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Population regulation and diversity-stability relationships in ecological time-series

Thesis submitted by

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To the memory of Andrée Thibaut and Paulette Frache

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Statement of the Contribution of Others

1.1. Contribution of all authors to co-authored papers

Chapter 2

Loïc Thibaut conceived the project, designed and performed the analyses and wrote the first draft of the manuscript.

Sean Connolly assisted in developing the approach and argument, assisted in the interpretation of the results, and made suggestions on and edits to multiple drafts of the paper.

Hugh Sweatman provided the data, provided expert advice for classifying herbivorous fishes into functional groups, assisted in the interpretation of the results, and provided helpful comments on and edits to the manuscript.

Chapter 3

Loïc Thibaut conceived the project, derived the mathematical results, co-developed the approach and argument, designed and performed the analyses, and wrote the first draft of the manuscript.

Sean Connolly co-developed the approach and argument and made suggestions on and edits to multiple drafts of the paper.

Chapter 4

Loïc Thibaut conceived the project, designed and performed the analyses, and wrote the first draft of the manuscript.

Sean Connolly assisted in developing the approach and argument and made suggestions on and edits to multiple drafts of the paper.

1.2. Other contributions

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Chapter 2

- The graphics team at the Australian Institute of Marine Science prepared Figure 2.1.
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Chapter 3

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Contributions of all authors to papers (signed)

Chapter #	Details of publication	Nature and extent of the intellectual input of each author	I confirm the candidate's contribution to this paper and consent to the inclusion of the paper in this thesis
2	Thibaut, L. M., S. R. Connolly, and H. P. A. Sweatman. 2012. Diversity and stability of herbivorous fishes on coral reefs. Ecology **93**:891-901.	Loïc Thibaut conceived the project, designed and performed the analyses and wrote the first draft of the manuscript. Sean Connolly assisted in developing the approach and argument, assisted in the interpretation of the results, and made suggestions on and edits to multiple drafts of the paper. Hugh Sweatman provided the data, provided expert advice for classifying herbivorous fishes into functional groups, assisted in the interpretation of the results, and provided helpful comments on and edits to the manuscript.	Prof. Sean Connolly Dr. Hugh Sweatman
3	Thibaut, L. M. and S. R. Connolly. 2013. Understanding diversity–stability relationships: towards a unified model of portfolio effects. Ecology Letters **16**:140-150.	Loïc Thibaut conceived the project, derived the mathematical results, co-developed the approach and argument, designed and performed the analyses, and wrote the first draft of the manuscript. Sean Connolly co-developed the approach and argument and made suggestions on and edits to multiple drafts of the paper.	Prof. Sean Connolly
4	Thibaut, L. M. and S. R. Connolly. Strong evidence for weak density-dependence in population dynamics. In prep.	Loïc Thibaut conceived the project, designed and performed the analyses, and wrote the first draft of the manuscript. Sean Connolly assisted in developing the approach and argument and made suggestions on and edits to multiple drafts of the paper.	Prof. Sean Connolly

Abstract

Biodiversity can provide insurance against ecosystem collapse by stabilizing assemblages that perform critical 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. The overall aim of this thesis was to develop a quantitative approach to estimate the extent to which diversity stabilizes communities, and to apply this approach to herbivory on coral reefs.

In chapter 2, I examined herbivory on the Great Barrier Reef. On coral reefs, herbivory helps maintain coral dominated states, so volatility in levels of herbivory has important implications for reef ecosystems. In this chapter, I 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, I 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 than explicitly includes terms for both mechanisms. I found that portfolio effects operate strongly in herbivorous fishes, as shown by nearly independent fluctuations in abundances over time. Moreover, I found strong evidence for high response diversity, with nearly independent responses to environmental fluctuations. In contrast, I found little evidence that the portfolio effect in this system was enhanced by compensatory ecological interactions. My results show that portfolio effects are driven principally by response diversity for herbivorous fishes on coral reefs. I conclude that portfolio effects can be very strong in nature, and that, for coral reefs in particular, response diversity on coral reefs may help maintain herbivory above the threshold levels hypothesized to trigger regime shifts.

In chapter 3, I developed a theoretical framework to understand diversity-stability relationships (DSRs) in nature, in order to overcome shortcomings in past approaches that became apparent during the work for Chapter 2. Specifically, DSRs are analysed using a variety of different population and community properties, most of which are adopted from theory that makes several restrictive assumptions that are unlikely to be reflected in nature. Here, I constructed a simple synthesis and generalization of previous theory for the DSR. I showed that community stability is a product of two quantities: the synchrony of population fluctuations, and an average species-level population stability that is weighted by relative abundance. Weighted average population stability can be decomposed to consider effects of the mean-variance scaling of abundance, changes in mean abundance with diversity, and differences in species' mean abundance in monoculture. My framework makes explicit how unevenness in the abundances of species in real communities influences the DSR, which occurs both through effects on community synchrony, and effects on weighted average population variability. This theory provides a more robust framework for analysing the results of empirical studies of the DSR, and facilitates the integration of findings from real and model communities.

Observation error is pervasive in ecological time-series and can have important implications for estimating and identifying the drivers of stability in community time-series. In chapter 4, I used a model which explicitly accounts for observation error to assess the strength of evidence for population regulation in time-series from the Global Population Dynamics Database (GPDD). The extent to which populations in nature are regulated by density-dependent processes is unresolved. While experiments increasingly find evidence of strong density-dependence, unmanipulated population time series yield much more ambiguous evidence of regulation. In this chapter, I re-examined the evidence for density-dependence in time series of population sizes in nature, by conducting an aggregate analysis of the populations in the GPDD. I found that density-dependence is likely over-estimated when it is fitted independently for each population, even when accounting for observation error. However, in the aggregate, very strong evidence for weak, but non-zero, density-dependence remains. Rather than falling into categories of density-dependent and density-independent dynamics, differences in support for density-dependence are likely the result of differences in statistical power. My findings suggest that the observational record does indeed contain strong support for density-dependence, but that its intensity is likely weaker than is detected in laboratory and field experiments.

The findings from my latter two chapters have important implications for the assessment of diversity-stability relationships from the analysis of ecological time series. Specifically, the framework developed in chapter 3 shows that the DSR can be partitioned into an effect of synchrony and an effect of population variability. Consequently, the role and importance of several ecological drivers of the DSR can be disentangled by considering separately their effect on community synchrony and population variability. Finally, chapter 4 illustrates that observation error should be explicitly accounted for to ensure sound inferences about the processes driving fluctuations in species' abundances.

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Chapter 1. Introduction

Understanding what drives the stability of ecological systems is of considerable theoretical and practical interest and has been a central question in ecology since the inception of the discipline (Elton 1927). For example, the Newfoundland cod fishery collapsed unexpectedly in 1994 despite being actively managed by the Canadian Department of Fisheries and Oceans, with dramatic economic and ecological consequences (Roughgarden and Smith 1996). More recently, concerns about the consequences of the worldwide loss of biodiversity has sparked renewed interest in the relationship between diversity and stability in ecosystems (Tilman and Downing 1994, Tilman 1996, Ives and Carpenter 2007). Comprehending what drives the stability of ecological systems is therefore essential for our understanding of their functioning and critical to ensure our capacity to manage them against collapse in an increasingly anthropogenically influenced world.

Defining stability has been a key challenge for research on the stability of ecological systems. A plethora of concepts and definitions associated with stability have been introduced (Pimm 1984, Ives and Carpenter 2007). The difficulty of defining stability is three-fold. Firstly, ecological systems can display a range of radically different dynamics. For example, some systems have a single stable equilibrium point. In such systems, the time needed to return to equilibrium after perturbation has been used as stability metric (Pimm 1984). Other systems can exhibit more complex dynamics, such as periodic cycles (Krebs et al. 2001), chaos (Costantino et al. 1997) or alternate stable states (Scheffer et al. 2001) and appropriate measures of stability vary accordingly (Ives and Carpenter 2007). Secondly, the nature of the environmental perturbation regime is key to defining stability. For example some studies consider that environmental conditions fluctuate frequently and randomly around average (constant) conditions (e.g. Ives et al. 2003) while others focus on the response of the system to rare, catastrophic perturbations (e.g. Mumby et al. 2007). Thirdly, the definition of stability depends on the quantity of interest. For example, some studies focus on the stability of the population size of a focal species, while others consider the dynamics of an aggregated property of a community, such as the total abundance or the species richness. Consequently, the choice of a stability measure is dictated by the assumptions we make about the dynamics of the system, the variable of interest and the environmental regime considered. In this thesis, I use the temporal variability of the total abundance of a functional group or guild as an inverse measure of stability (cf. Tilman 1996, Doak et al. 1998).

My original overall goal was to develop a quantitative approach to estimate the extent to which diversity stabilizes communities, and to apply this approach to herbivory on coral reefs. I began, in chapter 2, by examining herbivory on the Great Barrier Reef.

On coral reefs, herbivorous fishes play a critical role on ecosystem function by mediating competition between corals and macroalgae for space. Vacant space on the substrate opened by recurrent perturbations such as storms, cyclones or bleaching, is colonized by macroalgae under conditions of low herbivory, leading to inhibition of coral recruitment and coral overgrowth. Once initiated, this process is hard to reverse and can result in large scale phase-shifts where previously coral-dominated systems become dominated by algae (Hughes 1994, Bellwood et al. 2004). Consequently the magnitude of the temporal variability of herbivory is important to the control of macroalgae on coral reefs and to their maintenance in a coral-dominated state.

Asynchrony in the fluctuations of species' abundances is the key mechanism underlying the stabilizing effect of species diversity on aggregate community properties (Doak et al. 1998, Tilman et al. 1998, Yachi and Loreau 1999, Loreau 2010). Therefore I used community asynchrony to quantify the strength of the diversity-stability relationship for herbivorous fish. Community asynchrony, in turn, is driven by two mechanisms: competitive interactions among species and differential responses to environmental fluctuations (response diversity). Competition between species can generate strong asynchrony in species' fluctuations because a decrease in 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 response diversity promotes asynchrony in species' fluctuations.

The extent to which interspecific ecological interactions and response diversity contribute to the diversity-stability relationship is contentious and has never been assessed in natural assemblages. Theoretical studies suggest that interspecific competition has little influence on the DSR, because the stabilizing effect resulting from competition-driven asynchronous dynamics is compensated by the destabilizing effect of competition on population variability (Ives et al. 1999, Ives and Hughes 2002). In contrast, a recent study suggests that competition has a destabilizing effect (Loreau and Mazancourt 2013). The quantitative approach I developed in chapter 2 is the first study that disentangles the relative contributions of ecological interactions and response diversity to the diversity–stability relationship in a natural ecological community.

Using an extensive dataset of time-series of abundances on 35 reefs of the GBR, I first quantified the strength of asynchrony in temporal fluctuations of abundance among herbivorous fishes. Then, by fitting a model of community dynamics that explicitly includes terms for compensatory interactions and response diversity, I estimated their relative contribution to the stabilising effect of species diversity. My results show that response diversity is the main driver of the stabilizing effect of species diversity for herbivorous fishes on the GBR, with important implications for the management of coral reefs.

1.1. Population synchrony and community stability

The approach I developed in chapter 2 is based on the positive relationship between community asynchrony and the stabilizing effect of species' diversity on the total abundance of the community. This relationship has been established in many empirical and theoretical studies (Doak et al. 1998, Tilman et al. 1998, Yachi and Loreau 1999, Loreau 2010). However there is no consensus about how community asynchrony should be measured and how it contributes to the diversity-stability relationship. This is the question I address in chapter 3.

In chapter 3, I developed a theoretical framework to understand diversity-stability relationships in nature. Following years of theoretical debate about the relationship between diversity and stability in ecological systems, biodiversity experiments have found that aggregate community properties, such as total abundance or productivity tend to fluctuate less in species-rich communities, a phenomenon commonly termed the portfolio effect. Theoretical studies have identified four determinants of the portfolio effect: community asynchrony, evenness of abundance among constituent species, the relationship between total community abundance and diversity and the way in which temporal variability in abundance scales with its mean. However, predictions from portfolio effect theory have been increasingly at odds with results from empirical studies, leading to calls for the development of a new theory which relaxes several of the restrictive assumptions made by existing theory (Grman et al. 2010, Mikkelson et al. 2011).

Generalizing existing theory, I produce a simple model of portfolio effects that shows that community variability is the product of two quantities: community synchrony and weighted average population variability. This relationship is robust to arbitrary violation of the evenness assumption and is much more general than previous models of the portfolio effect. Weighted average population variability can in turn be decomposed to consider effects of the mean-variance scaling of abundance, changes in mean abundance with diversity and differences in species' mean abundance in monoculture. Using this framework, I show how evenness in the abundances of a community's constituent species influences the diversity-stability relationship through combined effects on community synchrony and weighted average population stability. Finally, I illustrate how this framework helps to resolve the apparent contradictions between conflicting results from empirical studies and portfolio effect theory. Community synchrony, weighted average population variability and the way they change with diversity are the key elements to understand diversity-stability relationships. Most empirical studies do not report these quantities, although most have collected the data to do so, suggesting that a re-examination of existing data could improve our understanding of diversity-stability relationships in natural communities.

1.2. Observation error and quantifying ecological stability

Ecological time-series of population counts inevitably contain errors of measurement, where the population size recorded is different from the actual true population size. Ignoring observation error in the analysis of time series can bias parameter estimates and compromise the inferences drawn from fits of population and community dynamics models to data (De Valpine and Hastings 2002, Polansky et al. 2009). For example, ignoring observation error in studies of population regulation leads to over-estimation of the strength of density dependence (Freckleton et al. 2006). In population viability analyses, extinction risk can be under-estimated when observation error is ignored (Nadeem and Lele 2012). Similarly, ignoring observation error can potentially have important implications for estimating and identifying the drivers of stability in community time-series. For example, errors of observation among species are typically assumed to be uncorrelated, as would be the case if environmental conditions do not affect the observation process. Consequently, ignoring observation error could spuriously decrease the strength of correlation between species responses to environmental fluctuations, resulting in an over-estimate of response diversity.

In chapter 4, I used a model which explicitly accounts for observation error to assess the strength of evidence for population regulation in ecological time-series from the Global Population Dynamics Database (GPDD). The extent to which natural populations are regulated has been a contentious issue in ecology for nearly a century. The debate seemed to come to an end when several studies found strong evidence for population regulation in large collections of time-series of population sizes (Brook and Bradshaw 2006, Sibly et al. 2007). However, more recently, the conclusions of these studies have been challenged on the ground that they did not acknowledge for uncertainty in abundance estimates (observation error) (Knape and de Valpine 2012, Lebreton and Gimenez 2013). Observation error is pervasive in ecological time-series, and, unless it is explicitly accounted for, it can lead to the detection of strong negative density-dependence even though density-dependence is weak or absent (Freckleton et al. 2006). Indeed, a recent analysis of the patterns of density dependence in the GPDD found that the strength of evidence for population regulation decreased substantially when observation error is accounted for, suggesting that density-dependence has been overestimated in early analyses. Some authors have even suggested that the patterns of density-dependence previously detected in the GPDD could be entirely driven by observation error (Holmes et al. 2007). Alternatively, the reduced rate of detection of statistically significant density-dependence could result from the loss of statistical power associated with the explicit incorporation of observation error. Indeed the detection of density-dependence in single time-series of population counts with observation error is notoriously difficult, owing to the large uncertainty in estimates of the strength of density-dependence (Dennis et al. 2006, Dennis et al. 2010). To overcome this difficulty, I conduct an aggregate analysis of the GPDD, considering evidence for density-dependence across all time-series.

My population by population results match closely those of previous studies: statistically significant density-dependence is detected in only 16% of the time-series. However, in the aggregate, I find very strong evidence for density-dependence, even though its intensity is weaker than suggested by averaging estimates from separate fits to individual time-series. This indicates that density-dependence might be over-estimated when based on analysis of a single time-series in isolation, even though observation error has been accounted for. Moreover, I find no evidence that individual time-series fall into categories of density-dependent and density-independent dynamics, suggesting that differences in support for density-dependence are likely the result of differences in statistical power. Overall my findings suggest that the observational record does indeed contain strong support for density-dependence, but that its intensity is likely weaker than is detected in laboratory and field experiments.

Chapter 2 has been published in *Ecology* (Thibaut et al. 2012), © 2012 by the Ecological Society of America. Chapter 3 has been published in *Ecology Letters* (Thibaut and Connolly 2013), © 2012 Blackwell Publishing Ltd/CNRS. Chapter 4 has been submitted for publication. Chapter 2 has been co-authored with Sean Connolly and Hugh Sweatman, and chapter 3 and 4 have been co-authored with Sean Connolly.

Chapter 2. Diversity and stability of herbivorous fishes on coral reefs

2.1. Introduction

The relationship between species diversity and 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 I 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 influence 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, more than 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 chapter addresses these difficulties using a multiple-scale approach in which species that have similar ecological functions are grouped together for analysis. First, I quantify the portfolio effect and analyze ecological interactions and response diversity among these functional groups. I then conduct a similar analysis within functional groups by modeling the ecological interactions and response diversity between subsets of species within functional groups. This approach allows me 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 (Burkepile 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 chapter, I estimate the strength of the diversity-stability relationship for herbivorous fishes on Australia's Great Barrier Reef, and I develop and apply a new approach to quantify the relative contributions of ecological interactions and response diversity to this relationship. My 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, I estimate spatial variation in the overall strength of the portfolio effect, of ecological interactions, and of response diversity, both between and within herbivore functional groups. I then examine 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.

2.2. Material and Methods

Overview of approach

I analyze 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 is used to analyze the portfolio effect both between functional groups and within functional groups. For each analysis, three statistics related to the diversity-stability relationship are 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, I use 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 come 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. My dataset is based on 35 reefs spread across a large proportion of the Great Barrier Reef province (Figure 2-1). The surveys started in 1993 and are continuing, although the number of years of surveys varies from reef to reef (see Table A-1 in Appendix A). At each reef, there are three distinct sites on the north-east flank of the reef. Each site contains five permanently marked 50m transects running parallel to the reef crest. Trained observers assess 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 are used: small, sedentary species are surveyed on 1 m wide transects, while larger, more mobile species are surveyed on 5 m wide transects. Therefore, abundances were standardized to density for analysis.

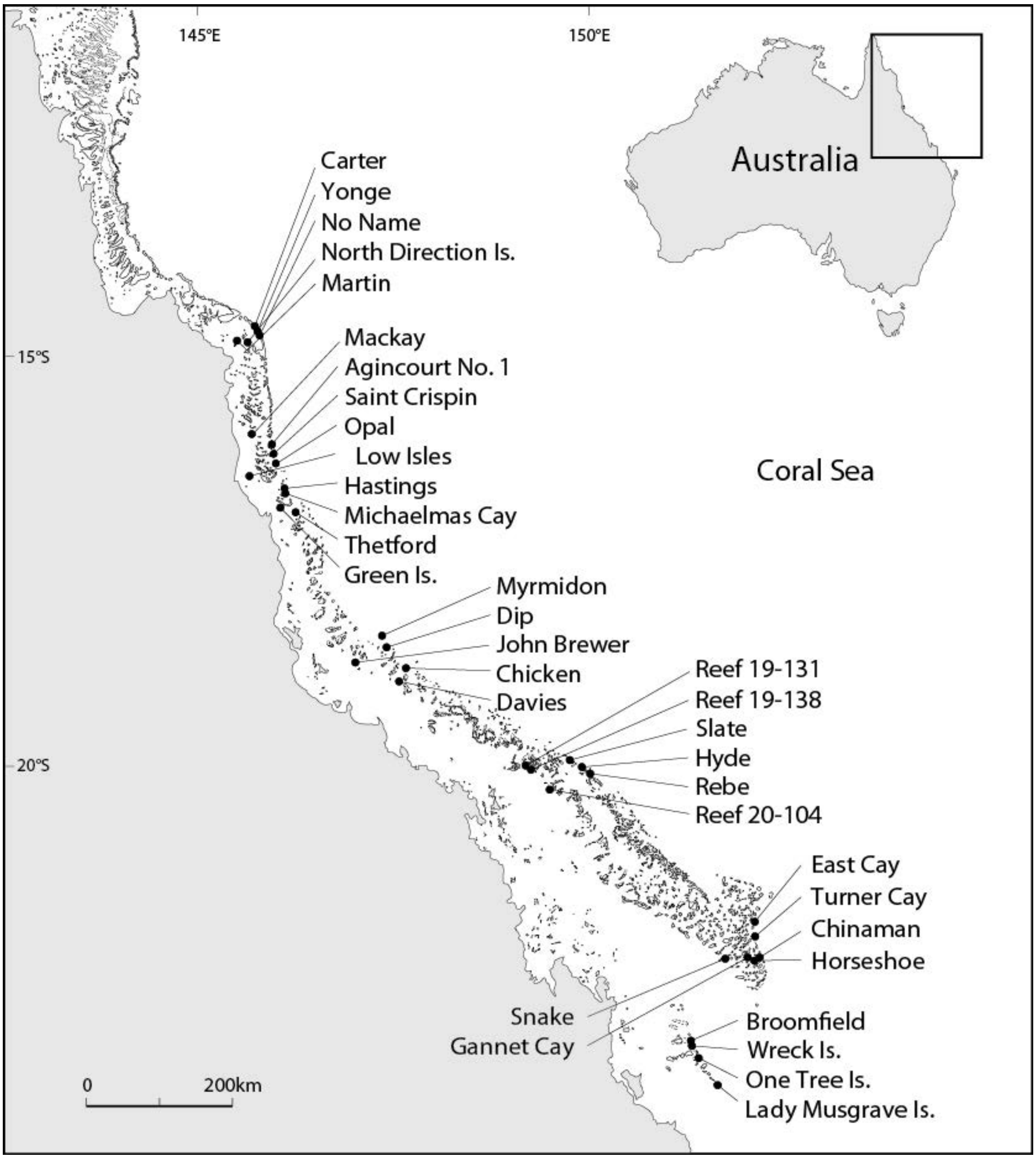

Figure 2-1.—Map of the Great Barrier Reef of Australia showing the location of the 35 reefs included in this study.

I 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 A-2 in Appendix A.1). 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 sub-group 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 co-existence of multiple functional groups is caused by asynchrony of fluctuations in abundance of those groups over time (Gonzalez and Loreau 2009). To quantify the strength of this portfolio effect, I use the average pair-wise cross-correlations between abundances of the functional groups over time, a standard approach for estimating community-wide patterns of synchrony (Bjornstad et al. 1999). I 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, I fitted our time-series to a model of community dynamics that explicitly included terms for each of the mechanisms. More specifically, I tested two models involving different functional relationships 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 A.2), so I used the Gompertz model in all of my analyses.

Specifically, my 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 (2003), observation error can bias the estimates for ecological interactions and response diversity. Therefore, to disentangle observation error from responses to environmental fluctuations, I 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 my model, I 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, I 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 dataset, ecological interactions can be parameterized at different levels: equivalent interactions for all reefs in the dataset, different interactions for each reef, or different interactions for each site within each reef. To determine the optimal parameterization, I 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:

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

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). I assumed that both $r_{i,r,s}^{t}$ and $e_{i,r,s,u}^{t}$ were normally distributed with mean zero.

Between-groups analysis.—Once the model had been fitted to the data, I calculated two statistics representing the two processes underlying the diversity-stability relationship: ecological interactions and response diversity. Firstly, I 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, I 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, I 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, I averaged all $b_{i,i,r}$). 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, I estimated the degree of synchrony between groups in the responses to environmental fluctuations. I 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, I calculated, for each pair of groups i and j, the correlation coefficient between $r_{i,r,s,t}$ and $r_{j,r,s,t}$). I then averaged these correlation coefficients over all pairs of groups for each reef. I term this quantity the "Environmental Response Synchrony Index" (ERSI).

Within-groups analysis.—Fitting a model of three interacting functional groups allowed me to assess the extent to which diversity of functional groups influenced ecological stability. However, species diversity within functional groups may also influence stability. Here, I face 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, I 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. I repeated this procedure 9 times for each functional group.

The rationale for the above 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. I 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).

2.3. Results

The portfolio effect was found to operate strongly in the community of herbivorous reef fishes on the GBR 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. I 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 (Figure 2-2A).

Overall, I 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, Figure 2-2B). The within-groups analysis indicated that response diversity was similarly high among Territorial and Roving Grazer species, but somewhat weaker for Scrapers (Figure 2-2B).

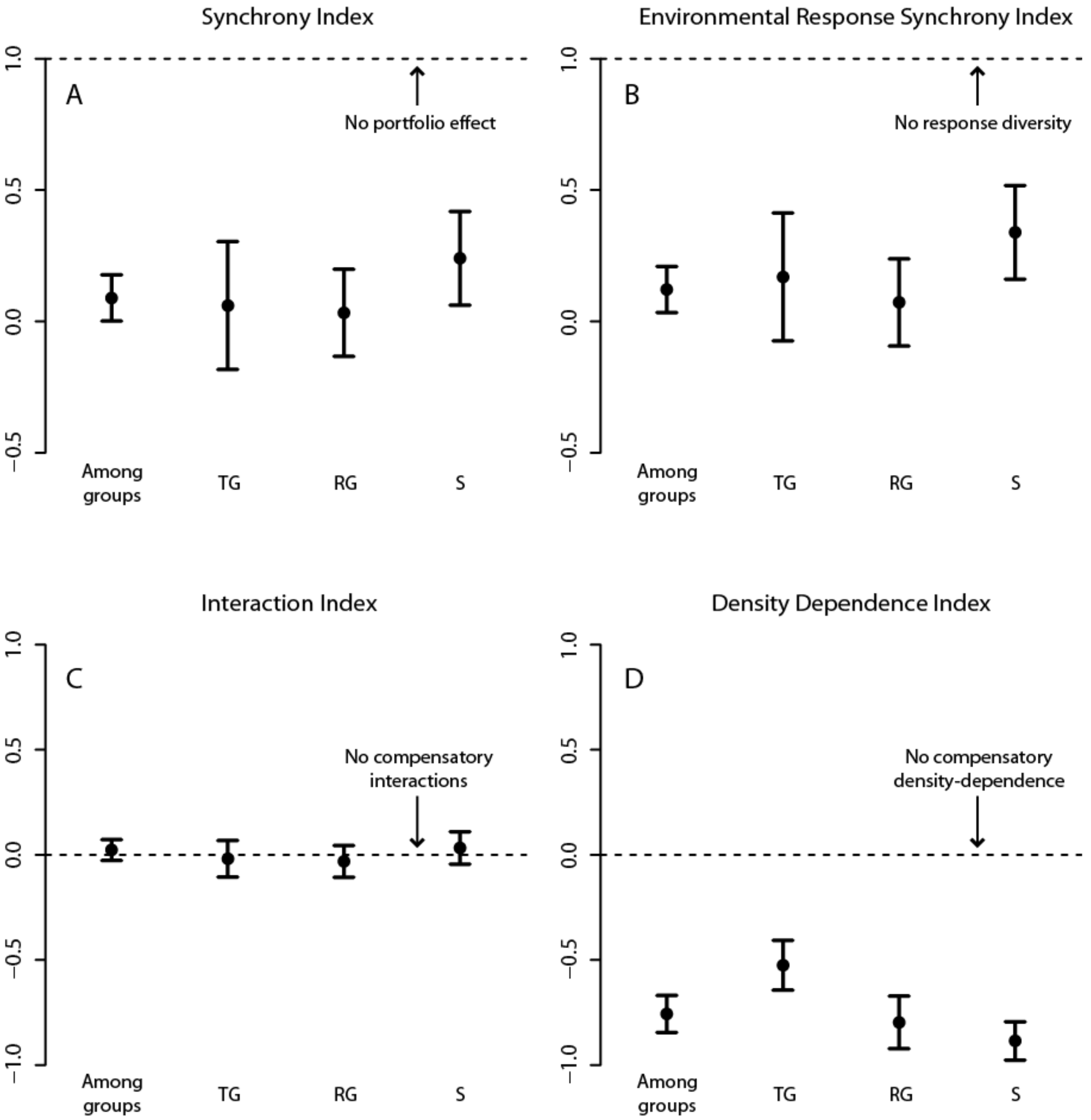

Figure 2-2.—Mean values and standard deviation for the (A) Synchrony, (B) Environmental Response Synchrony, (C) Interaction, and (D) Density-dependence Indices.“Among–Groups” refers to the analysis of interactions between the functional groups, while “TG”, “RG” and “S” refer to the within-group, random-subset analyses for the Territorial Grazers, Roving Grazers and Scrapers functional groups, respectively. Note that the lowest possible value for the synchrony indices is -1/2 for the among-groups analysis and -1 for the within-groups analyses. In (A) and (B), the dashed line indicates the Synchrony Index corresponding to complete absence of a portfolio effect.

In (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 (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.

As noted above, my 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 (Figure 2-2A-C). This suggests that that average between-group interaction strength varied spatially from weakly competitive to weakly facilitative. Very similar results were obtained for the within-groups analysis (Figure 2-2C, Table 2-1). In contrast, within group interactions were always strongly competitive, as shown by consistently large, negative Density-Dependence Indices (Figure 2-2D).

Table 2-1.—Results of multiple linear regressions of Synchrony Index against Interaction Index and Environmental Response Synchrony Index for between-groups and within-group analyses.Between groups is the analysis based on fluctuations in abundance of the three functional groups (cf. Figure 2-2). TG, RG, and S refer to analyses of the fluctuations of abundance of the random subgroups 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. ¤ $p<0.1$, * $p<0.05$, ** $p<0.01$, *** $p< 0.001$.

Dataset	Overall Regression		Environmental Response Synchrony Index		Interaction Index	
	Signif.	R^2	Coef.	R^2	Coef.	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

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 (Figure 2-3, Table 2-1). 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 2-1). 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 2-1). 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 by response diversity, as was the case in the between-groups analysis (Table 2-1). 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 2-1).

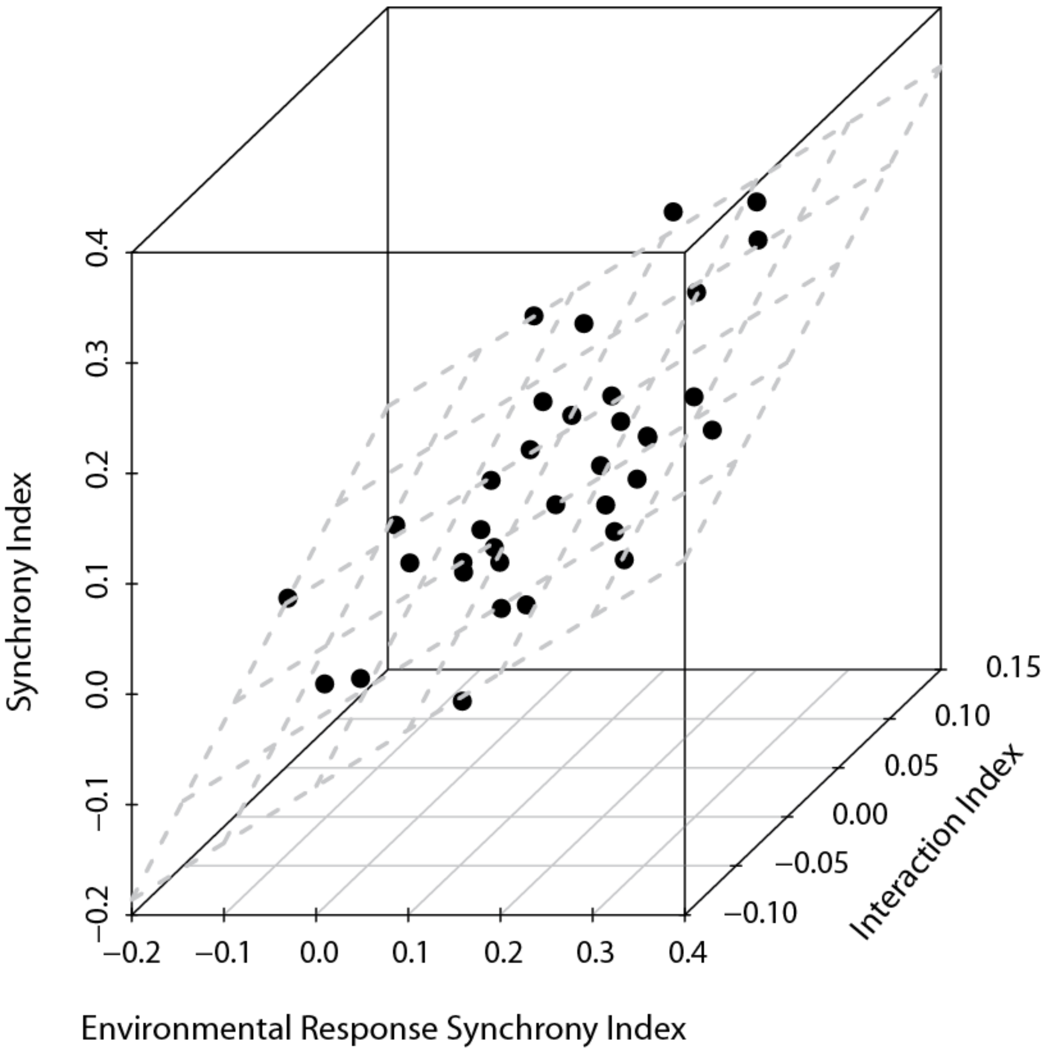

Figure 2-3.—Multiple regression of Synchrony Index on Interaction Index and Environmental Response Synchrony Index. Each point represents a reef (n=35), and the dashed grid shows the fit of the regression model. See Table 2-1 for regression statistics.

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

For my within-groups analysis, I 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 my 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 A.3). This means that the portfolio effect and response diversity for species within functional groups are likely to be stronger than my 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 A.3), meaning that species interactions are likely to be even weaker than the estimates from my 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. I 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 & 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 my Synchrony Index. However, the two statistics appear to yield very similar conclusions: when I applied their statistic to my data, I found an average correlation of 0.1 across the 35 reefs, identical to my 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 my 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 I 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 et al. 1990). However, given the ecological differences between these species and the pomacentrids that constitute the rest of this group, I repeated my between-groups and within-Territorial Grazers analyses with the two *Acanthurus* species excluded. My 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. Figure 2-2). Similarly, all terms that were significant in the original regression analyses (Table 2-1) remained significant in the revised analyses. These results indicate that my 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, I found little evidence in this system that the portfolio effect was enhanced by compensatory ecological interactions, either between functional groups or within them. Instead, I 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. Roughgarden 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 & 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). My findings are consistent with these results and support a Gleasonian view of herbivorous reef fish assemblages in which the effects of inter-specific 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 my results to this potential effect, I 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). I then repeated my between-groups analysis, and I 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. Figure 2-2). Moreover, all terms that were significant in my original regression analyses (Table 2-1) remained significant in the modified analyses. While not a comprehensive accounting of inter-specific differences in biomass (which will vary among individuals within species, as well as between species), the fact that I obtained very similar results, despite a range of body size of about three orders of magnitude among species, indicates that my 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 my measure of abundance**.**

In contrast to between-group interactions, which were, on average, near zero, I 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, then I would have expected my within-groups 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 my 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 my estimates of the strength of density-dependence are, if anything, stronger in the Roving Grazers and Scrapers than in the Territorial Grazers (Figure 2-2D), 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, I have used a new approach to quantifying the portfolio effect which allows the roles of compensatory ecological interactions and response diversity, the underlying drivers of the portfolio effect, to be disentangled. I 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. My 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). My 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).

In this chapter, I used the average correlation coefficient (SI) to quantify the degree of asynchrony among functional groups of herbivorous fishes, a common practice in studies of spatial and temporal fluctuations of abundances (e.g. Bjornstad et al. 1999, Valone and Barber 2008). A problem with this approach is that, in real communities, species may differ substantially in their variances, so some between-species correlations are likely to be more important to overall community stability than others. Consequently, two communities with the same mean correlation coefficient could differ substantially in their synchrony (see Appendix B.1 for an example). There is no consensus about how community asynchrony should be measured and how it contributes to the diversity-stability relationship. Consequently, I turn to this problem in Chapter 3.

Chapter 3. Understanding diversity-stability relationships: towards a unified model of portfolio effects

3.1. Introduction

In nature, many species' ecological roles are essential for ecosystem functioning or for the provision of ecosystem services to human societies (Lawton 1994, Worm et al. 2006, Cardinale et al. 2012). For example, species that forage for pollen or nectar facilitate reproduction in the plants on which they forage, a function that is essential for the maintenance of plant populations, including in agricultural ecosystems (McGregor 1976, Hoehn et al. 2008). On coral reefs, grazing by fishes helps to maintain healthy, coral-dominated reefs (Bellwood et al. 2004). One essential service provided by biodiversity is to stabilize the overall abundance of an assemblage of organisms that provides a particular ecosystem service or function, thereby making it less vulnerable to fluctuations in the abundances of individual populations. This phenomenon, or components of it, have been characterized using a variety of terms (e.g., statistical averaging, portfolio effect, covariance effect, insurance hypothesis, stabilizing effect: (Doak et al. 1998, Tilman et al. 1998, Yachi and Loreau 1999, Loreau 2010). For simplicity, I here refer to the relationship between the number of populations and temporal stability of total community abundance as the "diversity-stability relationship", or DSR, and the tendency for DSRs to be positive (i.e., for stability to increase with diversity), as the "portfolio effect". This definition of the latter term is consistent with its use in other disciplines, such as finance (Markowitz 1952, 1987), and with its original use in the context of the DSR (Tilman et al. 1998, contra Tilman 1999).

In both model and experimental communities, stability is typically taken to be inversely related to the coefficient of variation of some measure of ecosystem function, such as total community abundance. The DSR is the relationship between this measure of stability, and diversity (here defined as the number of constituent populations). Usually diversity is quantified as species richness, but communities can be stabilized by diversity at other levels of organization as well, such as functional groups (Bai et al. 2004) or number of phenotypes within populations (Norberg et al. 2001). Various proposed statistical formalisms for the DSR have suggested that, at least in principle, it may be positive or negative (Tilman 1999, Lhomme and Winkel 2002). However, stochastic competition models have consistently found portfolio effects (e.g. Lehman and Tilman 2000, Ives and Hughes 2002, Loreau and de Mazancourt 2008). Similarly, two decades of experimental research into DSRs indicates that portfolio effects are overwhelmingly present, but that their strength and magnitude varies considerably (Campbell et al. 2011). However, inverse portfolio effects, where stability decreases with diversity, also can occur in nature (DeClerck et al. 2006, Yang et al. 2011).

Several community properties have been identified as important determinants of the portfolio effect. Four that have received particular attention are asynchrony in population fluctuations, evenness of abundance, effects of diversity on total community abundance, and the way in which temporal variability in abundance scales with its mean (Cottingham et al. 2001). Firstly, theoretical studies indicate that portfolio effects should strengthen as asynchrony in the fluctuations of a community's constituent populations increases (Doak et al. 1998, Loreau 2010). Despite its importance in diversity-stability relationships, however, there is no consensus about how asynchrony should be measured, or about how it contributes to the DSR. A variety of metrics have been proposed, including coefficients of pairwise correlations of species' fluctuations in abundance (Doak et al. 1998), summed species-level variances and covariances (Tilman 1999), and total community variance relative to that of a perfectly synchronous community (Loreau and de Mazancourt 2008). All of these metrics are still used in empirical studies (e.g., Mikkelson et al. 2011, Roscher et al. 2011, Thibaut et al. 2012). Secondly, models of the DSR also predict that the portfolio effect will be stronger where evenness of mean abundance among populations is greater (Doak et al. 1998, Lhomme and Winkel 2002): when evenness is very low, the rarest species make a limited contribution to overall stabilization of function at the community level, compared to when evenness is high. However, researchers have found positive relationships between evenness and stability (Mikkelson et al. 2011), no relationship (Isbell et al. 2009), and even negative relationships (van Ruijven and Berendse 2007), leading to calls for the development of theory to better understand how evenness affects community stability (Grman et al. 2010, Mikkelson et al. 2011). Thirdly, mean community biomass often increases with increasing diversity (Duffy 2009, Cardinale et al. 2012), a phenomenon sometimes termed "overyielding" (Tilman 1999), and several empirical studies have identified overyielding as a mechanism driving the DSR (Tilman et al. 2006, Isbell et al. 2009, Hector et al. 2010). Finally, there is a well-known tendency for the temporal variance in population abundance to exhibit a power-law relationship with the mean (Taylor 1961). Theoretical studies have suggested that stability should increase as the value of the exponent of this mean-variance scaling relationship increases above unity (Tilman et al. 1998, Tilman 1999). However some experimental studies have found contrary results (Valone and Hoffman 2003, van Ruijven and Berendse 2007, Yang et al. 2011).

A comprehensive understanding of the combined effects of synchrony, overyielding, mean-variance scaling, and evenness on the diversity-stability relationship has been hampered by the need to make idealized assumptions about some of these phenomena when investigating effects of others. For example, in order to examine the effect of evenness, Doak et al. (1998) assumed that all between-species correlations are equal, and that total community size is independent of diversity (no overyielding). Tilman's (1999) framework assumes perfect evenness (all species' mean abundances are equal), and independence of species fluctuations (all $\rho_{ij}=0$), in order to examine the effect of overyielding. Similarly, community-dynamic approaches have made strong symmetry assumptions (e.g., all species have the same intrinsic growth rates, carrying capacities, competition coefficients, and between-species correlations in responses to environmental fluctuations: (Ives and Hughes 2002, Loreau 2010). These assumptions have come under increasing criticism, particularly in empirical studies that have obtained anomalous results (such as "inverse" portfolio effects, where communities become less stable as diversity increases) under conditions where particular simplifying assumptions are violated (e.g., Valone and Hoffman 2003, Steiner et al. 2005, van Ruijven and Berendse 2007, Grman et al. 2010, Yang et al. 2011).

An additional challenge to understanding the DSR is teasing apart the factors that drive the relationship between community stability, and stability of the individual populations that constitute the community. In a meta-analysis, Campbell *et al.* (2011) found strongly bimodal responses of population stability with diversity: some studies find that diversity stabilizes populations, while a comparable number of studies find that diversity de-stabilizes populations. Because either of these contrasting population-level responses may occur in assemblages exhibiting portfolio effects at the community level, clarifying the relationship between population stability and overall community stability has been identified as a critical knowledge gap in our understanding of the DSR (Vogt et al. 2006, Campbell et al. 2011).

In order to generalize the theory that we use to understand the DSR, and to place earlier theoretical and empirical findings in a broader context, I here synthesize key elements of previous approaches (e.g., Doak et al. 1998, Tilman 1999, Loreau 2010), in order to produce a simple model of portfolio effects that makes explicit how community stability relates to the stability of a community's constituent populations, and in turn how asynchrony, overyielding, mean-variance scaling, and evenness influence this relationship. Analysis of this model reveals that the DSR is the product of a synchrony effect and a weighted average population variability effect, a simple expression that is robust to the presence or absence of overyielding, and to differences in means or variances of species abundances (i.e., arbitrary violation of the evenness assumption). Weighted average population variability can be further decomposed into an overyielding-related effect and a single-species variability effect. This synthetic framework clarifies the sometimes counter-intuitive ways that evenness can affect the DSR, and helps to explain apparent inconsistencies among alternative statistical frameworks, empirical studies of the DSR, and theoretical studies based on analysis of community-dynamic models. It also suggests some additional assumptions common to DSR theory that are likely to be violated in nature, but whose effects on the DSR have received little or no attention to date.

3.2. Towards a unified model of portfolio effects

Following previous theory for the portfolio effect (e.g., Doak et al. 1998, Tilman 1999, Loreau 2010), I here treat species abundances as stationary random variables (i.e., abundances fluctuate over time, with a fixed mean and variance). Thus, a community of n species can be described with a vector of mean species abundances, $\mathbf{m}_n$ and a variance-covariance matrix of abundances, $\mathbf{V}_n$:

$$\mathbf{m}_n = \begin{pmatrix} m_n^s(1) \\ \vdots \\ m_n^s(n) \end{pmatrix} \tag{3.1a}$$

$$\mathbf{V}_n = \begin{pmatrix} v_n^s(1,1) & \cdots & v_n^s(1,n) \\ \vdots & \ddots & \vdots \\ v_n^s(n,1) & \ldots & v_n^s(n,n) \end{pmatrix} \tag{3.1b}$$

where

$$v_n^s(i,j) = \rho_{ij}\sqrt{v_n^s(i,i)v_n^s(j,j)} \tag{3.1c}$$

In eq. (3.1), and throughout this chapter, I use the superscript c to designate community level quantities, and the superscript s for species-level quantities. n is the number of species in the community. m denotes mean abundances, and v variances and covariances. Thus, $m_n^s(i)$ denotes the mean abundance of species i, $v_n^s(i,i)$ the variance (over time) of abundance of species i, and $v_n^s(i,j)$ the temporal covariance of abundances of species i and j, in a community of n species. By definition, the covariances depend on the species-specific variances, and a coefficient, ρ_{ij}, characterizing the temporal correlation between the abundances of the two species.

Measuring Asynchrony

Of particular interest in analyses of the portfolio effect has been the development of measures of community synchrony. In early work, community synchrony was defined using the correlation coefficients in eq. (3.1c), which were assumed to be the same for all pairs of species in the community ($\rho_{ij}=\rho$ for all i,j) (Doak et al. 1998, Tilman 1999). Because, in real communities, correlation coefficients will differ between different pairs of species, based on the idiosyncratic characteristics that determine their interactions and responses to environmental fluctuations, most empirical analyses rely on the mean of the correlation coefficients, $\bar{\rho}$ (Valone and Barber 2008, Thibaut et al. 2012), which is bounded in the range $\left[-\frac{1}{n-1}, 1\right]$. A problem with this approach is that, in real communities, species may differ substantially in their variances, so some between-species correlations are likely to be more important to overall community stability than others. Consequently, two communities with the same mean correlation coefficient could differ substantially in their synchrony (see Appendix B.1 for an example).

An alternative approach to measuring synchrony considers the sum of the species-level variances (diagonal elements of eq. 3.1b) and the sum of the between-species covariances (off-diagonal elements of eq. 3.1b). Tilman (1999) argued that these two quantities measure different drivers of asynchrony: the former a "portfolio effect"—the benefit of diversity due to statistical averaging (a narrower definition of the term than used in this chapter)—and the latter a "covariance effect", which represents the stabilizing effect of compensatory interactions (e.g., the tendency for a species to increase in abundance from competitive release, when another species decreases).

However, while there is still some disagreement in the literature about the utility of summed covariances as an indicator of compensatory interactions, there is now broad consensus that summed variances and covariances do not partition statistical averaging and compensatory interaction effects (Ives and Carpenter 2007, Houlahan et al. 2008, Loreau and de Mazancourt 2008, Ranta et al. 2008) .

More recently, Loreau & de Mazancourt (2008) proposed quantifying community synchrony using the statistic:

$$\phi = \frac{\sum_{ij} v_n^s(i,j)}{\left(\sum_i \sqrt{v_n^s(i,i)}\right)^2} = \frac{v_n^c}{\left(\sum_i \sqrt{v_n^s(i,i)}\right)^2} \tag{3.2}$$

(also see Loreau 2010). Here, the scalar $\boldsymbol{v_n^c}$ indicates the variance of total community abundance for a community of n species, which, by definition, is the sum of all elements of the community variance-covariance matrix (the summed variances plus the summed covariances). The denominator is the variance of a hypothetical community with the same species-level variances, but in the presence of perfect synchrony (Loreau and de Mazancourt 2008). One advantage of ϕ, hereafter termed the "synchrony index", is that it makes no assumptions about the particular distribution of values for the pairwise correlation coefficients. This is because the off-diagonal elements of the community variance-covariance matrix influence ϕ only through their combined effect on the total community variance in abundance, $v_n{}^c$, which can be measured directly in the aggregate (i.e., without separate estimation of pairwise covariances). ϕ is also normalized, independent of diversity: it always varies between zero (when total community abundance is constant), and one (when fluctuations are perfectly synchronous). Finally, in contrast to the mean correlation coefficient, it explicitly incorporates the effects of unequal species-level variances on synchrony (see Appendix B.1).

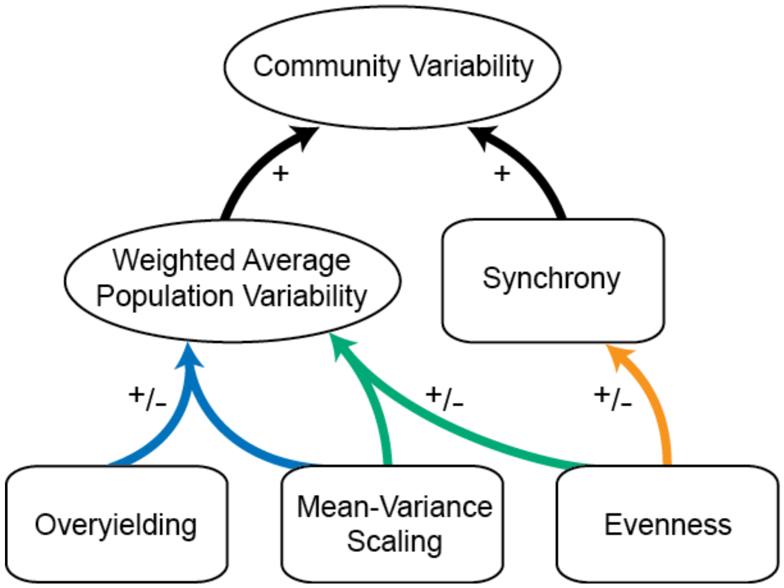

Figure 3-1.—Schematic illustrating how population and community variability (ellipses) are influenced by the four determinants of the DSR highlighted in the Introduction: synchrony of population fluctuations, evenness, overyielding, and the way variance in population fluctuations scales with the mean (rectangles). Arrows merge where an effect arises from an interaction between two determinants. "+" indicates that an effect is positive (e.g., community variability increases as synchrony increases), and "+/-" indicates that an effect may be either positive or negative.

Unifying Population and Community Variability

We can derive a very general relationship for the relationship between population and community variability by taking advantage of the synchrony index, re-arranging eq. (3.2), and rescaling our measure of community variability from total variance to CV:

$$CV_n^c = \sqrt{\phi}\widetilde{CV}_n^s \tag{3.3}$$

where CV_n^c is the coefficient of variation of total community abundance, for a community of n species, and $\widetilde{CV}_n^s$ is the average species-level coefficient of variation for a community of n species, weighted by species' relative mean abundance:

$$\widetilde{CV}_n^s = \sum_i \frac{m_n^s(i)}{m_n^c} \frac{\sqrt{v_n^s(i,i)}}{m_n^s(i)} \tag{3.4}$$

(see Appendix B.2 for derivation). m_n^c is the temporal mean of total community abundance (i.e., the sum of species-level mean abundances). Eq. (3.3) shows that the dimensionless community variability in abundance is completely determined by the weighted average species-level coefficient of variation, and the synchrony index ϕ (Figure 3-1, black arrows). In eq. (3.3), dimensionless population and community variability are linearly proportional to one another, with a constant of proportionality that depends on how synchronous the fluctuations of different species are. When fluctuations are highly synchronous (ϕ~1), community variability tracks population variability. When fluctuations are less synchronous (ϕ is smaller), population variability is damped at the community level. The fact that population variability is a weighted average in eq. (3.3) indicates that the variability of more abundant populations make larger contributions to overall community variability.

Equation (3.3) is much more general than previous DSR models. In particular, it makes no assumptions about evenness of mean abundances, about the distribution of variances or correlation coefficients in the covariance matrix, or about the direct ecological interactions or responses to environmental fluctuations that influence those variances and correlation coefficients. Note that, because $\phi \leq 1$, community variability is never greater than population variability.

To examine more specifically the role of overyielding and mean-variance scaling, I extend eq. (3.3) by making two further assumptions that have reasonably broad empirical support. Firstly, I assume that temporal variance in species' population sizes scale with their means according to Taylor's (1961) power law:

$$v_n^s = a(m_n^s)^b \tag{3.5}$$

where a and b are coefficients relating mean and variance of abundance. Secondly, both species and community mean abundance may vary as a function of diversity. I model this phenomenon using Tilman's (1999) functional form for this relationship, modified to allow unequal mean abundances:

$$m_n^c = \sum_i m_n^s(i) = \sum_i \frac{m_1(i)}{n^x}, \tag{3.6}$$

where $m_1(i)$ is the abundance of species i in monoculture, and x drives how the total abundance of the community changes with diversity. If x=1, the abundance of the total community is fixed, independent of diversity, as is assumed in many theoretical studies of the DSR (sensu Doak et al. 1998, Ives et al. 1999, Loreau 2010). "Overyielding" occurs whenever x<1: the mean of total community abundance increases with diversity. If 0<x<1, this increasing community abundance is accompanied by decreases in mean species abundance with diversity; if x=0, mean species abundances are independent of diversity; and if x<0, mean species abundance actually increases with diversity. Finally, if x>1, mean community abundance and mean species abundances both decrease with diversity (underyielding).

Incorporating eqs. (3.5) and (3.6) into eq. (3.3), I extend my framework to explicitly include the effect of overyielding on the DSR:

$$CV_n^c = \sqrt{\phi}\,\sqrt{n^{(2-b)x}}\,\widetilde{CV}_1 \tag{3.7}$$

(see Appendix B.3 for derivation). This essentially sub-divides species-level population variability into two components: an "average single species variability" term, $\widetilde{CV}_1$, which represents species' weighted average CV in monoculture, and a "mean-abundance effect", $\sqrt{n^{(2-b)x}}$, which characterizes how $\widetilde{CV}_n^s$ changes with diversity as a consequence of associated systematic changes in mean abundance (Figure3-1, blue arrows). Eq. (3.7) generalizes Tilman's (1999) model considering the effect of overyielding on the portfolio effect, which assumes that all species have the same mean abundance, and species' fluctuations in abundance are uncorrelated with one another. Similarly, it can be considered a generalization of eq. 5.8 in Loreau (2010), who considered the special case of no overyielding and perfect evenness. Note that, if the mean-abundance effect increases with diversity, then changes in mean species abundances associated with increasing diversity tend to be destabilizing at both population and community levels. In contrast, if the mean-abundance effect decreases with diversity, then changes in mean species abundance associated with increasing diversity are stabilizing at both population and community levels.

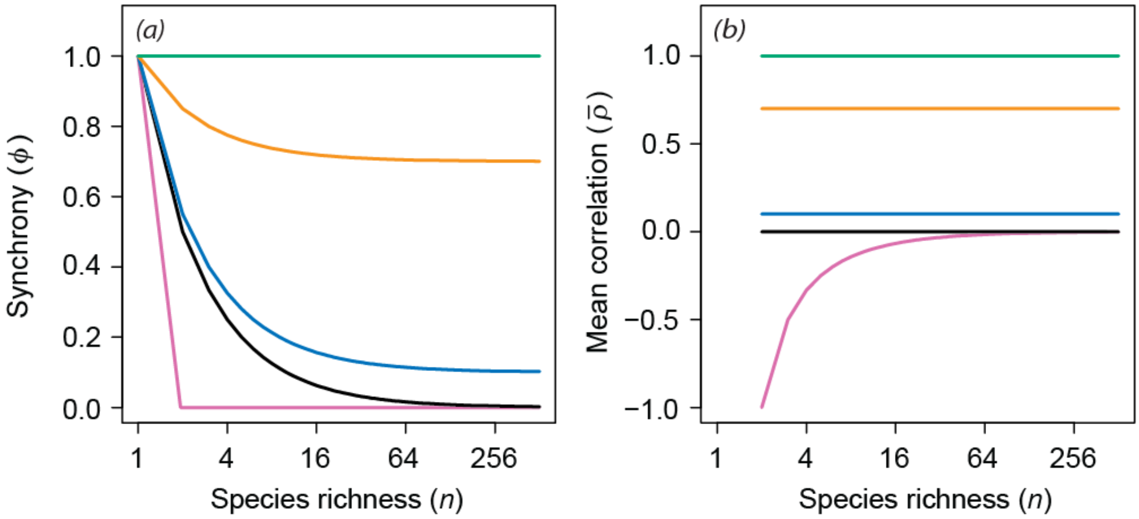

Figure 3-2.— Illustration of relationship between diversity-dependence of (a) the synchrony index, ϕ, and (b) the mean correlation coefficient, $\bar{\rho}$, under the assumption of equal population variances. The green line shows the limiting case of perfect synchrony ($\bar{\rho} = 1, \phi = 1$). The magenta line shows the limiting case of perfect asynchrony ($\bar{\rho} = -\frac{1}{n-1}, \phi = 0$ whenever $n>1$). For the orange, blue, and black lines, $\bar{\rho}$ is constant, independent of diversity (at 0.7, 0.1, and 0, respectively), so ϕ is calculated from eq. (3.8) using the specified value of $\bar{\rho}$. Because $\bar{\rho}$ is only defined for $n>1$, the lines in panel (b) commence at $n=2$. Note that species richness is plotted on a logarithmic scale.

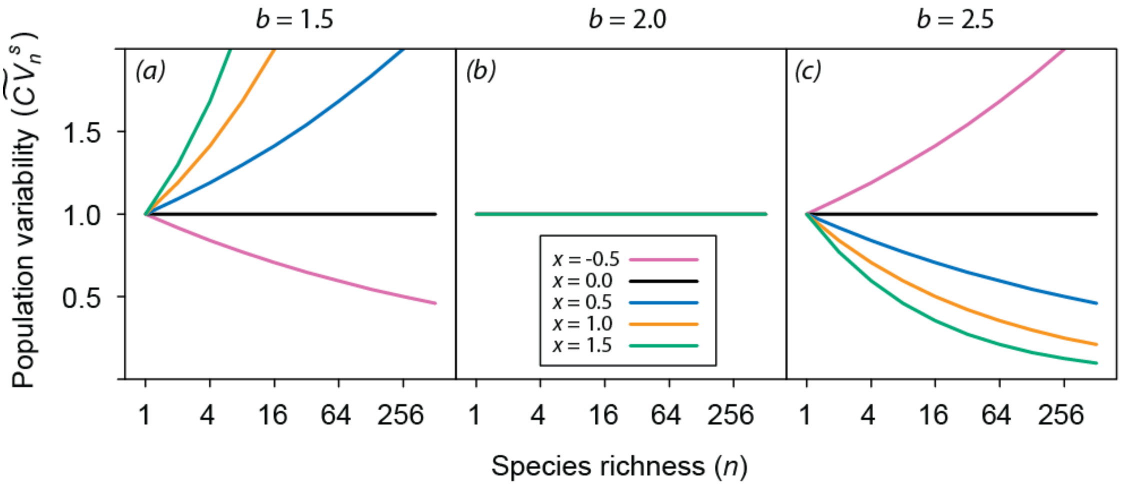

Figure 3-3.— Illustration of the diversity-dependence of the mean-abundance effect for mean-variance scaling exponents of (a) b=1.5, (b) b=2, and (c) b=2.5. Results are qualitatively identical to (a) whenever b<2, and to (c) whenever b>2. The different-colored lines show the mean-abundance effect for different values of the overyielding coefficient, x, as indicated in the figure. Note that all lines are super-imposed when b=2. Species richness is plotted on a logarithmic scale.

Synchrony, Overyielding, Evenness, and the Portfolio Effect

Eq. (3.3) makes explicit how portfolio effects arise from changes in synchrony and population variability with species richness. To understand how synchrony is likely to change with diversity, it is helpful to consider the relationship between ϕ and the mean correlation coefficient, $\bar{\rho}$, derived by Loreau (2010):

$$\phi = \frac{1+(n-1)\bar{\rho}}{n} = \frac{1}{n}(1-\bar{\rho}) + \bar{\rho} \qquad (3.8)$$

Eq. (3.8) holds only for the special case when all species have the same variances, but is still useful for thinking about the implications of different community structures for the diversity-dependence of synchrony. For instance, in the limiting case of perfect synchrony, $\bar{\rho} = 1$ and ϕ=1, regardless of diversity (Figure 3-2, green line). Conversely, for perfect asynchrony, $\bar{\rho} = -\frac{1}{n-1}$, and ϕ=0 everywhere (except in monoculture, where ϕ=1) (Figure 3-2, magenta line). For the special case of a community of non-interacting species, fluctuations in abundance between species are correlated only due to similarities in their responses to environmental fluctuations, so pairwise correlation coefficients are constant, independent of diversity (Ives et al. 1999). If $\bar{\rho}$ is small, ϕ decreases strongly with diversity (Figure 3-2, black and blue lines), while if $\bar{\rho}$ is large, then ϕ is less strongly diversity-dependent (Figure 3-2, orange line). This tendency for ϕ to decline asymptotically with diversity also occurs in the presence of competition (see Appendix B.4), and there are good reasons to expect this tendency to be common in nature. Firstly, ϕ=1 in monoculture, and must decline from this value as diversity increases if species are not perfectly positively correlated. Secondly, as diversity becomes large, each additional species makes a progressively smaller marginal contribution to the overall mean correlation coefficient, implying that chages in $\bar{\rho}$ (and thus, by eq. 3.8, ϕ) will become smaller and smaller as diversity increases.

Although the influence of overyielding on population variability has been investigated previously, these studies have tended to focus on the ranges $0<x<1$ and $1<b<2$ (e.g., Lhomme and Winkel 2002). In this range, the mean-abundance effect causes population variability to increase with diversity (Fig. 3.3a, blue line). The focus on $1 \leq b \leq 2$ was likely due to a belief that exceptions to this range are rare (e.g., Kilpatrick and Ives 2003). However, a growing number of studies report scaling exponents >2 (e.g., Valone and Hoffman 2003, Vogt et al. 2006, van Ruijven and Berendse 2007). Similarly, a focus on $0 \leq x \leq 1$ makes sense for manipulations of diversity under fixed environmental conditions, where x reflects mainly the combined effects of competition and niche partitioning (Tilman 1999, Lehman and Tilman 2000). However, in nature, diversity often covaries with environmental conditions that influence mean abundance in other ways, and DSR studies along natural gradients have found both cases of underyielding ($x>1$; Yang et al. 2011), and cases where mean species abundance actually increases with diversity ($x<0$: Valone and Hoffman 2003). Considering this broader range of parameter values, the mean-abundance effect can be seen to have both positive and negative effects on population variability (Figure 3-3). The direction of the mean-abundance effect depends on whether mean species abundance decreases with species richness or not ($x>0$ or $x<0$), and whether species-level variances scale less than or more than quadratically with the mean ($b<2$ or $b>2$). Specifically, if mean species abundance decreases with species richness ($x>0$), then the mean-abundance effect is de-stabilizing at the population level when variance scales less than quadratically with mean species abundance ($b<2$), and stabilizing when $b>2$ (compare blue, orange, and green lines in Fig. 3.3a,c). If mean species abundance increases with species richness ($x<0$), then mean-variance scaling has the opposite effect (compare magenta lines in Fig. 3-3a,c).

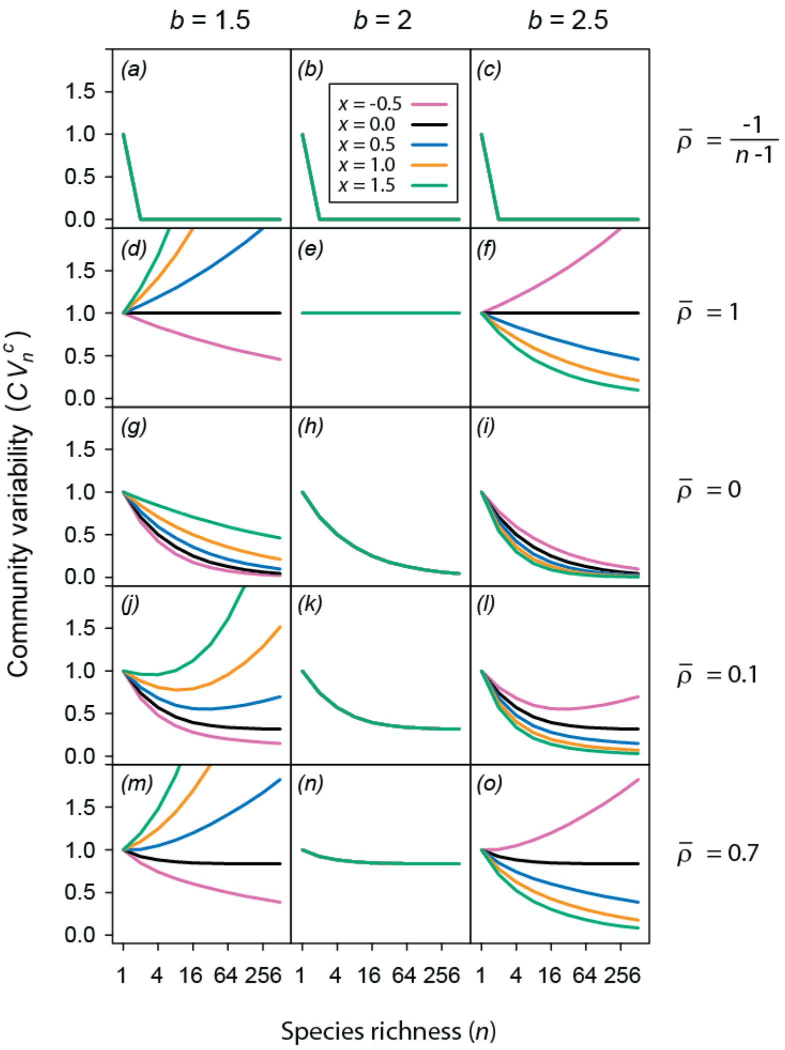

Figure 3-4.— Combined influences of synchrony and the mean-abundance effect on community variability. The left column of panels shows *b*=1.5 (cf. Fig. 3-3a), the middle column *b*=2 (cf. Fig. 3-3b), and the right column *b*=2.5 (cf. Fig. 3-3c). Rows of panels incorporate different models of synchrony from Fig. 3-2 (calculated from eq. 3.8 using the values of the mean correlation coefficient to the right of each row on the panel above). Colored lines represent different values of the overyielding coefficient, *x*, as in Fig. 3-3 (as indicated by the legend on the panel above). Note that all lines are super-imposed when *b*=2, or $\bar{\rho} = -1/(n-1)$. Species richness is plotted on a logarithmic scale.

Figure 3-4 illustrates how the DSR may be influenced by the interaction between community synchrony and the mean-abundance effect. Several non-intuitive results are worth highlighting. Firstly, a portfolio effect can be apparent even when synchrony is perfect, if population variability decreases with species richness (Figure 3-4f, blue, orange and green lines). Secondly, Figure 3-4 shows that inverse portfolio effects are possible (e.g., Figure 3-4m). Thirdly, when population variability and synchrony act in opposite directions, non-monotonic DSRs can be produced, for which community variability initially decreases with species richness, then increases. For instance, when $\bar{\rho} = 0.1$, independent of diversity, ϕ decreases asymptotically towards 0.1 as richness increases (eq. 3.8). Thus, its response to diversity may dominate the DSR at low diversity, while population variability dominates at high diversity (compare blue line in Figure 3.2a with orange lines in Figures 3.3a and 3.4j).

Considering the effect of unevenness in light of eqs. (3.3) and (3.7) indicates that it may actually increase or decrease community variability, and may increase or decrease the strength of the portfolio effect, depending on its effects on the synchrony index, ϕ, and on species population variability $\widetilde{CV}_n^s$. The effect of evenness on ϕ (Figure 3.1, orange arrow) depends on the how the population sizes of the different species fluctuate relative to one another (i.e., on the structure of the covariance matrix, $\mathbf{V_n}$ [eq. 3.1b]). Previous consideration of the effect of evenness on the DSR has assumed, implicitly or explicitly, that the populations of all species pairs are equally correlated (all ρ_{ij}=ρ: see, e.g., Doak *et al.* 1998). However, in the general case where the ρ_{ij} differ, the effect of unevenness is more contingent. For example, consider an assemblage in which population fluctuations of most species are highly synchronous, except for one species, whose fluctuations are strongly negatively correlated with all the other species (as in Appendix B.1). For this community, the portfolio effect will be maximized when this latter species is disproportionately abundant (or, more precisely, contributes disproportionately to the total community variance). Moreover, non-intuitive effects of evenness can emerge even when correlation coefficients are independent of relative abundance. For example, in Figure 3.5a, I generated hypothetical communities by drawing species' mean abundances at random from a lognormal distribution, and I assigned pairwise correlation coefficients at random with respect to abundance such that the expected mean correlation coefficient is zero, regardless of evenness or diversity. (I achieved the latter by exploiting a hyperspherical parameterization of the correlation matrix (Pinheiro and Bates 1996). By drawing each parameter from a uniform distribution on $[0,\pi]$, I sample from the entire universe of possible correlation matrices where, on average, the mean correlation coefficient is zero.) When there is perfect evenness, ϕ for the randomly assembled community is identical to the theoretical prediction (eq. 3.7 with $\bar{\rho} = 0$). As evenness decreases, synchrony increases, consistent with the hypothesis that unevenness is de-stabilizing at the community level. However, the same asymptotic value is approached at high diversity, so the effect of this is to cause synchrony to decrease more gradually with diversity when unevenness is higher (Figure 3.5a).

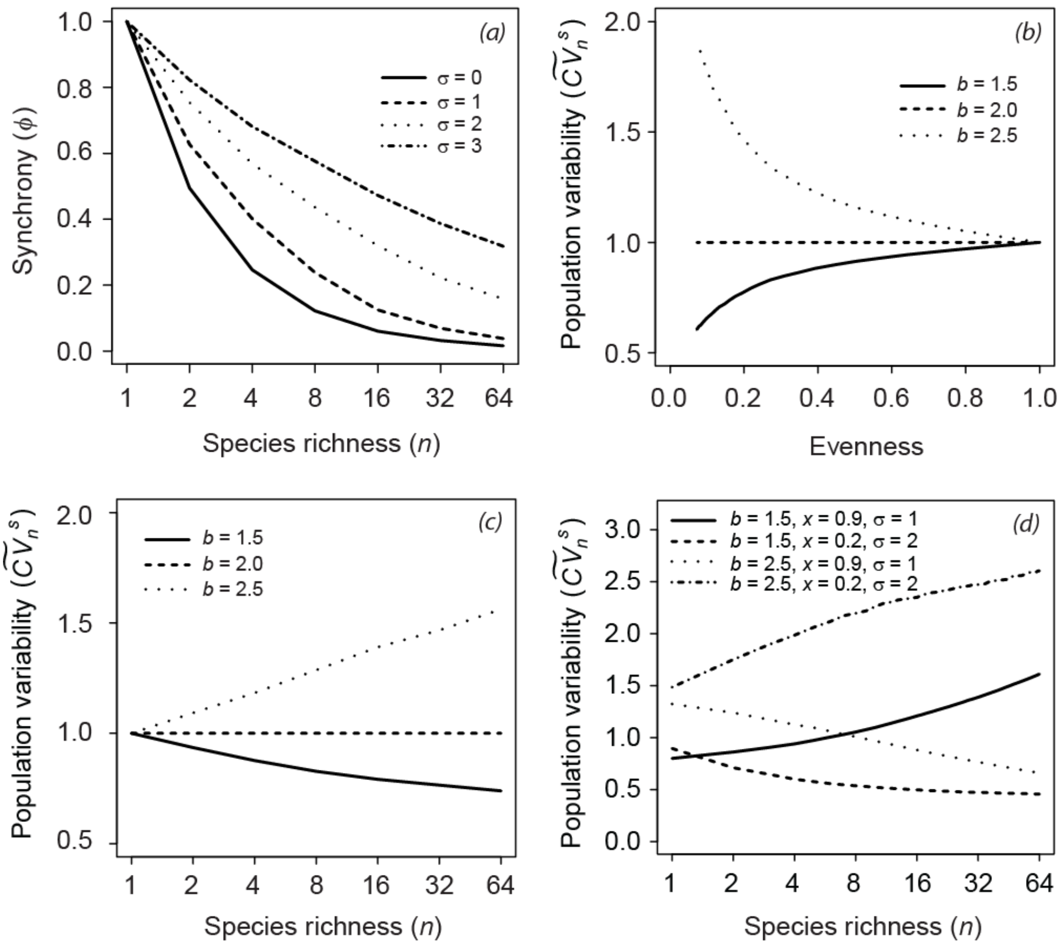

Figure 3-5.— Illustration of effects of unevenness on the DSR. In all panels, species abundances are drawn from a lognormal distribution with mean of log-abundance μ=1, and mean-variance scaling coefficient a=1. (a) Diversity-dependence of synchrony for different levels of unevenness, generated using the specified standard deviation of log abundance, σ. For all curves, b=2 and correlation coefficients were assigned randomly as described in the text. (b) $\widetilde{CV}_n^s$ as a function of evenness (communities were simulated using $0 \leq \sigma \leq 3$, and evenness quantified using the index E_{var}: Smith and Wilson (1996). (c) $\widetilde{CV}_n^s$ versus diversity, illustrating the effect of b. For all lines, σ=2 and x=0. (d) $\widetilde{CV}_n^s$ versus diversity, illustrating the interaction between evenness and mean-abundance effects. Note the log-scale for species richness.

Evenness can also influence weighted average population variability, $\widetilde{CV}_n^s$, but its qualitative effect depends upon the nature of mean-variance scaling (Figure 3.1, green arrows). Specifically, as evenness decreases, $\widetilde{CV}_n^s$ decreases when species' population variability scales less than quadratically with the mean ($b<2$), and increases when $b>2$ (Fig. 3.5b). This is because weighted average population variability becomes progressively less dominated by the more abundant species as evenness increases. In particular, when $b<2$, CV decreases with mean abundance. As evenness decreases, the most abundant species occupy a progressively larger fraction of the community, and thus population variability becomes progressively more dominated by these low-variability populations.

This relationship between evenness and population variability implies that unevenness can alter the way in which population variability changes with species richness, even when species are assembled randomly into communities with respect to their mean abundances. It is easiest to understand this effect by considering first the special case when species' mean abundances are independent of diversity ($x=0$, so the mean-abundance effect in eq. [3.7] is unity). In this case, unevenness tends to cause population variability to decrease with diversity when $b<2$, and to increase when $b>2$ (Figure 3.5c). I interpret this result as follows. As diversity increases, the likelihood of the assemblage, by chance, containing a species with very high mean abundance increases. The populations of these highly-abundant species will be more or less stable than the populations of species with average mean abundance, depending on whether $b<2$ or $b>2$, respectively. Of course, there is also a progressively greater likelihood of including species with unusually small mean abundances as diversity increases. However, because $\widetilde{CV}_n^s$ is a weighted average, the effect of sampling further out in the abundant tail of the distribution outweighs the countervailing effect of sampling further out in the rare tail. This interpretation is supported by simulations using a wide variety of shapes of species-abundance distributions (including symmetrical, left, and right-skewed distributions), and by the fact that, in contrast to $\widetilde{CV}_n^s$, unweighted population variability exhibit no trends with diversity when x=0, regardless of b (results not shown).

The nature of the interaction between unevenness and the mean-variance scaling parameter b implies that, when species' abundances differ (i.e., unevenness is present) and species' mean abundances tend to decrease with species richness (x>0), mean-variance scaling may actually act in countervailing ways along a diversity gradient. For instance, when x>0 and b<2, the mean-abundance effect is de-stabilizing at the population level, but the effect of unevenness is stabilizing (e.g., compare Figure 3.3a, blue line, and Figure 3.5c, solid line), whereas the opposite occurs when b>2 (e.g., Figure 3.3c, blue line, and Figure 3.5c, dotted line). This makes sense: increasing unevenness will tend to make the most abundant species – which dominate the weighted average population variability – increasingly more abundant relative to the average species mean abundance. Consequently, populations will be more stable if b<2 and less stable if b>2. Conversely, x>0 will tend to reduce all species' mean abundances as diversity increases, so populations will become less stable if b<2, and more stable if b>2. Thus, whether population variability is stabilized or destabilized by unevenness depends upon the magnitude of the overyielding parameter, x, relative to the among-species variance in mean abundances (i.e., the extent of unevenness), and on whether b<2 or b>2 (Figure 3.5d).

Of course, along natural diversity gradients, species may not be added at random with respect to their mean abundances, with implications for how population variability changes with species richness. For example, species' colonization abilities are sometimes hypothesized to be negatively correlated with their resource-use efficiency, (and thus population density at equilibrium: e.g., Tilman and Downing 1994). In such cases, succession would be expected to commence with species that have colonizer strategies, low resource-use efficiency, and thus low equilibrium abundance, and to progress by adding poorer colonizers that have greater resource-use efficiency and higher equilibrium abundances (Tilman and Downing 1994). Because these conditions imply that species tend to be added to communities in order of progressively increasing mean abundances, weighted average population variability would tend to decrease with species richness if $b<2$ (because species with higher mean abundances have lower CV when $b<2$, and these species are increasingly represented as species richness increases). Conversely, weighted average population variability would increase with species richness under these conditions if $b>2$.

3.3. Diversity and stability in nature

The model in eq. (3.3) shows that there are two key elements to making explicit the relationship between population and community variability. The first is to define community synchrony in terms of the synchrony index ϕ of Loreau & de Mazancourt (2008). The second is to measure population variability as a weighted average across species. The resulting relationship is extremely general. It holds regardless of extent or nature of unevenness of abundances among species, and regardless of the pattern of variances or covariances of species' abundances. Thus, it is robust to the nature of overyielding (if it is present), or the nature of the mean-variance scaling of species' abundances. Consequently, it offers a promising framework for understanding the broad range of relationships between population and community variability observed in natural and experimental systems.

The fact that portfolio effects are commonly found even in the presence of increasing population variability suggests that synchrony tends to decrease with diversity in DSR studies, consistent with our conjecture that this pattern is likely to be common in nature. There have been only two empirical studies that explicitly quantify the diversity-dependence of synchrony, but both exhibit an asymptotic decline that is consistent with a small, positive mean correlation coefficient that remains approximately constant as diversity changes. Specifically, Roscher *et al.* (2011) found that synchrony decreased strongly with diversity, from a median of ~0.55 when n=2 to ~0.1 when n=60, which is similar to what would be expected for a community with $\bar{\rho}\sim 0.1$ (cf. Figure 5.2a, blue line). Similarly, Isbell *et al.* (2009) found that synchrony decreased from ~0.6 to ~0.3 as diversity increased from 2 to 8, consistent with $\bar{\rho}\sim 0.2$. Of course, given that species are often added non-randomly along natural diversity gradients, and the idiosyncratic nature of species' responses to environmental fluctuations, there are likely to be exceptions to any general tendency for ϕ to decrease monotonically with diversity. An advantage of the framework in eq. (3.3) is that it makes no implicit simplifying assumptions about community structure that impose a particular functional form on this relationship.

The potential diversity-dependence of synchrony, along with eq. (3.3), offers an explanation for why studies of the DSR find a variety of different relationships between population and community variability. For instance, in a study of a natural diversity gradient among patches of boreal forest habitat, DeClerck *et al.* (2006) found that population variability increased with diversity, and between species correlation coefficients were positive and large. The large correlation coefficients suggest that ϕ exhibited relatively little change with diversity in this system, because its value would have been dominated by the second term in eq. (3.8), which is independent of diversity. In this case, the DSR would be driven by how population variability changes with diversity, and, indeed, that appears to be precisely what happens: this study documented one of the very few empirical examples of an inverse portfolio effect in the literature. Conversely, in the experimental grassland communities of Roscher *et al.* (2011), synchrony was strongly diversity-dependent, so a portfolio effect could be apparent in spite of the fact that population variability increased with diversity.

Eq. (3.7) extends the framework in eq. (3.3) to separate out the contribution of overyielding to population variability, and shows that overyielding and mean-variance scaling can have a broader range of effects than has been assumed in the literature (Figures 3-3,3-4). For instance, many empirical studies that have found both portfolio effects, and evidence of overyielding (i.e., $x<1$), have invoked the latter as a key mechanism driving the former (Valone and Hoffman 2003, Tilman et al. 2006, Isbell et al. 2009, Hector et al. 2010, Roscher et al. 2011), based on early analytical work suggesting that overyielding can induce a stabilizing effect of diversity at the community level (Tilman 1999). Similarly, some empirical studies have reported b as a measure of the intensity of the DSR, with any value of $b>1$ being taken as evidence that the portfolio effect is operating (e.g. Steiner et al. 2005, Polley et al. 2007, Isbell et al. 2009, Roscher et al. 2011), because simple analytical models have suggested that diversity should stabilize communities when the mean-variance scaling exponent $b>1$, and de-stabilize them when $b<1$ (Tilman et al. 1998, Tilman 1999, Loreau 2010). However, the derivation of these two conditions is sensitive to particular combinations of simplifying assumptions (see Appendix B.5). In fact, eq (3.7) shows that, in general, the key determinants of the stabilizing or destabilizing effect of overyielding, at both population and community levels, are whether mean species abundance decreases ($x>0$) or increases ($x<0$) with diversity, and on whether species-level variances scale more ($b>2$) or less ($b<2$) than quadratically with the mean (Figure 3-3).

The strength of the portfolio effect is widely believed to be enhanced whenever evenness is greater, and this effect has been reproduced in the few theoretical studies that have relaxed the evenness assumption (Doak et al. 1998, Loreau 2010). This makes intuitive sense: if a community is dominated by one species, then adding rare species will produce only a small reduction in total community variance, which will be dominated by the abundant species' population variability. However, eqs. (3.3) and (3.7) show how evenness may actually increase or decrease community stability, depending on its combined effects on synchrony and population variability. This context-dependence may help to explain why there is a lack of consistency in empirical relationships between stability, evenness, and diversity (Steiner et al. 2005, Polley et al. 2007, van Ruijven and Berendse 2007, Isbell et al. 2009, Grman et al. 2010, Mikkelson et al. 2011). For instance, several empirical studies have found that, when averaged over all species in the community, $b<2$ (i.e., larger populations are more stable: Bai et al. 2004, Leps 2004, Steiner et al. 2005, Polley et al. 2007, Roscher et al. 2011). This implies a stabilizing effect of unevenness at the community level, although there is some evidence that species-specific deviations from the mean-variance scaling relationship may play an additional role (Grman et al. 2010: see Future Directions, below) .

In decomposing population variability into a mean-abundance effect and a single-species variability effect, two assumptions were made that are more restrictive than those used in the derivation of our more general model unifying population and community variability: power-law scaling of the temporal mean and variance of abundance, and a monotonic change in mean abundance with diversity. Because there is strong support for both such relationships in nature, and they are commonly examined in both theory and experiments of the DSR, these additional assumptions may seem, at first, to be relatively innocuous. However, their inclusion in eq. (3.7) implies the additional assumptions that the mean-variance scaling exponent, and the overyielding coefficient, are the same for all species in the community, and do not vary as functions of diversity. In nature, the extent to which these assumptions are violated varies between systems. For instance, Yang *et al.* (2011) found that a single mean-variance scaling exponent explained >90% of the variation in temporal variances in alpine meadow communities (also see, e.g., Isbell *et al.* 2009), but van Ruijven & Berendse (2007), also studying herbaceous plants, found a nearly fourfold variation in the mean-variance scaling exponent among species. If mean-variance scaling exponents vary independently of species' relative abundances and responses to overyielding, then I would not expect the relationships shown in Figure 3-3 to be qualitatively affected, and this is consistent with the results of preliminary simulations (not shown). However, covariation between mean-variance scaling parameters and species' relative abundances could change the way weighted average population variability changes with diversity. For instance, if disproportionately abundant species have lower than average *b*, then

$\widetilde{CV}_n^s$ will tend to be smaller than predicted by eq. (3.7), because more stable species contribute disproportionately to the weighted average. There is empirical evidence for such relationships. For instance, Grman *et al.* (2010), examining residuals of an aggregate mean-variance scaling relationship, found evidence that disproportionately abundant species had smaller mean-variance scaling exponents than less abundant species.

Finally, although eq. (3.3) unifies population and community variability under a much broader range of conditions than previous models, it does retain one assumption of nearly all DSR theory that is likely to be violated to some degree, particularly in experimental manipulations of diversity gradients: that the community is fluctuating around a stochastic equilibrium ("stationarity"). Few DSR studies explicitly address the stationarity assumption (see (Tilman et al. 2006, Grman et al. 2010) for exceptions). Nevertheless, in most experimental diversity manipulations, stationarity is likely to be violated, at least to some degree. There are certainly some circumstances in which estimates of the portfolio effect could be biased by non-stationary dynamics. For example, if a competitively-structured community begins with all species abundances well below, or well above, their equilibrium values, then most species will tend to increase or decrease, respectively, and exhibit much more synchronous dynamics, and higher species-level variances, than they would exhibit at equilibrium. Conversely, an assemblage that begins with some species well below, and others well above, their equilibrium values, dynamics may appear initially highly asynchronous relative to equilibrium, as over-abundant species persistently decline and under-abundant species increase towards their respective equilibria.

A comprehensive assessment of how these biases may influence empirical estimates of DSRs in nature is not possible, since few studies report evidence for or against underlying temporal trends in species abundances. However, two findings from recent meta-analyses suggest that experimental estimates of DSRs are unlikely to be consistently biased, relative to DSRs on natural diversity gradients. Firstly, one might expect shorter experiments to be more dominated by transient dynamics, but there does not appear to be any relationship between experiment duration and the effect of diversity on either population or community variability. Secondly, there are no significant differences in the mean effect sizes of DSR studies that involve direct diversity manipulations, indirect manipulations, or that use natural diversity gradients (Campbell *et al.* 2011; also see (Jiang and Pu 2009)). However, studies of the DSR on natural diversity gradients do exhibit greater among-study variability than manipulative studies (Campbell et al. 2011).Thus, natural diversity gradients produce more instances in which portfolio effects do not occur (e.g., Rodriguez and Hawkins 2000, DeClerck et al. 2006), but they also produce instances of very strong portfolio effects (e.g., McNaughton 1985, Mouillot et al. 2005, Romanuk et al. 2009). This indicates that the non-random addition of species that occurs along natural diversity gradients adds more complexity to the community-level effects of diversity than may be apparent in experimental studies (Mittelbach et al. 2001, Huston and McBride 2002), and highlights the importance of having a framework for understanding DSRs that is robust to idiosyncratic changes in species' mean abundances, variances, and covariances with increasing diversity, such as eq. (3.3).

3.4. Conclusions and future directions

The framework developed here makes explicit the relationships between several phenomena that previous theoretical and empirical studies have found to have important effects on the diversity-stability relationship, by relaxing several important simplifying assumptions that have been employed in various combinations in previous work. It makes explicit how the DSR depends on how two quantities change with diversity: the weighted average species-level variability $(\widetilde{CV_n^s})$, and community synchrony (ϕ). Moreover, it clarifies how the strength of overyielding (x), and the slope of the mean-variance scaling relationship (b), interact to influence population and community variability. Both species-level variability and synchrony depend on evenness, and, in most cases, are likely to vary as a function of diversity. This synthesis reveals important interactions between these different phenomena that influence the strength, and even the direction, of the DSR.

My framework also suggests several particularly promising areas for further work. In particular, the synchrony index, ϕ is the key community property linking population and community variability. Only three empirical studies to date have explicitly estimated this quantity (Isbell et al. 2009, Roscher et al. 2011, Yang et al. 2011). However, virtually all empirical studies of the DSR collect the data necessary to estimate ϕ, meaning that a re-examination of existing data has the potential to rapidly flesh out our understanding of how ϕ changes with diversity in different types of assemblages. Similarly, population-level variability is universally understood to have a key influence on the DSR, but the way population variability is measured is inconsistent. Some studies quantify population variability separately by species; others compute (unweighted) averages across species at each diversity level; still others compute means and variances separately for all species at all diversity levels, and examine the aggregate relationship for systematic changes with diversity. Indeed, this inconsistency has been identified as a key barrier to our understanding of the relationship between population and community variability (Campbell et al. 2011). Eq. (3.3) reveals that the critical measure of population variability, at least from the standpoint of the DSR, is a weighted average, $\widetilde{CV}_n^s$. To date, no empirical studies of the DSR have measured population variability in this way (although most studies will have collected the data necessary to do so), suggesting that a re-examination of population variability and synchrony in empirical studies of the DSR may offer fresh insights into diversity-stability relationships in nature.

The development of portfolio effect theory by analysis of properties of the community covariance matrix (eq. 3.1b), or by analysis of community-dynamic models, have often been seen as mutually exclusive alternatives (Loreau 2010). However, statistical frameworks such as that proposed here can provide a common language for the interpretation and comparative analysis of studies of the DSR in both empirical and model communities. Community-dynamic models produce long-run means and variances of population and community abundance, and thus their outputs can be interpreted within the framework outlined here, just as empirical data can. Such approaches can reveal how particular assumptions about population dynamics and species interactions impose particular constraints on the diversity dependence of community synchrony (Loreau 2010), and average population variability (Tilman 1999), as well as on the particular components of species-level variability, such as the nature of the mean-variance scaling relationship (e.g., Tilman 1999, Kilpatrick and Ives 2003).

Chapter 4. Strong evidence for weak density-dependence in population dynamics

4.1. Introduction

The extent to which natural populations are regulated, and the relative importance of internal processes such as density dependence versus environmental forcing, has raged in the ecological literature for at least 60 years (Andrewartha and Birch 1954, Hassell et al. 1976). Population regulation has important implications for population replenishment, for the resilience of populations buffeted by environmental perturbations, and thus for the stability of ecosystem functions performed by populations (Chesson and Warner 1981, Dennis et al. 2006, Thibaut et al. 2012). Population regulation also has evolutionary implications, influencing the nature of selection (Charlesworth 1971). In addition to its fundamental importance to ecological and evolutionary dynamics, accurate assessments of the existence and strength of density-dependence have important practical applications for the sustainable exploitation of populations, population viability analysis, pest control and eco-toxicology (Hilborn et al. 1995, Freckleton et al. 2006)

Until recently, many field experiments failed to detect density-dependence (Osenberg et al. 2002), leading some researchers to challenge the assumption that density-dependent processes are widespread in nature (Sale and Tolimieri 2000). This has been somewhat surprising, given that the conceptual issues underpinning the population regulation debate largely have been resolved (Turchin 1995). “Negative” density-dependence, whereby a population’s per-capita population growth rate is a decreasing function of population size, must occur at sufficiently many times and places to ensure population persistence (Hixon et al. 2002). In a meta-analysis of reef fish studies, Osenberg *et al.* (2002) suggested a resolution to the apparent discrepancy between ecological theory, according to which density-dependence should be nearly ubiquitous, and the apparent absence of evidence for density-dependence in a large proportion of field experiments. Specifically, there is strong evidence for density-dependent recruitment in the aggregate (i.e., across experiments), even though support for density-dependence in individual studies often falls short of the conventional threshold of P=0.05. Indeed, studies failing to find density-dependence did not yield markedly weaker estimates of the strength of density-dependence; rather, they inherited larger confidence intervals due, presumably, to greater levels of environmental stochasticity. More recently, a broad range of laboratory and field experiments have been conducted, the overwhelming majority of which have also detected strong density-dependence (e.g., 35 out of 41 in a systematic literature review: see Table C-1 in Appendix C.2).

Ecologists also have sought to evaluate the generality of density-dependence by analysing ensembles of population time series. Such analyses have focused on the Global Population Dynamics Database (GPDD), a dataset that now contains over 5000 time series of a large range of taxa (zooplankton, birds, mammals, fishes, reptiles, etc.), covering durations of up to 120 years (NERC Centre for Population Biology 1999). The earliest of these studies found evidence for relatively strong density-dependence in the majority of time series (Sibly et al. 2005, Brook and Bradshaw 2006, Sibly et al. 2007). However, the models used in these studies implicitly assume that there is no observation error, and the unexplained variation in the data is overwhelmingly dominated by process noise (i.e., stochasticity in population growth). More recent analyses of the GPDD, which explicitly account for both observation error and process noise, have found much weaker evidence for density-dependence. For instance, Knape & deValpine (2012) found that the proportion of time series exhibiting significant density-dependence falls from 56% to just 16% when observation error is incorporated. Moreover, when density-dependence is detected (or its existence assumed), the estimated strength of density dependence tends to be weaker when observation error is accounted for (Freckleton et al. 2006, Ziebarth et al. 2010, Knape and de Valpine 2012).

These more recent studies raise the possibility that density dependence has been over-estimated in early analyses, possibly substantially so, a conclusion that would be at odds with the apparently growing evidence for density-dependence from experimental studies. However, an alternative possibility is that the explicit incorporation of observation error increases the uncertainty associated with estimates of density-dependence, and thus the reduced frequency with which it is detected may be largely due to reduced statistical power. One way to resolve this is to consider the evidence for density-dependence in the aggregate (i.e., across time series), much as Osenberg *et al.* (2002) overcame the limitations of individual studies by meta-analysing estimates of the strength of density-dependence from a large sample of experimental studies.

Here, I re-examine the evidence for density-dependence in the GPDD, by conducting an aggregate analysis of the entire database. I first conduct an analysis using the conventional approach of fitting density-dependent and density-independent models to each of the data sets independently, but combining likelihoods across data sets to produce an overall estimate of the strength of evidence for density-dependence. However, because the information about density-dependence in individual time series can vary due to a broad range of factors such as time series length and magnitude of environmental noise, I also consider two reduced-parameter density-dependent models that leverage information across data sets. My findings suggest resolutions, both to the apparent ambiguity in the evidence for density-dependence in observational time series, and the seeming inconsistency between conclusions from experimental and observational studies of density-dependence.

4.2. Methods

I analyzed the same 627 population time series that were considered by Knape and deValpine (2012). These data consisted of all time series in the GPDD (http://www3.imperial.ac.uk/cpb/databases/gpdd) with at least 15 distinct years of observation, and for which abundances were sampled at annual intervals (Knape and de Valpine 2012).

To account for both observation error and process noise in the estimation of density-dependence, I use the Gompertz model, which has been found to describe the relationship between per capita growth rate and population size better than alternatives, such as the discrete-time logistic (Rotella et al. 1996, Brook and Bradshaw 2006, Thibaut et al. 2012). It also has the advantage of being linear on a logarithmic scale, facilitating its application in time series analysis. Specifically, the Gompertz model follows:

$$N_{t+1} = N_t \exp(a + (b-1)\ln N_t + e_t(0, \sigma^2)), \tag{4.1}$$

where N_t is population size, a is the density-independent exponential growth rate, b is an inverse measure of the strength of density-dependence ($b<1$ indicates density-dependent dynamics), and e_t is an independent random perturbation to the exponential growth rate due to fluctuating environmental conditions (i.e., process noise). Defining $x_t = \ln(N_t)$, eq. (4.1) becomes linearized:

$$x_{t+1} = a + bx_t + e_t(0, \sigma^2) \tag{4.2a}$$

Eq. (4.2a) is typically called the "state equation", because it represents the dynamics of the true unobserved state. To incorporate observation error, I couple eq. (4.2a) with an observation equation that links observations of the system with the corresponding true states. Specifically, if y_t denotes the observed log-abundance at time t, I can write:

$$y_t = x_t + f_t(0, \tau^2) \tag{4.2b}$$

where f_t is an independent random deviation of observed abundance y_t from true abundance x_t due to observation error. Eqs. (4.2a) and (4.2b) together constitute the "Gompertz state space model" (hereafter termed the GSS model: Dennis *et al.* 2006). Because eq. (4.2) is linear, I can employ an algorithm known as the Kalman filter to obtain maximum likelihood estimates of a, b, and the standard deviations due to process noise and observation error (hereafter designated σ and τ, respectively) (see Appendix C.1).

Two of the variants of the GSS model that I fit to each time series follow the convention of previous tests of density-dependence in population time series. In the full density-dependent model, all four GSS model parameters (a, b, σ, and τ) are estimated separately for each time series. In the density-independent model, b is fixed at one. The key feature of this latter model is that the discrete-time per-unit-abundance growth rate, defined as $\ln\left(\frac{n_{t+1}}{n_t}\right)$, is independent of population size.

In a conventional meta-analysis, an estimate of an effect of interest, with its associated precision, is extracted from each individual study, and these estimates used to produce a kind of weighted average effect size, where each study's contribution to the overall estimate is weighted by its precision (Cochran and Carroll 1953). However, these approaches assume that the sampling distribution of the statistic is approximately Gaussian. Unfortunately, the sampling distribution of estimates of the strength of density-dependence are extremely poorly behaved for many of our data sets: the sampling distribution of b in many datasets is highly asymmetric in idiosyncratic ways, sometimes with evidence of multi-modality (see Figure 4-1).

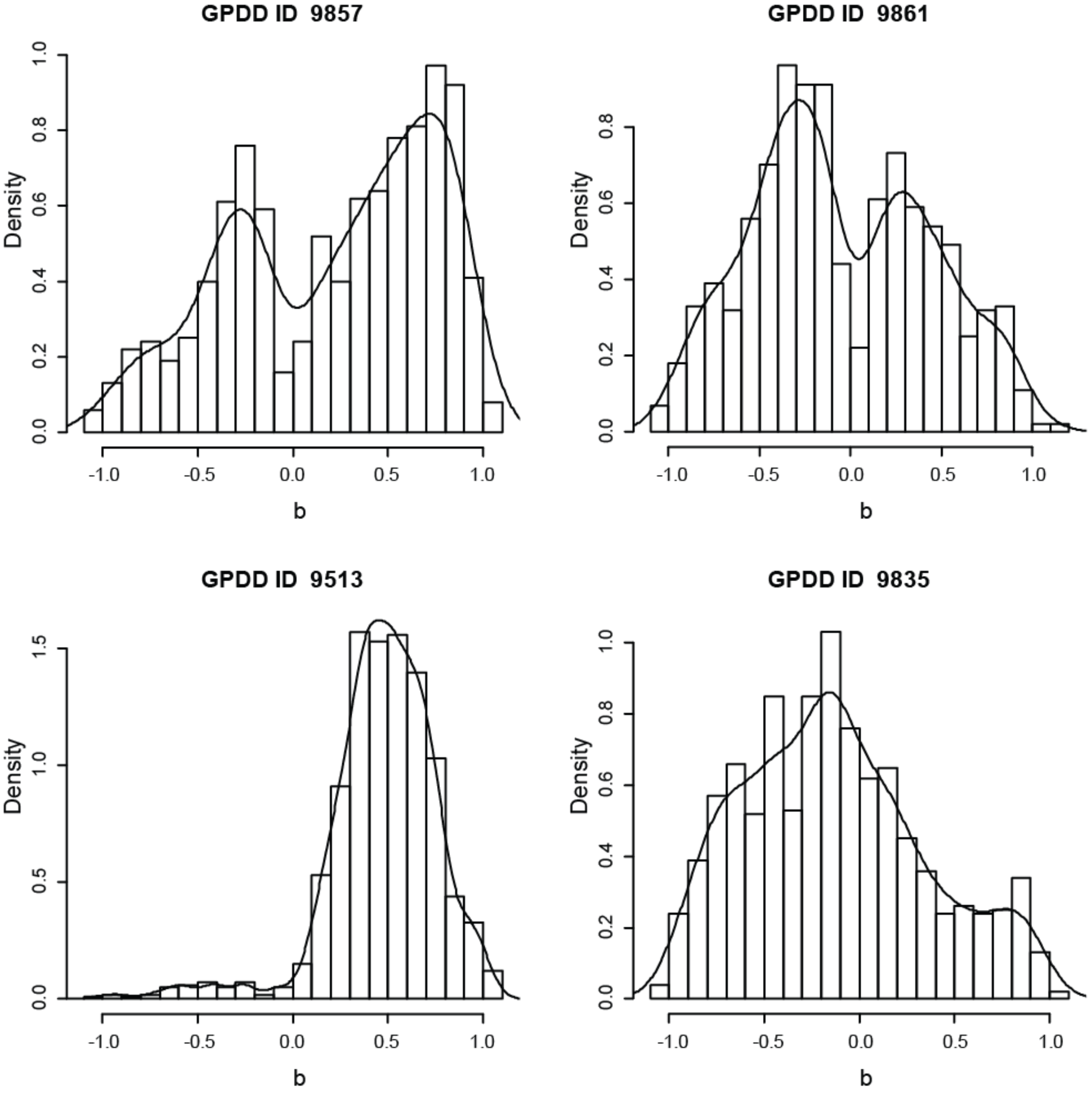

Figure 4-1.— Parametric bootstrap distributions of the density-dependence parameter (*b*) for 4 representative time-series. GPDD ID refers to the unique identification code for the time series in the GPDD. The solid line is a kernel density estimator fitted to the bootstrap distribution.

Due to the poor statistical behaviour of independent estimates of b for each time series, I adopt two alternative approaches to estimating the overall strength of evidence for density-dependence in the dataset. Specifically, I fit all the time series in an omnibus analysis, where each time series has its own values of a, σ, and τ, but where there is a common strength of density-dependence, b, for all data sets (hereafter termed the "common-b" model). Thus there are $3\ n + 1$ estimated parameters, where n is the number of time series being analyzed. I also fit a random effects model, in which there is an overall mean value of b, and an among-population variance of b, and each time series' b value is a random draw from this distribution (hereafter the "random-b" model). Thus, the common-b model is analogous to a fixed effects meta-analysis, where there is a single "true" b value and differences in estimates of b among data sets reflect only sampling error, and the random-b model is akin to a random-effects meta-analysis, where each study has a different "true" effect size, which is drawn from an overall distribution of effect sizes (Kontopantelis and Reeves 2012). The random-b model contains the common-b model as a special case, which in turn contains the density-independent model as a special case (in the former, the variance of the random effect is zero, and in the latter, the common value of b is equal to1).

The common-b model assumes that the strength of density-dependence is the same for all populations in the GPDD. This hypothesis is not biologically realistic, since there is no reason to expect that all populations are governed by the same density-dependence parameter. However, here, the purpose of the common-b model is not to test whether the strength of density dependence varies among populations, but to provide a model that can be compared with the density-independent model, but which, unlike the full density-dependent model, has a similar number of parameters.

Consequently, if the density-independent model outperforms the full model, but the common-*b* model outperforms the density-independent model, it will indicate that the former statistical result is a consequence of lack of data within individual data sets to estimate a distinct strength of density-dependence, rather than an absence of evidence for density-dependent regulation in general.

After fitting each of my four models (full density-dependent, density-independent, common-*b*, and random-*b*) to the data using maximum likelihood methods, I compared their relative fit using two different model selection criteria: AIC_c (Akaike's Information Criterion with the standard bias-correction for small sample size: Burnham and Anderson 2003) and BIC (Bayesian Information Criterion: Schwarz 1978). In addition, I compared the fit of the full density-dependent and density-independent models using a parametric bootstrap version of the likelihood ratio test (hereafter PBLR). The PBLR is like a standard likelihood ratio test, except that the expected distribution of log-likelihood ratios under the null hypothesis of no density-dependence is generated explicitly by simulation from the density-independent model, to avoid biases associated with using the χ^2 distribution as the null distribution (Dennis and Taper 1994, Knape and de Valpine 2012). For this latter test, for every time series, I simulated 1000 time series using the best-fit parameters of the density-independent model. Then I fitted both the density-independent and full density-dependent models to the simulated time series, and calculated the Likelihood Ratio between the two fitted models. If the observed likelihood ratio was larger than the 95th quantile of the likelihood ratios from the simulated data, I considered that there was significant evidence for density-dependence. Computational constraints prevented me obtaining null distributions for the "common-*b*" and "random-*b*" models, because fitting and assessing convergence of these models was quite time consuming (often involving detailed visual inspection of model fits that could take a day or more for each simulated dataset of 627 time series); thus, replicating the procedure for 1000 simulated datasets was not logistically feasible.

Finally, I evaluated the biological plausibility of our model fits by examining the density-independent growth parameters produced by the fitted density-dependent models. A recent review has suggested that fitted models with density-dependence can imply unrealistically high values of the density-independent growth rate a (Lebreton and Gimenez 2013). Because estimates of the density-independent and density-dependent parameters have strong statistical covariances (Lebreton and Gimenez 2013), unrealistic values of density-independent growth rates would undermine the plausibility of estimates of the strength of density-dependence as well (Delean et al. 2013). Therefore, I examined the distribution of density-independent parameter values (a) across data sets for our density-dependent models.

Table 4-1.—Results of model selection. # pars is the number of estimated parameters in the model, NLL is the negative of the maximum log-likelihood, AICc is Akaike's Information Criterion corrected for small sample bias, and BIC is the Bayesian (or Schwarz) Information Criterion.

	# pars	NLL	ΔAICc	ΔBIC
Full density-dependent model	2508	18646	0	4209
Common-*b* model	1882	19665	486	0
Random-*b* model	1883	19665	488	10
Density-independent model	1881	20214	1582	1089

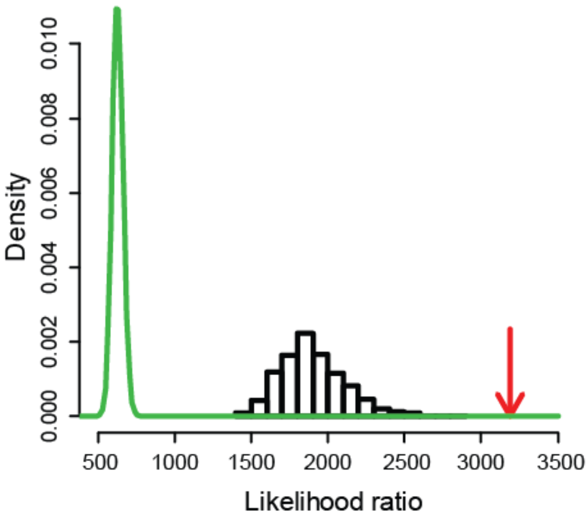

Figure 4-2.—Ordinary and parametric bootstrap likelihood ratio (PBLR) tests. The green line shows the theoretical Chi-square distribution (i.e., the standard asymptotic null distribution), and the histogram shows the parametric bootstrap distribution of the likelihood ratio statistic. The vertical red arrow indicates the observed Likelihood Ratio statistic.

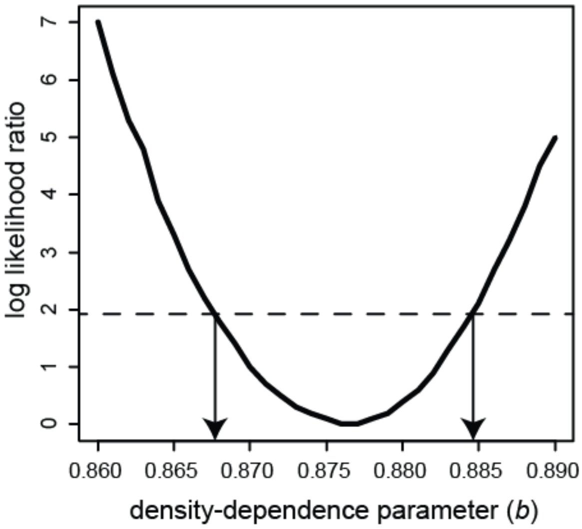

Figure 4-3.— Profile likelihood intervals for the strength of density-dependence in the “common-*b*” density-dependent model. The 95% confidence interval falls

between the two downward-pointing vertical arrows. The maximum likelihood estimate of *b,* 0.876, is at the minimum of the log-likelihood ratio function.

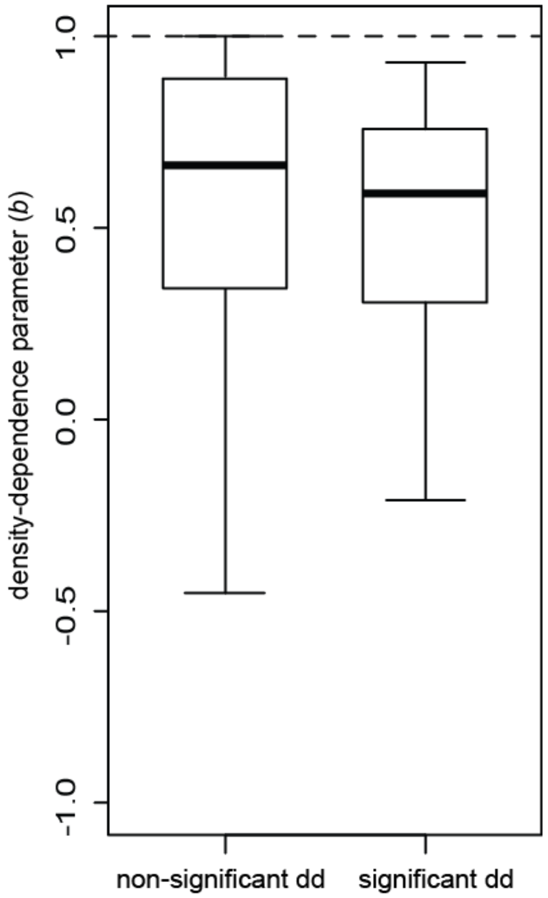

Figure 4-4.— Boxplots of the estimated strength of density-dependence (*b*) produced by the full model, for the time series in which the evidence for density-dependence was statistically significant (right), and the time series for which it was not significant (left). The horizontal dashed line indicates the value of *b* corresponding to no density-dependence. Smaller values of *b* indicate stronger density-dependence.

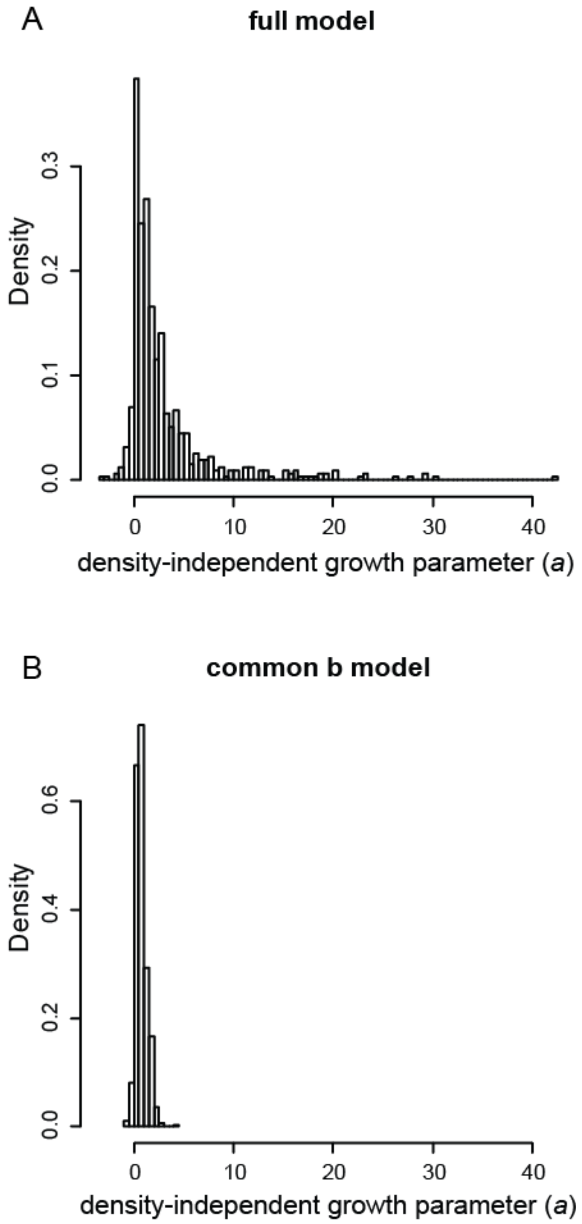

Figure 4-5.— Histogram of estimates of the Gompertz density-independent growth parameter, *a*, for (A) the full model, and (B) the common-*b* model. A histogram of *a* for the random-*b* model is not shown, because it is virtually identical to that of the common-*b* model.

4.3. Results

Considering the individual time series separately, my results correspond closely with those of Knape & de Valpine (2012): among the 627 time series analysed, only 102 (~16%) exhibited significant density dependence, according to the PBLR. Nevertheless, at the whole dataset level, if I focus only on the full density-dependent model and the density-independent model, the results are ambiguous. The PBLR (Figure 4-2) and AICc (Table 4-1) favour the full density-dependent model over the density-independent model. Consistent with this, a bootstrap estimate of the average strength of density-dependence across all 627 time series suggests that density-dependence is strong: $\bar{b} = 0.59$ (95% CI: 0.50-0.68). However, BIC strongly favours the density-independent model (Table 4-1).

The ambiguity in the evidence for density-dependence disappears, however, when I consider the common-b and random-b models. Both of these models outperform the density-independent model on both AICc and BIC, with the common-b model slightly favoured over the random-b model. Moreover, in contrast to the full density-dependent model, where estimates of b for individual time series often indicate pathological statistical behaviour of the density-dependent parameter (e.g., Figure 4-1), the log-likelihood profile for the common value of b behaves very well: it is approximately parabolic in shape, with the density-independent special case (b=1) clearly outside of the 95% confidence intervals (Figure 4-3). On the other hand, it indicates substantially weaker density-dependence (b=0.88 [0.868 0.885 95% CI]) than was suggested by averaging the independent estimates of b_i from the full density-dependent model.

My analyses also provide no evidence that the time series are divided into groups of density-independent versus density-dependent dynamics. For the full density-dependent model (where each density-dependent parameter was estimated separately), a comparison of the distributions of the estimated strength of density dependence for the datasets with and without statistically significant density-dependence yields no evidence of bimodality (Figure 4-4). The mean value of the density-dependent parameter b is very similar in the two subgroups of data, although there is greater variability among estimates of b for the time series not exhibiting significant density-dependence. Consistent with this, the common-b model was favoured over the random-b model, contrary to what I would expect if there were evidence of substantial heterogeneity in the existence or strength of density-dependence in the data.

Further support for the common-b model as more biologically plausible than the full model is apparent from inspection of the estimated density-independent growth rates. When the Gompertz model is fitted independently to each data set, the density-independent growth parameter a corresponds to geometric growth factors ($\propto \exp(a)$) that differ by up to 40 orders of magnitude, a far greater range of variation than in the common-b model (Figure 4-5). It is particularly revealing to examine the demographic parameters for species represented multiple times in the GPDD. For example, if I consider the demographic parameters for the Dickcissel (*Spiza americana*) among the 11 time series analysed, I find that the density-independent growth factor $\exp(a)$ varies by more than 3 orders of magnitude (from exp(0.01) to more than exp(7)), whereas, in the common-b model, the corresponding range of variation is only a factor of about 1.5 (from exp(0.12) to exp(0.52)).

4.4. Discussion

A recent analysis of population time series, which takes explicit account of observation error, has raised questions about the strength of evidence for density-dependence in natural populations (Knape and de Valpine 2012). My population-by-population results are consistent with that study. However, my findings also indicate that, in the aggregate, there is strong evidence for density-dependence in the Global Population Dynamics Database, but that the intensity of density dependence is weak. The strong support for density-dependence is most apparent in the much greater support for the common-*b* model over the density-independent model, while the evidence that density-dependence is weak is apparent from the much greater biological plausibility of the density-independent growth rates yielded by the common-*b* relative to the full density-dependent model. That density-dependence is consistently weak is supported by the lack of evidence for heterogeneity in estimates of *b*, either in the comparison between the common-*b* and random-*b* models, or in the distributions of estimates of *b* between the subsets of populations that do and do not exhibit statistically significant density-dependence individually.

The seeming erosion of evidence for strong density-dependence in observational time series studies, which accompanied explicitly accounting for both observation and process error, has been at odds with evidence from experimental studies of density-dependence (e.g., Table C-1). It is notoriously difficult to detect density-dependence in sequential censuses of populations (e.g. Gaston and Lawton 1987, Fowler et al. 2006). In general, experimental studies have tended to find strong evidence for density-dependence; however, these studies commonly impose very large differences in density among treatments, and, especially in laboratory studies, reduce the effects of other, potentially confounding sources of variation in population growth (Fowler et al. 2006). The controlled nature and small scale of experimental studies also might reasonably be expected to reduce observation error, compared to many observational time series. These factors would both increase the expected magnitude of density-dependent effects, and reduce the magnitude of both process noise and observation error, making density-dependence easier to detect (Osenberg et al. 2002).

In addition to the above factors, experimental studies are, of necessity, small-scale, relative to the scale of interbreeding populations in nature: field experiments typically focus on habitat patches or relatively small sub-populations, while laboratory studies typically generate populations that are comparatively small, and inhabit a relatively homogeneous environment, than would be the case for those populations in nature (e.g. Pearl 1927, Gause 1934, Hazlerigg et al. 2012, Boström-Einarsson et al. 2013). Thus, the extent to which strong density-dependence at the patch level might scale up to regulate population size at the meta-population level has been a key point of contention in the debate about density-dependence (Sale and Tolimieri 2000). Our findings support the hypothesis that these local-scale density-dependent effects do, in fact, scale up to have a detectable effect on population regulation, consistent with both metapopulation theory (Hanski 1991, Hixon et al. 2002) and with a recent laboratory meta-population experiment (Strevens and Bonsall 2011). Such effects may be quite heterogeneous among populations: for instance, in an experimental study, Schmitt & Holbrook (2007) found large variation in the strength of density-dependence among 6 local populations of a reef fish, due to local variation in predator abundance. Because density-dependent processes act on individuals in response to their local environment, such heterogeneity among local habitat patches could well weaken the apparent strength of density-dependence at the whole-population level, particularly if population dynamics are asynchronous among habitat patches (Wang et al. 2009).

One striking difference between the full density-dependent model on the one hand, and the common-*b* and random-*b* models on the other, is the average strength of density-dependence. That the full density-dependent model produces much stronger average strength of regulation implies that the time series that produce weak density-dependence have more information in them than the time series that produce strong density-dependence. Consistent with this, time series yielding very weak density-dependence ($b>0.9$) tended to be long time series of (especially) birds and mammals. In the subset of data I analysed, birds, fishes, mammals, and insects each constitute about a quarter of the time series (only 9 time series did not fall into one of these four groups). Indeed, a simple linear model with the full model estimate of *b* as the response variable indicated that longer time series produced weaker estimates of density-dependence than short ones, with estimates of density-dependence strongest for fishes, then insects, then mammals and birds (see Table 4-2).

Table 4-2.—Results of linear regression of the density-dependent parameter (*b*) against the length of the time-series and the taxon of the focal species. Time-series were grouped in 5 taxon classes: Aves (188), Insecta (156), Mammalia (130), Osteichtyes(144) and Other (9).

	d.f.	Sum of squares	Mean squares	F	P-value
Taxon	4	10.1	2.5	12	<.001 ***
Length	1	4.6	4.6	22	<.001 ***

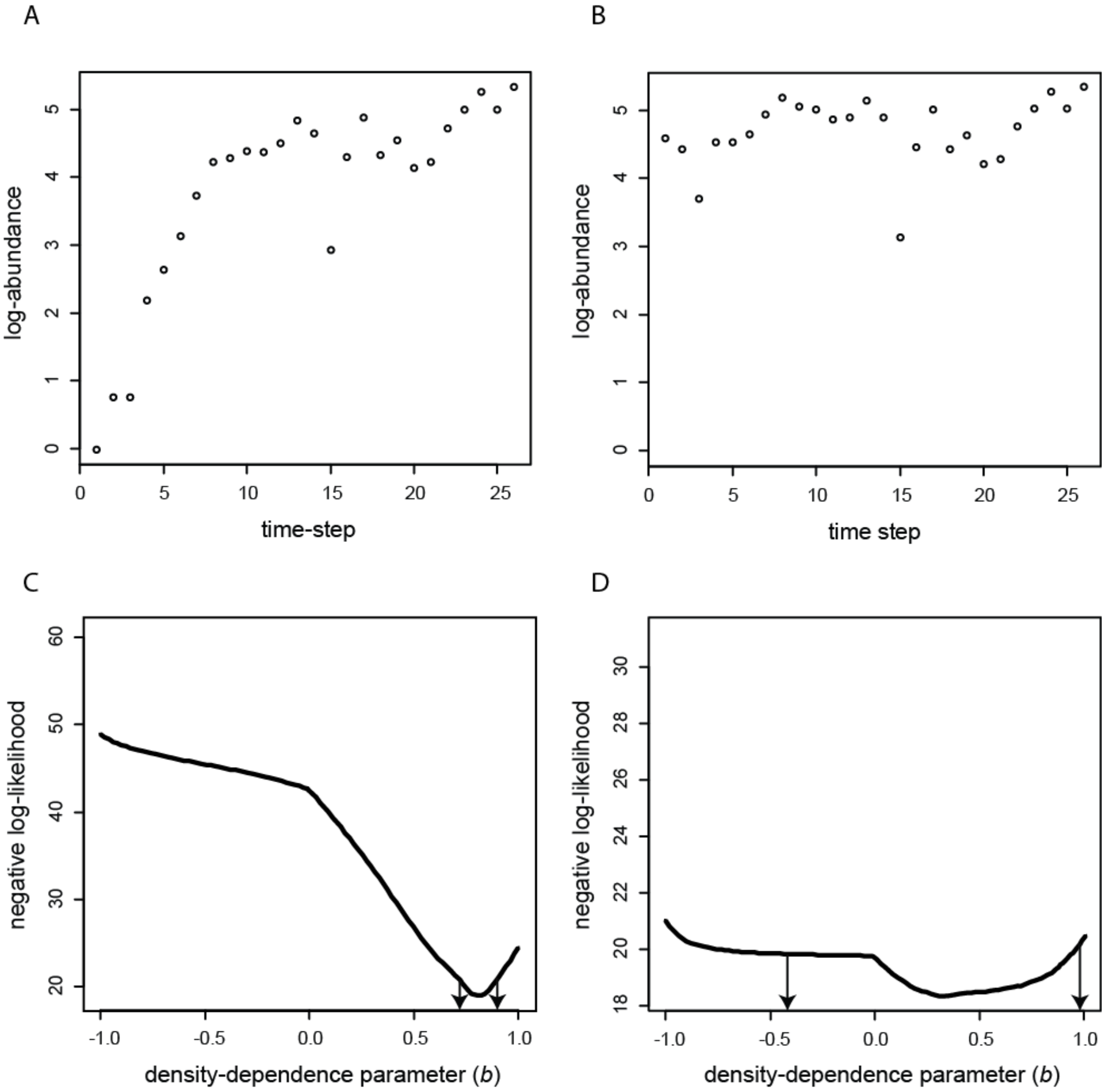

Figure 4-6.— Simulated observations of Gompertz population dynamics, incorporating process and observation error (A) starting far below carrying capacity, and (B) starting at carrying capacity (a=0.92, b=0.8, σ^2 =0.3, and τ^2=0.3 in both cases). Lower panels show log-likelihood profiles for (C) the time series starting far from carrying capacity, and (D) the time series starting at carrying capacity. The vertical arrows on the log-likelihood profiles indicate the 95% confidence interval.

One factor likely contributing to the relatively low power to detect density-dependence in individual time series is the nature of the fluctuations in the data. Information about density-dependence is clearest when excursions to low density occur that are substantially larger in magnitude than typical interannual environmental fluctuations (i.e., rare catastrophes), after which recovery towards carrying capacity might be expected to occur (Figure 4-6). Few such excursions to low density occur naturally in the GPDD, whereas experimental studies typically impose large differences in abundance among treatments (Fowler et al. 2006). This suggests that organisms subject to episodic disturbances on a frequency that is comparable to that of expected recovery to equilibrium (e.g., reef corals: Osborne et al. 2011) may be particularly well-suited to assessments of the strength of evidence for density-dependence in nature.

Another factor potentially influencing the detection of density-dependence is differences in the taxonomic coverage of observational and experimental data sets. While the GPDD contains time series of insects, plankton, and fish (taxa that dominate experimental studies of density-dependence), it also contains time series for many organisms that tend to be relatively large, long-lived, and have relatively small litter sizes (e.g., half of the time series I analysed were for birds or mammals), compared to the insects, planktonic micro-organisms, and fish that dominate experimental studies. Short-lived, highly fecund organisms are more likely to have the capacity to increase rapidly towards, or overshoot, carrying capacity, inducing rapid changes in resource availability per-capita and thus severe density-dependence such as mass starvation or the attraction of large numbers of predators (Herrando-Pérez et al. 2012). In contrast, longer-lived organisms that produce few offspring at a time may respond by delays in reaching reproductive maturity, reductions in litter size, and other non-lethal density-dependent responses as resources become limiting. Indeed, a recent review of density-dependence in ungulates argued that these milder forms of density-dependence are typically those that are first observed as resources become limiting (Bonenfant et al. 2009).

Finally, the need to estimate both density-dependent and density-independent components of population growth may itself complicate the process of detecting density-dependence. These two parameters typically covary positively and strongly: very large density-independent growth rates coupled with strong density-dependence often fit the same data nearly as well as low density-independent growth rates coupled with weak density-dependence, creating ridges in the likelihood surface that imply substantial uncertainty about the value of both. Consequently, imposing constraints on the density-independent growth rate using other sources of information has been identified as one way to improve the detection and estimation of density-dependence (Lebreton and Gimenez 2013). Two potential sources of such information are independent experimental estimates of the density-independent growth rate, or the use of allometric relationships (Fenchel 1974). Recently, Delean et al. (2013) employed allometric relationships to impose priors on the density-independent growth rate. They found that the prior dominated the posterior distribution of the density-independent growth rate, which is consistent our finding that time series frequently contain very little information about this parameter.

4.5. Conclusions

Accounting for both observation error and process noise is critical to avoid over-estimation of the strength of density-dependence (Knape and de Valpine 2012, Lebreton and Gimenez 2013). Unfortunately, doing so also reduces drastically the statistical power to detect the existence of density-dependence. Previous workers have suggested three ways to mitigate this problem in the collection of time series. First, collecting longer time series will strengthen statistical power, although power to detect density-dependence increases very slowly with time series length (Dennis et al. 2006). Secondly, replicated sampling, where multiple observations of population size are collected at each time step, can considerably improve inference by teasing apart observation error and process noise (Dennis et al. 2010). Finally, time series with large excursions from carrying capacity contain much more information on density-dependence than time series of population fluctuating around carrying-capacity (see Fig. S2 in Supplementary Information for an example). However, most existing time series are relatively short, do not include replicate observations of density, and lack large excursions from carrying capacity. Nevertheless, there is a need to use the information in these studies as effectively as possible to understand how populations are regulated in nature. Our findings show one way to strengthen our inferences about this: by using statistical models that leverage information from multiple time series to mutually inform one another. For the GPDD, such an approach reveals that, despite the loss of statistical power associated with accounting for observation error and process noise, there is strong evidence that density dependence is common in nature, but that it is weaker in strength than either experimental studies or early analyses of population time series suggest.

Chapter 5. General discussion

5.1. Summary of key findings

In chapter 2, I developed a quantitative approach to measure the stabilizing effect of species richness on herbivory on coral reefs. My results show that this effect is strong, with nearly independent fluctuations among herbivorous fishes. Furthermore, I found that differential responses to environmental fluctuations among herbivorous fishes is the main driver of the portfolio effect in this community. Ecological compensatory interactions, such as competition, also contribute significantly to the portfolio effect but to a much lesser extent. My results support the current view among coral reef researchers that herbivorous fish diversity provides insurance against catastrophic shift from dominance by corals towards dominance by macroalgae (Burkepile and Hay 2008, Adam et al. 2015).

In chapter 3, I developed a framework to understand diversity-stability relationships in ecological communities. I established a general mathematical relationship relating community variability to population variability. This relationship shows that community variability is always smaller than weighted-average population variability, and that the factor by which it is smaller is the square root of the community synchrony index (Φ). Additionally, I showed how the weighted-average population variability depends on the mean-variance scaling of abundance, changes in abundance with diversity and differences in species' mean abundance in monoculture. My results reveal important interactions between these phenomena that influence the strength, and even the direction, of the diversity-stability relationship. Furthermore, I studied how evenness in abundances alters the diversity-stability relationship through combined effects on community synchrony and weighted-average population variability. Contrary to the widely held view that evenness has a stabilizing effect, my results reveal that evenness can be either stabilizing or destabilizing, depending on the nature of the mean-variance scaling and whether species' mean abundances tend to decrease as species richness increases. This framework appears to have the potential to reconcile seemingly conflicting results from empirical and theoretical studies.

In chapter 4, I assessed the strength of evidence for population regulation in the Global Population Dynamics Database. I found that individual time-series of population sizes contain little information about density-dependence, and that separate analyses of these time-series are likely to over-estimate its strength, even when observation error is accounted for. In contrast, I find very strong evidence for density-dependence when performing an analysis across all time-series, although its magnitude is weak. This finding suggests that leveraging information from multiple time-series allows stronger inferences about density-dependence in population time-series, and helps to explain the apparent inconsistencies between experimental studies, recent analyses of population time-series, and ecological theory.

My findings in chapters 3 and 4 have important implications for quantifying how biodiversity stabilizes communities. In chapter 2, I used an average correlation coefficient to quantify community synchrony. As I have shown in chapter 3, a better metric of community synchrony for quantifying diversity-stability relationships is Φ. Further analyses of the data from Chapter 2 show that Φ and the Synchrony Index are strongly correlated ($\rho = 0.76$), suggesting that my conclusions are unlikely to be affected by my use of the average correlation coefficient. Nevertheless, in future, studies of diversity-stability relationships should use Φ, since the average correlation coefficient may not always be well-correlated with community synchrony, particularly when abundances are uneven within the community (Appendix B.1).

Additionally, the linear mixed-effect model framework that I used in chapter 2 does not explicitly account for observation error. Instead, I have taken advantage of the replicated sampling design to estimate a yearly random effect, representing random perturbations to the intrinsic growth rate due to environmental fluctuations at the reef scale. The residual variation is assumed to be due to observation error and other sources of unexplained variation, including heterogeneity and stochasticity at the sub-reef scale. Although this approach explicitly accounts for two sources of stochastic fluctuations, reef-scale environmental fluctuations and residual variation, it is not, strictly speaking, a process noise and observation error model, because it does not keep track of an estimate of the true (unobserved) population size. At each time-step, the population size next year is predicted from the observed population size this year, which is assumed to be accurate. Then the deviation between the predicted and observed value is partitioned between reef-scale process noise (due to environmental fluctuations) and residual error. Clearly these two steps make inconsistent assumptions: the prediction step assumes that observations are accurate, while the partitioning step assumes the opposite. In contrast, a state-space model approach, such as that I developed in chapter 4, would keep track of the true unobserved population size and use it to make one-step-ahead predictions.

A complete assessment of the potential biases induced by the hierarchical analytical approach I have used in chapter 2 would require fitting a state-space model to the data and comparing the results. Unfortunately, accurate estimation of state-space models' parameters requires longer time-series than available in this dataset. However, there are good reasons to think that my results are robust. Firstly, using a state-space model is unlikely to change the estimates of response diversity. Response diversity is calculated from the covariance matrix of process noise among species, and it is hard to imagine how the statistical model I used would systematically bias the patterns of covariance among species at the reef scale. Secondly, the simplified model is likely to produce over estimates of density-dependence, since process-noise only models are known to do this (chapter 4). Consequently, we can expect the density-dependence index to be biased low. My analysis however does not focus on density-dependence, but rather the interaction index (II) , the average of the interaction strengths between species. The extent to which ignoring observation error can systematically bias estimates of interaction strengths between species is unknown (Ives et al. 2003). However, it is likely that there will be negative covariances among interaction parameters, because a decrease in one parameter needs to be compensated by an increase in another parameter so that the predicted average abundance remains close to the average of the data. Consequently, elements of the community matrix are likely to be biased in compensatory ways: some coefficients will be biased low while some others will be biased high. By averaging interaction strengths over all species pairs, I would expect my index to have mitigated the impact of any such biases.

5.2. Caveats

Functional form of density-dependence

Analysing population dynamics using time-series of abundances requires choosing a functional form of density-dependence to characterize the expected deterministic dynamics in the absence of stochasticity. Popular choices for the functional form include the θ-logistic model (e.g. Sibly et al. 2005, Brook and Bradshaw 2006, Sæther et al. 2008), the Ricker model (e.g. Brannstrom and Sumpter 2006, Abbott 2011) and the Gompertz model (e.g. Pollard et al. 1987, Dennis et al. 2006, Knape and de Valpine 2012). These models are phenomenological models, in the sense that the density-dependence of birth and death terms are not explicitly derived from mechanistic assumptions. The lack of biological assumptions makes it difficult to assess objectively the suitability of a particular model for the dynamics of a specific population. Consequently, the choice of the model is often done *a priori*, based on personal preference, or based on considerations of analytical tractability.

Analytical tractability might explain the popularity of the Gompertz model in ecological analysis of time-series (Dennis et al. 2006). When expressed in log-abundances, the Gompertz model is linear. Under the assumption that observation error can be ignored, and that environmentally-driven random fluctuations of growth rates are normally distributed on the log-abundance scale, the resulting model can be fitted to time-series using simple linear regression. Additionally, if both process noise and observation error are considered, and if observation error also is assumed to be normally distributed on the log-abundance scale, the Gompertz model becomes a linear Gaussian state-space model that can be fitted to time-series using the Kalman Filter. Software packages to perform Kalman filtering exist that are designed to be accessible to ecologists (e.g. Holmes et al. 2012).

If the Gompertz model is chosen for statistical convenience rather than for ecological reasons, one could legitimately question its suitability for analysing ecological time-series analysis. However, studies that have compared multiple functional forms of density-dependence consistently find that the Gompertz model performs at least as well as other models for time-series of natural population abundances. For example, Brook & Bradshaw (2006), analysing a large collection of time-series, found that the Gompertz model consistently outperformed the θ-logistic and the Ricker model for a wide range of taxa. Moreover, Knape & de Valpine (2012), in an extensive analysis of the GPDD found that the Ricker and the Gompertz model lead to very similar distributions of the strength of density-dependence among time-series, suggesting that the relative strength of density-dependence is robust to the choice of the functional form. Using data from laboratory experiments, Ferguson & Ponciano (2014) compared the performance of alternative functional forms for population viability analysis. They found that the form of density-dependence had a moderate effect on predictions, but that these effects were small compared to removing density-dependence entirely. The Ricker model performed best for populations embedded within simple communities (one consumer, multiple resources) whereas the Gompertz model outperformed other models for populations embedded within complex communities (multiple consumers, multiple resources). They conclude that the Gompertz model may be a better model for larger communities, where interactions with others species play a role in population regulation, as is the case for most populations in nature (including the herbivore assemblage analysed in chapter 2). These experimental findings suggest that the Gompertz model is a good candidate for analysing the dynamics of natural populations.

Statistical distribution of observation error

In the analysis of time-series of population abundances, observation error usually refers to any discrepancy between the true unobserved population size and the recorded population size. Observation error results from the interaction of multiple processes involved in the collection of data, such as miscounts made by the observer or sampling error. Indeed, estimates of population sizes are rarely based on exhaustive censuses of individuals, but rather on samples. Consequently, some sampling error will affect population size estimates with a magnitude and a distribution dependent on the sampling design and on the spatial distribution of the population. For simple sampling designs and under simplifying assumptions, the distribution of observation error can be derived directly. For example, counting individuals from a population randomly distributed in space results in a Poisson-distributed sampling error. However, for many ecological time-series, there is no natural way of determining the distribution of observation error. In such cases, the choice of the distribution of observation error is often dictated by analytical tractability, as noted above in the context of using the Kalman Filter to fit population time series.

In contrast to the functional form of density-dependence, there are compelling reasons to think that the choice of the error model can influence inferences on population-dynamic parameters. For example, in a simulation study, Knape et al. (2011) found that selecting an incorrect distribution of observation error could result in severe over-estimation of density-dependence. Additionally, they tested whether the true distribution of observation error could be identified from the data by arbitrating between several error models with model selection criteria. They found that, when using single time-series, the model of observation is commonly mis-identified, in some instances in 70% of the cases. In contrast, when using replicated time-series, the correct model was identified in most cases. Consequently, unless replicated time-series are available, the correct error model will likely not be identifiable from the analysis of the data.

Acknowledging for observation error in the analysis of population and community time-series is a necessity for reliable inference, but it remains a challenging task. Firstly, it is notoriously difficult to tease apart process noise from observation error in short ecological time-series (Dennis et al. 2006, Dennis et al. 2010, Lebreton and Gimenez 2013). Estimates of the variance of process noise and observation error tend to be strongly negatively correlated, often resulting in a large variance for one source of variability and a small variance for the other. Secondly, the choice of the error model itself has important implications for parameter estimation. Analysing replicated time-series considerably improves parameter estimation (Dennis et al. 2010), and may allow to select an appropriate model of observation error (Knape et al. 2011). Unfortunately, most time-series are not replicated. Nevertheless, some recent developments may help to address these issues. First, Knape et al. (2013) have developed a new method for analysing population time-series when estimates of population sizes are accompanied by standard errors. This method performs as well or even better than the joint analysis of replicated time-series when the number of replicates is small. Second, when the true observation model is incompletely known, flexible distributions for observation error can be used to incorporate prior information about general features of the observation error distribution, such as left or right skew (Hosack et al. 2012). These two approaches could be useful, for instance, if the magnitude or form of observation error can be estimated post-hoc from other studies that mimic the focal study's sampling design, but with replication. Finally, using weakly informative priors on demographic parameters can dramatically increase estimation efficiency (Lebreton and Gimenez 2013).

5.3. Future directions

Ecological drivers of the diversity-stability relationship (DSR)

The extent to which interspecific ecological interactions and response diversity contribute to the diversity-stability relationship remains an open question. Early theoretical studies suggested that interspecific competition has little influence on the DSR, because the stabilizing effect resulting from competition-driven asynchronous dynamics is compensated by the destabilizing effect of competition on population variability (Ives et al. 1999, Ives and Hughes 2002). In contrast, a recent study suggests that competition has a destabilizing effect (Loreau and Mazancourt 2013). However these theoretical predictions are at odds with the findings of Chapter 2, which found that compensatory interactions have a weak but significant stabilizing effect on herbivory.

Existing theory typically assumes strong symmetry in the community's population dynamics (all species have identical values for some parameters). This assumption has been relaxed only for simple communities of two interacting species, or through simulation of larger communities, yielding different conclusions about diversity-stability relationships depending on details of model structure and parameter values (Ives et al. 1999, Hughes and Roughgarden 2000, Ives et al. 2000, Fowler et al. 2012, Loreau and Mazancourt 2013). The interpretation of community-dynamic models within the framework developed in Chapter 3 opens the way to re-examine the relationship between ecological interactions, response diversity and their influence on the diversity-stability relationship for realistic communities. For example, using this framework, a recent study characterized how functional distance between species and the relative importance of predation and competition drive the diversity-stability relationship in complex communities (Bauer et al. 2014).

Disentangling the relative contribution of levels of organization to the DSR

The mounting evidence that portfolio effects operate strongly in natural communities has important implications for conservation. Species diversity can stabilize critical ecosystem functions, such as herbivory on coral reefs. This stabilization, in turn, can provide insurance against regime shifts when those functions are key for keeping the system in a particular basin of attraction (Standish et al. 2014, Adam et al. 2015). In many cases, the assemblage of species performing a particular function is itself composed of several functional groups. For example, on coral reefs, herbivorous fishes can be classified as Territorial grazers, Roving grazers and Scrapers.

Conservation of both species diversity and functional diversity are commonly identified as goals in ecosystem management. Therefore, determining which level of organization contributes most to the DSR is of considerable interest for informing conservation decisions. The framework developed in Chapter 3 could be extended to allow estimation of the relative contribution of within-group asynchrony and among-group asynchrony to overall community asynchrony.

5.4. Conclusions

The results of this thesis support the view that positive diversity-stability relationships might be common, but not ubiquitous, in natural assemblages. Ultimately, the strength and direction of the diversity-stability relationship depends on the interplay of several ecological drivers of fluctuations in species' abundances. The analysis of time-series with community dynamics models can provide useful insights on the relative importance of these ecological drivers. For example, I have shown that, when the drivers of population synchrony are partitioned between response diversity and compensatory interactions, the former is the main determinant of the diversity-stability relationship for herbivorous fishes on coral reefs. The DSR itself can be partitioned into an effect of synchrony, and an effect of population variability, when these are quantified as the community synchrony index (Φ) and the weighted-average population variability. Because population and community-dynamic processes affect both average population variability and community synchrony, their role on the strength and direction of the DSR can be disentangled by considering separately their effect on community synchrony and population variability. However, my final chapter indicates that there is still some important work to do in terms of understanding DSRs in community time series, in order to more rigorously account for the effects of observation error, and thereby better ensure sound inferences about the magnitudes of the processes driving fluctuations of the communities being sampled.

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Appendix A. Supplementary material for chapter 2

A.1. Functional groups and reefs surveyed

Table A-1.—Survey reefs and period of surveys.

Reef	Period surveyed
Low Isles Reef	1997 – 2004
Green Island Reef	1993 – 2004
Mackay Reef	1995 – 2004
Hastings Reef	1993 – 2009
Michaelmas Reef	1993 – 2004
Thetford Reef	1994 – 2009
Agincourt Reefs (No. 1)	1994 – 2009
St. Crispin Reef	1995 – 2009
Opal Reef	1995 – 2004
Broomfield Reef	1995 – 2009
Wreck Island Reef	1996 – 2004
One Tree Reef	1995 – 2004
Lady Musgrave Reef	1995 – 2009
Martin Reef	1995 – 2004
North Direction Reef	1994 – 2004
Carter Reef	1995 – 2004
Yonge Reef	1993 – 2004
No Name Reef	1994 – 2004
Gannett Cay Reef	1993 – 2004

Snake Reef	1993 – 2004
Chinaman Reef	1993 – 2009
Horseshoe Reef	1995 – 2004
East Cay Reef	1994 – 2009
Turner Reef	1994 – 2004
John Brewer Reef	1993 – 2004
Davies Reef	1993 – 2004
Myrmidon Reef	1993 – 2004
Dip Reef	1995 – 2004
Chicken Reef	1994 – 2009
Reef 19-131	1996 – 2004
Reef 19-138	1994 – 2004
Reef 20-104	1993 – 2004
Slate Reef	1995 – 2004
Hyde Reef	1994 – 2004
Rebe Reef	1994 – 2004

Table A-2.—List of functional groups' constituent species.

Territorial Grazers	Roving Grazers	Scrapers
Acanthurus lineatus	*Acanthurus maculiceps*	*Bolbometapon muricatum*
Acanthurus nigricans	*Acanthurus nigrofuscus*	*Calotomus carolinus*
Chrysiptera biocellata	*Acanthurus triostegus*	*Cetoscarus bicolor*
Chrysiptera rex	*Naso lituratus*	*Chlorurus bleekeri*
Dischistodus melanotus	*Naso tuberosus*	*Chlorurus japanensis*
Dischistodus prosopotaenia	*Naso unicornus*	*Chlorurus microrhinos*
Dischistodus pseudochrysopoecilus	*Siganus doliatus*	*Chlorurus sordidus*
Hemiglyphidodon plagiometopon	*Siganus fuscescens*	*Hipposcarus longiceps*
Plectroglyphidodon lacrymatus	*Siganus lineatus*	*Scarus altipinnis*
Pomacentrus bankanensis	*Siganus punctatissimus*	*Scarus chameleon*
Pomacentrus chrysurus	*Siganus punctatus*	*Scarus dimidiatus*
Pomacentrus grammnorhyncus	*Siganus spinus*	*Scarus flavipectoralis*
Pomacentrus wardi	*Zebrasoma scopas*	*Scarus forsteni*
Stegastes apicalis	*Zebrasoma veliferum*	*Scarus frenatus*
Stegastes fasciolatus		*Scarus ghobban*

Stegastes gascoynei	*Scarus globiceps*
Stegastes nigricans	*Scarus longipinnus*
	Scarus niger
	Scarus oviceps
	Scarus psittacus
	Scarus rivulatus
	Scarus rubroviolaceus
	Scarus schlegeli
	Scarus spinus

A.2. Selection of functional form

To establish the functional relationship between per capita growth rate and abundance, I fitted two different models to the abundance data: a discrete time version of the Lotka-Volterra model (Ives and Carpenter 2007) and a discrete time version of the Gompertz model (Ives et al. 2003). In these models, the change in abundance of group i at time t on reef r at site s, transect u, $n_{i,r,s,u}^{t}$, is modeled as:

Gompertz model:

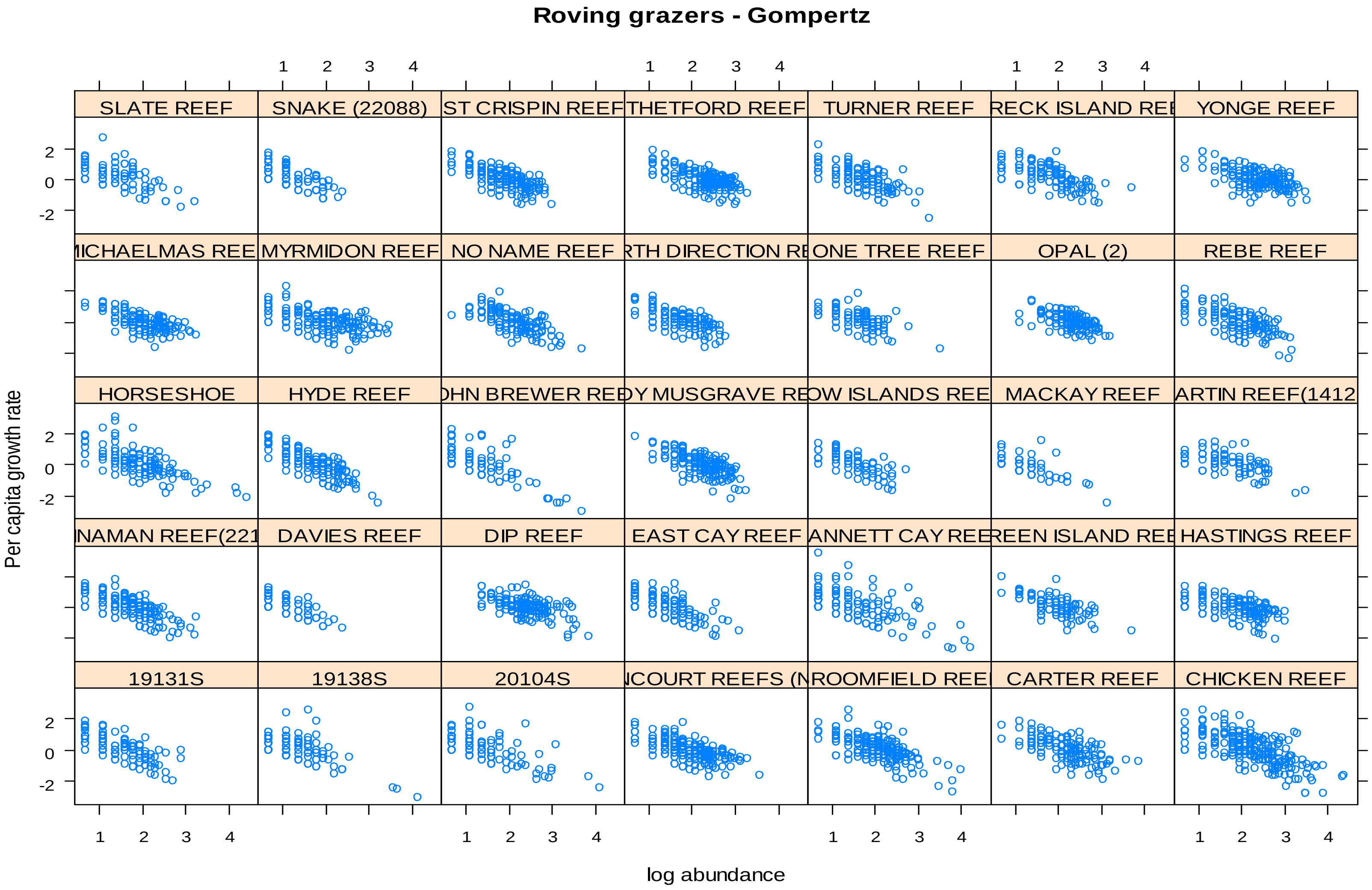
$$\log\left(n_{i,r,s,u}^{t+1}\right) - \log\left(n_{i,r,s,u}^{t}\right) = a_{i,r} + \sum_{j=1}^{3} b_{i,j,r} \log\left(n_{j,r,s,u}^{t}\right) + r_{i,r,s}^{t} + e_{i,r,s,u}^{t}$$

Lotka-Volterra model:

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

Note that both models have exactly the same structure and differ only in the functional relationship between per capita growth rate and abundance: per-capita growth rate declines linearly with abundance in the Lotka-Volterra model, but linearly with log-abundance in the Gompertz model. Note also that the Lotka-Volterra model is essentially a multi-species extension of the “ricker-logistic”, which preserves the linearity between per-capita growth rate and abundance, while preventing negative population sizes.

I fitted both models and compared the fits using Akaike Information Criteria, which strongly favored the Gompertz model. The better fit of the Gompertz model is also supported by visual inspection of model fit. Specifically, plots of per-capita growth rate against log-abundance for all three functional groups exhibit linearly decreasing relationships, consistent with Gompertz model assumptions), but nonlinear relationships with abundance on an arithmetic scale, in violation of Lotka-Volterra model assumptions. Figure A-1 illustrates this, using the roving grazer data.


Roving grazers - Gompertz
SLATE REEF
SNAKE (22088)
ST CRISPIN REEF
THETFORD REEF
TURNER REEF
RECK ISLAND REE
YONGE REEF
IICHAELMAS REE
MYRMIDON REEF
NO NAME REEF
RTH DIRECTION RE
ONE TREE REEF
OPAL (2)
REBE REEF
HORSESHOE
HYDE REEF
OHN BREWER REE
DY MUSGRAVE RE
OW ISLANDS REE
MACKAY REEF
ARTIN REEF(1412
NAMAN REEF(221
DAVIES REEF
DIP REEF
EAST CAY REEF
ANNETT CAY REE
REEN ISLAND REE
HASTINGS REEF
19131S
19138S
20104S
ICOURT REEFS (N
ROOMFIELD REE
CARTER REEF
CHICKEN REEF
Per capita growth rate
log abundance
1
2
3
4
-2
0
2

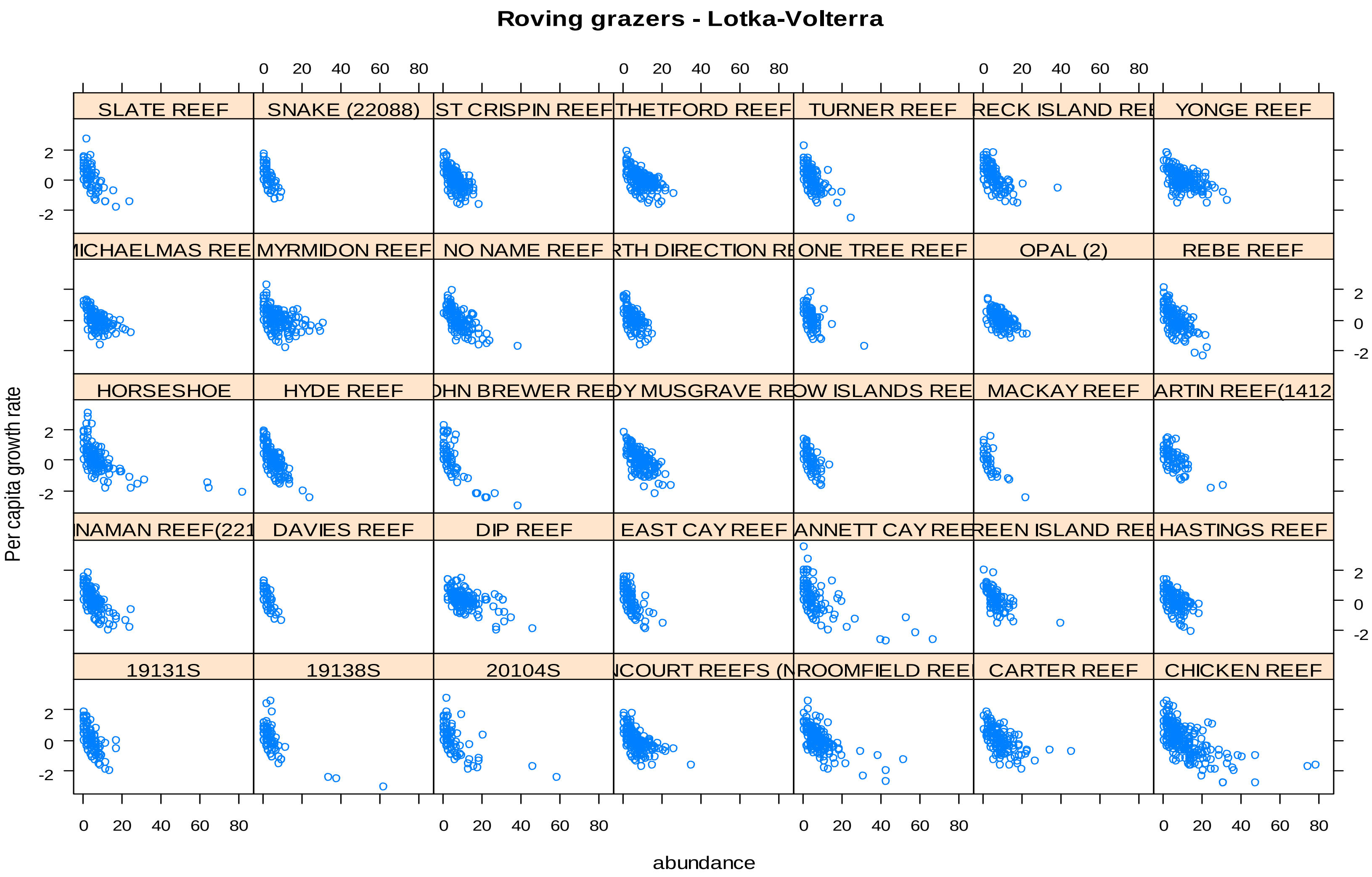

Roving grazers - Lotka-Volterra

Figure A-1. — Biplots of *per capita* growth rate versus either log-abundance (for the Gompertz model) or arithmetically-scaled abundance (for the Lotka-Volterra model) for the Roving Grazers.The non linearity of the relationship is conspicuous for the Lotka-Volterra model.

A.3. Effect of grouping species on indices

Effect of grouping species on Synchrony Index estimates

To examine the effect of pooling species into subgroups on estimates of the Synchrony Index, I consider, for simplicity, a community composed of 2$\mathbf{n}$ species, each with variance $\boldsymbol{V}$ and correlation coefficient $\boldsymbol{\alpha}$ between the abundances of all pairs of species; thus, the species-level Synchrony Index is $\boldsymbol{\alpha}$. I consider the effect of splitting the community into 2 groups of $\boldsymbol{n}$ species each, and seek to determine the Synchrony Index for the two subgroups (this is the quantity actually estimated in our empirical analyses). Following the definition of the correlation coefficient, the subgroup-level Synchrony Index is:

$$\alpha_{est} = \frac{\sigma(group_1, group_2)}{\sqrt{\sigma^2(group_1) * \sigma^2(group_2)}} \tag{A.1}$$

Where $\boldsymbol{group_1}$ and $\boldsymbol{group_2}$ represent the total abundance of the two subgroups, $\boldsymbol{\sigma(group_1,group_2)}$ is the covariance between subgroups, and $\boldsymbol{\sigma^2(group_1)}$ and $\boldsymbol{\sigma^2(group_2)}$ are the variances.

Now I consider how the subgroup variances depend on the species-level variances. The total variance of a subgroup is a function of its constituent species-level variances and covariances, according to the definition of the variance of a sum (e.g. Pitman 1993):

$$\sigma^2\left(\sum_{i=1}^{n} x_i\right) = \sum_{i=1}^{n} \sigma^2(x_i) + \sum_{i \neq j} \sigma(x_i, x_j)$$

(A.2)

If I denote the species-level variances are *V*, and the species-level covariances α, this simplifies to:

$$\sigma^2(group_1) = \sigma^2(group_2) = n * V + n * (n-1) * \alpha * V$$

(A.3)

Also, the covariance between groups is the sum of the pairwise covariances of species of different groups:

$$\text{covar}(group_1, group_2) = \sum_{i \in group1, j \in group2} \text{covar}(sp_i, sp_j) = n^2 * \alpha * V$$

(A.4)

Substituting eqs. (A.3) and (A.4) into (A.1), I obtain the subgroup-level Synchrony Index as a function of the species-level Synchrony Index:

$$\alpha_{est} = \frac{n * \alpha}{1 + (n-1) * \alpha}$$

Knowing that $\boldsymbol{\alpha}$ is a correlation coefficient and therefore less than or equal to 1, it follows that

$$\frac{\alpha_{est}}{\alpha} = \frac{n}{1 + (n-1) * \alpha} \geq 1$$

Because this ratio is always positive and bigger than 1, the quantity estimated in our analyses—the between subgroup Synchrony Index—is an overestimate of species-level Synchrony. This is illustrated in Figure A-2 for a community of 10 species split in two groups of 5. The same argument applies for the Environmental Response Synchrony Index.

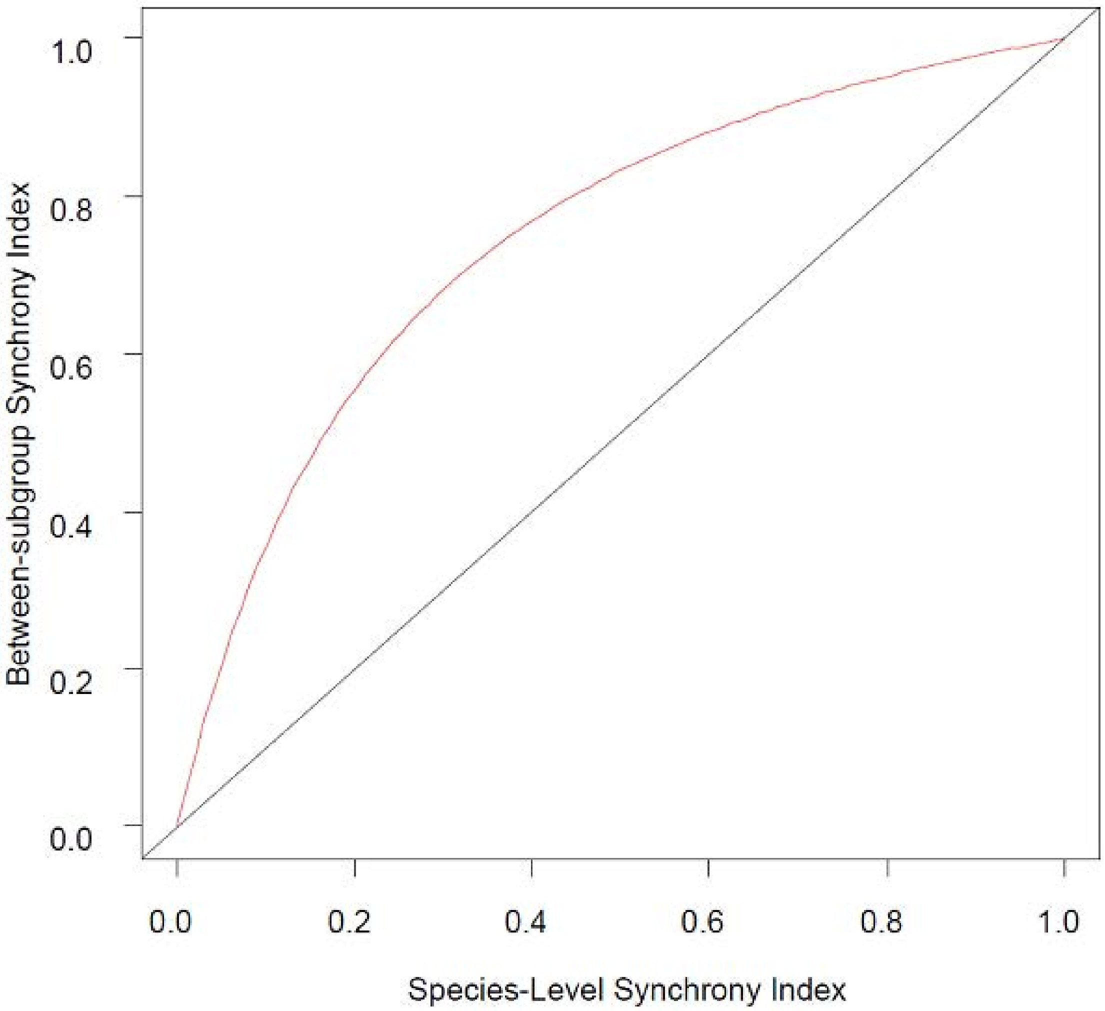


Figure A-2. — Bias resulting from calculating the Synchrony Index between groups instead of doing it at species level. The dashed line is the unity line (species level synchrony index = between-subgroup Synchrony Index).

Effect of grouping species on Interaction Index estimates

I used a simulation study to determine whether pooling species into subgroups biases the Interaction Index, relative to the true species-level interactions. I assembled communities of 3, 5 and 10 species with varying values of the Interaction Index. Again, for simplicity, I assume that all species had the same growth rate, density-dependent parameter (b) and the same effects on one other ($a_{ij}=a$ for all i,j). Negative values of a (which is equivalent to the species-level Interaction Index) correspond to a community where diffuse competition takes place, while positive values of the interaction Index indicates that diffuse facilitation occurs. The resulting community matrix **B** had the following format:

$$B = \begin{pmatrix} b & a & \dots & a \\ a & b & \ddots & \vdots \\ \vdots & \ddots & \ddots & a \\ a & \dots & a & b \end{pmatrix}$$

Only communities having a stable equilibrium are of interest to our analysis, and I therefore determined the stability conditions of this model. It can be shown that **B** has (n-1) eigenvalues equal to b-a and one eigenvalue equal to $a(n\text{-}1)+b$, where n is the number of species in the community. The conditions for the existence of a stable equilibrium (all eigenvalues have a magnitude less than one) can then be written as follows:

$$-\frac{2}{n} < a < \frac{2}{n}$$

$$if\ a \geq 0, \qquad a - 1 < b < 1 - a(n-1)$$

$$if\ a \leq 0, \qquad -1 - a(n-1) < b < a + 1$$

For each value of n, I assembled 10 communities with an Interaction Index varying within the stability ranges shown above. A value of b was chosen in the middle of the range of values that ensure stability ($b = a(2-n)/2$). For each community, simulations of community dynamics were run to produce 1000 replicate time-series of community abundances over 100 time steps. Once the data had been simulated, the n species were split into two randomly drawn groups, and the between-subgroup Interaction Index estimated, following the same procedure I used for the empirical data. Finally, I calculated the ratio of the estimated (between-subgroup) Interaction Index between the two groups and the species-level Interaction Index (a) that was used to generate the simulated data. A ratio with a magnitude above 1 implies that the subgroup-level Interaction Index is larger in magnitude than the actual species-level interaction index; a positive ratio implies that the estimated Interaction Index is in the same direction as the true species-level index. Our results show this ratio is consistently both positive and greater than 1, regardless of the magnitude or sign of the true interaction index (e.g., Figure A-3). This indicates that the subgroups analysis tends to correctly estimate the sign, and to overestimate the strength, of species-level interactions. Qualitatively identical results were obtained for all values of n, the number of species in the community, with the biases tending to be larger in magnitude for a larger number of species, suggesting that subgroup-based analyses of high diversity communities are particularly likely to overestimate, rather than underestimate, the species-level interaction strengths.

In another series of simulations, I varied b, the strength of density-dependence. Except for some borderline cases, where the community was on the threshold of instability (i.e., the leading eigenvalue’s magnitude was very close to one), the results were qualitatively similar, with the Interaction Index estimate biased away from zero, relative to the species-level interaction strength.

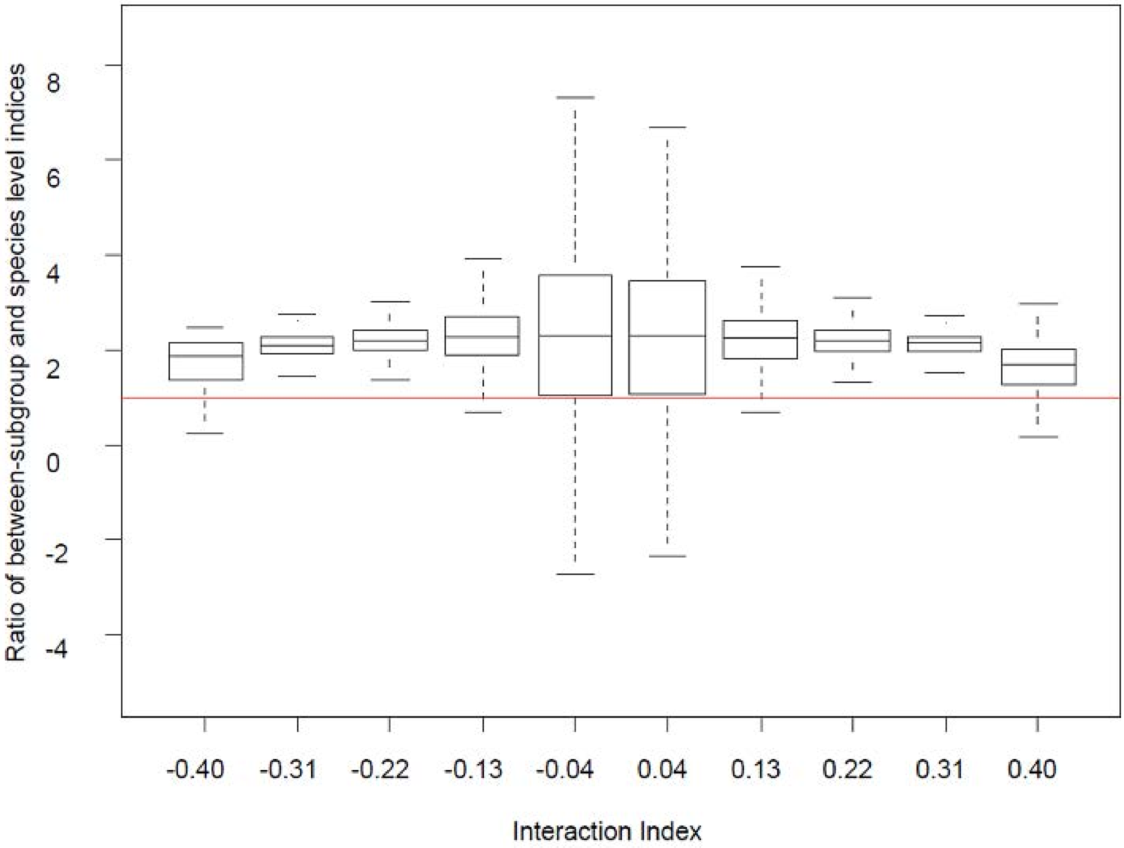


Figure A-3. — Ratio of the between-subgroup interaction index over the species-level interaction index, for a community of 5 species, as a function of the species-level interaction index. Each boxplot summarizes the results of 1000 simulation for a given between-species interaction index. The horizontal red line indicates a ratio of 1.

Appendix B. Supplementary material for chapter 3

B.1. Effects of unequal variances on the mean correlation coefficient and synchrony index

A major shortcoming of the mean correlation coefficient as a measure of community synchrony is that it is not robust to unequal variances. In contrast, the synchrony index ϕ implicitly accounts for the different effects of species with large versus small variances on total community variance. This can be illustrated with a simple toy example comparing two community covariance matrices, which differ only in the inequality of their variances.

Consider a community of n species, where the first n-1 species are perfectly correlated with each other $(\rho = 1)$, and the n^{th} species is perfectly negatively correlated with the other n species $(\rho = -1)$. First, consider the case where all species have the same variance, v. Then, the community covariance matrix is:

$$\mathbf{V}_n = \begin{pmatrix} v & \dots & v & -v \\ \vdots & \ddots & \vdots & \vdots \\ v & \cdots & v & -v \\ -v & \cdots & -v & v \end{pmatrix} \tag{B.1.1}$$

The synchrony index for this community (from eq. 3.2) is:

$$\phi = \frac{\sum_{ij} v_n^s(i,j)}{\left(\sum_i \sqrt{v_n^s(i,i)}\right)^2} = \frac{(n-1)^2 v + v - 2(n-1)v}{n^2 v} = \frac{(n-2)^2}{n^2} \tag{B.1.2}$$

and the mean correlation coefficient is:

$$\bar{\rho} = \left(\frac{(n-1)n}{2}\right)^{-1}\left((1)\frac{(n-1)(n-2)}{2} + (-1)(n-1)\right) = \frac{n-4}{n} \qquad \text{(B.1.3)}$$

When there are only two species in the community (n=2), they are perfectly negatively correlated, and, consistent with this, $\phi = 0$ and $\bar{\rho} = -1$. As n increases, the negatively correlated species contributes a smaller and smaller portion of the total community variance, and the community variability is increasingly dominated by the perfectly synchronized species. Accordingly, both the synchrony index and the mean correlation coefficient converge to 1 as $n \to \infty$.

Now consider a community with the same correlation coefficients, and where the first n-1 species still have variance v, but where the variance of the n^{th} species is now $(n\text{-}1)^2v$:

$$\mathbf{V}_n = \begin{pmatrix} v & \cdots & v & -(n-1)v \\ \vdots & \ddots & \vdots & \vdots \\ v & \cdots & v & -(n-1)v \\ -(n-1)v & \cdots & -(n-1)v & (n-1)^2 v \end{pmatrix} \qquad \text{(B.1.4)}$$

Note that this community is perfectly asynchronous: the total community variance (sum of all of the covariance matrix elements) is zero (i.e., total community size remains constant over time), as long as there is more than one species in the community. This is reflected in the synchrony index, which is now zero for any n>1:

$$\phi = \frac{\sum_{ij} v_n^s(i,j)}{\left(\sum_i \sqrt{v_n^s(i,i)}\right)^2} = \frac{0}{4(n-1)^2 v} = 0 \qquad \text{(B.1.5)}$$

In contrast, the mean correlation coefficient is the same as for the community with equal variances (eq. B.1.3, above). In other words, even though this community is perfectly asynchronous (it remains constant over time), the mean correlation coefficient actually still converges to the opposite extreme (perfect synchrony, $\bar{\rho} = 1$) as species richness increases.

The problematic behavior of the mean correlation coefficient for the unequal community arises because the contribution of the negatively correlated species to the mean correlation is the same as the contribution of all the other species (and thus makes a proportionately smaller contribution at larger *n*), even though it contributes very disproportionately to the total variance of the community in the second example for all n.

B.2. Derivation of relationship between population and community variability

To derive eq. (3.3), I re-arrange eq. (3.2) by solving for community variance:

$$v_n^c = \phi\left(\sum_i \sqrt{v_n^s(i)}\right)^2 \tag{B.2.1}$$

I then divide both sides by temporal mean of total community abundance, $m_n{}^c$ (i.e., the sum of mean abundances of all species in the community):

$$CV_n^c = \frac{\sqrt{v_n^c}}{m_n^c} = \frac{\sqrt{\phi\left(\sum_i \sqrt{v_n^s(i)}\right)^2}}{m_n^c} \tag{B.2.2}$$

This allows me to express community variability as a dimensionless quantity: the coefficient of variation of total community abundance, CV_n^c. I then factor out the synchrony index:

$$CV_n^c = \frac{\sqrt{\phi\left(\sum_i \sqrt{v_n^s(i)}\right)^2}}{\sum_i m_n^s(i)} = \sqrt{\phi}\,\frac{\sum_i \sqrt{v_n^s(i)}}{\sum_i m_n^s(i)} \tag{B.2.3}$$

Equation (3.3) says that community variability is simply the product of a synchrony effect, $\sqrt{\phi}$, and a population variability effect. One way to express the population variability is as the average standard deviation of species abundance, divided by the average mean species abundance. We can see this more clearly by dividing the right-hand numerator and denominator in (B.2.3) by the number of species, *n*:

$$CV_n^c = \frac{\sqrt{\phi\left(\sum_i \sqrt{v_n^s(i)}\right)^2}}{\sum_i m_n^s(i)} = \sqrt{\phi}\,\frac{\frac{1}{n}\sum_i \sqrt{v_n^s(i)}}{\frac{1}{n}\sum_i m_n^s(i)} \tag{B.2.4}$$

However, the link between population and community variability can be expressed more intuitively by recognizing that the ratio in eq. (B.2.4) is equivalent to a weighted average of each species' coefficient of variation, where the weighting is by each species' relative mean abundance. We can do this by first pulling the sum in the numerator out in front of the fraction:

$$CV_n^c = \sqrt{\phi}\,\frac{\sum_i \sqrt{v_n^s(i)}}{\sum_i m_n^s(i)} = \sqrt{\phi}\sum_i \frac{\sqrt{v_n^s(i)}}{\sum_j m_n^s(j)}, \tag{B.2.5}$$

and then multiplying through by $m_n^s(i) \big/ m_n^s(i)$

$$CV_n^c = \sqrt{\phi}\sum_i \frac{\sqrt{v_n^s(i)}}{\sum_j m_n^s(j)} = \sqrt{\phi}\sum_i \frac{m_n^s(i)}{\sum_j m_n^s(j)}\,\frac{\sqrt{v_n^s(i)}}{m_n^s(i)} = \sqrt{\phi}\,\widetilde{CV}_n^s \tag{B.2.6}$$

The term inside the sum in eq. (B.2.6) is simply the relative mean abundance of species i (i.e., mean abundance relative to the mean total community abundance), times the coefficient of variation of abundance of species i. That is, the sum represents a weighted average species-level coefficient of variation, where the weighting is by species' relative abundance. Thus, for instance, in the special case where all species have the same mean abundance, $\widetilde{CV}_n^s$ collapses to a normal unweighted average CV.

B.3. Derivation of relationship between mean-abundance effect and population variability

To derive eq (3.7) in the main text, we first rewrite eq. (3.4), using the mean-variance scaling relationship from eq. (3.5):

$$\widetilde{CV}_n^s = \frac{\sum_i \sqrt{v_n^s(i)}}{\sum_i m_n^s(i)} = \frac{\sum_i \sqrt{a\left(m_n^s(i)\right)^b}}{\sum_i m_n^s(i)} \tag{B.3.1}$$

Then, we substitute the right-hand side of eq. (3.6) for $m_n^s(i)$ in eq. (B.3.1), and factor out the n^x terms in the resulting numerator and denominator:

$$\widetilde{CV}_n^s = \frac{\sum_i \sqrt{a\left(m_n^s(i)\right)^b}}{\sum_i m_n^s(i)} = \frac{\sum_i \sqrt{a\left(\frac{m_1(i)}{n^x}\right)^b}}{\sum_i \frac{m_1(i)}{n^x}} = \frac{\sqrt{\left(\frac{1}{n^x}\right)^b}}{\frac{1}{n^x}} \frac{\sum_i \sqrt{a\left(m_1(i)\right)^b}}{\sum_i m_1(i)}. \tag{B.3.2}$$

We then simplify the left-most fraction on the right-hand side of eq. (B.3.2), to obtain:

$$\widetilde{CV}_n^s = \frac{n^{-\frac{xb}{2}}}{n^{-x}} \frac{\sum_i \sqrt{a\left(m_1(i)\right)^b}}{\sum_i m_1(i)} = \sqrt{n^{(2-b)x}} \frac{\sum_i \sqrt{a\left(m_1(i)\right)^b}}{\sum_i m_1(i)}. \tag{B.3.3}$$

Next, analogous to the derivation of $\widetilde{CV}_n^s$ (Appendix B.2, eqs. B.2.3-B.2.5), we note that the fraction on the far right-hand side of eq. (B.3.3) is equivalent to the weighted average of species' CV in monoculture:

$$\widetilde{CV}_n^s = \sqrt{n^{(2-b)x}} \frac{\sum_i \sqrt{a\left(m_1(i)\right)^b}}{\sum_i m_1(i)} = \sqrt{n^{(2-b)x}} \frac{\sum_i \sqrt{v_1(i)}}{\sum_i m_1(i)} = \sqrt{n^{(2-b)x}}\, \widetilde{CV}_1. \tag{B.3.4}$$

Substituting the right-hand side of the above equation into eq. (3.3) in the main text, we obtain eq. (3.7).

B.4. Effect of direct interactions on diversity-dependence of synchrony

To investigate the effect of incorporating direct interactions on the tendency for the synchrony index, ϕ, to decrease with diversity, we calculate synchrony from the analytical results of Ives *et al.* (1999) and Ives *et al.* (2003). Specifically, we consider the discrete-time Lotka-Volterra model of symmetric, diffuse competition:

$$N_i(t+1) = N_i(t) \cdot \exp\left[r\left(1 - \frac{N_i(t)+\alpha\sum_{j\neq i}^{n} N_j(t)}{K}\right)\right] \cdot \exp(\epsilon_i(t)) \qquad \text{(B.4.1)}$$

where $N_i(t)$ is population size of species i and time t, r =intrinsic growth rate, K = Carrying capacity, α = competition coefficient, and $\varepsilon_i(t)$ is a random perturbation to the growth rate due to environmental fluctuations (drawn for all n species in the community from a multivariate normal distribution with variances σ_e^2 and correlation coefficients ρ_e). Note that the ρ_e represent the correlations in species' responses to environmental fluctuations, which will, in general, be different from correlations in the overall fluctuations in abundance (ρ) used in the calculation of $\bar{\rho}$ and ϕ. Ives & Hughes (2002) derive a first-order Taylor series approximation of the model above:

$$n_i(t+1) = \left(1 - r\frac{N_i^*}{K}\right) n_i(t) - r\alpha\frac{N_i^*}{K}\sum_{j\neq i} n_j(t) + e_i(t) \qquad \text{(B.4.2)}$$

where $n_i(t)$ is abundance of species i, expressed as a perturbation from equilibrium at time t, N_i^* is the equilibrium population size of species i, and $e_i(t)$ is a re-scaled random perturbation to the growth rate ($e_i(t) = N_i^*\epsilon_i(t)$: Ives & Hughes 2002). Because this approximation is linear in N_i, the covariance matrix (eq. 1b) can be solved numerically (see eqs 15-17 in Ives *et al.* 2003). From this, we can calculate the mean correlation coefficient, $\bar{\rho}$, and the synchrony index, as described in the main text.

Note that, when $\alpha = 0$, species are non-interacting, so $\bar{\rho} = \rho_e$ and ϕ exhibits the same pattern of diversity dependence as for the corresponding values of $\bar{\rho}$ in the main text (compare orange lines in Figure B-1 with the orange, blue, and black lines in Figure 3.2a). As α increases, the qualitative pattern of an asymptotic decline in ϕ is preserved (Figure B-1: compare different colored lines of the same line type). However, because competition makes species' dynamics less synchronous, ϕ decreases more rapidly, and to a lower value, compared to the equivalent non-interactive case, but the asymptotic shape of the decline is qualitatively unchanged (Figure B-1).

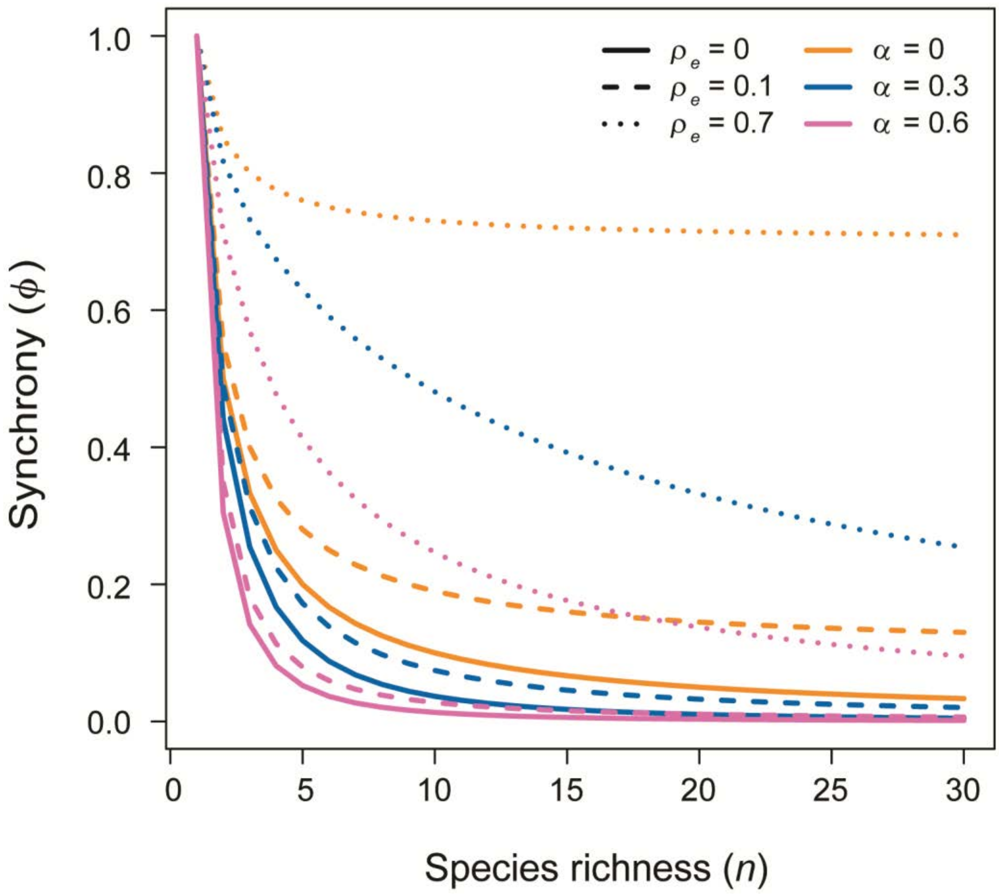


Figure B-1.— Diversity-dependence of the synchrony index under the discrete-time version of the Lotka-Volterra model, for the special case of symmetric, diffuse competition (eq. B.4.1). For all graphs, r=1, K=100, and α and ρ_e differ between lines as indicated on the figure panel. Note that, to better illustrate the asymptotic nature of the decline in synchrony, species richness is here plotted on an arithmetic scale (in contrast to the figures in the main text).

B.5. Overyielding, porfolio effects, and the "threshold" of b=1

In Tilman's (1999) analytical model, $1 \leq b \leq 2$, $\rho=0$, and only values of $0 \leq x \leq 1$ are considered. For this special case, synchrony decreases inversely with diversity towards zero ($\phi=n^{-1}$ [eq. 3.8], black line in Figure 3.2), and thus eq. (3.7) simplifies to:

$$CV_n^c = \widetilde{CV}_1 \sqrt{n^{(2-b)x}} \sqrt{n^{-1}}$$

Because $0<x<1$ and $1<b<2$, the mean-abundance effect increases with diversity, driving the increase in population variability with diversity (e.g., Figure 3.3a, orange line). However, because it increases more slowly than synchrony decreases, there is still a portfolio effect (Figure 3.4g). As overyielding increases (x decreases below 1), the increase in the mean-abundance effect with diversity becomes progressively weaker (Figure 3.3a), and so the overall portfolio effect becomes stronger (Figure 3.4g). Thus, overyielding promotes portfolio effects here by reducing the de-stabilization of species abundances, allowing the diversity-dependence of synchrony to dominate the community-level response.

These countervailing effects of overyielding and diversity-dependent synchrony are present in the experimental study of Roscher et al. (2011). They found $1<b<2$, and that community abundance increases, but species abundance decreases, with diversity (implying $0<x<1$). This should tend to cause population variability to increase with diversity. However, synchrony declines strongly with diversity towards a value close to zero (similar to what is implied by the $\rho=0$ assumption in Tilman's model). Consequently, at the community level, diversity-dependent synchrony outweighs the decreasing population stability, and a portfolio effect is observed.

Similarly, the threshold *b*=1 is derived from models sharing two key assumptions: constant community size, independent of diversity (i.e., *x*=1, no overyielding), and independence of species' fluctuations in abundance (i.e., all ρ=0). This corresponds to the special case above, with *x*=1:

$$CV_n^c = \widetilde{CV}_1\sqrt{n^{(2-b)}}\sqrt{n^{-1}} = \widetilde{CV}_1\sqrt{n^{(1-b)}}$$

Clearly, in this specific case, there is a portfolio effect when *b*>1, and an inverse portfolio effect when *b*<1. However, the result is highly sensitive to this particular combination of assumptions. Whenever either assumption is violated (as they will almost always be in nature), *b*=1 ceases to be a threshold defining portfolio effects.

Appendix C. Supplementary material for chapter 4

C.1. Model likelihoods

The Kalman filter provides a way of fitting stochastic time series when the true state of the system is uncertain, due to observation error. In a nutshell, the approach works because a Cholesky decomposition of the theoretical variance-covariance matrix of the observations at each time step, when multiplied by the vector of observations, produces a vector of transformed observations that are independently and identically distributed. That is, the transformation removes the serial correlation structure that arises from the fact that population sizes are dependent on population sizes at previous time steps. In fact, the Kalman filter is simply an very efficient algorithm to compute the Cholesky decomposition of the theoretical variance-covariance matrix of the observations for space-space models (Eubank and Wang 2002).

Specifically, any Gaussian linear state-space model, such as the Gompertz model, can be written as (following the notation of Durbin and Koopman 2012):

$$\alpha_{t+1} = T\alpha_t + R\eta_t$$

$$y_t = Z\alpha_t + \epsilon_t$$

$$\eta_t \sim N(0, Q)$$

$$\epsilon_t \sim N(0, H)$$

$$t = 1, \dots, n$$

where α_t is a $m \times 1$ vector denoting the unobserved (true) state of the system at time t, y_t is a $p \times 1$ vector of observations at time t, T is an $m \times m$ matrix whose elements define the functional dependence of α_{t+1} on α_t, R is a $m \times r$ matrix characterizing the process noise in the system, Z is a $p \times m$ matrix describing the effect of the true state on the observed state at time t, and Q and H are positive-definite matrices of dimensions $r \times r$ and $p \times p$ respectively, giving the variance-covariance matrix for the vectors of error terms η_t and ϵ_t, which are hypothesized to be serially independent and independent of each other. The matrices T, R, Z, Q and H are assumed to depend on the elements of an unknown parameter vector Ψ.

The Kalman filter is then the following set of five recursive equations:

$$v_t = y_t - Zx_t \tag{C.1a}$$

$$F_t = ZP_tZ' + H \tag{C.1b}$$

$$K_t = TP_tZ'F_t^{-1} \tag{C.1c}$$

$$x_{t+1} = Tx_t + K_tv_t \tag{C.1d}$$

$$P_{t+1} = TP_tT' + RQR' - K_tF_tK_t' \tag{C.1e}$$

Where v_t is known as the innovation at time t, F_t is the variance matrix of v_t, K_t is the Kalman gain and P_t is the variance matrix of the unobserved state vector α_t.

A disadvantage of the Kalman filter is its notational complexity. Dennis *et al.* (2006) proposed a way of expressing the Gompertz state space form that reduced the number of recursive equations from five to two. Specifically, one can set $\alpha_t = \begin{pmatrix} a \\ x_t \end{pmatrix}$ for

t=1,…,*n*, $T = \begin{pmatrix} 1 & 0 \\ 1 & b \end{pmatrix}$, $R = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$, $Q = \sigma^2$, $Z = (0 \quad 1)$, and $H = \tau^2$,

where a, b, σ^2, and τ^2 are the Gompertz model parameters as specified in the main text.With this formulation, 3 elements of P_t are always 0 (because a is a constant in α_t), and thus one element of K_t is always 0:

$$P_t = \begin{pmatrix} 0 & 0 \\ 0 & p_t \end{pmatrix}$$

$$K_t = \begin{pmatrix} 0 \\ k_t \end{pmatrix}$$

Using this notation, and substituting into system (S.1), the kalman filter equations for the Gompertz model become:

$$v_t = y_t - x_t \tag{C.2a}$$

$$F_t = p_t + \tau^2 \tag{C.2b}$$

$$k_t = b p_t F_t^{-1} \tag{C.2c}$$

$$x_{t+1} = a + b x_t + k_t v_t \tag{C.2d}$$

$$p_{t+1} = b^2 p_t + \sigma^2 - b^2 p_t (p_t F_t^{-1}) \tag{C.2e}$$

Each of these equations has an intuitive interpretation that aids in understanding how the Kalman filter works. Here, v_t is a residual (observed minus predicted state at time *t*). F_t is the total variance of the observed relative to the true (unknown) state: the sum of the variance in the predicted state, p_t (due to a combination of observation error from previous states, and process noise), and the variance of the observation of the state at time t, τ^2. k_t is termed the "kalman gain", and measures the information about the true state of the system provided by the observation, relative to the predicted state: $p_tF_t^{-1}$ is the ratio of the variance of the predicted state to the total variance: if it is close to zero, the variance based on the prediction from the previous time step is close to zero, compared to the total variance, so we trust the prediction. If it is close to unity, then the total variance is almost entirely due to the variance in the predicted state, so we trust the observation. This relative weighting influences the both the predicted state at time $t+1$, x_{t+1}, and the variance in the predicted state at $t+1$, p_{t+1}, in intuitive ways. As the $p_tF_t^{-1}$ approaches zero, observation error at time t dominates the total variance, so k_t approaches zero and the predicted state at $t+1$ in eq. (C.2d) is based overwhelmingly on the predicted state at time t. Similarly, the variance in the predicted state at time $t+1$ (eq. C.2e) depends on the variance in the predicted state at time t, plus the process noise associated with population growth between time t and $t+1$, which has variance σ^2 (i.e., the last term drops out). Conversely, as $p_tF_t^{-1}$ approaches unity, observation error is negligible, k_t approaches b, and eq. (C.2d) approaches $x_{t+1} = a + by_t$(i.e., we rely on the observation at the previous time step). For analogous reasons, the variance in the predicted state at time t cancels out in eq. (C.2e) (due to the fact that our observation of the state at time t is reliable), so the variance in the predicted state at time $t+1$ depends only on the process noise between time t and time $t+1$.

We can simplify system (C.2) by re-arranging eq. (C.2e):

$$p_{t+1} = b^2p_t(1 - p_tF_t^{-1}) + \sigma^2 = b^2p_t(F_t - p_t)F_t^{-1} + \sigma^2 = b^2\tau^2p_tF_t^{-1} + \sigma^2$$

By substituting eq. (C.2c) for k_t in eq. (C.2d), solving eq. (C.2b) to obtain $p_t = F_t - \tau^2$, and substituting this into eq. (C.2e), the last two recursive equations become sufficient to carry out the calculations:

$$x_{t+1} = a + b\left(x_t + \frac{F_t - \tau^2}{F_t}(y_t - x_t)\right) \tag{C.3a}$$

$$F_{t+1} = b^2\tau^2\frac{F_t - \tau^2}{F_t} + \sigma^2 + \tau^2 \tag{C.3b}$$

(Dennis et al. 2006).

The log-likelihood for this model can be calculated in standard fashion, by recognizing that the residuals between observed states and the estimated true states are now independent, normally-distributed random variables with mean zero and variance F_t.

The recursion (C.3) does not account for missing observations. For the Gompertz model, this includes years when zero individuals were observed (due to the log-transformation of abundance). Such cases are relatively common in the GPDD (281 time series contain at least one missing value or zero abundance estimate). Fortunately, it is straightforward to extend the approach to handle this problem. When an observation, y_t is missing, it is still necessary to generate a predicted true state (and variance associated with the true state). I do this with a simple prediction step. In my original matrix notation this is:

$$\alpha_{t+1} = T\alpha_t$$

$$P_{t+1} = TP_tT' + RQR'$$

The corresponding simple expressions are found in the same way as above:

$$x_{t+1} = a + bx_t$$

$$F_{t+1} = b^2(F_t - \tau^2) + \sigma^2 + \tau^2$$

It is also necessary to choose initial values, x_1 and F_1, to start the Kalman filter. Here, I follow Knape and deValpine (2012) and employ the "large variance" approach:

$$x_1 = y_1$$

$$F_1 = 10$$

This approach assumes that we have very little information about the initial state (recall that x is abundance on a log scale, so $F_1=10$ implies a variance of e^{10} individuals on an arithmetic scale). Alternatively, it is straightforward to derive analytical expressions for exact diffuse initial conditions, where the variance F_0 is assumed to be infinite instead of very large (de Jong 1991). However I favoured the large variance approach so that my results could be directly compared with those of (Knape and de Valpine 2012). I also repeated the analyses using exact diffuse conditions and found qualitatively identical results.

As noted in the main text, I fit all of the time series in a single analysis. Thus, the full density-dependent model has log-likelihood:

$$\log\left[L\left(\boldsymbol{a}, \boldsymbol{b}, \boldsymbol{\sigma}, \boldsymbol{\tau} \middle| \boldsymbol{y_1}, \boldsymbol{y_2}, \dots, \boldsymbol{y_D}\right)\right] = \sum_i \sum_t \log\left[f\left(y_{i,t} - x_{i,t} \middle| 0, F_{i,t}\right)\right]$$

where **a, b, σ,** and **τ** are vectors of the Gompertz model parameters (one for each data set), The $\boldsymbol{y_i}$ represent each of the D time series, and $f\left(y_{i,t} - x_{i,t} | 0, F_{i,t}\right)$ is the normal distribution with mean zero and variance $F_{i,t}$. The density-independent model is identical, except with all b_i=1. Similarly, the constant b model sets all $b_i=\mu_b$ (but this single μ_b is estimated, rather than being fixed as in the density-independent model). Finally, the log-likelihood for the random b model follows the standard formula for mixture distributions:

$$\begin{aligned}\log\left[L\left(\boldsymbol{a},\mu_b,v_b,\boldsymbol{\sigma},\boldsymbol{\tau}\middle|\boldsymbol{y_1},\boldsymbol{y_2},\dots,\boldsymbol{y_D}\right)\right]\\ =\sum_i\sum_t\int_{b_i}\log\left[f\left(y_{i,t}-x_{i,t}|0,F_{i,t}\right)f(b_i|\mu_b,v_b)\right]db_i\end{aligned}$$

where μ_b is the mean value of the density-dependent parameter, and $v_b$is the among-time series variance in the strength of density-dependence. Effectively, this computes a weighted-average likelihood for each possible value of b_i, where the weighting is according to the relative probability of that value of b_i, given the among-time series mean and variance μ_b and v_b.

I fitted the alternative models in *ADMB* (Fournier et al. 2012), with the exception of the random b model, which we fitted using *ADMB-RE*. The integrated likelihood was calculated using Gauss-Hermite quadrature with 20 sample points.

C.2. Literature survey for experimental studies of density-dependence

I queried the Web of Science using the keywords “density-dependen*” and “experiment*” and restricted the search to the research area “Environmental sciences, ecology”. I recorded a study as finding density dependence (“yes”) only when all tested responses indicated density-dependence, “no” when all tested responses failed to indicate density-dependence, and “ambiguous” when at least one tested response exhibited density-dependence, and at least one failed to exhibit density-dependence.

Table C-1.—Summary of a systematic literature survey for experimental studies of density-dependence.

Reference	Field/Lab	Taxon	Density-dependence	Notes
(Clay and Shaw 1981)	Field	Plant *Diamorpha smallii*	yes	3 components of fecundity are density-dependent
(Stapanian and Smith 1984)	Field	Plant (nuts) *Juglans nigra* *Quercus macrocarpa* *Quercus muehlenbergii*	yes	Survival is density-dependent
(Olfafsson 1986)	Field	Bivalve *Macoma balthica*	ambiguous	Growth is density-dependent in muddy sand but not in sand

(Shaw and Antonovics 1986)	Field	Plant *Salvia lyrata*	yes	Seedling mortality and growth are density-dependent
(Ellison 1987)	Lab.	Plant *Atriplex triangulari*	yes	Mortality and fecundity are density-dependent
(Shaw 1987)	Field	Plant *Salvia lyrata*	no	Effect of adult density on fecundity, survival and growth is non-significant.
(Vanbuskirk 1987)	Lab.	Insect *Pachydiplax longipennis*	yes	Survival and growth are density-dependent
(Smith et al. 1988)	Lab.	Crustacea *Daphnia* *Ceriodaphnia*	yes	Growth rate is density-dependent

(Wang 1989)	Lab.	Insect *Diaphania indica*	yes	Larval development rate, larval survival and adult fecundity are density-dependent
(Reed 1990)	Field	Plant *Pterygophora californica*	yes	Growth, reproduction, and recruitment are density-dependent
(Gould et al. 1990)	Field	Insect *Lymantria dispa*	yes	Mortality is density-dependent
(Martin et al. 1991)	Field	Fish *Neophylax fuscus* *Pycnopsyche guttifer*	ambiguous	Survival of larvae is density-dependent for *N. fuscus*, but not for *P. guttifer*
(Goater 1992)	Lab.	Worm *Rhabdias bufonis*	yes	Growth and fecundity are density-dependent

(Ostfeld and Canham 1995)	Field	Mammal *Microtus pennsylvanicus*	yes	Reproductive rate and recruitment are density-dependent
(Johnson et al. 1995)	Field	Insect *Epitheca cynosura*	yes	Survival of larvae is density-dependent
(Wagner and Wise 1996)	Field & Lab.	Spider *Schizocosa ocreata*	yes	Mortality is density-dependent
(Both 1998)	Field	Bird *Parus major*	yes	Reproductive output is density-dependent
(Post et al. 1999)	Field	Fish *Onchorynchus mykiss*	yes	Growth is density-dependent

(Tanaka et al. 1999)	Field	Mollusk *Pomacea canaliculata*	yes	Growth and reproductive output are density-dependent
(Wilson and Osenberg 2002)	Field	Fish *Gobiosoma evelynae* *G. prochilos*	yes	Settlement and survival are density-dependent
(Moe et al. 2002)	Lab	Insect *Lucilia sericata*	yes	Reproductive rate is density-dependent, juvenile survival is facilitated at low density and hampered at high density
(Biro et al. 2003)	Field	Fish *Onchorynchus mykiss*	yes	Mortality is density-dependent

(Hildrew et al. 2004)	Field	Insect *Sialis fuliginosa*	yes	Survival is density-dependent
(Stewart et al. 2005)	Field	Mammal *Cervus elaphus*	yes	Physical condition and reproductive output are density-dependent
(Einum and Nislow 2005)	Field	Fish *Salmo salar*	yes	Survival of juveniles is density-dependent
(Guelda et al. 2005)	Field	Crustacea *Bosmina longirostris* cyclopoid copepods	yes	Population growth rate is density dependent when food is limiting
(Steele and Forrester 2005)	Field	Fish *Coryphopterus glaucofraenum*	yes	Mortality is density-dependent

(Gunnarsson et al. 2006)	Field	Bird *Anas platyrhynchos*	yes	Survival of ducklings is density-dependent
(Craig et al. 2007)	Field	Fish *Leiostomus xanthurus*	yes	Growth and mortality are density-dependent
(Gunnarsson and Elmberg 2008)	Field	Bird *Anas platyrhynchos*	yes	Nest survival is density-dependent
(Brouwer et al. 2009)	Field	Bird *Acrocephalus sechellensis*	yes	Reproductive output is density-dependent
(Fordham et al. 2009)	Field	Reptile *Chelodina rugosa*	yes	Reproductive output is density-dependent
(Gunton and Kunin 2009)	Field	Plant *Silene latifolia*	yes	Reproductive output is density-dependent

(Nicolaus et al. 2009)	Field	Bird *Parus major*	yes	Clutch size is density-dependent
(Loman and Lardner 2009)	Field	Frog *Rana arvalis* *Rana temporaria*	ambiguous	Growth is density-dependent for *R. arvalis* but not for *R. temporaria*
(Forrester et al. 2011)	Field	Fish *Coryphopterus glaucofraenum*	yes	Reproductive output is density-dependent
(Leicht-Young et al. 2011)	Field	Plant *Celastrus orbiculatus* *Celastrus scandens*	no	Survival exhibits positive (inverse) density-dependence
(Stewart et al. 2011)	Field	Mammal *Odocoileus hemionus Cervus elaphus*	yes	Diet quality decreases with density

(Flockhart et al. 2012)	Lab	Insect *Danaus plexippus*	yes	Larval survival is density-dependent
(Bassar et al. 2013)	Field	Fish *Poecilia reticulata*	yes	Survival of juveniles and reproductive output are density-dependent
(Gripenberg et al. 2014)	Field	Five forest tree species	ambiguous	Seed germination is density-dependent for one species among 5