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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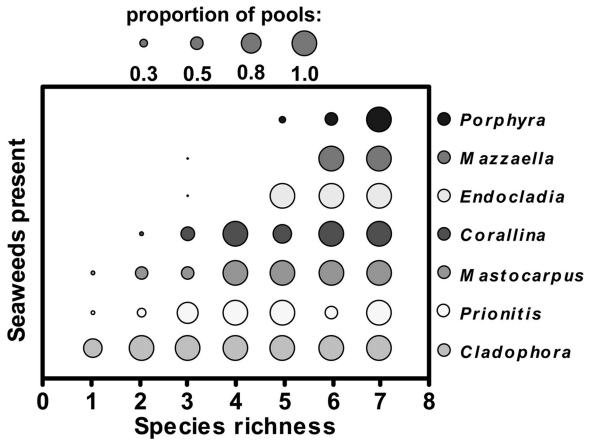

Fig. 1. Seaweed species composition in tide pools containing different numbers of macroalgal species. For each level of richness, the proportion of pools containing each species is indicated by the size of the dot. Changes in tide pool seaweed species composition were nonrandom; low-diversity (one to two species) tide pools contained predominately *Cladophora*, whereas all seven species were commonly found in high-diversity (six to seven species) pools.

changes in diversity on seaweeds' acquisition of water-column ammonium. Specifically, we created one-, three-, six-, and seven-species assemblages in tide pool microcosms which mimicked the diversity gradient we observed in the field. We compared the ammonium use of these realistic seaweed assemblages with uptake by assemblages constructed randomly from the same group of seven species and found striking differences in the effects of random and nonrandom changes in diversity (Fig. 2). Realistic increases in diversity—those based on our survey data—resulted in enhanced utilization of ammonium ($F_{1,283}$ = 71.4, $P < 0.001$). In contrast, we observed no relationship between diversity and ammonium uptake when the diversity gradient was composed of assemblages randomly selected from the local species pool ($F_{1,282}$ = 0.3, P = 0.619).

We also evaluated these relationships between diversity and nitrogen uptake using a modeling approach. Our models allowed us to increase replication, enhancing the statistical power of our analyses. For each level of richness (one to seven species), we randomly generated 500 assemblages, for a total of 3,500 assemblages. In the scenario where diversity changed randomly, species were randomly selected without replacement. In the scenario for realistic diversity changes, assemblages were constrained by the diversity patterns we observed in the field [see supporting information (SI) Table 2]. Because the ammonium uptake coefficient of an assemblage is the average of the uptake coefficients of the component species (see below; 24), we averaged the uptake values of the species in an assemblage (Table 1) to calculate the assemblage's uptake coefficient. Our model results were similar to those we obtained experimentally (Fig. 3). Realistic increases in species richness were associated with enhanced use of water-column ammonium (χ^2 = 2542.13, $P < 0.001$), but there was no relationship between diversity and ammonium uptake when assemblages comprised random sets of species (χ^2 = 1.86, P = 0.173). Furthermore, the uptake coefficients of the model assemblages were not different from those of the experimental assemblages for either realistic (P = 0.770) or random (P = 0.280) changes in diversity.

We also used the model to examine whether altering the relative abundances of species influenced our results. Our experiment and initial model both assumed equal abundances of species. Whereas this was a reasonable approximation of evenness patterns in the pools (see *Materials and Methods*), one

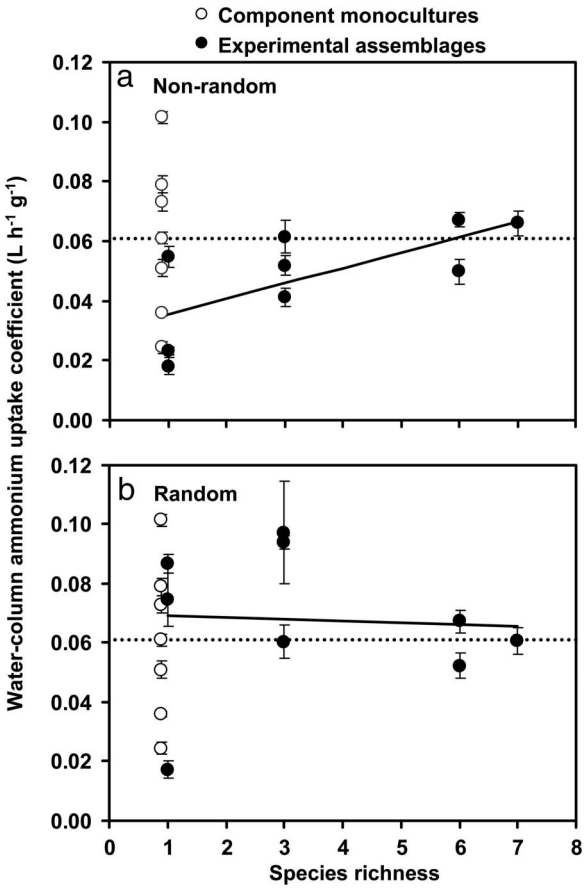

Fig. 2. Influences of random versus nonrandom diversity changes on the relationship between species richness and ammonium use by experimental assemblages of tide pool seaweeds. Values are ammonium uptake coefficients (L h^{-1} g^{-1}). Open circles show the monoculture uptake coefficients for all species, filled circles show the values for our experimental assemblages, and dotted horizontal lines indicate the weighted averages of all seven monocultures. (*a*) Realistic, nonrandom increases in species richness were associated with enhanced use of water-column ammonium ($F_{1,283}$ = 71.4, $P < 0.001$), and uptake of the single-species experimental assemblages was lower than the average of the seven monocultures (P = 0.014). (*b*) In contrast, there was no relationship between diversity and ammonium uptake when assemblages were composed of random sets of species ($F_{1,282}$ = 0.3, P = 0.619), and uptake values of experimental assemblages were never different from the average of the seven monocultures ($P > 0.239$). Error bars are ±1 standard error.

species (*Cladophora*) was relatively more abundant and one (*Mastocarpus papillatus*) was relatively less abundant than the others ($P < 0.001$ in both cases). We therefore reran the model using relative abundances that reflected those in natural tide pools and found results that were similar to our initial model for

Table 1. Water-column ammonium uptake by tide pool seaweeds. Values for uptake coefficients are means ± standard errors

Species	Uptake coefficients (L h^{-1} g^{-1})
Porphyra	0.102 ± 0.002
Mazzaella	0.079 ± 0.003
Endocladia	0.061 ± 0.002
Corallina	0.036 ± 0.001
Mastocarpus	0.051 ± 0.003
Prionitis	0.073 ± 0.003
Cladophora	0.024 ± 0.002

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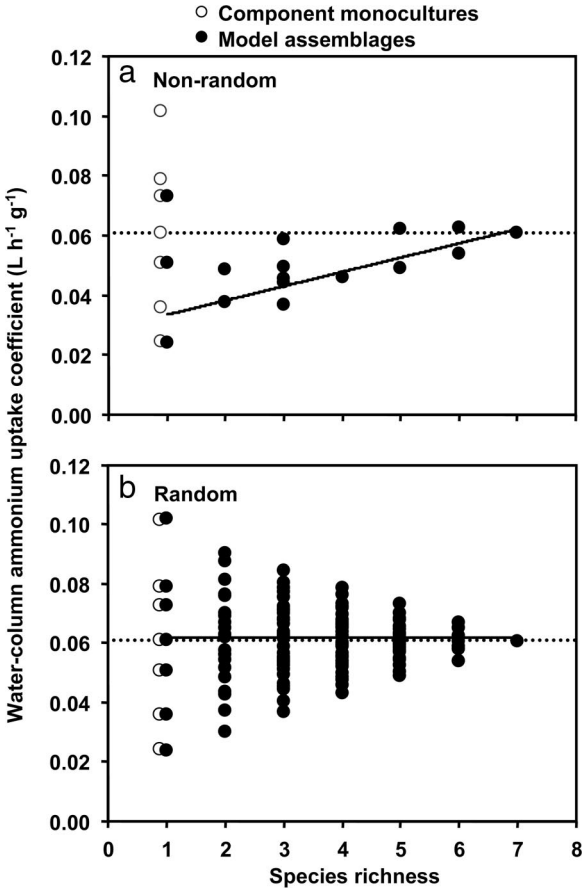

Fig. 3. Effects of random versus nonrandom diversity changes on the relationship between species richness and ammonium use by model assemblages of tide pool seaweeds. Values are ammonium uptake coefficients (liter h^{-1} g^{-1}). Open circles show the monoculture uptake coefficients for all species, filled circles show the values for the model assemblages, and dotted horizontal lines indicate the average uptake of the seven monocultures. Uptake coefficients of model assemblages were calculated as the average uptake of the constituent seaweed species. Results are based on 500 assemblages at each level of richness. (*a*) When assemblages were constrained based on field survey results, increases in species richness were associated with enhanced use of water-column ammonium ($\chi^2 = 2542.13$, $P < 0.001$). (*b*) In contrast, there was no relationship between diversity and ammonium uptake when assemblages were composed of random sets of species ($\chi^2 = 1.86$, $P = 0.173$).

both realistic ($\chi^2 = 2{,}757.57$, $P < 0.001$) and random ($\chi^2 = 3.06$, $P = 0.080$) diversity changes.

The increase in water-column ammonium use with increasing diversity in realistic seaweed assemblages arose because of the functional attributes of the seaweed species present in low- and high-diversity assemblages. Our previous work indicates that observed relationships between ammonium uptake and diversity are due to species identity effects (21, 24). A comparison of ammonium uptake by the three-, six-, and seven-species polycultures and their component monocultures indicated that the ammonium uptake ability of a polyculture was no different from that predicted by the component species ($t < 1.05$, df = 62, $P > 0.3$). The increase in ammonium use with realistic increases in diversity is therefore based on differences in species' abilities to use water-column ammonium. Specifically, *Cladophora*, which was the dominant species in low-diversity assemblages (Fig. 1), requires very little water-column ammonium (Table 1), as all of its nitrogen requirements are met by invertebrate meiofauna living within its filaments (25). In contrast, *Porphyra perforata*, which was only present in high-diversity (at least five species) pools (Fig. 1), has a very high demand for water-column nitrogen (Table 1) (24). However, the results we observed were not simply due to negligible nitrogen uptake by *Cladophora*. We ran a six-species model that lacked *Cladophora* and found that realistic increases in diversity were still associated with increased nitrogen use ($\chi^2 = 400.11$, $P < 0.001$), whereas random diversity changes had no effect on nitrogen uptake ($\chi^2 = 0.55$, $P = 0.457$). As diversity increases in natural tide pools, species with low usage of water-column ammonium (e.g., *Cladophora* and *Mastocarpus*) are supplemented by species with high uptake rates (e.g., *Porphyra* and *Mazzaella flaccida*), and the assemblage collectively acquires more ammonium, converging on the ammonium uptake coefficient predicted by the seven seaweed species in monoculture (Figs. 2*a* and 3*a*). When diversity gradients are based on assemblages randomly selected from the local species pool, a species with a high uptake coefficient is just as likely to be included in a low-diversity assemblage as a species with a low uptake coefficient. There is no relationship between diversity and ammonium uptake, and uptake coefficients are never different from the weighted average of the seven component monocultures ($P > 0.2$) (Figs. 2*b* and 3*b*).

Along with other recent experiments and models evaluating the consequences of realistic extinction scenarios (6–9, 15, 26–28), our study indicates that nonrandom changes in biodiversity can have very different effects on ecosystem functioning than random changes. Diversity changes (associated with local extinctions, invasions, or natural environmental variability) do not occur randomly in natural systems (5, 29). Instead, some species are more susceptible than others to environmental perturbations (6, 7), which results in nested patterns of species occurrences along a diversity gradient (Fig. 1) (15, 21). Our results also suggest that even when water-column nutrient use by a diverse seaweed assemblage is the simple weighted average of the component species' uptake abilities (i.e., species identity effects; 30), realistic changes in diversity can have profound consequences for seaweeds' use of limiting nutrients, at least over the short-term time scale of a tidal cycle. When a species' susceptibility to loss from an ecosystem is related to its functional characteristics, as it is in this case (species with the highest uptake coefficients were only present in more diverse assemblages), realistic declines in diversity will alter ecosystem functioning (12, 28, 31). A recent metaanalysis of biodiversity–ecosystem function experiments found that whereas the average performance of a multispecies assemblage is higher than predicted by the traits of the component species, diverse assemblages seldom out-perform the most productive species (13). Species identity effects, such as the effects of seaweed composition on ammonium uptake that we describe here, are therefore common mechanisms for diversity effects on ecosystem functioning. An understanding of how species performance relates to realistic diversity gradients (e.g., whether more productive species are more often found in more diverse assemblages; ref. 32) is essential to our ability to predict the consequences of declining biodiversity.

Materials and Methods

Experimental Organisms. Assemblages were composed of 7 intertidal seaweed species found in the Bodega Marine Reserve on the northern California coast, USA: *Cladophora columbiana*, *Corallina vancouveriensis*, *Endocladia muricata*, *Mastocarpus papillatus*, *Mazzaella flaccida*, *Porphyra perforata*, and *Prionitis lyallii*. These species collectively comprise >96% of seaweed biomass in surveyed tide pools (25), so our assemblages were reasonable representations of those found in nature. Algae were maintained in ambient running seawater (≈25 μmol NO_3^- and ≈5 μmol NH_4^+) for the brief period (<4 h) between collection and experimental uptake trials. Because we were interested in seaweeds' net utilization of water-column ammonium as our metric of ecosystem functioning, we did not disturb the invertebrate meiofauna associated with the seaweeds. This was particularly important for *Cladophora*,

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°C). All trials were conducted outside, under natural and nonlimiting light conditions (1682 $\pm$ 81 μmol photons m^{-2} 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 between 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 μmol/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 μmol/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 microcosm'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 (μmol h^{-1} 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 (L h^{-1} 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 μmol/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 $\approx$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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