

Functional consequences of realistic biodiversity changes in a marine ecosystem

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Declines in biodiversity have prompted concern over the consequences of species loss for the goods and services provided by natural ecosystems. However, relatively few studies have evaluated the functional consequences of realistic, nonrandom changes in biodiversity. Instead, most designs have used randomly selected assemblages from a local species pool to construct diversity gradients. It is therefore difficult, based on current evidence, to predict the functional consequences of realistic declines in biodiversity. In this study, we used tide pool microcosms to demonstrate that the effects of real-world changes in biodiversity may be very different from those of random diversity changes. Specifically, we measured the relationship between the diversity of a seaweed assemblage and its ability to use nitrogen, a key limiting nutrient in nearshore marine systems. We quantified nitrogen uptake using both experimental and model seaweed assemblages and found that natural increases in diversity resulted in enhanced rates of nitrogen use, whereas random diversity changes had no effect on nitrogen uptake. Our results suggest that understanding the real-world consequences of declining biodiversity will require addressing changes in species performance along natural diversity gradients and understanding the relationships between species' susceptibility to loss and their contributions to ecosystem functioning.

ammonium | diversity | ecosystem function | nitrogen | species identity

Motivated by global declines in biodiversity (1, 2), many studies have documented important links between the number of species in an ecosystem and the functioning (e.g., productivity, elemental cycling, and trophic transfer of energy) of that system (3, 4). Based on this body of work, we are beginning to understand how and why changes in diversity influence ecosystem functioning. However, most studies have used random assemblages of the species in a given ecosystem to construct gradients of diversity (5), and the few that have explicitly considered nonrandom extinction scenarios have relied primarily on modeling approaches to predict the consequences of diversity loss (refs. 6 and 7; but see refs. 8 and 9). After early experiments that used natural diversity gradients (10, 11) were criticized for containing "hidden treatments" (12) (i.e., the effects of species richness could not be separated from the effects of the factors driving diversity) most work evaluating the functional consequences of changing biodiversity has used random species assemblages. Whereas this approach is attractive from a theoretical perspective—it has provided insights into some mechanisms by which a more diverse assemblage can result in enhanced functioning (13, 14)—diversity does not change randomly. Instead, the number of species in a community is influenced by a variety of factors (e.g., physical stress, nutrient availability, consumer pressure, habitat destruction), which results in nonrandom diversity gradients in natural systems (5, 15).

For example, the diversity of seaweeds on rocky shorelines is determined by a combination of processes, including physical disturbance (16), herbivory (17–19), abiotic stress (20), and nutrient availability (18, 19, 21). Because seaweeds can account for the majority of primary productivity in temperate coastal

ecosystems (22), understanding the causes and consequences of variation in marine benthic algal diversity is essential to our knowledge of energy flow, nutrient fluxes, and productivity in nearshore marine systems. We focus, in particular, on seaweed diversity changes in high-intertidal pools, which are isolated from the ocean for extended periods during low tide. Tide pools provide an ideal model system for evaluating the effects of realistic biodiversity change on functioning, as several potential factors influencing tide pool seaweed diversity (e.g., herbivory, disturbance, nutrient availability) have been well-studied (17, 18, 21, 23). High-intertidal pools are, for the most part, closed systems, which enabled us to easily measure nutrient uptake by seaweeds under ecologically relevant conditions.

In this study, we used a diversity gradient based on our surveys of intertidal pools on the coast of California to evaluate the effects of realistic diversity changes on nutrient use by seaweed assemblages. We also quantified the relationship between diversity and nutrient uptake using randomly selected assemblages from the same suite of seaweed species. These measurements allowed us to explicitly compare the effects of realistic versus random biodiversity changes on nutrient fluxes in a marine ecosystem.

Results and Discussion

The composition of seaweed assemblages changed nonrandomly as diversity increased (Fig. 1). Specifically, in our surveys of 50 tide pools in the Bodega Marine Reserve in northern California, we found that low-diversity (1–2 species) tide pools were dominated by the filamentous green seaweed *Cladophora columbiana*. As diversity increased, *Cladophora* was supplemented by other seaweed species, so that high-diversity (six to seven species) pools typically contained all seven common macroalgal species. We also surveyed abundances of common invertebrates in many of the tide pools. We found that seaweed diversity was unrelated to either mussel or herbivore abundances ($F_{1,35} = 1.05$, $P = 0.314$ and $F_{1,35} = 0.06$, $P = 0.802$, respectively), suggesting that neither local-scale nutrient loading (which is closely related to mussel abundance per volume; ref. 21) nor herbivory were responsible for diversity patterns in northern California tide pools. Instead, it appears that diversity in these pools may be mediated primarily by disturbance, as all of the pools with five species or more were located in areas protected from heavy surf.

The capacity for seaweed productivity is often set by nutrient availability (18), and we therefore used these nonrandom diversity patterns in natural tide pools to test the effects of realistic

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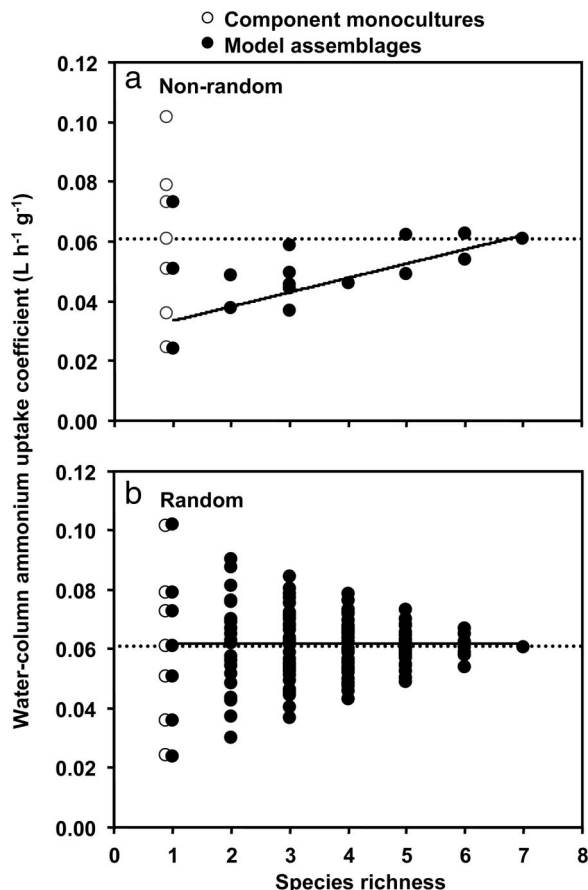
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which dominates low-diversity tide pools and uniquely harbors substantial abundances of invertebrates (25). These invertebrates contribute all of the nitrogen *Cladophora* requires, and *Cladophora* does not use water-column ammonium, despite its high total nitrogen demand. Furthermore, based on our measurements of water-column ammonium concentrations above *Cladophora* turfs, virtually none of the nitrogen excreted by invertebrate meiofauna within a *Cladophora* turf is exported into the adjacent tide pool water (25).

Determination of Random and Nonrandom Assemblages. Random assemblages were constructed by selecting from all possible combinations of the seven species at each richness level. Nonrandom assemblages were based on actual combinations of species found in natural tide pools at different levels of species richness (Fig. 1). Each nonrandom assemblage was weighted based on the frequency with which it occurred in surveys of 50 tide pools in the Bodega Marine Reserve. For example, when a tide pool contained one seaweed species, that species was *Cladophora* in 75.0% of the pools, *Prionitis* in 12.5% of the pools, and *Mastocarpus* in the remaining 12.5% of the pools. These percentages, and similar data for three-, six-, and seven-species combinations (SI Table 2), were used to weight which assemblages were randomly selected for ammonium uptake trials from the ones we observed in the field at each richness level. Compositions of the experimental assemblages are included in SI Table 3. We used richness levels of one (three independently selected assemblages), three (three assemblages), six (two assemblages), and seven (one assemblage containing all species) species to evaluate the effects of random versus nonrandom changes in diversity on ammonium uptake.

Ammonium Uptake. Measurements of nitrogen uptake were conducted on each of the seven species (monocultures) and on both random and nonrandom three-, six-, and seven-species assemblages as described above. Uptake was measured in 0.4-liter tide-pool microcosms, which were maintained at ambient seawater temperatures ($13.4 \pm 0.6^\circ\text{C}$). All trials were conducted outside, under natural and nonlimiting light conditions ($1682 \pm 81 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$), to ensure that light availability did not limit nitrogen uptake.

Nitrogen-depleted seawater and 24 g of algae were added to each microcosm. Our previous studies have shown that nitrogen dynamics in microcosms of this size are similar to those in natural tide pools (24, 25). Multispecies assemblages were composed of equal masses of each of the component species. Our field surveys and previous studies suggest that there is no relationship between algal diversity and biomass ($F_{1,49} = 0.5$, $P = 0.480$) and that tide pools typically support a given amount of algal biomass (g/liter), which is partitioned among the species present (21). Furthermore, we found no relationship among species richness (for $S > 1$) and species evenness ($F_{1,40} = 2.3$, $P = 0.131$), and assemblages with high evenness (i.e., biomass was equally partitioned among the component species) were found at all richness levels. We also found that model results were similar when species' relative abundances were changed slightly to reflect actual values in natural tide pools (see *Results and Discussion*). Thus, our replacement-series design is an ecologically relevant representation of tide pool community structure.

Seaweeds were supplied with initial ammonium concentrations of 2, 4, 8, 12, 20, 30, 40, and 60 $\mu\text{mol/liter}$ in 0.4 liters of seawater. These spanned the range of ammonium concentrations observed in natural tide pools; the average concentration in tide pools is $\approx 24 \mu\text{mol/liter}$ (21). Ammonium uptake was quantified in four replicate microcosms at each initial concentration, for a total of 32 replicates of each macroalgal assemblage. The water in the microcosms was not stirred, to simulate the still-water conditions experienced by seaweeds in tide pools. Water samples were collected at 0, 15, 30, and 45 min and analyzed for ammonium concentrations. The change in each micro-

cosm's ammonium concentration over the 45-min incubation period was divided by the dry tissue mass of the algae in that microcosm to calculate the biomass-specific uptake rate ($\mu\text{mol h}^{-1} \text{ g}^{-1}$) as a function of initial nitrogen concentration.

Analyses of Experimental Data. Because of still-water conditions, diffusion was the primary mechanism of ammonium uptake, uptake rates did not saturate, and relationships between uptake and concentration were linear (21, 24, 33). We used the slopes of the relationships between nitrogen uptake and concentration as coefficients ($\text{L h}^{-1} \text{ g}^{-1}$) describing the uptake capabilities of each of the monocultures and polycultures (24). These coefficients summarized the uptake across ammonium concentrations ranging from 2 to 60 $\mu\text{mol/liter}$, but we observed similar rankings of species and assemblages at all concentrations across the gradient. Based on the regression analysis for each species or assemblage, we calculated independent estimates of uptake coefficients for each of the 32 microcosms across the ammonium concentration gradient. To elucidate the mechanisms underlying the relationship between diversity and ammonium uptake, we evaluated the potential for overyielding in three-, six-, and seven-species assemblages by comparing polyculture uptake coefficients with coefficients predicted by the component monocultures (Table 1) (24). Each species' contribution to a predicted uptake coefficient was weighted by its proportion of the dry tissue mass in each polyculture. The variance associated with each monoculture uptake coefficient was calculated using regression analyses, and the predicted polyculture variance was calculated by pooling the variances of each component monoculture, weighted by their proportional biomass.

Model Assemblages. Our experimental analyses were limited to three replicates at each of three richness levels, which only allowed us to include a small number of the possible species combinations. This was especially evident for the random assemblages, where we were able to include only 9 of 123 possible combinations across the diversity gradient. To verify that our results were robust, we used a modeling approach to evaluate the same concepts using higher replication. Because the ammonium uptake coefficient of a tide pool seaweed assemblage is the average of the uptake coefficients of the constituent species (see *Results and Discussion*; ref. 24), we generated both random and realistic assemblages and used the uptake coefficients of the component monocultures (Table 1) to calculate the uptake coefficient of each assemblage. Realistic assemblages were generated using random sampling constrained to reflect the assemblages present in our field surveys (SI Table 2). Random assemblages were generated using random sampling without replacement. We generated 500 assemblages at each richness level, for a total of 3,500 assemblages in each diversity gradient. We found that ≈ 500 assemblages per level were necessary to include relatively equal proportions of all possible species assemblages. As in other models that have evaluated the consequences of biodiversity change (34), variance declined as richness increased (Fig. 3), so we used generalized linear models with gamma distributions and identity links (PROC GENMOD, SAS) to evaluate the relationships between richness and nitrogen uptake. For both random and realistic diversity-uptake relationships, results of these analyses were similar to those obtained using traditional regression approaches.

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