

Complementarity in marine biodiversity manipulations: Reconciling divergent evidence from field and mesocosm experiments

John J. Stachowicz^{a,b,1}, Rebecca J. Best^{a,b}, Matthew E. S. Bracken^c, and Michael H. Graham^d

^aDepartment of Evolution and Ecology and Center for Population Biology, University of California, Davis, CA 95616; ^bBodega Marine Laboratory, Bodega Bay, CA 94923; ^cMarine Science Center, Northeastern University, Nahant, MA 01908; and ^dMoss Landing Marine Labs, Moss Landing, CA 95039

Edited by Robert T. Paine, University of Washington, Seattle, WA, and approved October 8, 2008 (received for review July 3, 2008)

Mounting concern over the loss of marine biodiversity has increased the urgency of understanding its consequences. This urgency spurred the publication of many short-term studies, which often report weak effects of diversity (species richness) driven by the presence of key species (the sampling effect). Longer-term field experiments are slowly accumulating, and they more often report strong diversity effects driven by species complementarity, calling into question the generality of earlier findings. However, differences among study systems in which short- and long-term studies are conducted currently limit our ability to assess whether these differences are simply due to biological or environmental differences among systems. In this paper, we compared the effect of intertidal seaweed species richness on biomass accumulation in mesocosms and field experiments using the same pool of species. We found that seaweed species richness increased biomass accumulation in field experiments in both short (2-month) and long (3-year) experiments, although effects were stronger in the long-term experiment. In contrast, richness had no effect in mesocosm experiments, where biomass accumulation was completely a function of species identity. We argue that the short-term experiments, like many published experiments on the topic, detect only a subset of possible mechanisms that operate in the field over the longer term because they lack sufficient environmental heterogeneity to allow expression of niche differences, and they are of insufficient length to capture population-level responses, such as recruitment. Many published experiments, therefore, likely underestimate the strength of diversity on ecosystem processes in natural ecosystems.

diversity–ecosystem function | seaweed | species identity | intertidal | algae

A growing body of research addresses the functional consequences of diversity for ecosystem processes. Although reviews and metaanalysis of this literature do suggest an effect of diversity (usually manipulated as species richness) that is consistent across ecosystems and taxa when averaged over many studies (1–3), there is considerable variation in the strength of this effect, even among experiments conducted within similar ecological systems. Although it should not be surprising that diversity, like most ecological drivers, will vary in importance in space and time, understanding the causes of this variation is important because it would allow us to better predict the conditions and ecosystems in which the consequences of diversity loss will be the greatest.

However, our ability to use existing data to rigorously assess the biological or environmental determinants of variation in the strength of diversity effects (we use this term interchangeably with effects of species richness) is currently limited by important differences in approaches and methodologies specific to particular study systems. For example, consider the effects of producer species richness on biomass production, probably the most commonly investigated type of diversity effect (2, 4). Many studies of terrestrial plant species richness have found diversity effects, but this pattern has been less general in marine systems,

where many studies find weak or no effects (reviewed in ref. 3). Although it is tempting to conclude that diversity's importance varies with differences in life form (algae vs. vascular plants) or physical medium (water vs. soil and air), differences in the details of experiments conducted in marine vs. terrestrial systems could also drive this pattern. First, most marine manipulations of producer species richness are of short duration relative to analogous terrestrial experiments. The mean duration of marine producer species richness experiments listed in Stachowicz *et al.* (3) is 2.5 months (median = 3 weeks), whereas the mean duration of terrestrial experiments in Cardinale *et al.* (1) is 2.5 years (median = 2 years). Within terrestrial experiments, the strength of diversity effects increases over time (5, 6), and metaanalysis has suggested that many studies that find weak diversity effects are of insufficient duration for the mechanisms that underlie such effects to be manifested (1). Second, for important logistical reasons, marine algal species richness manipulations are often conducted in mesocosms (e.g., see refs. 7–10). However, theory suggests that the reduced heterogeneity and limited duration characteristic of many mesocosm experiments might reduce opportunities for the expression of complementarity among species (11, 12). Third, even when experiments are conducted in the field, in many cases these involve transplanting adults onto artificial substrates that may also lack heterogeneity (e.g., see refs. 7, 8, and 13), limiting them to examining mechanisms that involve growth of individual ramets rather than population phenomena that include recruitment or clonal spread.

In marine algal experiments that adopt methods analogous to terrestrial ones (field experiments, long duration, allowing population processes and not just individual growth; e.g., refs. 14 and 15), strong diversity effects are more common. Still, even among marine studies, confounded variation in systems and methodologies hampers efforts to explain differences in outcome. Although longer-term studies do tend to find strong effects, these studies are also from colder temperate regions, are conducted intertidally, and are in the field (14–16). In contrast, studies that find weak or no effects often involve subtidal taxa and are shorter term and/or conducted in mesocosms (7, 8, 17). This severely limits our ability to use existing data to ascertain when diversity really is and is not an important driver of ecosystem processes.

Application of multiple experimental approaches within the same biological system could help resolve the extent to which

Author contributions: J.J.S., R.J.B., M.E.S.B., and M.H.G. designed research; J.J.S., R.J.B., M.E.S.B., and M.H.G. performed research; J.J.S. analyzed data; and J.J.S. and R.J.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: jstachowicz@ucdavis.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0806425105/DCSupplemental.

© 2008 by The National Academy of Sciences of the USA

existing results are the result of methodological differences vs. specific characteristics of different systems. Such studies might also help assess the relative importance of different types of mechanisms that might underlie a positive diversity–productivity relationship. For example, previous work has identified a range of potential mechanisms that might underlie the effects of seaweed species richness on biomass accumulation (10, 14, 15). Some of these mechanisms should operate in short-term “assembly” experiments where response variables largely reflect growth or photosynthetic rate of existing adult thalli. For experiments with intertidal algae, these might include complementarity of photosynthesis in air vs. water (18, 19) or complementary affinities for different forms of limiting nutrients (10). If these mechanisms are the primary drivers of diversity effects, then short-term mesocosms and long-term field experiments should show similar results, assuming field experiments are not overwhelmed by other factors. Other mechanisms, such as microhabitat differentiation, temporal complementarity, and facilitation, might be more likely to operate in longer-term experiments that follow populations over time and allow external recruitment, or experiments that are conducted on naturally heterogeneous substrata (14, 15). If these mechanisms predominate, long-term field experiments should show diversity effects, whereas mesocosm or short-term field experiments should produce weak or no effects.

In this paper we examine the effect of seaweed species richness (as a measure of diversity) on biomass production (as a measure of ecosystem functioning) using 3 approaches: first, a short-term mesocosm experiment using transplanted adult thalli; second, a short-term field experiment measuring the production of individual thalli that naturally recruited to experimentally established high- and low-richness assemblages; and third, a long-term (3-year) field experiment in which production was measured in plots in which species richness was manipulated. Adding a short-term field experiment under naturally heterogeneous conditions allowed us to separate duration and heterogeneity to some extent, unlike most current experiments in which heterogeneity and experimental duration positively covary. All experiments were conducted at Bodega Marine Reserve, Bodega Bay, CA (38°19.2'N, 123°04.4'W), in mid-high intertidal portions of rocky reefs, where 4 common perennial taxa (the turf-forming red alga *Endocladia muricata*, the foliose red alga *Mastocarpus papillatus*, the canopy-forming brown alga *Pelvetiopsis limitata*, and the turf-forming green alga *Cladophora columbiana*) comprise >85% of seaweed cover and are typically organized in a patchwork mosaic that appears to be maintained by a combination of disturbance, competition, and herbivory (refs. 20–22, but see ref. 23). We compared and contrasted findings from each of these experiments in an effort to both resolve whether differences in the strength of diversity effects in the literature are due to experimental procedure vs. study system and address more generally which types of potential mechanisms underlie significant diversity–productivity relationships.

Results

The effect of seaweed species richness on seaweed biomass differed dramatically between short-term field, mesocosm, and long-term field experiments. After 1 month in intertidal mesocosms, there was no effect of species richness on the change in total seaweed mass, as biomass change in polyculture was exactly the average of the component species monocultures (Fig. 1A). However, there were strong differences among monocultures in biomass accumulation, with *Cladophora* and *Pelvetiopsis* increasing in biomass much faster than *Mastocarpus* and *Endocladia*. Thus, in the mesocosm experiment, partitioning treatment effects into richness and identity (24) found a strong effect of species identity on biomass ($F_{3,90} = 37.3$, $P < 0.001$, $\omega^2 = 0.53$; see refs. 24 and 25 and *Methods* for details on statistical analysis),

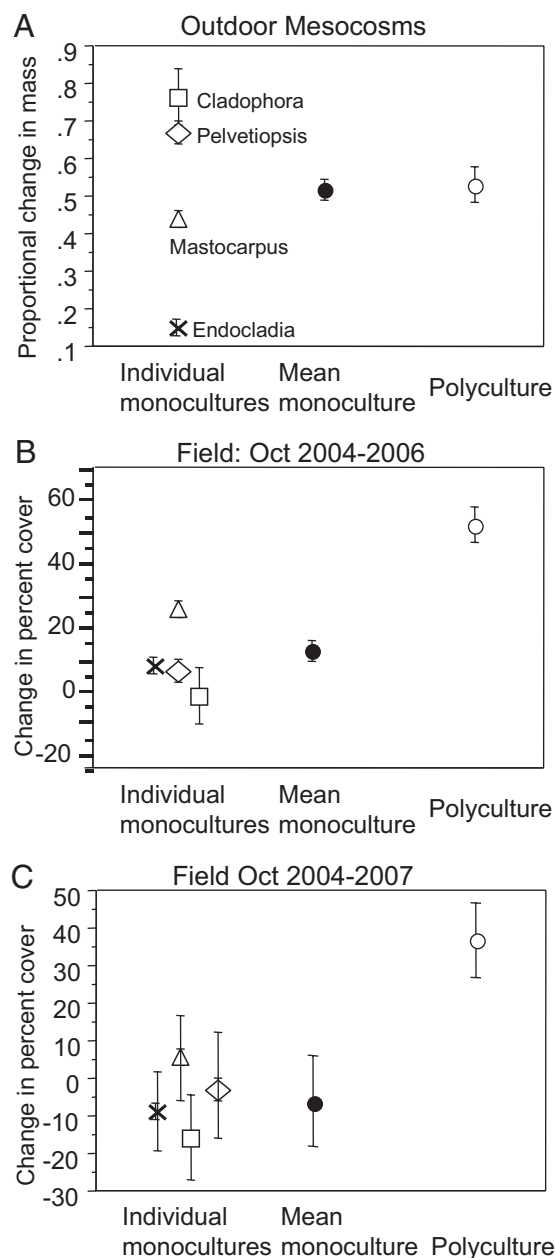


Fig. 1. Effect of seaweed richness and composition on proportional biomass change in outdoor mesocosms (A) and change in cover in the field after 2 and 3 years (B and C, respectively). Analysis by ANOVA. Partitioning treatment effects into a richness (monocultures vs. polyculture) and identity (among monoculture) component reveals a strong effect of diversity and weak effects of identity in the field experiment, and no effect of diversity and a strong effect of identity in the mesocosm experiment.

whereas there was no effect of richness ($F_{1,90} = 0.18$, $P = 0.66$, $\omega^2 = 0$). Growth differed slightly between the 2 time periods over which the mesocosm experiment was run (block $F_{1,90} = 7.02$, $P = 0.01$, $\omega^2 = 0.03$), but there was no block \times treatment interaction ($F_{4,90} = 2.27$, $P = 0.07$). In contrast, the change in seaweed cover over 3 years in the field experiment was strongly influenced by seaweed species richness ($F_{1,42} = 19.1$, $P < 0.0001$, $\omega^2 = 0.18$) but not by identity ($F_{3,42} = 1.05$, $P = 0.38$, $\omega^2 = 0.001$; Fig. 1C). Monocultures increased negligibly in cover on average over 3 years (although they did change seasonally in cover; see ref. 15), whereas polyculture cover increased 40% over the same time

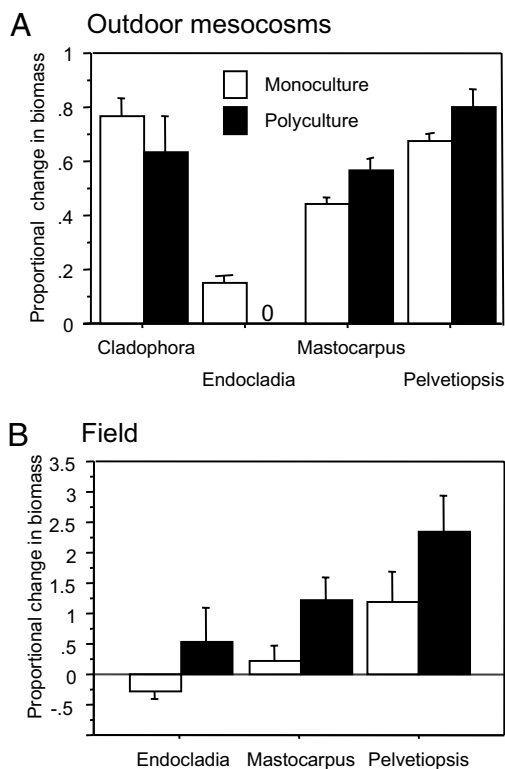


Fig. 2. Fractional change in biomass for each species of algae grown in mesocosms (A) or the field plots (B) in monoculture and polyculture. Biomass increments in mesocosm are from direct weighing; field data are estimates using the product of survival and growth. Analysis is by 2-way ANOVA (separate analyses for A and B) with species richness and identity as fixed factors.

period. After 2 years, the effect sizes were similar, although overall cover in both monoculture and polyculture was higher (Fig. 1B). The magnitude of these changes in each treatment differed among seasons and years, but the effect of species richness was always greater than that of identity (for more details, see ref. 15). There were no differences in average hourly desiccation rates between field and mesocosm experiments as measured by water loss of agar blocks. The rate of mass loss per hour was $0.86\% \pm 0.27\%$ in the mesocosm vs. $0.64\% \pm 0.08\%$ in the field for foggy conditions ($t = 0.495$, $P > 0.25$) and $4.83\% \pm 0.53\%$ in the mesocosm vs. $4.34\% \pm 0.29\%$ in the field for sunny conditions ($t = 0.38$, $P > 0.25$).

When we compared integrated measures of performance of individuals in the short-term (2-month) field experiment (e.g., growth \times survival; see *Methods*) with biomass change of individual species in the mesocosms by using ANOVA, species richness increased biomass accumulation in the field but not in mesocosm (Fig. 2). Comparisons of individual morphological measures for each species are included in the online [supporting information \(SI\) Text](#) and in [Fig. S1](#). In the field, total standardized growth of individual thalli was affected by plot-level species richness ($F_{1,61} = 8.23$, $P = 0.005$) and the identity of the species being measured ($F_{2,61} = 7.39$, $P = 0.001$), but not by the interaction between the two ($F_{2,61} = 0.088$, $P = 0.92$). There was no significant effect of block ($F_{11,52} = 1.10$, $P = 0.31$), so it was removed from the model. The magnitude of the effect of species identity ($\omega^2 = 0.15$) was greater than that of richness ($\omega^2 = 0.09$). Results of the short-term field experiment were qualitatively similar after 1 vs. 2 months. In contrast, in the mesocosm, algal growth was affected strongly by species identity ($F_{3,141} = 57.4$, $P < 0.0001$) but not richness ($F_{1,141} = 0.001$, $P = 0.87$). There was a weak interaction between species identity and richness in the

mesocosm ($F_{3,141} = 3.84$, $P = 0.024$), reflecting the fact that seaweeds with a turf morphology (*Endocladia* and *Cladophora*) performed better in monoculture than in polyculture, whereas algae with larger, upright thalli (*Mastocarpus* and *Pelvetiopsis*) performed better in polyculture than in monoculture. Still, the magnitude of differences in growth among species ($\omega^2 = 0.47$) was much greater than the effect size of the interaction ($\omega^2 = 0.02$), suggesting that the effect of species richness in mesocosms was negligible. There were significant effects of block ($F_{1,141} = 11.2$) and block \times species identity interaction ($F_{3,141} = 5.95$) in the mesocosm experiment, but these were an order of magnitude smaller than the main effect of species identity ($\omega^2 = 0.03$ and 0.04 , respectively). Thus, change in biomass of marked thalli was affected by both the species richness of the plot and the species identity of the tagged individual in the field, but only by species identity in mesocosms.

Discussion

We found that seaweed species richness increased biomass accumulation in both short- and long-term field experiments, whereas in mesocosms the richness effect was negligible and biomass accumulation was largely a function of species identity. This occurred in part because in the field, individuals of each species performed better in polyculture than monoculture (Fig. 2B), whereas in mesocosms the marginally greater performance of 2 species in polyculture came at the expense of reduced performance by 2 other species (Fig. 2A), leading to no net difference between the average monoculture and the polyculture (Fig. 1A). Across experiments, 3 main factors correlated positively with strong diversity effects: experimental duration, environmental heterogeneity, and the ability of the experiment to measure population responses (e.g., recruitment) in addition to individual growth and survival. Each of these likely contributed to the observed differences among our experiments. Below, we discuss each of these factors in more depth and examine how our results might help explain apparently contradictory outcomes among previous manipulations of marine algal species richness that might otherwise be attributed to idiosyncratic differences among study systems.

Our results support the idea that experimental duration influences the strength of the diversity effect. More detailed analysis of the time series of the field experiment (15) shows that effects of algal richness on total cover first emerged after 9 months ($\omega^2 = 0.10$ to 0.20), then strengthened until reaching their full strength after 18–24 months ($\omega^2 = 0.25$ to 0.35). In contrast, the mesocosm experiment, in which species richness had no effect, measured growth over only 5 weeks. Further, among field experiments, the diversity effect on change in cover was stronger in the long-term than in the short-term experiment ($\omega^2 = 0.18$ vs. 0.09 ; Figs. 1 and 2). That the importance of diversity and species complementarity increases over longer time scales is also supported by metaanalysis of multiple experiments of varying experimental duration (1). This can occur because longer experiments encounter greater temporal variation in conditions, which facilitates the expression of differences among species in response to seasonal or other climatic change (e.g., temporal complementarity; ref. 26). Increasing biomass in diverse plots could also be a function of greater resistance to, or resilience from, extreme events (16, 27, 28), which happen infrequently but with greater probability in longer experiments. The strength of complementarity among species can also increase with experimental duration simply because it takes time for sufficient interactions among species to occur to allow the expression of niche differences and overcome initial effects of rapid growth (1, 12). Finally, longer experiments are more likely to measure population processes, such as recruitment of new individuals, opening up additional mechanisms by which diversity can act, such as facilitation of early life history stages (29, 30).

That time (directly or indirectly) is not the only factor generating differences between field and mesocosm results is supported by the contrast between short-term field and mesocosm experiments. These experiments were of similar duration, but biomass accumulation was greater in polyculture for all measured species in the field, whereas in mesocosms, upright species tended to perform better in polyculture and turf species did better in monoculture, likely because of asymmetric competition for light. What mechanisms underlie the effect of species richness on biomass change in the field in the short-term measurement of individual growth that do not operate in the mesocosms? There was significant mortality in the field for *Mastocarpus* and *Pelvetiopsis* (Fig. S1), suggesting that there were some agents of stress or mortality in the field that were not present in the mesocosms, despite no difference in desiccation rates as measured by agar blocks. In the field, desiccation was reduced in the polycultures compared with the monoculture (15), which could have contributed to enhanced growth and survival, particularly of the small individuals we marked in the short-term experiment, which can be more susceptible to desiccation than adult plants (29). Whether this was a direct effect of diversity or an indirect effect of the higher biomass in diverse field plots is unknown. Other stressors absent from mesocosms, such as grazers and waves, also could have contributed to mortality in the field. Previous studies at our location found that limpets decreased the abundance of the species that we observed to have high mortality rates (*Mastocarpus* and *Pelvetiopsis*) while increasing the abundance of the species that we observed to have low mortality (*Endocladia*) (20). Further, the abundance of some grazing limpets and littorine snails is greater in monoculture plots of some species than in polyculture (J.J.S., unpublished data); thus, increased grazing intensity could have contributed to lower growth and survival of individual algae in field monocultures (Fig. 2).

Because of the generality of the likely mechanisms involved in the differences between field and mesocosm experiments, we suspect our results are robust to our choice of particular species to include in the manipulation. For example, *Ulva* and *Porphyr*a comprise most of the rest of the cover in our plots not attributable to the 4 target species. Had we included these in our experiments, short-term mesocosm experiments would likely find that monocultures of these have greater biomass accumulation than the polyculture because of their rapid growth rates and the lack of herbivores and other agents of mortality in the mesocosms. In our field plots, the abundance of *Ulva* and *Porphyr*a is highly seasonal, with *Ulva* reaching peak biomass in July and *Porphyr*a in October, and is reduced to low levels where grazers are active (20). In our long-term field experiments, monocultures of each could have achieved high cover seasonally, but there would also have been long periods of the year with low cover. In contrast, over the course of an entire year, polycultures would have maintained high cover due to temporal complementarity in seasonal abundance among ephemeral species and because perennials would have helped maintain some cover during times of year when ephemerals are rare. In other words, just as we found using only the 4 perennials, effects of species richness in longer-term field experiments would be strong, whereas in mesocosms, algal production would be mostly a function of species identity.

Indeed, our results are likely generalizable beyond intertidal algae, because the differences we found between field vs. mesocosm and short- vs. long-term experiments are predicted by theoretical arguments (11, 12) and parallel differences between separate field and mesocosm studies of the effects of algal species richness on ecosystem functioning by other authors. For example, Bruno *et al.* (7) found that algal species richness had little, if any, effect on biomass production in 2.5- to 5-week mesocosm experiments, whereas 2 longer-term field manipulations (>1 year) found strong effects (14, 15). However Bruno *et al.* (7, 8) also performed field experiments with the same species pool and still found weak or no

effect of species richness, so the distinction is not simply due to the field setting. Two major differences between the field experiments that found effects of species richness and those that did not are (i) the duration of the experiment and (ii) whether treatments were produced by assembling transplanted individuals vs. deleting species in situ on natural substrates. This second difference is also illustrated by the comparison of 2 experiments examining the effect of functional group diversity on invasion success. When Arenas *et al.* (31) manipulated functional group richness by assembling small monocultures of each functional group growing on natural rock pieces into various combinations, the species largely remained as separate monocultures, interacting weakly and failing to exhibit niche differentiation via canopy layering (31). No effect of richness on invasion by other seaweeds was observed in this experiment. Given additional time to interact, it is possible that understory species (which depleted bare space but not light) and canopy species (which depleted light but not bare space) might have acted to complementarily reduce overall resource levels and invasion success. Such “multivariate complementarity” (in the sense of ref. 10) was found in an experiment of similar duration in which high-diversity communities were created by using deletion experiments (32). These studies corroborate the conclusion that experiments finding strong effects of diversity are often those in which treatments develop by weeding communities on natural substrate, whereas assembly experiments often find stronger “identity” effects unless they are of long duration.

This is not to say that short-term assembly experiments cannot find strong diversity effects. Rather, the mechanisms underlying these effects likely include a more restricted set of possibilities than longer-term deletion experiments. Short-term assembly experiments usually measure growth or photosynthetic rate of transplanted individuals (individually or in aggregate), whereas longer-term and field experiments will also incorporate population-level phenomena, such as mortality rates, sexual recruitment, and clonal spread across a heterogeneous environment. Based on our lack of finding a diversity effect in short-term mesocosms, we conclude that mechanisms that should be expressed under these conditions, such as nutrient complementarity (10) or tradeoffs between photosynthetic rate in air and water (18, 19), are unlikely to be primary drivers of the species richness effect we observed in the field. The weak effects of diversity in short-term experiments in general suggest that mechanisms that cause enhanced per capita growth or photosynthetic rates may be relatively unimportant. Instead, the fact that the greatest effect of richness is found in longer-term field experiments suggests a stronger effect of diversity on population-level processes, including recruitment, survival, and growth of new individuals. Because of the time required for such processes to affect total algal cover, the effect of diversity on total cover may be weak at first and strengthen over time (5, 15).

Our results highlight the importance of recognizing the strengths and weaknesses of different approaches to understanding diversity–function relationships and explicitly considering what different experiments can and cannot tell us about the way diversity affects ecosystem function. Short-term mesocosm-based experiments can detect only a subset of potential mechanisms, and thus conclusions from these experiments that diversity has small or negligible effects must be treated with caution, despite the consistent results. We agree with Cardinale *et al.* (1) and suggest that this may have led to an underestimation of the strength of diversity effects in experiments performed to date on algal assemblages, most of which are short and have treatments produced by assembly of adult thalli (3). However, when mesocosm experiments are combined with longer-term, field-based studies, there is a synergism such that the mechanisms underlying diversity effects in field experiments become clearer. Rather than advocate exclusively for one design over another, we suggest that short-term assembly experiments and

longer-term experiments on natural substrate in combination might allow one to better elucidate the mechanisms that do and do not operate to link diversity and function.

Methods

Long-Term Field Experiment. We manipulated the number and identity of species in 72 1.5-m-diameter plots in the field for 3 years. We summarize our approach here and refer the reader to Stachowicz *et al.* (15) for more detail. Plots were blocked based on spatial proximity, then randomly assigned within each block to 1 of 6 treatments: a *Pelvetiopsis* monoculture, a *Mastocarpus* monoculture, an *Endocladia* monoculture, a *Cladophora* monoculture, a 4-species polyculture consisting of only the 4 target seaweed species, and an unmanipulated control. We created monocultures by removing all seaweeds except 1 target species and polycultures by removing all seaweeds except the 4 target species. To avoid confounding species richness and composition with disturbance or biomass removal, we removed additional biomass of target species from plots in which less initial weeding was required. In polycultures, this meant removing an amount of all 4 seaweed species to achieve a similar biomass removal to monocultures; extra biomass removal in polycultures was distributed among the 4 species in proportion to their abundance in the plot. As a result, neither biomass removed nor postweeding percent cover differed among treatments when algal cover was assessed immediately after the establishment of the treatments. Because of seaweed regrowth from holdfasts and recruitment of new individuals, we continued to weed plots throughout the experiment by removing nontarget species to maintain the treatments. Percent cover of all algae in plots was measured quarterly by using a 1-m-diameter hoop marked with 102 points distributed in a stratified-random manner. This left a 25-cm radial buffer on the boundary of each plot to minimize edge effects. In our analysis of the data we focused on the change in total seaweed cover (all species in a plot combined) from the beginning to the end of the 3-year experiment, although results are qualitatively similar if data from year 2 are used (15).

To compare the effect of species richness and composition on the change in algal cover we performed a 1-factor ANOVA (with blocking), with algal assemblage as the independent variable with 5 levels (4 monocultures and 1 polyculture). We partitioned the treatment sums of squares into an a priori contrast between the polyculture and the monoculture treatments (richness effect, $df = 1$) (24). The residual treatment effect is then due to variation among monocultures, and thus consists of a test of variation in cover due to species identity ($df = 3$). Significance of richness and identity effects was assessed by using the mean-square error as the denominator in the F test. To compare the relative effect size of richness and identity we calculated omega-squared (ω^2) for each (25).

Short-Term Field Experiment. We conducted short-term field experiments examining the effect of species richness (monoculture vs. polyculture) on the growth and survival of marked individual plants of 3 species: *Endocladia*, *Mastocarpus*, and *Pelvetiopsis*. We marked 5 individuals from each species present in each plot (monoculture and polyculture) by placing a small dab of epoxy on the substrate near the base of each individual and using die tools to embed a number into the epoxy. Initial distance from marked thalli to their nearest neighbor did not differ between monoculture and polyculture ($P > 0.5$, t test). For all species, we selected small individuals because many of these species have maximum sizes set by environmental constraints and because larger individuals sometimes coalesce and can be more difficult to track reliably. We were unable to measure the growth of individual plants of *Cladophora* because there were few small individuals that were sufficiently distinct to track, and it was impossible to reliably distinguish individuals in larger clumps.

Because we wanted individuals to experience natural substrate and environmental conditions, we could not remove plants for weighing during the experiment. Instead, we tracked survival and took several measures of size of each plant initially, after 1 month, and after 2 months. It was impossible to obtain estimates over longer time scales because of mounting mortality, loss of markers, and coalescence with other individuals. We measured survival by recording the number of plants that disappeared from one sampling period to the next; only individuals for which their marker could be relocated and the plant was clearly missing were considered "dead." Measures of growth tracked changes in area or volume of the thallus, although specific methods differed among species, depending on their morphology and growth habit (see *SI Text* for more detail). We used growth and survival data to estimate plot-level biomass change of each species in each individual plot in the field by calculating an integrated measure of plant performance. For *Pelvetiopsis*, we did this by multiplying the change in the number of apical tips of each

surviving individual by the individual survival rate. For *Mastocarpus*, we multiplied change in individual biomass (length \times number of fronds) by survival probability. Finally, for *Endocladia*, we multiplied change in turf area by survival probability. We examined whether standardized biomass production (% change) varied both among species and between monoculture and polyculture by using a 2-way ANOVA with plot species richness (monoculture vs. polyculture), species identity (*Endocladia*, *Pelvetiopsis*, *Mastocarpus*), and their interaction as factors and calculated metrics of effect size (ω^2) for each.

Mesocosm Experiment. We examined the effect of the same species from the long-term field experiment in monoculture and polyculture on the growth of individual species and total biomass change in an outdoor intertidal mesocosm. Assemblages were created by attaching each of the 4 intertidal seaweed species to 15 \times 15 cm squares of 1-cm plastic mesh with transparent fishing line, as has been done in other experiments (7). Each square was attached to the top of a concrete block that elevated it 20 cm above of the bottom of a 3.75-m-diameter outdoor pool. The pool was located \approx 200 m inland from our field plots and less than 100 m from the nearest shoreline. Filtered seawater flowed into the pool through a central high-pressure sprinkler that ensured adequate water movement and provided some mist during low tide to mimic the sea spray that plots typically encounter in the field. We performed 10 replicates of each monoculture and polyculture, and we repeated the entire experiment a second time and analyzed the experiment using the 2 trials as blocks in time. The initial biomass of algae in each assemblage was \approx 48 g wet weight, chosen to mimic the biomass per unit area found in our polyculture and control plots in the field. Polycultures started with 12 g wet weight of each species, interspersed within the square.

We collected the algae for this experiment from the shore near our field plots, using juvenile individuals to allow scope for vegetative growth during the experiment. *P. limitata* individuals and clumps of *C. columbiana* were scraped directly off the rocks, with minimal damage to holdfasts. To avoid damaging the less robust and horizontally spreading *E. muricata* and *M. papillatus*, respectively, we collected individuals of these 2 species found growing on the shells of mussels (*Mytilus californianus*). We chipped away most of the shell, leaving only the portion of shell holding the algae, and fastened it to the mesh square. Experimental duration (5 weeks) was chosen to be similar to that in published mesocosm studies (see review in ref. 3) to facilitate comparisons. At the end of the experiment, we subtracted the mass of the shell from both initial and final measurements. Wet weight for each species in each plot was recorded at the beginning, middle, and end of each 1-month experiment. Each individual seaweed was immersed in seawater for 1 h to ensure that it was fully hydrated, then weighed after excess water was removed by using a salad spinner.

We established an artificial tidal cycle in the pool that produced alternating periods of about 6.25 h of exposure and submersion to produce similar levels of desiccation in field and mesocosm experiments. "Tides" were caused by attaching a timer-controlled irrigation valve to a drain in the pool (see ref. 33 for details). We set the time of morning low tide in the pool to coincide with that in the field, advancing by \approx 1 h each day. More precise matching of the mixed-semidiurnal tidal cycle in the field was not feasible given the variation in the flow rate of the sea water system due to changing demand in other sections of the marine lab. We assessed how desiccation rates during "low tides" in our mesocosms compared with rates in field plots by measuring the change in mass of 2 \times 2 \times 1 cm blocks of agar gel mixed in a ratio of 1 L of hot water to 14 g of agar powder. We deployed cooled agar blocks on 10 bare concrete blocks and on bare spots within our field plots during 1 foggy/overcast day and 1 sunny day while the experiment was running. We weighed each block before and after exposure during low tide. To minimize the effects of spatial variation in horizontal flow rate and/or shading throughout the pool, all concrete blocks were placed in a new randomly generated configuration every 5 days.

Data on total biomass change of algae were analyzed as for the long-term field experiment, with treatment partitioned into 2 orthogonal contrasts representing tests of the effects of species richness and identity. We conducted a separate analysis of biomass change of individual species in polyculture and monocultures and analyzed these by using 2-way ANOVA as for the short-term field experiment. In both cases, we used ω^2 as a measure of effect size to compare the magnitude of the effect of species identity vs. species richness in the field vs. mesocosms.

ACKNOWLEDGMENTS. We thank many graduate and undergraduate students who contributed to the maintenance of the field experiment, but especially Ambre Chaudoin and Kirsten Sellheim for help in all phases of the field and mesocosm experiments. Kristin Aquilino, Kyle Edwards, and Kirsten Sellheim provided useful feedback on earlier drafts. Funding was provided by the National Science Foundation through Grants OCE 0351779 (to J.J.S.) and OCE 0351778 (to M.H.G.).

1. Cardinale BJ, et al. (2007) Impacts of plant diversity on biomass production increase through time due to species complementarity: A meta-analysis of 44 experiments. *Proc Natl Acad Sci USA* 104:18123–18128.
2. Hooper DU, et al. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol Monogr* 75:3–35.
3. Stachowicz JJ, Bruno JF, Duffy JE (2007) Consequences of biodiversity for marine communities and ecosystems. *Annu Rev Ecol Syst* 38:739–766.
4. Cardinale BJ, et al. (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989–992.
5. Tilman D, et al. (2001) Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845.
6. Tilman D, Knops JMH, Wedin D, Reich PB (2002) In *Biodiversity and Ecosystem Functioning. Synthesis and Perspectives*, eds Loreau M, Naeem S, Inchausti P (Oxford Univ Press, Oxford), pp 21–35.
7. Bruno JF, Boyer KE, Duffy JE, Lee SC, Kertesz JS (2005) Effects of macroalgal species identity and richness on primary production in benthic marine communities. *Ecol Lett* 8:1165–1174.
8. Bruno JF, et al. (2006) Partitioning effects of algal species identity and richness on benthic marine primary production. *Oikos* 115:170–178.
9. Kertesz JS (2006) The role of biodiversity in a fluctuating environment. M.S. thesis (San Francisco State Univ, San Francisco).
10. Bracken MES, Stachowicz JJ (2006) Seaweed diversity enhances nitrogen uptake via complementary use of nitrate and ammonium. *Ecology* 87:2397–2403.
11. Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proc Natl Acad Sci USA* 96:1463–1468.
12. Pacala SW, Tilman D (2001) In *The Functional Consequences of Biodiversity*, eds Kinzig AP, Pacala SW, Tilman D (Princeton Univ Press, Princeton), pp 151–166.
13. White LF, Shurin J (2007) Diversity effects on invasion vary with life history stage in marine macroalgae. *Oikos* 116:1193–1203.
14. Allison G (2004) The influence of species diversity and stress intensity on community resistance and resilience. *Ecol Monogr* 74:117–134.
15. Stachowicz JJ, Graham MH, Bracken MES, Szoboszlai AI (2008) Diversity increases cover and stability of rocky intertidal seaweed assemblages. *Ecology* 89:3008–3019.
16. Hughes AR, Stachowicz JJ (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc Natl Acad Sci USA* 101:8998–9002.
17. Moore TN, Fairweather PG (2006) Decay of multiple species of seagrass detritus is dominated by species identity, with an important influence of mixing litters. *Oikos* 114:329–337.
18. Bell EC (1993) Photosynthetic response to temperature and desiccation of the intertidal alga *Mastocarpus papillatus*. *Mar Biol* 117:337–346.
19. Johnson WS, Gigon A, Gulmon SL, Mooney HA (1974) Comparative photosynthetic capacities of intertidal algae under exposed and submerged conditions. *Ecology* 55:450–453.
20. Sousa WP (1984) Intertidal mosaics: Patch size, propagule availability, and spatially variable patterns of succession. *Ecology* 65:1918–1935.
21. Foster MS, de Vogelaere AP, Harrold C, Pearse JS, Thum AB (1988) Causes of spatial and temporal patterns in rocky intertidal communities of central and northern California. *Mem Calif Acad Sci* 9:1–45.
22. Foster MS, de Vogelaere AP, Oliver JS, Pearse JS, Harrold C (1991) In *Ecosystems of the World: Intertidal and Littoral Ecosystems*, eds Mathieson AC, Nienhuis PH (Elsevier, Amsterdam), pp 235–272.
23. Foster MS, Nigg EW, Kiguchi LM, Hardin DD, Pearse JS (2003) Temporal variation and succession in algal-dominated high-intertidal assemblage. *J Exp Mar Biol Ecol* 289:15–39.
24. Duffy JE, Richardson JP, France KE (2005) Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. *Ecol Lett* 8:301–309.
25. Graham MH, Edwards MS (2001) Statistical significance versus fit: Estimating the importance of individual factors in ecological analysis of variance. *Oikos* 93:505–513.
26. Stachowicz JJ, Fried H, Whitlatch RB, Osman RW (2002) Biodiversity, invasion resistance and marine ecosystem function: Reconciling pattern and process. *Ecology* 83:2575–2590.
27. Tilman D, Downing JA (1994) Biodiversity and stability in grasslands. *Nature* 367:363–365.
28. Reusch TBH, Ehlers A, Haemmerli A, Worm B (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc Natl Acad Sci USA* 102:2826–2831.
29. Brawley SH, Johnson LE (1991) Survival of fucooid embryos in the intertidal zone depends upon developmental stage and microhabitat. *J Phycol* 27:179–186.
30. Bertness MD, Leonard GH, Levine JM, Schmidt PR, Ingraham AO (1999) Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80:2711–2726.
31. Arenas F, Sanchez I, Hawkins SJ, Jenkins SR (2006) The invasibility of marine algal assemblages: Role of functional diversity and identity. *Ecology* 87:2851–2861.
32. Britton-Simmons KH (2006) Functional group diversity, resource preemption and the genesis of invasion resistance in a community of marine algae. *Oikos* 113:395–401.
33. Bracken MES (2004) Invertebrate-mediated nutrient loading increases growth of an intertidal macroalga. *J Phycol* 40:1032–1041.