The Effect of Genetic Diversity on Ecosystem Functioning in Vegetated Coastal Ecosystems

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ABSTRACT

In species-poor communities, genetic diversity potentially plays an important role for ecosystem functioning, though this is still largely unexplored in marine and estuarine ecosystems. We studied how genetic diversity (sensu genotypic diversity and/or allelic richness) affects ecosystem functioning in marine habitat-forming plant communities. First, we conducted a 15-month field experiment in the highly seasonal Baltic Sea and established mono- and polycultures of different genotypes and genotype combinations of *Zostera marina*. Second, we reviewed existing literature and performed a meta-analysis of 12 studies including this study. We found no evidence of positive genetic diversity effects on shoot production in the field experiment, but diversity enhanced community stability over time. The literature review revealed that a majority of the included studies observed positive effects of

genetic diversity on ecosystem functions such as primary production and nutrient uptake. The results from the meta-analysis support the hypothesis that genetic diversity effects on productivity are stronger during or after periods of stress. These diversity effects were also more positive in the field compared to mesocosm studies. Our results indicate that genetic diversity has positive effects on ecosystem functioning, particularly during increased environmental stress. Thus, local genetic diversity should be preserved especially in species-poor ecosystems, where it potentially provides insurance against environmental change.

Key words: allelic richness; eelgrass; genotypic diversity; saltmarsh; SAV; seagrass; environmental stress; wetland.

INTRODUCTION

Biodiversity is an important driver of ecosystem functioning (Cardinale and others 2006; O'Connor and Byrnes 2014; Gamfeldt and others 2015). Di-

verse communities are hypothesized to be able to maintain functioning during increased environmental stress (that is, insurance hypothesis) due to species redundancy when more resistant species maintain functioning, while more sensitive species are not able to or are lost from the community (Yachi and Loreau 1999). Genetic diversity may functionally replace species diversity (Hughes and others 2008) and may thus not only be necessary for evolutionary processes but also increase ecosystem functioning and enhance stability.

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Genetic diversity, for example, increases pest control in agricultural crops (summarized by Tooker and Frank 2013), resistance to diseases, tolerance to environmental changes, productivity (summarized by Jump and others 2009), seed production (Dostàlek and others 2010), colonization success (Crawford and Whitney 2010), resistance and resilience (Hughes and Stachowicz 2004, 2009, 2011), and recovery after stress events (Reusch and others 2005).

Many marine macrophyte habitats such as salt-marshes and seagrass meadows are among the most productive communities on Earth (Duarte and Chiscano 1999) and sustain and provide many important and valuable ecosystem processes and services (Barbier and others 2011). Characteristically, these habitats are formed by only one or a few foundation species, and genetic diversity, rather than species diversity, likely plays a major role for the functioning of these ecosystems. For example, genetic diversity enhances the stability of seagrass systems during increased environmental stress (Reusch and others 2005; Ehlers and others 2008; Hughes and Stachowicz 2004, 2009) improves the water quality in wetland areas (Tomimatsu and others 2014) and increases the productivity of salt-marshes (Wang and others 2012).

The number of studies investigating genetic diversity patterns in marine and estuarine ecosystems has increased during the past decade. Although it is commonly acknowledged that genetic diversity is important and should be preserved to maintain evolutionary potential, we still lack a consensus about the effects of genetic diversity on ecosystem functioning, whether it benefits ecosystems and in which particular circumstances it does so. Some studies suggest that positive diversity effects mainly operate under sufficiently stressful conditions (Hughes and Stachowicz 2004, 2009, 2011), whereas others propose that it may simply take a longer time for positive diversity effects to develop (Wang and others 2012). If diversity effects are strengthened in stressful conditions, in theory, these should be conspicuous in areas with high seasonal stress, as observed by Hughes and Stachowicz (2009).

Although the importance of genetic diversity on ecosystem functioning has been explored on several occasions in seagrass systems (for example, Reusch and others 2005 and Hughes and Stachowicz 2004, 2009), to our knowledge, none of these studies present results from a long-term experiment in a highly seasonal system. Therefore, in this study, we aimed to test the relative importance of genotypic diversity of eelgrass (*Zostera marina*) for community production and persistence

in a highly seasonal estuarine environment, the Baltic Sea, over two growth seasons by conducting a 15-month field experiment. More specifically, we wanted to investigate (1) how eelgrass shoot production differs between mono- and polyculture communities, (2) whether genotypically diverse eelgrass assemblages are temporally more stable, and (3) whether diverse communities show greater survival compared to single-genotype communities. As previous studies have shown that genetic diversity affects the stability and primary production of eelgrass (Hughes and Stachowicz 2004, 2009; Reusch and others 2005), we hypothesized that more diverse eelgrass assemblages would have higher shoot production, and show less temporal variability (that is, higher stability) and greater survival compared to assemblages with low diversity. To compare the observed patterns with other studies, we reviewed the existing literature. Furthermore, to estimate the relative importance of genetic diversity on ecosystem functioning, we conducted a meta-analysis on genetic diversity experiments conducted in marine and estuarine vegetated ecosystems. We expected to find positive effects of genetic diversity on community performance, but predicted that these effects would vary depending on the environmental conditions and the duration of the experiments in question. More specifically, we hypothesized that positive diversity effects would be stronger during periods of stress (O'Connor and Byrnes 2014). As environmental variability often decreases in more controlled settings, we predicted that diversity effects would be more easily detectable in mesocosms than field studies. Finally, as biological interactions may take a long time to develop (Cardinale and others 2012), we hypothesized that genetic diversity would be stronger in experiments with longer duration.

MATERIALS AND METHODS

Study Species and Region

Eelgrass (*Zostera marina*), a temperate seagrass species, has a wide distribution in the Northern Hemisphere. It reproduces both clonally and sexually and commonly forms monospecific meadows with varying degrees of genotypic diversity (Olsen and others 2004; Reusch and Boström 2011). In the nontidal brackish Baltic Sea, eelgrass grows at its distribution limit (5.5 psu, Boström and others 2003). Here, eelgrass persistence mainly relies on vegetative reproduction, which has resulted in highly reduced genotypic diversity compared to more central populations (Olsen and others 2004;

Reusch and Boström 2011). In this area, one patch or meadow typically consists of only one single genotype (Reusch and others 1999; Reusch and Boström 2011; Salo and others 2015). The species-poor northern Baltic Sea is a highly seasonal environment with water temperatures varying between 0 and 22°C and daylight hours between 6 and 19 h in the winter and summer seasons, respectively. The growth season of benthic vegetation usually lasts from May to September. During winter, sea ice cover can block most of the light emitted during the few daylight hours for several weeks or months (average ice cover duration of the study area is 4–8 weeks, Finnish Meteorological Institute), constraining eelgrass to light levels close to or below its light compensation point (Touchette and Burkholder 2000). Furthermore, during the growth season, eutrophication increases the competition and shading from phytoplankton and ephemeral macroalgal mats (HELCOM 2009), consequently forming a serious threat to eelgrass (Gustafsson and Boström 2014).

Experimental Design

All the plants used in the experiment were collected at Sandön, N Baltic Sea (60°02.164'N, 22°20.47'E) where several clones occur within a small area (Salo and others 2015). To identify possible donor clones, DNA samples from 10 to 20 shoots around 13 ID-tagged patches were collected and analyzed using nine polymorphic microsatellite loci (Reusch and Boström 2011). A patch was considered a single clone if all sampled shoots from the patch were the same genotype (Salo and others 2015). Four identified clones (A, B, C, D) that formed patches larger than 3 m in diameter in shallow water (1.6–3 m depth) were chosen as donor clones. In June 2011, individual ramets from each clone were carefully collected with the minimum length of rhizomes being four internodes.

The plants were moved to the experimental site (Fårö, 59°55.219'N, 21°47.711'E), and transplanted in a sandy vegetation-free area. This site has frequently been used in manipulative field experiments involving plant transplantation (Salo and others 2009, 2015; Gustafsson and Boström 2011, 2013) and is hence highly suitable for analogous studies. The study site is further described in detail by Salo and others (2009) and Gustafsson and Boström (2011). The treatments consisted of monocultures of each genotype and three polycultures. The polycultures were composed of two randomly chosen combinations of three genotypes (ABC and ABD) and one combination including all

four genotypes (ABCD). Due to the limited number of shoots per genotype, we were compelled to limit the experimental design in such that of the four available three-genotype combinations, only two were randomly chosen. This also allowed us to include a four-genotype combination as the highest diversity treatment. Treatment plots were assembled according to a replacement design (Harper 1977), with 24 shoots (ramets) in each plot. Thus, monocultures consisted of 24 shoots of one genotype and polycultures of eight or six shoots of each of the three or four genotypes, respectively. Each monoculture and polyculture treatment was replicated four times. A shoot with intact rhizome was attached to a 21 × 21 cm plastic grid and planted in the sediment at about 5 cm depth using SCUBA. The distance between any shoot was more than 4 cm corresponding to a shoot density of about 545 shoots m⁻², which is within the natural range of shoot densities observed in the Baltic Sea (Boström and others 2003). The plots were transplanted randomly in two rows parallel to the shore. The distance between neighboring plots was more than 2 m to allow free spatial expansion of the plots. The water depth in the experimental area was 1.5–1.8 m during mean sea level.

The planned length of the experiment was set to three growth seasons (ca 2.5 years) but pack-ice wiped out a majority of the plots during the second winter, preventing any of the planned assessments of the final genotypic composition of polycultures. Thus, the final experimental duration was 463 days, from June 2011 to September 2012, covering two growth seasons and one winter. The water temperature and irradiance at canopy height were measured every 4 h using light and temperature loggers (HOBO Pendant®, 8 K, Onset, USA), except during August 31 to October 5, 2011, when no loggers were deployed. The loggers were calibrated with an underwater quantum sensor (Li-193SA, Li-Cor, USA). Shoot densities and survival of plots were assessed seven times during the experiment: in July, August, and October 2011, and in April, June, July, and September 2012. If any living shoots were visible, the plot was classified as survived. No data from November to March are available as ice conditions prevented visits to the experimental site during this time.

Statistical Analyses

Temporal differences in mono- and polyculture shoot densities were analyzed using univariate repeated measures permutational analysis in

PERMANOVA+ (v2.0.3) in PRIMER 6 (v6.1.13). Prior to the analysis, the data were square root transformed to reduce the weight of the highest shoot densities and to improve the dispersion of the data. Time and diversity treatment were considered fixed factors, and plot a random factor nested under diversity treatment. As a measure of stability, we calculated the coefficient of variation (hereafter CV) of shoot density across genotype combinations in mono- and polycultures. The data were analyzed using repeated measures permutational analysis with time and diversity treatment as fixed factors and genotype combination as a random factor nested under diversity treatment. The differing number of mono- and polycultures led to an unbalanced design but this was accounted for by adjusting the degrees of freedom and by using type III sum of squares to maintain the independence of hypothesis (Anderson and others 2008). Resemblance matrices were based on Euclidean distances, and all permutations were run 9999 times. The dispersion of the data was inspected using PERMDISP-analysis and MDS-plots. The plot survival of mono- and polycultures was based on shoot density calculations and it was analyzed with Chi-square log-rank analysis.

Although we could not compare the observed and expected performance of individual genotypes in polycultures (see above), we compared (1) the performance of monocultures by analyzing the final number of shoots in monocultures by permutational univariate analysis, with genotype as a fixed factor, and (2) the proportional deviation of the observed total yield in polycultures from its expected yield (D_T) based on monoculture yields of the individual genotypes (Loreau 1998). One-sample T-tests (IBM SPSS 22) were further used to analyze whether the overall performance of the polycultures was greater (>0) or less (<0) than expected. Values close to zero indicate that the polyculture performed as expected, positive values indicate overyielding and negative underyielding (Loreau 1998). All given values are mean $\pm$ SE, except for the polyculture yield and the effect size values, which are mean $\pm$ 95% confidence intervals.

Literature Review

We conducted literature searches to identify studies that have investigated the impacts of genetic (genotypic or allelic) diversity on ecosystem functioning in marine and estuarine foundation species. Literature searches were conducted on Web of Science and Google Scholar between October 7 and

November 3, 2015, using the search terms “marine macrophyte”/“seagrass”/“salt marsh”/“macroalgae”/“seaweed” AND “genotypic diversity”/“genotypic richness”/“genetic diversity”. Of all hits, we limited our review to experimental studies manipulating genotypic or allelic diversity and to studies following the development of natural vegetation with varying degrees of genetic diversity. In addition to studies using marine organisms as model species, we also included studies on freshwater plant species that commonly grow in estuarine environments. In total, 16 studies (15 peer-reviewed publications and this study) met the above-mentioned requirements.

Meta-analysis

Twelve of the 16 studies reported findings in a format that could be used to calculate effect sizes. Thus, we extracted data from these studies and compared effect sizes among diversity treatments using meta-analysis. If available, we concentrated on measures reflecting productivity (primary and seed production). As many of the reported results were likely to correlate (for example, shoot density, biomass, spatial spread), only one variable was used per experiment. The chosen variable was then extracted separately for all the reported levels of diversity. In total, we performed 26 comparisons between the lowest diversity and high(er) diversity. Most studies only controlled for or reported one component of genetic diversity (either genotypic or allelic richness). Thus, the risk of confounding either these two, or other types of genetic diversity (Hughes and others 2008) with the selected diversity measure was potentially high. Therefore, the importance of the studied diversity metric may have been overestimated, and we decided to pool all the data to examine general genetic diversity patterns.

The effect size was calculated as Hedges' g by calculating Cohen's d and multiplying it with correction factor J according to Nakagawa and Cuthill (2007) and Borenstein and others (2009). We used pooled standard deviations in the calculations. If studies reported results for more than two diversity levels (low and high), we calculated d for all the reported levels separately. Data from studies reporting results for several separately applied stressors were further split into different calculations. We calculated seven separate mean effect size statistics: studies without stress events ($n = 14$), studies with stress events ($n = 12$), short-term (< 1 year, $n = 18$) and long-term studies (> 1 year,

$n = 8$), mesocosm ($n = 12$) and field studies ($n = 14$), and one for the whole dataset ($n = 26$). We calculated 95% confidence intervals for the mean effect sizes and considered the effects significant if they did not overlap zero.

RESULTS

Field Experiment

Both temperature and light levels varied greatly during the experiment due to the high seasonality of the study region. The water temperature varied between -0.1°C (February 2012) and 22.3°C (July 2011), whereas the lowest midday light levels were recorded in December 2011 ($21.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) and highest in June 2012 ($1250 \mu\text{mol m}^{-2} \text{s}^{-1}$, Figure 1A). The genotypes from the shallowest depth at the donor site (A and D) were the most and least productive, respectively, and the genotypes from the deeper area (B and C) were in the midrange of productivity, which suggests that the genotypes acclimatized rapidly to the new conditions.

Shoot densities were affected by seasonality (time; $P = 0.001$, Table 1). On average, the highest shoot densities in 2011 and 2012 (17.1 ± 1.7 and 33 ± 8.0) were measured in August and September, respectively, whereas shoot densities were lowest after the break-up of the ice cover in April 2011 (7.6 ± 1.6 , Figure 1B). However, the dispersion of the data increased during the last time points (July–September 2012) potentially affecting the results for factor time (PERMDISP $P = 0.0001$).

Although genetic diversity had no direct effect on shoot densities (Tables 1 and 2), it had a stabilizing effect on shoot density. The CV increased with time ($P = 0.0001$), but polycultures had a consistently lower CV through time ($P = 0.027$, Table 1; Figure 2A). Although nonsignificant ($X^2(1, n = 28) = 2.78$, $P = 0.095$), polycultures also tended to have higher plot survival: 91.7% of polyculture plots survived until September 2012 compared to a 62.5% survival among monoculture plots (Figure 2B).

Monocultures of different genotypes did not differ in their final shoot densities (Pseudo- $F_{3,12} = 1.372$, $P = 0.294$, Figure 3A). ABC and ABD polycultures performed as expected based on monoculture performances ($t = 0.671$, $P = 0.550$ and $t = -1.764$, $P = 0.176$, respectively, Figure 3B), whereas the third polyculture ABCD had lower than expected performance ($t = -3.870$, $P = 0.031$, Figure 3B).

Literature Review

Of the 16 studies that met our review requirements, 13 explored the effects of genotypic diversity on ecosystem functioning, two investigated allelic richness, whereas only one study examined both these aspects of genetic diversity (Table 3). Submerged aquatic vegetation (SAV) encompassing seagrasses and freshwater plants commonly occurring in estuaries were the most popular model organisms. All allelic richness studies and 11 of 14 genotypic diversity studies focused on SAV, whereas only three studies contained wetland or saltmarsh species and none included macroalgae. All studies were conducted in the Northern Hemisphere covering regions from subtropical to cold temperate (Table 3). The average duration of the studies was 13.6 ± 2.4 months, varying from three to 39 months (Figure 4A). Three studies investigated natural vegetation formations, whereas man-made plots were established in the field in eight studies and five studies were conducted in mesocosms (Figure 4B). The number of genotypes used in the manipulative experiments varied from one to nine, with levels of diversity ranging from two to four. In studies using natural vegetation formations, genotypic richness ranged from one to 40. Allelic richness was defined as low, medium, or high. In eight of the 16 included studies plant communities were subjected to stress. Stressors ranged from “naturally occurring” such as impacts of eutrophication and fish farms, grazing events, algal blooms, and heat waves, to purposely caused stress, for example, biomass removal, heat wave simulations, and induced grazing (Figure 4C). A more varying set of stressors was applied in the mesocosm studies compared to the field studies and included, for example, effects of different grazers, epiphyte loading, and simulated heat waves. If a stressor was applied in the field, it usually consisted of physical removal of plant biomass (Table 3).

A clear majority (that is, 12) of the total 16 studies included in the literature review observed positive effects of genetic diversity on ecosystem functioning (Figure 4D). Of these 12 studies, four observed positive diversity effects (that is, enhanced resistance or recovery) only after increased or high levels of stress (Table 3), whereas eight studies recorded positive diversity effects in ambient (nonstressed) conditions. Two studies found neutral or only slightly positive diversity effects. Both these studies lasted for a relatively short time (< 6 months) and may have been terminated before diversity effects could be discernible, especially

Figure 1. A Water temperature and light measurements (PAR) at canopy height during the field experiment. The light values were recorded at 12 AM (daylight saving time) or 11 AM (standard time). For illustrational reasons, the light levels are averaged over two adjacent days. No measurements from September 2011. **B** Average shoot densities ($\pm$ SE) in mono- and polycultures during the experimental duration. The *dashed line* indicates the change of year.

as one of the included studies reported that positive diversity effects might only become visible after 10 months. Only two studies found a negative correlation between genetic diversity and tolerance of stress events, but these were observations from natural plant assemblages that had been subjected to stress for a long time before the observations started.

Meta-analysis

The Meta-analysis revealed that when all studies (that is, 12 studies) were combined, genetic diver-

sity did not have an effect on productivity (primary and seed production) (1.04 ± 1.20 ; average $\pm 95\%$ CI). However, when looking at specific studies in more detail, diversity had a positive effect on productivity in stress treatments (Figure 5A, 0.47 ± 0.34). In ambient treatments, genetic diversity also tended to affect productivity positively, but the variability was higher leading to a nonsignificant effect (Figure 5A, 1.52 ± 2.32). The lower variability observed in stress treatments is likely partly due to a shorter duration of the studies; the average duration of studies applying stress was 9.3 ± 3.2 months, whereas the average duration of

Table 1. PERMANOVA on Final Shoot Densities and the Variability in Shoot Densities Measured as the Coefficient of Variation (CV)

	df	MS	Pseudo-F	P
<i>Shoot density</i>				
Time	6	23.5	13.7	0.0001
Diversity	1	13.7	0.62	0.4365
Plot (diversity)	26	21.9	12.8	0.0001
Time × diversity	6	0.21	0.12	0.9928
Residual	156	1.7		
<i>CV</i>				
Time	6	1.06	17.5	0.0001
Diversity	1	1.09	6.03	0.0272
Genotypes (diversity)	5	0.18	2.98	0.0253
Time × diversity	6	0.08	1.26	0.3139
Residual	30	0.06		

Table 2. Survival of Experimental Plots and Average Final Shoot Density in All Plots

Treatment	Genotype(s)	Survival of plots (%)	Shoot density
Monoculture	A	75	71.5 ± 36.3
Monoculture	B	50	16.0 ± 13.2
Monoculture	C	100	42.3 ± 24.3
Monoculture	D	25	11.8 ± 11.8
Polyculture	ABC	100	58.0 ± 22.0
Polyculture	ABD	75	17.5 ± 8.8
Polyculture	ABCD	100	14.0 ± 5.5

studies without stress was 14.4 ± 3.2 months. Diversity had a positive effect on productivity in short-term studies (0.39 ± 0.24), although in long-term studies, the average diversity effect was over six times higher (2.50 ± 4.37), but also more variable and nonsignificant (Figure 5B). However, the comparison of short- and long-term experiments was slightly imbalanced (Figure 5B), which may have affected the variability to some extent. A majority (>60%) of the short-term studies were stress experiments, whereas the long-term studies focused on productivity under ambient conditions (Table 3), likely contributing to the larger variability found in long-term studies. Often, variability is thought to decrease in more controlled settings, such as mesocosms. Surprisingly, the genetic diversity effects on production were more variable in mesocosm studies, whereas in field experiments, the diversity effects were clearly positive with lower variability (Figure 5C; 1.62 ± 2.78 and 0.54 ± 0.22 , respectively).

DISCUSSION

An increasing number of studies suggest that genetic diversity increases the functioning of ecosystems (for example, Stachowicz and others 2007;

Hughes and others 2008), particularly under harsh conditions (Jahnke and others 2015). This has been proposed to be of special importance in species-poor communities (for example, Reusch and others 2005; Tooker and Frank 2013), such as many marine and estuarine macrophyte-dominated ecosystems. To investigate the importance of genetic diversity (genotypic and/or allelic richness) for ecosystem functioning in vegetated coastal ecosystems, we conducted a long-term field experiment, reviewed existing literature, and performed a meta-analysis on relevant studies. We did not find any clear diversity effects on production in our field experiment, but genetic diversity enhanced community stability over time. Of the studies that we reviewed, a majority found indications of genetic diversity affecting ecosystem processes positively, especially productivity. The meta-analysis supported the hypothesis that diversity effects are more frequent and easily observable during or after periods of stress.

Field Experiment

In seasonal environments, seagrass communities follow annual dynamics in their shoot densities and standing biomass stock (Sand-Jensen 1975). Leaf

Figure 2. **A** Effects of genetic diversity on the temporal variability in shoot densities (measured as the coefficient of variation, $CV \pm SE$) and **B** the plot survival based on shoot densities in mono- and polycultures.

formation is slower in low temperatures (Nejrup and Pedersen 2008; Olesen and others 2015), and in response to decreasing irradiation, shoot densities decrease in autumn to reduce self-shading (Olesen and Sand-Jensen 1993). Low irradiation forces seagrasses to rely on their carbohydrate storages to carry on fundamental metabolism (Alcoverro and others 1999; Gustafsson and Boström 2013; Salo and others 2015). Thus, supporting less biomass during long periods of low irradiation increases the probability of eelgrass survival without a full depletion of resources. In this study, the biomass senescence in autumn and the overall low shoot production during the long and dark winter were also obvious by the low shoot densities in October 2011 and low standing shoot density after the break-up of ice in April 2012 (Figure 1B).

Increased environmental stress during the winter season can increase shoot densities in genetically diverse seagrass assemblages (Hughes and Stachowicz 2009). Such patterns were not found in this study, likely due to the more extreme winter

Figure 3. **A** Final number of shoots ($\pm SE$) in different monoculture treatments. **B** D_T ($\pm 95\% CI$) based on expected versus observed total polyculture yield. Positive and negative values indicate over- and underyielding, respectively.

season in the Baltic Sea compared to Bodega Bay, California (latitude 60° vs. latitude 38° , respectively). Natural stress in the wintertime, caused by, for example, low light availability, can be very severe in our study system. In addition, intra-specific interactions between shoots, such as increased light competition and protection from physical forces can both weaken or strengthen diversity effects on productivity, respectively. Overall, high shoot density influences eelgrass production positively in the Baltic Sea (Worm and Reusch 2000). The lack of diversity effects could thus be either due to weak interactions between and within genotypes or due to environmental stress. The nonsignificant effect of genetic diversity further corroborates that environmental stress rather than intraspecific interactions seems to be a key driver of population dynamics in our system.

Eelgrass genotypes differ in, for example, the susceptibility to grazing (Tomas and others 2011), shoot densities, and nutrient uptake (Hughes and others 2009), and responses to low light conditions (Salo and others 2015). Hence, in theory, plots including “fitter” and “more tolerant” genotypes should perform better during stressful times and vice versa. Overall, monocultures of genotypes B and D tended to have lower shoot densities, which

Table 3. Summary of the Studies Included in the Literature Review

Type of study	Richness measure	Habitat type	Species	Location	Experimental units	Allelic or genotypic richness
Natural study	Genotypic	Seagrass/SAV	<i>Posidonia oceanica</i>	Mediterranean (several sites from Cyprus to Spain)	4 impacted and 4 control meadows	Natural diversity (18-32)
Natural study	Genotypic	Seagrass/SAV	<i>P. oceanica</i>	Mediterranean (several sites from Cyprus to Spain)	30 meadows	Natural diversity (5-40)
Natural study	Genotypic	Seagrass/SAV	<i>Zostera marina</i>	N California	In total 48 plots within a meadow at 3 field sites	Natural diversity (1-15)
Field experiment	Allelic	Seagrass/SAV	<i>Z. marina</i>	San Diego Bay, California	14 plots	Low and high
Field experiment	Allelic	Seagrass/SAV	<i>Z. marina</i>	Virginia coastal bay system	32 plots from seeds	Low and high
Field experiment	Genotypic	Seagrass/SAV	<i>Z. marina</i>	Bodega bay, California	24 plots	1, 2, 4, 8
Field experiment	Genotypic	Seagrass/SAV	<i>Z. marina</i>	SW Baltic Sea, Germany	48 plots	1, 3, and 6
Field experiment	Genotypic	Seagrass/SAV	<i>Z. marina</i>	Bodega harbor, California	48 plots	1 and 6
Field experiment	Genotypic	Seagrass/SAV	<i>Z. marina</i>	N Baltic Sea, Finland	28 plots	1, 3, and 4
Field experiment	Genotypic	Wetland/Saltmarsh	<i>Spartina alterniflora</i>	Yangtze Estuary, China	42 plots	1, 3, and 6
Field experiment	Genotypic	Wetland/Saltmarsh	<i>S. alterniflora</i>	Florida, NE Gulf of Mexico	73 plots	1, 3, and 6
Mesocosm experiment	Allelic and genotypic	Seagrass/SAV	<i>Zostera noltii</i>	Ria Formosa, Portugal	36 plots	Low, medium, and high (A) and 3, 6, and 9 (G)
Mesocosm experiment	Genotypic	Seagrass/SAV	<i>Z. marina</i>	SW Baltic Sea, Germany	48 plots	1, 3, and 6
Mesocosm experiment	Genotypic	Seagrass/SAV	<i>Z. marina</i>	Bodega Bay, California	60 plots	1 and 4
Mesocosm experiment	Genotypic	Seagrass/SAV	<i>Vallisneria americana</i>	Chesapeake Bay	120 plots	2, 4, and 8
Mesocosm experiment	Genotypic	Wetland/Saltmarsh	<i>Phragmites australis</i>	Osaki, Japan	58 plots	1 and 6

Table 3. continued

Type of study	Duration (months)	Stressors	Findings	Div. effects	Study
Natural study	Not given	Fish farm impacts	Mortality increased with diversity	Negative	Diaz-Almela and others 2007
Natural study	10-13	Org. matter, nutrients	Mortality increased with diversity. No trend when most extremely disturbed sites were excluded	Negative	Arnaud-Haond and others 2010
Natural study	2 sampling dates 4-6 months apart	–	Higher shoot density in more diverse plots during winter (but no difference in summer)	Positive (but small)	Hughes and Stachowicz 2009
Field experiment	22	–	Higher shoot density in more diverse plots	Positive	Williams 2001*
Field experiment	39	–	Higher shoot density and abundance of epifauna in plots with higher richness. Plots with high richness survived longer	Positive	Reynolds and others 2012*
Field experiment	10	Grazing	Higher resistance and faster recovery in more diverse plots. More efficient resource use and higher abundance of infauna in more diverse plots after the stress event	Positive (only after the stress event)	Hughes and Stachowicz 2004*
Field experiment	4.5	Natural heat wave	Faster recovery in more diverse plots. Higher abundance of epifauna in high diversity plots	Positive	Reusch and others 2005*
Field experiment	24	Biomass removal (low and high intensity), algal bloom	Diversity enhanced resilience in terms of shoot production after high intensity stress events	Positive (only after high intensity stress event)	Hughes and Stachowicz 2011*
Field experiment	15	–	Lower variability in diverse plots. No impacts of diversity on shoot density	Neutral or positive	This study*
Field experiment	17	–	Diversity enhanced spatial spread and shoot production, but no effects on plant biomass or shoot density	Positive (but only after 10 months)	Wang and others 2012*

Table 3. continued

Type of study	Duration (months)	Stressors	Findings	Div. effects	Study
Field experiment	11	–	Spatial spread and plant density increased with genotypic diversity in plots with low trait diversity. No or slightly negative diversity effect in high trait plots. Stem height decreased slightly with increasing diversity	Mainly positive	Hughes 2014*
Mesocosm experiment	10.5	Diatom bloom	A: Higher resistance (shoot density) after the stress event in plots with higher richness. No differences in resilience between richness treatments G: Higher resistance (shoot density) in more diverse plots after the stress event. No differences in resilience between diversity treatments	Positive (both due to differences in allelic and genotypic richness)	Massa and others 2013
Mesocosm experiment	4	Temperature	Shoot density increased with diversity over time. Biomass not affected by diversity. No diversity x temperature effects	positive	Ehlers and others 2008*
Mesocosm experiment	3	Epiphytic algae and grazing	Diversity enhanced seagrass biomass in one of the five grazing treatments	Neutral or positive	Hughes and others 2010*
Mesocosm experiment	5.5	–	Flowering time and probability of both female and male plants flowering in the same population increased with genotypic diversity. Functional diversity increased with genotypic diversity, but did not contribute notably to the measured variation	Positive/neutral	Engelhardt and others 2014*
Mesocosm experiment	17	–	Diversity enhanced biomass production and water quality (nitrogen removal)	Positive	Tomimatsu and others 2014*

Natural study refers to studies exploring natural vegetation formations, whereas field experiments included man-made vegetation plots. Data from the studies marked with asterisks (after the reference) were included in the meta-analysis.

was also reflected in the lower than expected performance of the ABCD polyculture (Table 2; Figure 3B), further indicating the importance of genotypic identity for shoot production. However, due to loss of plots to ice scouring during the second winter, we are missing data on the actual contribution of individual genotypes to the final shoot densities in polycultures and therefore cannot confirm whether the observed patterns were due to dominance of genotypes with specific traits or to complementarity between genotypes (Loreau and others 2001).

The variability in shoot densities increased with time (Figure 2A). Despite the overall increasing temporal variability among diversity treatments, polycultures showed less variability compared to monocultures, supporting the hypothesis that diversity promotes community stability (Hughes and others 2008; Cardinale and others 2012; O'Connor and Byrnes 2014). Many marginal populations tend to have lower diversity compared to more central populations (Johanneson and André 2006), which may increase their vulnerability (Procaccini and others 2007). Although the results suggest that increased genetic diversity promotes temporal stability and therefore likely benefits these plant communities; in this highly seasonal environment, the predominant asexual reproduction (Reusch and Boström 2011) and low genetic diversity (Olsen and others 2004; Johanneson and André 2006; Reusch and Boström 2011) minimize the possibility of evolutionary rescue of N. Baltic eelgrass populations. As these clones differ in their traits (Salo and others 2015), efforts should be made to preserve seagrass meadows both locally and regionally, and consequently conserve the existing regional diversity in a species-poor environment. For possible future restoration efforts, we suggest that genetic diversity is increased artificially by combining different locally adapted genotypes.

Literature Review and Meta-analysis

A majority of the reviewed studies reported positive or neutral diversity effects (14 out of 16 studies), and only two studies reported negative effects of genetic diversity on ecosystem functioning. Diaz-Almela and others (2007) and Arnaud-Haond and others (2010) observed that mortality increased with diversity over time in stressed (contaminated) and control meadows. In the latter study, the negative diversity effects disappeared when the most contaminated sites were excluded from the analysis. The above-mentioned studies did not include manipulative experiments, but rather field observations of the effects of genetic diversity on

primary production in assemblages with natural genetic diversity. The authors of both studies concluded that the observed negative effects could be caused by long-term stress on local genetic diversity prior to the observations made rather than by genetic diversity per se (Diaz-Almela and others 2007; Arnaud-Haond and others 2010).

In studies where the relationship between the richness of diversity components and ecosystem functioning is explored, the underlying mechanisms behind potential richness effects are frequently divided into selection and complementarity effects (Loreau and Hector 2001; O'Connor and Byrnes 2014). In our review, we found five studies where the observed positive diversity effects were partitioned. Hughes and others (2010), for example, discovered that complementarity in resource use led to higher production, whereas Wang and others (2012) found evidence of a selection effect at play (that is, higher performance in polycultures due to one or a few well-performing genotypes) causing enhanced productivity. Reusch and others (2005), Hughes and Stachowicz (2011), and Tomimatsu and others (2014), in turn, found indications of both mechanisms working simultaneously. However, the efforts to separate different aspects of diversity such as allelic and genotypic richness were rarer. Only Massa and others (2013) controlled for both allelic richness and genotypic diversity and found that these have confounding effects on community resistance and are very difficult if not entirely impossible to separate. Such issues may easily lead to the overestimation of the importance of either diversity component for ecosystem functioning. Hughes (2014) on the other hand is the only one to date who has investigated whether diversity effects in vegetated coastal ecosystems depend on trait diversity. She observed that functional differences within and among different genotypes affect diversity effects, especially in plots with low genotypic diversity. In general, genotypic diversity had a positive effect on plant performance when trait diversity was low, whereas these effects were neutral or even slightly negative when trait diversity was high (Hughes 2014). Thus, genotypic identity, allelic richness, and the traits different genotypes possess are all expressed within genetic diversity effects, and specifically how strongly such effects influence functioning in plant assemblages.

The importance of genetic diversity may vary depending on the age of the studied community (Wang and others 2012), differences among genotypes including trait diversity (Hughes 2014), confounded genetic characteristics such as allelic or genotypic richness (Massa and others 2013), the

Figure 4. Summary of the literature review: **A** duration of studies, **B** type of experiment, **C** stressors used in the studies, and **D** observed genetic diversity effects.

Figure 5. Mean effects ($\pm 95\%$ CI) of genetic diversity on productivity (primary and seed production) in **A** ambient treatments (no stress treatment), stress treatments, and all treatments, **B** short-term (< 1 year), long-term (> 1 year) studies and all study durations and **C** mesocosm studies, field studies, and both study types. The number above each data point indicates the number of comparisons used in the calculation.

stressor (Hughes and Stachowicz 2004, 2009; Massa and others 2013), and the intensity of stress (Hughes and Stachowicz 2011), among others.

Positive genetic diversity effects are usually stronger during or after periods of stress (Hughes and Stachowicz 2004, 2009, 2011), and this pattern was also supported by our meta-analysis (Figure 5A). Likewise, diversity effects may increase with time (for example, Cardinale and others 2007, 2012; Stachowicz and others 2008; Wang and others 2012) as different underlying mechanisms may take time to develop, become stronger and of greater importance (Cardinale and others 2007, 2012; Stachowicz and others 2008). Accordingly, we observed an over six times higher average effect of genetic diversity on production (albeit non-significant) in the long-term studies compared to the short-term studies. Although not all comparisons yielded significant results, the biological importance of genetic diversity for production was primarily positive (Figure 5).

To conclude, genetic diversity did not affect eelgrass production in our field study, but the community stability of shoot production was enhanced over time. Despite the lack of a clear coupling between diversity and production in our particular experiment, the meta-analysis revealed positive effects of genetic diversity on productivity (including primary and seed production) in marine and estuarine plant communities, especially during or after periods of stress and in field studies. There are many underlying mechanisms and factors that all potentially influence the strength and direction of diversity effects such as allelic richness, trait diversity, and environmental settings, and these should be taken into account when planning restoration efforts. Furthermore, in the face of climate change, it becomes paramount to preserve local genetic diversity, especially in species-poor ecosystems where insurance against environmental change is likely provided by genetic rather than species richness.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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