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

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Abstract

Marine ecosystems are experiencing rapid and pervasive loss of species. Understanding the consequences of species loss 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 174 marine experiments from 42 studies that have 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 or 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 most 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 BEF relationship. We found that, for response variables categorised as 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 losses 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.

Key words: aquatic, marine, species richness, meta-analysis, production, consumption, biogeochemical flux, power-function, biodiversity and ecosystem functioning

Introduction

In the current era of global change, marine systems are heavily impacted by human activities including overexploitation, eutrophication, pollution, and species introductions (Burrows et al. 2011, Halpern et al. 2008, Hoegh-Guldberg and Bruno 2010) 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 (Beaugrand et al. 2010, Byrnes et al. 2007, Dulvy et al. 2003, Hawkins et al. 2009, Jones et al. 1994, Sax and Gaines 2003). Given that marine systems worldwide provide a variety of valuable ecosystem services (Barbier et al. 2010, MEA 2005), and previous evidence suggest such services can be linked to changes in biodiversity (Balvanera et al. 2006, Cardinale et al. 2012), 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 1990's (Naeem et al. 1994, Tilman and Downing 1994), consensus is now emerging that declines in biodiversity generally have negative consequences for a range of ecosystem functions (Balvanera et al. 2006, Cardinale et al. 2011, Cardinale et al. 2012, Naeem et al. 2009). Even though early reviews of the biodiversity-ecosystem functioning field concluded that research in the marine realm was lagging behind (Emmerson and Huxham 2002, Hooper et al. 2005), progress has been made and the number of studies in marine systems has increased rapidly over the past few years (Cardinale et al. 2011, O'Connor and Byrnes 2013, Solan et al. 2012, Stachowicz et al. 2007, Worm et al. 2006). Indeed, marine studies have been instrumental in shifting the focus towards higher trophic levels, specifically looking at herbivory and predation (Bruno and O'Connor 2005, Duffy 2002, Duffy et al. 2003, Gamfeldt and Hillebrand 2008, O'Connor and Crowe 2005, Stachowicz et al. 2007), and how these interact across multiple trophic levels (Bruno et al. 2008, Douglass et al. 2008, Gamfeldt et al. 2005). Marine studies contributed substantially to our understanding of the role of predator diversity (Byrnes et al. 2006, Griffen 2006, Griffin et al. 2008, Griffin and Silliman 2011, O'Connor and Bruno 2009, O'Connor et al. 2008), and have helped elucidate the role of random vs. ordered scenarios of species loss (Bracken et al. 2008, Bracken and Low 2012, Solan et al. 2004). 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.

85   2001, Solan et al. 2004), used controlled experiments to further our understanding
about the relative roles of species density, identity and diversity (Benedetti-Cecchi
2006, Byrnes and Stachowicz 2009, Griffin et al. 2008, O'Connor and Crowe 2005),
and explored how connectivity among communities alters such relationships (France
and Duffy 2006).

90   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

95   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 report any measures of effect size. Rather it simply tallied
the studies that reported a significant relationship between richness and functioning in

100   marine experiments. Thus, stronger forms of inference and a larger data sample are
needed to synthesize the marine data.

          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 174 marine experiments that manipulated the

105   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) of the relationship between species
richness and ecosystem responses in marine systems for multiple functions. Finally,

110   we discuss shortcomings of the current literature and suggest fruitful future research
topics.

Methods

The data

115   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 174 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. 2011,
Cardinale et al. 2009). 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); we therefore 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. (i)
"(biodiversity OR diversity OR richness) AND function* AND marine", and (ii)
"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 experiments analyzed in this paper.

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 studies 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 (e.g. Ieno et al. 2006,
Norling et al. 2007, Raffaelli et al. 2003), 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.

27% 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

155 at the peak of the growing season or at the end of an experiment has been analyzed and discussed as a proxy for the rate of production of biomass (e.g. 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.

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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,

165 i.e., highest or lowest function value (depending on whether a higher or lower response was predicted to be optimal from theory, see below), 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

170 difference in the response variable Y between the average value of the most species-rich polyculture (S_{max}) and the average value of these same species grown in monoculture ($Y_{AveMono}$): $\ln(Y_{Smax}/Y_{AveMono})$. 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 defined as $\ln(Y_{Smax}/Y_{extMono})$, where Y_{Smax} is the response variable in the

175 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, i.e., whether the function was predicted to be maximized or minimized with increasing diversity.

180 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

185 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,

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Thebault & Loreau 2003, Ives et al. 2005, Duffy et al. 2007). However, there is 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

190   consumer production may respond positively as 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

195   which the predicted direction of a diversity effect might be conflicted. The first (Gustafsson and Bostrom 2009) hypothesized a positive effect of seagrass richness on the amount of epifauna because increasing diversity increases seagrass structural habitat. The second study (Gamfeldt et al. 2005) tested the effect of algal prey richness on herbivore biomass. Since all prey species were edible the authors

200   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 & O'Connor 2005 and Blake & Duffy 2010 studies). The definition of the expected direction has

205   implications for the construction of LR_{ext}. When the expected direction was negative, e.g., the response was expected to be minimized with increasing diversity, then we simply inverted the ratio (X_{mono}/X_{poly}), or $1/LR_{ext}$.

        For papers that included multiple sampling points over time, we used only data from the last sampling point (see e.g. Griffin et al. 2013) as this is least likely to

210   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. We included study as a random effect to account for the variation due to an experiment being in a particular study. To investigate the overall effect of species richness, we calculated a mean log response

215   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

220   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. 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 vs those conducted in the field) from exerting an inordinate influence on the mean log ratios (as in Cardinale et al. 2006, Cardinale et al. 2011, Griffin et al. 2013). We further parsed the mean log ratios by trophic level, habitat, trophic direction, and response type (state vs. 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 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. Again, 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 (Michaelis-Menten), as well as a null model including only the random factor (see R code Appendix 1 in Supplementary material 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 then used the coefficients from these most parsimonious models to predict the overall effect of richness on each of the three different function categories. Finally, we 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, Cardinale et al. 2011) which fit a separate set of curves to each individual experiment, and then used vote-counting

255   based on the type of relationship with the lowest AIC value for each experiment. All analyses were done in R (version 3.0.2, R Development Core Team, 2013) using the package *nlme* (Pinheiro et al. 2013). All R code is available in Appendix 1, and the data in Appendix 2.

260   <u>Results</u>

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

265   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 to change this general

270   picture. Only two studies looked at bottom-up effects of producer richness on consumer production, which was 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

275   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 (Fig. A1).

Effects of species richness by trophic groups

280   For production, LR_{net} - the level of production of the most species-rich polyculture relative to the *average* monoculture – was positive for both primary producers and herbivores (Fig. 4), reflecting the general trend (Fig. 3). Meanwhile, there was no equivalent effect of richness on production of either carnivores or mixed feeders, though the low sample sizes for these trophic groups must be noted (Fig. 4).

285   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 23 experiments from 5 studies, of which 2 studies see (Bracken et al. 2008, Bracken

and Stachowicz 2006) contributed 19 experiments. The results are thus strongly
driven by these studies. However, detailed exploration of the response ratios for these
5 studies shows that the removal of any of those 5 studies did not qualitatively change
the result (Fig. A2).

The pattern for LR_{ext} - the level of functioning of the most species-rich
polyculture relative to the most extreme monoculture - 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}). 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 vs. rate variables
There was only one small difference between the state and rate log response variables
(Fig. A3). While biogeochemical fluxes were positive for LR_{net} overall (Fig. 3) their
confidence interval overlapped zero for state variables (Fig. A3). Note, however, the
low sample size for the state variables, which was 5 experiments from 3 studies.

Curve-fitting

The functional form that best captured the effect of diversity on production was the linear function (Akaike weight = 0.93, Table 3 and Fig. 6a). For consumption, the power function was the best model (Akaike weight = 1.00, Table 3 and Fig. 6b). Output from the models indicates that the coefficients for both production and consumption were positive (β_{prod} = 0.17 and 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 functions, likely representing the paucity of studies relative 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 the similar patterns to other well-studied ecosystem functions; 4) the shape of the richness-functioning relationship followed a linear function for production and a saturating 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 (e.g. Cardinale et al. 2006, Cardinale et al. 2011), and thus suggests a high degree of generality in our understanding of the effects of changing species richness for ecosystem function.

We found that species-rich marine assemblages followed a previously reported general trend in biodiversity experiments that 'transgressive overyielding' (i.e. mixtures of species performing better than their most extreme single species) was uncommon. 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).

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 (Byrnes et al. 2013, Duffy et al. 2003, Gamfeldt et al. 2008, Zavaleta et al. 2010). It should be noted that the common approach to comparing mixtures to the most extreme monoculture has been suggested to be biased towards more extreme estimates of single species averages, 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 (Fig. A1), but note that our data set only included two experiments that studies 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 and 5).

Predicting the effects of species losses 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, although data limitations did not allow similarly robust estimations for biogeochemical fluxes. Previous analyses have found broad support for saturating relationships between richness and functions (including strong support for power-functions), consistent with our result for consumption. This suggests a diminishing return with increases in species richness. However, our finding that production appears to generally respond to species richness in a linear fashion is a departure from previous findings. Direct comparisons to previous syntheses are constrained by the different approaches used to judge the relative support for different functional forms. 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 effect, 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 power relationship for consumption with a lower median number of species (3) and a smaller range of maximum species richness (3-9). 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.

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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 e.g. Stachowicz et al.

430   2008) 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, Reich et al. 2012, Stachowicz et al. 2008) and environmental heterogeneity can influence the diversity-function relationship (Dyson et al. 2007, Griffin et al. 2009, Raffaelli 2006;

435   but see Gamfeldt and Hillebrand 2011, Weis et al. 2008). Our current knowledge about the role of spatial heterogeneity in affecting the biodiversity-functioning relationship is limited.

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

440   (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, Eklof et al. 2012, Godbold 2012). Furthermore, while we know that indirect effects can just as strongly influence functioning as direct effects (Alsterberg et al. 2013, Eisenhauer et al. 2013, Wootton 2002), indirect and

445   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. But if acidification also affects biodiversity it may indirectly affect primary production negatively. The net outcome may be difficult to predict.

Third, most studies have been assembly experiments in which communities

450   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 (Crowe et

455   al. 2011, Davies et al. 2011, Maggi et al. 2009, O'Connor and Crowe 2005, Walker and Thompson 2010). 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

460   species – a key assumption of the substitutive design used in most assembly

experiments.

Fourth, while local biodiversity can change and even increase due to invasive

species (Byrnes et al. 2007, Sax and Gaines 2003), we know little about the effects of

increases in richness – in any system (but see Byrnes and Stachowicz 2009, Karlson

465   et al. 2011). Coastal and estuarine systems are vulnerable to invasive species (Cohen

and Carlton 1998) and thus represent ideal communities with which to explore this

question.

Fifth, experiments have focused on single functions, but simultaneously

considering multiple functions may affect the importance of biodiversity, either

470   positively or negatively (Byrnes et al. 2013, 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

475   management.

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

480   functional traits and/or evolutionary differences (e.g., Best et al. 2013, Cadotte 2013,

Griffin et al. 2009, Griffin et al. 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

485   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

490   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

495   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

500   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. Finally, while observational studies can provide an illusion of being

505   large-scale by spreading replicated sampling over large areas, in many cases the individual sampling units are small (e.g., $1m^{-2}$ benthic grabs, or quadrats on the rocky shore) and may have questionable relevance to truly scaling-up our understanding of diversity-function linkages.

510   *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

515   long history of ecosystem ecology and biogeochemistry in marine biology and oceanography, we are uniquely poised to have a large contribution to this area of biodiversity-ecosystem functioning research.

Second, we highlight a need to increase our knowledge of marine biodiversity-ecosystem functioning relationships in salt marsh and pelagic habitats. Both were

520   underrepresented in our sample, and as such their results were less conclusive (although we note that several important studies in these systems, such as Finke & Denno 2005, Lee et al 1985, were excluded because they did not meet our criteria for inclusion). Notably, at the time of our literature search there had not been a single study with mangrove or coral reef systems.

525   Third, 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

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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 (Menge

530   1972, Paine 1969, 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.

Last, given the differences in our curve fitting versus previous studies (Cardinale et al. 2006, 2011), we suggest that marine studies need to increase the

535   range of species diversity manipulated whenever possible in order to facilitate the cross-comparability of our results to those of other systems.

We also note that we know almost nothing about how diversity at one trophic level affects the standing stock biomass and production at higher trophic levels (but see Lefcheck et al. 2012). Our data set included only two experiments (Gamfeldt et al.

540   2005, Gustafsson and Bostrom 2009). Furthermore, our analyses did not consider trophic cascades, of which there are many prominent examples in the marine realm (Eriksson et al. 2009, Estes et al. 1998, 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

545   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 e.g. Bruno and Cardinale 2008, Duffy et al. 2007, Preisser et al. 2005). Further studies are necessary if we are

550   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,

555   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

560   spatial scale and heterogeneity, realistic local extinction scenarios, and other

environmental factors (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. 2009, Tomimatsu et al. 2013). Unique opportunities for testing the potential

565 importance of diversity in influencing ecosystem processes may arise in the growing number of restoration projects in marine systems (see e.g. Doherty and Zedler for a case study in salt marshes). We also need to explicitly consider ecosystem services (Cardinale et al. 2012), since it is unclear how functions link to the processes human society is interested in (Balvanera et al. 2014). Only by expanding the scope of our

570 research can we get a more thorough understanding of the consequences of changes in marine biodiversity.

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multiple ecosystem functions in grassland communities requires higher biodiversity. - Proc. Nat. Acad. Sci. USA 107: 1443-1446.

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

Paper	System	Number of experiments
Blake and Duffy (2010)	Seagrass	12
Boyer et al. (2009)	Hard substrate	12
Bracken et al. (2008)	Hard substrate	16
Bracken and Stachowicz (2006)	Hard substrate	3
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 (2009)	Hard substrate	2
Byrnes and Stachowicz (2009)	Hard substrate	1
Callaway et al. (2003)	Salt marsh	3
Dam and Lopes (2003)	Pelagic	6
Douglass et al. (2008)	Hard substrate	20
Duffy et al. (2001)	Seagrass	2
Duffy et al. (2003)	Seagrass	2
Duffy et al. (2005)	Seagrass	4
Ericson et al. (2009)	Hard substrate	2
Foster et al. (1999)	Hard substrate	3
Gamfeldt et al. (2005)	Pelagic	9
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	2
Gustafsson and Boström (2009)	Seagrass	2
Hillebrand et al. (2009)	Hard substrate	2
Ieno et al. (2006)	Soft substrate	3
Jaschinski et al. (2009)	Seagrass	2
Karlson et al. (2010)	Soft substrate	3
Karlson et al. (2011)	Soft substrate	4
Matthiessen et al. (2007)	Hard substrate	8
Mermillod-Blondin et al. (2005)	Soft substrate	5
Moore and Fairweather (2006)	Seagrass	1
Moorthi et al. (2008)	Soft substrate	6
Murray and Marcus (2002)	Pelagic	3
Norling et al. (2007)	Soft substrate	5
O'Connor and Bruno (2009)	Hard substrate	2
O'Connor et al. (2008)	Hard substrate	1
Salo et al. (2009)	Seagrass	4
Stachowicz et al. (2008)	Hard substrate	1
Stachowicz et al. (2008)	Hard substrate	1
Vanelslander et al. (2009)	Soft substrate	1

1000 **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}, number 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}, number 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} hr^{-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)

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Table 3. Results from AIC analyses for each function category and species richness-function curve relationship.

Production	AIC	AIC weight	Delta AIC
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

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Figure legends

Figure 1. A global map showing the location of the experiments included in this meta-analysis.

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).

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.

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.

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.

Supplementary Appendices

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).
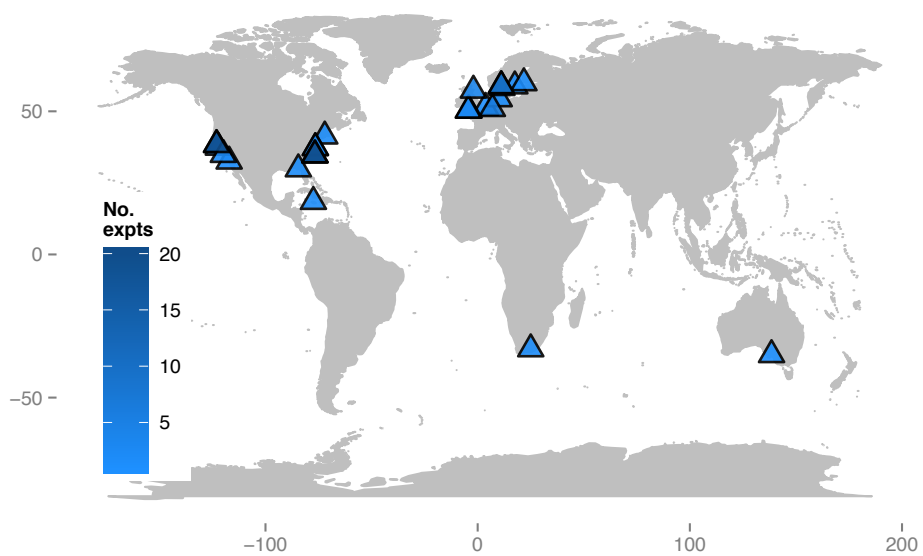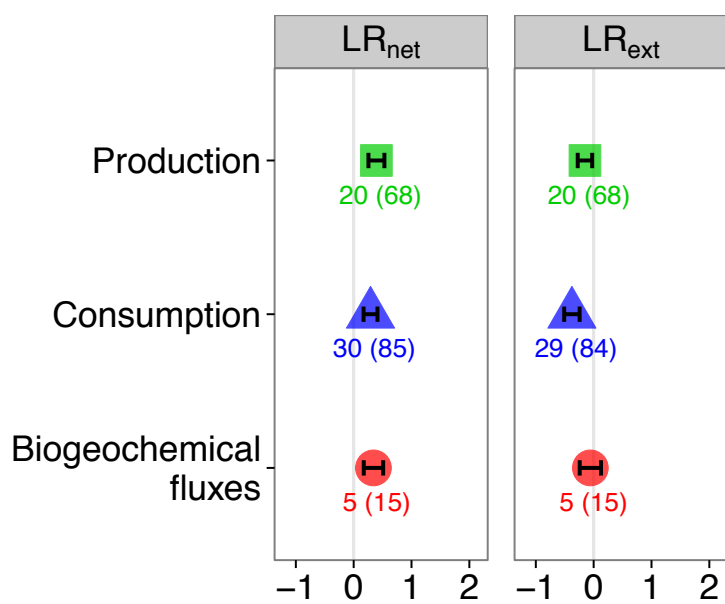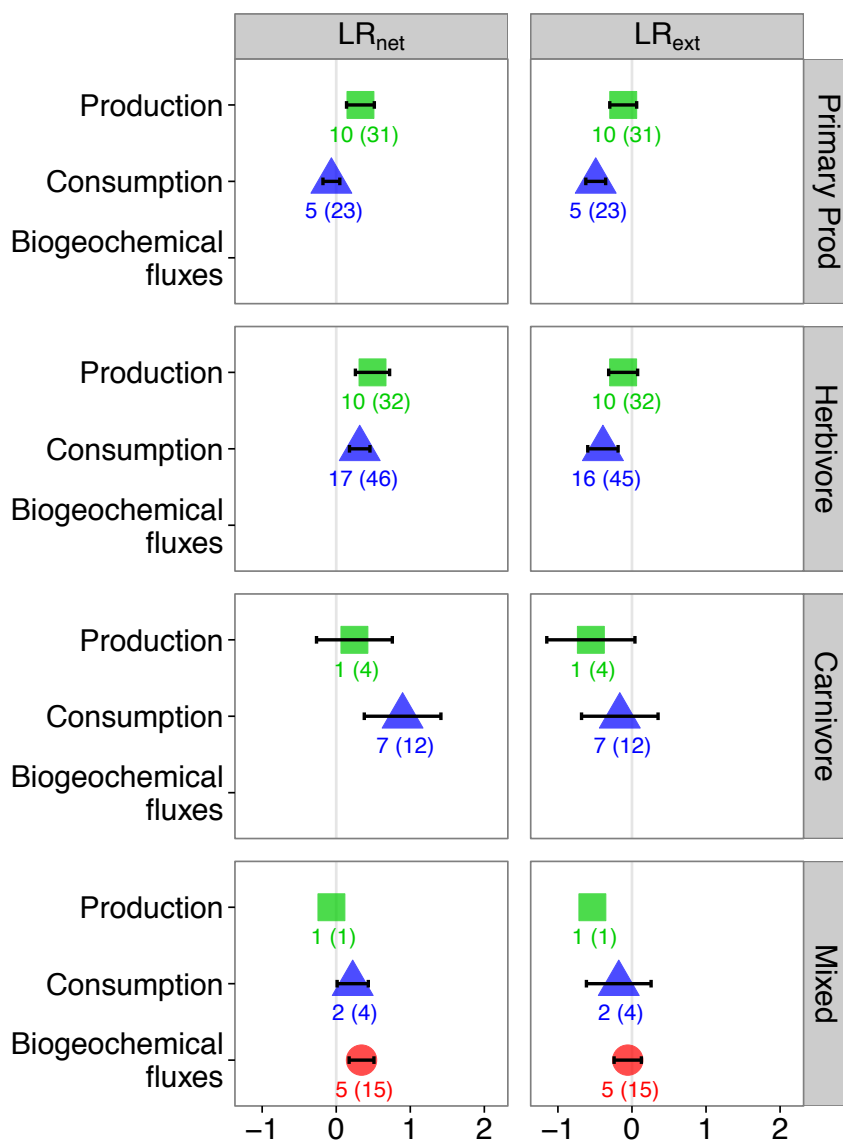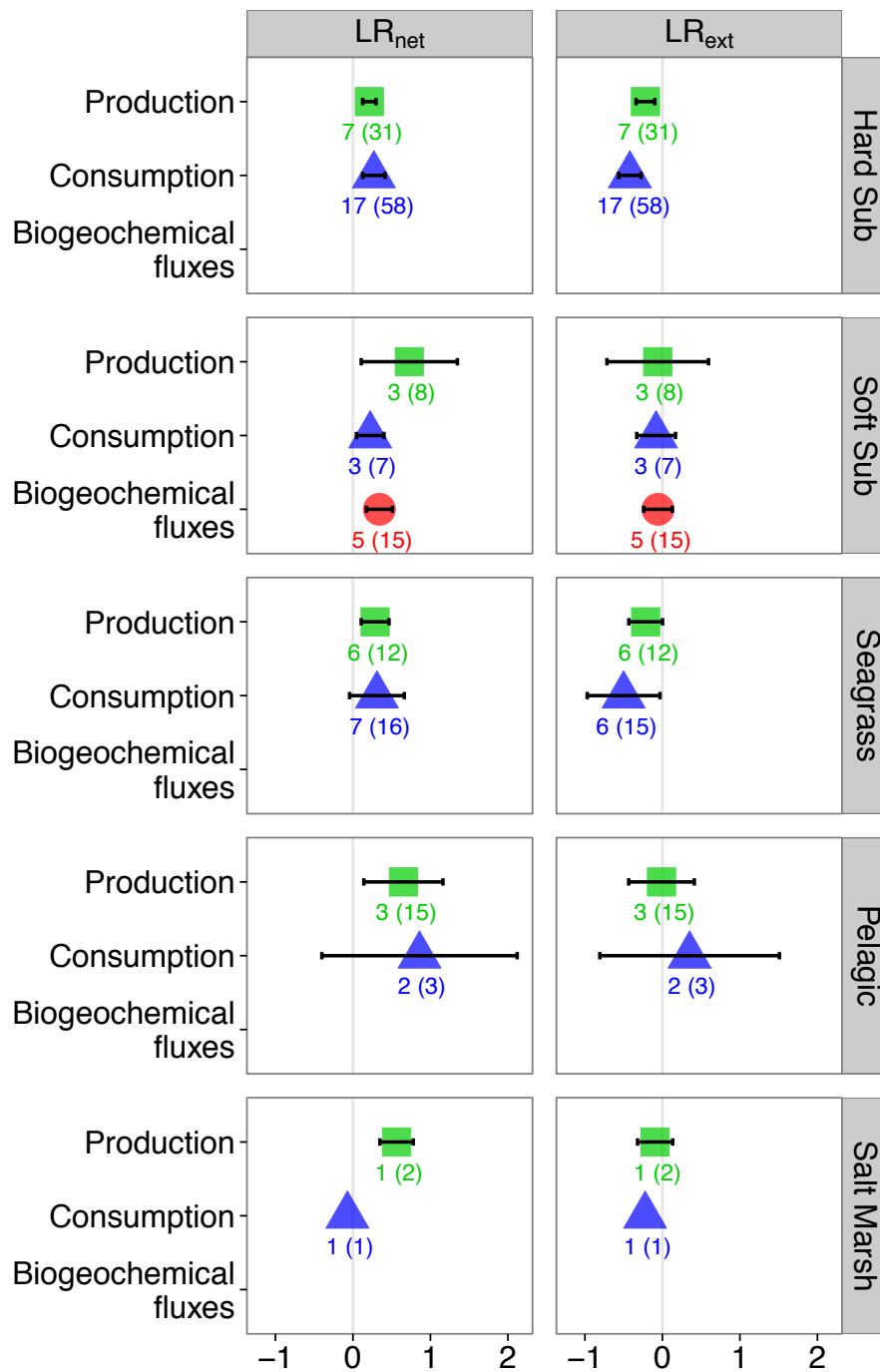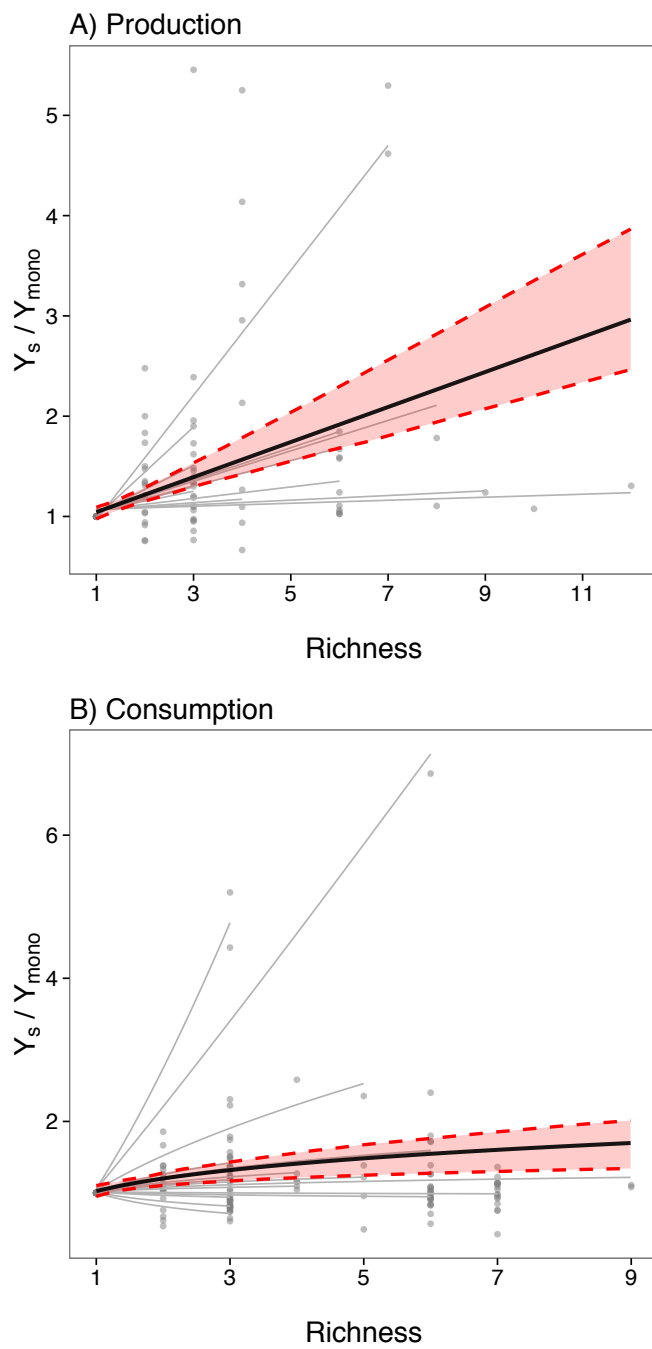
1040   **Figure 1**.
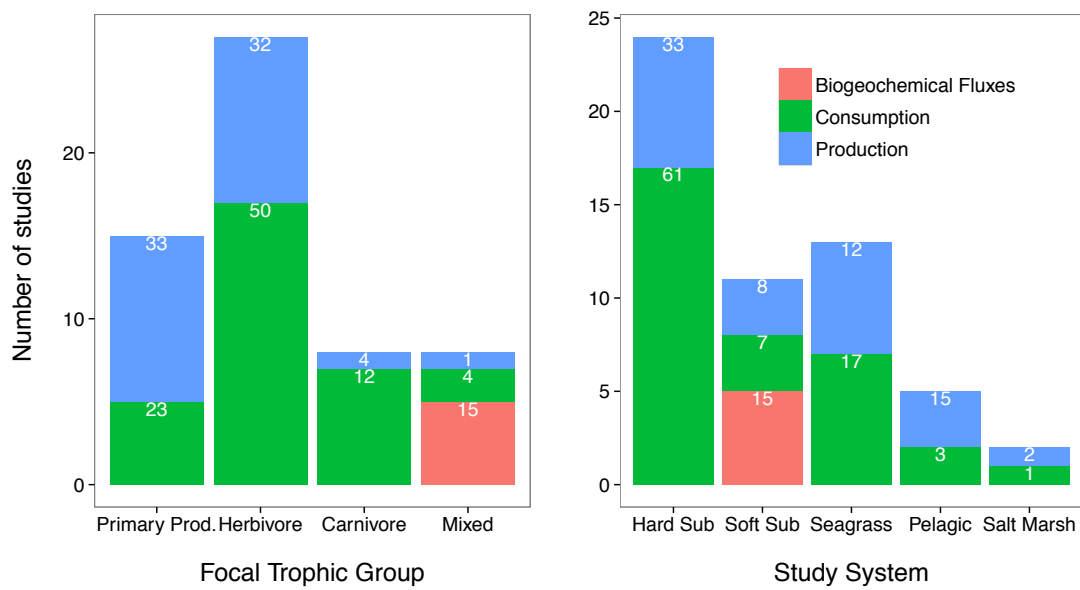
Figure 2.

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Figure 3.

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Figure 4.

Figure 5.

Figure 6.