Notes

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Ecological impacts of genotypic diversity in the clonal seagrass *Zostera marina*

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Abstract. Genetic diversity, like species diversity, can have important consequences for communities and ecosystems. However, little is known about whether the effects of genetic diversity demonstrated in experimental assemblages are of sufficient strength to generate patterns in natural systems. We conducted a survey of eelgrass (*Zostera marina*) to examine the correlation between eelgrass clonal diversity and two metrics of community structure across two seasons: shoot density (reflective of habitat quality) and biomass of epiphytic algae (as a measure of food resource availability). Eelgrass clonal diversity was not related to epiphyte biomass in either winter or summer. Interestingly, there was a positive relationship between eelgrass clonal diversity and shoot density only in the winter, when eelgrass experiences stress from abiotic and biotic factors. The magnitude of this correlation was similar to that of other factors known to affect shoot density such as tidal elevation or position in the bed. In contrast, summer shoot density and diversity were uncorrelated. This natural pattern is consistent with previous experimental results in which diversity positively affected shoot density only during periods of abiotic or biotic stress, suggesting that the effects of clonal diversity are sufficiently strong to influence shoot density in the field, despite the presence of potentially confounding environmental gradients.

Key words: biodiversity–ecosystem function; clonal diversity; community genetics; disturbance–stability; eelgrass; genetic diversity; primary production; richness; Zostera marina.

Introduction

The functional consequences of biodiversity have been the focus of considerable empirical and theoretical research (Kinzig et al. 2002, Loreau et al. 2002). As with species diversity, genetic diversity within species can have important ecological consequences (reviewed by Hughes et al. 2008). For instance, genetically diverse plant mixtures can have higher fitness than monocultures (Ellstrand and Antonovics 1985, Johnson et al. 2006). In addition, plant genetic diversity in a variety of systems can enhance secondary productivity by influencing the diversity and abundance of associated invertebrates (Hughes and Stachowicz 2004, Wimp et al. 2004, Reusch et al. 2005, Crutsinger et al. 2006, Johnson et al. 2006). Genetic diversity can also have important effects on community dynamics, both between predators and prey/parasites or pathogens and their hosts (Mundt 2002, Yoshida et al. 2003, 2007). Furthermore, genetic diversity can increase the stability of systems and enhance resistance to or recovery from disturbance (see references in Hughes et al. 2008).

Studies of the community or ecosystem impacts of species and genetic diversity have typically focused on whether these variables have statistically significant effects on the process of interest through controlled experimentation. Yet we generally have little understanding of the relative importance or magnitude of these effects compared to other variables, a common situation in ecological research (Graham and Edwards 2001). To assess just how important genetic diversity is to ecosystem function, we need to understand whether its effect is similar in magnitude to other key factors, or if the effect of genetic diversity is more often overwhelmed by other variables. (For example, positive experimental relationships between plant species diversity and invasion resistance can be reversed in natural settings when plant species diversity is strongly correlated with seedling recruitment; Levine 2000.) However,

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the logistical difficulties of conducting factorial manipulations of genetic diversity with other factors are formidable, especially when the experimental design calls for replicating all genotypes in monoculture to separate effects of genotypic identity from diversity. Furthermore, experiments using assembled communities address only whether diversity can affect ecosystem processes, but pairing existing experiments with surveys may better assess whether natural variation in diversity actually does correlate with function in the field.

Building on previous manipulative experiments that demonstrated a positive effect of clonal richness on seagrass communities during both biotic (grazing; Hughes and Stachowicz 2004) and abiotic (temperature stress; Reusch et al. 2005) disturbances, we examine spatial patterns of small-scale (1 m^2) genotypic diversity and performance of a clonal marine flowering plant, eelgrass (*Zostera marina*). We use these data specifically to address two questions regarding the ecological consequences of natural variation in genotypic diversity. First we assess the correlation between eelgrass clonal diversity and eelgrass shoot density. We focused on shoot density because it is a nondestructive proxy for aboveground production, and it is an important component of habitat complexity in these systems (Williams and Heck 2001). Second, we examined the relationship between eelgrass clonal diversity and the biomass of epiphytic algae that grows on eelgrass. The effect of epiphytes and grazers on seagrass growth varied among plants in a common garden experiment (Hays 2005), suggesting there could be a genetic component to the epiphyte–seagrass interaction. We did not specify a priori whether this relationship is likely to be negative or positive: epiphytes are a key factor in recent widespread seagrass declines (Hughes et al. 2004), emphasizing their negative effects on the plant itself. However, epiphytes can also have neutral or even positive impacts on seagrasses (Williams and Ruckelshaus 1993), and they serve as food for many of the small invertebrate taxa living within seagrass whose grazing can mitigate their negative effects (Howard and Short 1986, Williams and Ruckelshaus 1993, Hughes et al. 2004). We use a multiple regression approach that includes other factors known to influence shoot density and epiphyte biomass such as tidal elevation and position relative to the perimeter of the eelgrass bed (see *Materials and methods*) to allow us to assess the relative importance of clonal richness to eelgrass shoot density in natural eelgrass systems.

Given that experimental studies in this system have found strongest effects of eelgrass genotypic diversity in the presence of disturbance or stress, we hypothesized that the relationship between eelgrass clonal diversity and ecological performance would be stronger during the portion of the year when eelgrass experiences more stressful conditions. Thus, we quantified eelgrass shoot density and epiphyte biomass under both stressful winter conditions and under benign summer conditions. Stress and disturbance are greater in the winter in our study areas in northern California (as evidenced by reduced shoot density; see *Results*) because winter brings grazing by migratory birds, desiccation from midday low-tide exposure, and decreased photoperiod. During the summer, stress and disturbance are less frequent: vertebrate grazers are rare, photoperiod is increased, and desiccation stress is reduced because of the prevalence of fog and the occurrence of low tides in the early morning.

Materials and Methods

Study system

Eelgrass is a dominant species in many shallow bays and estuaries throughout North America and Europe, and it greatly enhances primary and secondary production, nutrient cycling, and sediment stabilization (Williams and Heck 2001). As with many clonal plants, eelgrass can reproduce sexually and clonally, potentially creating wide variation in genotypic diversity at small spatial scales. We surveyed plots for clonal richness at a total of seven sites spread across three regions in northern California (see Plate 1); for detailed site information, see Appendix A. Based on previous research in seagrass systems, we hypothesized that tidal height and distance to the habitat perimeter would significantly influence seagrass and epiphyte abundance due to corresponding variation in abiotic (e.g., light, temperature, hydrodynamic forces) and biotic (e.g., grazing) factors (Irlandi 1997, Williams and Heck 2001, Bologna and Heck 2002, Borowitzka et al. 2006). Thus, at each site we established four permanent 1-m^2 quadrats within a contiguous eelgrass bed at each of three tidal elevations in relation to mean lower low water (MLLW): high intertidal (HI; >0–0.5 m MLLW); low intertidal (LI; 0 to −0.5 m MLLW); and subtidal (S; −0.5 to −1.0 m MLLW; see Appendix A for further information about tidal heights). At each tidal level two quadrats were located in the interior of the bed and two were located on the edge of the bed. Some sites were part of a larger, continuous eelgrass bed (particularly in the subtidal), so we do not have equal numbers of edge and interior plots (Appendix B). In addition, at one site (Sacramento Landing) we were only able to sample three quadrats in the high intertidal due to the low abundance of eelgrass (Appendix B). All quadrats were at least 5 m apart.

Survey of eelgrass clonal richness and ecological variables

We collected tissue samples during the summer from 25 randomly selected shoots in each 1-m^2 plot (see Appendix B for sampling dates). Using the same sampling intensity in plots of different density allowed us to maintain statistical independence between genetic diversity and shoot density to explore the relationship

between these two variables, which was a key goal of our study. A preliminary survey indicated that this sampling intensity was sufficient to characterize plot diversity (data not shown). Fresh tissue samples from the field were stored on ice for transport to the laboratory and then frozen at −80°C. We utilized five DNA microsatellite loci known to exhibit high variability in this system (Hughes and Stachowicz 2004). Briefly, DNA was extracted using a modified CTAB protocol (Doyle and Doyle 1987), amplified via polymerase chain reaction (PCR), run using 6% polyacrylimide gel electrophoresis, visualized using silver nitrate staining, and manually scored against a pUC/M13 sequence ladder. For further description of the methods, please see Hughes and Stachowicz (2004).

We quantified eelgrass shoot density and epiphytic algal biomass in each quadrat in the summer at the same time the clonal diversity samples were collected (Appendix B). Because correlations between diversity and eelgrass community structure may vary seasonally, we also quantified these ecological variables in the same quadrats in the winter (Appendix B). We did not resample plots for clonal diversity in the winter because eelgrass seedling recruitment occurs in the spring in northern California (R. Hughes, *unpublished data*) and thus would not have caused an increase in diversity over this time period. Clonal richness could have declined due to competitive exclusion or disturbance between sampling times, but our previous experiments at one site showed that diversity changes within a single year were minimal (Hughes and Stachowicz 2004; R. Hughes, *unpublished data*). Shoot density was assessed by counting the number of shoots in a haphazardly chosen 0.25×0.25 m quadrat within each 1-m^2 plot. These measurements were only performed in the high and low intertidal plots that could be sampled reliably at low tide. Counts using scuba were not possible due to logistical constraints and limited visibility underwater. Epiphytic algal biomass of three randomly chosen shoots in each plot was measured following Williams and Ruckelshaus (1993).

Statistical analyses: relationship between eelgrass clonal richness and ecological variables

Different metrics of genetic diversity may yield different relationships with a given response variable (Arnaud-Haond et al. 2007, Hughes et al. 2008). Thus, we evaluated the consistency of our results using four metrics of genetic diversity. First, we examined clonal richness (R) using a modified ratio of the number of unique genotypes (G) to the total number of shoots analyzed (N) in which one is subtracted from both the numerator and denominator (Arnaud-Haond et al. 2007). Second, we examined clonal diversity using the Shannon-Wiener index (H') of clonal diversity (Arnaud-Haond et al. 2007). We then included a metric of clonal diversity that is less sensitive to variation in the total number of individuals (i.e., shoots) in a plot: the negative slope of the power distribution of the number of shoots of a given genotype (β; Arnaud-Haond et al. 2007). Finally, we calculated average multilocus heterozygosity (H; the proportion of genotyped loci for which an individual was heterozygous) for each plot. Clonal richness, diversity, and the slope of the power distribution were all calculated using GenClone 2.0 (S. Arnaud-Haond and K. Belkhir, *unpublished software*). Unless otherwise specified, we present statistical results from the richness analyses; we note differences between these results and those from other metrics of diversity when applicable.

To determine the relationship between eelgrass clonal richness and community structure in the summer, we ran individual mixed stepwise regressions of eelgrass shoot density and epiphyte biomass on richness (and other diversity estimators) at the summer sampling date (i.e., the ecological measurements were taken at the same time as the genetic samples). Analyses of the relationship between clonal richness and epiphyte biomass included quadrats from all three tidal levels, while the analyses of eelgrass shoot density necessarily only included high and low intertidal quadrats. In all stepwise regression analyses, we included site, tidal elevation, position, richness, and each of the two-variable interactions as the possible model variables. We could not include all possible interactions due to limited degrees of freedom. We set the probability to enter and leave the model at 0.10. All response variables were log-transformed to meet assumptions of normality and homoscedasticity. Stepwise regressions were conducted using JMP 5.0 (SAS Institute, Cary, North Carolina, USA).

To analyze the relationship between clonal richness and eelgrass community structure in the winter, we conducted two separate analyses. First, we ran mixed stepwise regressions of epiphyte biomass and eelgrass shoot density on richness (and other diversity estimators) for the sites in which these variables were measured the winter after the tissue samples were taken (Appendix B). In the second analysis, we included the site (Blake's Landing; Appendix B) in which epiphyte biomass and eelgrass shoot density were quantified the winter before the eelgrass tissue samples were collected (i.e., seedling recruitment could have occurred in between the two sampling dates). These analyses yielded qualitatively and quantitatively similar results (see *Results*), suggesting that any changes in richness that occurred between sampling dates at Blake's Landing did not affect our results. Thus, we present the second, more inclusive analysis.

Statistical analyses: relative importance of clonal richness and environmental variables

To assess the relative importance of eelgrass clonal richness vs. other factors correlated with shoot density

and epiphyte biomass (i.e., site, tidal elevation, and position in the bed) for a given response variable, we calculated two measures of effect magnitude: partial eta squared (η^2) and omega squared (ω^2) (Graham and Edwards 2001, Olejnik and Algina 2003). We assumed that negative estimates indicated negligible effects and set them to zero (Graham and Edwards 2001). Because many of the interactions had ω^2 values of zero or below zero, we used two models: (1) site, tidal elevation, position, richness, and all possible two-factor interactions; and (2) site, tidal elevation, position, and richness main effects only.

Results

Relationship between eelgrass clonal richness and ecological variables

We identified a total of 324 unique genotypes out of 1618 samples. There was a low probability of the same multilocus genotype occurring by chance due to sexual reproduction given the frequency of alleles at each locus across the entire data set ($P_{gen} < 0.001$; Arnaud-Haond et al. 2007); thus, we consider samples with identical genotypes to be clonemates. The number of genotypes per plot ranged from 1 to 15, with a mean of 4.1 genotypes and a median of 3.0 genotypes (Fig. 1a). The distributions of clonal richness and the negative slope of the power distribution were very similar, with most of the plots having very low values (Fig. 1a, c). Clonal diversity was more evenly distributed among plots in the lower half of the distribution (Fig. 1b), whereas heterozygosity was skewed toward higher values (Fig. 1d).

Eelgrass clonal richness did not meet the specifications for inclusion in the model for summer shoot density (Fig. 2a; see Appendix C: Table C1 for complete statistics). In contrast, the model for winter shoot density (model, $R^2 = 0.47$) included a positive correlation between eelgrass clonal richness and shoot density ($F_{1,40} = 5.01$, $P = 0.03$; Fig. 2b), with significant differences among sites ($F_{5,40} = 5.76$, $P = 0.0004$) but no interaction between the two variables. Excluding the site where density was measured prior to genotypic diversity (BL) did not change this relationship (richness, $F_{1,32} = 5.01$, $P = 0.03$; site, $F_{4,32} = 6.55$, $P = 0.0006$), although the omission of this site did increase the significance of a positive correlation between shoot density and tidal elevation ($F_{1,32} = 5.33$, $P = 0.03$). A quantile regression revealed that the relationship between eelgrass clonal richness and winter shoot density was strongest at intermediate shoot densities (see Appendix D for details of quantile regression).

Eelgrass clonal diversity showed a similar relationship with winter shoot density (Appendix C: Table C2). The slope of the distribution of shoots into genotype size classes was also generally positively correlated with winter shoot density; however, a negative relationship at one site (SL) led to a significant interaction with site in the stepwise regression (site × β interaction, $F = 6.24$, $P = 0.0005$; Appendix C: Table C3). Average heterozygosity (Appendix C: Table C4) did not meet the specifications for inclusion in the model for shoot density in either season.

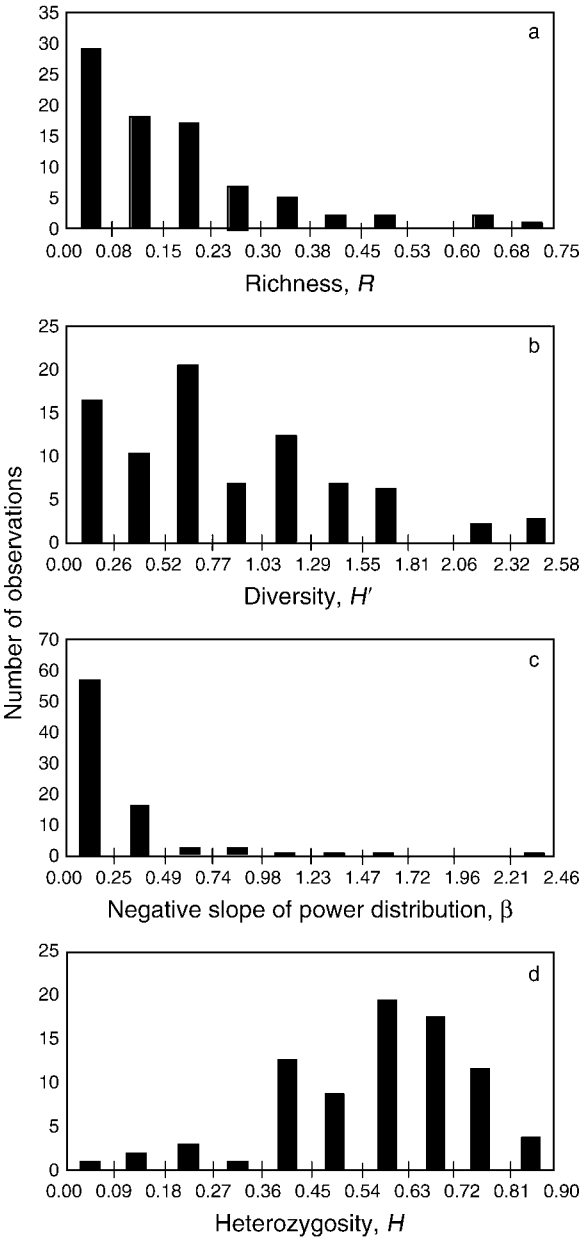

FIG. 1. Distribution of small-scale clonal diversity in Bodega Bay and Tomales Bay, California, USA: frequency histograms of (a) clonal richness (R; mean = 0.17, median = 0.11), (b) clonal diversity (H'; mean = 0.84, median = 0.69), (c) β, the negative slope of the power distribution (mean = 0.24, median = 0.13), and (d) average plot heterozygosity (H; mean = 0.57, median = 0.60).

PLATE 1. Intertidal portions of an eelgrass (*Zostera marina*) bed in Bodega Harbor, California (USA), are exposed during a morning low tide in the summer. Flags mark a 1-m^2 research plot. Photo credit: Kristen Selheim.

Clonal richness, diversity, and the slope of the genotype size class distribution did not show a significant relationship with epiphyte biomass in either season (Appendix C). However, plot heterozygosity did meet the specifications for the model for winter epiphyte biomass: there was a trend for plots with higher heterozygosity to have lower epiphyte biomass (heterozygosity, $F = 3.66$, $P = 0.06$; Appendix C: Table C4). As expected, site, tidal elevation, and position relative to the habitat perimeter explained significant variation in epiphyte biomass and summer shoot density. We summarize these results in Appendix C: Fig. C1.

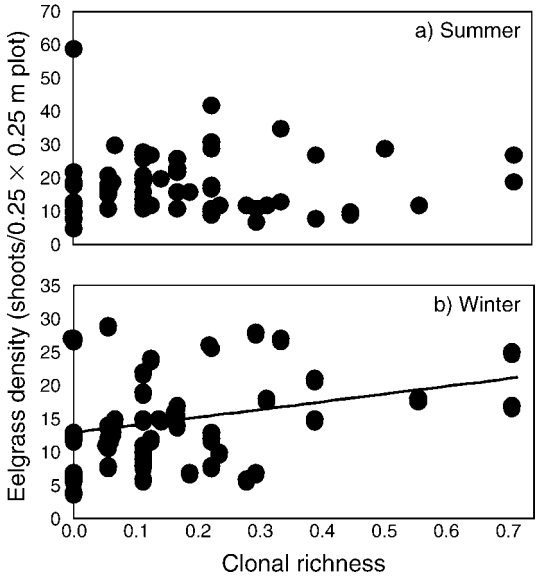

FIG. 2. Relationship between clonal richness (R) and eelgrass shoot density. Results are similar for other metrics of clonal diversity. (a) Summer eelgrass shoot density. (b) Regression analysis of clonal richness and winter shoot density. The line indicates that richness is positively correlated with winter shoot density.

Relative importance of eelgrass clonal richness and environmental variables

Our comparison of the relative importance of genotypic richness and environmental variables revealed that site is the key correlate of eelgrass shoot density and epiphyte biomass, regardless of season or the metric used (Table 1a). In addition, the interaction between site and position was often of high relative importance (Table 1a). Clonal richness (R) is clearly not the most important correlate of shoot density, but richness and its interactions did have similar partial η^2 values as tidal elevation and position in the bed (Table 1a), two factors well known to affect shoot density. For example, the magnitude of the clonal richness relationship with winter shoot density is 0.054, which is comparable to tidal elevation (0.042), while the site × richness interaction had an even larger magnitude (0.283). The value of ω^2 (Table 1a) for many factors and interactions was negligible due to the large impacts of site, complicating comparisons among them. When we restricted the analyses to main effects (Table 1b), the estimates of richness were still small relative to the role of site, yet were generally as large or larger than position in the bed and comparable to tidal height. Relative importance did not vary greatly between clonal richness, diversity, or the slope of the power distribution (data not shown).

TABLE 1. Relative importance of eelgrass clonal richness and environmental variables for shoot density and epiphyte biomass.

	Shoot density						Epiphyte biomass					
	Summer			Winter			Summer			Winter		
Factor	df	η^2	ω^2	df	η^2	ω^2	df	η^2	ω^2	df	η^2	ω^2
a) Full model												
Site	6	**0.396**	**0.525**	5	**0.687**	**0.236**	6	**0.823**	**0.436**	5	**0.669**	**0.373**
Tide	1	0.004	0.000	1	0.042	0.000	2	0.319	0.041	2	0.114	0.015
Position	1	0.004	0.000	1	0.173	0.006	1	0.116	0.010	1	0.030	0.001
Richness	1	0.003	0.000	1	0.054	0.000	1	0.022	0.000	1	0.032	0.001
Site × richness	6	0.029	0.000	5	0.283	0.000	6	0.084	0.000	5	0.170	0.013
Tide × richness	1	0.000	0.000	1	0.056	0.000	2	0.072	0.003	2	0.095	0.010
Position × richness	1	0.024	0.015	1	0.118	0.000	1	0.000	0.000	1	0.001	0.000
Site × tide	6	0.071	0.029	5	0.281	0.000	12	*0.525*	*0.080*	10	*0.298*	*0.029*
Site × position	6	*0.158*	*0.124*	1	*0.329*	*0.056*	6	0.173	0.007	5	0.151	0.008
Tide × position	1	0.007	0.000	1	0.005	0.000	2	0.029	0.000	2	0.010	0.000
b) Main effects model												
Site	6	**0.491**	**0.357**	5	**0.441**	**0.319**	6	**0.690**	**0.599**	**5**	**0.596**	**0.523**
Tide	1	0.304	0.172	1	0.095	0.038	2	0.223	0.076	2	0.127	0.048
Position	1	0.003	0.000	1	0.051	0.013	1	0.032	0.005	1	0.016	0.000
Richness	1	0.000	0.000	1	0.072	0.025	1	0.035	0.006	1	0.016	0.000

Notes: Definitions of measures of effect magnitude: $\eta^2 =$ (effect sum of squares)/(effect sum of squares + error sum of squares); $\omega^2 =$ (effect sum of squares − effect degrees of freedom × error mean square)/(error mean square + total sum of squares). Boldface indicates the most important factor. Italics indicate the second most important factor.

Thus the results suggest that the importance of clonal richness for patterns of shoot density is small, but it is still of similar magnitude to other factors correlated with within-site variation.

DISCUSSION

Patterns of clonal richness and shoot density across sites in this study suggest that positive experimental effects of eelgrass genetic diversity (Williams 2001, Hughes and Stachowicz 2004, Reusch et al. 2005) can influence patterns of shoot density in natural populations, at least in some seasons. Although one might expect a positive correlation between shoot density and the number of genotypes due to a sampling artifact (more shoots should result in more genotypes), there was no correlation between these variables in the summer despite an identical sampling method, suggesting that these correlations are not a methodological artifact. In addition, a metric of diversity that is robust to variation in shoot density across plots (β) yielded similar results. However, site effects (representing unmeasured large-scale environmental variables) generally showed a much stronger relationship with eelgrass shoot density and epiphyte biomass than other factors, suggesting clonal richness may be best at explaining variation within sites. In addition, our results for shoot density are limited to high and low intertidal eelgrass; further work is needed to determine whether similar patterns hold in the subtidal region.

Eelgrass at our sites is exposed to several potential abiotic stresses during the winter that do not occur in summer (e.g., reduced light levels, desiccation during daytime low tides, lowered salinity from winter rains) and that may contribute to the positive relationship between diversity and eelgrass standing stock at this time of year (cf. Reusch et al. 2005). In addition, although we did not quantify grazing in this study, our sites annually host migratory brant geese (*Branta bernicla* subsp. *nigricans*) from December to February (R. Hughes, *personal observation*), and these geese preferentially graze eelgrass (Ganter 2000). Hughes and Stachowicz (2004) found that more diverse plots lost fewer shoots to grazing than plots with one or a few genotypes; thus, grazing pressure could also contribute to the positive diversity–density relationship. Increasing variation with decreasing genotypic richness is indeed consistent with the "wedge" shape in Fig. 2b, although there are relatively few plots with high richness: in summer, all plots have relatively high shoot density, regardless of genotypic richness (Fig. 2a). Because diverse plots lose few shoots due to grazing (Hughes and Stachowicz 2004), those plots with high genotypic richness could maintain high density regardless of grazing, while low richness plots should exhibit greater variation in density depending on whether or not they experience grazing, which can be spatially patchy (Ganter 2000).

Our results highlight that the relationship between genetic diversity and a response variable of interest can depend on the metric of diversity used (Arnaud-Haond et al. 2007, Hughes et al. 2008). In particular, plot heterozygosity yielded different patterns than clonal richness/diversity: heterozygosity was not related to eelgrass shoot density in either season, but it showed a weak, negative relationship with winter epiphyte biomass. These differences are perhaps not surprising given

that clonal richness and diversity estimate genetic variation across individuals in a population (i.e., the number of unique genotypes or trait values in a plot) whereas heterozygosity provides an estimate of the average degree of genetic variation within individuals in a plot. Given links between individual-level heterozygosity and performance/fitness in seagrasses (Williams 2001, Hammerli and Reusch 2003) and other taxa (Britten 1996), plots with higher heterozygosity may on average include genotypes that are better able to compete with epiphytic algae, leading to lower overall epiphyte biomass. However, the particular mechanism leading to the relationship between heterozygosity and winter epiphyte biomass is unclear. Furthermore, a weak positive relationship between eelgrass shoot density and epiphyte biomass in the summer ($R^2 = 0.07$, $P = 0.03$) and no relationship in the winter ($R^2 = 0.01$, $P > 0.05$) suggest that epiphytes do not have a strong negative impact on eelgrass in this system.

Our results have important implications for seagrass restoration efforts, which are often required in coastal areas to mitigate development. First, it is clear that individual site characteristics play an overriding role in determining shoot density and other metrics of eelgrass community structure. Nonetheless, within sites, the success of beds at surviving periods of stress may be influenced by genetic diversity. Restored eelgrass beds often have lower genetic (allozyme) diversity than natural beds (Williams and Davis 1996), and may therefore be more vulnerable to disturbance (Hughes and Stachowicz 2004, Reusch et al. 2005); our results and others (Williams 2001, Reusch et al. 2005) suggest that future restoration efforts should incorporate genetically diverse source material to enhance transplant success and survival. In addition, the positive effects of plant clonal diversity may cascade up to affect associated invertebrate communities (Hughes and Stachowicz 2004, Reusch et al. 2005, Crutsinger et al. 2006, Johnson et al. 2006). Although we did not find a relationship between eelgrass clonal richness and the biomass of epiphytic algae that these invertebrates primarily consume, eelgrass clonal diversity could still influence invertebrate abundances or diversity via its effects on shoot density and habitat quality. In addition, plot-level heterozygosity may affect epiphyte abundance independent of clonal diversity. The emerging body of work on the ecological effects of genetic diversity suggests that conservation and restoration efforts should include consideration of genetic diversity not only for long-term evolutionary potential, but also for short-term ecological success. These and other positive associations between genetic and species diversity (Booth and Grime 2003, Vellend 2003, 2005) underscore the potential generality of biodiversity effects across multiple levels of biological organization.

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Literature Cited

Arnaud-Haond, S., C. M. Duarte, F. Alberto, and E. A. Serrao. 2007. Standardizing methods to address clonality in population studies. Molecular Ecology 16:5115–5139.

Bologna, P. A. X., and K. L. Heck, Jr. 2002. Impact of habitat edges on density and secondary production of seagrass-associated fauna. Estuaries 25:1033–1044.

Booth, R. E., and J. P. Grime. 2003. Effects of genetic impoverishment on plant community diversity. Journal of Ecology 91:721–730.

Borowitzka, M. A., P. Lavery, and M. van Keulen. 2006. Epiphytes of seagrasses. Pages 441–461 *in* A. W. Larkum, R. J. Orth, and C. M. Duarte, editors. Seagrasses: biology, ecology, and conservation. Springer, Dordrecht, The Netherlands.

Britten, H. B. 1996. Meta-analysis of the association between multilocus heterozygosity and fitness. Evolution 50:2158–2164.

Crutsinger, G. M., M. D. Collins, J. A. Fordyce, Z. Gompert, C. C. Nice, and N. J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313:966–968.

Doyle, J. J., and J. L. Doyle. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemical Bulletin 19:11–15.

Ellstrand, N. C., and J. Antonovics. 1985. Experimental studies of the evolutionary significance of sexual reproduction. II. A test of the density-dependent selection hypothesis. Evolution 39:657–666.

Ganter, B. 2000. Seagrass (*Zostera* spp.) as food for brent geese (*Branta bernicla*): an overview. Helgoland Marine Research 54:63–70.

Graham, M. H., and M. S. Edwards. 2001. Statistical significance versus fit: estimating the importance of individual factors in ecological analysis of variance. Oikos 93:505–513.

Hammerli, A., and T. B. H. Reusch. 2003. Inbreeding depression influences genet size distribution in a marine angiosperm. Molecular Ecology 12:619–629.

Hays, C. G. 2005. Effect of nutrient availability, grazer assemblage and seagrass source population on the interaction between *Thalassia testudinum* (turtle grass) and its algal epiphytes. Journal of Experimental Marine Biology and Ecology 314:53–68.

Howard, R. K., and F. T. Short. 1986. Seagrass growth and survivorship under the influence of epiphyte grazers. Aquatic Botany 24:287–302.

Hughes, A. R., K. J. Bando, L. F. Rodriguez, and S. L. Williams. 2004. Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. Marine Ecology Progress Series 282:87–99.

Hughes, A. R., B. D. Inouye, M. T. J. Johnson, M. Vellend, and N. Underwood. 2008. Ecological consequences of genetic diversity. Ecology Letters 11:609–623.

Hughes, A. R., and J. J. Stachowicz. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proceedings of the National Academy of Sciences (USA) 101:8998–9002.

Irlandi, E. A. 1997. Seagrass patch size and survivorship of an infaunal bivalve. Oikos 78:511–518.

Johnson, M. T. J., M. J. Lajeunesse, and A. A. Agrawal. 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. Ecology Letters 9:24–34.

Kinzig, A. P., S. W. Pacala, and D. Tilman. 2002. The functional consequences of biodiversity. Princeton University Press, Princeton, New Jersey, USA.

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854.

Loreau, M., S. Naeem, and P. Inchausti. 2002. Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford, UK.

Mundt, C. C. 2002. Use of multiline cultivars and cultivar mixtures for disease management. Annual Review of Phytopathology 40:381–410.

Olejnik, S., and J. Algina. 2003. Generalized eta and omega squared statistics: measures of effect size for some common research designs. Psychological Methods 8:434–447.

Reusch, T. B. H., A. Ehlers, A. Haemmerli, and B. Worm. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. Proceedings of the National Academy of Sciences (USA) 102:2826–2831.

Vellend, M. 2003. Island biogeography of genes and species. American Naturalist 162:358–365.

Vellend, M. 2005. Species diversity and genetic diversity: parallel processes and correlated patterns. American Naturalist 166:199–215.

Williams, S. L. 2001. Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. Ecological Applications 11:1472–1488.

Williams, S. L., and C. A. Davis. 1996. Population genetic analyses of transplanted eelgrass (*Zostera marina*) beds reveal reduced genetic diversity in southern California. Restoration Ecology 4:163–180.

Williams, S. L., and K. L. J. Heck. 2001. Seagrass community ecology. Pages 317–337 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer Associates, Sunderland, Massachusetts, USA.

Williams, S. L., and M. H. Ruckelshaus. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. Ecology 74:904–918.

Wimp, G. M., W. P. Young, S. A. Woolbright, G. D. Martinsen, P. Keim, and T. G. Whitham. 2004. Conserving plant genetic diversity for dependent animal communities. Ecology Letters 7:776–780.

Yoshida, T., S. P. Ellner, L. E. Jones, B. J. M. Bohannan, R. E. Lenski, and N. G. Hairston, Jr. 2007. Cryptic population dynamics: rapid evolution masks trophic interactions. PLoS Biology 5:1868–1879.

Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussman, and N. G. Hairston, Jr. 2003. Rapid evolution drives ecological dynamics in a predator–prey system. Nature 424:303–306.

APPENDIX A

Detailed information on seven sites across three regions in northern California (*Ecological Archives* E090-093-A1).

APPENDIX B

The survey sampling design (*Ecological Archives* E090-093-A2).

APPENDIX C

Results of statistical analyses of the relationship between site, tidal elevation, position, eelgrass diversity, and eelgrass ecological variables for different genetic diversity metrics (*Ecological Archives* E090-093-A3).

APPENDIX D

A quantile regression analysis for winter shoot density (*Ecological Archives* E090-093-A4).