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Experimental Warming Enhances Effects of Eelgrass Genetic Diversity Via Temperature-Induced Niche Differentiation

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Abstract

Genetic diversity within coastal foundation species can enhance species and ecosystem resilience to ocean warming and marine heatwaves. However, the effects of diversity on ecosystem function are often context-dependent and mechanisms underpinning, such contingency, remain poorly understood. To test the relationship between genetic diversity and resilience to warming in a coastal foundation species, we planted eelgrass (*Zostera marina*) pots at two levels of genotypic richness (1 genotype monocultures or 4 genotype mixtures) and exposed these pots to warming events of different frequencies (sustained or alternating) in mesocosms for four months (mid-summer to late fall). Our results revealed that in monocultures warming reduced pot biomass by 15.8% but warming led to overyielding in mixtures by 33.3%. In contrast, mixture biomass at control temperatures underyielded by 13.2%. Overyielding of mixtures during sustained warming was driven by positive complementarity, which appears to be the result of warming-induced shifts in the relative performance of genotypes over time. We propose that high temperature stress created a tradeoff, such that some genotypes experienced greater photoinhibiton during mid-summer while other genotypes were light limited during the late fall. Thus, seasonal differences in temperature and light conditions in the warming treatment generated asynchrony in genotype peak performance, freed genotypes from competitive interactions, and allowed overyielding via complementarity to occur. While we demonstrate that the effects of diversity on ecosystem function depend on environmental context as well as trait variation among genotypes, our results underscore that maintaining or restoring genetic diversity could dramatically improve the resilience of coastal foundation species to future ocean warming.

Keywords Biodiversity-ecosystem functioning · Complementarity · Niche differentiation · Environmental heterogeneity · Ocean warming · *Zostera marina*

Introduction

The conservation of coastal ecosystems depends on management and restoration practices that reinforce ecosystem resilience (i.e., the ability to resist and recover from disturbance, sensu Bernhardt and Leslie 2013). Maintaining biodiversity is often highlighted as a core characteristic of good management practices in coastal and marine ecosystems (Levin and Lubchenco 2008; Palumbi et al. 2008; Bernhardt and Leslie 2013), as biodiversity can enhance the function and stability of these ecosystems (Worm et al. 2006). However, the positive influence of biodiversity on ecosystem function is context dependent (Fridley 2001; Healy et al. 2008) and is conditional on both niche differentiation among community members and sufficient environmental heterogeneity to allow niche differentiation to be expressed (Stachowicz et al. 2008a, b; Weis et al. 2008; Whalen et al. 2016). The maximum benefits of diversity for ecosystem function are more likely to occur when niche differentiation leads to complementarity in resource use (over space or time) or facilitation (Stachowicz et al. 2007; Tilman et al. 2014; Marquard et al. 2016). Thus, to predict diversity-based mechanisms of ecological resilience

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Susan L. Williams is deceased.

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requires knowledge of trait variation among community members, an understanding of how specific traits impact acquisition of limiting resources (Fridley 2002; Lambers et al. 2004), and how the strength of species interactions is modified by environmental stress (Baert et al. 2018). Understanding the mechanisms and context dependencies of diversity-function relationships is critical for usefully applying them to restoration and conservation in a changing climate (Cardinale et al. 2011).

The increasing frequency and intensity of marine heatwaves is a major threat to coastal ecosystems and is commonly associated with decline of foundation species and disruption of ecosystem services (Wernberg et al. 2013; Thomson et al. 2015; Arias-Ortiz et al. 2018, reviewed in Smale et al. 2019). Greater genetic diversity has commonly been linked to improved resilience to thermal stress in a range of marine foundation species, including seagrasses (Reusch et al. 2005), kelps (Wernberg et al. 2018), and corals (Hume et al. 2016). Across all of these foundation species, genetically based variation in the photokinetics of photosystem II has repeatedly been demonstrated to underlie diversity in thermal tolerance both within (Suwa et al. 2008; Wernberg et al. 2018; DuBois et al. 2019) and among populations (Berkelmans and van Oppen 2006; Winters et al. 2011; Howells et al. 2012). Photosystem II, the first protein in the light-dependent reactions of oxygenic photosynthesis, is highly sensitive to increased temperature and can be inhibited at even low levels of heat stress (Bita and Gerats 2013). It is possible that variation in key photokinetic traits could be a primary factor driving intraspecific niche differentiation in thermal tolerance in oxygenic photosynthetic organisms (plants, algae, and cyanobacteria), although direct manipulation of intraspecific variation in this trait has yet to be linked to diversity effects on ecosystem function.

Eelgrass (*Zostera marina*) is a species of temperate seagrass that inhabits sheltered coastlines throughout the Northern Hemisphere, and as a foundation species, it greatly contributes to local productivity and provides numerous ecosystem services (Moore and Short 2006). However, eelgrass meadows are in decline worldwide do to various anthropogenic stressors (Waycott et al. 2009), potentially resulting in the loss of genetic diversity within eelgrass populations (Alberte et al. 1994). Similarly, eelgrass meadows restored by transplantation can have reduced genetic diversity (Williams and Davis 1996; Williams and Orth 1998). Williams (2001) was the first to link greater genetic diversity in eelgrass to higher vegetative production and greater seedling germination success under high temperatures. Subsequent manipulative field experiments found that greater genetic diversity (i.e., genotypic richness) in eelgrass enhances resilience to marine heatwaves (Reusch et al. 2005) and other disturbances (Hughes and Stachowicz 2004, 2011). The basis for these genetic diversity effects is genotypic variation in eelgrass traits causing differential response to a myriad of environmental factors (Tomas et al. 2011; Salo et al. 2015; Reynolds et al. 2016), and such trait diversity is directly linked to enhanced biomass production in the field (Abbott et al. 2017). Maintenance of eelgrass genetic diversity to enhance restoration success is now recognized as an important goal by management programs around the globe (Alberte et al. 1994; Campanella et al. 2010; Tanaka et al. 2011; Reynolds et al. 2012; Ort et al. 2014; Unsworth et al. 2015; Harenčár et al. 2018; Kim et al. 2019). However, the mechanistic link between genotypic variation in specific traits and eelgrass productivity across environmental contexts remains unknown, preventing managers from truly understanding under what circumstances restoration will maximally benefit from genetic diversity.

Here, we expand on our previous research, which demonstrated that in common garden, the relative performance of eelgrass genotypes from Bodega Harbor, CA, shifted during a marine heatwave and that this shift depended on differences in genotype traits (DuBois et al. 2019). Specifically, shifts in genotype relative performance were highly correlated with genotypic variation in photoinhibition of photosystem II under periods of high temperature stress and genotypic variation in efficiency of light capture of photosystem II under periods of light limitation. Based on these observations, we hypothesized that genetically based diversity in photosynthetic traits could enhance eelgrass productivity when environmental conditions fluctuated between periods of high temperature stress and light limitation. However, because DuBois et al. (2019) was an observational study of genotypes grown in monoculture, we were unable to directly link shifts in genotype relative performance to temperature or test how genotypic variation in key traits could lead to emergent effects of diversity. To investigate these mechanisms, we planted Bodega Harbor eelgrass at different levels of genotypic richness and exposed these pots to simulated ocean warming of different frequencies (sustained or alternating). By examining genotype response in monoculture and mixtures, we are able to partition diversity effects into different mechanisms (i.e., complementarity or selection) and based on previous knowledge of traits driving genotype productivity across environmental contexts propose trait-based explanations for the observed diversity effects.

Methods

Genotype Collection and Common Garden Propagation

We maintained 40 eelgrass (*Zostera marina*) genotypes (distinguished using 11 microsatellite loci) collected from four sites in Bodega Harbor, CA (see Abbott et al. 2018 for map and GPS coordinates) in an outdoor common garden under ambient conditions for three years. We previously found that these genotypes vary greatly across 17 different traits related to light and nutrient acquisition and biomass allocation (Abbott et al. 2018). Productivity of these genotypes also varies under average and elevated temperatures (Reynolds et al. 2016; DuBois et al. 2019).

Experimental Design: Diversity Manipulation and Ocean Warming Simulation

In July 2015, we selected eight genotypes from among these 40 that encompassed the range in trait values previously measured for Bodega Harbor eelgrass (Hughes et al. 2009; Abbott et al. 2018; DuBois et al. 2019). We harvested 75 clonal shoots from each genotype, standardizing rhizome length to 3 cm and shoot length to 30 cm so that the starting biomass of all individuals was approximately equal. We planted monocultures and mixtures of these genotypes in pots (8 cm^3) filled with sieved and homogenized sediment from Bodega Harbor. For planting, we used a replacement design, with monocultures comprised of four shoots of the same genotype and mixtures comprised of four shoots, with each from a different genotype randomly selected from the pool of eight genotypes. We created ten unique mixture combinations so that each of the eight genotypes was represented five times in mixture (with a different set of neighboring genotypes in each combination), and each combination was replicated once in each temperature treatment (see Fig. 1 for the experimental design). Pot shoot densities were within the range of field densities reported for Bodega Harbor (averaging approximately 250–800 shoots m^{-2} or 1.6–5.1 shoots per pot) (Hughes and Stachowicz 2011; Ha and Williams 2018). We tagged shoots with numbered and colored cable ties so that individual ramets could be identified as they expanded through growth of new clonal side shoots. We placed 10 pots in a mesocosm (dimensions = 60 cm × 30 cm × 60 cm; volume = 113 L) with each mesocosm containing all eight monocultures and two mixtures, for a total of 15 mesocosms. We supplied mesocosms with flow-through sand-filtered seawater at approximately 60 L h^{-1}.

We allowed shoots to recover from transplanting for two weeks, after which we initiated temperature treatments keeping five mesocosms at control temperatures (15.0 ± 1.2 °C, mean ± SD), warming five mesocosms (18.2 ± 1.3 °C), and five mesocosms that alternated between the control and warm treatments every two weeks (averaging 16.3 ± 1.7 °C). The warm treatment approximated the maximum temperatures reached in Bodega Bay during the 2014 marine heatwave in the Northern Pacific, named "The Blob" (Sanford et al. 2019). Because Bodega Bay during 2015 was also an unusually warm summer due to El Niño conditions (Sanford et al. 2019), we achieved our control temperature by first chilling seawater in a header sump (Aqua Logic Delta Star in-line titanium chiller). The 30-year average summer sea surface temperature for Bodega Bay during the summer months (July–September) is 13.0 ± 0.6 °C, with heatwave conditions occurring above 15 °C. Consequently, even with chilling genotypes in the control treatment experienced warmer than average temperatures. We achieved our warming treatment by first warming seawater in a header sump using three titanium emersion heaters (Process Technologies, L-shape, 1000 or 1800 W). Temperature treatments were maintained for 4 months, from mid-July to mid-November.

We measured leaf growth rates using the "hole punch" method (see Dennison 1987) on the originally planted terminal shoot of every individual ramet three times during the experiment, in early August (1 month of treatment), early September (2 months of treatment), and early November (4 months of treatment). We measured growth rates when the alternating temperature treatment was in the second week of exposure to warming (see Fig. 1).

At the end of the experiment we carefully separated the individual genets planted in each pot, as all shoots remained connected to the originally planted shoot that we identified with a tag. We divided each genet into aboveground, root, and rhizome tissues and then weighed tissue types separately after drying at 60 °C in a drying oven for several weeks.

Data Analysis

To investigate pot-level response to temperature treatments by pot genotypic richness, we first removed from the analysis any pots in which one of the four initially transplanted shoots died. By removing pots with three or fewer shoots from our analysis, we removed any confounding impacts of differential shoot density (Polley et al. 2003; Brooks and Crowe 2018) and retained our initial genotypic richness treatments. For biomass analyses, this resulted in the removal of 35 pots (23%), and for growth rate analyses, this resulted in the removal of 21 pots (14%). There was no differential mortality of genotypes across temperature treatments or diversity treatments, and genotype replication was even across temperature and diversity treatments (see Online Resource 1). For the mixtures, this did cause uneven representation of the ten different genotype combinations across temperature treatment. We determined that our results were not driven by this uneven design (i.e., our results were not driven by the removal of relatively underperforming mixture combinations from the warm treatment or relatively overperforming mixture combinations from the control treatment). We determined this by rerunning all mixture analyses with only combinations that were present across all temperature treatments (which did not alter our results) and by inspecting the distribution of combination conditional modes when combination was specified as a random effect in our mixed effect model analyses (combinations were

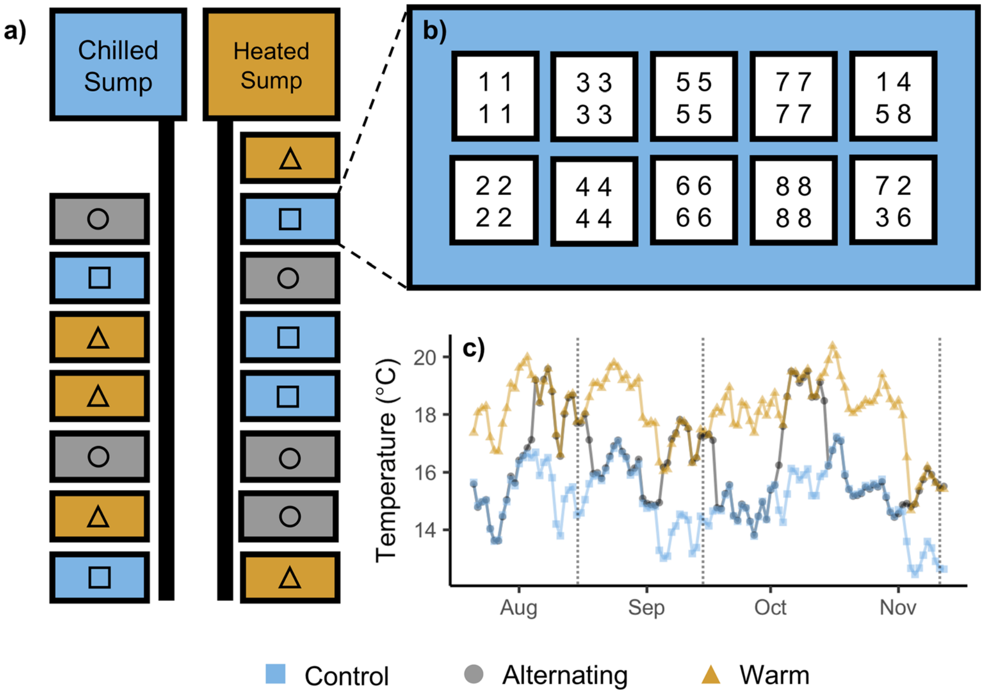

Fig. 1 Experimental design. (**a**) We applied three temperature treatments: control (squares), warming (triangles), and alternating between control and warming (circles) to five mesocosms each. (**b**) We planted eelgrass pots at two levels of genotypic richness, monocultures (1–8), or mixture, with four shoots planted in each pot. We randomly assigned genotypes to mixtures for a total of 10 unique combinations represented once in each temperature treatment. We placed 10 pots (all 8 monocultures and two mixtures) within each of the 15 mesocosms. (**c**) We maintained temperature treatments for four months (July–November); the figure shows daily mean temperature, the constant 3 °C of separation between control and warm treatments, and the alternating temperature treatment switching between control and warm every two weeks. Vertical dashed lines denote the three times we measured leaf growth rates throughout the experiment

normally distributed even after removal of mixtures that had three or fewer shoots) (see Online Resource 1).

We investigated the average response of monocultures and mixtures across each temperature treatment by first summing biomass (above + belowground biomass) across all shoots within each pot. We did the same for leaf growth rates taken during the September time point (i.e., during peak productivity). We determined the effect of temperature on average pot-level monoculture biomass and September growth by specifying a linear mixed effects model with temperature as the fixed effect and genotype identity as the random effect. We used the average performance of each genotype in monoculture at each temperature to construct the expected pot-level performance for each mixture. We then determined the effect of temperature on average pot-level mixture biomass and September growth for both the observed mixture performance and the expected mixture performance using a linear mixed effects model. We specified an interaction between the fixed effects of temperature and type (i.e., observed or expected), and we also specified a random effect of combination. Expected mixture performance is virtually the same as average monoculture performance with very slight differences due to removal of specific replicate combinations from particular temperature treatments because of shoot mortality.

We next assessed how individual genotype performance varied as a function of genotype identity, temperature, and diversity. We used linear mixed effects models on individual shoot response, with data consisting of genotype response within monoculture averaged by pot (i.e., averaging the four sub-replicates) and genotype response within mixture as the response of the single shoot of that genotype within a pot. We tested for interactions between the three fixed effects and compared models using AIC. For biomass, we specified an independent fixed effect of genotype and a 2-way interaction between the fixed effects of temperature and richness. For September growth, we specified 2-way interactions between the fixed effects of genotype and temperature as well as temperature and richness. For both models, we specified a random effect of mesocosm. To visualize the effect of diversity on each genotype's yield across different temperature treatments, we calculated percent deviation (D_i) of genotype yield in mixture relative to average genotype yield in monoculture (Hooper and Dukes 2004). Positive values of D_i reveal overyielding in mixtures (better performance of that genotype when grown with other genotypes when compared with being grown with clone mates). In the mixed effects models on individual shoot response, differential temperature effects on D_i would cause a temperature × diversity interaction.

To further differentiate among classes of mechanisms underpinning mixture response to temperature treatments, we used the additive partitioning equation of Loreau and Hector (2001), which separates the net effect of diversity into the complementarity effect and the selection effect. Complementarity is the occurrence of greater species (or genotype) performance in mixture than expected from performance in monoculture caused by resource partitioning or facilitation. Selection effect (also termed sampling effect) refers to the greater statistical probability of including a species (or genotype) with a dominant effect in an assemblage as species richness increases. For biomass and September growth, we compared strength of each component of the net diversity effect across temperature treatments by specifying linear mixed effect models, with an interaction between the main effects of mechanism (i.e., complementarity vs sampling) and temperature, and the random effect of combination.

To investigate possible mechanisms of complementarity, we first examined temporal shifts in relative genotype performance over the course of the experiment. We ranked each genotype by leaf growth rate at each of the three time points (August, September, and November) and under each temperature treatment. We then calculated Spearman's rank correlation coefficient between genotype ranks during August and genotype ranks during September and November to determine if genotype rank was consistent throughout the experiment. Second, we used root to aboveground biomass ratios as an indicator of increased competitive interactions among plants due to belowground resource limitation (Aerts et al. 1991). We compared observed root to aboveground biomass ratios in a mixture to the expected root to aboveground biomass ratios in mixture based on monoculture performance using, a linear mixed effects model with an interaction between the fixed effects of temperature and type (i.e., observed vs expected), and a random effect of composition.

For all linear mixed effects models, we tested contrasts between estimated marginal means using the Tukey's method. We checked the residuals of these models and the distribution of conditional models for normality using a Shapiro-Wilk test. For complete summaries of all linear mixed effects models, see Online Resource 1. All data analyses were conducted in R Version 3.6.2 (The R Foundation for Statistical Computing 2020) and also with the R-package "lme4" (version 1.1–21).

Results

Impact of Temperature on Monoculture and Mixture Pots

After four months of temperature treatment, warming reduced pot biomass in monoculture by 15.8% relative to controls ($t_{85} = 2.93$, $p = 0.012$, Fig. 2a). In contrast, monoculture leaf growth rates in September (i.e., two months of treatment) were elevated under both alternating and warming temperature treatments by 23.8 and 13.2%, respectively ($t_{94.1} = -7.08$, $p < 0.001$ and $t_{94.1} = -4.12$, $p = 0.037$, Fig. 2b). However, the negative impact of warming on biomass in monoculture was counteracted in genotypically rich pots. Mixtures in the warm temperature treatment had 33.3% more biomass than expected ($t_{27.2} = -4.39$, $p = 0.0002$), a robust signal of overyielding (Fig. 3a). In contrast, biomass in mixtures at control temperatures underyielded by 13.2% ($t_{27.2} = 2.51$, $p = 0.019$), resulting in a strong interaction between temperature treatment and the effect of diversity on biomass ($x^2(2) = 26.94$, $p < 0.0001$, Fig. 3a). Observed September growth in mixtures underyielded by 8.3% in the control temperature treatment compared with their expected yield ($t_{35.1} = 1.82$, $p = 0.078$, Fig. 3b), but under alternating or warmed temperature

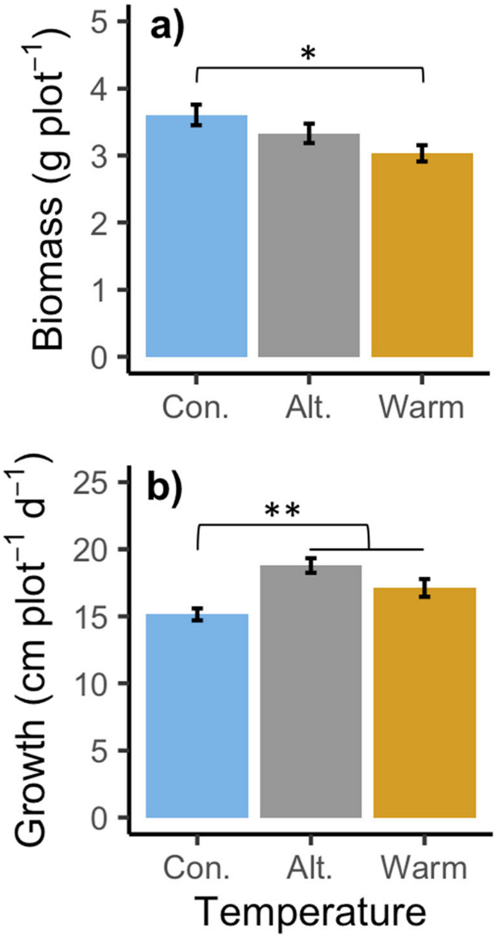

Fig. 2 Effect of temperature treatments (control, alternating, and warming) on (**a**) pot biomass in monoculture after four months (i.e., November) and on (**b**) pot leaf growth rate in monoculture over a 2-week period at the midpoint of the experiment (i.e., September). Values are mean ± SE. Asterisks indicate significance of depicted contrast (**$p < 0.01$ and *$p < 0.05$). $N = 31$–32

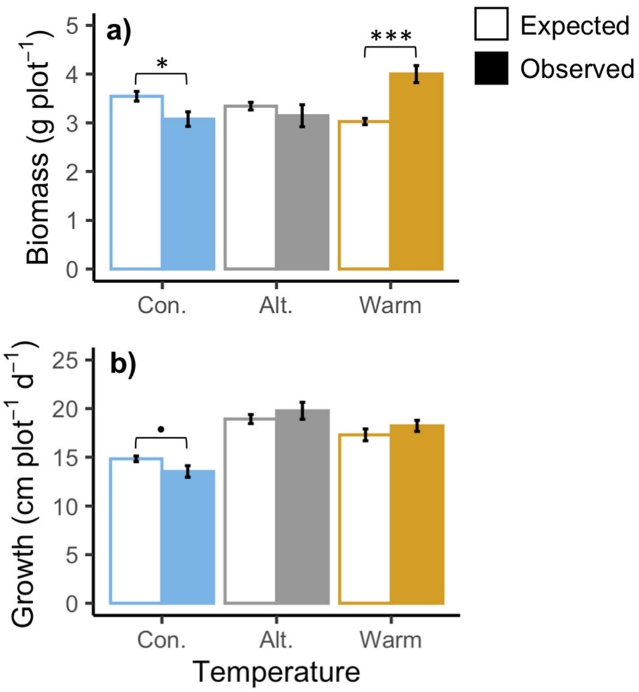

Fig. 3 Effect of temperature treatments (control, alternating, and warming) on observed (dark bars) and expected (calculated with monoculture values) performance as measured by (**a**) biomass after four months (i.e., November) and (**b**) growth at the midpoint of the experiment (i.e., September). Values are mean ± SE. Asterisks indicate significance of depicted contrast (***$p < 0.001$, *$p < 0.05$, and •$p < 0.1$). $N = 5$–9

treatments, there was no effect of diversity on yield resulting in an interactive effect of temperature and diversity on growth ($x^2(2) = 6.29$, $p = 0.043$, Fig. 3b).

Genotypic Differences in Response to Temperature and Diversity

Overall, there were biomass differences among genotypes ($x^2(7) = 51.08$, $p < 0.0001$), driven primarily by G3 and G6 (Fig. 4a), but no support for a genotype × temperature interaction (G × E effect) with most genotypes producing slightly less biomass under alternating and warming temperature treatments. In contrast, there was support for a genotype × temperature interaction for September leaf growth ($x^2(14) = 22.06$, $p = 0.077$, Fig. 4b), where G2, G4, G5, and G8 grew faster under alternating and warm temperature treatments, G1, G6, and G7 grew faster only under alternating conditions, and G3's growth was not impacted strongly by temperature. For both biomass and September growth, temperature interacted with richness in a similar pattern across all genotypes ($x^2(2) = 17.74$, $p = 0.0001$ and $x^2(2) = 6.19$, $p = 0.045$, respectively), where genotype percent deviation in mixture relative to monoculture tended to be negative at control temperatures (i.e., underyielding) and positive at warm temperatures (i.e., overyielding) (Fig. 4c, d).

Diversity Mechanisms

Positive complementarity effects completely drove the strong diversity effects observed for biomass after four months of temperature treatment (Fig. 5a), with the complementarity effect greater than the selection effect under warm temperatures ($t_{45.1} = 4.78$, $p = 0.0001$) and the complementarity effect lesser (more strongly negative) than the selection effect under

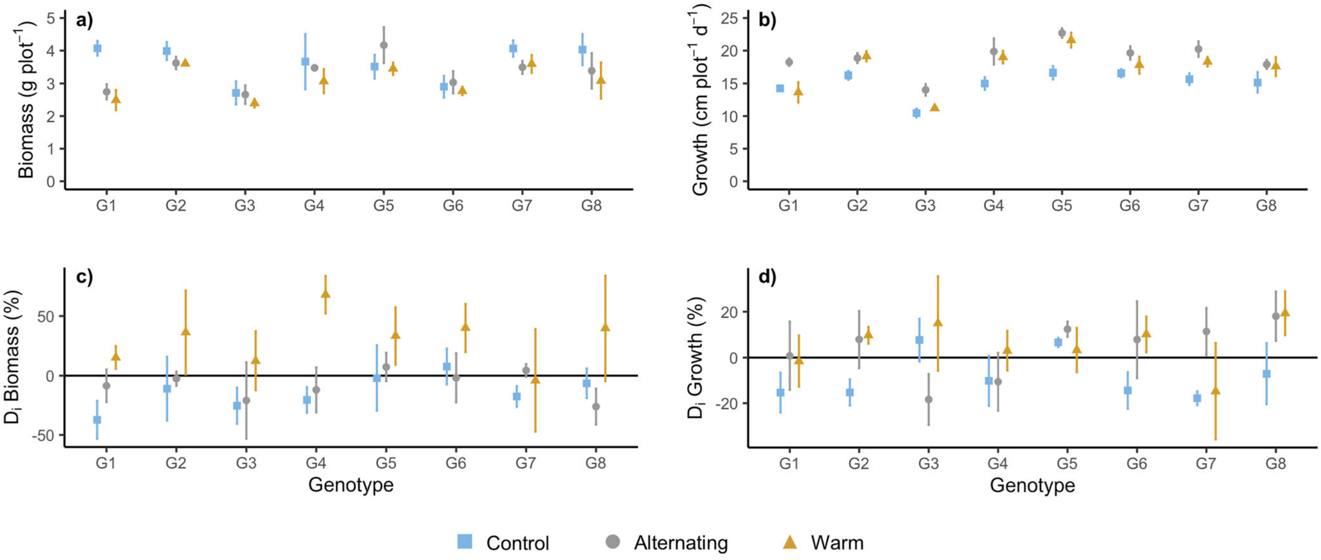

Fig. 4 Genotype monoculture (G1–G8) response to control (square), alternating (circle), and warm (triangle) temperatures as measured by (**a**) biomass after four months of treatment (i.e., November) and (**b**) leaf growth rate at the midpoint of the experiment (i.e., September). Percent deviation (D_i) of genotype yield in mixture relative to yield in monoculture at each temperature treatment as measured by (**c**) biomass after four months of treatment and (**d**) leaf growth rate after two months of treatment. Negative values of D_i indicate underyielding, and positive values of D_i indicate overyielding. Values are mean ± SE. $N = 3$–5

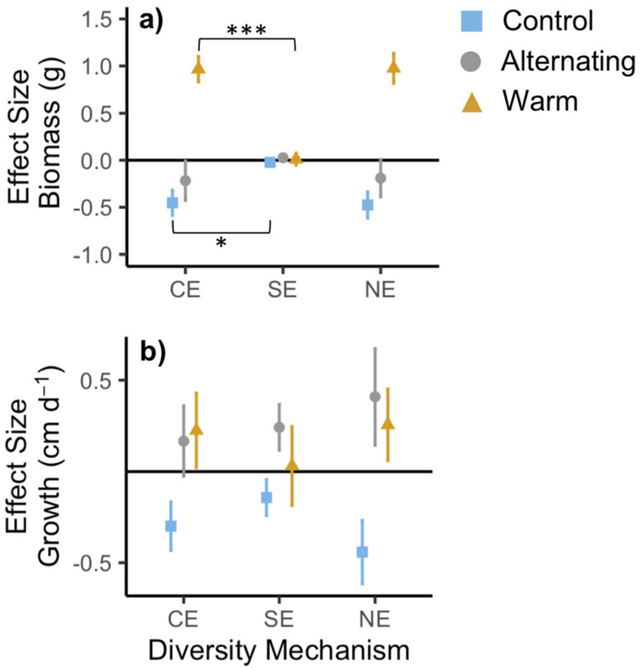

Fig. 5 Partitioning of net diversity effects (NE) into the complementarity effect (CE) and the selection effect (SE) for each temperature treatment (control: squares, alternating: circles, and warming: triangles) as measured by (**a**) pot biomass after four months of treatment (i.e., November) and (**b**) pot leaf growth rate at the midpoint of the experiment (i.e., September). Values are mean ± SE. Asterisks indicate significance of depicted contrast (***$p < 0.001$, *$p < 0.05$). $N = 5$–9

control conditions ($t_{45.1} = -2.55$, $p = 0.037$). Complementarity and selection effects equally contributed to the weaker and highly variable diversity effect identified for September growth midway through the experiment (Fig. 5b). Under the warm temperature treatment positive complementarity and a near-zero selection effect combined to cause a positive net effect of diversity, with mixtures under warm conditions growing on average 0.25 cm d^{-1} more than expected (about 1.4%), which was not detectable when comparing observed and expected yields for mixtures (see Fig. 3b). In contrast, negative complementary and selection effects combined to reduce growth in mixture under the control temperature treatment. Negative complementarity effects indicate the mutual inhibition of competitors, and negative selection effects indicate that genotypes that performed poorly in monoculture performed better in mixture.

Evidence for Temporal and Spatial Resource Partitioning

In mixtures, a seasonal shift in genotype performance ranked by leaf growth was detected only under the warm temperature treatment possibly indicating temporal partitioning of resources (Fig. 6). Under control temperatures, genotype rank was highly consistent between August and September ($R_s = 0.81$, $p = 0.01$, Fig. 6a) and August and November ($R_s = 0.67$, $p = 0.07$, Fig. 6b). Under the alternating temperature, treatment genotype rank was consistent between August and September ($R_s = 0.67$, $p = 0.07$, Fig. 6c) and August and November ($R_s = 0.69$, $p = 0.06$, Fig. 6d). However, at warm temperatures, genotype rank was highly variable and not correlated between time points ($p = 0.21$, Fig. 6e, and $p = 0.49$, Fig. 6f).

Genotypic richness altered eelgrass biomass allocation only at control temperatures, with observed root to aboveground biomass ratios 40% greater than expected based on monoculture performance ($t_{26.6} = -1.947$, $p = 0.062$, Fig. 7). This enhanced allocation to roots is common indication of increased competition for belowground resources (Aerts et al. 1991). We detected the opposite pattern under alternating and warm temperatures (temperature × observed/expected interaction: $x^2(2) = 7.36$, $p = 0.025$), in which observed root to aboveground biomass ratios were less than expected, suggesting belowground resources may have been less limiting under those conditions.

Discussion

Variability in the relationship between biodiversity and ecosystem functioning can be explained by considering environmental context and specificity of mechanism (Fridley 2001). Our results reveal that the strength and direction of genotypic richness effects on eelgrass (*Zostera marina*) biomass and leaf growth rate depend on temperature (Figs. 3 and 4) and likely reflect temperature-driven shifts in niche differentiation among genotypes. At warm temperatures, by the end of the experiment, nearly all genotypes achieved higher biomass in mixtures than monocultures (Fig. 4c), whereas short-term growth measurements taken throughout the experiment indicate that the relative performance of genotypes shifted seasonally (Fig. 6e, f) because only a few genotypes overyielded at any particular time point (Fig. 4d). Therefore, the emergence of overyielding via positive complementarity at warm temperatures (Fig. 5a) was likely because different genotypes benefitted from being in mixtures during different seasons allowing all genotypes to achieve a greater increase in biomass over the course of the experiment. Identifying the traits responsible for the variability in seasonal niches among genotypes at warm temperatures, but not at control temperatures, is key to developing a predictive understanding of the role of diversity in this ecosystem.

We propose that seasonal niche differentiation occurs because warm temperatures cause asynchrony in genotype ability to use light of different intensities, which changes throughout the year. This could occur via the following two mechanisms: enhanced photoinhibition during the summer and increasing the importance of photosynthetic efficiency during the late fall (see Fig. 8). Because our mesocosms were outside

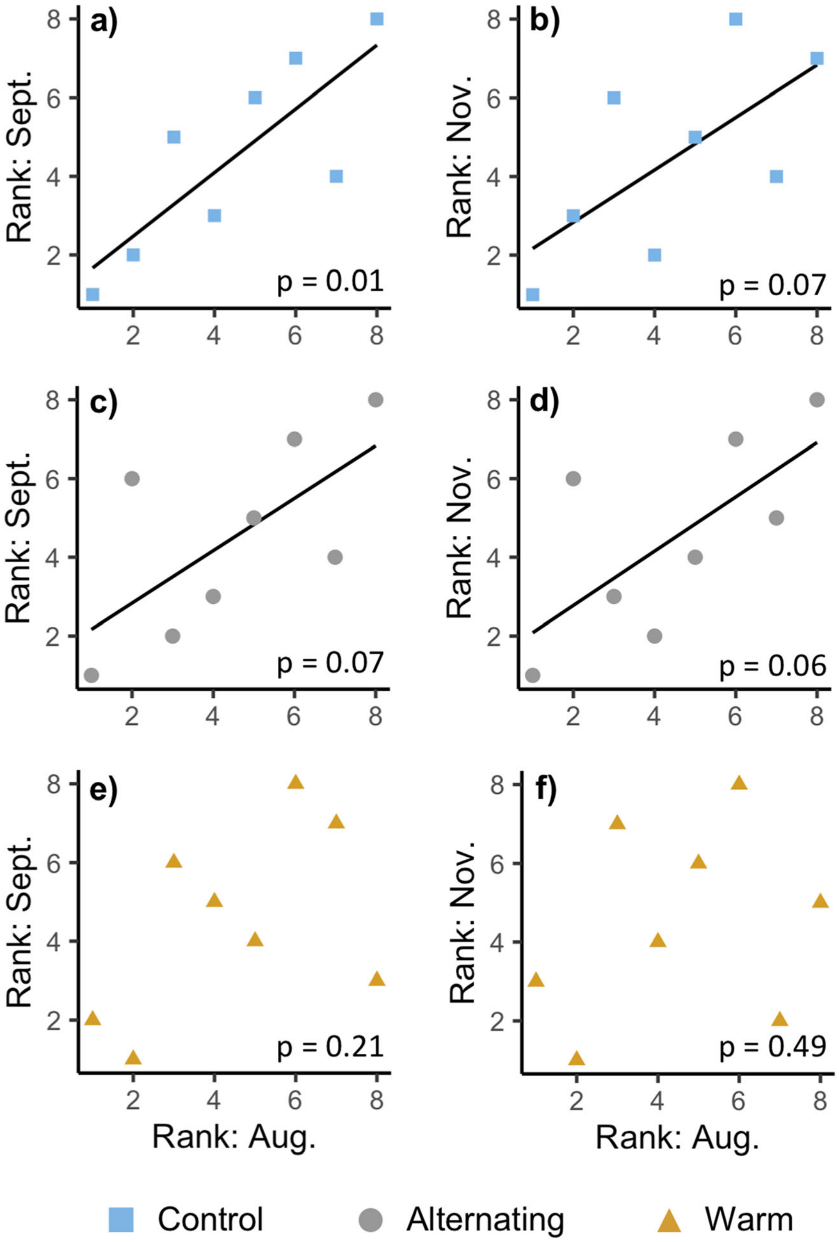

Fig. 6 Rank order of genotype performance (G1–G8) during August compared with rank order of genotype performance in September and November at control (**a**, **b**), alternating (**c**, **d**), and warm (**e**, **f**) temperatures. Rank order was determined using average leaf growth rate of genotype in mixture over a two-week period

and supplied with flow-through seawater, conditions in the warming treatment ranged from extremely high temperature and intense light in August (19 °C, 13 h photoperiod) to moderately elevated temperature and low light in November (16 °C, 8.5 h photoperiod). Our previous work demonstrates that eelgrass genotypes from Bodega Harbor (grown in common garden) seasonally vary in relative performance because some genotypes are more sensitive to photoinhibition under conditions of high temperature and intense light (17 °C, 12 h photoperiod) while other genotypes have much higher photosynthetic efficiency under conditions of lower temperature and light (11 °C, 9 h photoperiod) (DuBois et al. 2019). Variation in genotype seasonal niches, driven by differences in photoinhibition and photosynthetic efficiency expressed during thermal stress, would cause asynchrony in genotype carbon limitation and release individuals from competing for limited belowground resources (i.e., nitrogen) (Roscher et al. 2016). Indeed, genotype performance rank order shifted seasonally only in the warming treatment (Fig. 6), as previously demonstrated by DuBois et al. (2019).

Differences in phenology and temporal partitioning of resources is often the mechanism identified when overyielding via complementarity is observed in species diverse plant and marine invertebrate assemblages (Tilman et al. 1997; Hooper 1998; Stachowicz et al. 2002; Stachowicz and Byrnes 2006; Douda et al. 2018), but our work also demonstrates how complementarity can be context dependent. A similar mechanism was detected in the brown algae, *Fucus vesiculosus*, where

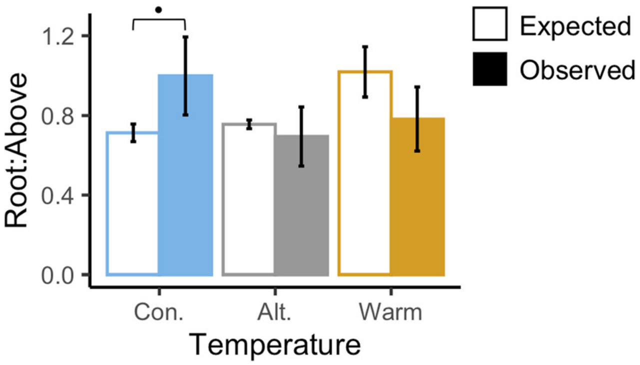

Fig. 7 Effect of temperature treatments (control, alternating, and warming) on observed (dark bars) root to aboveground biomass ratios compared with the expected (light bars) root to aboveground biomass ratios (calculated with monoculture values) in mixture after four months. Values are mean ± SE. Asterisks indicate significance of depicted contrast (•$p < 0.1$). $N = 5–9$

genotypic variation in sensitivity to photoinhibition under warming led to variation in carbon limitation and higher long-term survival of diverse genotype assemblages (Al-Janabi et al. 2016). Additionally, kelp (*Ecklonia radiata*) population performance and resilience to a marine heatwave were strongly linked to population genetic diversity and population variability in photosynthetic efficiency (Wernberg et al. 2018). In contrast, at the range of temperatures experienced under control conditions, genotypes did not express different seasonal niches (see Fig. 8a, c) as demonstrated by the stability of relative genotype performance across seasons (Fig. 6a, b).

Moving from stressful to benign conditions can reduce environmental heterogeneity and increase competition (Bulleri et al. 2016). Greater allocation to root biomass in relation to aboveground biomass is a common phenotypic response in plants that increases competitive ability for belowground resources (i.e., nutrients) (Aerts et al. 1991; Ehlers et al. 2016). At control temperatures, observed root to aboveground biomass ratios in mixtures were 40% greater than expected based on root to aboveground biomass ratios in monoculture (Fig. 7), and this response coincided with mixtures underyielding by 13.2% (Fig. 3a) because of negative

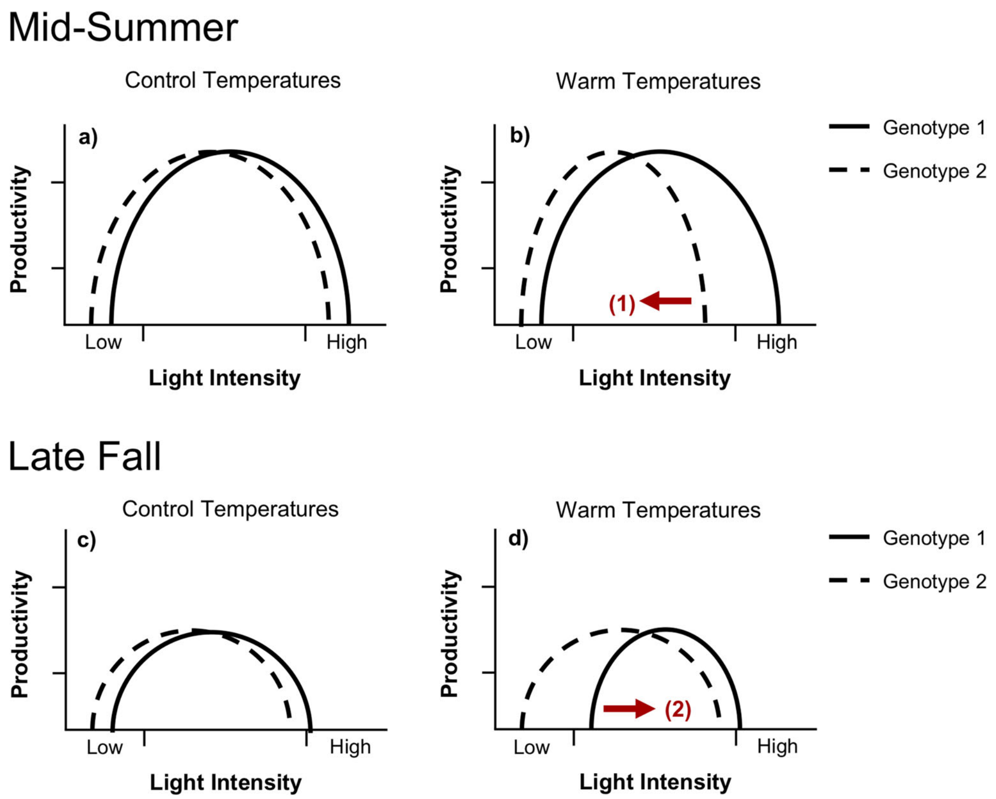

Fig. 8 Schematic depicting possible mechanism underlying increased complementarity with experimental warming, based on a tradeoff between sensitivity to high-light photoinhibition and low-light efficiency at elevated temperatures (shown by DuBois et al. (2019)). Niche differentiation among genotypes in light utilization increases at warmer temperatures, for hypothetical genotypes 1 (solid line) and 2 (dashed line). (**a**) During mid-summer (i.e., the warmest temperatures and highest light intensities), under control temperatures, both genotypes overlap in productivity across all light intensities. (**b**) Under the warming treatment, genotype 2 is less productive at high light intensities due to increased sensitivity to photoinhibition (arrow 1). (**c**) During late fall (i.e., when light is limiting and productivity is reduced overall), under control temperatures, genotypes overlap in productivity across all light intensities. (**d**) Under the warming treatment, genotype 1 is less productive at low light intensities because reduced photosynthetic efficiency increases the intensity of light required to reach the light compensation point (arrow 2). Thus, over time, the relative productivity of genotype 1 and genotype 2 switches at higher temperatures but remains the same at control temperatures (see Fig. 6)

complementarity (Fig. 5a). Conversely, at warm temperatures root to aboveground biomass ratios in mixtures were less than expected, which suggests that when genotypes in mixtures are released from competition via temporal resource partitioning no shifts in root to aboveground resource allocations are induced (Fig. 7). Together, these results suggest that the underyielding of mixtures at control temperatures was caused by increased synchrony in competition for sediment nutrients and mutual inhibition of competitors. Mutual inhibition of competitors (i.e., negative complementarity) in biodiversity-ecosystem function studies is reported less often but appears to occur under conditions of low resource complexity (Becker et al. 2012; Roscher et al. 2016), which is often the case in mesocosms (Stachowicz et al. 2008a) and especially in our control treatments which lacked seasonal niche differentiation caused by thermal stress. However, a similar phenomenon was also reported by Hughes and Hughes and Stachowicz (2011) in which genotypically diverse eelgrass pots initially underyielded compared with monocultures prior to disturbance. While the observation of negative diversity effects in mesocosm and the field in this species highlights the need for careful consideration of how genetic diversity can reduce productivity in some situations the increasing benefits of diversity in a warming ocean will likely outweigh the slight negative effects of diversity on biomass accumulation during benign periods.

That the alternating temperature treatment was intermediate between the two other treatments also supports our proposed explanation that thermal stress could enhance niche differentiation among genotypes. If niche differentiation between genotypes were fixed and dependent solely on temperature, then we might have expected the greatest diversity effects in the alternating temperature treatment as the greater temperature variation would have increased the expression of temporal niche differences (Chesson et al. 2002). However, we found no diversity effect under the alternating temperature treatment (Fig. 3), which could reflect that these mixtures alternated between underyielding and overyielding when alternated between control and warm temperatures. Wang et al. (2019) found that in species-rich grasslands alternating between underyielding and overyielding occurs over a heterogeneous landscape, and at a global scale results in a zero net diversity effect on the magnitude of productivity but greatly enhances stability of productivity. Similarly, our work highlights that the relationship between the strength of diversity effects and environmental heterogeneity may not be straightforward when environmental conditions themselves alter the extent to which species or genotypes exhibit niche differentiation.

Although there are relatively few data comparing the magnitude of effects of diversity versus anthropogenic stressors on ecosystem function (Cardinale et al. 2011 ; Isbell et al. 2013), our results show that diversity effects are comparable to, or even greater than, the effects of warming. Warming reduced monoculture biomass by 15.8% (Fig. 2a), yet at warm temperatures, genotypically rich pots produced 33.3% more biomass than expected (Fig. 3a), completely reversing the negative effect of warming detected in monocultures. The magnitude of overyielding detected here is similar to that found in a field experiment where biomass of genotypically rich eelgrass plots within an eelgrass meadow overyielded by 26% after experiencing a summer-long heatwave (Reusch et al. 2005).

Our results demonstrate that biodiversity effects on ecosystem function are context dependent and that a mechanistic understanding of diversity-function relationships requires knowledge of trait diversity relevant to limiting resources. Our results also support the idea that the strength and direction of complementarity can vary across environmental contexts because of shifting resource availability (Roscher et al. 2016) and that complementarity effects become stronger than selection effects over time (Cardinale et al. 2011; Stachowicz et al. 2008b; Marquard et al. 2016). However, because the positive effects of genotypic richness completely mask the negative effects of ocean warming it is possible that simultaneous loss of genetic diversity (and trait diversity) could cause dramatic and unexpected loss of ecosystem function (Bulleri et al. 2016). Therefore, regular monitoring for changes in baseline genetic diversity could provide an early warning of increased vulnerability of coastal ecosystems to warming ocean temperatures and is critical to improving the success of restoration and conservation efforts (Mijangos et al. 2015; O’Leary et al. 2017). While the monitoring of genetic diversity is broadly promoted for seagrasses (Williams 2001; Reynolds et al. 2012) and salt marshes (Travis et al. 2002; Ryan et al. 2007; Tumas et al. 2018), such monitoring is limited and just recently occurring in coral (Shearer et al. 2009) and oyster reefs (Hornick and Plough 2019; Hughes et al. 2019) and remains understudied for kelp forests (Layton et al. 2020) and mangroves (Sandilyan and Kathiresan 2012). As ocean warming continues, variation in photokinetic traits could be a key mechanism underpinning genetic diversity effects for the many marine foundation species that are primary producers.

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