Biogeochemical implications of biodiversity and community structure across multiple coastal ecosystems

Jacob E. Allgeier,[1,4] Craig A. Layman,[1] Peter J. Mumby,[2] and Amy D. Rosemond[3]

[1]*Department of Applied Ecology, North Carolina State University, 127 David Clark Labs, Raleigh, North Carolina 27695-7617 USA*
[2]*Marine Spatial Ecology Lab, University of Queensland, St. Lucia, Brisbane, Queensland 4072 Australia*
[3]*Odum School of Ecology, University of Georgia, 140 East Green Street, Athens, Georgia 30602 USA*

Abstract. Small-scale experiments and theory suggest that ecological functions provided by communities become more stable with increased species richness. Whether these patterns manifest at regional spatial scales and within species-rich communities (e.g., coral reefs) is largely unknown. We quantified five biogeochemical processes, and an aggregate measure of multifunctionality, in species-rich coastal fish communities to test three questions: (1) Do previously predicted biodiversity–ecosystem-function relationships hold across large spatial scales and in highly diverse communities? (2) Can additional covariates of community structure improve these relationships? (3) What is the role of community biomass and functional group diversity in maintaining biogeochemical processes under various scenarios of species loss across ecosystem types? These questions were tested across a large regional gradient of coral reef, mangrove and seagrass ecosystems. Statistical models demonstrated that species richness and the mean maximum body size per species strongly predicted biogeochemical processes in all ecosystem types, but functional group diversity was only a weak predictor. Simulating three scenarios of species loss demonstrated that conserving community biomass alone increased the ability for communities to maintain ecosystem processes. Multifunctionality of biogeochemical processes was maintained least in simulations that conserved biomass and community structure, underscoring the relative lack of importance of community structure in maintaining multiple simultaneous ecosystem functions in this system. Findings suggest that conserving community biomass alone may be sufficient to sustain certain biogeochemical processes, but when considering conservation of multiple simultaneous biogeochemical processes, management efforts should focus first on species richness.

Key words: consumer-driven nutrient recycling; coral reef; diversity; ecosystem function; fish; food web; mangrove; nitrogen; nutrient storage and supply; phosphorus; richness; seagrass.

Introduction

A primary rationale for conservation of biodiversity is that species loss may undermine our ability to meet the rising demand for ecosystem services for growing human populations. Small-scale experiments and theory suggest that increased species richness or functional group richness is positively correlated with various ecosystem functions (e.g., biomass, nutrient and energy cycling, etc. [Loreau et al. 2001, Hooper et al. 2005]). The nature of biodiversity–ecosystem-function relationships, and the mechanisms by which they are governed (i.e., species dominance vs. species diversity), have been well studied in model communities (Tilman et al. 1997), yet our understanding remains limited in three primary ways. First, studies have largely focused on simple food webs that do not always encompass the levels of diversity found in many ecosystems, including many of those at

most risk (e.g., tropical rainforests and coral reefs [Duffy 2009, Hillebrand and Matthiessen 2009, Cardinale et al. 2012, Naeem et al. 2012]). Second, the extent to which biodiversity–ecosystem-function relationships hold across space is not well understood, particularly across large spatial scales of the same ecosystem type (Duffy 2009, Hillebrand and Matthiessen 2009, Cardinale et al. 2012, Naeem et al. 2012, but see Maestre et al. 2012). Third, biodiversity studies tend to occlude other possible community characteristics (e.g., trophic structure, body size, etc.) that may additionally mediate ecosystem functioning.

Coastal marine ecosystems, including coral reefs, mangroves, and seagrass beds, are among the most species-rich and productive ecosystems in the world. Despite yielding critical ecosystem services for society, they are also among the most heavily impacted by humans (Worm et al. 2006), e.g., resulting in drastic declines of coastal fisheries on which humans rely (Jackson et al. 2001). While ecological implications of such declines have been widely studied from a food web (i.e., top-down) perspective (Pauly et al. 1998, Essing-

ton et al. 2006), the role of fishes in mediating biogeochemical pathways (Vanni 2002), a critical ecosystem function (Naeem et al. 2012), is not well recognized. Namely, through stoichiometric processes of assimilation (storage in biomass) and regeneration (excretion), fishes are among the largest pools (Maranger et al. 2008) and fluxes of nutrients (Allgeier et al. 2013, Burkepile et al. 2013) in oligotrophic coastal waters, regulating energy and material pathways within these energetically efficient ecosystems (Deangelis 1980). These stoichiometric processes are governed by traits that are unique to each species, and thus provide a framework to understand mechanisms through which biodiversity mediates ecosystem function (Vanni et al. 2002).

Here we test basic biodiversity–ecosystem-function relationships using an extensive data set of 172 marine fish communities in six coastal ecosystem types across the Northern Antilles (Figs. 1, 2). Specifically, we ask three primary questions: (1) Do previously predicted biodiversity–ecosystem-function relationships hold across large spatial scales and in highly diverse communities? (2) Can additional covariates of community structure improve these relationships? (3) What is the role of community biomass and functional group diversity (i.e., trophic structure) in maintaining biogeochemical processes under various scenarios of species loss across ecosystem types?

To test these questions we quantify five biogeochemical processes of nutrient storage and supply (for nitrogen, N, and phosphorus, P), and an aggregate measure of multifunctionality (M) for 144 species across mangrove, seagrass, and four coral reef ecosystems. We apply statistical analyses to explore how variability in diversity metrics and community structure found across geographic gradients (and within different ecosystem types) affect consumer-mediated biogeochemical processes at the ecosystem level. We then simulate hypothetical scenarios of species loss to further explore the importance of species richness, community biomass, and functional group diversity for these same biogeochemical processes.

Methods

Study design

To address our focal questions, we first applied hierarchical mixed-effects models to test relationships between biodiversity and community structure, and biogeochemical processes (Question 1; Fig. 1B). We then simulated three scenarios of species loss, and applied qualitative and quantitative assessments of the degree to which biomass and functional group diversity (i.e., trophic structure) help maintain biogeochemical processes across all ecosystem types (Question 2; Fig. 1C). This study represents a companion to Allgeier et al. (2014), but here the focus is on biodiversity–ecosystem-function relationships, not the ecological implications of the ratio

of nutrient supply for these ecosystem types, namely coral reefs (Allgeier et al. 2014).

Our study used two primary data sets: survey data and a large quantitative data set on fish nutrient content and excretion. Survey data is from Mumby et al. (2006), and consists of identification and size estimates of 71 729 fish across 172 communities. The excretion data is from Allgeier et al. (2014) and consists of models for which processes of C, N, and P storage and N and P supply can be estimated as a function of wet mass for 144 fish species. The analysis consisted of three steps: (1) model all processes, plus multifunctionality (M), onto every fish in the data set; (2) quantify aggregate processes for each community and apply these data to hierarchical models (Question 1 and 2); (3) Conduct simulations for three scenarios of species loss for the average community of fish from each ecosystem type. (Question 3)

Surveys

We surveyed 172 fish communities across 82 sites within six different ecosystems (*Acropora* reef, gorgonian plains [see Plate 1], mangroves, *Montastraea* reef, patch reef, seagrass) across seven different islands in the Northern Antilles with relatively low fishing pressure (i.e., the Bahamas and Turks and Caicos [Mumby et al. 2006, Harborne et al. 2008]). Surveys consisted of multiple transects (typically 8–10), which were averaged per area following Mumby et al. (2006) and Harborne et al. (2008).

Models for nutrient excretion

Bayesian statistics allow parameters to be estimated based on observed distributions (the observed data), and prior distributions that allow knowledge from previous studies to be applied explicitly and quantitatively (McCarthy 2007). In this study, we used Bayesian statistics to develop models that predict excretion rate as a function of wet mass by informing empirical data (the observed data) with bioenergetics models (used to generate the priors), thus incorporating the two most widely applied methods to estimate fish excretion (Schreck and Moyle 1990b, Schaus et al. 1997, Whiles et al. 2009) into singular models of nutrient excretion by fishes. The modeling approach was developed such that if the empirical data were robust then the final model would primarily reflect these data (i.e., the priors developed from the bioenergetics model would only minimally inform the output). When the empirical data were not robust, due to lack of individual empirical measurements on rare species or high variability in the data, the final model would then be more of a reflection of the bioenergetics models (i.e., the priors would have more influence on the output). In doing so, this approach allowed us to underpin extensive empirical data to produce robust models with realistic error and fill gaps in the empirical data set for which empirical data was incomplete.

Fig. 1. Hierarchical conceptual model of research and hypotheses. (A) Empirical data used in statistical models to test for biodiversity effects, including the empirical survey data set, stoichiometric data set, and the total species and percentage of biomass accounted for by our study. (B) Hypotheses for biodiversity effects: (i) species richness has either a positive saturating nonlinear, or positive linear, relationship with ecosystem processes; (ii) species dominance, i.e., the degree to which individual species have disproportionate influence on ecosystem processes, here quantified with diversity indices (e.g., Simpson's diversity index), may be either positively or negatively related to ecosystem process; (iii) functional group (FG) diversity, here calculated using diversity indices for FGs, may be either positively or negatively related to ecosystem processes. (C) Three scenarios of species loss used in simulation models in this study: (i) no replacement, i.e., random removal of species without compensation; (ii) biomass, i.e., random removal with compensation to maintain total community biomass; and (iii) biomass + FG, i.e., random removal with compensation to maintain total community biomass and functional group diversity (i.e., trophic structure). The three plots are examples of potential outcomes from simulations, including bifurcation (left panel). (D) Hypothesized strength of model variance structure produced from the different scenarios of species loss (indicated by color) at each level of species richness associated with each ecosystem type.
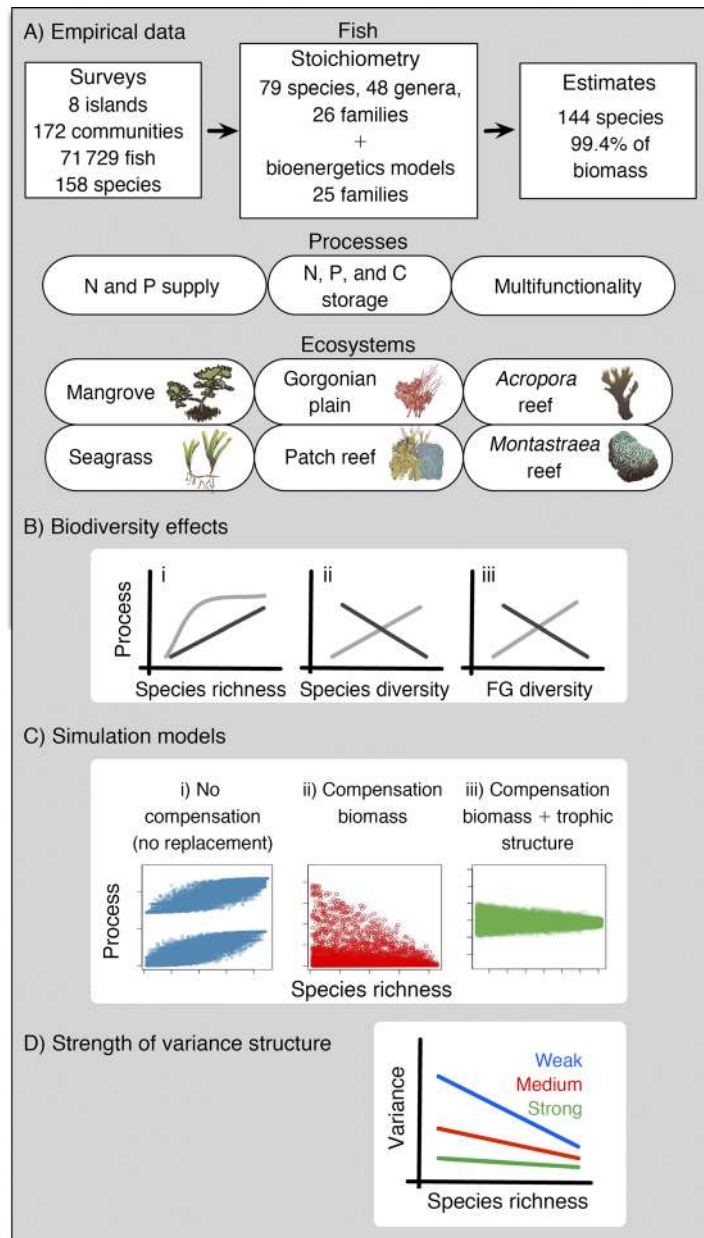
This modeling process consisted of four steps:

1) Bioenergetics models were developed for each family (and in some cases at the genus level) in our data set to estimate excretion rates of N and P for a given mass of an individual fish.

2) These data were run in an initial Bayesian simple linear regression analysis (using uninformative priors), to generate parameter estimates for the slope and intercept of each model ($y = mx + b$, where y is excretion rate, x is the wet mass of an individual, m is the slope, and b is the intercept) (see detailed methods for bioenergetics models in *Methods* and Appendix A).

3) A second Bayesian simple linear regression analysis was conducted using the empirical data. In this case, we used the posterior distributions (i.e., the mode and standard deviation) for the slope and intercept generated in Step 2 as the priors for the model (McCarthy 2007). In this way, we were able to take advantage of all available data and multiple approaches to generate robust estimates of nutrient supply by fishes.

4) The posterior distributions of these final estimates for the slope and intercept were then used to calculate the excretion rate for every fish within our survey data set. See *Ecosystem modeling* for further explanation.
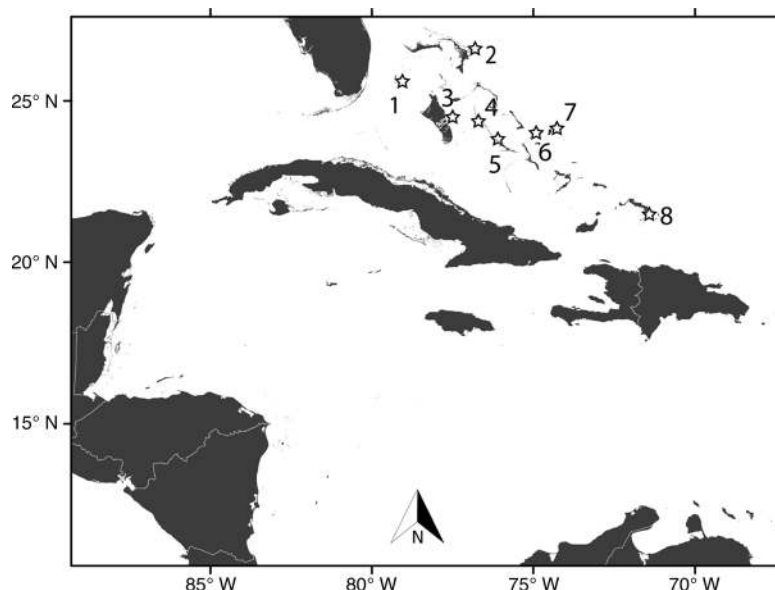
FIG. 2. Map of region where surveys were conducted. For simplicity, only the islands upon which multiple surveys were conducted are identified. Numbers represent Bimini, 1; Abaco, 2; Andros, 3; Exuma Cays Land and Sea Park, 4; Lee Stocking Island, 5; Conception Island, 6; San Salvador, 7; South Turks and Caicos, 8.

Bioenergetics models

Bioenergetics models use a mass balance approach given a priori knowledge of the natural history (e.g., diet, feeding activity), physiology (e.g., stoichiometry of predator and prey, assimilation efficiency of nutrients, consumption rates, energy density of prey) and environmental conditions (temperature) to estimate nutrient excretion (Schreck and Moyle 1990b, Hanson et al. 1997). We followed the approach to construct bioenergetics models, and used the same diet stoichiometry data as found in Allgeier et al. (2013, 2014). In total, bioenergetic models for 31 genus and 25 families within our surveys were developed (Appendix A).

Empirical excretion estimates

All fish were captured using hook and line or traps on Abaco Island, the Bahamas between 2008–2011. Fish were captured in coral reef, mangrove, and seagrass ecosystem types representing all of the ecosystem types for which excretion rates were modeled herein. Fish were pooled across ecosystem type, such that individuals from a given species could have been caught in any one or all ecosystems. We accounted for potential differences in resource availability across ecosystem type, which would be predicted to affect recycling rates, in two ways: (1) individuals within a given species were often collected from different ecosystem types and potential variation across ecosystem type was pooled, and thus accounted for, in our empirical models, and (2) we modeled error for diet nutrient content in our bioenergetics models (Appendix A). Excretion rates, for nitrogen-NH_4^+ and soluble reactive phosphorus (SRP), were measured in

situ following the methodologies of Schaus et al. (1997), as modified by Whiles et al. (2009). Values were control corrected through the use of multiple (typically $n = 6$) identical control incubation bags without fish (see Appendix B for details on nutrient analyses). Each fish used for excretion experiments ($n = 665$ individual fish, 79 species, 46 genera and 26 families; size range: 2–107 cm) was weighed for wet mass and measured to standard length. Fish were identified, and dissected to remove stomach contents, and then frozen for transport to the University of Georgia's (UGA) Odum School of Ecology and processed for elemental content (C, N, and P). UGA's Institutional Animal Care and Use Committee approved protocols for the capture and handling of fish (AUP #A2009-10003-0) were used. Water samples (filtered with 0.45-μm Whatman nylon membrane filters) were immediately placed on ice and, within 10 hours, analyzed for NH_4 using the methodologies of Taylor et al. (2007), or frozen for transport to UGA for SRP analyses using the ascorbic acid method and colorimetric analyses (APHA 1995; Appendix B).

Bayesian excretion models

Previous research on fish nutrient stoichiometry has shown that variation within families is relatively constrained (Vanni et al. 2002). As such, we used genus- or family-level bioenergetics models to inform empirical data in a Bayesian framework (i.e., bioenergetics models were employed to constrain excess variance in empirical excretion models when present). To further illustrate this approach, we follow each step taken to generate the final equation (excretion rate = wet mass × slope + intercept) with an example species: gray snapper (Lutjanus griseus).

Step 1: A genus-level bioenergetics model for *Lutjanus* was developed. Step 2: A Bayesian simple linear analyses was run using the size-specific data generated from the bioenergetics model. Step 3: A second Bayesian simple linear analysis was run using the empirical excretion data (i.e., collected from individual gray snapper; $n = 70$ fish), whereby the priors for this model were determined by the estimates for the slope and intercept calculated from the bioenergetics data in Step 2. Step 4: The estimates (and standard deviation) for the slope and intercept from this final model were applied to calculate the excretion rate for all gray snapper found within the data set using Monte Carlo simulations (see *Ecosystem modeling*).

In the case of the gray snapper models, the empirical data were robust and thus the priors generated from the bioenergetics model had little influence on the final model (e.g., the slope from the empirical data alone, the bioenergetics model, and the final model were empirical $m = 0.000018$, bioenergetic $m = 0.0001$, final $m = 0.000022$). In cases where the empirical data was less robust, the bioenergetics model would have more influence on the final slope estimate. In all cases, the prior estimates influenced the variance associated with each parameter estimate. To account for all potential sources of error we used Monte Carlo simulations to perpetuate uncertainty into our final estimates of excretion for each individual fish (see *Ecosystem modeling*).

All models were constructed at the level of taxonomic resolution for which we had optimal data. For example, if there were not sufficient empirical data at the species level to generate significant linear models of wet mass vs. excretion (at $\alpha = 0.1$, typically more than eight individuals), data would be pooled among species within the same genus and informed with the appropriate genus-level bioenergetics model. Using this approach, we developed 27 species-, 25 genus-, and 16 family-level models. With these models nutrient supply and storage could be estimated for 144 of the 158 species. Using this approach we accounted for 99.4% of the biomass of fishes within the field surveys.

All models were run with three chains for 50 000 iterations with a burn-in period of 1000. Data for excretion models were not transformed and assumptions of normality were met. Bayesian analysis was run using the *rjags* package in R (R Core Development Team 2012).

Ecosystem modeling

Excretion estimates were modeled onto each individual fish ($n = 71\,729$ fish) using the equations generated from the Bayesian models, within all communities ($n = 172$ communities, within 82 independent sites), to quantify species-level and then aggregate community-level rates of N and P supply and storage. Fish nutrient supply is a function of body size, organism identity, and diet (Schreck and Moyle 1990a, Vanni et al. 2002). As such, we used Monte Carlo simulations to model

uncertainty into our estimates of fish nutrient supply for individual fish within the data set. For each fish, we sampled from the posterior distribution of both the slope and intercept from our Bayesian excretion models to calculate 1000 mass-based species-specific excretion estimates (Robert and Casella 2010). These values were summed to provide a distribution of community-level aggregate estimates ($n = 1000$) of N and P supply. We applied the same methodology to calculate nutrient storage, whereas, in this case, we sampled 1000 times from the normal distribution (mean ± standard deviation) associated with our stoichiometric estimates for body nutrient content at each taxonomic level (typically genus or species). In doing so, we modeled realistic estimates of error into each step of our analysis to create a range of values that represent a realistic distribution of nutrient supply and storage for every fish and the entire community. Because we sampled from a normal distributions for each estimate, this error propagation approach should not inherently alter the mean value of the aggregate community-level excretion, but instead provide information as to how much variability there may be in this mean as a result of potential error and natural variability.

Hierarchical mixed-effects models

We used hierarchical mixed effects models and information theory (Akaike information criterion, AIC_c [Burnham and Anderson 2002]), to explore the relationship between the aggregate supply, and storage of nutrients and multifunctionality (M) and community assembly. To do so, we ran six separate models, one for each of the ecosystem processes of interest and for M. All models included the same six parameters: species richness, species diversity (SD, the reciprocal of Simpson's index [Simpson 1949]), functional group diversity (FGD), mean trophic level (TL), mean maximum size of each species within the community (L_{max}) calculated following Nicholson and Jennings (2004), and skewness of the size frequency distribution of the community (S_{size} [Joanes and Gill 1998]; Appendix C). Biomass has long been recognized to be a strong predictor of stoichiometric properties (Sterner and Elser 2002) and, in the case of this study, was directly used to calculate our response values. For this reason, we did not include biomass as a predictor in our models (Appendix C). Models for N and P storage and recycling were similar to those published in Allgeier et al. (2014), which examined the roles of the same explanatory variables on nutrient content (N, P) as well as stoichiometry (N:P) in fish excretion and storage. The present analysis uses most of the same data, but tests the relative strength of predictor variables by employing a different model structure in which data were standardized to allow for more formal comparisons of predictor strengths (i.e., allowing quantitative assessment of the relative effect size and direction of each predictor). Here we also test the effects of species loss on biogeochemical response

variables, including carbon and multifunctionality (both not included in Allgeier et al. [2014]).

Multifunctionality was calculated following Maestre et al. (2012), whereby we calculated the average of the Z scores for each ecosystem process of interest. Z scores were calculated from log-transformed normalized data as Z score $= (x - \mu)/\sigma$; where x is the site-level ecosystem process, μ is the mean value for all sites, and σ is the standard deviation of all sites. This index was chosen for three primary reasons: (1) it follows a normal distribution (Kolomgorov-Smirnof test, df $= 81$, $P = 0.18$ when calculated for use in mixed-effects models, Kolomgorov-Smirnof test, df $= 143$, $P = 0.79$, when calculated for simulation models) and thus is applicable to the modeling approach we used herein, (2) all of our response variables were positively correlated, and (3) Z scores do not constrain the variability found in the raw data (Maestre et al. 2012).

We averaged the 172 fish communities at the site level ($n = 82$ sites) to account for variability that may exist within sites. Site and ecosystem were held as random effects in all models to control for the confounding effects that may be present due to site or ecosystem differences. In all cases, both random effects were for the intercept only as the random slope, or random intercept and slope, models were always significantly different ($P > 0.001$) and selected against using Akaike's information criterion (Zuur et al. 2009). Models were run using the *lme4* package in R (R Development Core Team 2012). All response variables, as well as richness, SD, FGD, and L_{max}, were log-transformed to ensure linear relationships and all predictors were standardized in order to make comparisons among estimates. In all cases, model assumptions of normality and homogeneity of variance were met (Appendix C).

Simulation models

We conducted three types of simulations of community disassembly: (1) random removal without replacement (the null model, hereafter, no-replacement models), (2) removal with compensation of biomass by any remaining species (hereafter, biomass models), and (3) removal with compensation of biomass whereby the biomass of all FG remained constant for each species combination (hereafter, biomass + FG models). In each case whereby biomass was compensated due to species loss, the proportion of biomass for each simulated community was kept within ±2.5% of the mean biomass for its respective ecosystem type. All simulations were initially parameterized using the nonrandom average community structure and richness associated with each ecosystem type and the entire coastal ecosystem, as calculated in our surveys (*Acropora* reef, 68 species; gorgonian plains, 98 species; mangroves, 48 species; *Montastraea* reef, 114 species; patch reef, 86 species; seagrass, 45 species; entire region, 144 species). For each level of species richness, we simulated 500 combinations of communities (created from random draws of species

until that given level of richness was achieved) to create distinct communities. For each community, the aggregate sum of each ecosystem process and M was calculated.

Our simulations may not precisely mirror real scenarios of community disassembly, as we had to limit the complexity through which species loss occurred (increasingly complex scenarios would both be nearly impossible due to the complexity of unknown ecological interactions and would render model simulations intractable). For example, in real coral reef ecosystems, species loss can coincide with replacement by other species whereby the biomass of the community can be maintained or even exceed the biomass of the historical community (e.g., the loss of key predators causes top-down release of prey species allowing their proliferation). Our biomass simulations sought to approximate this reality by generating all (or at least most) potential combinations of communities that could arise from such a scenario. These simulations likely generated species combinations that are not probable (e.g., a community in which only predators remained) detracting from realism in some cases. Nonetheless, these simulations allow us to isolate the specific role of community biomass in maintaining consumer-mediated biogeochemical processes, and thus it provides important theoretical and applied perspective into these ecosystems and the biodiversity–ecosystem-function literature.

Simulations allowed for two tests. First, a qualitative assessment of the variance associated with each process within each ecosystem type. Here we were primarily looking for obvious bifurcations in the simulated data. Bifurcations indicate disproportionate effects on ecosystem processes by single (or a few) species on a given ecosystem process (i.e., species identity [Solan et al. 2004, Bunker et al. 2005, McIntyre et al. 2007]), whereby, when this species is lost, a fundamental shift in aggregate ecosystem process occurs. Bifurcations allow inference regarding the degree of disproportionate species effects (i.e., species identity effects; Fig. 1C, panel i).

A second test quantified the variance associated with the response axis for each simulation. In the case of our study, the variance represents a measure of how well a given process was maintained under all species combinations for any given level of richness, and in particular allows a more quantitative measure of data bifurcation. That is, if all species contributed relatively equally to a given process, i.e., high species evenness (Tilman et al. 1997), then the variance would be equal for all levels of species richness. Conversely, when a single (or few) species has a disproportionate role in this process, i.e., species identity (Tilman et al. 1997), as would be indicated by a bifurcation in the data, then the variance would be expected to be greater. As such, comparing how much variation exists among ecosystem types and, importantly, among different scenarios of species loss, allows inference to be made regarding the relative

PLATE 1. Nassau grouper, one of the more dominant species in our study, on a typical gorgonian-dominated reef in the Bahamas. Photo credit: C. A. Layman.

importance of maintaining community biomass or functional group diversity (i.e., trophic structure) in the face of species loss. To do this, the normalized root mean squared error (NRMSE; [100 × RMSE/max(response) − min(response)]) was calculated for each simulation (Moore et al. 2010). A generalized linear model was then applied for each biogeochemical process, to assess the relationship between NRMSE of each ecosystem type and the initial species richness of the community. The slope and the intercept (here the mean because the data were centered) were then used to make comparisons among the three scenarios of species loss.

RESULTS

Hierarchical linear mixed-effects models and information theory (Akaike information criterion corrected for sample size; AIC_c [Burnham and Anderson 2002]) revealed that best predictors of all ecosystem processes were species richness (i.e., positive saturating relationship; gray line Fig. 1B, panel i, Table 1; see Appendix D for raw plots of richness against all ecosystem processes) and mean L_{max} of individuals in the community (positive relationship, Table 1). Because the parameters were standardized (Gelman and Hill 2007), estimates indicate a relative effect size. As such, richness was the best predictor of all ecosystem processes, followed by L_{max}, though their relative importance was very similar in the multifunctionality, M, models. For all processes, with the exception of M, species diversity (i.e., Simpson's index [SD], negative relationship; black line in Fig. 1B, panel ii) was included in all top models ($\Delta AIC < 10$), but in all cases the effect of this

predictor was weak relative to richness or L_{max} (Table 1; see Appendix D for untransformed plots of SD against ecosystem processes). Functional group diversity (i.e., trophic groups, FGD) was positively related to all ecosystem process and negatively related to M but, importantly, was both weak in effect size and not included in all top models (Table 1). Mean TL was the only other predictor that was present in all top models for M (always negative), but also had a small effect size relative to richness or L_{max}. TL was also an important predictor for P supply (positive relationship) and, in this case, had a relatively strong effect size and was included in all models. The skewness of size distribution (S_{size}) was found to have relatively weak relationships with all processes except P supply and N storage (both positive). However with all models, removing any parameter other than richness or L_{max} from the model does not substantially alter the R^2 or AIC values, emphasizing the overwhelming importance of these two parameters for the global model. To explore the importance of these two parameters further, we ran the P supply model without either richness or L_{max}. The R^2 and AIC_c values changed to 0.70 (a decrease of 0.22) and ~150 (an increase of 100), respectively, further highlighting the importance of richness and L_{max} for model fit. This additional test, however, also demonstrated that the model without these parameters (driven only by TL and FGD) still did remarkably well, explaining 70% of the variance in the data.

Simulations allowed for qualitative and quantitative assessment of the role of biomass and functional group diversity (i.e., trophic structure) for maintaining biogeochemical processes under different scenarios of

TABLE 1. Results from hierarchical mixed effects models exploring the relationship between aggregate nitrogen (N) and phosphorous (P) supply, and N, P, and carbon (C) storage of nutrients and mutlifunctionality (M) and six independent variables of community assembly.

Richness	SD	FGD	Mean TL	S_{size}	L_{max}	R^2	AIC	AIC$_c$	ΔAIC
P supply									
1.40	−0.58	0.19	0.31	0.19	1.02	0.92	−63.56	150.20	0.00
1.46	−0.48		0.33	0.18	1.04	0.92	−65.44	151.40	1.16
1.56	−0.61	0.17	0.35		0.89	0.92	−67.10	154.70	4.48
1.61	−0.53		0.37		0.91	0.91	−68.52	155.00	4.81
N supply									
1.62	−0.54		0.18		0.58	0.92	−58.57	135.10	0.00
1.60	−0.57	0.06	0.17		0.57	0.92	−58.38	137.30	2.15
1.61	−0.54		0.17	0.01	0.58	0.92	−58.55	137.60	2.47
1.49	−0.48				0.65	0.91	−61.57	138.60	3.53
1.58	−0.57	0.07	0.17	0.02	0.58	0.92	−58.31	139.70	4.60
1.47	−0.48			0.05	0.67	0.91	−61.32	140.60	5.49
1.48	−0.51	0.04			0.64	0.91	−61.47	140.90	5.79
1.45	−0.52	0.06		0.05	0.66	0.91	−61.13	142.80	7.64
P storage									
1.56	−0.46			0.18	1.19	0.93	−73.31	164.60	0.00
1.68	−0.50		0.12	0.16	1.13	0.93	−72.27	165.00	0.44
1.56	−0.54	0.12		0.19	1.18	0.93	−72.85	166.20	1.60
1.78	−0.53		0.15		1.03	0.93	−74.26	166.50	1.90
1.78	−0.68	0.19	0.14	0.17	1.07	0.93	−71.96	167.00	2.42
1.63	−0.48				1.10	0.93	−75.77	167.10	2.46
1.80	−0.59	0.08	0.15		1.02	0.93	−74.08	168.70	4.07
1.64	−0.52	0.06			1.09	0.93	−75.67	169.30	4.71
N storage									
1.71	−0.53		0.14	0.16	1.15	0.93	−70.17	160.80	0.00
1.58	−0.49			0.19	1.23	0.93	−71.90	161.80	0.94
1.68	−0.60	0.14	0.13	0.17	1.12	0.93	−69.35	161.80	0.96
1.56	−0.59	0.16		0.19	1.19	0.93	−70.77	162.00	1.21
1.85	−0.57		0.17		1.03	0.93	−72.34	162.70	1.82
1.84	−0.64	0.12	0.17		1.01	0.93	−71.75	164.00	3.17
1.66	−0.50				1.12	0.92	−74.48	164.50	3.64
1.77	−0.69	0.17			1.04	0.92	−74.53	167.00	6.20
C storage									
1.71	−0.53		0.15	0.15	1.14	0.93	−69.46	159.40	0.00
1.68	−0.59	0.12	0.14	0.16	1.12	0.93	−68.79	160.70	1.26
1.85	−0.57		0.18		1.03	0.93	−71.48	160.90	1.50
1.57	−0.49			0.18	1.23	0.93	−71.54	161.10	1.63
1.54	−0.57	0.15		0.19	1.20	0.93	−70.56	161.60	2.19
1.83	−0.63	0.11	0.18		1.01	0.93	−70.99	162.50	3.05
1.65	−0.50				1.12	0.92	−74.10	163.70	4.29
1.67	−0.60	0.14			1.10	0.93	−73.57	165.10	5.70
M									
0.14	−0.05		−0.08		0.11	0.72	53.70	−89.40	0.00
0.12		−0.04	−0.07		0.11	0.72	53.21	−88.40	0.98
0.10			−0.08		0.10	0.71	51.77	−88.00	1.40
0.14	−0.04	−0.02	−0.07		0.11	0.72	54.25	−88.00	1.44
0.15	−0.05		−0.07	−0.01	0.11	0.72	54.00	−87.50	1.93
0.13		−0.04	−0.07	−0.01	0.10	0.72	53.43	−86.40	3.08
0.15	−0.04	−0.03	−0.07	−0.01	0.10	0.73	54.54	−86.00	3.45
0.10			−0.08	−0.01	0.10	0.71	51.84	−85.70	3.73

Notes: Variables include species richness (richness), the number of species within a community; species diversity (SD) and functional group diversity (FGD), both measured by the reciprocal Simpsons' diversity index at the species level and functional group level based on discrete trophic delineations, respectively; mean trophic level (mean TL) and mean maximum size per species within the community (L_{max}); skewness of the size frequency distribution of the community (S_{size}); Akaike's information criterion (AIC); AIC corrected for sample size (AIC$_c$); and the change in AIC attributable to this model (ΔAIC). Top models (ΔAIC < 10) are shown for each response, with models decreasing in support from top to bottom. Empty cells indicate that the parameter was not in a model; the sign of the values associated with each parameter indicates the direction of change. Predictor variables were all standardized for ease of comparison among parameter estimates.

species loss. Qualitatively, three general patterns emerged (Fig. 1C, panels i–iii, Fig. 3). Bifurcations in simulated data (Fig. 1C, panel i) indicate disproportionate species effects on ecosystem processes (hereafter, species-identity effects), and thus the sensitivity of these ecosystem processes to species loss. While bifurcations might be mitigated by the compensatory dynamics of the simulations, e.g., the maintenance of community bio-

mass, the general paucity of bifurcations across all simulations suggests that contributions to nutrient cycling is relatively evenly dispersed across communities (i.e., species diversity, not species identity, may be driving biodiversity effects for most scenarios of species loss; Fig. 3, Appendix D: Figs. D1–D3). Data clouds that indicate a sharp reduction in variance with increasing species richness (Fig. 1C, panel ii), indicate that with increased species richness the range at which communities can affect biogeochemical processes substantially increases. Data clouds with less reduction in variance (Fig. 1C, panel iii) indicate that the identity of species present in the community tends to be less important for that particular biogeochemical process; this tended to occur in both scenarios in which biomass was compensated and for processes of storage. The increased propensity for communities to have larger rates of supply and storage with decreased species richness is a result of communities that are dominated by species that have large effects on biogeochemical processes in the biomass-only and the biomass + FG scenarios. For example, when simulating communities with species richness of two, a possible outcome is that the only two species remaining have relatively high recycling rates (or store large amounts of nutrients). In this case, if this community of two high impact species has the same biomass as a community with 80 species (including many species with a lower recycling rate of nutrients), the net outcome will be a substantially larger community level nutrient supply.

To quantitatively assess the degree to which biomass and functional group diversity affects the maintenance of biogeochemical processes under scenarios of species loss, we conducted simple linear regression analyses on the NRMSE for each process across all ecosystem types (i.e., for each simulation). The slopes of the two scenarios of species loss in which community biomass was maintained (both biomass-only and biomass + FG) was significantly less than the no-replacement scenarios (the latter of which effectively functions as the null model), for all three processes of storage (Fig. 4B; Table 2). There was no significant effect for either supply process or M (Fig. 4B; Table 2). With the exception of P storage, slopes did not differ between the biomass-only and biomass + FG scenarios (though, in all cases but M, slopes increased but not significantly). The mean variance of the two scenarios of species loss in which community biomass was maintained (both biomass-only and the biomass + FG) was significantly less than the no-replacement scenarios for all three processes of storage. The exceptions were processes of supply and M, whereby difference in the three scenarios were not different, or were significantly greater, respectively (Table 2).

DISCUSSION

Biodiversity–ecosystem-function research often relies on small-scale experiments that capture limited gradi-

ents of species richness, or meta-analyses and global scale analyses that may overlook important ecosystem-specific details. As such, there has been a consistent call for increased efforts to bridge these scales of research (Duffy 2009, Hillebrand and Matthiessen 2009, Cardinale et al. 2012, Naeem et al. 2012). Our study tackles this challenge by quantifying patterns of process across an unprecedented spatial scale in species-rich ecosystems. Our study also incorporates additional factors that may be important to consider as to how biogeochemical processes will change in the face of species loss. Results from our study underscore the importance of absolute species number as being a remarkably reliable predictor of biogeochemical processes, across large spatial scales and multiple ecosystem types. Our analyses did not include a temporal component, but using simulations we provide qualitative evidence that high levels of species richness increases the ability of ecosystems to maintain high functioning, whereby species loss had only potentially disproportionate effects in the coastal ecosystem with the lowest initial species richness (seagrass ecosystems). Importantly, our research also highlights the importance of the maintenance of community biomass, but not community structure, for biogeochemical processes. That is, we demonstrate that community biomass alone is nearly sufficient to maintain biogeochemical processes in the face of species loss.

Hierarchical models revealed the importance of different biodiversity and community characteristics with surprising consistencies across different biogeochemical processes. Most notable was that species richness was retained in all models for all processes, and in each case had the largest effect size of any parameter. It should be noted that, because we were unable to measure empirical excretion rates for all species, and thus relied to some extent on bioenergetics models at the family or genus level to estimate species-level excretion, our approach may mask potential differences among species. In this sense, our findings that the importance of species richness for biogeochemical processes is conservative. This strongly supports previous biodiversity–ecosystem-function research and provides a needed test of this relationship across space. Maestre et al. (2012) recently found that species richness was among the most important predictors of multi-functionality across an impressive global scale of different dryland ecosystem types. Our study takes a similar approach but makes comparisons within multiple ecosystem types across a large region of the Caribbean (e.g., coral reefs among similar islands). Interestingly, though richness was the strongest predictor of multifunctionality in the Maestre et al. (2012) study, the support for this parameter was relatively weak (e.g., $R^2 = 0.03$, $P = 0.009$ for relationships between multifunctionality and species richness using transformed data). In our study, species richness was the best predictor for all processes, and explained a large proportion of the variance in the data as a single
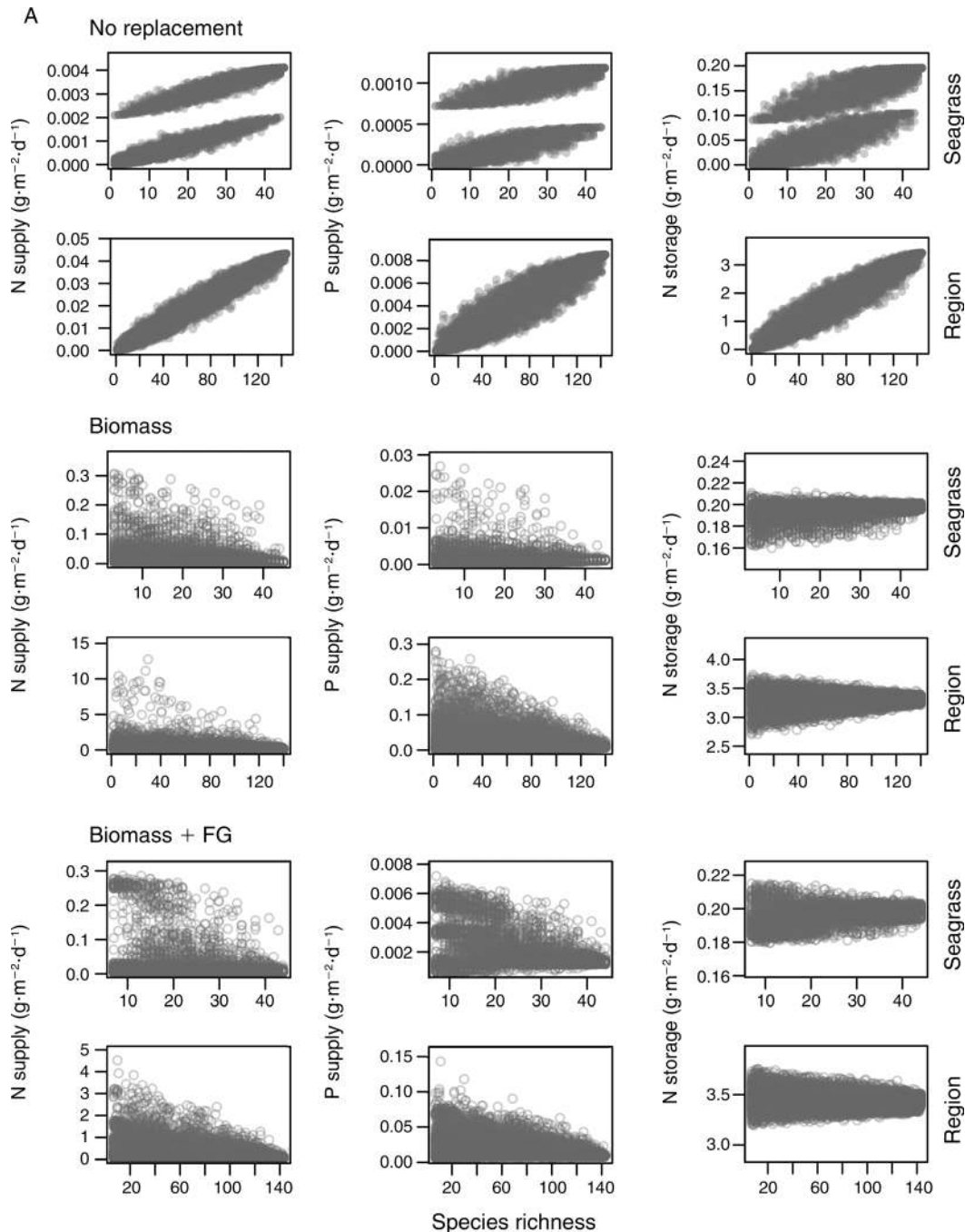
Fig. 3. Results from probabilistic simulation models for the three different scenarios of species loss within a given community: no replacement, biomass, and biomass + FG. Only fish communities associated with seagrass ecosystems and the entire region are shown for simplicity (for all others, see Appendix D: Figs. D1–D3). For each biplot, the y-axis is the rate for each of the five processes and multifunctionality (M). Each data point within a graph indicates the aggregate process rate for each simulated community with its corresponding species richness (x-axis).

predictor ($R^2 = 0.57$, $P < 0.001$ for relationships between the same index of multifunctionality and species richness using transformed data). Regardless of the strength of support for these relationships, collectively, these studies provide consistent results that suggest

species richness is a very important predictor of ecosystem processes and multifunctionality.

Two additional measures of biodiversity, species diversity (i.e., Simpson's index; SD), and functional group diversity (FGD), had relatively weak effects in
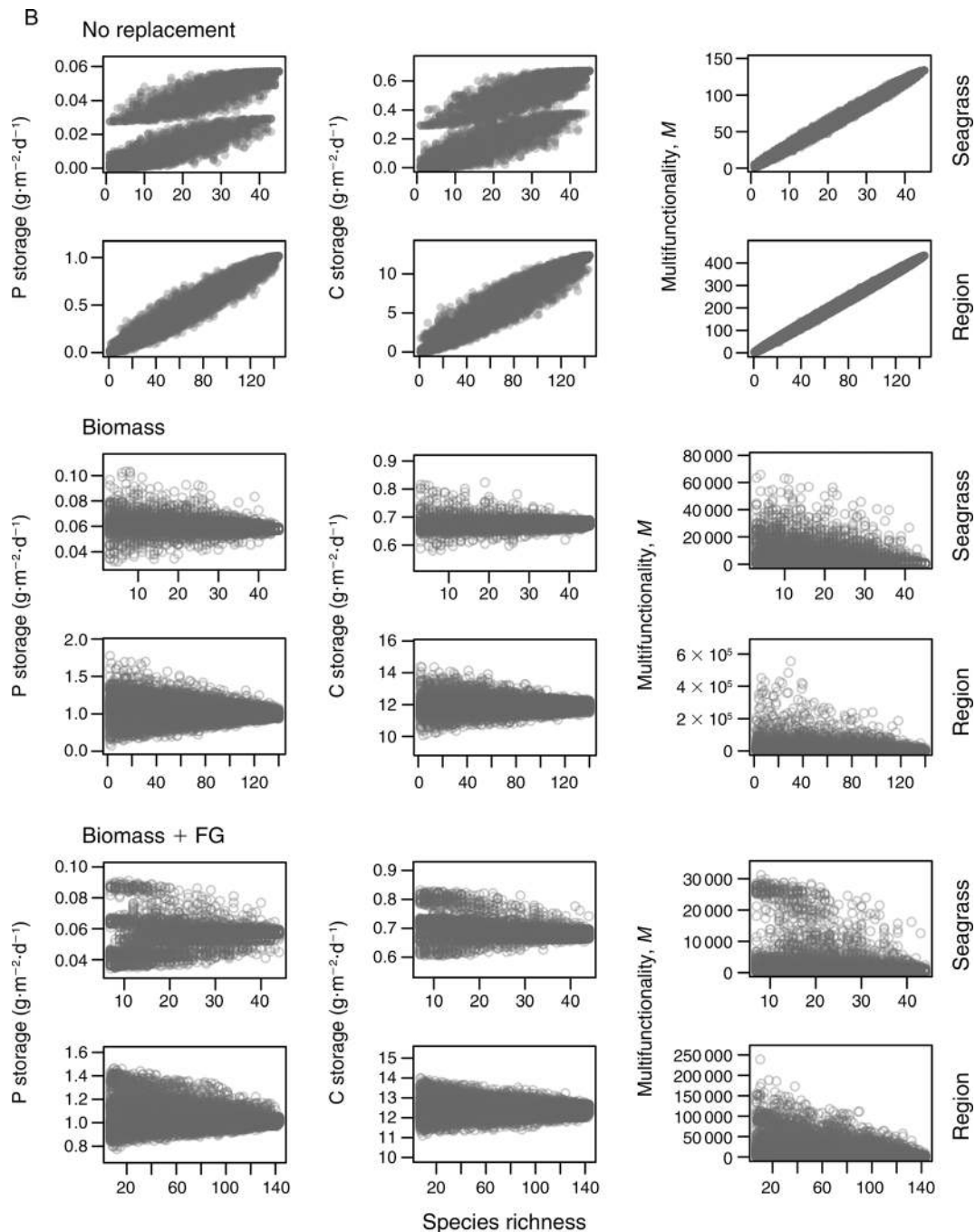
FIG. 3. Continued.

comparison to species richness. SD was negatively related to all responses (Table 1) and, though it was present in the top models for all processes (with the exception of M), it was always associated with a relatively weak effect size. The negative relationship in our global models suggests that higher biogeochemical processes were found when species assemblages had relatively uneven diversity, but this trend is notably driven by seagrass ecosystems. Further, it is notable that the SD–ecosystem-function relationships were positive when regressed independently (Appendix D). The opposing directions (between the independent regressions and the global model) and the weak nature of all of the relationships ($R^2 < 0.15$ for all independent processes), underscores the relative lack of importance of SD for ecosystem function (Gelman

and Hill 2007). FGD, on the other hand, was not present in most top models. The exception to this was for P supply, for which the relationship was positive. This finding may be intuitive in that a more even distribution of functional groups within a community would suggest more predators are present. Predators supply P at higher rates than other groups due to the fact that their diet is rich in P (Schindler and Eby 1997, Allgeier et al. 2013). All slopes for FGD were positive, with the exception of M, which suggests that certain functional groups tend to disproportionately enhance multifunctionality, underscoring the importance of the identity of functional groups. But it is important to highlight that effect sizes for FGD in all models suggest that these trends are relatively unimportant in explaining variance associated with the different ecosystem processes. The relatively weak role of functional group diversity in our study is an important finding, as it contrasts many previous expectations (Naeem and Li 1997, Diaz and Cabido 2001, Duffy et al. 2007, Weigelt et al. 2008).

Basic community structure has also been shown to be important for ecological functions (Duffy et al. 2007, McIntyre et al. 2007). Exploring the relative importance of three parameters of community structure for biogeochemical processing revealed mixed support for this hypothesis. In particular, the mean maximum body size per species within each community, L_{max}, had strong and consistent relationships with the different ecosystem processes, and remained in the top model for every process (including M). A community that is characterized with a high L_{max} also tends to have high relative biomass (correlation $r = 0.64$; using the natural log of both parameters), and because many of these processes scale with biomass the strong relationship would be expected. The strong positive relationship between TL and P supply is likewise supported by previous work, whereby predatory fish have been shown to excrete high amounts of P relative to lower trophic level organisms (Schindler and Eby 1997). Finally, TL is the only parameter that had opposing slopes for M and other parameters. Two factors can be inferred from the relatively weak, negative relationship between TL and M. First, different trophic groups have varying degrees of influence on different processes (e.g., predators supply more P and herbivores more N, relative to body size [Schindler and Eby 1997, Allgeier et al. 2013]). Second, the trophic structure of a community is relatively unimportant for predicting multiple simultaneous functions, a finding that is supported by our simulations.

Given our findings from the statistical models, we extended our analyses through the use of simulations to further explore how communities would respond under various scenarios of species loss (reduction in richness) in which additional measures of community structure were maintained (e.g., biomass and function group

diversity). Previous work has shown that the biomass of single (or few) species can drive ecosystem function (i.e., overyielding [Cottingham et al. 2001]), a factor we were unable to test for in our statistical models given that biomass was directly used to calculate each response variable. Further, it is widely regarded that functional group diversity is important for the maintenance of ecosystem function (Diaz and Cabido 2001, Duffy et al. 2007, Weigelt et al. 2008), a previous finding that our statistical models refute. To provide additional tests of the influence of these two community characteristics (functional group diversity and biomass) on the maintenance of biogeochemical processes, we simulated three scenarios of species loss. Specifically, simulations were conducted whereby species loss occurred (1) randomly (null model); (2) randomly, but biomass loss (due to species loss) was compensated by the increase in biomass of other species (randomly chosen) that remained within the species pool; and (3) randomly, but the biomass of the community was maintained through compensation by increase in biomass of species within the same functional group as the species lost (Fig. 1C, panels i–iii, respectively). In doing so, we were able to explore two aspects of each community: the relative importance of biomass and the structure of the community for biogeochemical processes and the degree to which species identity or diversity maintained these processes (i.e., the degree to which a given process can be sustained under various levels of biodiversity).

Bifurcations produced from simulations indicate strongly disproportionate effects on ecosystem processes by single (or a few) species on a given ecosystem process (Solan et al. 2004, Bunker et al. 2005, McIntyre et al. 2007), whereby when this species is lost, a fundamental shift in aggregate ecosystem process occurs (Fig. 1C, panel i). While bifurcations might be mitigated by the compensatory dynamics of the simulations, e.g., the maintenance of community biomass, the general paucity of bifurcations across all simulations suggests that the roles of nutrient cycling are relatively evenly dispersed across these communities (i.e., species diversity, not species identity, may be driving biodiversity effects for most scenarios of species loss; Fig. 3, Figs. D1–D3). Exceptions are found in two cases. First, bifurcations were found within the processes that are most strongly driven by species-specific traits as opposed to biomass, e.g., P supply and storage (Fig. 3, Figs. D1–D3), suggesting that in these cases certain species have such dominant traits that they are driving these processes. Second, bifurcations emerged in the seagrass bed communities under the biomass + FG model scenarios, and strongly so under the no-replacement scenarios (Fig. 3, Figs. D1–D3), suggesting strong disproportionate species effects (species identity) in these communities. For example, total N supply by seagrass fish communities ($n = 45$ species, the lowest richness) was dominated by a single species of *Belonidae* (49%). As such, the loss of this one species would disproportion-
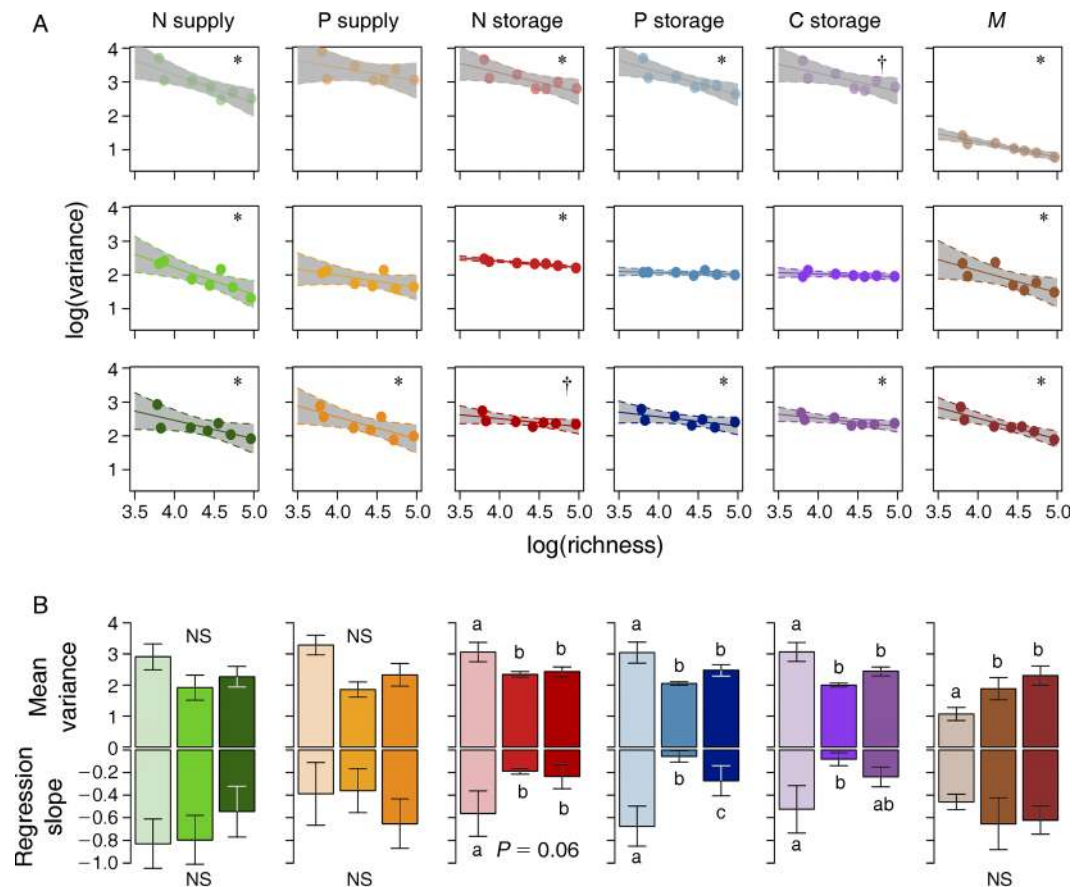
Fig. 4. (A) Relationship between model variance structure (normalized root mean square error; NRMSE, log-transformed) and species richness (log-transformed) for each fish community associated with each ecosystem type and across the entire region († $P < 0.1$; * $P < 0.05$; gray bands indicate 95% confidence intervals). (B) Bar plots of the mean value of the variance for each regression (top) and the slope for each regression (bottom). Error bars indicate SD of the mean and different letters indicate significant differences ($P < 0.05$) between bars within each individual plot; NS indicates not significant. Each color is associated with a given ecosystem process or M. Color shade indicates the type of simulation model: light, no replacement (left bar of each plot); medium, biomass (middle bar in each plot); dark, biomass + FG (right bar of each plot).

ately reduce N supply, as is represented by the obvious bifurcation in the data (Fig. 3, Figs. D1–D3). Interestingly, the only model scenario that produced indications of bifurcations for M in any ecosystem was the biomass + FG (Fig. 3, Figs. D1–D3), suggesting that the degree of overlap in species-level multifunctionality may be less within functional groups than among species across functional groups. This finding is consistent with the negative FG diversity and TL effects with M in our statistical models. This finding contrasts expectations of redundancy among species within the same functional groups (Loreau 2004, Hooper et al. 2005).

The biodiversity insurance hypothesis suggests that ecosystem processes are maintained by differences in species' responses to temporal environmental fluctuations (Cottingham et al. 2001). Insurance effects are typically measured over temporal scales (Yachi and Loreau 1999), allowing covariance among species' responses to be calculated (Cottingham et al. 2001).

Here, given that we did not have time-series data available for our communities, meaningful covariance of species responses over time could not be generated. Yet, comparing the collective variance for each simulation model across all ecosystem types allows meaningful inference regarding the ability of a given community to maintain ecosystem processes under various scenarios of species loss. In our analysis, the degree to which biodiversity maintained a given process was indicated by the slope between the NRMSE and initial richness of a given ecosystem type. The relative steepness of the slope indicates the relative importance of biodiversity for maintaining that process as it is associated with each scenario of species loss (Fig. 4).

Findings from this analysis demonstrated three main conclusions. First, maintaining community biomass negates the relative importance of biodiversity for all three processes of storage, i.e., the slopes for the models with biomass compensation is significantly less than the

JACOB E. ALLGEIER ET AL.

Table 2. Results from linear regression models for each ecosystem process for relationships between model variance structure (normalized root mean square error; NRMSE, log-transformed) and species richness (richness, log-transformed) for each fish community associated with each ecosystem type and across the entire region.

Parameter	Estimate	SE	t	P
N Supply				
Intercept	5.40	0.97	5.57	0.000
NR–B	1.13	1.37	0.83	0.420
BF–B	−0.76	1.36	−0.56	0.584
BF–NR	−1.89	1.35	−1.40	0.183
Slope	−0.80	0.22	−3.61	0.003
Slope NR–B	−0.03	0.31	−0.11	0.915
Slope BF–B	0.25	0.31	0.81	0.431
Slope BF–NR	0.28	0.31	0.92	0.372
P Supply				
Intercept	3.44	1.03	3.34	0.005
NR–B	1.55	1.45	1.06	0.304
BF–B	1.73	1.44	1.20	0.248
BF–NR	0.18	1.44	0.13	0.900
Slope	−0.36	0.23	−1.54	0.144
Slope NR–B	−0.03	0.33	−0.08	0.936
Slope BF–B	−0.29	0.33	−0.88	0.390
Slope BF–NR	−0.26	0.33	−0.80	0.434
N Storage				
Intercept	3.16	0.59	5.40	0.000
NR–B	2.36	0.83	2.85	0.012
BF–B	0.29	0.82	0.35	0.733
BF–NR	−2.07	0.82	−2.53	0.023
Slope	−0.19	0.13	−1.41	0.179
Slope NR–B	−0.38	0.19	−1.99	0.065
Slope BF–B	−0.05	0.19	−0.25	0.807
Slope BF–NR	0.33	0.19	1.76	0.099
P Storage				
Intercept	2.30	0.58	3.97	0.001
NR–B	3.69	0.82	4.51	0.000
BF–B	1.36	0.81	1.68	0.115
BF–NR	−2.33	0.81	−2.88	0.012
Slope	−0.06	0.13	−0.43	0.673
Slope NR–B	−0.62	0.19	−3.32	0.005
Slope BF–B	−0.22	0.19	−1.17	0.261
Slope BF–NR	0.40	0.18	2.17	0.046
C Storage				
Intercept	2.35	0.60	3.94	0.001
NR–B	3.01	0.84	3.56	0.003
BF–B	1.12	0.84	1.34	0.200
BF–NR	−1.89	0.83	−2.26	0.039
Slope	−0.08	0.14	−0.59	0.561
Slope NR–B	−0.44	0.19	−2.31	0.035
Slope BF–B	−0.16	0.19	−0.82	0.423
Slope BF–NR	0.29	0.19	1.51	0.152
M				
Intercept	4.74	0.68	6.93	0.000
NR–B	−1.66	0.97	−1.72	0.107
BF–B	0.27	0.96	0.28	0.780
BF–NR	−0.16	0.22	−0.74	0.473
Slope	−0.65	0.16	−4.20	0.001
Slope NR–B	0.19	0.22	0.87	0.396
Slope BF–B	0.03	0.22	0.15	0.887
Slope BF–NR	−0.16	0.22	−0.74	0.473

Notes: Values associate with graphs in Fig. 4. Abbreviations are B, biomass-only simulations; NR, random simulation (null); BF, biomass + FG simulations. The dash indicates comparisons between two simulation types. Response values are centered, thus intercept values indicate mean NMRSE values for all ecosystem types.

no-replacement models (Fig. 4). This finding is largely intuitive for both N and C storage in that differences among species in N or C body nutrient content have not typically been observed in fishes (Sterner and George 2000, Vanni et al. 2002), thus suggesting the role of biodiversity for these processes are likely minimal. However, P nutrient content has been found to vary relatively dramatically among fishes, particularly in species-rich communities (Vanni et al. 2002), and as such would be expected to have been influenced by the diversity of the community present. Second, the lack of significant effect for either supply process or M (Fig. 4B; Table 2) indicates that these processes are more strongly regulated by species-specific traits than community biomass. This conclusion is supported by previous research suggesting the importance of biodiversity for N and P supply (Vanni et al. 2002), as well as M (Hector and Bagchi 2007). Finally, the finding that, with the exception of P storage, slopes did not differ between the biomass-only and biomass + FG scenarios (though in all cases but M slopes increased but not significantly), emphasizes that maintaining functional group diversity does not generally enhance the maintenance of ecosystem function. The general significance of the finding is that while trophic complexity and functional group diversity has been widely cited for its importance for food web stability in aquatic food webs (Pauly et al. 1998, Duffy et al. 2005, 2007), these data instead suggest that species richness and biomass are most critical for maintaining biogeochemical processes.

The mean variance for each model provides an additional measure of the degree to which biogeochemical processes are maintained in the face of species loss, allowing inference regarding the relative importance of disproportionate species effects (species identity) for these processes, whereby the greater the variance the stronger the role of species identity. Similar to findings from the slope of these relationships, maintaining community biomass for all storage processes increased the overall ability of all communities to maintain these functions, but this did not improve when additionally maintaining functional group diversity (Fig. 4B; Table 2). M appears to be more strongly regulated by species-specific traits than by biomass or functional group diversity, as it was the only process in which mean variance decreased with greater regulation of community structure (Fig. 4). It is noteworthy that there were no significant differences in either the slope or the mean variance for either of the supply models (though there is a notable nonsignificant difference). This underscores the importance of species diversity for these two properties (i.e., supply of N and P) more so than all other processes quantified herein. This finding may be of critical significance for these ecosystems given the recent evidence of the important role that fish nutrient supply has been documented to have in these ecosystems (Allgeier et al. 2013, 2014, Burkepile et al. 2013, Layman et al. 2013).

Our findings collectively demonstrate that (1) community biomass is an extremely important regulating factor for independent biogeochemical processes, but its relative importance can vary depending on the process; (2) additional maintenance of functional group diversity, i.e., community trophic structure, does not increase the ability of a community to maintain any independent or simultaneous biogeochemical process, consistent with the weak role of functional group diversity in our statistical models, but contrary to some expectations (Hooper et al. 2005, Duffy et al. 2007, Hillebrand and Matthiessen 2009); and (3) species-specific traits are substantially more important for maintaining multifunctionality than any other singular process, emphasizing the fact that we are likely underestimating the role of species richness for biogeochemical processing (and, likely, other important functions) at the ecosystem scale. As such, a critical conclusion to this study is that species loss, irrespective of the maintenance of community structure, will drastically alter biogeochemical processing in these coastal ecosystems.

Improving our understanding of biogeochemical processes in coastal ecosystems is greatly needed if we are to implement more effective measures to ensure the future health of these important systems. Consumer regulation of nutrient pathways may provide a baseline from which to better understand these processes because fishes can constitute a critical role in these cycles (Pomeroy 1974, Kitchell et al. 1979, Vanni 2002). Our study emphasizes that the role of coastal fish communities in maintaining these ecosystem functions warrants immediate conservation attention given the susceptibility of communities to species loss. We underscore that maintaining the biodiversity and biomass of these communities needs to be a central goal of management strategies. The implications of this research for conservation efforts may be significant as it provides a complementary framework to understand how anthropogenic impacts, e.g., overharvesting of species, are affecting these imperiled ecosystems.

Literature Cited

Allgeier, J. E., C. A. Layman, P. J. Mumby, and A. D. Rosemond. 2014. Consumer driven nutrient stoichiometry in coral reef ecosystems. Global Change Biology 20:2459–2472.

Allgeier, J. E., L. A. Yeager, and C. A. Layman. 2013. Consumers regulate nutrient limitation regimes and primary production in seagrass ecosystems. Ecology 94:521–529.

APHA. 1995. Standard methods for the examination of water and wastewater. American Public Health Association, Washington, D.C., USA.

Bunker, D. E., F. DeClerck, J. C. Bradford, R. K. Colwell, I. Perfecto, O. L. Phillips, M. Sankaran, and S. Naeem. 2005. Species loss and aboveground carbon storage in a tropical forest. Science 310:1029–1031.

Burkepile, D. E., J. E. Allgeier, A. A. Shantz, C. E. Pritchard, N. P. Lemoine, L. H. Bhatti, and C. A. Layman. 2013. Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. Scientific Reports 3.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Cottingham, K. L., B. L. Brown, and J. T. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecology Letters 4:72–85.

Deangelis, D. L. 1980. Energy-flow, nutrient cycling, and ecosystem resilience. Ecology 61:764–771.

Diaz, S., and M. Cabido. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution 16:646–655.

Duffy, J. E. 2009. Why biodiversity is important to the functioning of real-world ecosystems. Frontiers in Ecology and the Environment 7:437–444.

Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thebault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecology Letters 10:522–538.

Duffy, J. E., J. P. Richardson, and K. E. France. 2005. Ecosystem consequences of diversity depend on food chain length in estuarine vegetation. Ecology Letters 8:301–309.

Essington, T. E., A. H. Beaudreau, and J. Wiedenmann. 2006. Fishing through marine food webs. Proceedings of the National Academy of Sciences USA 103:3171–3175.

Gelman, A., and J. Hill. 2007. Data analysis using regression. Cambridge University Press, New York, New York, USA.

Hanson, P. C., T. B. Johnson, D. E. Schindle, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin System Sea Grant Institute, Madison, Wisconsin, USA.

Harborne, A. R., P. J. Mumby, C. V. Kappel, C. P. Dahlgren, F. Micheli, K. E. Holmes, J. N. Sanchirico, K. Broad, I. A. Elliott, and D. R. Brumbaugh. 2008. Reserve effects and natural variation in coral reef communities. Journal of Applied Ecology 45:1010–1018.

Hector, A., and R. Bagchi. 2007. Biodiversity and ecosystem multifunctionality. Nature 448:188–190.

Hillebrand, H., and B. Matthiessen. 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. Ecology Letters 12:1405–1419.

Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

Joanes, D. N., and C. A. Gill. 1998. Comparing measures of sample skewness and kurtosis. Journal of the Royal Statistical Society Series D 47:183–189.

Kitchell, J. F., R. V. Oneill, D. Webb, G. W. Gallepp, S. M. Bartell, J. F. Koonce, and B. S. Ausmus. 1979. Consumer regulation of nutrient cycling. BioScience 29:28–34.

Layman, C. A., J. E. Allgeier, L. A. Yeager, and E. W. Stoner. 2013. Thresholds of ecosystem response to nutrient enrichment from fish aggregations. Ecology 94:530–536.

Loreau, M. 2004. Does functional redundancy exist? Oikos 104:606–611.

Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments (vol 412, pg 72, 2001). Nature 413:548–548.

Loreau, M., et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808.

Maestre, F. T., et al. 2012. Plant species richness and ecosystem multifunctionality in global drylands. Science 335:214–218.

Maranger, R., N. Caraco, J. Duhamel, and M. Amyot. 2008. Nitrogen transfer from sea to land via commercial fisheries. Nature Geoscience 1:111–113.

McCarthy, M. A. 2007. Bayesian methods for ecology. Cambridge University Press, Cambridge, UK.

McIntyre, P. B., L. E. Jones, A. S. Flecker, and M. J. Vanni. 2007. Fish extinctions alter nutrient recycling in tropical freshwaters. Proceedings of the National Academy of Sciences USA 104:4461–4466.

Moore, D. S., G. P. McCabe, and B. Craig. 2010. Introduction to the practice of statistics. W. H. Freeman, Gordonsville, Virginia, USA.

Mumby, P. J., et al. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98–101.

Naeem, S., J. E. Duffy, and E. Zavaleta. 2012. The functions of biological diversity in an age of extinction. Science 336:1401–1406.

Naeem, S., and S. B. Li. 1997. Biodiversity enhances ecosystem reliability. Nature 390:507–509.

Nicholson, M. D., and S. Jennings. 2004. Testing candidate indicators to support ecosystem-based management: the power of monitoring surveys to detect temporal trends in fish community metrics. Ices Journal of Marine Science 61:35–42.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and J. F. Torres. 1998. Fishing down marine food webs. Science 279:860–863.

Pomeroy, L. R. 1974. The ocean's food web, a changing paradigm. BioScience 24:9.

R Core Development Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Robert, C. P., and G. Casella. 2010. Introducing Monte Carlo methods with R. Springer Science, New York, New York, USA.

Schaus, M. H., M. J. Vanni, T. E. Wissing, M. T. Bremigan, J. E. Garvey, and R. A. Stein. 1997. Nitrogen and phosphorous excretion by detritivorous gizzard shad in a reservoir ecosystem. Limnology and Oceanography 42:1386–1397.

Schindler, D. E., and L. A. Eby. 1997. Stoichiometry of fishes and their prey: implications for nutrient recycling. Ecology 78:1816–1831.

Schreck, C. B., and P. B. Moyle, editors. 1990a. Methods for fish biology. American Fisheries Society, Bethesda, Maryland, USA.

Schreck, C. B., and P. B. Moyle. 1990b. Methods for fish biology. American Fisheries Society, Bethesda, Maryland, USA.

Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.

Solan, M., B. J. Cardinale, A. L. Downing, K. A. M. Engelhardt, J. L. Ruesink, and D. S. Srivastava. 2004. Extinction and ecosystem function in the marine benthos. Science 306:1177–1180.

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, New Jersey, USA.

Sterner, R. W., and N. B. George. 2000. Carbon, nitrogen, and phosphorus stoichiometry of cyprinid fishes. Ecology 81:127–140.

Taylor, B. W., C. F. Keep, R. O. Hall, B. J. Koch, L. M. Tronstad, A. S. Flecker, and A. J. Ulseth. 2007. Improving the fluorometric ammonium method: matrix effects, background fluorescence, and standard additions. Journal of the North American Benthological Society 26:167–177.

Tilman, D., C. L. Lehman, and K. T. Thomson. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. Proceedings of the National Academy of Sciences USA 94:1857–1861.

Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annual Review of Ecology and Systematics 33:341–370.

Vanni, M. J., A. S. Flecker, J. M. Hood, and J. L. Headworth. 2002. Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. Ecology Letters 5:285–293.

Weigelt, A., J. Schumacher, C. Roscher, and B. Schmid. 2008. Does biodiversity increase spatial stability in plant community biomass? Ecology Letters 11:338–347.

Whiles, M. R., A. D. Huryn, B. W. Taylor, and J. D. Reeve. 2009. Influence of handling stress and fasting on estimates of ammonium excretion by tadpoles and fish: recommendations for designing excretion experiments. Limnology and Oceanography—Methods 7:1–7.

Worm, B., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790.

Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Sciences USA 96:1463–1468.

Zuur, A. F., E. I. Ieno, N. J. Walker, A. A. Saveliev, and M. S. Graham. 2009. Mixed effects models and extension in ecology. Springer Science, New York, New York, USA.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–D are available online: http://dx.doi.org/10.1890/14-0331.1.sm