity within key species may be equally, or in some cases 53 more important, than species diversity in determining ecosystem functioning (Cook-Patton et al. 54 2011, Latta et al. 2011). However, genotypic richness is just one measure of intraspecific 55 diversity and more direct measures of genetic differentiation or functional diversity may be more 56 mechanistically related to ecological outcomes. Yet, few studies have directly compared the 57 influence of different intraspecific diversity metrics on community function. 58 Although the genotypic or species richness of an assemblage is often assumed to be a 59 rough proxy for trait diversity, with greater trait diversity promoting resource partitioning and 60 increased production, it is unlikely that each species or genotype is equally distinct. Direct 61 measurements of functional trait dissimilarity can be a better predictor of diversity effects than 62 species richness (Heemsbergen et al. 2004; Wojdak and Mittelbach 2007). However, measuring 63 traits can be labor intensive, traits may be plastic, and choosing which traits matter to ecological 64 processes *a priori* is often challenging and context dependent (Naeem and Wright 2003). 65 Consequently, interest in using measures of genetic distance as proxies for functional diversity 66 has increased (Felsenstein 1985; Harvey and Pagel 1991). Phylogenetic diversity of multispecies 67 assemblages (e.g., total branch length in a phylogeny) is often a better predictor of assemblage 68 productivity than the number of species or functional groups (Cadotte et al. 2008; Cadotte et al.

69 2009; Flynn et al. 2011). However, because not all traits that might influence ecosystem

70	functions are evolutionarily conserved (Cavender-Bares 2004, 2006; Moles et al. 2005; Silverton
71	et al. 2006; Best and Stachowicz 2013; Best et al. 2013), the relationship between overall
72	phylogenetic distance and ecological processes can vary (Burns and Strauss 2011; Narwani et al.
73	2013; Godoy et al. 2014).
74	Analogously, genetic relatedness or allelic diversity within species could be more closely
75	linked to trait diversity and assemblage performance than genotype richness (Stachowicz et al.
76	2013, Massa et al. 2013, Fischer et al. 2017). However there is considerable uncertainty in this
77	relationship. For example, under strong selection trait differentiation can exceed (McKay and
78	Latta 2002) or be less than (Petit et al. 2001) the amount predicted by overall genetic relatedness,
79	resulting in little correlation between trait and genetic distance (Reed and Frankham 2001;
80	McKay and Latta 2002; Abbott et al. in review). Genetic relatedness among individuals within a
81	species could also have direct effects (independent of traits) on assemblage or individual
82	performance due to inbreeding or outbreeding depression (e.g. Charlesworth and Charlesworth
83	1987; Ralls et al. 1988; Crnokrak and Roff 1999; Keller and Waller 2002) or kin recognition
84	(Dudley and File 2011). Thus, the number of genotypes (richness) and their relatedness may
85	have unique effects on performance such that the question is not as simple as, "which metric best
86	captures overall trait diversity and predicts functioning?"
87	To assess the independent and interactive effects of these different dimensions of
88	diversity, we factorially manipulated the genotypic richness and genetic relatedness of
89	assemblages of the seagrass Zostera marina (eelgrass) in the field. Eelgrass provides critical
90	habitat for fishes and invertebrates, while buffering shorelines from erosion and playing a key
91	role in nutrient and carbon cycling (Williams and Heck 2001). Because many of these functions

92 are correlated with standing plant biomass, we measured plant growth and biomass as response

93 variables, as well as the abundance and diversity of epifaunal invertebrates. Eelgrass reproduces 94 sexually and vegetatively, forming extensive monospecific meadows where genotypic richness varies at scales of meters (1-15 genotypes m⁻² in northern California, Hughes and Stachowicz 95 96 2009). Eelgrass genotypes differ in traits such as growth rate, nutrient uptake, photosynthetic 97 efficiency, phenolic content, susceptibility to herbivores, and detrital production (Ehlers et al. 98 2008; Hughes et al. 2009; Tomas et al. 2011; Abbott et al. in review) that are thought to underlie 99 the effects of genotypic richness (Hughes and Stachowicz 2004, 2011; Reusch et al. 2005; Massa 100 et al. 2013). We previously measured these traits for all the genotypes used in our experiment, 101 allowing us to explore the influence of trait diversity as an underlying mechanism relating the 102 different dimensions of genetic diversity on assemblage performance.

103

104 Methods

105 We used 41 unique genotypes to create a factorial field experiment, crossing genotypic richness 106 (2 or 6 genotypes) and relatedness (low, medium, and high, defined below). We used a large 107 number of genotypes to minimize identity effects and create assemblages that cover a wide range 108 of relatedness. We collected the 41 genotypes across three tidal heights at five sites in Bodega 109 Harbor, CA in May 2012 (Abbott et al. in review) and propagated them in outdoor tanks at the 110 UC Davis Bodega Marine Laboratory to produce enough shoots for deployment in a field 111 experiment in the summer of 2013. We estimated the relatedness of the 41 genotypes using 11 112 microsatellite loci selected from a pool of >30 loci designed specifically for Zostera marina 113 (Reusch et al. 1999; Reusch 2000; Oetjen and Reusch 2007; Oetjen et al. 2010; Abbott and 114 Stachowicz 2016). We determined the relatedness of all possible genotype pairs using a 115 regression-based measure of the number of shared alleles, calibrated by the frequency of those

116 alleles in the population (estimated using 220 unique genotypes collected at the same time as the 117 41) using the program STORM (Frasier 2008). We calculated the relatedness of eelgrass in the 118 six-genotype treatments as the average relatedness of all pairwise combinations of the six 119 genotypes. 120 121 Selecting assemblages 122 Our treatments consisted of two levels of genotype richness, two or six genotypes, and three 123 levels of relatedness within each richness level: less related than expected by chance (low), as 124 related as expected by chance (mid), and more related than expected by chance (high). "By 125 chance" here refers to expected values based on a random draw from the 41 genotypes. We 126 selected genotype combinations for these treatments to minimize genotypic identity effects and 127 standardize variation in relatedness among replicates within treatment (Table 1, see appendix A 128 for a list of all genotype combinations used). 129 We wanted to test explicitly the role of richness and relatedness in general, while 130 minimizing identity effects, thus each replicate of a given treatment contained a different 131 assemblage of genotypes. This required using a large number of genotypes, and as a result, our 132 experiment did not contain monocultures of each genotype. We avoided confounding our

133 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

137 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 andtwo different tidal heights.

141

142 Field Experiment

143 In July 2013 we planted 12 replicates of each of the six treatments (two levels of richness 144 crossed with three levels of relatedness) in a randomized block design, with plots in a grid with 145 12 rows (each row is a block) and six columns, for a total of 72 plots. Although the slope of the 146 shore was gradual at our location (< 0.5 m difference between any plots) and the entire 147 experiment was > 20 m from the edge of a bed, these blocks paralleled the shore to account for 148 effects of elevation/depth (Abbott and Stachowicz 2016). We randomly assigned each treatment 149 to one of the six columns for each of the 12 rows. We established this grid within an existing 150 eelgrass bed in Bodega Harbor, CA by clearing seventy-two 70 cm by 60 cm plots of seagrass. 151 We then inserted plastic containers (40.4 cm long x 32.7 cm wide x 15.2 cm deep) lined with 2 152 mm diameter mesh into the center of each plot and filled them within 3 cm of the top with 153 homogenized, sieved, field-collected sediment. We planted 12 shoots in each plot: six of each 154 genotype for the two-genotype plots and two of each genotype for the six-genotype plots. Prior 155 to planting, we removed all epibionts from each shoot and standardized them to 30 cm of shoot 156 and 2.5 cm of rhizome. We harvested the experiment 16 months later in October 2014 (after two 157 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

162 traveled from the base of the sheath x shoot width). We estimated epifaunal community 163 composition in each plot by collecting three eelgrass shoots from each plot and quickly 164 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 165 166 identification to the lowest taxonomic level possible. For analyses we used two measures of 167 invertebrate abundance: (1) we standardized abundance by the dry weight of the shoots of 168 eelgrass from which the invertebrates were collected, and (2) we estimated the total plot-level 169 abundance of invertebrates by multiplying the abundance per gram of eelgrass sampled by the 170 total mass of aboveground biomass from each plot at the end of the experiment. Because it is 171 unlikely that richness scales linearly with the mass of eelgrass either sampled or in the plot as a 172 whole, we used cumulative richness from all three sampled shoots in analyses. 173 We next harvested all of the eelgrass from each container. Each physically connected 174 section of eelgrass (group of ramets) was placed into individually labeled Ziploc bags and 175 transported a short distance (~ 2.5 km) back to the laboratory, where they were stored in a 176 refrigerator or frozen until processing. For each group of connected ramets we took a single leaf 177 tissue sample for genetic analysis so that we could attribute biomass unambiguously to a 178 genotype. We divided the final biomass of each ramet into shoots, roots, and rhizome, and

179 weighed each after drying at 60°C for at least 48 hours.

180

181 *Trait diversity*

We previously measured significant variation among these 41 genotypes for 17 traits when
grown in a common garden (Abbott et al. in review). 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 (Hughes et al. 2009; Reynolds et al. 2016).
Multivariate trait distance was uncorrelated with estimates of pairwise relatedness for these
genotypes (Abbott et al. in review), 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; Clark et al. 2012; Schleuter et al. 2010). This allowed us to
include trait diversity as a predictor in models of biomass accumulation along with genotypic
richness and relatedness.

208	
209	Re-genotyping
210	In addition to the genotype samples we took at harvest, in November 2013 and May 2014 we
211	collected 2 cm long pieces of leaf from each group of shoots we estimated to be part of the same
212	physiologically connected ramet in the field in each plot in order to assess genotypic composition
213	of the plots and how it changed over time. The tissue samples collected for genotyping were
214	processed in the same manner as in the original genetic analysis. Each sample was identified as
215	one the original 41 genotypes or a new unique genotype. By the end of the experiment new
216	"invader" genotypes established in 16 of the 72 plots, but overall they composed less than 3% of
217	the total eelgrass biomass. Within plots where invaders established, on average they composed
218	less than 10% of total plot biomass. There were no effects of richness, relatedness, or trait
219	diversity of eelgrass in a plot on the likelihood of an invader establishing (Appendix B).
220	
221	Statistical analysis
222	Not all genotypes survived in plots in which they were planted, so we assessed whether
223	there was any effect of the initial planted diversity (richness, relatedness, and trait diversity) on
224	patterns of mortality and survival of genotypes. Because we detected no such effects (see
225	Appendix C), and because nearly two-thirds (44/68) of the genotypes that were lost during the
226	experiment had already been lost from the plots by November 2013 (four months into the
227	experiment), whereas all performance/functioning response variables were measured at the end
228	of the experiment (October 2014), we used the final genotypic composition rather than initial
229	composition to calculate plot-level realized diversity metrics. In addition to richness, relatedness,
230	and trait diversity, we also included genotypic evenness as a realized diversity metric in our

231	models to account for the differences in the relative abundance of genotypes in each plot at the
232	end of the experiment. Because we included genotypic evenness separately in the model, we
233	assumed an equal abundance of all genotypes in each plot at the end of the experiment for our
234	calculation of trait diversity. We did this to avoid systematic correlations between trait diversity
235	and other parameters in the model. Some of the plots only had one genotype left at the end of the
236	experiment; these plots all have a trait diversity and evenness of zero and richness and
237	relatedness of one. We repeated our analyses with planted diversity metrics, but none of these
238	was ever correlated with final performance (see Results).
239	We performed analyses using R 3.0.3 or R 3.3.3 (R Core Team 2014, 2017). We used
240	logistic regression (glm function from the stats package in R; R Core Team 2014) to test the
241	effects of planted genotypic richness, relatedness, and trait diversity, on the likelihood that no
242	shoots survive at the end of the experiment. For plots in which at least one genotype survived,
243	we performed separate analyses of genotype survival for those planted with two genotypes and
244	six genotypes. In two- genotype plots, we performed a logistic regression, testing the effects of
245	planted genotypic richness, relatedness, and trait diversity on whether both genotypes survived.
246	For the six-genotype plots we used the proportion of surviving genotypes as a continuous
247	response variable and used a generalized linear mixed model with the richness, relatedness, and
248	trait diversity of planted genotypes as fixed effects, and block as a random effect, using a
249	Bayesian approach in the MCMCglmm package in R (Hadfield 2010).
250	We used the same type of generalized linear mixed models (MCMCglmm package in R)
251	to assess the effects of our realized diversity metrics on the performance and functioning of the
252	eelgrass plots (eelgrass above and belowground biomass and leaf growth rate, and invertebrate
253	grazer abundance and richness). For these models we specified a Gaussian distribution for the

254	response variables and used priors that corresponded to an inverse-Gamma distribution, with
255	shape and scale parameters equal to 0.001. We evaluated relative performance of our models
256	using the model deviance information criterion (DIC). DIC is a Bayesian generalization of the
257	Akaike information criterion (AIC) that is particularly suited to comparing models that
258	use Markov chain Monte Carlo (MCMC) to obtain posterior distributions (Spiegelhalter et al.
259	2002). Similar to AIC, DIC measures model accuracy while penalizing excessive model
260	complexity (additional parameters), with a lower DIC score indicating a preferred model. We
261	tested univariate models for each diversity metric (realized richness, relatedness, trait diversity,
262	and evenness), a full model that included all four metrics, and all possible two and three variable
263	models. For simplicity only the best performing two and three variable models are presented in
264	the results.

265

266 **Results**

267 Survivorship

Eelgrass failed to establish permanently (complete mortality) in 22 of 72 plots. We found no 268 269 effect of the initial planted genotypic richness, average relatedness, or trait diversity of the 270 genotypes in a plot on the likelihood of complete mortality (Appendix C). Most of these plots 271 never produced any new shoots and died within a few months of the initial planting, suggesting 272 that complete mortality resulted from the failure of the transplants to establish, likely due to 273 dislodgement by currents, burrowing organisms or floating algal mats, rather than interactions 274 among shoots. Because complete mortality was independent of treatment, we excluded these 275 plots from the rest of the analyses.

276 Within the plots in which eelgrass remained at the end of the experiment, neither the 277 richness, relatedness, and trait diversity of planted genotypes, nor their interactions affected the 278 proportion of genotypes surviving or any of our measures of plant performance or animal 279 community diversity (Appendices C and D). The lack of effect of planted diversity is probably 280 because most (65%) of the genotypes that were lost from a plot in which they were planted were 281 lost within the first 4 months of the experiment. Thus, for the vast majority of the duration of the 282 experiment the genotypic composition in each plot was similar to that measured at the end of the 283 experiment.

284

285 *Plant biomass and growth*

286 Realized richness and relatedness (calculated using observed genotypic composition at the end of 287 the experiment) independently influenced several measures of plant biomass. For example, the 288 model that best explained variation in final belowground biomass included both richness, which 289 was positively correlated with biomass, and relatedness, which was negatively correlated with 290 biomass (Table 2, Fig. 1). A model that also included evenness with richness and relatedness 291 performed similarly (Δ DIC = 0.56, Table 2), suggesting that evenness also positively influenced 292 belowground biomass (as seen in univariate analyses), but not enough to improve model 293 performance while adding an additional variable. For above ground biomass the best performing 294 model included richness and evenness having a positive affect on biomass and relatedness 295 having a negative affect, although a model that did not include relatedness performed essentially 296 the same (Δ DIC = 0.12, Table 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

299 for explaining eelgrass biomass, although richness had a greater effect. In practice, richness and 300 evenness are often combined to calculate the diversity (e.g., Shannon index) of an assemblage. 301 Because genotypic Shannon diversity combines two measures of diversity that we found to be 302 important, and it is a ubiquitous metric used to characterize the diversity of natural communities, 303 we decided to run models that replaced the richness and evenness of eelgrass plots with their 304 genotypic diversity. Unsurprisingly, by combining information about richness and evenness into 305 a single metric and reducing the number of parameters, model performance increased when using 306 genotypic diversity (Δ DIC = 1.46 for below and 2.84 for above ground biomass when comparing 307 the best performing models, Tables 2 and 4). Genotypic diversity proved to be the strongest 308 predictor of eelgrass biomass, however relatedness was also included in the best performing 309 models for both below and aboveground biomass (Table 2).

310 A consistent positive correlation between trait diversity and diversity of genotypes, both 311 for single traits and multivariate trait indices, suggests that trait diversity may mechanistically 312 account for the effect of genotypic diversity on plant performance (Fig. 3). Trait diversity was 313 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 314 315 stronger predictor. Trait diversity was positively correlated with belowground and aboveground 316 biomass in univariate analyses (Table 2, Fig. 1), and the performance of the full model, which 317 included trait diversity, was not greatly reduced compared to the best performing model (Δ DIC 318 = 2.36 for below and 1.57 for above ground 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

322 were positively correlated with biomass; however, as with our multivariate trait diversity metric, 323 the strong correlation between trait and genotypic diversity meant that these factors dropped out 324 of multi-factor models once Shannon genotypic diversity was included (Appendix E). 325 Leaf growth over the last two weeks of the experiments was weakly positively affected 326 by relatedness, but not by any other dimension of diversity (Appendix F). The association of 327 high relatedness with low biomass (Fig. 1) likely reduced self-shading and contributed to higher 328 leaf growth rates in high-relatedness plots. Despite high leaf growth rates, standing biomass was 329 lower in these plots, suggesting that turnover rates, leaf number, or herbivory rates vary with 330 relatedness in such a way to reduce standing stock. The low belowground biomass in realized 331 monocultures, combined with the high aboveground growth, resulted in a higher ratio of above to 332 belowground biomass in plots with one genotype compared to plots with multiple genotypes (Fig. 333 4). By definition, realized monocultures have zero trait diversity or genotypic diversity, and a 334 richness and relatedness of one. Therefore, we also ran models excluding all realized 335 monocultures to determine whether this drove the effects we observed, which it did not 336 (Appendix G).

337

338 *Invertebrate Community Response*

The best performing model of invertebrate abundance contained only trait diversity (Table 3).
Total estimated invertebrate abundance in an entire plot increased with eelgrass trait diversity
(Table 3, Fig. 5), even when only considering plots with > 1 genotype (Appendix G). The
abundance of invertebrate grazers per unit mass of eelgrass sampled decreased with increasing
relatedness, the only predictor showing any effect in univariate analyses (Table 3, Fig. 5).
However, adding trait diversity to the model including relatedness modestly improved model fit

345	(delta AIC = 1.5) largely due to the difference between single and multi-genotype plots
346	(Appendix G). The species richness of invertebrate grazers in the eelgrass samples from each
347	plot was uncorrelated with any of the realized eelgrass diversity metrics Appendix G and H).
348	
349	Discussion
350	Considerable current research examines the utility of different diversity measures for describing
351	the species diversity - ecosystem functioning relationship (Cadotte et al. 2008; Cadotte et al.
352	2009; Flynn et al. 2011; Fischer et al. 2017). However, we show that different metrics of
353	intraspecific diversity capture fundamentally different components of biodiversity and should be
354	treated as complementary rather than competing dimensions of biodiversity that influence
355	assemblage performance. Eelgrass assemblages with more genotypes and greater evenness of
356	genotypes (genotypic diversity) attained higher plot-level biomass, whereas relatedness
357	decreased biomass independently of genotypic and trait diversity. Furthermore, our use of
358	multiple metrics clarified particular mechanisms underlying this relationship, as more
359	genotypically diverse plots had higher trait diversity (Fig. 3), suggesting that niche
360	differentiation among genotypes and more efficient use of available resources (e.g. Loreau 2001)
361	at the plot level leads to greater eelgrass biomass accumulation. Although our study focuses on
362	intraspecific diversity in a key habitat-forming species, the same principles should apply to
363	diversity at any level of biological organization.
364	Genotypic richness showed a strong positive relationship with eelgrass biomass,
365	consistent with previous studies (Hughes and Stachowicz 2004, 2011; Reusch et al. 2005). By
366	statistically partitioning diversity effects, these studies highlighted the importance of
367	complementarity (Reusch et al. 2005; Hughes and Stachowicz 2011), but never clearly revealed

368 a trait-based mechanism, our study showed that the evenness of eelgrass assemblages also 369 positively influenced eelgrass biomass. Species evenness can affect community function (e.g. 370 Wilsey and Potvin 2000, Polley et al. 2003, Mulder et al. 2004), but the influence of intraspecifc 371 genotypic evenness on function is less clear. Our finding that genotypic Shannon diversity, a 372 measure that includes both richness and evenness, best predicted biomass accumulation implies 373 that resource partitioning among genotypes promotes both coexistence at similar relative 374 abundances (Chesson 2000) and higher assemblage performance (Tilman 1999). 375 Although eelgrass genotypic diversity explained greater variation in biomass than trait 376 diversity, without knowing which traits are most important to intraspecific interactions, a 377 multivariate measure of trait differentiation may not provide the best measure for how trait 378 differences influence assemblage performance. Our multivariate trait index could be less 379 correlated with eelgrass biomass than simple genotypic richness either because we failed to 380 measure some relevant traits or because our index contains some irrelevant traits that weaken the 381 correlation between differentiation and performance. Because we measured 17 different traits 382 related to light and nutrient acquisition, biomass production above and below ground, rates of 383 clonal spread, and resistance to herbivores, the failure to measure an unidentified trait seems an 384 unlikely explanation. Unfortunately the links between trait combinations and performance are 385 likely to be complex, and different traits may be most relevant to predicting performance of 386 different sets of genotypes. Furthermore, differentiation in some traits can lead to either 387 complementarity or dominance, depending on heterogeneity in environmental conditions and the 388 nature and magnitude of tradeoffs among traits (Mayfield and Levine 2010). Without tradeoffs, 389 for example, genotypes with lower requirements for some limiting resource would likely 390 outcompete others, and the greater the variation in traits, the greater the difference in competitive

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391	ability and the more likely competitive exclusion will occur (Abbott and Stachowicz 2016).
392	Differences in certain traits and environmental conditions may be more likely to lead to trade-
393	offs and thus only some subset of traits may influence how well trait diversity predicts
394	performance (Kraft 2015).
395	In contrast to the strong positive effects of genotypic richness and diversity, the
396	relatedness of eelgrass genotypes reduced eelgrass biomass. Because relatedness and trait
397	differences for the genotypes used in this study were uncorrelated (Abbott et al. in review), this
398	effect cannot be attributed to low trait diversity in high relatedness plots. Relatedness could have
399	direct effects on performance as some plants allocate fewer resources to root competition when
400	in the presence of individuals of the same species (Mahall and Callaway 1991, 1996), genotype
401	(Gersani et al. 2001; Falik et al. 2003; Gruntman and Novoplansky 2004), or close kin (Dudley
402	and File 2011). Our finding that the ratio of above to belowground biomass was higher for plots
403	that only had one genotype left at the end of experiment (realized monocultures) than those with
404	multiple genotypes (Fig. 4) could be evidence of self vs. non-self recognition, with reduced
405	allocation to intense belowground competition in the presence of closely related individuals.
406	Eelgrass trait diversity increased invertebrate grazer abundance at the plot scale, either
407	because trait diversity leads to higher plant biomass and greater habitat volume (Borer et al.
408	2012; Best et al. 2014), or because different grazer taxa prefer different genotypes as food or
409	habitat (Reynolds et al. in press Oikos). Trait diversity did affect eelgrass biomass, although not
410	as strongly as other variables that were uncorrelated with invertebrate abundance, suggesting that
411	higher aboveground biomass is not the only mechanism involved. Several amphipods and
412	isopods prefer different microhabitats within eelgrass beds at this site (Lürig et al. 2016), and the

413 presence of genotypes with different heights, widths, or leaf traits may have influenced414 invertebrate biomass.

415 Our results, combined with those of previous studies, show a consistent pattern of 416 genotypic richness/diversity enhancing the productivity of eelgrass assemblages (Hughes and 417 Stachowicz 2004, 2011; Reusch et al. 2005; Stachowicz et al. 2013). Our study indicates that 418 trait diversity among genotypes contributes to these effects and also influences the eelgrass-419 associated invertebrate community. The influence of relatedness on performance is more 420 enigmatic. Previous studies of relatedness were confounded by a spurious positive correlation 421 between relatedness and trait differentiation in a small sample of genotypes (Stachowicz et al. 422 2013). In the present study trait diversity and relatedness were uncorrelated, making the negative 423 relationship between relatedness and biomass, and the positive relationship between relatedness 424 and invertebrate grazer density more difficult to interpret. It is clear that the diversity metrics we 425 tested influenced eelgrass performance in distinct ways; however, it remains unclear why 426 relatedness influenced eelgrass and invertebrate grazers the way it did. 427 Understanding the relationship between biodiversity and ecosystem functioning is a 428 major focus of modern ecology (e.g. Tilman 1999; Schmid 2002), and one of the main lines of 429 inquiry has been the aspects of biodiversity (richness, genetic distance, functional diversity) that 430 best predict ecosystem functioning (e.g. Flynn et al. 2011, Venail et al. 2015). While many 431 studies have asked these questions about diversity among species, few have extended the 432 approach to multiple dimensions of intraspecific variation, particularly within the marine realm. 433 Each of our diversity metrics affected some community function, but the lack of correlation 434 among certain metrics suggests they represent independent dimensions of biodiversity with 435 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.

442

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685 Tables:

Table 1. Range and variance of relatedness values for each level of richness x relatedness. 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

690	genotypes in the	12 replicate pl	lots at each re	latedness level.
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		Distantly related	Intermediate relatedness	Closely related
	2 genotype plots	0		
	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
	6 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
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698	Table 2. Summary of generalized linear mixed model results for the effects of realized diversity
699	metrics on below and aboveground biomass of eelgrass. Block was included as a random effect
700	in all models; but block effect results are omitted for brevity. Models are presented with posterior
701	means (Bayes estimates), 95% credible intervals (equivalent to 95% confidence intervals), and
702	pMCMC values (probability of the estimate overlapping zero). Section A shows results for
703	models including genotypic richness and evenness separately and section B shows results
704	including genotypic (Shannon) diversity in the place of richness and evenness. Results for the
705	best performing models are in bold.
706	

		Belowground biomass					Aboveground biomass				
	Models using final diversity metrics	Post mean	Lower CI	Upper CI	рМС- MC	DIC	Post mean	Lower CI	Upper CI	pMC- MC	DIC
A	Richness+relatedness +trait diversity+ evenness				0	305.41					321.72
	Richness	1.95	0.32	3.37	0.01		1.51	-0.28	3.42	0.11	
	Relatedness	-3.01	-6.36	0.54	0.09		-3.06	-6.87	0.73	0.12	
	Trait diversity	-0.06	-0.43	0.33	0.78		-0.12	-0.61	0.33	0.62	
	Evenness	3.31	-2.24	8.10	0.19		5.47	-0.71	11.35	0.07	
	Richness+Relatedness +evenness					303.61					320.15
	Richness	1.78	0.73	2.93	0.007		1.18	-0.15	2.46	0.08	
	Relatedness	-2.94	-6.34	0.20	0.07		-2.89	-6.67	0.96	0.14	
	Evenness	3.10	-1.97	7.78	0.23		5.04	-1.06	10.65	0.10	
	Richness+relatedness					303.05					-
	Richness	1.89	0.97	3.05	<0.001		-	-	-	-	
	Relatedness	-4.11	-6.43	-1.05	0.006		-	-	-	-	
	Richness+evenness					-					320.27

	Richness	-	-	-	-		1.50	0.27	2.78	0.02	
	Evenness	-	-	-	-		7.50	2.74	12.33	0.001	
	Richness					310.40					327.61
	Richness	2.69	1.67	3.68	< 0.001		2.25	1.03	3.49	< 0.001	
	Relatedness					311.89					323.72
	Relatedness	-6.52	-9.21	-4.03	< 0.001		-6.43	-9.79	-3.71	< 0.001	
	Trait diversity					316.71					330.96
	Trait diversity	0.56	0.27	0.81	< 0.001		0.48	0.21	0.84	0.004	
	Evenness					317.19					324.01
	Evenness	9.10	5.18	13.97	< 0.001		10.06	5.56	15.03	< 0.001	
B	Genotypic diversity + relatedness + trait diversity			~		303.38					319.18
	Genotypic diversity	6.69	2.25	11.86	0.009		7.06	1.84	12.55	0.01	
	Relatedness	-3.19	-6.18	-0.19	0.05		-3.81	-7.34	-0.27	0.03	
	Trait diversity	0.07	-0.25	0.38	0.66		-0.06	-0.42	0.37	0.74	
	Genotypic diversity + relatedness					301.59					317.31
	Genotypic diversity	7.20	3.24	10.91	0.001		6.55	1.73	10.74	0.003	
	Relatedness	-3.37	-6.30	-0.34	0.03		-3.64	-6.87	-0.015	0.04	
	Genotypic diversity					305.15					319.78

Table 3. Summary of generalized linear mixed model results for the effects of realized diversity

708 metrics on invertebrate grazer abundance at the plot level and per unit eelgrass biomasss.

709 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 in

712 bold.

	Inverteb	orate abund	lance (/plo	ot)		Inverte	orate abund	lance (/g e	elgrass)	
Models using final diversity metrics	Post mean	Lower CI	Upper CI	рМС- MC	DIC	Post mean	Lower CI	Upper CI	рМС- MC	DIC
Relatedness+richness+ evenness+trait diversity			6		663.36					356.48
Richness	-12.74	-69.49	39.80	0.67		-2.25	-4.97	0.47	0.13	
Relatedness	-17.10	-134.9	109.3	0.79		5.79	-0.46	11.54	0.06	
Trait diversity	12.84	-1.78	25.53	0.07		0.87	0.22	1.58	0.01	
Evenness	-7.43	-193.1	169.9	0.95		-5.25	-13.78	4.69	0.26	
Richness+relatedness+ trait diversity					661.32					355.01
Richness	-12.48	-63.90	45.41	0.66		-2.07	-4.64	0.83	0.15	
Relatedness	-13.18	-114.9	85.04	0.77		7.48	2.41	12.27	<0.00 1	
Trait diversity	12.64	-0.88	26.57	0.08		0.75	0.14	1.54	0.04	
Relatedness+trait diversity					-					355.23
Relatedness	-	-	-	-		8.03	2.85	13.26	<0.00 1	
Trait diversity	-	-	-	-		0.38	-0.08	0.89	0.11	
Richness+trait diversity					659.24					-
Richness	-11.24	-64.76	40.30	0.66		-	-	-	-	
Trait diversity	13.26	1.01	26.22	0.03		-	-	-	-	

Richness					661.64					364.20
Richness	31.23	-3.47	65.50	0.08		-1.01	-2.92	0.83	0.30	
Relatedness					662.18					356.71
Relatedness	-73.12	-160.5	13.06	0.11		6.12	1.55	10.70	0.01	
Trait diversity					657.48					364.27
Trait diversity	11.11	2.78	19.04	0.01		-0.01	-0.46	0.47	0.94	
Evenness					662.98					361.03
Evenness	95.01	-34.53	244.2	0.18		-7.55	-14.38	-0.31	0.04	

714	Figures legends:
715	Figure 1. Effects of realized genotypic richness (A), relatedness (B), trait diversity (C), evenness
716	(D), and Shannon diversity (E) on aboveground biomass. See Table 2 for statistical analysis.
717	Different symbols are used to denote the richness of genotypes in each plot; the legend is in the
718	bottom right corner of plot E.
719	
720	Figure 2. Same as figure 1 but with belowground biomass as the response variable.
721	
722	Figure 3. Relationship between genotypic richness and trait diversity.
723	
724	Figure 4. Relationship between the ratio of above to belowground eelgrass biomass and the
725	relatedness of eelgrass in each plot (A) and the mean ratio of above to belowground biomass in
726	plots with only one genotype (realized monoculture) compared to plots with multiple genotypes
727	(realized polycultures) at the end of the experiment (B). Different symbols in plot A are used to
728	denote the richness of genotypes in each plot. The error bars in plot B are 95% confidence
729	intervals.
730	
731	Figure 5. Effects of trait diversity on the abundance of invertebrate grazers per plot (A) and of
732	relatedness on invertebrate abundance per gram of eelgrass sampled (B). See Table 3 for
733	analyses. Different symbols are used to denote the richness of genotypes in each plot and the
734	legend is in the upper left corner of plot B.
735	
736	











- 1 Appendix A: Genotypic composition of all plots
- 2 Table A1. Genotypic composition of each plot for the field experiment. Plots were arranged in a
- 3 grid with 12 blocks along a slight tidal gradient and 6 plots (one of each treatment) in a row
- 4 (position) in each block. The table gives the block and position of each plot and lists the
- 5 genotypes that were planted in it. It also gives the pairwise relatedness of genotypes in the two-
- 6 genotype plots and average pairwise relatedness in the 6 genotype plots. A range of the
- 7 relatedness of all pairwise combinations of the 6 genotypes is included for the six-genotype
- 8 plots.

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									Relatedness	Range of
Block	Position	Treatment	Genotype 1	Genotype 2	Genotype 3	Genotype 4	Genotype 5	Genotype 6	(pairswise	pairwise
									or average)	relatedness
A	1	2-high	CCS9	DPHI4	-	-	-	-	0.46	-
В	4	2-high	DPS19	MMS10	-	-	-	-	0.31	-
С	3	2-high	MMHI1	MMHI7	-	-	-	-	0.87	-
D	6	2-high	DPHI2	WPHI4	-	-	-	-	0.52	-
E	5	2-high	WPH13	MMHI15	-	-	-	-	0.66	-
F	3	2-high	CCS14	MMLI15	-	-	-	-	0.41	-
G	1	2-high	J4	WPL15	-	-	-	-	0.33	-
Н	2	2-high	DPHI14	WPS20	-	-	-	-	0.36	-
I	6	2-high	MMS8	WPS3	-	-	-	-	0.56	-
J	3	2-high	CCHI12	J14	-	-	-	-	0.41	-
K	6	2-high	CCHI12	WPHI12	-	-	-	-	0.41	-
L	6	2-high	CCLI6	CCLI2	-	-	-	-	0.41	-
Α	4	2-mid	CCHI1	WPLI12	-	-	-	-	0.02	-
В	5	2-mid	CCHI17	CCL16	-	-	-	-	-0.04	-
С	4	2-mid	CCS14	DPLI18	-	-	-	-	0.06	-
D	2	2-mid	DPS9	WPHI4	-	-	-	-	-0.02	-
E	2	2-mid	CCS17	MMLI12	-	-	-	-	-0.01	-
F	6	2-mid	DPHI10	MMLI15	-	-	-	-	0.03	-
G	3	2-mid	DPHI14	DPLI18	-	-	-	-	0.00	-
Н	5	2-mid	DPHI6	MMHI8	-	-	-	-	-0.09	-
Ι	5	2-mid	WPLI15	WPS9	-	-	-	-	0.00	-
J	5	2-mid	DPLI7	J6	-	-	-	-	0.01	-
K	1	2-mid	DPS14	MMLI17	-	-	-	-	-0.17	-
L	5	2-mid	MMS17	WPHI3	-	-	-	-	-0.03	-
A	6	2-low	CCS17	DPHI6	-	-	-	-	-0.61	-
в	3	2-low	J6	WPLI15	-	-	-	-	-0.38	-
С	2	2-low	DPHI14	J4	-	-	-	-	-0.45	-
D	4	2-low	CCLI2	DPHI6	-	-	-	-	-0.56	-
Е	1	2-low	CCS9	WPS9	-	-	-	-	-0.40	-
F	2	2-low	DPHI2	MMLI12	-	-	-	-	-0.69	-
G	2	2-low	DPHI4	DPS9	-	-	-	-	-0.50	-
Н	6	2-low	DPLI10	WPL15	-	-	-	-	-0.50	-
Ι	2	2-low	MMHI1	WPS20	-	-	-	-	-0.43	-
J	6	2-low	J4	WPHI12	-	-	-	-	-0.44	-
Κ	5	2-low	DPLI7	MMHI15	-	-	-	-	-0.49	-
L	1	2-low	MMLI17	WPS3	-	-	-	-	-0.66	-
A	3	6-high	CCHI12	CCLI2	CCS17	J14	WPHI3	WPHI12	0.39	0.25 to 0.45
В	1	6-high	CCS14	CCS9	DPHI14	J6	MMLI15	MMS10	0.41	0.07 to 0.65
С	1	6-high	CCS17	CCS9	DPHI14	J6	MMS8	WPLI12	0.41	0.11 to 0.65
D	5	6-high	CCS9	DPHI14	DPHI4	J14	J6	MMS10	0.41	0.18 to 0.64
Е	6	6-high	CCHI12	CCL16	CCS9	DPHI10	J14	MMS10	0.38	0.004 to 0.56
F	4	6-high	CCS14	DPS14	J6	MMS10	MMS8	WPL112	0.45	0.24 to 0.71
G	4	6-high	CCLI6	CCLI2	CCS17	J14	MMH11	WPHI12	0.39	0.20 to 0.80
H	1	6-high	CCL12	CCS14	DPHI14	DPL110	WPHI3	MMHI15	0.39	0.20 to 0.70
I	4	6-high	CCL12	DPHI10	DPHI14	DPHI2	J6	MMHI15	0.43	0.21 to 0.67
J	4	6-high	CCL12	CCS17	DPL110	MMH11	WPHI12	WPH13	0.40	0.20 to 0.80
ĸ	2	6-high	CCS17	DPHI10	DPHI2	.J6	MMH11	WPHI4	0.42	0.09 to 0.66
L	4	6-high	CCS17	DPHI10	MMH11	MMHI7	WPH13	WPHI4	0.41	0.11 to 0.87
A		6-mid	CCH117	CCL16	CCS14	.16	MMHI7	WPS3	0.02	-0.21 to 0.4
B	6	6-mid	CCH117	DPS9	MMS10	WPHI4	WPL15	WPS3	0.04	-0.21 to 0.29
c	6	6-mid	DPS14	MML115	MML117	WPHI3	WPHI4	WPS9	-0.11	-0.53 to 0.15
Ď	3	6-mid	DPL110	DPS14	MML117	MMS17	MMHI15	WPS9	-0.02	-0.15 to 0.15
E	4	6-mid	CCH11	DPL110	J14	MMS8	WPL115	WPHI4	0.04	-0.17 to 0.25
F	1	6-mid	CCL16	CCS14	DPS9	MML112	WPL15	WPS3	0.05	-0.32 to 0.16
G	6	6-mid	CCHI12	CCL16	DPHI14	DPL110	DPS19	MMS8	0.03	-0.18 to 0.22
н	ĩ	6-mid	DPHI10	DPHI4	DPS14	MML117	WPHI12	WPS20	0.06	-0.21 to 0.31
I	3	6-mid	CCHI1	CCL12	DPHI2	DPS9	WPI 112	WPI 15	0.04	-0.13 to 0.40
I	1	6-mid	CCH117	CCL16	CCS17	DPHI4	DPS14	WPL115	0.05	-0.24 to 0.28
ĸ	4	6-mid	CCHU	DPH14	DPS10	16	MMH11	MMS8	0.03	-0 15 to 0 29
T	2	6-mid	CCH117	0000	J6	14	WPHI3	WPHI4	0.05	-0.25 to 0.25
A	2	6-low	DPS19	14	MMHI7	MMHI8	WPL115	WPS20	-0.42	-0.79 to -0.12
R	2	6-low	CCH112	CCH117	DPI 118	DPI 17	WPI 15	MMS17	-0.42	-0 74 to -0.07
с С	2 5	6-low	DPS10		MMH17	MMI 112	MMS17	W/DI 115	-0.44	-0.68 to .0.07
D	5	6 low	CCHI12	CCLIG	DDI 110	DDC0	MMINIOT /	MMI 117	-0.44	-0.00 to -0.07
D E	1	0-10W	DBL 110	DBS10	DrL118 MMU112	DP59 MMC17	WDI 115	WIVILII/	-0.41	-0.76 to 0.004
E	5	6 low	CCUU	CCU112	DDI 17	MMT 115	WPLIID MMITTO	WPH14	-0.45	-0.70 to -0.12
Г	5 E	6 low		DBS10	DPLI/	IVIIVILII 3 MMT 117	MMC17	WPLID	-0.49	-0.70 to -0.12
П	2	0-10W	DrHI0	DPUIA	DP39	MN/THO	MMU 115	WPED	-0.47	-0./8 to -0.14
т	4	0-10W	DBIII10	DPHI0	DPLI/	MM 112	MMC17	WDI 115	-0.43	-0.00 10 -0.09
1	1	0-10W	DPHI10	DPLIT	DPLI/	MML112	MMS1/	WPL115	-0.43	-0.81 to -0.14
J	2	0-low	CCHII2	DPLI/	MML112	MML115	WPL115	WPL15	-0.45	-0.80 to -0.13
ĸ	3	6-low	CCL16	MMLI12	DPL118	DPLI/	MMS17	WPHI4	-0.44	-0.81 to-0.14
L	3	6-low	CCHI12	DPL118	DPS9	MMH18	MMLI17	wPS9	-0.43	-0.76 to -0.18

10 Table A2. The number of plots in which each genotype was planted for each of the treatment

11 combinations (2 or 6 genotypes and distantly related (low), intermediately related (mid), or

12 closely related (high). No genotype occurred in more than half of the replicates for a particular

13 treatment combination (6/12 replicates), and all genotypes occurred in both 2 and 6 genotype

14 treatments and at least two levels of relatedness.

		6 genotypes			2 genotypes		
Genotype	High	Mid	Low	High	mid	low	
CCHI1	0	3	1	0	1	0	
CCHI12	2	1	5	2	0	0	
CCHI17	0	4	1	0	1	0	
CCLI6	2	4	3	1	1	0	
CCLI2	5	1	0	1	1	0	
CCS14	3	2	0	1	0	1	
CCS17	6	1	0	0	1	1	
CCS9	4	1	0	1	0	1	
DPHI10	4	1	1	0	1	0	
DPHI14	5	1	0	1	1	1	
DPHI2	2	1	0	1	0	1	
DPHI4	1	3	0	1	0	1	
DPHI6	0	0	2	0	1	2	
DPLI10	2	3	0	0	0	1	
DPLI18	0	0	6	0	2	0	
DPLI7	0	0	6	0	1	1	
DPS14	1	4	0	0	1	0	
DPS19	0	2	4	1	0	0	
DPS9	0	3	5	0	1	1	
J14	4	1	0	1	0	0	
J4	0	1	1	1	0	2	
J6	6	3	0	0	1	1	
MMHI1	4	2	0	1	0	1	
MMHI7	1	1	2	1	0	0	
MMHI8	0	0	5	0	1	0	
MMLI12	0	1	4	0	1	1	
MMLI15	1	1	4	1	1	0	
MMLI7	0	3	2	0	1	1	
MMS10	4	1	0	1	0	0	
MMS17	0	1	6	0	1	0	
MMS8	2	3	0	1	0	0	
WPHI12	3	1	0	1	0	1	
WPHI3	4	2	0	1	1	0	
WPHI4	2	3	2	1	1	0	
MMHI15	2	1	0	1	0	1	
WPLI12	2	1	0	0	1	0	
WPLI15	0	2	6	0	1	1	
WPL15	0	3	3	1	0	1	
WPS20	0	1	1	1	0	1	
WPS3	0	3	0	1	0	1	
WPS9	0	2	2	0	1	1	

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19 Appendix B: Results from analyses of the likelihood of an invading genotype establishing in a 20 plot. We considered the establishment of invading genotypes as a binomial response and used 21 logistic regression (glm function from the stats package in R) to test the effects of the 22 relatedness, richness, and trait diversity of the genotypes in the plot on establishment. Because 23 we do not know when the invading genotypes established we used both the planted (based on 24 initial genotype composition, table B1) and realized (based on final genotype composition, table 25 B2) diversity metrics. Tables show the coefficients, their standard error, the Wald Z-statistic, and associated p-values (at α =0.05). Neither planted or realized diversity metrics had any effect on 26 27 the establishment of new genotypes.

Table B1.

	Inva	asion of r	new genoty	pes	
Models using initial diversity metrics	Coeff.	SE	Wald Z	Р	
Relatedness ^x richness +trait diversity			1		
Relatedness ^x richness	0.47	0.41	1.15	0.25	
Relatedness	-2.21	1.70	-1.30	0.19	
Richness	-0.11	0.19	-0.59	0.56	
Trait diversity	0.04	0.07	0.61	0.55	
Relatedness+richness +trait diversity					
Relatedness	-0.53	0.77	-0.69	0.50	
Richness	-0.13	0.18	-0.71	0.48	
Trait diversity	0.03	0.06	0.52	0.61	
Relatedness					
Relatedness	-0.50	0.76	-0.66	0.51	
Richness	-0.07	0.15	-0.51	0.61	
Relatedness					
Relatedness	-0.50	0.77	-0.65	0.52	

30 Table B2.

	In	vasion of 1	new genotyp	es
Models using final diversity metrics	Coeff.	SE	Wald Z	Р
Relatedness+richness +evenness +trait diversity				
Relatedness	0.41	0.77	0.53	0.60
Richness	0.28	0.34	0.81	0.42
Evenness	-1.98	3.29	-0.60	0.55
Trait diversity	-0.02	0.09	-0.18	0.86
Relatedness+richness+trait diversity				
Relatedness	0.43	0.76	0.66	0.57
Richness	0.23	0.24	0.96	0.34
evenness	-2.10	3.22	-0.65	0.52
Richness+evenness				
Richness	0.18	0.23	0.81	0.42
Evenness	-3.10	2.70	-1.15	0.25
Evenness				
Evenness	-2.21	2.39	-0.92	0.36

42 Appendix C: Results from analyses of the likelihood that a plot will experience complete

43 mortality across all plots (table C1) and the likelihood of exclusion in the two and six genotype

44 plots separately (tables C2 and C3).

45

46 Table C1. Table shows the coefficients, their standard error, the Wald Z-statistic, and associated

47 p-values (at α =0.05).

		Con Mor	nplete tality	
Models using initial diversity metrics	Coeff.	SE	Wald Z	Р
Relatedness ^x richness +trait diversity				
Relatedness ^x richness	-0.30	0.36	-0.83	0.41
Relatedness	0.26	1.41	0.19	0.85
Richness	0.14	0.16	0.89	0.37
Trait diversity	-0.04	0.05	-0.68	0.49
Relatedness+richness +trait diversity				
Relatedness	-0.78	0.68	-1.14	0.25
Richness	.14	0.16	0.86	0.39
Trait diversity	-0.04	0.05	-0.75	0.45
Relatedness				
Relatedness	-0.81	0.68	-1.19	0.23
Richness	0.07	0.13	0.53	0.60
Relatedness				
Relatedness	-0.81	0.68	-1.19	0.23

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50 Table C2. Model results for the effects of the relatedness and trait diversity of the initially

51 planted genotypes on the likelihood that one genotype would be excluded from the plot in the

- 52 two-genotype plots. Table shows the coefficients, their standard error, the Wald Z-statistic, and
- 53 associated p-values (at α =0.05).
- 54

	Coex	istence in	2-genotype	plots
Models using initial diversity metrics	Coeff.	SE	Wald Z	Р
Relatedness+trait diversity				
Relatedness	0.25	0.97	0.26	0.38
Trait Diversity	-0.07	0.08	-0.87	0.38
Relatedness				
Relatedness	0.14	0.94	0.15	0.88
Trait diversity				
Trait diversity	-0.07	0.08	-0.85	0.39

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Table C3. Model results for the effects of the relatedness and trait diversity of the initially planted genotypes on the survivorship of genotypes in the six-genotype plots. Block was included as a random effect; however, to save space results for block are not included in the table. Models are presented with posterior means (Bayes estimates), 95% credible intervals (equivalent to 95% confidence intervals), and pMCMC values (probability of the estimate overlapping zero).

	Su	rvivorship in	6 genotype p	olots	
Models using initial diversity metrics	Post mean	Lower CI	Upper CI	рМСМС	
Relatedness+trait diversity					
Relatedness	0.005	-0.26	0.32	0.98	
Trait diversity	0.009	-0.02	0.04	0.48	
Trait diversity					
Trait diversity	0.009	-0.02	0.03	0.48	

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64 **Appendix D:** Summary of generalized linear mixed model results for diversity metrics based on 65 initial eelgrass composition on belowground biomass, leaf growth rate, invertebrate grazer 66 richness (raw counts from eelgrass sampled), and invertebrate grazer abundance (per gram of 67 eelgrass sampled). Results for aboveground biomass were qualitatively similar to belowground 68 biomass and results invertebrate grazer abundance per plot were qualitatively similar to 69 invertebrate grazer abundance per gram of eelgrass sampled, and thus are not presented. 70 Predictor variables evaluated are based on the composition of genotypes at the beginning of the 71 experiment and include average genetic relatedness, genotypic richness, and trait diversity 72 (Rao's Q). Block was included as a random effect; however, to save space results for block are 73 not included in the table. Models are presented with posterior means (Bayes estimates), 95% 74 credible intervals (equivalent to 95% confidence intervals), and pMCMC values (probability of 75 the estimate overlapping zero). Initially, we found a significant negative correlation between trait 76 diversity and invertebrate abundance per gram of eelgrass sampled, but this relationship was 77 driven by one extreme point, which we determined to be an outlier using the Grubbs test for 78 single outliers (P = 0.004; Grubbs 1950).

		Below	ground b	iomass			Lea	f growth	rate	
Model using initial diversity metrics	Post mean	Lower CI	Upper CI	рМСМ С	DIC	Post mean	Lower CI	Upper CI	рМСМ С	DIC
Relatedness*richness+trait diversity					336.36					397.15
Relatedness *richness	1.07	-1.20	3.39	0.39		-0.52	-4.91	3.76	0.80	
Relatedness	-5.77	-15.12	3.28	0.256		8.75	-10.14	27.37	0.33	
Richness	0.49	-0.65	1.66	0.378		1.23	-0.73	3.43	0.24	
Trait diversity	0.029	-0.39	0.42	0.86		-0.26	-1.02	0.39	0.45	
Relatedness+richness+trait diversity					335.15					395.13
Relatedness	-1.88	-6.29	2.74	0.40		7.05	-2.17	15.5	0.14	
Richness	0.49	-0.80	1.5	0.37		1.19	-0.92	3.17	0.22	
Trait diversity	0.02	-0.37	0.43	0.90		-0.28	-0.10	0.39	0.42	
Relatedness + richness					332.81					393.76
Relatedness	-2.03	-6.65	2.56	0.40		6.86	-1.24	15.36	0.11	
Richness	0.54	-0.44	1.48	0.24		0.76	-0.97	2.46	0.37	
Richness					331.86					-
richness	0.51	-0.36	1.32	0.25		-	-	-	-	
Relatedness					-					392.55
relatedness	-	-	-	-		6.66	-1.25	15.38	0.12	
		Inver	tebrate ri	chness		Inv	ertebrate	abundanc	e (/g eelg	rass)
Relatedness*richness+trait diversity					211.24					366.08
Relatedness *richness	-0.43	-1.07	0.23	0.35		2.30	-0.93	5.60	0.174	
Relatedness	1.28	-1.38	3.77	0.42		-5.87	-20.33	7.47	0.40	
Richness	-0.13	-0.20	0.45	0.56		-0.58	-2.42	1.25	0.52	
Trait diversity	-0.03	-0.16	0.08	0.20		0.47	-0.23	1.17	0.21	
Relatedness+richness+trait diversity					211.3					366.61
Relatedness	-0.26	-1.53	1.15	0.73		2.06	-3.94	9.37	0.51	
Richness	0.14	-0.18	0.46	0.37		-0.69	-2.41	1.13	0.43	
Trait diversity	-0.03	-0.14	0.09	0.63		0.46	-0.28	1.12	0.21	
Richness + trait diversity					209.07					364.44
Richness	0.15	-0.17	0.47	0.34		-0.69	-2.64	1.04	0.47	
Trait diversity	-0.03	-0.14	0.08	0.59		0.46	-0.30	1.13	0.22	
Richness					207.40					-
Richness	0.10	-0.16	0.37	0.45		-	-	-	-	
Trait diversity					-					371.91
Trait diversity	-	-	-	-		0.28	-0.30	0.86	0.30	

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Appendix E: Table of pMCMC values (tests if the parameter is significantly different from zero, analogous to p-values at α =0.05) from analyses of the effects of individual traits of eelgrass genotypes in assemblages on belowground biomass, leaf growth rate, and invertebrate grazer richness. We analyzed the mean, variance, range, and maximum and minimum values of each trait for each plot. We looked at the effects of each trait individually in the model (A) and including any significant factors from our analyses with relatedness and genotypic diversity (B). Block was included as a random effect in all models.

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Table of pMCMC values		Below	ground bio	mass			Le	af Growt	ч			Inverte	ebrate rio	chness	
A)	model: tr	ait alone				model: tra	it alone				model: tra	ait alone			
Trait	Mean	Variation	Range	Мах	Min	Mean	Variation	Range	Мах	Min	Mean	Variation	Range	Max	Min
Alpha	0.71	0.09 .	0.004**	0.1	0.034*	0.63	0.34	0.21	0.21	0.83	0.99	0.94	0.62	0.76	0.94
Phenolic content	0.93	0.63	0.01^{*}	0.18	0.16	0.16	0.88	0.66	0.25	0.08 .	0.48	0.89	0.31	0.58	0.99
Ammonium uptake	0.69	0.2	0.002**	0.02*	0.11	0.29	0.48	0.43	0.39	0.89	0.57	0.69	0.42	0.9	0.22
Nitrate uptake	0.75	0.22	<0.001***	0.07 .	0.03*	0.56	0.38	0.39	0.37	0.89	0.42	0.29	0.59	0.94	0.22
Terminal shoot biomass	0.47	0.18	0.006**	0.23	0.002**	0.87	0.012*	0.03*	. 60.0	0.2	0.72	0.49	0.43	0.82	0.69
Rhizome biomass	0.56	<0.001***	<0.001***	0.03*	0.002**	0.46	0.432	0.38	0.87	0.24	0.67	0.31	0.41	0.98	0.51
Root biomass	0.56	0.02*	<0.001***	0.1	0.01*	0.08.	0.07 .	0.63	0.12	0.24	0.36	0.11	0.13	0.14	0.88
New shoot biomass	0.81	0.06 .	<0.001***	0.07 .	0.03*	0.19	0.06 .	0.29	0.13	0.45	0.67	0.27	0.41	0.76	0.45
Leaf growth biomass	0.7	0.12	<0.001***	0.16	0.01**	0.62	0.14	0.16	0.6	0.19	0.91	0.99	0.7	0.81	0.87
Leaf growth CM ²	0.88	0.12	<0.001***	0.05*	0.02*	0.36	0.12	0.1	0.75	0.11	0.92	0.45	0.34	0.39	0.74
Number of new shoots	0.45	0.002**	<0.001***	0.002**	0.06 .	0.67	0.93	0.84	0.78	0.47	0.15	0.85	0.96	0.23	0.25
Max shoot length	0.55	0.03*	<0.001***	0.08 .	0.008**	0.31	0.04*	0.07 .	0.63	0.07 .	0.19	0.77	0.45	0.13	0.33
Shoot width	0.34	0.12	<0.001***	0.004**	0.24	0.81	0.01^{*}	0.01^{*}	0.1	0.22	0.54	0.26	0.38	0.93	0.35
Rhizome diameter	0.58	0.16	0.004**	0.02*	0.16	0.45	0.11	. 60.0	0.05*	0.67	0.25	0.53	0.76	0.48	0.48
Max root length	0.29	<0.001***	<0.001***	0.04*	<0.001***	0.62	0.74	0.54	0.6	0.12	0.69	0.78	0.88	0.93	0.9
Total rhizome length	0.46	<0.001***	<0.001***	0.03*	<0.001***	0.39	0.7	0.87	0.81	0.59	0.87	0.26	0.21	0.58	0.49
above:belowground biomass	0.8	0.02*	<0.001***	0.006**	0.02*	0.43	0.03*	0.01*	0.04*	0.23	0.33	0.4	0.84	0.33	0.49
		Below	ground bio	omass			Le	af Growt	£			Inverte	ebrate ric	chness	
B)	model: tra	it + Relatedr	ess + diversi	ťy		model: tra	it + related	ness			model: tra	ait + relatedı	ness		
Trait	Mean	Variation	Range	Max	Min	Mean	Variation	Range	Max	Min	Mean	Variation	Range	Max	Min
Alpha	0.6	0.71	0.75	0.73	0.32	0.25	0.94	0.74	0.26	0.26	0.53	0.31	0.43	66.0	0.16
Phenolic content	0.92	0.22	0.24	0.69	0.49	0.16	0.62	0.63	0.1	0.2	0.63	0.7	0.79	0.97	0.75
Ammonium uptake	0.74	0.18	0.25	0.9	0.14	0.27	0.89	0.78	0.77	0.41	0.59	0.7	0.75	0.42	0.73
Nitrate uptake	0.47	0.84	0.88	0.77	0.49	0.59	0.7	0.93	0.75	0.68	0.54	0.1	0.12	0.62	0.07 .
Terminal shoot biomass	0.56	0.84	0.68	0.84	0.49	0.92	0.03*	0.47	0.16	0.15	0.93	0.94	0.92	0.78	0.66
Rhizome biomass	0.91	0.03*	0.19	0.58	0.43	0.76	0.81	0.87	0.7	0.74	0.88	0.86	0.62	0.76	0.73
Root biomass	0.51	0.77	0.39	0.41	0.93	0.29	0.01*	0.02*	0.06 .	0.5	0.13	0.23	0.52	0.14	0.19
New shoot biomass	0.78	66.0	0.77	0.66	0.74	0.33	0.004**	0.01*	0.04*	0.83	0.89	0.65	0.91	0.95	0.76
Leaf growth biomass	0.98	0.86	0.5	0.96	0.56	0.89	0.39	0.5	0.88	0.48	0.71	0.41	0.56	0.88	0.32
Leaf growth CM ²	0.49	0.42	0.24	0.34	0.76	0.7	0.27	0.37	0.39	0.89	0.69	0.92	0.9	0.7	0.61
Number of new shoots	0.41	0.26	0.13	0.17	0.89	0.78	0.28	0.36	0.48	0.98	0.23	0.2	0.24	0.06 .	0.58
Max shoot length	0.87	0.71	0.47	0.81	0.69	0.31	0.15	0.34	0.95	0.25	0.19	0.24	0.72	0.43	0.06 .
Shoot width	0.99	0.75	0.7	0.96	0.79	0.96	0.02*	0.06.	0.25	0.3	0.41	0.65	0.95	0.38	0.5
Rhizome diameter	0.6	0.94	0.77	0.85	0.69	0.53	0.27	0.34	0.19	0.92	0.16	0.19	0.53	0.12	0.76
Max root length	0.76	0.14	0.11	0.64	0.23	0.34	0.95	0.95	0.47	0.41	0.41	0.43	0.51	0.94	0.25
Total rhizome length	0.98	0.11	0.11	0.49	0.42	0.87	0.15	0.31	0.64	0.64	0.57	0.83	0.74	0.8	0.54
above:belowground biomass	0.76	0.65	0.47	0.71	0.64	0.76	0.07 .	0.11	0.14	0.41	0.11	0.1	0.44	0.03*	0.81

91 Appendix F: Summary of generalized linear mixed model results for the effects of realized 92 diversity metrics on the leaf growth in each plot. We only present results from analyses using all 93 plots with eelgrass at the end of the experiment because there were no significant results when 94 plots with only one genotype were excluded. The predictor variables evaluated are based on the 95 realized composition of genotypes at the end of the experiment and include for average genetic 96 relatedness, genotypic richness, genotypic evenness, and trait diversity (Rao's Q). Block was 97 included as a random effect; however, to save space results for block are not included in the 98 table. Models are presented with posterior means (Bayes estimates), 95% credible intervals (equivalent to 95% confidence intervals), and pMCMC values (probability of the estimate als, 99 100 overlapping zero). 101

-	L	eaf growth	all plots	with eelgra	ISS
Models using final diversity metrics	Post mean	Lower CI	Upper CI	рМСМС	DIC
Relatedness+richness+even ness+trait diversity					368.24
Relatedness	6.26	-1.15	13.66	0.10	
Richness	0.21	-3.36	3.43	0.90	
Evenness	3.06	-7.40	15.43	0.59	
Trait diversity	-0.10	-1.01	0.70	0.83	
Relatedness+evenness+trait diversity					366.20
Relatedness	6.33	-0.54	14.71	0.10	
Evenness	3.14	-8.47	14.17	0.59	
Trait diversity	-0.06	-0.60	0.61	0.82	
Relatedness+richness					364.11
Relatedness	6.27	-0.81	13.80	0.09	
Evenness	2.72	-9.82	13.12	0.60	
Relatedness					362.14
Relatedness	5.05	0.25	10.51	0.06	
Richness					365.15
Richness	-0.95	-3.15	0.92	0.35	
Evenness					364.94
Evenness	-3.80	-11.45	4.25	0.35	
Trait diversity					
Trait diversity	-0.27	-0.79	0.24	0.30	364.97

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103 Appendix G: Summary of generalized linear mixed model results for the effects of realized 104 diversity metrics on below and aboveground biomass (Table H1) and invertebrate richness and 105 abundance (Table H2) when plots with one genotype remaining at the end of the experiment 106 (realized monocultures) are excluded. Predictor variables evaluated are based on the composition 107 of genotypes at the end of the experiment and include average genetic relatedness, eelgrass 108 genotypic richness, genotypic evenness, and trait diversity (Rao's Q). Block was included as a 109 random effect; however, to save space results for block are not included in the table. Models are 110 presented with posterior means (Bayes estimates), 95% credible intervals (equivalent to 95% 111 confidence intervals), and pMCMC values (probability of the estimate overlapping zero).

- 113 Table G1. Effects of various realized diversity metrics on below and aboveground biomass
- 114 accumulation in plots where more than genotype remains at the end of the experiment (realized
- 115 monocultures excluded).

		Only p	lots with	more that	in one gen	otype at	the end o	f the exp	eriment	
		Below	ground b	iomass			Above	ground b	iomass	
Models using final unweighted diversity metrics	Post mean	Lower CI	Upper CI	рМС- МС	DIC	Post mean	Lower CI	Upper CI	рМС- MC	DIC
Relatedness+richness +evenness+trait diversity					243.51					248.26
Relatedness	-3.31	-7.59	0.62	0.12		-3.80	-7.84	0.66	0.09	
Richness	1.79	0.12	3.63	0.05		1.35	-0.44	3.27	0.15	
Evenness	2.57	-4.50	10.13	0.50		5.74	-2.55	13.07	0.14	
Trait diversity	-0.02	-0.47	0.41	0.97		-0.03	-0.48	0.49	0.90	
Relatedness+richness +evenness					241.65					246.71
Relatedness	-3.27	-7.16	0.79	0.11		-3.77	-7.89	0.64	0.07	
Richness	1.74	0.45	2.97	0.007		1.33	-0.05	2.56	0.04	
Evenness	2.80	-4.15	10.20	0.42		5.99	-1.76	13.14	0.12	
Relatedness+richness					239.40					245.82
Relatedness	-3.5	-7.18	0.54	0.07		-4.45	-9.07	-0.43	0.04	
Richness	1.65	0.44	2.81	0.002		1.05	-0.17	2.45	0.11	
Richness+evenness					-					-
Richness	-	-	-	-		-	-	-	-	
Evenness	-	-	-	-		-	-	-	-	
Relatedness					243.95					245.90
Relatedness	-3.84	-8.01	0.12	0.07		-4.59	-8.80	-0.31	0.04	
Richness					242.18					249.93
Richness	1.71	0.41	2.93	0.01		1.19	-0.29	2.51	0.10	
Evenness					248.78					250.58
Evenness	1.83	-5.80	9.65	0.63		5.89	-2.07	13.15	0.14	
Trait diversity										251.52
Trait diversity	0.36	-0.17	0.82	0.15	245.88	0.15	-0.23	0.53	0.45	

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- 123 Table G2. Effects of realized diversity metrics on invertebrate grazer a) richness (raw counts
- 124 from eelgrass sampled) and b) abundance (per gram of eelgrass sampled and scaled to plot) in
- 125 plots where more than genotype remains at the end of the experiment (realized monocultures
- 126 excluded).
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- 128 Table G1a:

Models using final diversity metrics	Post mean	Lower CI	Upper CI	рМС- MC	DIC
Relatedness+richness+ evenness+trait diversity					168.45
Relatedness	0.25	-1.22	1.79	0.75	
Richness	0.16	-0.47	0.79	0.62	
Evenness	-0.74	-3.45	1.81	0.56	
Trait diversity	-0.01	-0.19	0.15	0.91	
Relatedness+richness+ evenness					166.34
Relatedness	0.23	-1.37	1.58	0.74	
Richness	0.15	-0.29	0.65	0.55	
Evenness	-0.79	-3.54	1.68	0.54	
Richness+evenness					164.45
Richness	0.14	-0.30	0.62	0.56	
Evenness	-0.84	-3.52	1.75	0.52	
Relatedness					163.07
Relatedness	0.25	-1.26	1.65	0.74	
Richness					162.81
Richness	-0.15	-0.29	0.67	0.53	
Evenness					162.65
Evenness	-0.92	-3.39	1.64	0.47	
Trait diversity					163.06
Trait diversity	-0.02	-0.11	0.14	0.70	

Only plots with more than one genotype at the end of the experiment

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131 Table G2b:

	Inve	ertebrate a	bundance	e (/g eelg	rass)	I	nvertebra	te abunda	nce (/plo	ot)
Models using final diversity metrics	Post mean	Lower CI	Upper CI	рМС- MC	DIC	Post mean	Lower CI	Upper CI	рМС- MC	DIC
Relatedness+richness +evenness+trait diversity					286.25					520.92
Relatedness	7.39	0.72	14.26	0.04		5.53	-141.7	140.7	0.91	
Richness	-2.54	-5.54	0.33	0.08		-15.55	-72.38	39.71	0.59	
Evenness	-10.98	-23.46	1.80	0.09		-80.12	-314.8	168.8	0.50	
Trait diversity	0.56	-0.18	1.34	0.15		10.52	-5.43	25.65	0.18	
Relatedness+richness +evenness					286.89					-
Relatedness	7.71	0.72	14.37	0.03		-	-	-	-	
Richness	-1.25	-3.76	1.16	0.32		-	-	-	-	
Evenness	-11.01	-24.93	2.28	0.11		-	-	-	-	
Richness+evenness+ trait diversity					-					518.84
Richness	-	-	-	-		-16.19	-71.49	43.13	0.55	
Evenness	-	-	-	-		-73.36	-305.6	151.1	0.53	
Trait diversity	-	-	-	-		10.88	-4.65	26.31	0.18	
Relatedness+evenness					283.58					-
Relatedness	7.99	0.71	14.25	0.02		-	-	-	-	
Evenness	-8.79	-21.75	4.01	0.16		-	-	-	-	
Evenness+trait diversity					-					517.08
Evenness	-	-	-	-		-70.59	-291.6	168.6	0.56	
Trait diversity	-	-	-	-		7.81	-4.77	18.77	0.19	
Relatedness					280.44					517.78
Relatedness	8.60	2.00	15.53	0.008		15.11	-127.5	145.8	0.81	
Richness					290.51					517.51
Richness	-0.81	-3.12	1.71	0.52		10.68	-31.27	56.59	0.64	
Evenness					288.83					517.03
Evenness	-10.75	-24.27	1.92	0.10		-95.22	-324.4	140.2	0.42	
Trait diversity					287.77					515.54
Trait diversity	0.23	-0.37	0.84	0.45		8.62	-3.58	20.24	0.16	

Only plots with more than one genotype at the end of the experiment

Appendix H: Summary of generalized linear mixed model results for the effects of realized
diversity metrics on invertebrate grazer richness (raw counts from eelgrass sampled). Predictor
variables evaluated are based on the composition of genotypes at the end of the experiment and
include average genetic relatedness, eelgrass genotypic richness, genotypic evenness, and trait
diversity (Rao's Q). Block was included as a random effect; however, to save space results for
block are not included in the table. Models are presented with posterior means (Bayes estimates),
95% credible intervals (equivalent to 95% confidence intervals), and pMCMC values

141 (probability of the estimate overlapping zero).

	Invertebrate richness						
Models using final diversity metrics	Post mean	Lower CI	Upper CI	рМС- MC	DIC		
Relatedness+richness +evenness+trait diversity					209.65		
Relatedness	0.35	-0.94	1.51	0.580			
Richness	0.15	-0.46	0.75	0.61			
Evenness	-1.11	-3.02	0.93	0.28			
Trait diversity	-0.02	-0.17	0.14	0.82			
Relatedness+richness +evenness					207.78		
Relatedness	0.35	-0.98	1.58	0.59			
Richness	0.08	-0.32	0.52	0.68			
Evenness	-1.15	-2.91	0.85	0.23			
Relatedness+evenness					205.94		
Relatedness	0.27	-0.98	1.50	0.64			
Evenness	-1.10	-2.93	0.83	0.26			
Relatedness					205.43		
Relatedness	0.72	-0.29	1.59	0.12			
Richness					207.68		
Richness	-0.10	-0.49	0.27	0.62			
Evenness					204.16		
Evenness	-1.32	-2.66	0.15	0.07			
Trait diversity					206.93		
Trait diversity	-0.04	-0.13	0.05	0.31			

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