

Diversity and stability of herbivorous fishes on coral reefs

LOÏC M. THIBAUT,^{1,3} SEAN R. CONNOLLY,¹ AND HUGH P. A. SWEATMAN²

¹*School of Marine and Tropical Biology, and ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811 Australia*

²*Australian Institute of Marine Science, PMB 3, Townsville MC, Queensland 4810 Australia*

Abstract. Biodiversity may provide insurance against ecosystem collapse by stabilizing assemblages that perform particular ecological functions (the “portfolio effect”). However, the extent to which this occurs in nature and the importance of different mechanisms that generate portfolio effects remain controversial. On coral reefs, herbivory helps maintain coral dominated states, so volatility in levels of herbivory has important implications for reef ecosystems. Here, we used an extensive time series of abundances on 35 reefs of the Great Barrier Reef of Australia to quantify the strength of the portfolio effect for herbivorous fishes. Then, we disentangled the contributions of two mechanisms that underlie it (compensatory interactions and differential responses to environmental fluctuations [“response diversity”]) by fitting a community-dynamic model that explicitly includes terms for both mechanisms. We found that portfolio effects operate strongly in herbivorous fishes, as shown by nearly independent fluctuations in abundances over time. Moreover, we found strong evidence for high response diversity, with nearly independent responses to environmental fluctuations. In contrast, we found little evidence that the portfolio effect in this system was enhanced by compensatory ecological interactions. Our results show that portfolio effects are driven principally by response diversity for herbivorous fishes on coral reefs. We conclude that portfolio effects can be very strong in nature and that, for coral reefs in particular, response diversity may help maintain herbivory above the threshold levels that trigger regime shifts.

Key words: biodiversity; coral reefs; ecosystem function; functional diversity; herbivorous fishes; phase shift; portfolio effect; regime shift; response diversity; species richness; stability; temporal variability.

INTRODUCTION

The relationship between species diversity and the stability of ecological systems has been heavily debated in ecology since the middle of the last century, when the paradigm that diversity begets stability became established (e.g., MacArthur 1955). While this view was challenged by subsequent theoretical work (May 1973), increased availability of empirical data has revealed that species richness stabilizes aggregate community properties, such as productivity or total community abundance, when stability is defined as a tendency to fluctuate less, a phenomenon commonly termed the “portfolio effect” (Tilman 1996). These empirical findings motivated the development of new theory for the relationship between diversity and community stability (Doak et al. 1998, Tilman et al. 1998, Yachi and Loreau 1999). This work has identified asynchrony in the fluctuations of species’ abundances as the key mechanism underlying the stabilizing effect of species diversity. When species do not fluctuate in perfect synchrony, aggregate community properties are stabilized. The stabilizing effect is stronger as asynchrony

between species increases, and as the number of species increases.

The extent of asynchrony in fluctuations of abundance is determined by two basic kinds of processes: species–species interactions, such as competition or facilitation, and species–environment interactions, such as differences in species’ responses to environmental fluctuations. For example, competition between species can generate negative covariance (i.e., strong asynchrony) in two species’ abundances over time, because a decrease in the abundance of one species is likely to promote an increase in competitor abundance through competitive release. Similarly, if species respond differently to environmental fluctuations, then a year in which conditions are poor for one species will not necessarily be poor for other species; consequently, increases and decreases in abundance caused by environmental stochasticity are likely to be less pronounced at the assemblage level than at the level of individual species (hereafter we term this phenomenon “response diversity” following Elmqvist et al. 2003). To determine the relative importance of these different phenomena for the overall strength of the portfolio effect, a mechanistic approach is required that explicitly includes terms that characterize how species interactions and covariances in species’ responses to environmental fluctuations influ-

Manuscript received 26 September 2011; accepted 5 October 2011. Corresponding Editor: R. B. Aronson.

³ E-mail: Loic.Thibaut@jcu.edu.au

ence community dynamics (Cottingham et al. 2001, Ives and Carpenter 2007).

Disentangling the components that contribute to asynchronous population fluctuations in natural communities (hereafter termed “portfolio effect” for brevity) raises particular challenges. Firstly, the direction and strength of species interactions in species-rich communities cannot be evaluated by experimental approaches for simple logistical reasons. For example, >50 species of herbivorous fishes are common on the coral reefs of the Great Barrier Reef; it is clearly impossible to assess interaction strengths for all possible species pairs by experimental manipulation of fish densities. Therefore, broad-scale assessment of interaction strengths at the assemblage level must be approached indirectly, by fitting models of community dynamics that explicitly incorporate species interactions. In fact, even with such a modeling approach, the number of species that can be included explicitly is limited by the quantity of data available. This is because the number of estimated parameters increases with the square of the number of interacting populations, whereas the quantity of data (number of time series of abundances) increases only linearly with the number of interacting populations. Thus, the more interacting populations that are to be included in a model, the longer the time series required in order to estimate all the model parameters. Because even the longest ecological time series seldom exceed 20 years, this effectively limits the approach to a handful of species. Finally, most communities have a large number of rare species. Species with low abundances are more likely not to be recorded, producing proportionately large observation error and large numbers of zero abundances in the community time series, which hampers fitting community models to abundance data. This paper addresses these difficulties using a multiple-scale approach in which species that have similar ecological functions are grouped together for analysis. First, we quantified the portfolio effect and analyze ecological interactions and response diversity among these functional groups. We then conducted a similar analysis within functional groups by modeling the ecological interactions and response diversity between subsets of species within functional groups. This approach allowed us to examine the effects of species-level interactions on the portfolio effect, while avoiding the “curse of dimensionality” that precludes the estimation of interaction terms and environmental covariances for all pairs of species.

On coral reefs, herbivorous fishes can help to maintain coral cover by limiting the growth of macroalgae that compete with corals for space (Bellwood et al. 2004). These fishes can be classified into three functional groups. “Territorial grazers” are site-attached fishes that actively defend their territories against other herbivores. “Roving grazers” are relatively mobile herbivores that move around the reef in large schools feeding on superficial epilithic and macroalgae. “Scrapers” are

highly mobile fishes that consume epilithic algae and remove sediment by scraping the limestone surface of the reef. These three functional groups constitute the most important grazers of macroalgae on coral reefs (Sammarco and Carleton 1981, Choat 1991, McClanahan et al. 2003, Mumby et al. 2006). Moreover, theoretical models and empirical work both indicate that, when herbivory declines below threshold levels, macroalgae can rapidly colonize space made vacant by coral mortality. This, in turn, inhibits recruitment of corals, prompting a shift from dominance by corals towards dominance by macroalgae (Birkeland 1977, Hughes 1994). Moreover, such shifts may be difficult to reverse: There is some evidence that herbivorous fishes have a reduced ability to control macroalgae once macroalgae become highly abundant (Mumby et al. 2007, Hoey and Bellwood 2011). Thus, compensatory dynamics between functional groups of herbivorous fishes (i.e., a portfolio effect), due either to ecological interactions between groups or to differences in their responses to environmental fluctuations, can contribute to temporal stability in the control of macroalgae, which is critical to the maintenance of coral reefs. However, some experimental work indicates that control of macroalgal abundances is more effective where functional diversity of herbivores is higher (Burkpile and Hay 2008), suggesting that compensatory dynamics within functional groups (i.e., simultaneous stabilization of territorial grazing, roving grazing, and scraping via portfolio effects) are also likely to be important to the control of macroalgae on coral reefs.

In this paper, we estimated the strength of the diversity–stability relationship for herbivorous fishes on Australia’s Great Barrier Reef, and we developed and applied a new approach to quantify the relative contributions of ecological interactions and response diversity to this relationship. Our analyses provide the first quantitative picture of the strength of the portfolio effect and the importance of response diversity on coral reefs. Also, more broadly, they illustrate how the various mechanisms that give rise to the portfolio effect can be disentangled in species rich communities. Specifically, we estimated spatial variation in the overall strength of the portfolio effect, of ecological interactions, and of response diversity, both between and within herbivore functional groups. We then examined the overall magnitude of each of these and determine how spatial variation in the magnitude of the portfolio effect is explained by corresponding variation in the magnitude and direction of ecological interactions, and by the extent of response diversity.

MATERIALS AND METHODS

Overview of approach

We analyzed an extensive time series of abundances of herbivorous fishes from 35 reefs on the Great Barrier Reef (Sweatman et al. 2008). The same statistical approach was used to analyze the portfolio effect both

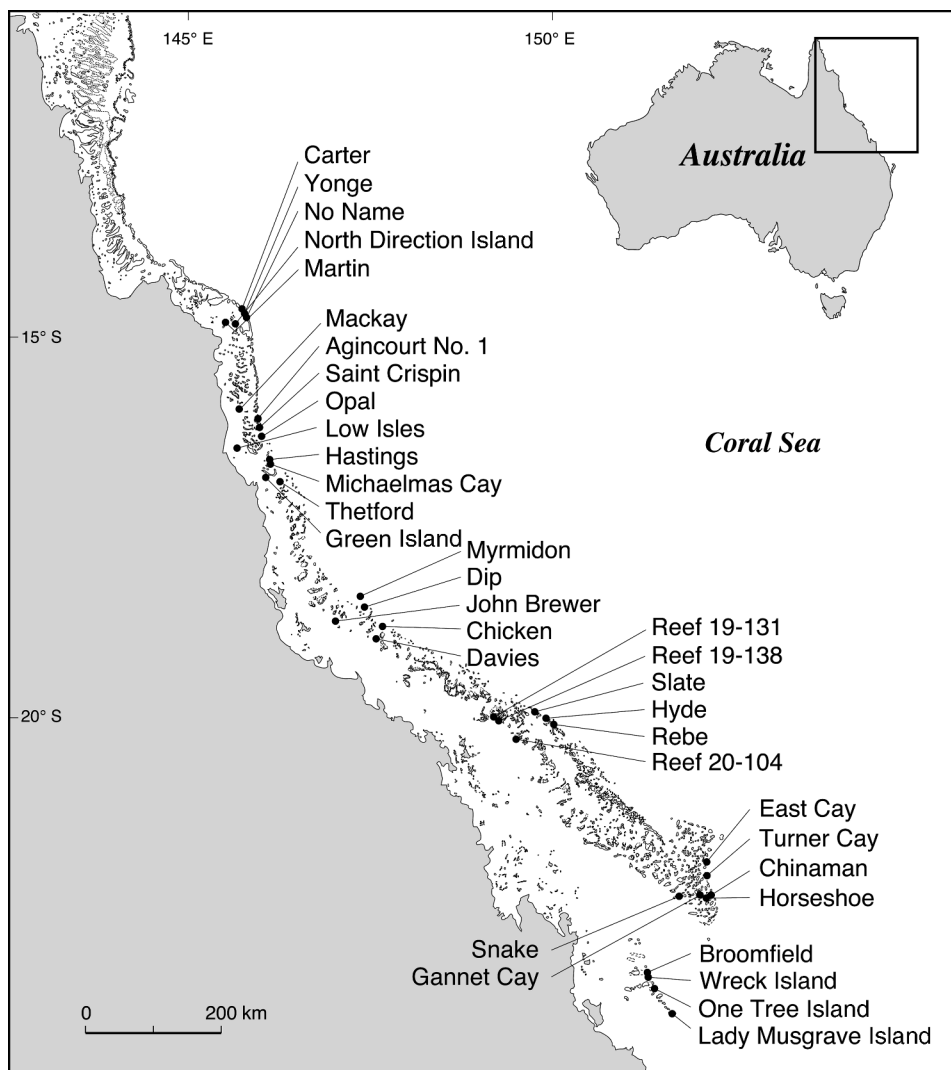


FIG. 1. Map of the Great Barrier Reef of Australia showing the location of the 35 reefs included in this study.

between functional groups and within functional groups. For each analysis, three statistics related to the diversity–stability relationship were calculated for each of 35 study reefs. The first statistic is an index of community synchrony obtained by quantifying the covariance in fluctuations of abundance between or within functional groups. The second statistic is a community-level index of interactions, which indicates whether the interactions between functional groups, or between species within functional groups, tend to be competitive or facilitative, and how strong those interactions are. The third statistic is an index of the synchrony of the responses to environmental fluctuations. The latter two statistics represent the mechanisms potentially driving the diversity–stability relationship, and must be estimated by fitting a model that explicitly characterizes their effects on community dynamics. Finally, we used a multiple regression to quantify how

much variation in the strength of the overall portfolio effect among sites is explained by spatial variation in response diversity and the direction and magnitude of species interactions.

Data

The data came from the surveys of fish communities and benthic cover conducted by the Australian Institute of Marine Science' Long Term Monitoring Program (LTMP) of the Great Barrier Reef (Sweatman et al. 2008). The sampling design and operational procedures are fully described elsewhere (Halford and Thompson 1996) and only summarized here. Our data set is based on 35 reefs spread across a large proportion of the Great Barrier Reef province (Fig. 1). The surveys started in 1993 and are continuing, although the number of years of surveys varies from reef to reef (see Table A1 in Appendix A). At each reef, there are three distinct sites

on the northeast flank of the reef. Each site contains five permanently marked 50-m transects running parallel to the reef crest. Trained observers assessed the abundance of 55 species of herbivorous fishes by underwater visual census; this includes most of the larger herbivorous fishes that can be effectively surveyed in this way. Two transect sizes were used: small, sedentary species were surveyed on 1 m wide transects, while larger, more mobile species were surveyed on 5 m wide transects. Therefore, abundances were standardized to density for analysis.

We classified the 55 surveyed species of herbivorous fishes into one of the three functional groups according to their behavior and feeding mode, based on the literature (see Table A2 in Appendix A). The territorial grazers were dominated by pomacentrid species that actively cultivate selected filamentous algae within their territories. However, this group also included two acanthurid species, *Acanthurus lineatus* and *Acanthurus nigricans*, which are also territorial and aggressive towards other herbivores, at least on the Great Barrier Reef (Choat and Bellwood 1985, Randall 1996). Field observations also suggest that *A. lineatus* may cultivate algae within its territories (D. Bellwood, *personal communication*). Roving grazers included all other acanthurid herbivores, along with siganids. These species are less site-attached than the territorial grazers, do not aggressively defend territories against other species of herbivore, and forage over larger areas, typically in schools. Scrapers consisted of all parrotfish species (formerly Scaridae, now a subgroup of the Labridae; Cowman et al. 2009): These are also highly mobile herbivores, but unlike roving grazers, these species forage by scraping the limestone surface of the reef with their beak-like teeth, removing epilithic algae and sediment in the process.

Quantifying portfolio effects

By definition, the degree of stabilization provided by the coexistence of multiple functional groups is caused by asynchrony of fluctuations in abundance of these groups over time (Gonzalez and Loreau 2009). To quantify the strength of this portfolio effect, we used the average pairwise cross-correlations between abundances of the functional groups over time, a standard approach for estimating community-wide patterns of synchrony (Bjornstad et al. 1999). We term this the “synchrony index” (SI), rather than “portfolio effect index,” because it is inversely related to the strength of the portfolio effect.

Mechanisms underlying portfolio effects

To disentangle the effect of between-group ecological interactions from that due to differences in responses to environmental fluctuations, we fitted our time series to a model of community dynamics that explicitly included terms for each of the mechanisms. More specifically, we tested two models involving different functional rela-

tionships for within- and between-group interactions: the Lotka-Volterra model, which assumes a linear relationship between abundance and per capita growth rate, and the Gompertz model (Ives et al. 2003), which assumes a linear relationship between log-abundance and per capita growth rate. Both visual inspection of model fits and formal model selection strongly favored the Gompertz model (see Appendix B), so we used the Gompertz model in all of our analyses.

Specifically, our model is a multivariate, discrete time, stochastic version of the Gompertz model (hereafter GMAR [Gompertz multivariate autoregressive model]). This model was first proposed by Ives et al. (2003) for estimating community stability from time-series data. It is well suited to this study because the model explicitly incorporates between-group and within-group interactions, as well as correlated responses to environmental fluctuations. However, as noted by Ives et al. (2003), observation error can bias the estimates for ecological interactions and response diversity. Therefore, to disentangle observation error from responses to environmental fluctuations, we allowed the per capita growth rate to vary from year to year by including a random effect in the model specification. For example, if a given year is a bad year, we expect the abundance to show a dip (represented by a negative random effect on population growth). Conversely, in a good year, we expect the population growth rate to be higher than otherwise predicted by the model, represented by a positive random effect. In our model, we treated the response to environmental fluctuations as a random effect on the site-level per capita increase in abundance, and treated variation in growth rate within sites as residual noise unexplained by the model, such as observation error. Note that this random-effects approach to response diversity means that, for each site, we estimated each group's year-to-year variance in abundance, and the between-group covariance in abundance, that is due to environmental fluctuations. This gave an overall picture of the variation in abundance that is due to response diversity, but it makes no assumptions about the specific environmental causes of particular ups and downs in abundance.

Given the hierarchical structure of the data set, ecological interactions can be parameterized at different levels: equivalent interactions for all reefs in the data set, different interactions for each reef, or different interactions for each site within each reef. To determine the optimal parameterization, we fitted alternative models representing each of those possibilities and used Akaike's Information Criterion (AIC) to identify the model best supported by the data. AIC strongly favored the model in which ecological interaction parameters were the same for different sites on the same reef, but differed between reefs.

One significant advantage of the GMAR model is that it is a linear autoregressive model on a logarithmic scale. Thus, the change in abundance of group i between time t

and time $t+1$ on reef r at site s , transect u , $n_{i,r,s,u}^t$, is modeled as

$$\log(n_{i,r,s,u}^{t+1}) - \log(n_{i,r,s,u}^t) = a_{i,r} + \sum_{j=1}^3 b_{i,j,r} \log(n_{j,r,s,u}^t) + r_{i,r,s}^t + e_{i,r,s,u}^t.$$

The left side of the equation is the per capita growth rate for group i , $a_{i,r}$ is the intrinsic growth rate of group i at reef r , $b_{i,j,r}$ represents the effect of group j on the growth rate of group i at reef r , $r_{i,r,s}^t$ is the random perturbation to the intrinsic growth rate of group i due to environmental fluctuations at time t , on reef r , site s , and $e_{i,r,s,u}^t$ is the residual variation in per capita growth rate (e.g., due to observation error). We assumed that both $r_{i,r,s}^t$ and $e_{i,r,s,u}^t$ were normally distributed with mean zero.

Between-group analysis.—Once the model had been fitted to the data, we calculated two statistics representing the two processes underlying the diversity–stability relationship: ecological interactions and response diversity. Firstly, we obtained a community-wide index of interactions between groups by averaging the between-group interaction strengths estimated from the model (i.e., for every reef r , we averaged all $b_{i,j,r}$ with $i \neq j$). The resulting between-group interaction index, hereafter “interaction index” (II), indicates the nature of the interactions in the community: A negative value indicates that competitive interactions are dominant in the community, while a positive value indicates that facilitative interactions are dominant (note that, like the synchrony index, larger, positive values of this index tend to weaken the portfolio effect). In order to compare the magnitude of between-group interactions and within-group interactions, we also calculated a within-group interaction index, hereafter “density-dependence index” (DDI), by averaging the within-group interaction strengths (i.e., for every reef r , we averaged all b_{ii}). A negative value would indicate that the within-group interactions tended to be compensatory (i.e., individuals reduced one another’s per capita growth rates). Secondly, for every reef, we estimated the degree of synchrony between groups in the responses to environmental fluctuations. We did this by first calculating, for each reef, the correlation coefficients between groups for the random effects on the intrinsic growth rate (i.e., for every reef r , we calculated, for each pair of groups i and j , the correlation coefficient between $r_{i,r,s,t}$ and $r_{j,r,s,t}$). We then averaged these correlation coefficients over all pairs of groups for each reef. We term this quantity the “environmental response synchrony index” (ERSI).

Within-group analysis.—Fitting a model of three interacting functional groups allowed us to assess the extent to which diversity of functional groups influenced ecological stability. However, species diversity within functional groups may also influence stability. Here, we faced the “curse of dimensionality”: The number of

estimated parameters increases with the square of the number of interacting populations in the multivariate Gompertz model, precluding an explicit species-level approach. Therefore, we devised a tractable test for diversity–stability relationships at this scale by randomly and repeatedly splitting each functional group into two subgroups of species, and then analyzing the community dynamics of the two subgroups. We repeated this procedure nine times for each functional group.

The rationale for the analysis is as follows. If within-group compensatory dynamics are driven by competition among species, then the between-subgroup II should tend to be negative. In contrast, if within-group compensatory dynamics are largely driven by within-species density dependence acting on different species independently, then the within-subgroup DDI should tend to be negative, while the between-subgroup II should be close to zero. However, it is important to bear in mind that the analysis of subgroups means the synchrony, interaction, and environmental response synchrony indices estimated in this way do not directly quantify average within-species DDI or species-level II. We therefore also assessed whether estimates of synchrony, interaction, density-dependence, and environmental response synchrony indices tended to be biased high or low when those species were pooled into subgroups for analysis, compared with the “true” underlying corresponding quantities (see *Discussion*).

RESULTS

The portfolio effect was found to operate strongly in the community of herbivorous reef fishes on the Great Barrier Reef at the level of functional groups, as indicated by nearly independent fluctuations of their abundances (average synchrony index ≈ 0.1). The range of values estimated across the 35 reefs, (−0.1 to 0.3), indicates that the strength of the portfolio effect varies geographically. We also found a strong portfolio effect operating within groups, among the territorial grazers and among the roving grazers. The diversity–stability relationship was weaker among scrapers, as shown by a higher average synchrony index (Fig. 2A).

Overall, we found strong evidence for high response diversity between and within functional groups. The responses of the three functional groups to environmental fluctuations were nearly independent (average environmental response synchrony index of 0.1 among reefs; Fig. 2B). The within-group analysis indicated that response diversity was similarly high among territorial and roving grazer species, but somewhat weaker for scrapers (Fig. 2B).

Our preliminary analysis found that different interaction parameters applied at each reef, indicating that interactions between functional groups did vary across reefs. However, these interactions had a mean close to zero, and were much less variable than the synchrony and environmental response synchrony indices (Fig. 2A–C). This suggests that that average between-group

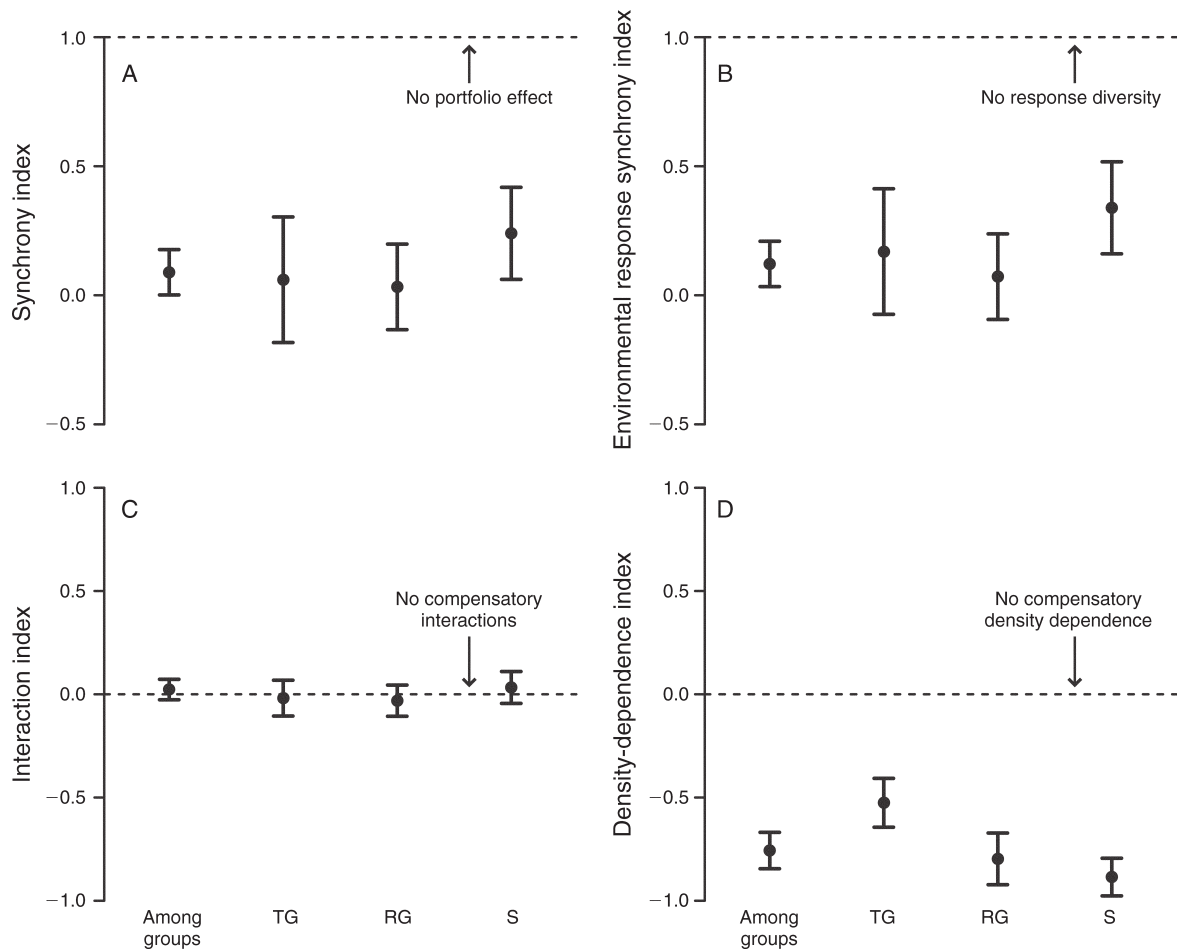


FIG. 2. Mean values and standard deviation for the (A) synchrony, (B) environmental response synchrony, (C) interaction, and (D) density-dependence indices (see *Materials and methods* for clarification of terms). “Among groups” refers to the analysis of interactions between the functional groups, while TG, RG, and S refer to the within-group, random-subset analyses for the territorial grazers, roving grazers, and scrapers functional groups of herbivorous fish, respectively. Note that the lowest possible value for the synchrony indices is -0.5 for the among-groups analysis and -1.0 for the within-group analyses. In panels A and B, the dashed line indicates the synchrony index corresponding to complete absence of a portfolio effect (see *Introduction*). In panel C, the dashed line indicates the absence of compensatory interactions: values below the line indicate compensatory interactions, while those above the line indicate facilitative interactions. Similarly, in panel D, values below the dashed line indicate compensatory (i.e., negative) density dependence, and those above the line indicate facilitative (i.e., positive) density dependence.

interaction strength varied spatially from weakly competitive to weakly facilitative. Very similar results were obtained for the within-group analysis (Fig. 2C, Table 1). In contrast, within-group interactions were always strongly competitive, as shown by consistently large, negative density-dependence indices (Fig. 2D).

Multiple regression was used to examine spatial variation in the synchrony index as a function of the interaction and environmental response synchrony indices. Response diversity was the principal driver of the portfolio effect, consistent with the previous analyses. Together, the interaction and the environmental response synchrony indices explained 69% of the variation in the overall synchrony index across the 35 reefs (Fig. 3, Table 1). However, the ERSI explained twice as much variation in community synchrony as the

interaction index did, indicating that response diversity was the main driver of the portfolio effect. Interactions between functional groups made a significant, but weaker contribution to the portfolio effect: Reefs with negative interactions between groups did tend to have lower synchrony indices, as evidenced by the significantly positive regression coefficient for the interaction index (Table 1). The relationship between response diversity and the overall portfolio effect also held within functional groups: In all cases, this relationship was positive, strong, and statistically significant, as in the between-groups analysis (Table 1). Ecological interactions had no statistically significant effect on the strength of the portfolio effect (as measured by the synchrony index) in scrapers and roving grazers, indicating that the portfolio effect was driven principally

TABLE 1. Results of multiple linear regressions of synchrony index against interaction index and environmental response synchrony index for between-groups and within-group analyses.

Data set	Overall regression		Environmental response synchrony index		Interaction index	
	Significance	R^2	Coefficient	R^2	Coefficient	R^2
Between groups	***	0.69	0.51***	0.43	0.90***	0.23
TG	***	0.67	0.45***	0.23	1.88***	0.53
RG	***	0.55	0.52***	0.49	0.59†	0.19
S	***	0.27	0.94***	0.27	0.13	0.02

Notes: Between groups is the analysis based on fluctuations in abundance of the three functional groups (cf. Fig. 2). TG, RG, and S refer to analyses of the fluctuations of abundance of the random subgroups of herbivorous fish within the territorial grazers, roving grazers, and scrapers, respectively. The overall R^2 value was partitioned between the two explanatory variables by performing a simple regression for each variable after checking that the two variables were not significantly correlated.

† $P < 0.1$; *** $P < 0.001$.

by response diversity, as was the case in the between-groups analysis (Table 1). In the territorial grazers functional group, ecological interactions explained more variation in the portfolio effect than did response diversity, although both effects were statistically significant (Table 1).

DISCUSSION

Herbivorous fishes provide a critical ecosystem function on coral reefs, consuming macroalgae and thereby facilitating the maintenance of reefs in coral-dominated states. Stability in the performance of this function has important implications for reef dynamics, since collapses in herbivore populations can provoke regime shifts to macroalgal-dominated states that may be difficult to reverse (Mumby et al. 2007, Hoey and Bellwood 2011). Our results show that the portfolio effect strongly stabilizes overall abundances of herbivorous fishes on the Great Barrier Reef. Fluctuations in abundances of the three functional groups were nearly independent of one another. Territorial grazers and roving grazers showed a similarly strong portfolio effect, whereas fluctuations in abundance of scrapers (parrotfishes) tended to be positively correlated, indicating a weaker portfolio effect. In addition, we found that high response diversity (demonstrated by nearly independent responses to environmental fluctuations across the three functional groups) was the main driver of this portfolio effect. Ecological interactions between functional groups also had a significant influence on the portfolio effect, but their effect was weaker than that of response diversity. We found similar results when considering portfolio effects within groups: Scrapers and roving grazers had high response diversity, and this explained much more of the variation in the portfolio effect among reefs than did ecological interactions. In territorial grazers, however, ecological interactions explained more of the variation in the portfolio effect for that group.

Assessing the mechanisms underlying the diversity–stability relationship in species-rich assemblages is particularly challenging, because as the number of

species increases, the number of model parameters increases more rapidly than the number of data points. Moreover, species-rich assemblages tend to have a large number of rare species that are only observed occasionally. These problems were circumvented by first analyzing the effect of multiple functional groups on stability, and then gaining insight into species-level effects by analyzing random assignment of species to subgroups within functional groups. Portfolio effects at both levels are important ecologically. Stability in the herbivorous fish community as a whole ensures that consumers of macroalgae are sufficiently abundant. However, differences in diet and foraging between functional groups, and the potentially synergistic effects of these differences

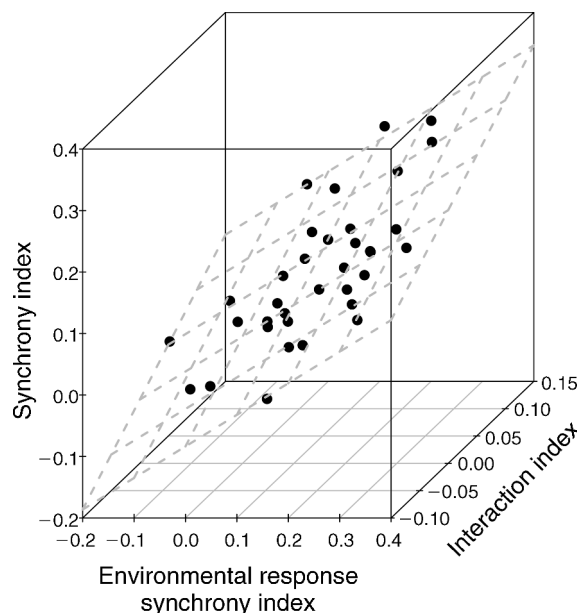


FIG. 3. Multiple regression of the synchrony index on the interaction index and environmental response synchrony index. Each point represents a reef ($n = 35$), and the dashed grid shows the fit of the regression model. See Table 1 for regression statistics.

on macroalgal control (Burkepile and Hay 2008), mean that stability in the abundances of each functional group is also ecologically significant.

For our within-group analysis, we used synchrony, interaction, and environmental response synchrony indices between random subgroups of species as proxies for the corresponding quantities for pairwise species interactions. Using random subgroups is likely to give a conservative basis for our two principal conclusions: that the portfolio effect operates strongly within and between groups, and that response diversity is the principal driver of this effect. Specifically, it is possible to show analytically that estimating both the synchrony and environmental response synchrony indices with this approach tends to lead to estimates that are higher than the corresponding species-level quantities (thus underestimating portfolio effects and response diversity; Appendix C). This means that the portfolio effect and response diversity for species within functional groups are likely to be stronger than our subgroup analyses suggest. Also, a simulation study of the effects of grouping on interaction indices suggests that the interaction index is biased away from zero when species are combined into subgroups (Appendix C), meaning that species interactions are likely to be even weaker than the estimates from our analyses of subgroups.

This is the first study that disentangles the relative contributions of ecological interactions and response diversity to the diversity–stability relationship in ecological communities. We found evidence for a remarkably strong portfolio effect in herbivorous coral reef fishes, with nearly independent fluctuations in abundance over time across the functional groups. Few studies have focused on the direct evaluation of the portfolio effect using empirical data, with the exception of Valone and Barber (2008), who analyzed long-term data from several terrestrial assemblages. Their portfolio effect statistic, a median Spearman rank correlation on the abundance of species pairs over time, is similar but not identical to our synchrony index. However, the two statistics appear to yield very similar conclusions: When we applied their statistic to our data, we found an average correlation of 0.1 across the 35 reefs, identical to our average synchrony index, and notably lower than the average value of 0.26 that they reported in terrestrial systems. Similarly, average values for territorial grazers and roving grazers were also remarkably lower (0.03 and 0.004, respectively) than those of the terrestrial assemblages, although the average value for scrapers, at 0.25, was similar to the terrestrial analyses. The lower synchrony index values in our data suggest that the diversity–stability relationship is stronger in herbivorous reef fishes than in the terrestrial assemblages previously studied.

Communities of coral reef fishes are among the most diverse vertebrate communities on earth, and this high species diversity is accompanied by high diversity of morphologies and behaviors (e.g., Ehrlich 1975). For

herbivorous fishes, this high functional diversity has been shown experimentally to enhance their capacity to control macroalgal abundance (Burkepile and Hay 2008). Even closely related species from the same functional groups can show striking differences in foraging patterns and habitat use. For example, Pomacentrid territorial grazers vary substantially in their degree of specialization in resource use and habitat requirements (Allen 1991), and a recent study has found that niche breadth explained most of the variance in species' mean response to coral decline (Wilson et al. 2008). It seems likely that this variety of strategies contributes to species' relatively independent responses to environmental fluctuations (i.e., high response diversity) that we found. Moreover, the lower response diversity among scrapers is consistent with their lower taxonomic and functional diversity compared with territorial and roving grazers. Scrapers all belong to one clade within the Labridae, which have a relatively recent evolutionary origin (Cowman et al. 2009), have similar morphologies and substantially overlapping foraging patterns (Bellwood and Choat 1990), and often form multi-specific schools (Overholtzer and Motta 2000). This comparatively strong ecological and morphological similarity may well explain why environmental fluctuations appear to affect species within this group more similarly than within the other groups.

In this context, it is worth noting that the territorial grazers were all pomacentrid species, with only two exceptions: *Acanthurus lineatus* and *Acanthurus nigricans*. Both of these species are reported as aggressive, and they are relatively site-attached, compared to roving grazers (Choat and Bellwood 1985, Randall 1996). However, given the ecological differences between these species and the pomacentrids that constitute the rest of this group, we repeated our between-groups and within-territorial grazers analyses with the two *Acanthurus* species excluded. Our modified estimates of the strength of the overall portfolio effect, response diversity, and ecological interactions were all within 0.01 of the values from the original analyses (cf. Fig. 2). Similarly, all terms that were significant in the original regression analyses (Table 1) remained significant in the revised analyses. These results indicate that our results are not sensitive to the decision to classify these species in the same functional group as the pomacentrid grazers.

In contrast to response diversity, we found little evidence in this system that the portfolio effect was enhanced by compensatory ecological interactions, either between functional groups or within them. Instead, we found that, when averaged over the community, interactions at different locations varied from weakly compensatory to weakly facilitative, with an average value near zero. There is a diversity of opinion about the relative importance of competition and facilitation in coral reef fishes. Although interspecific competition has been considered to be a major structuring factor in reef fish communities (e.g., Rough-

garden 1974, Sale 1977), recent studies have argued that the importance of facilitation has been overlooked in community ecology (Bruno et al. 2003, Hay et al. 2004). For instance, at the functional group level, conspicuous aggressive behavior of territorial grazers towards other herbivorous fishes has been assumed to indicate strong competitive interactions between territorial and roving grazers (e.g., Vine 1974, Jones 2005). However, the aggressive behavior of territorial grazers may be circumvented by schooling of roving herbivores (Robertson et al. 1976), and “farming” of algae by territorial species may, in fact, enhance the algal yield for roving grazers, resulting in facilitation (Russ 1987). Few studies have specifically assessed spatial variation in the nature and magnitude of interactions between herbivorous reef fishes, but the limited data indicate that species interactions are weak and spatially variable. For instance, Choat and Bellwood (1985) studied the interactions between parrotfishes and an abundant territorial grazer, *Acanthurus lineatus*. They found that the direction and magnitude of the interactions were site specific, which they attributed to local differences in habitat structure. Similarly, in the Caribbean, an extensive study of aggression among parrotfishes found that only 10% of the observed aggression was interspecific, while 90% of aggressive encounters involved conspecifics (Mumby and Wabnitz 2002). Our findings are consistent with these results and support a Gleasonian view of herbivorous reef fish assemblages in which the effects of interspecific interactions, while present, tend to be weak, diffuse, and variable (Gleason 1939).

Our study focuses specifically on the effects of diversity on the stability of abundance of herbivores, where abundance is defined as the number of individuals. However, from the standpoint of overall stability of levels of grazing, not all individuals make equal contributions. In particular, larger fishes are likely to graze more than smaller fishes. To investigate the robustness of our results to this potential effect, we converted each species' abundance to an approximate biomass, based on estimates of average size obtained from existing data (Kulbicki et al. 2005, Green and Bellwood 2009, Kulbicki et al. 2011). We then repeated our between-groups analysis, and we found that the modified estimates of the strength of the overall portfolio effect, of response diversity, and of ecological interactions, were within 0.04 of the values obtained in the original analysis (cf. Fig. 2). Moreover, all terms that were significant in our original regression analyses (Table 1) remained significant in the modified analyses. While not a comprehensive accounting of interspecific differences in biomass (which will vary among individuals within species, as well as between species), the fact that we obtained very similar results, despite a range of body size of about three orders of magnitude among species, indicates that our conclusion that there is a strong portfolio effect, and in particular high levels of

response diversity, is not sensitive to the use of numbers of individuals as our measure of abundance.

In contrast to between-group interactions, which were, on average, near zero, we found strong evidence for within-group density dependence. Such a result could indicate strong compensatory interactions among species within groups (e.g., strong competition among roving grazer species, or among territorial grazer species). If this were the case, we would have expected our within-group analyses to show negative interactions between subgroups. Instead, between-subgroup interactions were near zero, on average, while within-subgroup density dependence was strong, as in our between-groups analysis. This suggests that the strong density dependence within groups is mainly the result of the cumulative effects of intraspecific density dependence. This does not, of course, preclude the possibility that particular pairs of species may interact strongly, but if they do, negatively interacting and positively interacting species are largely canceling one another out at the functional group level.

Strong density dependence appears at odds with the Recruitment–Limitation Hypothesis (RLH), according to which post-settlement interactions are overwhelmed by random fluctuations in abundance due to the vagaries of larval recruitment (Doherty and Fowler 1994). Such high population variability has been invoked to propose that density dependence is not important in many reef fish populations (Sale and Tolimieri 2000). In contrast, a meta-analysis of reef fish studies found strong evidence for density dependence, even in the subset of studies that individually lacked sufficient statistical power to detect it (Osenberg et al. 2002). Subsequent work also indicates that density dependence is important in reef fishes, but most such studies have focused on relatively small, site-attached species (e.g., Johnson 2008, Samhouri et al. 2009). The fact that our estimates of the strength of density dependence are, if anything, stronger in the roving grazers and scrapers than in the territorial grazers (Fig. 2D), suggests that this process is also important in less site-attached reef fishes as well.

One of the key services provided by species diversity is the stabilization of ecosystem functioning: By means of the portfolio effect, species-rich communities can have less variable rates of production, consumption, detoxification, and other important processes (Naeem and Li 1997). This stabilizing effect can play an important role in the management of ecosystems, by reducing the risk that such functions will cross threshold levels that trigger major, ecosystem-level changes. Here, we have used a new approach to quantifying the portfolio effect that allows the roles of compensatory ecological interactions and response diversity, the underlying drivers of the portfolio effect, to be disentangled. We developed this approach in order to assess diversity–stability relationships among herbivorous fishes on coral reefs. In most of the world's reef ecosystems, fishes are the principal consumers of algae, and their grazing helps

keep space available for the recruitment and growth of corals. Our study reveals firstly that there is a strong portfolio effect both within and among functional groups of herbivorous fishes on the Great Barrier Reef. Secondly, this relationship is driven principally by response diversity: differences in how species respond to environmental fluctuations. These findings indicate that herbivorous fish diversity provides insurance against major environmentally induced collapses in herbivory that could potentially trigger macroalgal blooms on coral reefs, with its attendant adverse consequences for tourism and other reef-based economic activities that depend on high levels of coral cover (Pratchett et al. 2008). Our findings support calls to specify the conservation of functional diversity as an important goal in ecosystem management (Naeem and Li 1997, Bellwood et al. 2004).

ACKNOWLEDGMENTS

The authors thank D. Bellwood, J. H. Choat, R. Galzin, T. P. Hughes, A. MacNeil, and two anonymous reviewers for valuable comments and suggestions at various stages of the project. M. Kulbicki kindly provided access to his database on reef fish biomass. We gratefully acknowledge the staff of the Long Term Monitoring team at the Australian Institute of Marine Science for collection of the data with support from AIMS, the CRC Reef Research Centre and the Australian Government's Marine and Tropical Sciences Research Facility, and the High Performance Computing unit of James Cook University for facilitating numerical simulations. The Australian Research Council and James Cook University provided financial support for this research.

LITERATURE CITED

- Allen, G. R. 1991. Damselfishes of the world. Mergus, Melle, Germany.
- Bellwood, D. R., and H. J. Choat. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes* 28:189–214.
- Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nystrom. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.
- Birkeland, C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Pages 15–21 in *Proceedings of the Third International Coral Reef Symposium*. University of Miami, Miami, Florida USA.
- Bjornstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: analyzing patterns and processes of population asynchrony. *Trends in Ecology and Evolution* 14:427–432.
- Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.
- Burkepile, D. E., and M. E. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences USA* 105:16201–16206.
- Choat, J. H. 1991. The biology of herbivorous fishes on coral reefs. Academic, San Diego, California, USA.
- Choat, J. H., and D. R. Bellwood. 1985. Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation. *Marine Biology* 89:221–234.
- 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.
- Cowman, P. F., D. R. Bellwood, and L. van Herwerden. 2009. Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. *Molecular Phylogenetics and Evolution* 52:621–631.
- Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist* 151:264–276.
- Doherty, P., and T. Fowler. 1994. An empirical test of recruitment limitation in a coral-reef fish. *Science* 263:935–939.
- Ehrlich, P. R. 1975. The population biology of coral reef fishes. *Annual Review of Ecology and Systematics* 6:211–247.
- Elmqvist, T., C. Folke, M. Nystrom, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1:488–494.
- Gleason, H. A. 1939. The individualistic concept of the plant association. *American Midland Naturalist* 21:92–110.
- Gonzalez, A., and M. Loreau. 2009. The causes and consequences of compensatory dynamics in ecological communities. *Annual Review of Ecology, Evolution, and Systematics* 40:393–414.
- Green, A. L., and D. R. Bellwood. 2009. Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: A practical guide for coral reef managers in the Asia Pacific region. Working Paper Series Number 7. International Union for the Conservation of Nature (IUCN), Gland, Switzerland.
- Halford, A. R., and A. A. Thompson. 1996. Visual census surveys of reef fish. Standard operational procedure number 3. Australian Institute of Marine Science (AIMS), Townsville, Australia.
- Hay, M. E., J. D. Parker, D. E. Burkepile, C. C. Caudill, A. E. Wilson, Z. P. Hallinan, and A. D. Chequer. 2004. Mutualisms and aquatic community structure: the enemy of my enemy is my friend. *Annual Review of Ecology, Evolution, and Systematics* 35:175–197.
- Hoey, A. S., and D. R. Bellwood. 2011. Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecology Letters* 14:267–273.
- Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 1547–1551.
- Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317:58–62.
- Ives, A. R., B. Dennis, K. L. Cottingham, and S. R. Carpenter. 2003. Estimating community stability and ecological interactions from time-series data. *Ecological Monographs* 73:301–330.
- Johnson, D. 2008. Combined effects of condition and density on post-settlement survival and growth of a marine fish. *Oecologia* 155:43–52.
- Jones, K. M. M. 2005. The effect of territorial damselfish (family Pomacentridae) on the space use and behaviour of the coral reef fish, *Halichoeres bivittatus* (Bloch, 1791) (Family Labridae). *Journal of Experimental Marine Biology and Ecology* 324:99–111.
- Kulbicki, M., N. Guillemot, and M. Amand. 2005. A general approach to length-weight relationships for New Caledonian lagoon fishes. *Cybio* 29:235–252.
- Kulbicki, M., G. MouTham, L. Vigliola, L. Wantiez, E. Maldonado, P. Labrosse, and Y. Letourneur. 2011. Major coral reef fish species of the South Pacific with basic information on their biology and ecology. Report, Coral Reef Initiative for the Pacific (CRISP) and Institut de Recherche pour le Développement (IRD), Secretariat of the Pacific Community (SPC), Nouméa, New Caledonia.
- MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533–536.
- May, R. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.
- McClanahan, T. R., E. Sala, P. A. Stickels, B. A. Cokos, A. C. Baker, C. J. Starger, and S. H. Jones IV. 2003. Interaction

- between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. *Marine Ecology Progress Series* 261:135–147.
- Mumby, P. J., et al. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101.
- Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450:98–101.
- Mumby, P. J., and C. C. C. Wabnitz. 2002. Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. *Environmental Biology of Fishes* 63:265–279.
- Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390:507–509.
- Osenberg, C. W., C. M. St Mary, R. J. Schmitt, S. J. Holbrook, P. Chesson, and B. Byrne. 2002. Rethinking ecological inference: density dependence in reef fishes. *Ecology Letters* 5:715–721.
- Overholtzer, K. L., and P. J. Motta. 2000. Effects of mixed-species foraging groups on the feeding and aggression of juvenile parrotfishes. *Environmental Biology of Fishes* 58:345–354.
- Pratchett, M. S., P. L. Munday, S. K. Wilson, N. A. J. Graham, J. E. Cinner, D. R. Bellwood, G. P. Jones, N. V. C. Polunin, and T. R. McClanahan. 2008. Effects of climate-induced coral bleaching on coral-reef fishes: Ecological and economic consequences. Pages 251–296 in R. N. Gibson, R. J. A. Atkinson, and J. D. M. Gordon, editors. *Oceanography and marine biology: an annual review*. Volume 46. CRC Press-Taylor and Francis Group, Boca Raton, Florida, USA.
- Randall, J. E. 1996. *Fishes of the Great Barrier Reef and Coral Sea*. University of Hawaii Press, Honolulu, Hawaii, USA.
- Robertson, D. R., H. P. A. Sweatman, E. A. Fletcher, and M. G. Cleland. 1976. Schooling as a mechanism for circumventing territoriality of competitors. *Ecology* 57:1208–1220.
- Roughgarden, J. 1974. Species packing and competition function with illustrations from coral-reef fish. *Theoretical Population Biology* 5:163–186.
- Russ, G. R. 1987. Is rate of removal of algae by grazers reduced inside territories of tropical damselfishes. *Journal of Experimental Marine Biology and Ecology* 110:1–17.
- Sale, P. F. 1977. Maintenance of high diversity in coral-reef fish communities. *American Naturalist* 111:337–359.
- Sale, P. F., and N. Tolimieri. 2000. Density dependence at some time and place? *Oecologia* 124:166–171.
- Samhouri, J., R. Vance, G. Forrester, and M. Steele. 2009. Musical chairs mortality functions: density-dependent deaths caused by competition for unguarded refuges. *Oecologia* 160:257–265.
- Sammarco, P. W., and J. Carleton. 1981. Damselfish territoriality and coral community structure: reduced grazing, coral recruitment, and effects on coral spat. Pages 525–535 in E. D. Gomez, C. E. Birkeland, and R. W. Buddemeier, editors. *Proceedings of the 4th International Coral Reef Symposium*. University of the Philippines, Manila, Philippines.
- Sweatman, H., A. Cheal, G. Coleman, M. Emslie, K. Jones, M. Jonker, I. Miller, and K. Osborne. 2008. Long term monitoring of the Great Barrier Reef. Status report number 8. Australian Institute of Marine Science (AIMS), Townsville, Australia.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77:350–363.
- Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? *American Naturalist* 151:277–282.
- Valone, T. J., and N. A. Barber. 2008. An empirical evaluation of the insurance hypothesis in diversity–stability models. *Ecology* 89:522–531.
- Vine, P. J. 1974. Effects of algal grazing and aggressive behavior of fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral reef ecology. *Marine Biology* 24:131–136.
- Wilson, S. K., S. C. Burgess, A. J. Cheal, M. Emslie, R. Fisher, I. Miller, N. V. C. Polunin, and H. P. A. Sweatman. 2008. Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology* 77:220–228.
- 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.

SUPPLEMENTAL MATERIAL

Appendix A

Functional groups and reefs surveyed (*Ecological Archives* E093-079-A1).

Appendix B

Selection of functional form (*Ecological Archives* E093-079-A2).

Appendix C

Effect of grouping species on indices (*Ecological Archives* E093-079-A3).