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Realistic changes in seaweed biodiversity affect multiple ecosystem functions on a rocky shore

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Abstract. Given current threats to biodiversity, understanding the effects of diversity changes on the functions and services associated with intact ecosystems is of paramount importance. However, limited realism in most biodiversity studies makes it difficult to link the large and growing body of evidence for important functional consequences of biodiversity change to real-world losses of biodiversity. Here, we explored two methods of incorporating realism into biodiversity research: (1) the use of two-, five-, and eight-species assemblages that mimicked those that we observed in surveys of seaweed biodiversity patterns on a northern California (USA) rocky shore and the explicit comparison of those assemblages to random assemblages compiled from the same local species pool; and (2) the measurement of two fundamental ecosystem functions, nitrate uptake and photosynthesis, both of which contribute to growth of primary producers. Specifically, we measured nitrate uptake rates of seaweed assemblages as a function of initial nitrate concentrations and photosynthetic rates as a function of irradiance levels for both realistic and random assemblages of seaweeds. We only observed changes in ecosystem functioning along a richness gradient for realistic assemblages, and both maximum nitrate uptake rates (V_{\max}) and photosynthetic light use efficiency values ($\alpha_P = P_{\max}/I_K$) were higher in realistic assemblages than in random assemblages. Furthermore, the parameter affected by changes in richness depended on the function being measured. Both V_{\max} and α_P declined with increasing richness in nonrandom assemblages due to a combination of species identity effects (for V_{\max}) and overyielding effects (for both V_{\max} and α_P). In contrast, neither nitrate uptake efficiency values ($\alpha_N = V_{\max}/K_s$), nor maximum photosynthetic rates (P_{\max}) changed along the gradient in seaweed species richness. Furthermore, overyielding was only evident in realistic assemblages, and the parameters exhibiting overyielding, including V_{\max} , α_N , P_{\max} , and α_P , changed along a gradient in species richness. Our results suggest that in realistic assemblages of species (1) some functions may be maximized at low levels of species richness, and (2) it is not only diversity, per se, that is important for sustaining multiple ecosystem functions, but also the range of diversity values in an ecosystem.

Key words: *biodiversity; Bodega Marine Reserve, California, USA; ecosystem function; nonrandom; random; realistic; rocky intertidal; seaweed.*

INTRODUCTION

The plethora of recent experiments exploring the functional consequences of biodiversity changes have provided important insights into the mechanisms by which diversity affects ecosystem functions and services (Hooper et al. 2005, Cardinale et al. 2006, 2011). However, the vast majority of these studies have evaluated the effects of random diversity changes (Bracken et al. 2008, Selmants et al. 2012) on a single ecosystem function (Bracken and Stachowicz 2006, Hector and Bagchi 2007, Gamfeldt et al. 2008). This lack of realism has resulted in valid criticisms with respect to the conservation implications of research into

the effects of biodiversity on ecosystem functioning (Srivastava and Vellend 2005), which is particularly concerning because this body of work is motivated, at least in part, by the current global biodiversity crisis (Hooper et al. 2005). Making biodiversity research more relevant to the natural world, where changes in biodiversity are nonrandom (Selmants et al. 2012, Williams et al. 2013), therefore requires evaluating the effects of nonrandom diversity changes (those that mimic biodiversity gains and losses quantified in the field) on a variety of different functions (Duffy 2009, Naeem et al. 2012).

For example, the focus on a single response (usually biomass production) to experimental variation in biodiversity has led some researchers to conclude that ecosystem functioning typically saturates at a low level of richness (Schwartz et al. 2000, Cardinale et al. 2006). However, when multiple functions are considered together, higher richness is required for rates of overall

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functioning to be maximized (Hector and Bagchi 2007, Gamfeldt et al. 2008, Isbell et al. 2011, Maestre et al. 2012). For example, Duffy et al. (2003) considered a variety of functions co-occurring in seagrass ecosystems and found that different species were primarily responsible for mediating each function. Thus, a diverse community was required to maximize all functions simultaneously.

Researchers have also begun exploring the differences between the random-loss scenarios employed in most biodiversity experiments and more realistic, nonrandom changes in diversity that mimic patterns found in natural systems (Bracken et al. 2008, Selmants et al. 2012). For example, we found that in tide pools on rocky shores, realistic losses of seaweed species were associated with declines in ammonium uptake by seaweeds in those tide pools because species characterized by high rates of uptake were uniquely present in high-richness assemblages (Bracken et al. 2008). However, when a diversity gradient was generated by randomly selecting species from the local species pool, there was no relationship between uptake and seaweed species richness.

We expand on that previous work to evaluate the effects of nonrandom and random changes in seaweed diversity on two fundamental, but independent, aspects of ecosystem functioning: nitrate uptake and photosynthesis, both of which contribute to the production of biomass (Pedersen and Borum 1997, Loreau 1998, Bruno et al. 2005). We focused on seaweeds living on emergent intertidal substrata, not in tide pools, and therefore evaluated the uptake of nitrate, not ammonium, because ammonium accumulates in tide pools, but is scarce in well-mixed nearshore waters (Bracken and Nielsen 2004, Pfister 2007, Aquilino et al. 2009). By evaluating the effects of realistic biodiversity changes on the nitrate uptake and photosynthetic rates of seaweed assemblages, we combine two emerging ways in which realism is being incorporated into biodiversity research, the explicit comparison of realistic and random diversity changes and the simultaneous evaluation of multiple ecosystem functions.

MATERIALS AND METHODS

Field surveys and seaweed assemblages

Field surveys were conducted in the spring and summer of 2007 on wave-protected rocky intertidal reefs in the Bodega Marine Reserve, California, USA (38.32° N, 123.07° W; see Plate 1). Visual surveys were conducted using circular quadrats, 0.5 m in diameter, and all surveyed plots were located at the lower edge of the *Pelvetiopsis limitata* (Setchell) N. L. Gardner zone (1.7 ± 0.4 m above mean lower low water). We identified 21 unique seaweed assemblages, $n = 7$ each at three levels of seaweed species richness: two species, five species, and eight species. Because plots were all at the same tidal elevation and wave exposure, variation in seaweed richness was associated with local-scale effects.

Based on these surveys, we assembled algal communities that mimicked the species richness and relative abundance patterns on northern California rocky shores. All assemblages were comprised of 12 g (wet mass) of seaweeds, with biomass partitioned among component species to match their relative abundances in the field (Appendix). We also created 21 unique random assemblages of seaweeds. These assemblages were generated by randomly selecting, without replacement, from the entire set of seaweed species identified in our surveys to generate $n = 7$ each of two-species assemblages, five-species assemblages, and eight-species assemblages (Appendix). The relative abundance of each species in our random assemblages was based on the average abundance of that species in our field surveys. Thus, the identity of species in these assemblages was random, but their relative abundances matched field values. All seaweeds were collected from rocky intertidal reefs adjacent to the surveyed plots and maintained in ambient flowing seawater overnight after collection, which ensured full hydration before uptake and photosynthesis were evaluated in laboratory chambers.

Experimental chambers for measuring nitrate uptake and photosynthetic rates

We measured biomass-specific nitrate uptake and photosynthetic rates for each assemblage ($n = 21$ nonrandom and $n = 21$ random; Appendix) and for all component species present in any of the assemblages ($n = 17$ species; Table 1). Measurements were made in 16 2-L cylindrical chambers constructed of optically pure acrylic. The chambers were contained in a chilled, recirculating water jacket, also constructed of optically pure acrylic, which maintained chamber temperatures at $12.08 \pm 0.04^\circ\text{C}$. Each chamber was plumbed with a submersible pump (model LC-2-CP-MD; March Manufacturing, Glenville, Illinois, USA), which generated mean water velocities of 18.1 ± 3.1 cm/s (Pollak-Reibenwein and Jeoppen 2007) measured using an acoustic velocimeter (Vectrino, Nortek AS, Vangkroken, Norway). Mean turbulence intensities were $16.9 \pm 1.5\%$ of mean velocity, and maximum velocities reached 30.0 cm/s within individual chambers. High-velocity (>10 cm/s), turbulent flow conditions were necessary, as both nitrate uptake and photosynthesis rates of seaweeds are reduced at lower current speeds due to the formation of diffusion boundary layers (Hurd et al. 1996). At higher, more realistic current velocities, rates of nitrate uptake and photosynthesis typically show a saturation-type response to nitrate concentration and irradiance, respectively.

Nitrate uptake measurements

For nitrate uptake experiments, the water jacket around the experimental chambers was surrounded by four 129-cm, 54-W T5 HO light fixtures (model 1123; Current, Vista, California, USA) equipped with four SlimPac 10 000-K daylight and four 460-nm actinic

TABLE 1. Michaelis-Menten parameters for nitrate uptake and photosynthesis of seaweeds based on relationships between initial nitrate concentration ($\mu\text{mol/L}$) and biomass-specific nitrate uptake rates ($\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$) and between irradiance ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and biomass-specific rates of oxygen evolution ($\text{mg}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$).

Species	Nitrate uptake			Photosynthesis		
	V_{\max} ($\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$)	K_s ($\mu\text{mol/L}$)	α_N (V_{\max}/K_s)	P_{\max} ($\text{mg}/\text{h}/\text{g}$)	I_K ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	α_P (P_{\max}/I_K)
Chlorophyta						
<i>Cladophora columbiana</i>	6.3	3.3	1.91	3.5	439.9	0.008
<i>Ulva californica</i>	68.1	87.5	0.78	24.5	339.6	0.072
Rhodophyta						
<i>Callithamnion pikeanum</i>	1.7	5.2	0.32	14.9	171.6	0.087
<i>Corallina vancouveriensis</i>	0.1	12.7	0.01	5.0	855.4	0.006
<i>Endocladia muricata</i>	3.3	7.7	0.43	5.1	326.1	0.016
<i>Gelidium coulteri</i>	0.8	30.9	0.03	5.9	453.3	0.013
<i>Mastocarpus papillatus</i>	8.7	44.4	0.20	6.4	633.5	0.010
<i>Mazzaella flaccida</i>	8.9	27.7	0.32	7.0	501.6	0.014
<i>Microcladia borealis</i>	5.4	10.2	0.53	7.6	295.8	0.026
<i>Odonthalia floccosa</i>	7.3	16.7	0.44	7.8	368.3	0.021
<i>Plocamium violaceum</i>	1.2	1.5	0.77	7.8	122.9	0.064
<i>Polysiphonia hendryi</i>	2.2	3.9	0.57	10.9	282.9	0.038
<i>Pyropia perforata</i>	7.2	14.4	0.50	20.0	513.0	0.039
Ochrophyta						
<i>Analipus japonicus</i>	22.5	181.3	0.12	10.0	752.6	0.013
<i>Fucus gardneri</i>	2.7	9.0	0.30	8.8	294.3	0.030
<i>Leathesia difformis</i>	19.4	24.2	0.80	10.5	445.1	0.024
<i>Pelvetiopsis limitata</i>	4.7	17.1	0.28	6.0	740.4	0.008

Notes: Abbreviations are: V_{\max} , maximum nitrate uptake rate; K_s , initial concentration at $V_{\max}/2$; α_N , nitrate uptake efficiency; P_{\max} , maximum photosynthetic rate; I_K , irradiance level at $P_{\max}/2$; and α_P , photosynthetic light use efficiency. See <http://www.algaebase.org> for species authorities.

fluorescent bulbs. In addition, two similar 61-cm fixtures (model 1120) were placed at each end of the water jacket. These fixtures provided photosynthetically active radiation ($1873 \pm 40 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) within the chambers which was similar to that experienced by seaweeds in the field (Williams et al. 2013) and sufficient to saturate photosynthesis (see *Results*).

Uptake experiments were conducted in artificial seawater (33‰) prepared using Instant Ocean (Aquarium Systems, Mentor, Ohio, USA), spiked with a NaNO_3 stock solution. Initial nitrate concentrations in the chambers were $\sim 2, 15, 30,$ and $50 \mu\text{mol/L}$, which spanned the range of nitrate concentrations experienced by seaweeds on northern California rocky shores (~ 3 to $32 \mu\text{mol NO}_3^-/\text{L}$; Bracken et al. 2011). For each species and assemblage, we ran two replicates at each initial nitrate concentration. After allowing 10 min for equilibration, we collected 6 mL of water from each chamber every 15 min for 2 hr and analyzed nitrate concentrations using a QuickChem FIA 8500 autoanalyzer (Lachat Instruments, Loveland, Colorado, USA). Algae were dried to constant mass at 60°C to obtain the biomass of each species or assemblage. We then calculated the biomass-specific uptake rate of every assemblage and species ($\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$) as a function of the initial nitrate concentration ($\mu\text{mol/L}$).

Photosynthesis measurements

We measured net photosynthesis as the rate of oxygen evolution in random and nonrandom assemblages in the same chambers used for nitrogen uptake experiments,

though nitrate uptake and photosynthesis experiments were not run on the same seaweed individuals due to the need to reconfigure the chambers for measurement of nitrate and oxygen concentrations. For measurements of photosynthesis, the chambers were fitted with gas-tight lids into which temperature sensors and temperature-compensated oxygen optodes (FOXY R probes with MFPP-1000 LED; Ocean Optics, Dunedin, Florida, USA) were inserted through rubber septa. Photosynthesis was determined at five irradiance levels from 65 to $2200 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which spanned the range of light levels at intertidal sites in the Bodega Marine Reserve (i.e., <50 to $>1000 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; Wing and Patterson 1993). Light intensities were measured inside the seawater-filled chambers with a spherical sensor and meter (LI-193 and LI-250; LI-COR Biosciences, Lincoln, Nebraska, USA). Incubations were run for 10 min after allowing a 3-min acclimation period at each successively higher irradiance level. Oxygen saturation was avoided during incubations by sparging with N_2 gas to keep initial O_2 concentrations below 5 mg/L . Seawater pH remained below 8.5, so CO_2 was not limiting. The dissolved nitrate concentration in the ambient seawater was $\sim 22 \mu\text{mol/L}$ and was reduced by roughly half during long preliminary incubations of over one hour. As before, algae were dried to constant mass at 60°C to obtain the biomass of each species or assemblage. We then evaluated the biomass-specific photosynthetic rate of every assemblage and species ($\text{mg O}_2\cdot\text{h}^{-1}\cdot\text{g}^{-1}$) as a function of light intensity ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

*Parameters of nitrate uptake
and photosynthesis–irradiance relationships*

The nitrate uptake and photosynthesis–irradiance relationships were parameterized as rectangular hyperbolas. We used nonlinear curve-fitting techniques (PROC NLIN in SAS version 9.2; SAS Institute 2008) to determine the parameters of Michaelis-Menten relationships (Lobban and Harrison 1994) for each species and assemblage for rates of both nitrate uptake and oxygen evolution. For nitrate uptake rates,

$$V = (V_{\max} \times S)/(K_s + S) \quad (1)$$

where V ($\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$) was the uptake rate, V_{\max} ($\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$) was a parameter that defined the maximum uptake rate of the species or assemblage, S ($\mu\text{mol}/\text{L}$) was the initial nitrate concentration, and K_s ($\mu\text{mol}/\text{L}$) was a parameter that defined the initial concentration at $V_{\max}/2$. Similarly, for photosynthetic rates,

$$P = (P_{\max} \times I)/(I_K + I) \quad (2)$$

where P ($\text{mg}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$) was the rate of oxygen evolution, P_{\max} ($\text{mg}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$) was a parameter that defined the maximum rate of oxygen evolution of the species or assemblage, I ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was the irradiance level, and I_K ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was a parameter that defined the irradiance level at $P_{\max}/2$. Note that in this case, I_K does not represent saturating irradiance, but half-saturating irradiance. Michaelis-Menten fits were verified by comparing them to linear fits using the corrected Akaike information criterion (AIC_c; Burnham and Anderson 2002).

From the “typical” Michaelis-Menten parameters, we derived a third parameter, α , defined as

$$\alpha_N = V_{\max}/K_s \quad (3)$$

for nitrate uptake. This parameter is an index of nitrate uptake efficiency and represents the slope over the initial, non-saturating range of nitrate concentrations in the relationship between nitrate concentration and uptake (Harrison et al. 1989, Bracken et al. 2011). Similarly, for photosynthesis,

$$\alpha_P = P_{\max}/I_K \quad (4)$$

which is an index of light use efficiency and represents the initial slope of the photosynthesis–irradiance curve (Jassby and Platt 1976, Binzer and Middelboe 2005).

We focused our analyses on maximum nitrate uptake and photosynthetic rates (i.e., V_{\max} and P_{\max}), and nitrate uptake efficiency and light use efficiency values (i.e., α_N and α_P). V_{\max} describes maximum nitrate uptake rates of a species or assemblage, corresponding to nitrate use at high ambient nitrate concentrations, whereas α_N reflects nitrate use at low nitrate concentrations (Bracken et al. 2011). V_{\max} and α_N , therefore, represent different, but complementary aspects of that species’ or assemblage’s ability to use nitrate. Furthermore, whereas V_{\max} is often related to K_s (Harrison et al. 1989), α_N is not mathematically constrained by V_{\max} for

a species or assemblage ($P = 0.300$, $R^2 = 0.07$ for species in our data set; Table 1). Similarly, P_{\max} and α_P represent different, complementary aspects of a species’ or assemblage’s photosynthetic ability across gradients of light availability. However, α_P is often related to P_{\max} ($P < 0.001$, $R^2 = 0.54$ for species in our data set; Table 1), highlighting the fact that, in this system, species that are effective at photosynthesis at low light intensities are also characterized by high maximum photosynthetic rates.

We compared species performance in diverse assemblages to those predicted by the component species in those assemblages by calculating LR_{mean} as an indicator of non-transgressive overyielding as follows:

$$\text{LR}_{\text{mean}} = \ln(P/M) \quad (5)$$

where LR_{mean} referred to the log ratio of the parameters, P was the parameter (e.g., V_{\max} or α_P) of a given polyculture assemblage, and M was the predicted nitrate uptake or photosynthetic parameter of the assemblage based on the average of the component species’ parameters when measured in monoculture (Table 1), weighted by the mass of each of those species in the assemblage (Appendix; Cardinale et al. 2006, Brandt et al. 2012). LR_{mean} values > 0 were associated with greater performance of diverse assemblages than predicted by the component species and were therefore indicative of overyielding and complementarity. Note that LR_{mean} is equivalent to $\ln(D_T + 1)$ (Loreau 1998) and $\ln(D_{\text{mean}} + 1)$ (Bracken et al. 2011).

Statistical analyses

We analyzed our data using t tests and general linear models (PROC GLM in SAS version 9.2; SAS Institute 2008), with algal assemblages as experimental units. These experiments were designed to evaluate how nonrandom vs. random changes in seaweed diversity affected nitrate uptake and photosynthetic rates of seaweeds, and our GLMs evaluated a variety of response variables as functions of seaweed species richness. Response variables included parameters of the Michaelis-Menten relationship (i.e., V_{\max} , α_N , P_{\max} , and α_P), predicted parameter values of assemblages based on the weighted averages of the component species’ parameters, and LR_{mean} values for those parameters. All data were analyzed after verifying normal distributions and homogeneity of variances and transformed ($\ln[y+n]$, where $0 \leq n \leq 1$) as necessary to meet GLM assumptions.

We explored the role of species identity effects as factors explaining these relationships by examining how increases in richness were associated with the nitrate uptake and photosynthetic parameters predicted by the component species that made up those assemblages (i.e., variable M in Eq. 5). We also compared those parameters predicted based on species measured alone (i.e., in monoculture; Table 1) to parameters describing the performance of diverse assemblages composed of

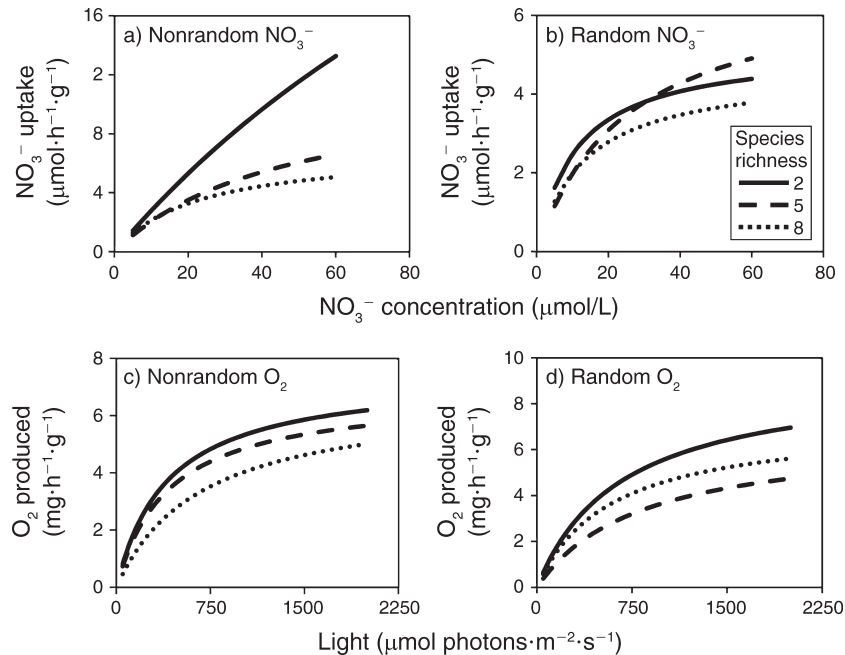


FIG. 1. Effects of nonrandom and random diversity changes on nitrate uptake and photosynthesis rates of seaweed assemblages. Curves are Michaelis-Menten fits of the relationship between (a, b) initial nitrate concentration and biomass-specific uptake and (c, d) light intensity and photosynthesis. Realistic, nonrandom increases in diversity were associated with declines in (a) nitrate uptake and (c) photosynthesis. In contrast, there was an idiosyncratic relationship between diversity and (b) nitrate uptake and (d) photosynthesis when assemblages were composed of random assemblages of species.

those species to assess how species richness effects (i.e., overyielding in nitrate uptake and photosynthetic parameters, LR_{mean}) changed with increases in seaweed richness.

To assess how ecosystem “multifunctionality” (sensu Hector and Bagchi 2007 as the collective value of multiple ecosystem functions considered together) changed along realistic and random diversity gradients, we averaged LR_{mean} values for nitrate uptake and photosynthetic parameters associated with each assemblage to generate average overyielding indices. These included an index of overyielding in nitrate uptake, calculated as the average LR_{mean} value for V_{max} and α_N ; an index of overyielding in photosynthesis, calculated as the average LR_{mean} value for P_{max} and α_P ; and an index combining both nitrate uptake and photosynthesis, calculated as the average LR_{mean} value for all 4 parameters (i.e., V_{max} , α_N , P_{max} , and α_P). Because α_N is associated with nitrate uptake at low ambient nitrate concentrations and V_{max} is associated with nitrate uptake at high concentrations, the collective index for nitrate uptake assessed overyielding across the range of available nitrate concentrations. Similarly, the collective index for photosynthesis assessed overyielding across light intensities.

RESULTS

For nonrandom assemblages of species, Michaelis-Menten fits to relationships between nitrate concentra-

tion and nitrate uptake highlighted a decline in nitrate uptake rates with increasing seaweed species richness; the five-species curve was nested within the two-species curve, and the eight-species curve was nested within the five-species curve (Fig. 1a). However, no relationship between richness and nitrate uptake was evident for random assemblages (Fig. 1b). Michaelis-Menten fits to relationships between irradiance and photosynthesis indicated a similar decline in photosynthetic rate with increasing richness for nonrandom seaweed assemblages (Fig. 1c), but were idiosyncratic between richness and photosynthetic rate for random assemblages (Fig. 1d).

To explore these patterns further, we evaluated relationships between Michaelis-Menten parameters and seaweed species richness in nonrandom and random assemblages. Maximum nitrate uptake rates (V_{max}) were 4.3 times higher in nonrandom assemblages than in random assemblages ($F_{1,38} = 19.0$, $P < 0.001$). Increases in richness were associated with declines in V_{max} values of nonrandom, realistic assemblages of seaweed species ($F_{1,19} = 15.0$, $P = 0.001$; Fig. 2a), but richness was unrelated to V_{max} values of nonrandom assemblages ($F_{1,19} < 0.1$, $P = 0.961$; Fig. 2b). In contrast, increases in richness were never associated with changes in the nitrate uptake efficiency (α_N) of seaweed assemblages, regardless of whether they were nonrandom ($F_{1,19} = 1.8$, $P = 0.200$; Fig. 2b) or random assemblages ($F_{1,19} = 2.7$, $P = 0.119$; Fig. 2b).

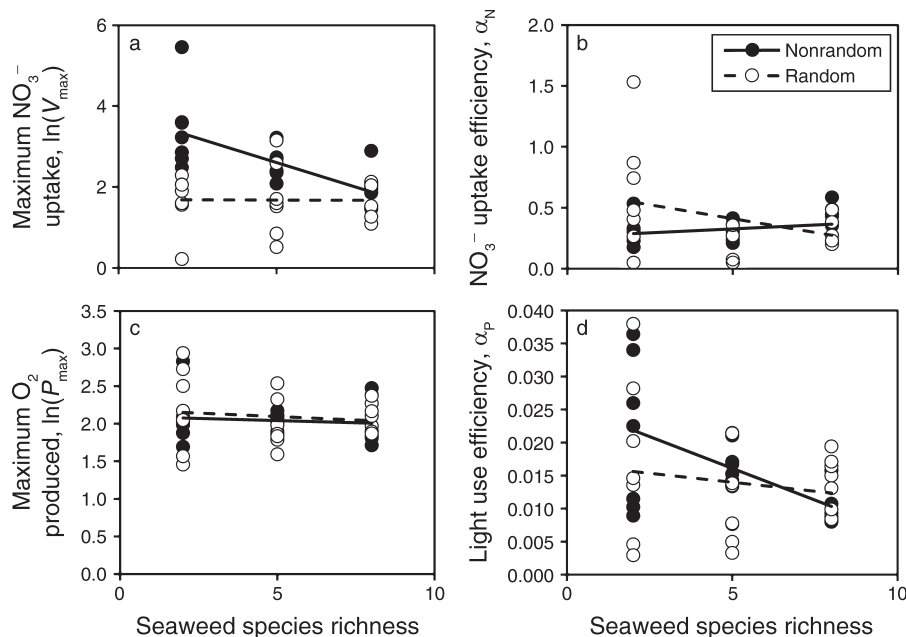


FIG. 2. Effects of nonrandom and random diversity changes on nitrate uptake and photosynthetic parameters. Values are parameters of Michaelis-Menten fits to relationships between (a, b) nitrate concentration and nitrate uptake rates and (c, d) irradiance and photosynthetic rates in seaweed assemblages (two-, five-, and eight-species assemblages). (a) Nonrandom increases in seaweed richness resulted in declines in maximum nitrate uptake rates (V_{\max} , originally measured in $\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$; $P=0.001$), but random changes in richness did not affect V_{\max} ($P=0.961$). (b) Neither nonrandom ($P=0.200$), nor random ($P=0.119$) increases in seaweed richness affected nitrate uptake efficiency ($\alpha_N = V_{\max}/K_s$, where K_s is measured in $\mu\text{mol/L}$). (c) Neither nonrandom ($P=0.637$), nor random ($P=0.603$) increases in richness affected maximum photosynthetic rates (P_{\max} , originally measured in $\text{mg}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$). (d) Nonrandom ($P=0.006$) but not random ($P=0.489$) increases in richness resulted in declines in light use efficiency ($\alpha_P = P_{\max}/I_K$, where I_K is measured in $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Solid symbols and solid lines indicate nonrandom assemblages, and open symbols and dashed lines indicate random assemblages.

Maximum photosynthetic rates (P_{\max}) were unrelated to either nonrandom ($F_{1,19} = 0.2$, $P = 0.637$; Fig. 2c) or random ($F_{1,19} = 0.3$, $P = 0.603$; Fig. 2c) increases in seaweed species richness. However, light use efficiency (α_P) values of nonrandom seaweed assemblages were 1.2 times higher than those in random assemblages ($F_{1,38} = 4.4$, $P = 0.043$), and α_P values of nonrandom assemblages declined with increases in seaweed species richness ($F_{1,19} = 9.8$, $P = 0.006$; Fig. 2d). Light use efficiency was unrelated to richness when assemblages were created randomly ($F_{1,19} = 0.5$, $P = 0.489$; Fig. 2d).

The decline in V_{\max} with realistic increases in richness was associated with both declines in V_{\max} values predicted by the component species in the seaweed assemblages ($F_{1,19} = 5.1$, $P = 0.036$; Fig. 3a) and declines in overyielding in V_{\max} ($F_{1,19} = 11.8$, $P = 0.003$; Fig. 3b). As the number of species in realistic seaweed assemblages increased, maximum nitrate rates of those assemblages, which initially exceeded those predicted by the species comprising them, declined so that they were no different from predicted values (Table 2). However, neither predicted V_{\max} values ($F_{1,19} = 0.3$, $P = 0.582$; Fig. 3a), nor overyielding in V_{\max} ($F_{1,19} = 0.7$, $P = 0.426$; Fig. 3b) declined with increasing richness when assemblages were randomly assembled from the local species pool. The decline in overyielding in V_{\max} with

nonrandom increases in richness was associated with positive overyielding at low richness (i.e., $\text{LR}_{\text{mean}} > 0$; for nonrandom, two-species assemblages, $t = 5.0$, $\text{df} = 6$, $P = 0.003$; Table 2), but no overyielding at intermediate (for nonrandom, five-species assemblages, $t = 2.2$, $\text{df} = 6$, $P = 0.066$; Table 2) or high levels of richness (for nonrandom, eight-species assemblages, one-sample $t = 0.4$, $\text{df} = 6$, $P = 0.674$; Table 2). Overyielding in α_N only occurred for nonrandom, eight-species assemblages ($t = 2.5$, $\text{df} = 6$, $P = 0.044$; Table 2). When we calculated the collective overyielding index for both nitrate uptake parameters, we found that overyielding coefficients were positive for both two-species ($t = 6.8$, $\text{df} = 6$, $P < 0.001$) and five-species ($t = 3.4$, $\text{df} = 6$, $P = 0.014$) nonrandom assemblages, but not for eight-species nonrandom assemblages ($t = 1.9$, $\text{df} = 6$, $P = 0.109$; Table 2).

The decline in light use efficiency (α_P) with realistic increases in richness was not paralleled by a similar decline in predicted α_P values ($F_{1,19} = 0.9$, $P = 0.356$; Fig. 4a), so that decline was not attributable to species identity effects. However, overyielding in light use efficiency ($\text{LR}_{\text{mean}} \alpha_P$) declined with nonrandom increases in richness ($F_{1,19} = 5.7$, $P = 0.027$; Fig. 4b). Neither predicted α_P values ($F_{1,19} = 0.4$, $P = 0.522$; Fig. 4a), nor overyielding in α_P ($F_{1,19} < 0.1$, $P = 0.903$; Fig. 4b) changed with random increases in seaweed species

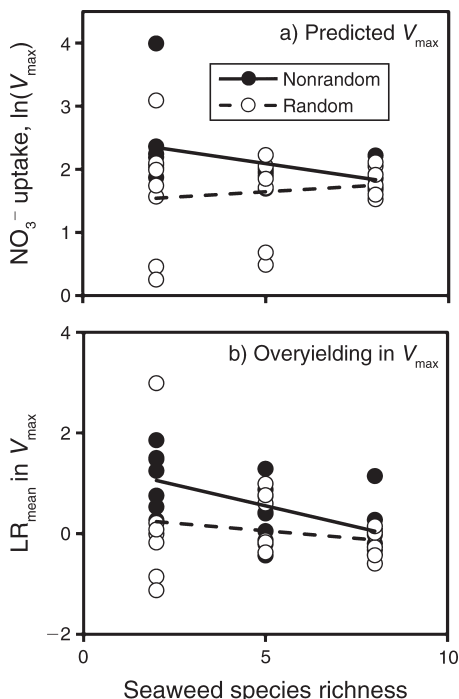


FIG. 3. Effects of species identity and overyielding effects on relationships between diversity change and nitrate uptake rates. (a) Based on uptake parameters of component species, nonrandom increases in seaweed richness were predicted to result in declines in maximum nitrate uptake rates (V_{max} ; $P = 0.036$), but random changes in richness were not predicted to affect V_{max} ($P = 0.582$). (b) Nonrandom increases in seaweed species richness were associated with declines in overyielding (log ratio, LR_{mean} ; see Eq. 5) in V_{max} ($P = 0.003$), but random changes in richness had no effect on overyielding in V_{max} ($P = 0.426$). Solid symbols and solid lines indicate nonrandom assemblages, and open symbols and dashed lines indicate random assemblages.

richness. The decline in LR_{mean} α_P with increasing richness was associated with no overyielding at low richness (for nonrandom, two-species assemblages, $t = 1.2$, $df = 6$, $P = 0.267$; Table 2), slight overyielding at

intermediate richness (for nonrandom, five-species assemblages, one-sample $t = 2.5$, $df = 6$, $P = 0.046$; Table 2) and underyielding (i.e., assemblages with α_P values lower than predicted based on component species) at high richness (for nonrandom, eight-species assemblages, $t = 3.0$, $df = 6$, $P = 0.023$; Table 2). Thus, eight-species assemblages were characterized by light use efficiency values lower than those predicted by the species comprising those assemblages. Overyielding in P_{max} only occurred for nonrandom, five-species assemblages ($t = 3.2$, $df = 6$, $P = 0.020$; Table 2) When we calculated the collective overyielding index for both photosynthetic parameters, we found that overyielding coefficients were positive only for five-species nonrandom assemblages ($t = 3.4$, $df = 6$, $P = 0.015$). For both two-species ($t = 0.7$, $df = 6$, $P = 0.484$) and five-species ($t = 1.0$, $df = 6$, $P = 0.362$) nonrandom assemblages, collective overyielding indices were not different from zero (Table 2).

When both nitrate uptake and photosynthesis were considered together (i.e., LR_{mean} values for all four parameters were averaged), overyielding was apparent for nonrandom two-species ($t = 4.1$, $df = 6$, $P = 0.007$) and five-species ($t = 3.8$, $df = 6$, $P = 0.009$) assemblages, but not for eight-species assemblages ($t = 0.9$, $df = 6$, $P = 0.387$; Table 2). Overyielding never occurred for any random assemblages ($P > 0.13$ in all cases).

DISCUSSION

By deliberately comparing the effects of random and nonrandom biodiversity changes on the rates of two fundamental ecosystem functions (i.e., nitrate uptake and photosynthetic rates), we have demonstrated, consistent with previous work (Bracken et al. 2008, Selman et al. 2012), that realistic, nonrandom changes in diversity can result in very different effects on functioning than random changes. This study also contributes unique insights to our understanding of both realistic biodiversity changes and multiple ecosystem functions, including our findings that (1) overyielding only occurred in realistic, nonrandom

TABLE 2. Overyielding coefficients (LR_{mean} values; means \pm SE) for parameters of Michaelis-Menten relationships for nitrate uptake and photosynthetic rates of seaweed assemblages.

Assemblage and species richness	Nitrate uptake			Photosynthesis	
	V_{max}	α_N	V_{max} and α_N	P_{max}	α_P
Nonrandom assemblages					
2 species	1.09 \pm 0.22**	0.15 \pm 0.22	0.62 \pm 0.09**	-0.08 \pm 0.08	0.29 \pm 0.24
5 species	0.48 \pm 0.21	0.10 \pm 0.07	0.29 \pm 0.08**	0.13 \pm 0.04*	0.28 \pm 0.11*
8 species	0.09 \pm 0.20	0.33 \pm 0.13*	0.21 \pm 0.11	0.07 \pm 0.11	-0.26 \pm 0.08*
Random assemblages					
2 species	0.16 \pm 0.51	0.87 \pm 0.47	0.51 \pm 0.47	0.18 \pm 0.24	<0.01 \pm 0.33
5 species	0.21 \pm 0.21	0.09 \pm 0.13	0.15 \pm 0.15	0.07 \pm 0.14	-0.27 \pm 0.30
8 species	-0.20 \pm 0.10	0.06 \pm 0.21	0.06 \pm 0.21	0.15 \pm 0.19	0.05 \pm 0.13

Notes: Values in columns with more than one parameter (V_{max} and α_N ; P_{max} and α_P ; V_{max} , α_N , P_{max} , and α_N) are the average LR_{mean} values, calculated for each assemblage, then averaged across all replicate assemblages. Statistical comparisons are based on one-sample t tests comparing the average across all assemblages to 0.

* $P < 0.05$; ** $P < 0.01$.

assemblages, (2) ecosystem functions can be maximized at low levels of species richness, and (3) the nitrate uptake and photosynthetic parameters exhibiting overyielding changed along a gradient in species richness.

Nonrandom assemblages achieved higher maximum nitrate uptake rates and greater light use efficiencies than random assemblages. Furthermore, whereas we found no effect of random diversity increases on either nitrate uptake or photosynthesis (Fig. 2), nonrandom increases in seaweed richness (i.e., from two to five to eight species) were associated with declines in maximum nitrate uptake rates (V_{max} ; Fig. 2a) and light use efficiency values (α_p ; Fig. 2d). This finding that realistic species losses resulted in increases in resource use and primary production contrasts sharply with consensus perspectives based on random diversity changes, which suggest that increases in producer richness typically result in enhanced primary production and resource assimilation rates (Cardinale et al. 2011).

For both maximum nitrate uptake and light use efficiency, we observed higher rates of ecosystem functioning at low (two-species) to intermediate (five-species) levels of richness in nonrandom seaweed assemblages, with performance in high-richness (eight-species) assemblages either equivalent to (nitrate uptake) or lower than (light use efficiency) predicted by the component species. In contrast, we never observed either overyielding or underyielding for any parameter in random assemblages of species (Table 2). Functioning of random assemblages did not change along the diversity gradient and was never different than predicted by the component species that comprised those assemblages. In contrast with our previous work in tide pools, where we found that ammonium uptake by seaweed assemblages could always be predicted based on the species comprising those assemblages (Bracken et al. 2008), here we found evidence for complementarity in nitrate uptake (i.e., $LR_{mean} > 0$ for V_{max} in two-species assemblages and for α_N in eight-species assemblages; Table 2) and show that on emergent substrata, both species identity effects and complementarity determine

TABLE 2. Extended.

Photosynthesis	Uptake and photosynthesis
P_{max} and α_p	V_{max} , α_N , P_{max} , and α_p
0.10 ± 0.14	$0.37 \pm 0.09^{**}$
$0.21 \pm 0.06^*$	$0.25 \pm 0.07^{**}$
-0.10 ± 0.10	0.06 ± 0.06
0.09 ± 0.27	0.30 ± 0.18
-0.10 ± 0.19	0.02 ± 0.14
0.10 ± 0.06	0.02 ± 0.10

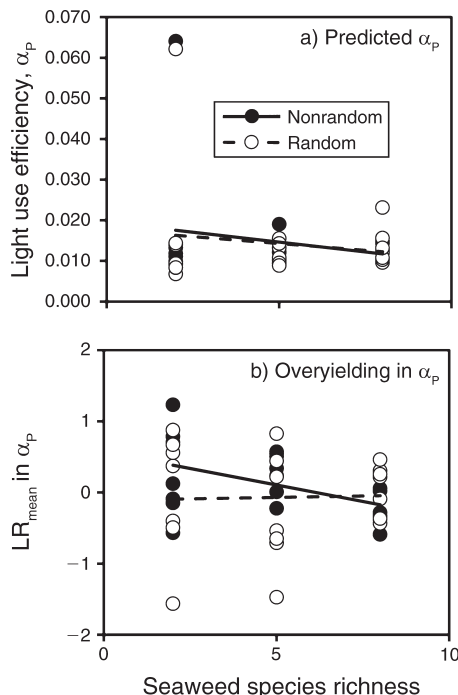


FIG. 4. Effects of species identity and overyielding effects on relationships between diversity change and light use efficiency. (a) Neither nonrandom ($P = 0.356$), nor random ($P = 0.522$) increases in richness affected predicted light use efficiency (α_p) values. (b) Nonrandom increases in richness were associated with declines in overyielding (LR_{mean}) in α_p ($P = 0.027$), but random changes in richness had no effect on overyielding in α_p ($P = 0.903$). Solid symbols and solid lines indicate nonrandom assemblages, and open symbols and dashed lines indicate random assemblages.

uptake of nitrate in a turbulent flow environment (Fig. 3).

Furthermore, by considering the responses of multiple functions along a diversity gradient, we found that different functions responded in different ways to realistic changes in diversity. Maximum nitrate uptake rates (V_{max}) of nonrandom assemblages, but not their nitrate uptake efficiencies (α_N), changed along the diversity gradient. In contrast, the maximum rate of photosynthesis (P_{max}) did not change with diversity, but light use efficiency (α_p) declined with increasing richness. In natural systems, multiple ecosystem functions respond simultaneously to changes in diversity, yet most biodiversity studies to date have focused on only a single response variable (Hector and Bagchi 2007, Gamfeldt et al. 2008). As studies consider multiple functions, understanding which aspects of those functions respond to changes in diversity (e.g., resource uptake efficiency, maximum resource uptake rates), as we highlight here, is critical. Many studies that measure the functional consequences of changes in biodiversity constrain the response variables they measure within a relatively limited range of environmental conditions. For example, the failure of some studies to find a relationship between



PLATE 1. Field surveys and experimental chambers used to examine the effects of change in seaweed diversity on nitrate uptake and photosynthetic rates: (left) intertidal surveys; (right) chambers arrayed in the chilled water jacket. Photo credits: (left) Bruce Nyden; (right) M. E. S. Bracken.

seaweed diversity and primary production may be because oxygen evolution rates are often measured at saturating irradiance levels (e.g., Bruno et al. 2006, Noël et al. 2010) instead of across the range of irradiance levels typical of many marine habitats.

In this intertidal ecosystem, ecosystem functioning tended to be maximized at low levels of species richness and decline as richness increased, a finding that parallels our previous work in the same system that spanned a broader range of environmental conditions (i.e., tidal elevations and herbivore abundances) and species richness values (up to 13 species per plot), where we found a negative relationship between nitrate uptake and richness after accounting for the effects of tide height and herbivores (Bracken et al. 2011). These results represent an important exception to most studies, which report a positive relationship between diversity and ecosystem functioning (Hooper et al. 2005, Cardinale et al. 2006, 2011), and likely reflect realistic changes in species composition along the richness gradient. For example, higher species diversity was likely associated with higher morphological diversity, resulting in increased self-shading in more diverse assemblages. Nonrandom, eight-species assemblages contained a disproportionate abundance of optically dense species such as *Corallina vancouveriensis* Yendo (Appendix). *Corallina* is characterized by very low light use efficiency ($\alpha_P = 0.006$; Table 1), and therefore, has the potential to reduce the light use efficiency of the assemblage.

Similarly, as species richness increased in nonrandom assemblages, the proportion of species characterized by higher V_{max} values declined, as reflected in the decline in predicted V_{max} values (Fig. 3). In nonrandom, two-species assemblages, a species with higher V_{max} but lower α_N (e.g., *Mastocarpus papillatus* [C. Agardh] Kützling) was typically paired with a species with lower V_{max} but higher α_N (e.g., *Cladophora columbiana* F. S. Collins, *Endocladia muricata* [Endlicher] J. Agardh, or *Pelvetiopsis limitata* [Setchell] N. L. Gardner; Table 1). These pairings should increase the V_{max} values of those assemblages because, as nitrate concentrations declined in our experimental chambers, and the species with higher V_{max} but lower α_N values became less effective at nitrate uptake, the species with lower V_{max} but higher α_N would become more effective at nitrate uptake. As richness increased in nonrandom assemblages, the proportion of *Mastocarpus* in those assemblages declined (Appendix), paralleled by a decline in the potential for complementarity via this mechanism.

Overyielding in one of the four parameters (V_{max} and α_N for NO_3^- , and P_{max} and α_P for O_2) occurred across the entire nonrandom gradient from two to eight species (i.e., V_{max} for two-species assemblages, P_{max} and α_P for five-species assemblages, and α_N for eight-species assemblages; Table 2), but no parameter independently exhibited overyielding across that entire gradient. When we averaged overyielding indices for all four parameters, we found evidence for overyielding, on average, in both

two-species and five-species nonrandom assemblages, and no evidence for underyielding in eight-species assemblages. Based on our field surveys of mid-shore, wave-protected areas in the Bodega Marine Reserve (Williams et al. 2013), 75% of 40 surveyed plots contain five or fewer species, and every plot contains at least two species, so, on average and conservatively, overyielding should occur in the majority of plots. Furthermore, 95% of plots contain eight or fewer species, so there is the potential for overyielding in at least one parameter to occur in virtually every plot in the field given the typical range of irradiance levels and nitrate concentrations at our study site (Wing and Patterson 1993, Bracken et al. 2011). However, if we had only considered one parameter (i.e., V_{\max} , α_N , P_{\max} , or α_P alone), we would have predicted overyielding in between 3% and 28% of plots in the field. By simultaneously considering multiple functions (i.e., nitrate uptake across a range of nitrate concentrations and photosynthetic rates across a range of light intensities), we were able to predict overyielding in the majority of plots surveyed.

Previous work that has considered multiple functions has highlighted the fact that higher richness is necessary to maintain multiple functions simultaneously because different species often affect different functions (Duffy et al. 2003, Hector and Bagchi 2007, Gamfeldt et al. 2008, Zavaleta et al. 2010). This work, based largely on random assemblages of species, predicts that multivariate complementarity (sensu Bracken and Stachowicz 2006) should be maximized in the most diverse assemblages. In contrast, we found, on average, a decline in overyielding with increasing richness. Furthermore, we show that, within this rocky shore ecosystem, patches of differing diversity are necessary in order to maximize levels of a variety of parameters related to nitrate uptake and primary production, especially in a temporally variable light and nutrient environment such as the one we consider here (Wing and Patterson 1993, Bracken et al. 2011).

Understanding the functional consequences of realistic biodiversity changes in real-world systems requires moving beyond the random-species loss scenarios that have characterized most biodiversity research (see also Solan et al. 2004, Zavaleta and Hulvey 2004, Bracken et al. 2008, Selmants et al. 2012) and evaluating not just one, but many ecosystem functions (Hector and Bagchi 2007, Gamfeldt et al. 2008, Zavaleta et al. 2010). Here, we have shown how unique insights can be gained by simultaneously addressing realistic diversity gradients and multiple functions. In particular, not only were the effects of nonrandom diversity changes different from the effects of random changes (random diversity changes never affected any ecosystem function or parameter estimate we considered), but average rates of ecosystem functioning were maximized at lower levels of species richness. Different parameters responded differently across gradients in both diversity (i.e., richness ranging from two to eight species) and availability of nitrate and

light (i.e., ambient available nitrate levels ranging from ~ 3 to $32 \mu\text{mol NO}_3^-/\text{L}$ and irradiance levels ranging from <50 to $>1000 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and overyielding in different functions occurred at different points along these gradients.

In this contribution, in addition to supporting earlier findings that realistic changes in biodiversity can have very different effects on functioning than random changes (Zavaleta and Hulvey 2004, Bracken et al. 2008, Isbell et al. 2011, Maestre et al. 2012, Selmants et al. 2012), we have provided empirical evidence that the effects of changing biodiversity are more apparent across multiple functions than for a single function. Furthermore, we highlight a novel attribute that emerged when we measured the responses of multiple functional parameters to realistic changes in biodiversity; different parameters were maximized at different levels of diversity. This finding implies that it is not only diversity that is important for ecosystem functioning (e.g., previous work suggesting that higher diversity results in enhanced functioning), but also the range of diversity values in an ecosystem. Our approaches and results illustrate the complex consequences of changing biodiversity in natural ecosystems (Duffy 2009).

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SUPPLEMENTAL MATERIAL

Appendix

Tables showing richness and biomass (grams wet tissue mass) of species in each experimental assemblage ([Ecological Archives E094-177-A1](#)).