

## Partitioning the effects of algal species identity and richness on benthic marine primary production

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Influential research in terrestrial habitats indicates that several ecosystem processes are related to plant biodiversity, yet these links remain poorly studied in marine ecosystems. We conducted one field and one mesocosm experiment to quantify the relative effects of macroalgal species identity and richness on primary production in coral reef macroalgal communities off the north coast of Jamaica. We measured production as the net accumulation of algal biomass in the absence of consumers and as photosynthetic rate using oxygen probes in sealed aquaria. We used two recently developed techniques to attribute deviations in expected relative yield to components associated with species identity or diversity and then to further partition diversity effects into mechanistic components based on dominance, trait-dependent complementarity, and trait-independent complementarity. Our results indicate that algal identity had far greater effects on absolute net growth and photosynthesis than richness. The most diverse mixture of macroalgae did not outperform the most productive monoculture or the average monoculture in either measure of primary production (i.e. we did not find evidence of either transgressive or non-transgressive overyielding). Trait-independent complementarity effects were positive but dominance and trait-dependent complementarity were both negative and became stronger when richness was increased. Thus the potentially positive influence of species interactions and niche partitioning on production were negated by dominance and other negative selection effects. These results demonstrate that the counteracting influence of component effects can diminish the net richness effects on production. This could explain frequently observed weak net richness effects in other aquatic and terrestrial systems and suggests that life history tradeoffs greatly reduce the potential for ecologically relevant plant biodiversity effects on ecosystem properties.

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The search for links between biodiversity and ecosystem processes has become a major theme in community ecology (Tilman 1999, Duffy 2002). An initial and still

widely addressed question is whether plant diversity is positively related to primary production (Loreau et al. 2001, Hooper et al. 2005). Several greenhouse and field

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experiments performed over the last ten years suggest that it can be (Tilman et al. 1996, Hooper and Vitousek 1997, Tilman et al. 2001, Fridley 2002), and the diversity–productivity hypothesis has reached near paradigm status (Naeem 2002, Hooper et al. 2005). However, the hypothesis remains untested in most terrestrial and freshwater systems and was only recently tested in the ocean (Bruno et al. 2005). Therefore, we cannot generalize far beyond the model grassland communities in which most relevant experiments have been performed. Furthermore, nearly all tests have measured net plant biomass accumulation as an indirect measure of primary production (Loreau et al. 2001). Plant biomass is an important community property and in some systems is likely positively related to gross productivity, especially when both parameters are driven by nutrient availability (Smith 1979). But because resource limitation effectively restricts primary production in dense plant assemblages (Harper 1977), in many cases the two are unrelated or even negatively related. For example, on coral reefs intense herbivory can remove most algal biomass yet maximize primary productivity (Carpenter 1986).

There is also still substantial confusion over what constitutes a diversity effect and how to untangle effects on ecosystem properties based solely on species diversity from the usually much stronger effects of species identity and composition. Furthermore, we are only beginning to develop analytical tools and experimental designs capable of deciphering the signals produced by the ecological and evolutionary mechanisms that ultimately drive “diversity effects” (Fox 2005). For instance, Fox (2005) recently devised a technique to partition the effect of diversity on production into three components: trait dependent complementarity, trait independent complementarity, and dominance. The strength of these components appear to be context dependent and in some cases opposite in sign (Loreau and Hector 2001, Bruno et al. 2005), explaining observed weak net diversity effects in some systems (Hector et al. 1999). If we can identify the biotic and abiotic factors that control the direction and magnitude of these components then we may be able to predict the conditions under which species diversity will have strong and ecologically relevant effects.

To advance our understanding of biodiversity effects on ecosystem properties we need experimental tests of the diversity–productivity hypothesis in other systems designed to quantify the relative effects of species composition and richness and to partition richness effects into components based on dominance and complementarity. Here we present two experimental tests of the general hypothesis that coral reef macroalgal species diversity can influence ecosystem functioning. We measured the effects of macroalgal identity and richness on primary production in a field experiment as

net biomass accumulation (over ten days) in the absence of herbivores and as net photosynthetic rate (over 20 min) in an outdoor mesocosm experiment. We also applied the techniques developed by Loreau and Hector (2001) and recently modified by Fox (2005) to our Jamaica growth measurements and the results of a recently published study with similar data (Bruno et al. 2005). This allowed us to partition the effects of dominance, trait-dependent complementarity and trait-independent complementarity on production. This analysis provides insight into the underlying mechanisms (including facilitation, competition, and niche partitioning) that are measured as net diversity effects.

There are several potential niche-based mechanisms through which macroalgal composition and diversity could influence benthic marine ecosystem processes. For example, primary productivity could be greater in diverse assemblages via resource partitioning (Loreau 1998). Or, environmental tolerances could vary among algal species, which could maximize productivity across environmental gradients or seasons (Yachi and Loreau 1999, Loreau et al. 2003, Cardinale et al. 2004). Facilitation could also enhance primary production via associational defenses when the presence of unpalatable species reduces the consumption of undefended neighbors (Hay 1986). Likewise, in physiologically stressful environments such as in rocky intertidal habitats, canopy-forming algae reduce thermal stress and facilitate neighboring species, thereby enhancing productivity and community resilience (Dayton 1971, Allison 2004). Finally, algal diversity and structural heterogeneity are generally positively related, which could reduce diffusive boundary layers and maximize metabolite delivery and thus productivity (Cardinale et al. 2002).

## Material and methods

Field and laboratory experiments were performed in Discovery Bay, Jamaica and at the Discovery Bay Marine Laboratory. Both experiments included replicated monocultures ( $n = 10$ ), a high-diversity ‘complete’ mixture containing all macroalgal species (10 in the field experiment and 12 in the aquaria experiment), and intermediate levels of richness in which the species composition in each replicate was independently determined by random draws from the experimental species pool. This design allows rigorous detection of transgressive and non-transgressive overyielding and the clear partitioning of the relative effects of species identity and richness (Loreau 1998). Non-transgressive overyielding occurs when mixture performance is greater than that of the average monoculture while transgressive overyielding requires mixture yield to exceed the most productive monoculture (Fridley 2001). Species selections, biomass, and richness levels in the field and aquaria experiments

were based on natural patterns of macroalgal community structure on Jamaican reefs. We quantified macroalgal community structure as macroalgal richness and biomass using SCUBA at three sites within Discovery Bay (1 m depth) and three nearby fore reef sites (5–8 m depth) in February 2004. We removed all macroalgae in ten randomly placed 25 × 25 cm quadrats (the same size as the working area of the algal communities in both experiments) at each site and identified (based on Littler and Littler 2000) and weighed each species in the laboratory.

Experimental algae were collected from the back reef of Discovery Bay, Jamaica (1–2 m depth). We created experimental fleshy macroalgae communities of varying composition and richness by attaching macroalgae to 32 × 32 cm black plastic Vexar screens. Multi-species screens contained at least two thalli of each species and individual and species positions on screens were determined randomly. Small grazers (e.g. amphipods and isopods) and other animals attached to the algae were removed by placing the algal screens in a bath of dilute pesticide (Sevin<sup>®</sup>, Bayer, 1-naphthyl methylcarbamate) with several rinses to remove pesticide residue (Carpenter 1986). Wet weights were determined after removing excess water from the algae using a salad spinner. Starting wet mass was the same across treatments (60 g in the field experiment and 120 g in the aquaria photosynthesis measurements, i.e. we used a replacement design).

### Field experiment

The field experiment measured net algal biomass accumulation over 10 days (beginning on 12 January, 2004) and included 14 treatments ( $n=10$ ): 10 monocultures and 4 multi-species mixtures of 2, 4, 8 and 10 species. Compared to similar experiments in terrestrial plant systems this is a relatively short duration, however, the macroalgae we used are far more ephemeral than perennial forbs: they grow and senesce faster, and rates of compositional turnover are much higher. Accurately measuring algal growth over long periods (i.e. months to years) in the field is very difficult because natural senescence and physical disturbance remove algal tissue and currents transport it away from the experimental plots.

Algal screens were placed in 2 × 1 × 0.5 m herbivore exclusion cages made of PVC frames and monofilament netting with 5 mm holes (1 replicate of each of the 14 treatments cage<sup>-1</sup>; an unreplicated block design in which cage is the blocking factor). Cages were suspended above a sand flat in the back reef (3 m depth), the algal screens were 1 m below the surface) at least 10 m from the nearest potential source populations of small grazers (which inhabit macroalgae and seagrass beds). A pilot study found that the combination of submerging the screens in a pesticide bath and isolating the cages on a

sand flat effectively excluded small grazers (that could fit through the holes in the cage netting) from the algal screens.

### Photosynthesis measurements

As a second and complementary measure of primary production we measured the effects of macroalgal identity and richness on net photosynthesis as the rate of daytime oxygen production. Photosynthesis measurements were made outdoors during February 2004 in 34-l sealed glass aquaria containing filtered seawater. Algae were collected and attached to screens 24 h prior to each run. Photosynthesis measurements were taken in filtered (100 µm) seawater with a Foxy fiber optic oxygen sensor (Ocean Optics). Each measurement was taken until oxygen concentration increased by 10% (usually 15–25 min). Each day (excluding cloudy days) we ran a single replicate of each of the 14 treatments (12 monocultures and polycultures of 6 and 12 species), plus one control with no algae in the aquaria in random order. Light, temperature, salinity and flow inside the aquaria were controlled such that they were very similar to field conditions in the Discovery Bay back reef. Photon flux density inside the aquaria was monitored with a LI-COR underwater quantum sensor and was regulated by shading with screens so that light was usually between 800 and 1000 µmol photons s<sup>-1</sup> m<sup>-2</sup> during photosynthesis measurements (mean light across all 140 runs was 904.2 µmol photons s<sup>-1</sup> m<sup>-2</sup> ± 10.2, mean ± 1 SE, min = 691, max = 1259). Temperature was monitored with StowAway<sup>®</sup> Tidbit<sup>®</sup> waterproof temperature loggers and varied <1°C during any given run. Temperature ranged from 27.8 to 30.8°C over all 140 runs and averaged 29.05°C ± 0.05. Water movement inside the aquaria was generated with two 120 GPH powerheads and was measured with a SonTek Acoustic Doppler Velocimeter. Horizontal free stream flow ranged from 0.1 to 26.7 cm s<sup>-1</sup> and averaged 5.5 ± 0.4 cm s<sup>-1</sup>, conditions similar to those in the Discovery Bay back reef (Genovese and Witman 2004) and other shallow back reef environments (Carpenter and Williams 1993).

### Analyses

We used one factor ANOVA in the fit model platform of JMP (version 5.0.1, SAS Institute) and LSM planned comparisons to test the independent effects of species identity and richness on log-transformed growth and photosynthetic rates. ANOVAs that included the complete mixtures (but not the intermediate richness treatments) and all monoculture levels were performed for both experiments. We then compared the polyculture values with the values from all pooled monocultures using planned comparisons; this is the test of the

richness effect and effectively tests for evidence of non-transgressive overyielding. The sums of squares calculated in this comparison can then be subtracted from the original model SS, leaving the residual SS which is attributable to variance among the monocultures and is thus a test of the species identity effect (Bruno et al. 2005, Duffy et al. 2005). Both effects were tested using the error MS from the original ANOVA as the denominator in the F-test. We also calculated the magnitude of effects ( $\omega^2$ , the relative contribution expressed as the percentage of the total variance) for the richness and identity factors (Kirk 1995, Graham and Edwards 2001).

We used Fox's tripartite equations (Fox 2005) to partition the macroalgal richness effect into its three component effects: dominance, trait-dependent complementarity, and trait-independent complementarity. This technique attributes differences in observed functioning of a diverse mixture relative to expected functioning based on monoculture performances of each species. The tripartite partitioning could only be applied to the growth data because we could not measure species-specific photosynthetic rates in polycultures. This partitioning is a modification of the widely used additive partition technique of Loreau and Hector (2001). Trait-independent complementarity is analogous to Loreau and Hector's (2001) complementarity effect, which when positive indicates that overall community growth in polycultures is increased presumably due to facilitation or niche partitioning (Loreau and Hector 2001). Trait-independent complementarity is positive when total yield of mixtures is greater than expected based on monoculture performances, the yield of a species in mixture does not depend on its yield in monoculture, and an increase in yield of any species does not come at the expense of other species.

The second component, trait-dependent complementarity, is also positive when species perform better in mixture than expected, but not at the expense of other species. Trait-dependent complementarity differs from trait-independent complementarity because it quantifies how much species' yields in mixture deviate from expectations based on monoculture performances. Fox (2005) also calls this "one-way" complementarity because it quantifies how much the benefit of growing in mixture is realized only by species with certain traits (e.g. high monoculture yield). The dominance effect measures the degree to which species perform better than expected in mixture (based on monoculture growth) at the expense of other species. A positive dominance effect indicates that the species that were the most productive in monoculture also dominate mixtures. We used linear regression analysis to determine whether macroalgal richness affected the magnitude or sign of each component. Values were square root transformed, with the

original sign preserved following Loreau and Hector (2001) and Fox (2005).

To expand the generality of the tripartite partitioning of macroalgal richness effects, we also analyzed the results of a recently published similar study of the effects of benthic macroalgal species identity and richness on primary production in North Carolina, USA (Bruno et al. 2005). The study included five independent experiments (three in outdoor mesocosms and two field experiments) of similar design to our Jamaica field experiment: each included four to nine algal species in monoculture and a complete mixture of all species ( $n = 10$  replicates treatment<sup>-1</sup>). Three of the five experiments also included intermediate levels of species richness (Bruno et al. 2005).

## Results

We found a total of 86 species in the 60 sampled 25 × 25 cm quadrats. Species richness ranged from 5 to 24, averaged 13.6 species quadrat<sup>-1</sup> ± 0.6 (mean ± 1 SE,  $n = 60$  pooled across all 6 sites), and varied significantly among sites (Fig. 1A; ANOVA:  $F = 13.46$ ,  $df = 5, 54$ ,  $P < 0.0001$ ). Macroalgal wet mass also varied substantially (Fig. 1B) and was significantly positively related to richness (Fig. 1C; linear regression analysis:  $F = 8.49$ ,  $df = 1, 58$ ,  $P = 0.005$ , adj.  $r^2 = 0.11$ ). In most plots, 75% of the total wet algal mass was made up by two or three species, and 494 of 818 (60%) species occurrences in the 60 sampled field plots were 1.0 g or less (or 1.6% the mass of the average plot).

The block factor (cage in the field experiment and day in the photosynthesis experiment) was not significant in either experiment (cage  $P = 0.84$ , day  $P = 0.41$ ) and was not included in final analyses. In both experiments ANOVA indicated that the richness effect was not statistically significant while the species identity effect was highly significant and explained nearly 50% of the variance in both analyses (Table 1). The net photosynthetic rate of one species (*Ceramium nitens*) was significantly greater than the 12 species mixture ( $P = 0.01$ ) (Fig. 2). The relative yields of eight of the ten species in the field experiment were positive, but mixture yield was significantly greater than monoculture yield for only two of those eight species (Table 2). There was no evidence of transgressive overyielding (i.e. complete mixture yield was never greater than all monocultures), and although production appeared to increase slightly with richness in the field experiment, this trend was not statistically significant ( $P = 0.089$ ; from ANOVA). The fastest growing species were red (e.g. *Acanthophora spicifera*) and green (e.g. *Chaetomorpha linum*) algae (Fig. 2). In the photosynthesis experiment mean temperature and light did not vary significantly among cages or treatments. Mean temperature had a slight effect on

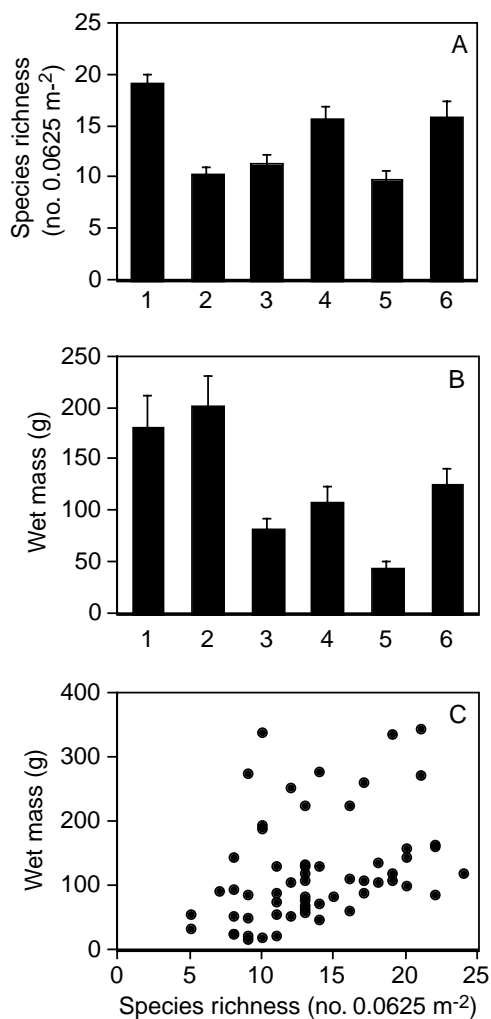


Fig. 1. Natural patterns of macroalgal (A) richness and (B) wet mass at six sites in Jamaica. Sites 1–3 are back reef sites and 4–6 are fore reef sites. Values are means  $\pm$  1 SE ( $n = 10$ ). (C) The relationship between macroalgal wet mass and richness within  $25 \times 25$  m quadrats (data are pooled from six sampled sites,  $n = 60$ ).

photosynthetic rate ( $P = 0.01$ , adj.  $r^2 = 0.04$ ), but mean light did not ( $P = 0.66$ , adj.  $r^2 = 0.006$ ). The effect size of each of the three partitioned diversity components was

essentially zero in the low richness treatments and increased with increasing richness (Fig. 3); dominance and trait-dependent complementarity becoming more negative and trait-independent complementarity becoming more strongly positive.

## Discussion

We found that macroalgal biomass was positively related to macroalgal species richness in the field in Jamaica. Such relationships between diversity and abundance, or biomass, are common in a variety of systems and taxa (Huston 1994, Schlöpfer and Schmid 1999, Emmerson and Huxham 2002), and are at least concordant with the hypothesis that plant richness can affect primary production. However, these static relationships may also reflect a response of diversity to variation in conditions among plots (Huston 1994, Lawton et al. 1998, Thompson et al. 2005). The primary analyses of our two experiments (Table 1) indicate that photosynthetic and growth rates were strongly influenced by species identity but not by richness. However, additional analyses suggest that there were subtle richness effects. For example, combined relative yields were 13% greater in mixture than in monoculture ( $t = 2.209$ ,  $df = 194$ ,  $P = 0.028$ ) and the relative yield total was  $1.179 \pm 0.08$ . Additionally, in both experiments, production of some multi-species treatments appeared to be slightly greater than that of the average monoculture (Fig. 2), although not significantly so. Overall, these results are very similar to those from a series of experiments in benthic macroalgal communities in North Carolina (Bruno et al. 2005) and are also concordant with recent studies in terrestrial plant (Fridley 2002, Hector et al. 2002, Hooper and Dukes 2004, Hooper et al. 2005), freshwater plant and microbial (Engelhardt and Ritchie 2002, Downing 2005), and salt marsh communities (Callaway et al. 2003). The overall lesson of these primary producer biodiversity experiments is that richness effects are subtle and compositional effects are much stronger. However, earlier work, generally in nutrient poor terrestrial grasslands, indicated that plant and functional group richness did have ecologically significant effects on

Table 1. Results of statistical analysis of the two experiments testing the effects of macroalgal species richness and identity on primary production. Richness and identity effects were tested with orthogonal planned contrasts. Effect sizes were estimated as  $\omega^2$  (Kirk 1995).

	SS	df	F	P	$\omega^2$
Field experiment					
Whole model	37712.1	10	11.7	0.0001	0.500
Richness effect	516.7	1	1.6	0.2070	0.003
Identity effect	37195.4	9	12.8	0.0001	0.497
Photosynthesis experiment					
Whole model	$2.40 \times 10^{-4}$	12	9.7	0.0001	0.445
Richness effect	$5.79 \times 10^{-6}$	1	2.8	0.0970	0.008
Identity effect	$2.44 \times 10^{-4}$	11	10.3	0.0001	0.437

Table 2. Production of each species in complete mixture (10 species) and monoculture in the field experiment. Values are mean change in biomass (%)  $\pm$  1 SE (n=10). Relative yield (RY)=normalized (to the starting biomass in mixture) performance in mixture/performance in monoculture. Statistical values are from 2-tailed t-test comparisons of production for each species in mixture and monoculture treatments. Significant values in boldface.

Species	Mixture	Monoculture	RY	t	P
<i>Acanthophora spicifera</i>	91.4 $\pm$ 26.1	61.7 $\pm$ 4.0	1.2	1.18	0.25
<i>Caulerpa racemosa</i>	45.7 $\pm$ 20.2	51.8 $\pm$ 12.4	1.0	-0.26	0.79
<i>Ceramium nitens</i>	49.4 $\pm$ 12.8	38.8 $\pm$ 12.9	1.1	0.59	0.56
<i>Chaetomorpha linum</i>	101.4 $\pm$ 22.1	64.9 $\pm$ 16.2	1.2	1.33	0.20
<i>Galaxaura rugosa</i>	33.4 $\pm$ 4.0	31.8 $\pm$ 1.6	1.0	0.35	0.73
<i>Gelidiella acerosa</i>	46.4 $\pm$ 4.5	27.4 $\pm$ 4.6	1.1	2.94	<b>0.008</b>
<i>Gracilaria damaecornis</i>	16.9 $\pm$ 4.9	24.5 $\pm$ 3.5	0.9	-1.22	0.24
<i>Halimeda opuntia</i>	33.0 $\pm$ 10.0	28.5 $\pm$ 6.3	1.0	0.38	0.71
<i>Laurencia poiteaui</i>	15.0 $\pm$ 23.7	-35.2 $\pm$ 6.6	1.8	2.04	<b>0.05</b>
<i>Sargassum polyceratum</i>	3.4 $\pm$ 33.5	-28.1 $\pm$ 13.8	1.4	0.904	0.38

primary production (Hooper and Vitousek 1997, Tilman et al. 2001). A challenge for future biodiversity research will be to resolve such contradictory results and identify the factors such as nutrient concentration and herbivore

abundance that influence the relative importance of plant richness effects (Mulder et al. 1999, Fridley 2002).

For logistical reasons we did not incorporate several important functional groups including encrusting and

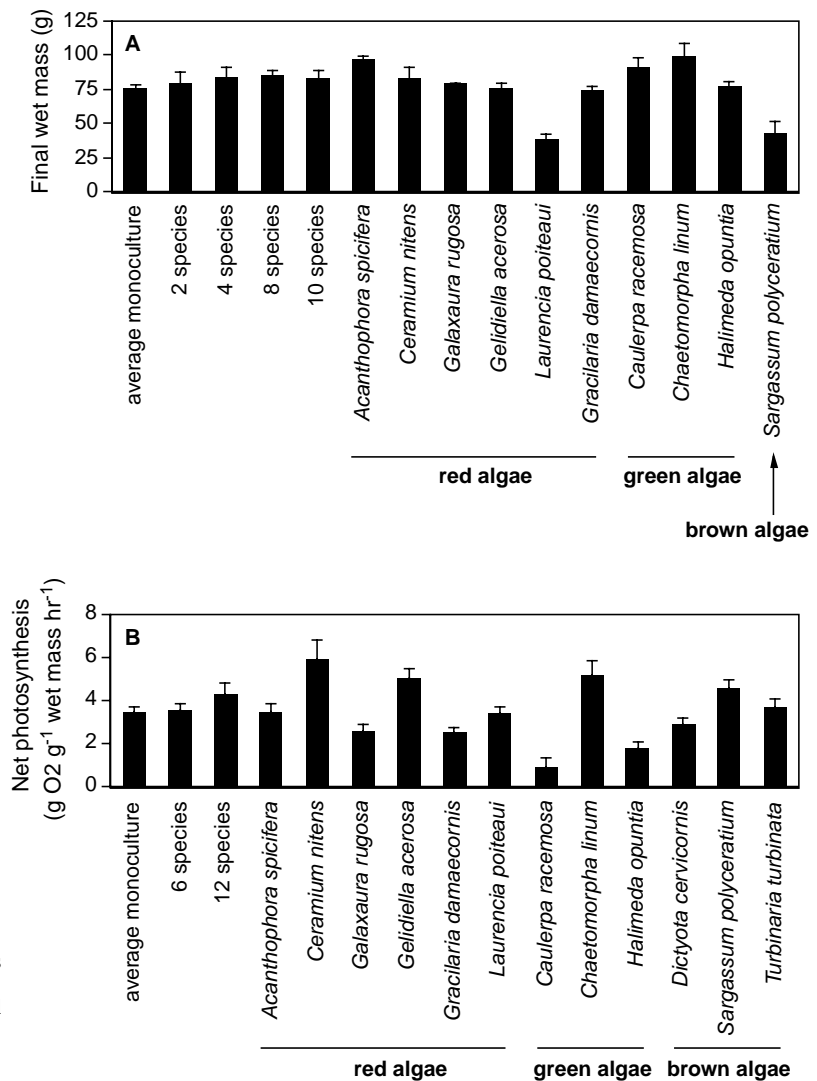


Fig. 2. Effects of algal species richness and identity on two measures of primary production. Values are means  $\pm$  1 SE. Sample size is 10 for all treatments and is 120 for the average monoculture, calculated as the mean of all monoculture replicates.

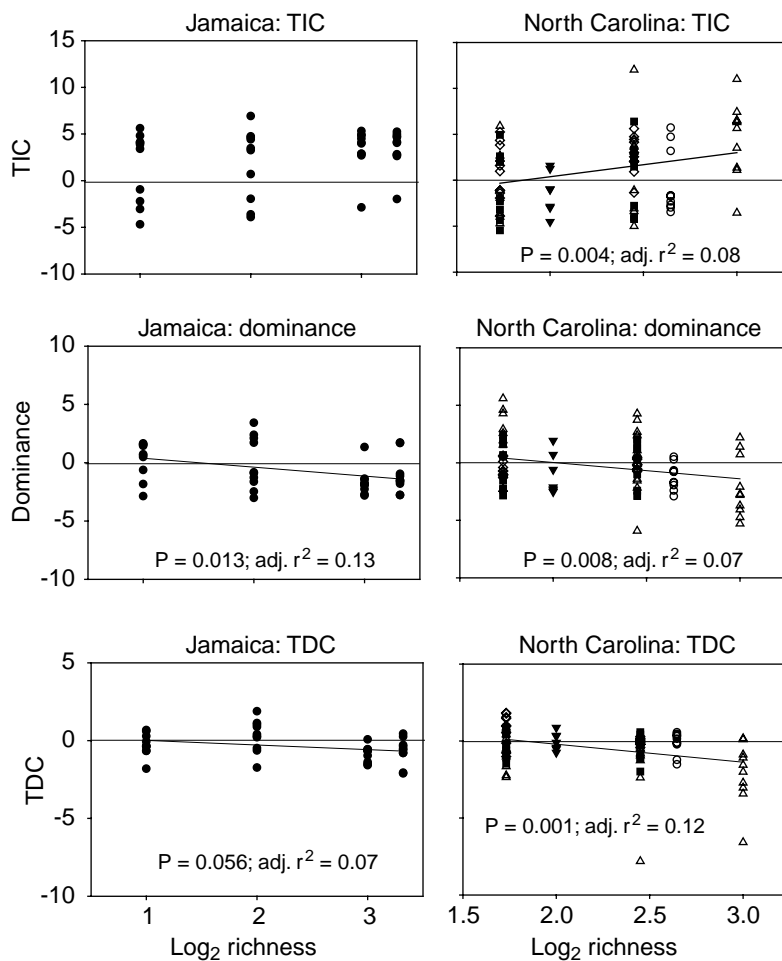


Fig. 3. Responses of effect sizes of trait-independent complementarity (TIC), dominance, and trait-dependent complementarity (TDC, after Fox 2005) to changes in macroalgal species richness. Data are from the Jamaica field experiment and from field (filled symbols) and mesocosm (open symbols) experiments from North Carolina (Bruno et al. 2005). Statistical results are from linear regression analysis.

small turf algae that are known to be important contributors to primary production in coral reef ecosystems (Carpenter 1986). Including these and other functional groups (Steneck and Dethier 1994) could have increased the degree of trait-dependent complementarity and the influence of richness. The maximum number of species in our field and photosynthesis polycultures was ten and twelve respectively. Field sampling at six nearby sites indicated that at the plot size used in our two experiments macroalgal richness naturally averages 14 and can reach at least 24 species. The effect size of species richness could be greater at higher richness levels, however, in most analogous terrestrial experiments, richness effects are detected and most important at relatively low levels; usually at 2–8 species (Loreau et al. 2001, Tilman et al. 2001). Additionally, species abundance distributions were highly skewed and most species were rare and only accounted for a small fraction of the biomass of a given plot (e.g. only 15% of 818 species occurrences in our field surveys constituted 10% of the average plot mass). The production of uncommon species could certainly be enhanced in very diverse plots,

but given their minimal contribution to total plant biomass, the effect would likely be modest.

Positive species richness effects on production caused by facilitation or niche partitioning could theoretically be offset by the negative effects of species interactions including the competitive suppression of highly productive species in diverse polycultures, resulting in weak or no net richness effects (Loreau and Hector 2001, Hooper and Dukes 2004). In both the Jamaica field experiment and the North Carolina experiments, trait-independent complementarity effects were positive. In contrast, dominance and trait-dependent complementarity were negative, indicating that species with low monoculture yields performed better than expected in mixture in comparison to species with higher monoculture yields. In other words, the most productive species did not dominate the polyculture treatments; in fact, they grew slower than expected based on their performance in monoculture. The absence of strong net macroalgal richness effects, despite positive trait-independent complementarity, indicates that increases in production in the high richness treatments via facilitation or other

mechanisms were largely negated by counteracting negative richness effects. As widely hypothesized (Tilman 1999, Loreau et al. 2001, Hooper et al. 2005), trait-independent complementarity increased with species richness in the North Carolina experiments. However, this increase was balanced by a similar increase in the strength of negative dominance and trait-dependent complementarity effects. Our results are largely concordant with those from several studies in terrestrial plant communities that reported small or negative dominance effects (Hooper and Dukes 2004), suggesting that the most productive plant in monoculture is not necessarily the most competitive species in mixture. Tradeoffs between competitive ability or other life history traits and fast growth are ubiquitous (Steneck and Dethier 1994, Pacala et al. 1996, Grime 1997, 2001, Tessier et al. 2000), and negative dominance and trait-dependent complementarity effects are probably common (Loreau and Hector 2001, Hooper and Dukes 2004, Bruno et al. 2005).

This study indicates that in coral reef ecosystems, the influence of macroalgal diversity on primary production is negligible, especially in comparison to species identity and other factors previously shown to be important including nutrient availability, flow velocity, and herbivore identity and abundance (Carpenter 1986, Carpenter and Williams 1993, Miller et al. 1999). Our analysis of the three component richness effects using Fox's (2005) tri-partite partitioning indicates that the positive effect of macroalgal richness on production caused primarily by trait-independent complementarity were nullified by negative dominance and trait-dependent complementarity effects. More generally, recent results from both aquatic and terrestrial systems suggest that the effects of plant richness on primary production are modest and sometimes undetectable, often because highly productive species fail to dominate diverse plant assemblages (Loreau and Hector 2001, Fridley 2002, Hector et al. 2002, Callaway et al. 2003, Hooper and Dukes 2004, Bruno et al. 2005). Given the enormous body of theoretical and empirical work on plant life history trait trade offs (Grime 2001, Rees et al. 2001) this conclusion is not surprising. Yet relatively high biomass and productivity are both sometimes mistakenly equated with competitive superiority (Huston 1997, Ives et al. 2005) which is clearly not always true; neither trait necessarily affects competitive ability, and some competitively dominant species allocate energy into fitness components other than adult soma such as anti-consumer deterrents and reproductive output (Pacala et al. 1996, Tessier et al. 2000). Likewise, critics of the original biodiversity experiments (Huston 1997) argued that the detected plant richness effects were caused by a "sampling probability effect" – the increased probability of including a highly productive species in diverse treatments (Loreau and Hector 2001). But this explana-

tion assumes that fast growing species dominate species rich plots, excluding or greatly reducing the abundance of other species (i.e. a positive dominance effect). Otherwise, the highest yielding species cannot increase community productivity to a level that would exceed that of the average monoculture simply via their presence (Ives et al. 2005) (i.e. not through positive interactions with other species and niche partitioning). We now know that this rarely occurs in biodiversity experiments, and when it occurs in nature the exclusion of slower growing species by high yield dominants causes a negative relationship between plant richness and biomass (Silvertown 1980, Huston 1994, Grime 2001, Thompson et al. 2005).

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