Marine biodiversity and ecosystem functioning: what's known and what's next?

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Marine ecosystems are experiencing rapid and pervasive changes in biodiversity and species composition. Understanding the ecosystem consequences of these changes is critical to effectively managing these systems. Over the last several years, numerous experimental manipulations of species richness have been performed, yet existing quantitative syntheses have focused on a just a subset of processes measured in experiments and, as such, have not summarized the full data available from marine systems. Here, we present the results of a meta-analysis of 110 marine experiments from 42 studies that manipulated the species richness of organisms across a range of taxa and trophic levels and analysed the consequences for various ecosystem processes (categorised as production, consumption or biogeochemical fluxes).

Our results show that, generally, mixtures of species tend to enhance levels of ecosystem function relative to the average component species in monoculture, but have no effect or a negative effect on functioning relative to the 'highest-performing' species. These results are largely consistent with those from other syntheses, and extend conclusions to ecological functions that are commonly measured in the marine realm (e.g. nutrient release from sediment bioturbation). For experiments that manipulated three or more levels of richness, we attempted to discern the functional form of the biodiversity–ecosystem functioning relationship. We found that, for response variables related to consumption, a power-function best described the relationship, which is also consistent with previous findings. However, we identified a linear relationship between richness and production. Combined, our results suggest that changes in the number of species will, on average, tend to alter the functioning of marine ecosystems. We outline several research frontiers that will allow us to more fully understand how, why, and when diversity may drive the functioning of marine ecosystems.

Synthesis

The oceans host an incredible number and variety of species. However, human activities are driving rapid changes in the marine environment. It is imperative we understand ecosystem consequences of any associated loss of species. We summarized data from 110 experiments that manipulated species diversity and evaluated resulting changes to a range of ecosystem responses. We show that losing species, on average, decreases productivity, growth, and a myriad of other processes related to how marine organisms capture and utilize resources. Finally, we suggest that the loss of species may have stronger consequences for some processes than others.

In the current era of global change, marine systems are heavily impacted by human activities including overexploitation, eutrophication, pollution and species introductions (Halpern et al. 2008, Hoegh-Guldberg and Bruno 2010, Burrows et al. 2011), and face unique threats such as ocean acidification (Doney et al. 2012). One consequence of these stressors is a documented change in species composition and richness (Jones et al. 1994, Sax and Gaines 2003, Dulvy et al. 2003, Byrnes et al. 2007, Hawkins et al. 2009, Beaugrand et al. 2010). Given that marine systems worldwide provide a variety of valuable ecosystem services (MEA 2005, Barbier

et al. 2010), and previous evidence suggest these services can be linked to changes in biodiversity (Cardinale et al. 2012, Balvanera et al. 2014), it is crucial to understand the consequences of biodiversity loss in the world's oceans.

Since the publication of the first experiments studying the effects of changes in biodiversity on ecosystem functioning in the early 1990s (Naeem et al. 1994, Tilman and Downing 1994), consensus is now emerging that declines in biodiversity have negative consequences for ecosystem functions such as production, resource use efficiency, and nutrient cycling (Loreau et al. 2001, Hooper et al. 2005, Balvanera et al.

2006, Naeem et al. 2009a, Schmid et al. 2009, Cardinale et al. 2012). Early reviews of biodiversity–ecosystem functioning noted that the marine realm was underrepresented (Emmerson and Huxham 2002, Hooper et al. 2005), but significant progress has been made and the number of manipulative studies in marine systems has increased rapidly over the past few years (Worm et al. 2006, Stachowicz et al. 2007, Cardinale et al. 2011, Solan et al. 2012, O'Connor and Byrnes 2013).

Indeed, marine studies have been instrumental in shifting the focus towards higher trophic levels, specifically looking at herbivory and predation (Duffy 2002, Duffy et al. 2003, Bruno and O'Connor 2005, O'Connor and Crowe 2005, Stachowicz et al. 2007, Gamfeldt and Hillebrand 2008), and how these interact across multiple trophic levels (Gamfeldt et al. 2005, Bruno et al. 2008, Douglass et al. 2008). Marine studies contributed substantially to our understanding of the role of predator diversity (Byrnes et al. 2006, Griffen 2006, Griffin et al. 2008, O'Connor et al. 2008, O'Connor and Bruno 2009, Griffin and Silliman 2011), and have helped elucidate the role of random vs. ordered scenarios of species loss (Solan et al. 2004, Bracken et al. 2008, Bracken and Low 2012). They have also investigated how biodiversity influences ecosystem processes that are generated non-trophically by ecosystem engineers (e.g. nutrient fluxes from bioturbation in soft-benthos) (Emmerson et al. 2001, Solan et al. 2004), used controlled experiments to further our understanding about the relative roles of species density, identity and diversity (O'Connor and Crowe 2005, Benedetti-Cecchi 2006, Griffin et al. 2008, Byrnes and Stachowicz 2009a), and explored how connectivity among communities alters such relationships (France and Duffy 2006, Matthiessen et al. 2007).

Worm and colleagues (Worm et al. 2006) provided the first quantitative meta-analysis of 32 marine experimental manipulations of either species or genetic richness, finding generally positive effects of diversity of either producers or consumers as compared to average monocultures for a wide variety of ecosystem functions. Following this, Stachowicz et al. (2007) published a more extensive review of 52 papers that manipulated the richness of not just species, but also functional groups or genotypes, in the marine realm. In total, those papers reported a significant effect of richness for about 70% of the experiments. The review by Stachowicz et al. (2007), however, did not quantify the size of the diversity effect. Rather, they simply tallied the studies that reported a significant relationship between richness and functioning in marine experiments.

In this paper, we provide an extensive quantitative summary of the current state of knowledge in marine biodiversity–ecosystem functioning research. We provide a rigorous meta-analysis of 110 marine experiments that manipulated the species richness and analysed some ecosystem response. We employ a mixed modelling framework to specifically test how changes in species richness affect a range of functions in different marine systems. We also provide the first estimates of the functional form (e.g. linear, logarithmic, etc.) of the relationship between species richness and ecosystem responses in marine systems. Finally, we discuss shortcomings of the current literature and suggest fruitful future research topics.

Methods

The data

To quantify the effects of changes in species richness on biomass production, consumption, and biogeochemical fluxes, we assembled a dataset of 42 studies that performed 110 experimental manipulations of species richness from 1999 to May 2011. For inclusion, studies must have manipulated the richness of ≥ 3 species, included treatments with all species together and each species alone, and used a substitutive design. A substitutive design means that total initial biomass (or response variable of choice) is held constant across richness levels, and is the most commonly employed design in biodiversity–ecosystem functioning research.

We began by extracting all marine studies from an existing, publicly available database used in previous meta-analyses of biodiversity effects (Cardinale et al. 2009, 2011). These syntheses focused solely on studies that examined how richness influenced resource capture and/or the production of biomass. They did not include many of the processes that are of interest in marine studies (e.g. bioturbation), therefore we supplemented the existing database in several ways. First, we added any studies reviewed in Stachowicz et al. (2007) that met our criteria for inclusion. Second, we searched ISI Web of Science using two search strings. 1) '(biodiversity OR diversity OR richness) AND function* AND marine', and 2) 'biodiversity AND function* AND marine'. This resulted in the addition of nine more studies that were not included in Cardinale et al. (2009), Cardinale et al. (2011) and Stachowicz et al. (2007). Table 1 lists all the studies and the number of experiments included in each study analyzed in this meta-analysis.

We categorized each experiment according to type of response variable (production, consumption, biogeochemical fluxes), study system (hard substrate, soft substrate, seagrass, pelagic, salt marsh), and focal trophic group (primary producers, herbivores, carnivores, mixed diet) (see Table 2 for an overview). We also categorized experiments based on whether the response variable was measured at the focal trophic group itself (i.e. producers, herbivores, carnivores, mixed feeders), at the level of their resources, or at the next trophic level up in the food web.

Biogeochemical fluxes have been a central focus in marine experiments that studied the effects of animal species richness on soft substrates (Raffaelli et al. 2003, Ieno et al. 2006, Norling et al. 2007), but the results have not been summarised prior to the present analysis. Examples of the different response variables are provided in Table 2. The geographical distribution of the studies is shown in Fig. 1, and the number of studies and experiments for each study system and focal trophic group are presented in Fig. 2.

Twenty-seven percent of the studies included in this meta-analysis used rates of ecological processes (e.g. the rate of oxygen production, rate of biomass production, or rate of resource depletion) as response variables. The remaining studies analyzed state variables (e.g. the standing stock biomass, volume or cover). These state variables have often been used as proxies for rates of ecological processes in the biodiversity-functioning literature. For example, the standing stock biomass of primary producers at the peak of the

Table 1. A list of the 42 studies included in the analyses, their study system, and the number of unique experiments within each study.

Paper	System	No. of experiments
Blake and Duffy 2010	seagrass	4
Boyer et al. 2009	hard substrate	8
Bracken et al. 2008	hard substrate	16
Bracken and Stachowicz 2006	hard substrate	1
Bruno et al. 2005	hard substrate	5
Bruno and O'Connor 2005	hard substrate	1
Bruno et al. 2006	hard substrate	2
Bruno et al. 2008	hard substrate	4
Byrnes et al. 2006	hard substrate	1
Byrnes and Stachowicz 2009a	hard substrate	1
Byrnes and Stachowicz 2009b	hard substrate	2
Callaway et al. 2003	salt marsh	1
Dam and Lopes 2003	pelagic	2
Douglass et al. 2008	hard substrate	10
Duffy et al. 2001	seagrass	1
Duffy et al. 2003	seagrass	1
Duffy et al. 2005	seagrass	2
Ericson et al. 2009	hard substrate	2
Foster et al. 1999	hard substrate	2
Gamfeldt et al. 2005	pelagic	7
Godbold et al. 2009	soft substrate	3
Griffin et al. 2008	hard substrate	2
Griffin et al. 2009	hard substrate	3
Griffin et al. 2010	hard substrate	1
Gustafsson and Boström 2009	seagrass	1
Hillebrand et al. 2009	hard substrate	2
Ieno et al. 2006	soft substrate	1
Jaschinski et al. 2009	seagrass	2
Karlson et al. 2010	soft substrate	1
Karlson et al. 2011	soft substrate	1
Matthiessen et al. 2007	hard substrate	2
Mermillod-Blondin et al. 2005	soft substrate	1
Moore and Fairweather 2006	seagrass	1
Moorthi et al. 2008	soft substrate	6
Murray and Marcus 2002	pelagic	2
Norling et al. 2007	soft substrate	1
O'Connor and Bruno 2009	hard substrate	2
O'Connor et al. 2008	hard substrate	1
Salo et al. 2009	seagrass	1
Stachowicz et al. 2008a	hard substrate	1
Stachowicz et al. 2008b	hard substrate	1
Vanelslander et al. 2009	soft substrate	1

growing season or at the end of an experiment has been analyzed and discussed as a proxy for the rate of production of biomass (Tilman et al. 1997). Since previous analyses have shown that rate- and state variables may respond differently to changes in biodiversity (Schmid et al. 2009), we also categorized the response variable as either rates or states.

Statistical analyses: log response ratios

From each experiment, we extracted the mean value of the response variable, its variance (standard deviation), and the sample size for each response at each level of richness. We also identified the single species with the most extreme performance, i.e. highest or lowest function value (depending on whether a higher or lower response was predicted to be optimal from theory), and recorded the mean value of functioning, variance in functioning, and sample size for that species by itself. This information allowed us to construct two common indices based on the log response ratio (LR, Hedges et al. 1999). The first, LR_{net}, is defined as the proportional difference in the response variable Y between the average value of the most species-rich polyculture (Y_{Smax}) and the average value of these same species grown in monoculture ($Y_{AveMono}$):

$$LR_{net} = \ln\left(\frac{Y_{Smax}}{Y_{AveMono}}\right)$$

An $LR_{net} > 0$ indicates that function in the diverse mixture is greater than the average species when grown alone. The second, LR_{ext}, is:

$$LR_{ext} = \ln\left(\frac{Y_{Smax}}{Y_{ExtMono}}\right)$$

where Y_{Smax} is the response variable in the most diverse polyculture in an experiment and $Y_{ExtMono}$ is the value of the most extreme monoculture. An $LR_{ext} > 0$ indicates that function in the diverse mixture is greater than function for the single most extreme species when alone.

For each response, we specified the expected direction of the diversity effect, i.e. whether the function was predicted to be maximized or minimized with increasing richness.

Table 2. A description of the different response variables included in each main category of function (production, consumption, biogeochemical fluxes), and their units. Some variables have been measured as both state and rate variables.

| Function category	Functions	Units
Production	- biomass/volume/abundance/cover/size - chlorophyll a - production of offspring or eggs - survival - hatching success - abundance of epifauna	weight volume^{-1} (e.g. g l^{-1}, no. volume^{-1}, O$_2$ time^{-1}, weight (e.g. g), weight area^{-2}, cover area^{-2}, shoots per plot, length (e.g. mm), numbers pair^{-1} (brood production or eggs), % (survival, gonad index, hatching success), weight time^{-1}, no. of eggs time^{-1}
Consumption	- biomass/volume/abundance/ - cover of resource or prey - nutrient uptake/incorporation - ingestion rate	weight volume^{-1} (e.g. g l^{-1}), number volume^{-1}, number/cover/weight/volume area^{-2}, l g^{-1} h^{-1}, proportional change, weight, mg g^{-1}, concentration (e.g. molar), weight time^{-1}
Biogeochemical fluxes	- water exchange - fluxes of nutrients - fecal production - oxygen flux and oxidized sediments	volume, concentration, concentration area^{-2} time^{-1}, number area^{-2} time^{-1}, number time^{-1}, depth (of O$_2$ layer)
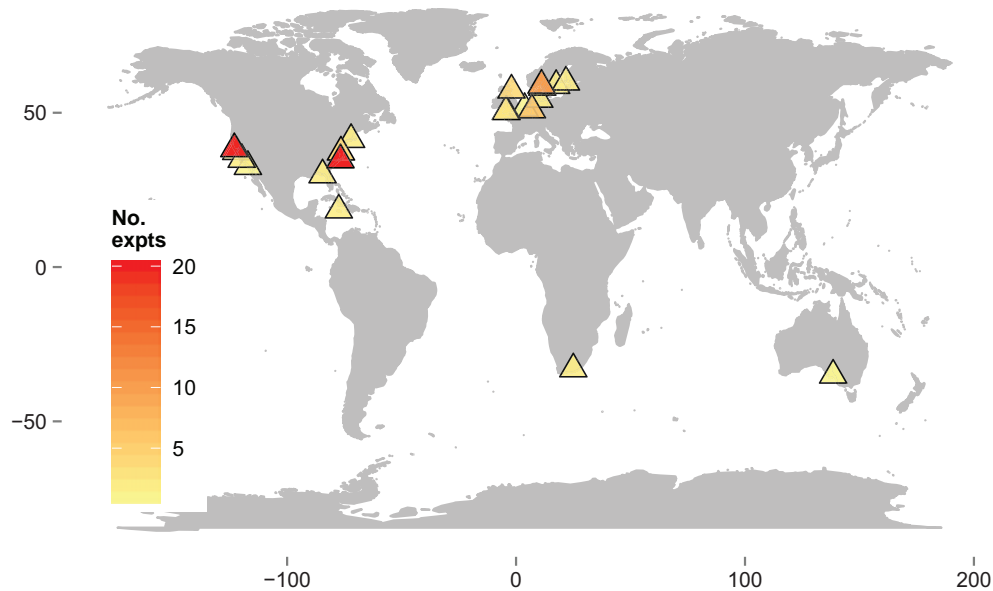
Figure 1. A global map showing the location of the experiments included in this meta-analysis.

Wherever possible, we relied on the predictions set forth by the authors of the original publication, or those suggested by ecological theory. For example, the expected effect of changes in diversity within a focal trophic level on processes within that same focal group is often expected to be positive (e.g. changes in diversity of plants enhances the standing stock biomass of plants, Loreau 1998). Similarly, the expected effect of diversity on the standing stock of the trophic level below the one that is being manipulated is expected to be negative (e.g. diversity enhances resource depletion, Thébault and Loreau 2003, Ives et al. 2005, Duffy et al. 2007).

However, there are a multitude of predictions for bottom–up effects of diversity, i.e. the effect of diversity on the trophic level above the one that is being manipulated. One possibility is that consumer production may respond positively to increased prey diversity because the diverse prey assemblage contains more and varied nutrients (the 'balanced diet' hypothesis); alternatively, consumer production might respond negatively to higher prey diversity if diverse prey assemblages have enhanced prey defenses (Duffy et al. 2007). We identified two experiments testing bottom–up effects of diversity, and for which the predicted direction of a diversity effect might be conflicted. The first (Gustafsson and Boström 2009) hypothesized a positive effect of seagrass richness on the amount of epifauna because increasing diversity can increase seagrass structural habitat. The second
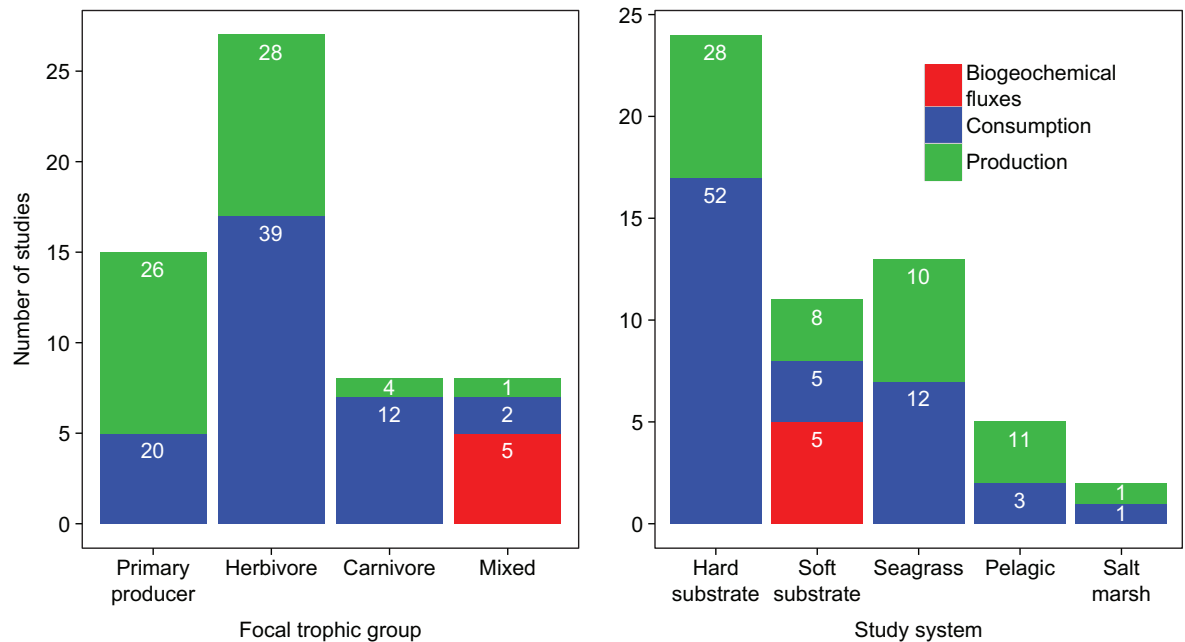

Figure 2. The number of studies and experiments for each function category (production, consumption, biogeochemical fluxes), trophic group (primary producer, herbivore, carnivore, mixed diet), and system (hard substrate, soft substrate, seagrass, pelagic, salt marsh).

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study (Gamfeldt et al. 2005) tested the effect of algal prey richness on herbivore biomass. Since all prey species were edible the authors hypothesized that the direction of a richness effect should be positive. Both these experiments were thus retained in our analyses.

We removed any experiments that measured effects exceeding > 1 trophic level away from the focal organisms whose diversity was manipulated (as some experiments in the Bruno and O'Connor 2005 and Blake and Duffy 2010 studies). When the expected direction was negative, e.g. the response was expected to be minimized with increasing diversity, then we simply inverted the ratio:$1/LR_{ext}$. For papers that included multiple sampling points over time, we used only data from the last sampling point (Poore et al. 2012), as this is least likely to be influenced by transient responses. When there were orthogonal experimental treatments (e.g. top predator present or absent), each level of the factors was considered an independent experiment.

To investigate the overall effect of species richness, we calculated a mean log response ratio for both LR_{net} and LR_{ext}, which was simply the unweighted average of the constituent log ratios. The variance of this statistic was the sample variance of the log ratios, which we used to construct 95% confidence intervals. We considered any mean log response ratio whose 95% CIs did not overlap zero to be significantly different from zero (either positively or negatively). We also calculated both variance- and sample size-weighted log response ratios for each study following Hedges et al. (1999), using the experiment standard deviations and sample sizes collected from the original publications. However, the inferences from these two weighted analyses were no different from the unweighted analysis (see code in Supplementary material). Therefore, we chose to present the unweighted analysis here, as it prevents more controlled studies (i.e. those conducted in the lab or in micro/mesocosms versus those conducted in the field) from exerting an inordinate influence on the mean log ratios (as in Cardinale et al. 2006, 2011, Griffin et al. 2013). We further parsed the mean log ratios by trophic level, habitat, trophic direction, and response type (state versus rate variables) and identified significant differences based on 95% CIs, as above. The definition of a rate variable is one that is reported as per unit time or proportional change.

Statistical analyses: curve-fitting

In addition to the analyses using log response ratios, we also analyzed the form of the relationship that best describes the effect of richness on functioning. For this purpose we used the 27 studies and 66 experiments in our database that manipulated three or more richness levels. We extracted the mean level of functioning at each level of richness (Y_S) relative to the average monoculture ($Y_{AveMono}$): $Y_S/Y_{AveMono}$ (sensu Cardinale et al. 2006), or the proportional change in functioning with each successive level of richness relative to the single-species treatments. We then regressed this response against richness in a non-linear mixed effects framework, allowing the slope and intercept of the richness effect to vary by study. Including study as a random effect allowed us to account for the variation due to an experiment being in a particular study when estimating the overall effect of richness on the response. We fitted our data using the following relationships: linear, logarithmic, power, and saturating
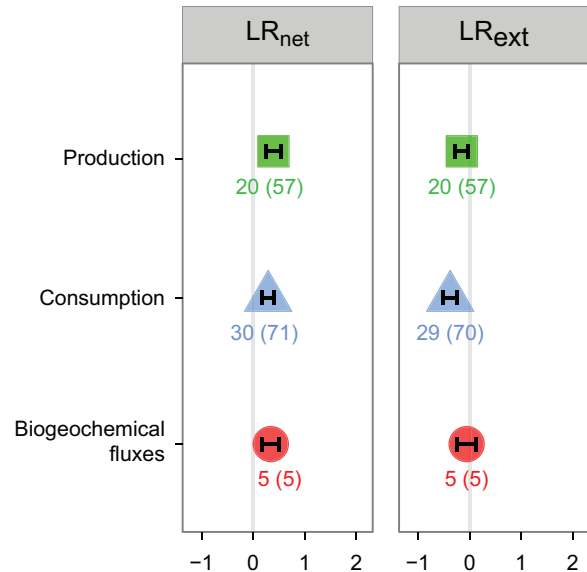

Figure 3. The log response ratios LR_{net} and LR_{ext} grouped by the three function categories: production, consumption and biogeochemical fluxes. The horizontal lines represent 95% confidence intervals.

(Michaelis–Menten), as well as a null model including only the random factor (see R code in Supplementary material Appendix 1 and Cardinale et al. 2011). Akaike weights were used to identify the most parsimonious model(s) for each response variable (Burnham and Anderson 2002).

We used the coefficients from the most parsimonious models to predict the overall effect of richness on each of the three different function categories (production, consumption, biogeochemical fluxes). We then randomly sampled our data and bootstrapped the model 999 times to arrive at an approximate 95% confidence band for the overall fit. This approach improves on previous efforts to categorize the shape of diversity–function relationships (Cardinale et al. 2006, 2011) which fitted a separate set of curves to each individual experiment, and then used vote-counting based on the type of relationship with the lowest AIC value for each experiment. All analyses were done in R (ver. 3.0.2) using the package *nlme* (Pinheiro et al. 2013). All R code is available in Supplementary material Appendix 1, and the data in Supplementary material Appendix 2.

Results

General effects of species richness

Across all marine systems and trophic groups, the most species-rich polyculture had higher levels of production, higher consumption, and higher biogeochemical fluxes than the average monoculture (LR_{net} was significantly positive for all three function categories based on 95% confidence intervals, Fig. 3). However, when compared to the monoculture with the most extreme value (LR_{ext}), polycultures show significantly lower levels of production and consumption, and similar levels for biogeochemical fluxes (Fig. 3).

Looking at experiments based on whether the response variable was measured at the focal or adjacent trophic level does little
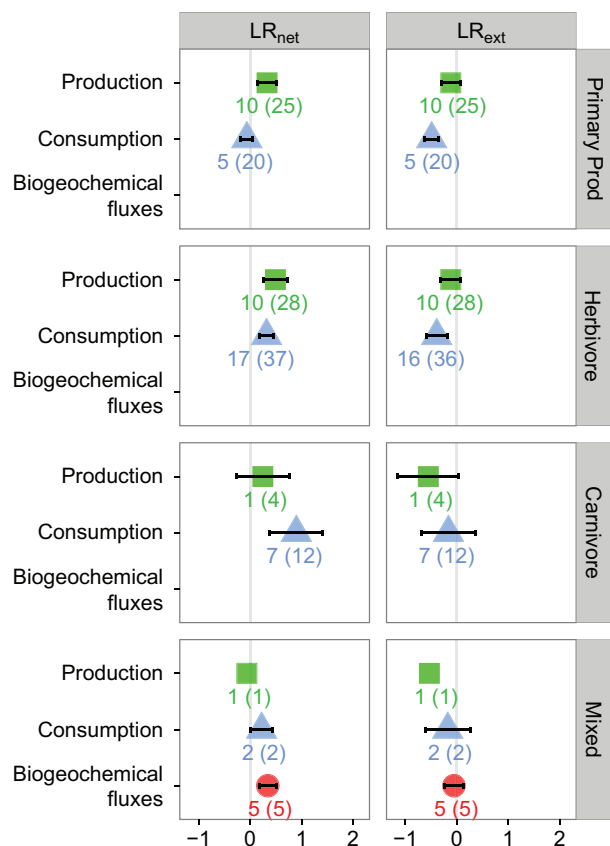
Figure 4. The log response ratios LR_{net} and LR_{ext} grouped by function category and trophic group. The horizontal lines represent 95% confidence intervals.

Figure 5. The log response ratios LR_{net} and LR_{ext} grouped by function category and system. The horizontal lines represent 95% confidence intervals.

to change this general picture. Only two studies looked at bottom–up effects of producer richness on consumer production, which is not different from zero, though we have little power to estimate that response ratio (Supplementary material Appendix 3, Fig. A1). For consumption, the response ratio is positive when we analyse the effects at the level of the resources (e.g. the effect of algal richness on nutrients in the water column). When we look at effects at the level of the focal trophic level (e.g. the effect of algal richness on algal biomass) the confidence interval overlaps zero (Supplementary material Appendix 3 Fig. A1).

Effects of species richness by trophic groups

For production, LR_{net} was positive for both primary producers and herbivores (Fig. 4), reflecting the general trend (Fig. 3). Meanwhile, there was no effect of richness on production of either carnivores or mixed feeders, though the low sample sizes for these trophic groups were likely responsible (Fig. 4).

For consumption, LR_{net} was positive for herbivores, carnivores and mixed feeders, but not for primary producers 'consuming' inorganic resources (Fig. 4). It should be noted that the data for primary producers and consumption is constrained to 20 experiments from five studies, of which two studies (Bracken and Stachowicz 2006, Bracken et al. 2008) contributed 17 experiments. The results are thus strongly driven by these studies. However, detailed exploration of the
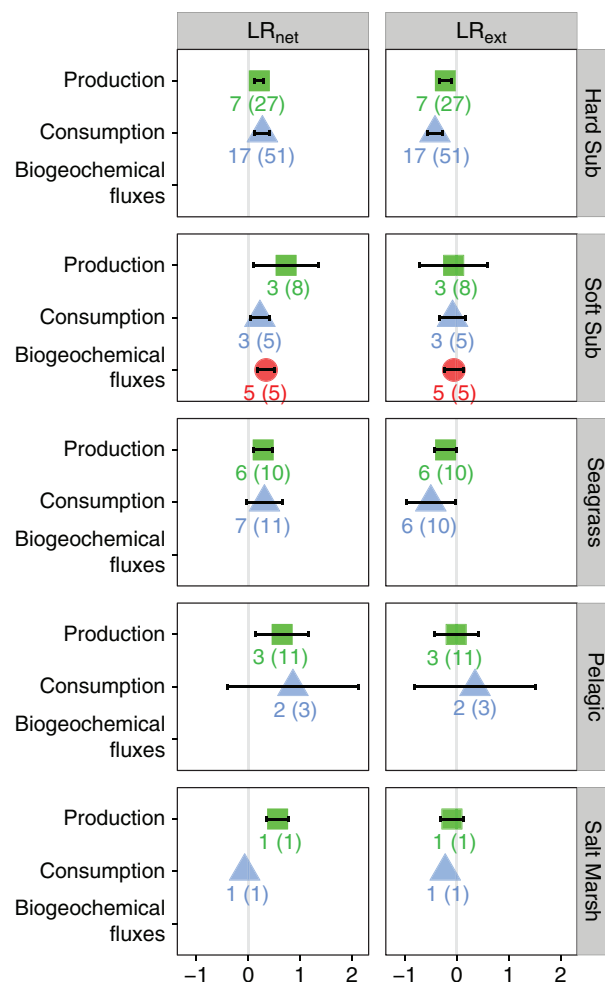
response ratios for these five studies shows that the removal of any of the five studies did not qualitatively change the result (Supplementary material Appendix 3 Fig. A2).

The pattern for LR_{ext} differed from those found for LR_{net}. For production, all trophic groups showed a marginally or non-significant trend in LR_{ext}. The most species-rich polyculture often had significantly lower functioning relative to the most extreme monoculture (Fig. 3). For consumption, the most species-rich polyculture performed more poorly than the most extreme monoculture (had a negative LR_{ext}) for both primary producers and herbivores, but for both carnivores and mixed feeders LR_{ext} did not differ from zero (Fig. 4). Biogeochemical fluxes were in all cases mediated by organisms considered to belong to a mixed feeding group, and therefore effects shown in Fig. 4 (both LR_{net} and LR_{ext}) reflected the same trends as seen in other groups; i.e. a positive LR_{net} and an LR_{ext} that did not differ from zero.

Effects of species richness by system

When results were parsed by type of marine system, we found consistent positive effects of richness on production across systems compared to the average monoculture (LR_{net}).

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Table 3. Results from AIC analyses for each function category and species richness–function curve relationship. Italics highlight the best-fitting models.

Function category	AIC	AIC weight	Delta AIC
Production			
Null	266.2	0.00	45.8
Linear	*220.4*	*0.93*	*0.0*
Logarithmic	225.6	0.069	5.2
Power	239.8	0.00	19.4
Saturating	245.4	0.00	25.0
Consumption			
Null	304.4	0.00	182
Linear	144.5	0.00	22.3
Logarithmic	139.5	0.00	17.3
Power	*122.2*	*1.00*	*0.0*
Saturating	321.7	0.00	200
Biogeochemical fluxes			
Null	39.7	0.00	13.4
Linear	26.8	0.22	0.6
Logarithmic	26.3	0.30	0.0
Power	26.6	0.26	0.3
Saturating	26.7	0.23	0.5

In contrast, there were positive effects on consumption only for hard and soft substrates (Fig. 5). However, we note that there were trends towards positive values of LR_{net} for consumption in both seagrass and pelagic systems, and that there were very low sample sizes across all three of the systems that are responsible for the wide confidence intervals on LR_{net}. Both hard substrate and seagrass systems showed negative effects of richness compared to the best-performing monoculture (LR_{ext}), while LR_{ext} was indistinguishable from zero for both soft substrate and pelagic systems. We note again the generally lower sample size for these systems.

State versus rate variables

There was only one small difference between the state and rate log response variables (Supplementary material Appendix 3 Fig. A3). While biogeochemical fluxes were positive for LR_{net} overall (Fig. 3) their confidence interval overlapped zero for state variables (Supplementary material Appendix 3 Fig. A3). Note, however, the low sample size for the state variables, which was three experiments from three studies.

Differences between types of experiments

We found only small, mostly non-significant differences between experiments that were performed in the lab, in mesocosms, and in the field (Supplementary material Appendix 3 Fig. A4). This resonates with the findings in Godbold (2012), which also found only subtle differences in effect size between lab- and field experiments.

Curve-fitting

The functional form that best captured the effect of diversity on production was the linear function (Akaike weight = 0.93, Table 3, Fig. 6a). For consumption, the power function was the best model (Akaike weight = 1.00, Table 3, Fig. 6b). Output from the models indicates that the coefficients for both production and consumption were positive (β_{prod} = 0.17 and

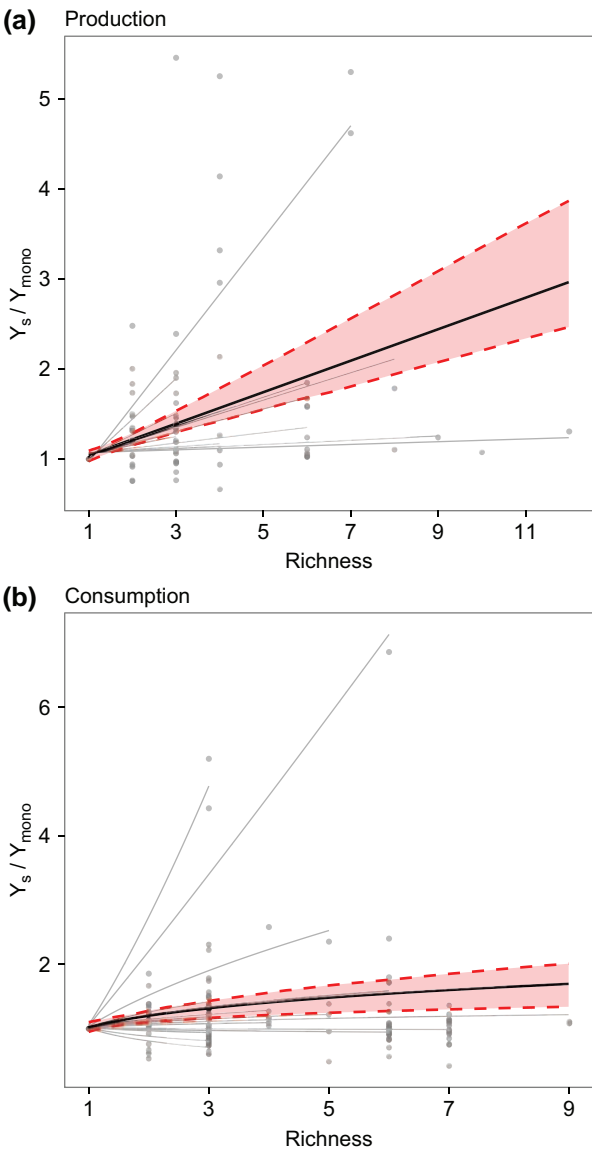**(a)** Production

(b) Consumption

Figure 6. The curve-fits for the function categories (a) production and (b) consumption with 999 bootstrapped models. 95% bootstrapped confidence interval shown by the red dashed lines.

β_{cons} = 0.23) and different from zero (p = 0.024 and p = 0.033 respectively). For biogeochemical fluxes there was nearly equivalent support for all forms, likely driven by the relative lack of studies compared to production and consumption, as opposed to any idiosyncratic response in nature (Table 3).

Discussion

What's known?

Our results provide the most comprehensive quantitative synthesis of marine biodiversity–ecosystem function studies to date. We found that: 1) the level of functioning achieved within species-rich assemblages was generally greater than the average of the component species in monoculture; 2) species-rich assemblages tended to have lower or similar levels of functioning compared to the species with the most

extreme monoculture; 3) the effects of species richness on biogeochemical fluxes, which to date have not been quantitatively summarised across studies, appeared to follow patterns similar to other well-studied ecosystem functions; 4) the shape of the richness–functioning relationship followed a linear function for production and a decelerating power-function for consumption. Our result that the most species-rich polycultures tend to produce more biomass, consume more resources, and have higher biogeochemical fluxes than the average monoculture (Fig. 3) matches the findings of previous meta-analyses (Balvanera et al. 2006, Cardinale et al. 2006, 2011, Stachowicz et al. 2007, Schmid et al. 2009, Godbold 2012), and thus suggests a high degree of generality in our understanding of the effects of changing species richness. Furthermore, we find the qualitative agreement between our marine meta-analysis and similar work in terrestrial systems to be striking; the relationship between diversity and ecosystem functioning as predicted by theory appears to be non-system specific.

We found that 'transgressive overyielding' (i.e. mixtures of species performing better than their most extreme single species in monoculture) was uncommon within species rich marine assemblages, consistent with previous general syntheses. Interestingly, our marine results in fact showed lower levels of production and consumption on average than their most extreme single species. This is consistent with functions analysed by previous synthesis of primary producer experiments (Cardinale et al. 2011). It also resonates well with the findings in many individual studies that the exact composition of species is just as important, or even more important, than species richness per se (Huston and McBride 2002, Bruno et al. 2005, Gustafsson and Boström 2009). The extent to which composition or richness matters most for ecosystem functioning remains to be synthesised.

Our findings might suggest that the focal function would not be compromised by species losses if the best-performing species could be conserved, and further, that management for the single 'best' species, under perfect knowledge, could increase single target functions. It is plausible that increasing richness may impose 'costs' to certain ecological functions, such as when competition or other forms of antagonism reduce the performance of highly functional species when they interact with other species in polyculture. The results suggest that we could, in fact, conserve ecosystem functioning with single species if the following assumptions hold. First, that we have perfect knowledge of the functional characteristics of each species that allow selection of the 'best' performing one. Second, that the single chosen species will remain the best performer through inevitable spatial and temporal changes in the environment. Third, though not an assumption per se, that choosing the single species is optimal also for the other functions we may be interested in maximizing. Multiple studies now show that the best performing species for one function is not necessarily the best performing species for all functions (Gamfeldt et al. 2008, Zavaleta et al. 2010, Byrnes et al. 2014). It should also be noted that the equal replication of each species in monoculture, a standard experimental design choice, may be biased towards finding extreme values in single-species treatments, thereby biasing against finding a consistent positive effect of LR_{ext} (Schmid et al. 2008). However, there has not yet been a satisfactory method for dealing with such biases presented in the literature.

Bottom–up effects of changes in species richness (effects of primary producers on herbivores) have previously been shown to differ from the top–down effects of changes in species richness (Cardinale et al. 2011). We found no such differences (Supplementary material Appendix 3 Fig. A1), but note that our data set only included two experiments that studied bottom–up effects. We thus had little power for this comparison. Responses to changes in species richness have also been shown to differ between state and rate variables (Schmid et al. 2009). We found only one such discrepancy, which was for biogeochemical fluxes for LR_{net}. One explanation for the only subtle differences might be that many of the rates included in our data are strongly related to the state variables measured. We cannot determine this from the data at hand, however. Future studies would benefit from explicitly comparing state and rate variables, e.g. by comparing the standing stock biomass of phytoplankton to the rate of phytoplankton production and respiration.

While the average effect of species richness on production (LR_{net}), consumption and biogeochemical fluxes is clear, we still see large variation in how it is manifested across trophic groups and functions. For example, there was no effect of primary producer richness on consumption, and no effect of carnivore richness on production (Fig. 4). Also, there was no effect of richness in pelagic or seagrass systems for consumption (Fig. 5). These results could represent real deviations from the general trend. However, since the trends in effects are mostly positive, another explanation is that they are an inevitable consequence of the lower number of studies available within some individual system-function or trophic group-function combinations. Indeed, all of the tests that did not show richness effects suffered from relatively small sample sizes (Fig. 4, 5). Thus, further investigations in these systems and trophic groups may shed light on this phenomenon.

Comparing the effect sizes for LR_{net} found in our study with those in previous meta-analyses of marine experiments (Table 4) indicates slightly weaker effects of changes in primary producer richness for the experiments included in our analysis. On the other hand, the effect of changes in carnivore richness on consumption is larger than for any other response category previously analysed – a finding consistent with a recent meta-analysis of carnivore richness effects across ecosystems (Griffin et al. 2013). On average, the effect sizes in all four meta-analyses are roughly of the same magnitude.

Predicting the consequences of changes in species richness requires an understanding of the form of the richness–functioning relationship. For production and consumption, we were able to estimate the general form of this relationship (Fig. 6), although data limitations did not allow similarly robust estimations for biogeochemical fluxes (Table 3). Previous analyses have found broad support for saturating relationships between richness and functioning (Cardinale et al. 2006, 2011). This form is generally consistent with the decelerating relationship observed for functions related to consumption (Fig. 6b).

However, our finding that production responds linearly to changes in species richness is a departure from previous

Table 4. Comparing the effect sizes (ES) in this study with those in previous meta-analyses: Cardinale et al. 2006 (C2006), Worm et al. 2006 (W2006), and Cardinale et al. 2011 (C2011). Effect sizes are for net log response ratios (LR_{net}) ± 95% confidence intervals. The number of experiments included in each meta-analysis is listed as subscript. PP = primary producers. Note that the term 'production' encompasses both standing stock and rates in G 2014, whereas it infers only standing stock in the other analyses.

Category	C2006 LR_{net}	W2006 LR_{net}	C2011 LR_{net}	G2014 LR_{net}
Standing stock*	$0.37 \pm 0.17_{34}$			
Resource depletion*	$0.37 \pm 0.17_{38}$			
PP, production		$0.58 \pm 0.15_{3}$	$0.42 \pm 0.15_{53}^{£}$	$0.33 \pm 0.19_{31}$
			$0.57 \pm 0.01_{2}^{\$}$	
PP, resource use		$0.18 \pm 0.06_{5}$		$-0.07 \pm 0.11_{23}^{ns}$
Consumers, production		$0.57 \pm 0.18_{6}$		$0.49 \pm 0.23_{32}$
Consumers, resource use		$0.32 \pm 0.19_{5}$		$0.32 \pm 0.14_{46}$
Carnivores, production				$0.25 \pm 0.51_{4}^{ns}$
Carnivores, resource use				$0.90 \pm 0.52_{12}$

*the effect sizes from Cardinale et al. (2006) are for aquatic systems in general, and include both marine and freshwater systems, and are not split by trophic groups
£marine coastal systems
$ estuarine systems
nsconfidence intervals overlapping zero

findings. We tentatively suggest that this could be the result of the generally low number of species in the studies that measured production (median = 4, range = 3–12), which could limit the potential for increasingly overlapping niches to saturate the richness–production relationship. In other words, the linear relationship could represent the initial linear rise in production at relatively low species richness levels present in a saturating relationship. On the other hand, we were able to identify a non-linear power relationship for consumption with a lower median (3) and a smaller range (3–9) of richness. Nonetheless, the small number of data points on the x-axis for each individual experiment is a serious limitation of our data set, and all conclusions based on the curve-fitting results should be interpreted with caution.

It should also be noted that comparisons to previous syntheses may be biased by the less sophisticated 'vote-counting' approach employed in earlier efforts (Cardinale et al. 2006, 2011). This approach has a lower statistical power to detect differences in the functional form, and thus power, paradoxically, decreases as more studies are added (Hedges and Olkin 1980). More importantly, the chance that two studies which have identical underlying functional forms will agree based on comparing significance tests (where $\alpha = 0.05$) is only ~90% (Gurevitch and Hedges 1999). The relatively high error rate may make it difficult to distinguish between functional forms that are relatively similar (e.g. logarithmic and saturating) but have different implications for functioning. Our AIC-based mixed model approach utilizes the entirety of the dataset and thus is a more powerful and rigorous approach to understanding the functional form of the BEF relationship. It should be noted, however, that the dataset is still limited by the number and breadth of studies that have already been conducted, and thus we again urge caution in interpreting these results.

Limitations of the experiments performed to date

There are numerous characteristics of the experimental studies included in our analysis that restrict our ability to extrapolate the results to nature. First, most studies have been short in duration and small in spatial scale (but see Stachowicz et al. 2008b) and have largely been performed in highly controlled and homogeneous environments, e.g. plastic or glass containers. Previous analyses have shown that the effect of species richness often increases with time (Cardinale et al. 2007, Stachowicz et al. 2008b, Reich et al. 2012) and environmental heterogeneity can influence the diversity–function relationship (Raffaelli 2006, Dyson et al. 2007, Griffin et al. 2009a; but see Weis et al. 2008, Gamfeldt and Hillebrand 2011). Our current knowledge about the role of temporal/spatial heterogeneity in affecting the biodiversity–functioning relationship is limited.

Second, the range of species diversity manipulated in the experiments to date. Given the differences in our curve fitting versus previous studies (Cardinale et al. 2006, 2011), we suggest that marine studies need to increase this range whenever possible in order to facilitate the cross-comparability of our results to those of other systems.

Third, most studies have been assembly experiments in which communities have been constructed by putting species together. More realistic inference may be gained from experiments in which species are removed from natural communities in the field (Diaz et al. 2003). There are only a few published removal experiments in marine systems, and these reveal effects of species richness that are equal to, or stronger than, the effects observed in the average lab assembly experiment (O'Connor and Crowe 2005, Maggi et al. 2009, Walker and Thompson 2010, Crowe et al. 2011, Davies et al. 2011). Removal experiments will be key for furthering our understanding of the role of biodiversity for functioning and complementing insights from the large number of assembly experiments performed to date. Removal experiments are also important for testing the compensatory ability of remaining species – a key assumption of the substitutive design used in most assembly experiments.

Fourth, experiments have focused on single functions, but simultaneously considering multiple functions may affect the importance of biodiversity, either positively or negatively

(Byrnes et al. 2014, Hensel and Silliman 2013). Marine environments provide numerous services, including food production, waste assimilation, shoreline protection, climate regulation, and recreation (MEA 2005) and understanding how diversity contributes to the simultaneous maintenance of the functions underlying these services is key to ensuring their effective conservation and management.

Fifth, the vast majority of studies have used a replacement series design in which the density (or other choice of measured unit) of the focal organisms is held constant across richness levels (Jolliffe 2000). This was the design of all the experiments included in our meta-analysis. By holding total density constant, the replacement design confounds changes in species richness with changes in density of component species. Studies that have explicitly studied the interactive effects of changes in number of species with changes in density indicate that density-dependent effects may be common (Underwood 1978, Benedetti-Cecchi 2004, O'Connor and Crowe 2005, Griffin et al. 2008, Byrnes and Stachowicz 2009a, Maggi et al. 2009, 2011). The absence of positive mean values of LR_{ext} in our analyses could potentially be a consequence of reduced density of component species with increasing levels of richness. A replacement series design may be especially problematic in systems where a single species drives most of the functioning, since reducing the density of such species in higher diversity treatments should lead to a decrease in ecosystem functioning independently of species richness. The fact that the LR_{ext} metric is often close to zero or negative, suggests that complementary and density-dependent effects may operate in opposite directions, but often with similar magnitude. One should note, however, that the choice of holding density constant across richness levels is less of an issue in studies that run long enough to allow population dynamics to occur.

Finally, marine biodiversity experiments have largely focused on species richness as a potential driver of functioning, while overlooking other aspects of biodiversity. Richness may fail to capture the degree of functional redundancy among species within an assemblage. Moving forward, it will be necessary to integrate functional traits and/or evolutionary differences (Griffin et al. 2009b, 2013, Best et al. 2013, Cadotte 2013) in investigating the relationship between diversity and functioning. Marine and terrestrial realms differ in terms of their phylogenetic diversity at higher levels. For example, 15 phyla are endemic to marine environments (Ray and Grassle 1991), and the primary producers in the ocean belong to several kingdoms whereas they are mainly from the Plantae kingdom on land (Guiry and Guiry 2013). A formal comparison of the relative importance of phylogenetic diversity for functioning between the two realms has yet to be performed.

Given the limited spatial scale of studies to date, and the resulting mismatch between our understanding of marine biodiversity–functioning relationships and the scales pertinent to management decisions, elucidating effects of diversity at larger scales is a key research frontier. Observational (i.e. correlational) studies provide one way forward because they do not require logistically-challenging manipulations (Emmerson and Raffaelli 2000), allowing the description of diversity–function relationships at scales of entire sites and regions (Godbold and Solan 2009, Mora et al. 2011). It may

be important to consider that observational studies across spatial environmental gradients assess the effects of variation in diversity resulting from a species sorting process at the scale of local communities; they do not necessarily address the effect of losing species from the entire regional species pool (as simulated by small-scale biodiversity experiments such as assessed here). Only the latter scenario would limit the number and type of species available for sorting at the local community scale. While diversity and function may be linked under both scenarios, the mechanisms, diversity–function relationships and management implications could vary widely. Furthermore, it is important to keep in mind in this context that an observed correlation does not necessarily equal causation between diversity and functioning. Finally, while observational studies can provide an illusion of being large-scale by spreading replicated sampling over large areas, in many cases the individual sampling units are small (e.g. 1 m^{-2} benthic grabs, or quadrats on the rocky shore) and may have questionable relevance to truly scaling-up our understanding of diversity-function linkages.

What's next?

Our results identify several key gaps in the field of marine biodiversity–ecosystem function research. First, while a few marine studies have explicitly measured biogeochemical fluxes, they are few in number relative to those that measure production and consumption, and have been confined to a single system. Given the long history of ecosystem ecology and biogeochemistry in marine biology and oceanography, marine biologists are uniquely poised to have a large contribution to this area of biodiversity–ecosystem functioning research.

Second, while meta-analyses and experiments show that the effects of changes in species richness are on par with the effects of other drivers of ecosystem change (Hooper et al. 2012, Tilman et al. 2012), we know little about the interactive effects of species richness and environmental factors, especially in marine systems (but see e.g. Blake and Duffy 2010, Eklöf et al. 2012, Godbold 2012). Furthermore, while we know that indirect effects can just as strongly influence functioning as direct effects (Wootton 2002, Alsterberg et al. 2013, Eisenhauer et al. 2013), indirect and interactive effects of changes in diversity and other factors must be explored further. As an example, acidification may have a direct and positive effect on primary production through increasing levels of CO_2. But if acidification also decreases biodiversity, it may indirectly negatively affect primary production. The net outcome may be difficult to predict and more research is needed in this area.

Third, while local biodiversity can change and even increase due to invasive species (Sax and Gaines 2003, Byrnes et al. 2007), we know little about the effects of *increases* in richness in any system (but see Byrnes and Stachowicz 2009b, Karlson et al. 2011). Coastal and estuarine systems are particularly vulnerable to invasive species (Cohen and Carlton 1998), and thus represent ideal communities with which to explore this question.

Fourth, we highlight a need to increase our knowledge of marine biodiversity–ecosystem functioning relationships in salt marsh and pelagic habitats. Both were underrepresented in our sample, and as such their results were less conclusive (although

we note that several important studies in these systems, such as Lee et al. 1985, Finke and Denno 2005, were excluded because they did not meet our criteria for inclusion).

Fifth, and as discussed above, future studies should explicitly consider manipulations of species density, such as combination additive-replacement designs or response surface designs, to disentangle density-dependent population processes and diversity effects. Density-dependent processes are pervasive ecological forces that shape natural communities. Biodiversity–ecosystem functioning experiments could prove more relevant for environmental management and conservation if they can inform on both the consequences of species loss and on the effects of reducing the population size of the most efficient species for a focal ecosystem process or service.

Last, while marine research has often led the way in the study of predation within the context of biodiversity–ecosystem functioning research, we still have only a relative handful of studies – and mostly in mesocosms – addressing the functional consequences of diversity within guilds of carnivorous predators. Again, research into the effects of predation has been a strength of marine ecology in the past (Paine 1969, Menge 1972, Wootton 1994). Given the importance of predation in marine systems, we suggest that marine research could break further ground in an appreciation of how changes in predator diversity can affect ecosystem functions.

While prey diversity generally increases standing stock biomass and production at higher trophic levels (Lefcheck et al. 2013), our marine-focused data set included only four experiments (Lee et al. 1991, Dam and Lopes 2003, Gamfeldt et al. 2005, Gustafsson and Boström 2009). Furthermore, our analyses did not consider trophic cascades, of which there are many prominent examples in the marine realm (Estes et al. 1998, Eriksson et al. 2009, Hughes et al. 2013). The few marine studies that have manipulated species richness and looked at the effects at two trophic levels down have found highly variable effects, ranging from weak to strong (Bruno and O'Connor 2005, Byrnes et al. 2006, Douglass et al. 2008). Several factors influence how the effects of predator diversity cascade down the food web, including the prevalence of omnivory, intra-guild interference and predation, as well as non-consumptive effects of predators on prey traits (reviewed by Preisser et al. 2005, Duffy et al. 2007, Bruno and Cardinale 2008). Further studies are necessary if we are to better understand how and when the diversity within and across trophic levels interacts to mediate trophic cascades.

The current literature on marine species richness and ecosystem functioning has a clear message: losing species will cause general reductions in ecosystem functions on average (see also Stachowicz et al. 2007, Worm et al. 2006). However, compared to the biodiversity–functioning field as a whole, the sample size for particular marine systems and function categories is low. At the same time, complementing the current literature with additional similar simplified experiments in the same systems will probably do little to change the overall picture presented in Fig. 3. What is now sorely needed is a new generation of experiments that target how spatial scale and heterogeneity, realistic local extinction scenarios, functional and phylogenetic composition, and other aspects

of environmental change (especially temperature, acidification and pollution) influence the relationship between different dimensions of biodiversity and ecosystem functioning, and under natural conditions across spatial and temporal scales (Naeem et al. 2009b, Tomimatsu et al. 2013). Unique opportunities for testing the potential importance of diversity in influencing ecosystem processes may arise in the growing number of restoration projects in marine systems (see Doherty and Zedler 2014 for a case study in salt marshes). We also need to explicitly link functions in these experiments to ecosystem services (Cardinale et al. 2012, Balvanera et al. 2014). Only by expanding the scope and relevance of future experiments can we gain a more thorough understanding of the consequences of changes in marine biodiversity.

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Supplementary material (available online as Appendix oik.01549 at <www.oikosjournal.org/readers/appendix>). Appendix 1. R code for data handling, analyses, and figure plotting. Appendix 2. Data as .txt file. Appendix 3. Supplementary figures/results. Including Fig. A1 (comparing response variables when measured at the focal [within] trophic level or at adjacent [bottom–up and top–down] trophic levels; Fig. A2 (jacknife simulations of removing individual studies from the effect of producer richness on consumption); Fig. A3 (state vs rate variables); Fig. A4 (comparing experiments performed in the field, in mesocosms and in the lab).