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LETTER

High response diversity and conspecific density-dependence, not species interactions, drive dynamics of coral reef fish communities

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Abstract

Species-to-species and species-to-environment interactions are key drivers of community dynamics. Disentangling these drivers in species-rich assemblages is challenging due to the high number of potentially interacting species (the 'curse of dimensionality'). We develop a process-based model that quantifies how intraspecific and interspecific interactions, and species' covarying responses to environmental fluctuations, jointly drive community dynamics. We fit the model to reef fish abundance time series from 41 reefs of Australia's Great Barrier Reef. We found that fluctuating relative abundances are driven by species' heterogenous responses to environmental fluctuations, whereas interspecific interactions are negligible. Species differences in long-term average abundances are driven by interspecific variation in the magnitudes of both conspecific density-dependence and density-independent growth rates. This study introduces a novel approach to overcoming the curse of dimensionality, which reveals highly individualistic dynamics in coral reef fish communities that imply a high level of niche structure.

KEYWORDS
community dynamics, latent variables, reef fish, regularized horseshoe, response diversity, species interactions, time series

INTRODUCTION

Understanding what drives variation in abundances of species in space and time is a core aim of ecology (Krebs, 2009). Populations respond to a combination of density-dependent and density-independent processes (Ohlberger et al., 2014; Sæther et al., 2016; Thibaut & Connolly, 2020). Species-to-environment interactions, such as variable species responses to environmental fluctuations, and covariations in those responses, are drivers of relative abundance dynamics. (Elmqvist et al., 2003; Thibaut et al., 2012; Thibaut & Connolly, 2013). Particularly, if species are not perfectly positively correlated in their responses to environmental fluctuations, their fluctuations in abundance will be less pronounced at the community level than at the individual species level (a phenomenon referred as 'response diversity', Elmqvist et al., 2003; and a key driver of diversity-stability relationships: Hautier et al., 2020; Zhao et al., 2022).

Interspecific interactions, such as competition and facilitation, also can influence species-abundance dynamics (Butterfield, 2009; Roughgarden, 1974; Tilman, 1994). Indeed, some of community ecology's classic studies identify species interactions with important demographic consequences (e.g., competitive [Connell, 1961], keystone species [Paine, 1966], predator–prey cycles [Stenseth et al., 1997; Krebs et al., 2017]). Conversely, several recent studies have found evidence of mainly weak or negligible interspecific interactions in time series data for marine microorganisms, moths, temperate fishes, crustaceans, birds and rodents communities (Mutshinda et al., 2009; Ovaskainen, Tikhonov, Dunson, et al., 2017; Sandal et al., 2022; but see Almaraz & Oro, 2011).

Evaluating the importance of interspecific interactions on community dynamics, and disentangling their effects from those of environmental covariances across species is critical for addressing many questions in community ecology (Loreau & de Mazancourt, 2013; Thébault &

Loreau, 2005; Tredennick et al., 2017). However, estimating these effects is particularly challenging in species-rich communities, due to the 'curse of dimensionality'. That is, the number of potential interspecific interaction strengths, and covariances in species' response to environmental fluctuations, that need to be estimated, increases quadratically with the number of species in the community (e.g., from 12 to 90 to 380 interaction terms and 6 to 45 to 190 environmental covariances as a community increases from 4 to 10 to 20 species, respectively).

In the absence of practical methods to estimate so many parameters, community ecologists have developed parsimonious biodiversity models that make strong simplifying assumptions about community dynamics. For instance, neutral theory of biodiversity assumes that individuals are demographically identical regardless of species, and all the variability in a community is driven by demographic stochasticity—random variation in the fates of individuals (e.g., birth, death and dispersal events; Hubbell, 2001). However, neutral models' ability to explain biodiversity patterns in real communities has been challenged (e.g., Brown et al., 2013; Chisholm et al., 2014; Connolly et al., 2014). Somewhat less restrictive, the stochastic community-dynamic theory of Engen and colleagues (Engen & Lande, 1996; Engen et al., 2002; hereafter the 'Engen model') allows for species differences in demographic rates and their fluctuations with environmental conditions. However, this theory still has restrictive assumptions (e.g., all species have equal intraspecific density dependence and temporal variance of fluctuations in population growth rate among species; interspecific interactions are negligible; responses to environmental fluctuations are independent [Engen & Lande, 1996]). How strongly these assumptions are violated, and how robust the inferences made from such models (e.g., Engen et al., 2002; Solbu et al., 2018), has been assessed only for a narrow range of parameter values (Tsai et al., 2022).

Such dimension-reduction approaches have been applied previously to coral reef fish assemblages. Static analyses of patterns of commonness and rarity reveal these communities do not follow species-abundance distributions expected from neutral dynamics (Connolly et al., 2014, 2017). Furthermore, the analysis of temporal dynamics of species-abundance distributions, using the Engen model, suggests that most of the variability in coral fish abundances is due to persistent heterogeneity in demographic characteristics among species, with smaller contribution due to environmental fluctuations (Tsai et al., 2022). However, species differences in the strength of density-dependence has been hypothesized to be an important driver of variation in abundance in other high-diversity assemblages like tropical forests (Comita et al., 2010; Johnson et al., 2012; LaManna et al., 2017; Mangan et al., 2010), and differential sensitivity of species to environmental fluctuations have been widely documented, including for reef fishes (Emslie et al., 2011; Hoey et al., 2016; Pratchett et al., 2011, 2015). Ideally, to draw robust inferences about community structure, we would like to confront community data with models that can account for such heterogeneities and interactions, where they are present (see, e.g., Hui et al., 2015; Ovaskainen, Tikhonov, Norberg, et al., 2017; Warton et al., 2015).

This study aims to evaluate the importance of among-species heterogeneity in demographic rates (particularly the strength of density dependence, and the sensitivity of species' density-independent growth rates to environmental fluctuations), species interactions, and response diversity as drivers of the temporal dynamics of reef fish assemblages on the Great Barrier Reef (GBR), Australia. Specifically, we develop a community dynamics model that is tractable, but that can estimate both species interactions and the variances and covariances of species' response to environmental fluctuations, without strong homogeneity assumptions, while making plausible biological assumptions about how those heterogeneous quantities are distributed among species. We fit this model to reef fish assemblage data, then evaluate the magnitude and importance of species interactions and response diversity as drivers of changes in abundance, and the relative importance of heterogeneity in density-independent and density-dependent demographic parameters in driving persistent variation in abundances among species. Additionally, we test our approach against simulated data, where we know a priori the interspecific interactions and species covariances in environmental fluctuations, to evaluate whether the model can successfully recover the 'true' parameters used to simulate the data, and in particular, to distinguish between covariation in species' abundances that is mediated by species interactions versus covariation mediated by environmental fluctuations. Our findings highlight highly heterogeneous and individualistic dynamics, with species interactions overwhelmingly negligibly small and response diversity relatively high. We also find that the substantial heterogeneity in species' long-term abundances is driven approximately equally by interspecific differences in density-dependent and density-independent components of population growth.

METHODS

Data collection

The GBR's reef fish communities have been surveyed by the Australian Institute of Marine Science' Long-Term Monitoring Program (LTMP) since 1995 (Emslie et al., 2020). Underwater visual surveys were conducted annually on the same 41 reefs (Figure 1) between 1995 and 2005, so here we focus on these reefs for this 11-year period. At each reef, there were three sites on the reef slope, usually on the north-east flank of the reef. Each site contained five permanently marked 50 m transects, approximately parallel to the reef crest between 6 m and 9 m. Observers recorded abundances of 208 species of reef fishes from

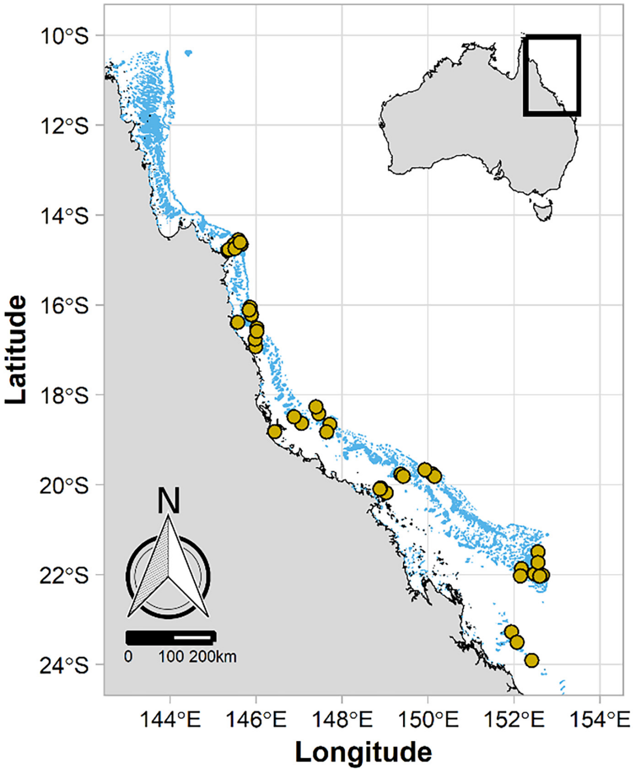

FIGURE 1 Map of the GBR showing the 41 sampled coral reefs in our analysis as yellow points. Mainland Australia and islands are represented in grey and coral reefs and cays are in light blue.

9 families: *Labridae* (including *Scarine* parrotfishes), *Pomacentridae*, *Siganidae*, *Chaetodontidae*, *Acanthuridae*, *Serranidae*, *Lutjanidae*, *Lenthrinidae* and *Zanclidae*. All fish estimated to be at least 1 year old were counted. All families were counted on 50 × 5 m transects, except pomacentrids, which were counted on 50 × 1 m transects, due to their small body sizes and site-attached life habits (see Emslie & Cheal, 2018 for detailed methodology).

The model

Abundance dynamics are assumed to follow the multivariate Gompertz model (Ives et al., 2003). This model has been used previously to model the dynamics of reef fishes (Thibaut et al., 2012; Tsai et al., 2022), and it characterizes the density-dependent dynamics of reef fishes better than models of logistic form, (Thibaut et al., 2012), as it does for many other taxa (Sibly et al., 2005; Thibaut & Connolly, 2020). The model follows:

$$\log\left(\mu_{i,t}\right) = a_i + \sum_{j=1}^{S} b_{i,j}\log\left(\mu_{j,t-1}\right) + e_{i,t} \tag{1}$$

or, in the matrix form:

$$\log\left(\boldsymbol{\mu}_t\right) = \boldsymbol{a} + \boldsymbol{B}\log\left(\boldsymbol{\mu}_{t-1}\right) + \boldsymbol{e}_t \tag{2}$$

where $\log(\boldsymbol{\mu}_t)$ is a vector containing species' estimated log-abundances at time t, $\boldsymbol{\mu}_t = (\mu_{1,t}, \mu_{2,t}, \mu_{3,t}, \ldots, \mu_{i,t})$. $\boldsymbol{a}$ is a vector containing species' estimated intrinsic rates of increase, $\boldsymbol{a} = (a_1, a_2, a_3, \ldots, a_i)$. $\mathbf{B}$ is a species-by-species interaction matrix whose off-diagonal elements, b_{ij}, indicate the effect of the abundance of species j on the per capita population growth rate of species i ($b_{ij} = 0$ for no interaction; $b_{ij} < 0$ for negative effects (e.g. competition); $b_{ij} > 0$ for positive effects (e.g. facilitation)), and whose diagonal elements, b_{ii}, represent the effect of the abundance of species i on its own population growth ($b_{ii} = 1$ for density-independent growth; $0 < b_{ii} < 1$ implies compensatory density-dependence, $b_{ii} < 0$ implies over-compensatory density-dependence). $\mathbf{e_t}$ is a vector of process error for each species, $\mathbf{e_t} = (e_{1,t}, e_{2,t}, e_{3,t}, \ldots, e_{i,t})$, which has a multivariate normal distribution with mean vector $\mathbf{0}$ and covariance matrix $\boldsymbol{\Sigma}$. This represents stochastic fluctuations in the intrinsic growth rate from year-to-year. Our use of fixed $\boldsymbol{a}$, $\mathbf{B}$, and $\boldsymbol{\Sigma}$ implies stationarity of the stochastic community-dynamic process; this assumption is consistent with the lack of clear abundance trends in the absolute or relative abundances of species (Figure S1).

We accounted for observation error by modelling the observed fish counts as Poisson-distributed:

$$y_{i,t} \sim \text{Poisson}\left(\mu_{i,t}\right), \tag{3}$$

where $y_{i,t}$ is the observed count of fish of species i at time t, $\mu_{i,t}$ is the (unobserved) abundance of species i at time t from Equation 1. Although we pooled fish counts at the reef scale to reduce the effect of overdispersion (i.e., extra-Poisson variation due to observation error), to the extent that such overdispersion is present in the data, we would expect it to be subsumed within the environmental covariance matrix, yielding some upward bias in the estimated species-specific variances due to environmental stochasticity.

Due to the use of different transect sizes to count Pomacentrids (50 × 1 m transect) and non-Pomacentrids (50 × 5 m transect), we modelled the Pomacentrid counts as:

$$y_{(\text{pom})\ i,t} \sim \text{Poisson}\left(\mu_{(\text{pom})\ i,t} / 5\right), \tag{4}$$

where $y_{(\text{pom})i,t}$ is the observed number of fish of the pomacentrid species i at time t, $\mu_{(\text{pom})i,t}$ is the mean abundance of the pomacentrid species i at time t per 250 m^2 (the area of the larger transect). The division by 5 accounts for the fact that pomacentrids were counted on transects that were a fifth the size of the normal transects. This obviates the need to exclude information by subsampling fishes counted on the larger transects (e.g., as in Connolly et al., 2005, 2009, 2017; Tsai et al., 2022).

Reducing dimensionality of the model

As species richness increases, the number of parameters in the interaction matrix **B** and the covariance matrix **Σ** increase quadratically. The interaction matrix **B** has S^2 free parameters, where S is the number of species. The covariance matrix **Σ** has $S(S+1)/2$ free parameters. Estimating that many parameters in species-rich assemblages would require long time-series data, which generally do not exist for community time series, particularly in marine systems.

To reduce the dimensionality of the covariance matrix, **Σ**, we used a factor analysis approach, similar to two previous analyses of high-diversity time series (Ovaskainen, Tikhonov, Dunson, et al., 2017; Sandal et al., 2022). This approach assumes that the observed data can be explained by a small number of latent variables, D ($D << S$), while still explaining the covariance of the observed data (Hui et al., 2015; Ovaskainen, Tikhonov, Norberg, et al., 2017; Warton et al., 2015). The logic is that environmentally-mediated fluctuations in abundances should be driven by a common set of environmental drivers (e.g., climatic variables, or other biological variables such as benthic composition), which in general may not be known or measured. Therefore, the variance–covariance matrix was estimated as

$$\boldsymbol{\Sigma} = \boldsymbol{\Lambda\Phi\Lambda}' + \Psi \tag{5}$$

where **Λ** is an $S \times D$ matrix of factor loadings, which can be interpreted as the response of species to the unknown drivers (i.e., latent variables). $\boldsymbol{\Phi}$ is the variance–covariance matrix of the latent variables and it is a $D \times D$ matrix (see Appendix S1). The covariance matrix $\boldsymbol{\Psi}$ is a diagonal matrix explaining the remaining variation (residual error) not captured by the factor loadings and the latent factors. The correlation in species responses to environmental fluctuations, $\boldsymbol{P}$, can be calculated from the variance–covariance matrix **Σ** as $P_{\mathrm{ij}} = \boldsymbol{\Sigma}_{ij} / \sqrt{\boldsymbol{\Sigma}_{ii}\boldsymbol{\Sigma}_{jj}}$. This changes the number of free parameters in the covariance matrix $(\boldsymbol{\Sigma = \Lambda\Phi\Lambda' + \Psi})$ from $S(S+1)/2$ to $D(S+(1-D)/2)$. Provided that $D<<S$, this substantially reduces the number of parameters required to calibrate the covariance matrix **Σ** (See Appendix S1 for further details and Figure 2 for prior choices and model structure).

With respect to the interaction matrix, **B**, we seek an approach in which most interactions will be weak or negligible, but which allows some interactions to be strong, and potentially asymmetric. To do this, we implemented the 'regularised horseshoe prior' (Piironen & Vehtari, 2017) as a prior distribution for our interspecific interaction terms. This distribution has high density around 0, but with heavy tails that allow some terms to be regularized far from zero (Figure S2). Here we apply the regularized horseshoe prior to estimate a full interaction matrix. See appendix S2 for further justification for our approach, and details about this prior and its implementation.

Because the main diagonal elements of the interaction matrix **B** represent effects of competition within species, which may come from a different distribution than the between-species effects, we estimate those terms using a Gaussian prior (see, e.g., Mutshinda et al., 2009; Bunin, 2017) (Figure 2).

Model fitting to data

To estimate the relative importance of interspecific interactions, intraspecific density dependence, and response diversity, we fitted our model (Figure 2) to the fish counts pooled at the reef scale. We also fitted a version with reef level random effects (see Appendix S3 and Figure S3).

We used the software program Stan (Stan Development Team, 2023), which uses Hamiltonian Monte Carlo (HMC) sampling, because this approach provides a greater range of tools to detect potential model pathologies that are not available for other MCMC algorithms, such as Gibbs samplers (Betancourt, 2016; Monnahan et al., 2017).

From the 208 species in the LTMP, we generated data subsets with 20 and 40 species, prioritizing species with the smallest proportion of zero counts observed across reefs and time (Table S1). Collectively, these represent 52.49% and 64.93% of the total number of observed individuals in the data, respectively. All counts were analysed at species level except for *Ctenochaetus* species, whose counts were grouped at the genus level and analysed as a pseudo-species, *Ctenochaetus spp*, due to the resemblance between the two occurring species in the GBR, *C. binotatus* and *C. striatus*. For each dataset we ran 4 chains, each with 10,000 iterations, 5000 iterations as warm up and 5000 as sampling. This left 20,000 samples in the posterior distribution of each parameter. We used weakly informative priors and prior predictive checks (see Figure 2 and Appendix S4), to ensure that posterior estimates were informed by the data. Model convergence was monitored by examining posterior chains and distributions, running 4 chains with different randomly chosen initial values, checking that the potential scale reduction factor (R-hat) was close to 1 for all parameters, and checking that the effective sample sizes were large (Figure S4). Model fit was assessed by posterior predictive checks (Figure S4). Model predictive accuracy and model selection were evaluated by leave one out cross validation (LOO-CV) (Vehtari et al., 2017), using the R package *loo* (Vehtari et al., 2023; Appendix S5). Comparing parameter estimates for the fits with 20 versus 40 species allowed us to assess the extent to which the use of only a subset of a community could bias those estimates.

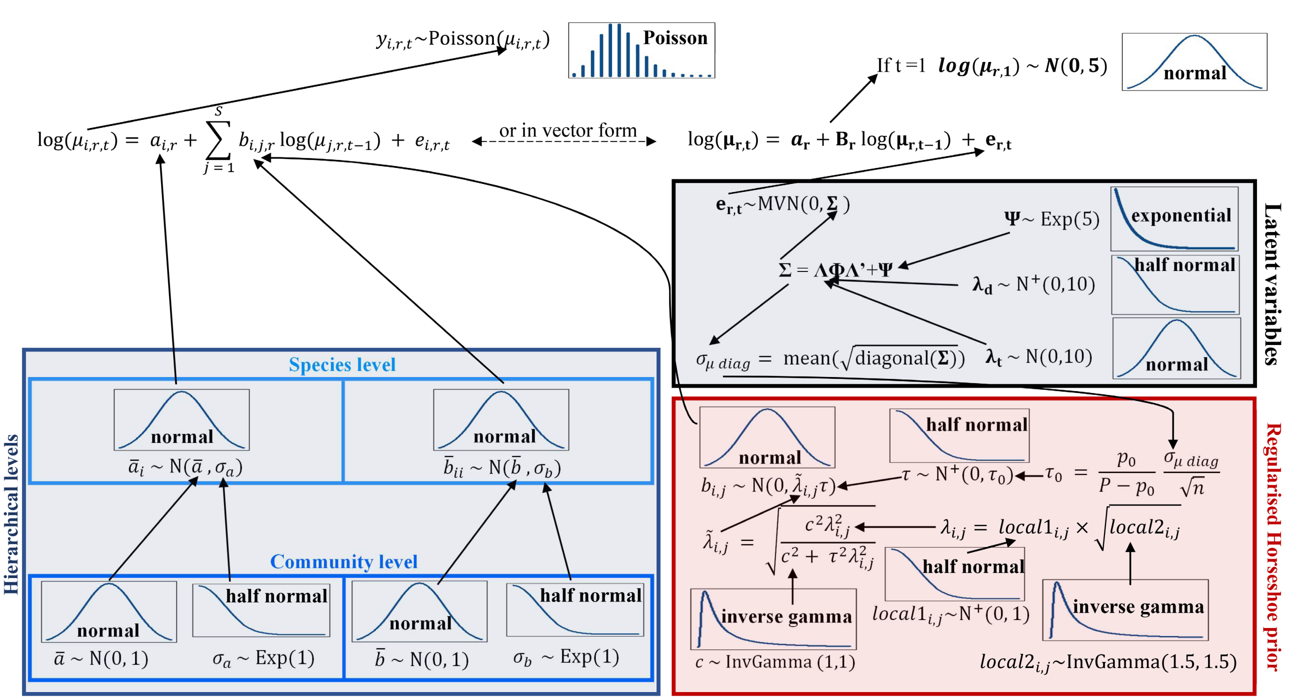

FIGURE 2 Schematic of the Poisson multivariate autoregressive Gompertz model. The blue box shows the random effects for the intrinsic growth rate and the within-species density dependence. There are two levels: the metacommunity parameters, and the parameters for each species. The red box shows the regularized horseshoe prior used to estimate the off-diagonal elements of the interaction matrix (between species density dependence). The black box shows the factor analysis component used to estimate the variance–covariance matrix. Note that λ_d stands for the diagonal elements of the factor loadings matrix $\boldsymbol{\Lambda}$, whereas λ_t stands for the lower triangular elements of the factor loadings matrix $\boldsymbol{\Lambda}$. Normal distributions are denoted with the standard deviation formulation (e.g., $N(0, 2)$ indicates a normal distribution with mean 0 and standard deviation of 2, not a variance of 2).

Simulation study

To assess the robustness of the parameter estimates and inferences produced in our analyses, we fit our models to simulated data with known parameter values. Specifically, we wished to verify that our approach could accurately estimate the off-diagonals of the interaction matrix **B** and the covariance matrix $\boldsymbol{\Sigma}$, and thereby successfully distinguish between covariances in abundance produced by species interactions versus correlated responses to environmental fluctuations. In the baseline simulation, we set interspecific interactions and environmental covariances to zero to determine whether model fits would erroneously identify non-zero interactions or covariances. In other simulations, we simulated non-zero environmental covariances and set the interspecific interactions terms to zero; we simulated communities where a subset of interspecific interactions was non-zero (this subset was small, ca. 10% of interactions, to allow interaction terms to be moderately large without compromising coexistence), but there were no environmental covariances; and we simulated communities with both non-zero environmental covariances and with some non-zero interspecific interactions. See Appendix S6 for further details.

RESULTS

Model fit to LTMP data

Model fits indicated very weak interspecific interactions, relative to conspecific density-dependence, but high response diversity. For interspecific interactions around 97% of estimated posterior means had magnitudes between −0.01 and 0.01, more than an order of magnitude smaller than the mean intraspecific density-dependence (Figure 3). In contrast, intraspecific density dependence was detected in all species, with mean b_{ii}<1 and centred around 0.86 (i.e., the mean strength of density-dependence 1 − 0.86 = 0.14: Figure 3).

In contrast to species interactions, species pairs exhibited a broad range of correlations in their responses to environmental fluctuations, with most weakly to moderately positively correlated, indicating reasonably strong response diversity: most of the posterior mean estimates for the correlation values were between 0 and 0.5 (Figure 4). The model with only 2 latent variables had the highest support. Model support decreased with increasing number of latent variables (Table S2) and the models with 10 and 12 latent variables did not converge. Model diagnostics indicated no convergence issues for the models with 2, 4, 6 and 8 latent variables. Thus, we

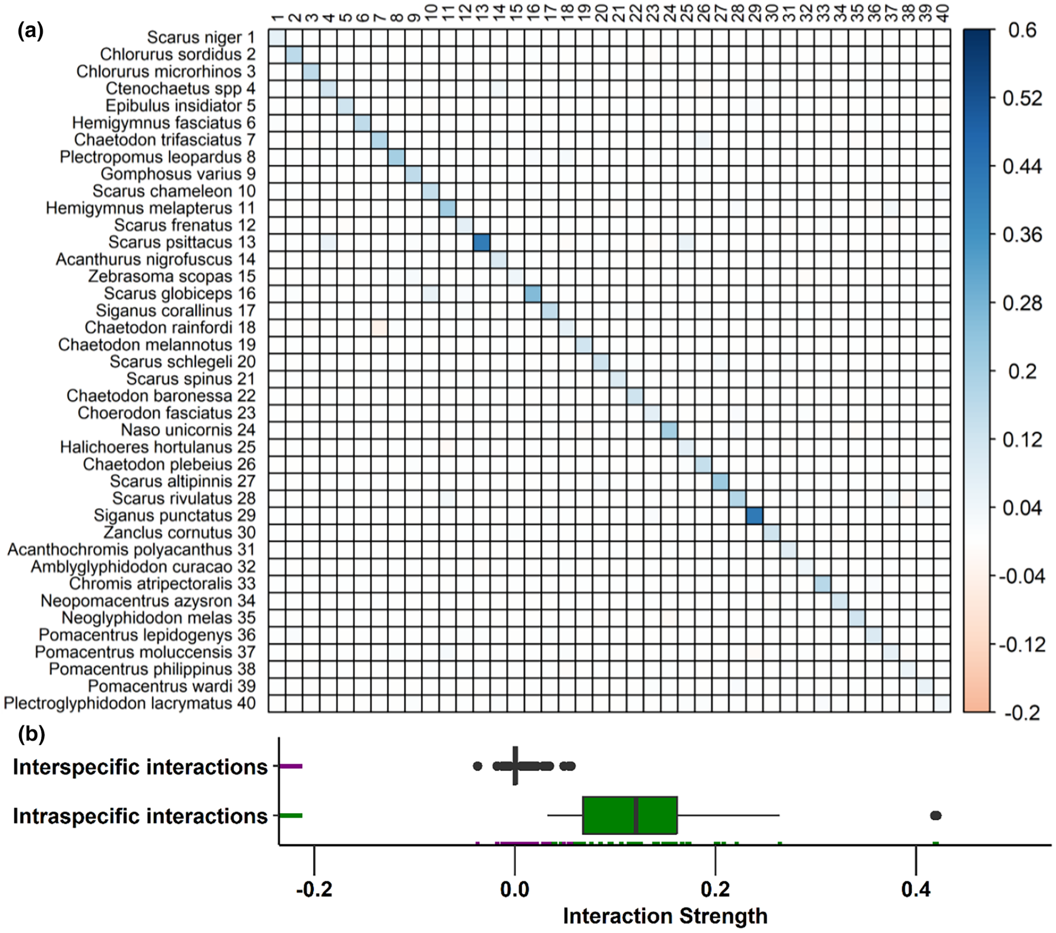

FIGURE 3 (a) Mean posterior estimates for the elements of the interaction matrix, B. (b) Distribution of posterior mean estimates for the elements of the interaction matrix. The off-diagonal elements are shown in the top boxplot (NB: b_{ij}=0 for no interaction; b_{ij}<0 for negative effects (e.g. competition); b_{ij}>0 for positive effects (e.g. facilitation)).The diagonal elements are shown in the bottom, green boxplot (NB: the diagonal elements are presented here as $1-b_{ii}$ [i.e., 1 minus the diagonal element], such that zero implies density-independent growth, and positive values imply negative density-dependence). The marks displayed along the horizontal axis represent each of the estimated posterior means for the diagonal elements in green and off diagonal elements in purple.

selected the model with two latent variables for our analysis. Overall, however, the number of latent variables had a small effect on the estimated interspecific correlations, with estimates remaining similar as the number of latent variables increased from 2 to 12 (Figure S5).

Overall, GBR fish assemblages exhibited similar magnitudes of variation in their species' mean intrinsic growth rates (CV_a=0.58), intraspecific density dependence (CV_b=0.64) and sensitivity to environmental fluctuations (CV_σ=0.59; Figure 5). The intrinsic growth rate parameter, *a*, varied among species but was consistently above zero (indicating capacity for recovery from low population density, i.e., persistence) with mean values from 0.03 to 0.5 (Figure 5a,b). Most species had mean intraspecific values ($1-b_{ii}$) below 0.25 and above 0, with only 3 species having intraspecific density dependence values above 0.25 (Figure 5c,d), indicating weakly compensatory density-dependence. The standard deviations of the temporal variation in the density-independent growth rate (i.e., the square root of the diagonal of $\mathbf{\Sigma}$) was right-skewed, with most species' mean values close to the overall metacommunity mean value 0.54, and species-specific posterior means ranging from 0.19 to 1.45 (Figure 5e,f).

We obtained consistent results regardless of whether models were fitted with or without reef-level random effects (Figure S6). Surprisingly, we found evidence of limited variability among reefs in intrinsic growth rates or intraspecific density dependence, for any species (Figure 6, Appendix S3) with overlapping posterior distributions. Similarly, results are robust to the number of species included in the analysis. Figure S7 compares parameter estimates from the model fits to 20 species and 40 species, for those species that appeared in both analyses: this shows that the model parameters were extremely similar in the two analyses (Figure S7a,c,d). The interspecific species interaction parameters did appear to experience somewhat stronger shrinkage towards zero for

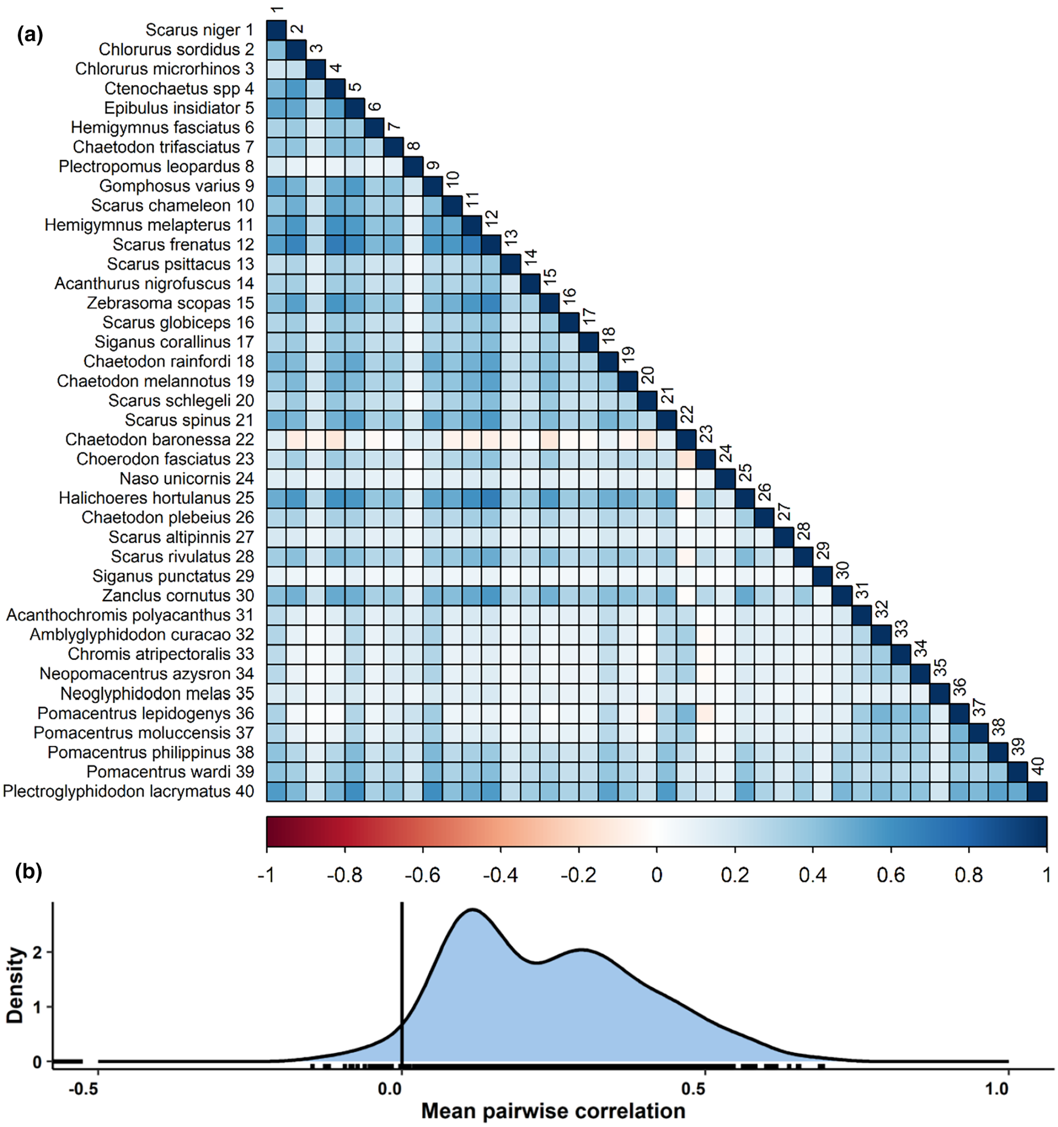

FIGURE 4 (a) Correlation plot showing the diagonal and the lower triangular elements of the correlation matrix, calculated from the variance–covariance matrix Σ as $P_{ij} = \Sigma_{ij} / \sqrt{\Sigma_{ii}\Sigma_{jj}}$. Each square shows the mean correlation estimate for a pair of species. (b) Density plot showing the distribution of posterior mean correlations. The black marks displayed along the horizontal axis represent each of the estimated posterior correlation means.

the model with a higher number of species (Figure S7b). However, most interactions were close to 0 in both analyses, and the few values farther away from zero did not show this shrinkage, indicating that the regularized horseshoe prior successfully allows nonzero interactions to escape the shrinkage to zero (see the following section 'Simulation study').

Simulation study

The simulation study indicated that the models successfully distinguished between zero and non-zero environmental correlations and interactions terms. Specifically, where these terms were zero, posterior means tended to be close to zero and had credible intervals encompassing zero. Conversely, when true parameter values were far from zero, posterior means and credible intervals correctly captured the direction and approximate magnitude of these effects, even when there were non-zero effects in off-diagonals of both the environmental correlation matrix and the interaction matrix (see Appendix S7 for detailed results).

DISCUSSION

We found that coral reef fish assemblages on the GBR exhibit a classically Gleasonian community structure (Gleason, 1939), with highly heterogenous responses to environmental fluctuations and no evidence of interspecific interactions playing a strong role in the dynamics of species relative abundances. Conversely, these

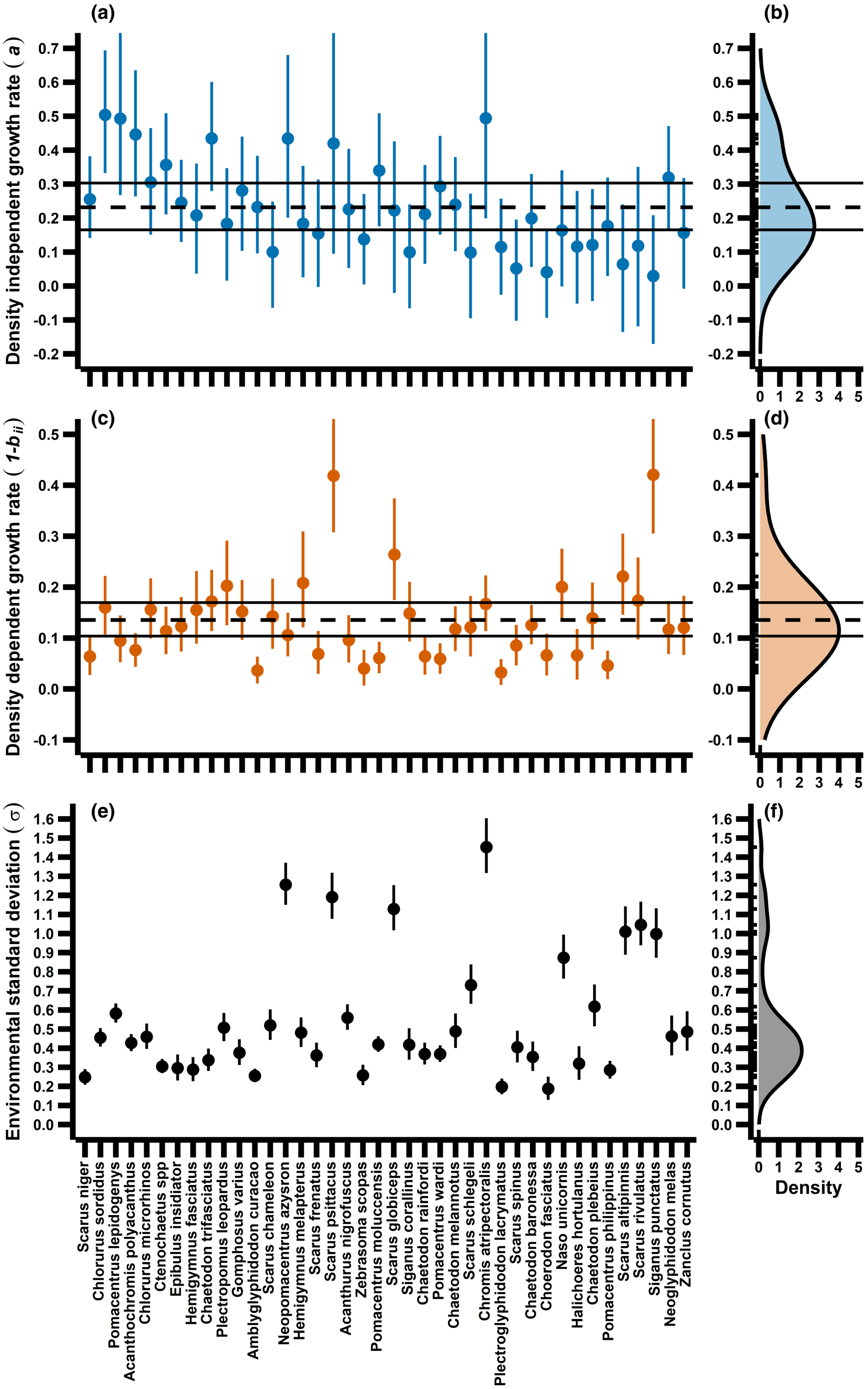

FIGURE 5 Interspecific heterogeneity in population-dynamic parameters. Panel (a) shows in blue each species posterior estimates for the density independent growth rate (i.e., intrinsic growth rate). Each dot represents a species posterior mean and the vertical lines represent the 95% credible intervals. Panel (b) shows the distribution across species of the posterior mean estimates from panel (a). Each of the black lines displayed along the vertical axis in panel (b) correspond to each species posterior mean density independent growth rate (i.e., the dots in panel (a)). The dashed horizontal line in panels (a) and (b) show the higher hierarchical metacommunity mean (see Figure 2 and Equations 1–3) and the two horizontal solid lines represent the upper and lower 95% credible intervals for that estimate. The same is displayed in orange for the species density dependent growth rate (i.e., intraspecific density dependence) estimates in panels (c) and (d), and black for the species environmental standard deviation (i.e., standard deviation in temporal abundance) estimates in panels (e) and (f). The species names on the horizontal axis for panels (a), (c) and (e), are sorted from the species with the lowest proportion of zero counts across reefs and years on the left, *Scarus niger*, to the species with the highest proportion of zero counts on the right, *Zanclus cornutus*.

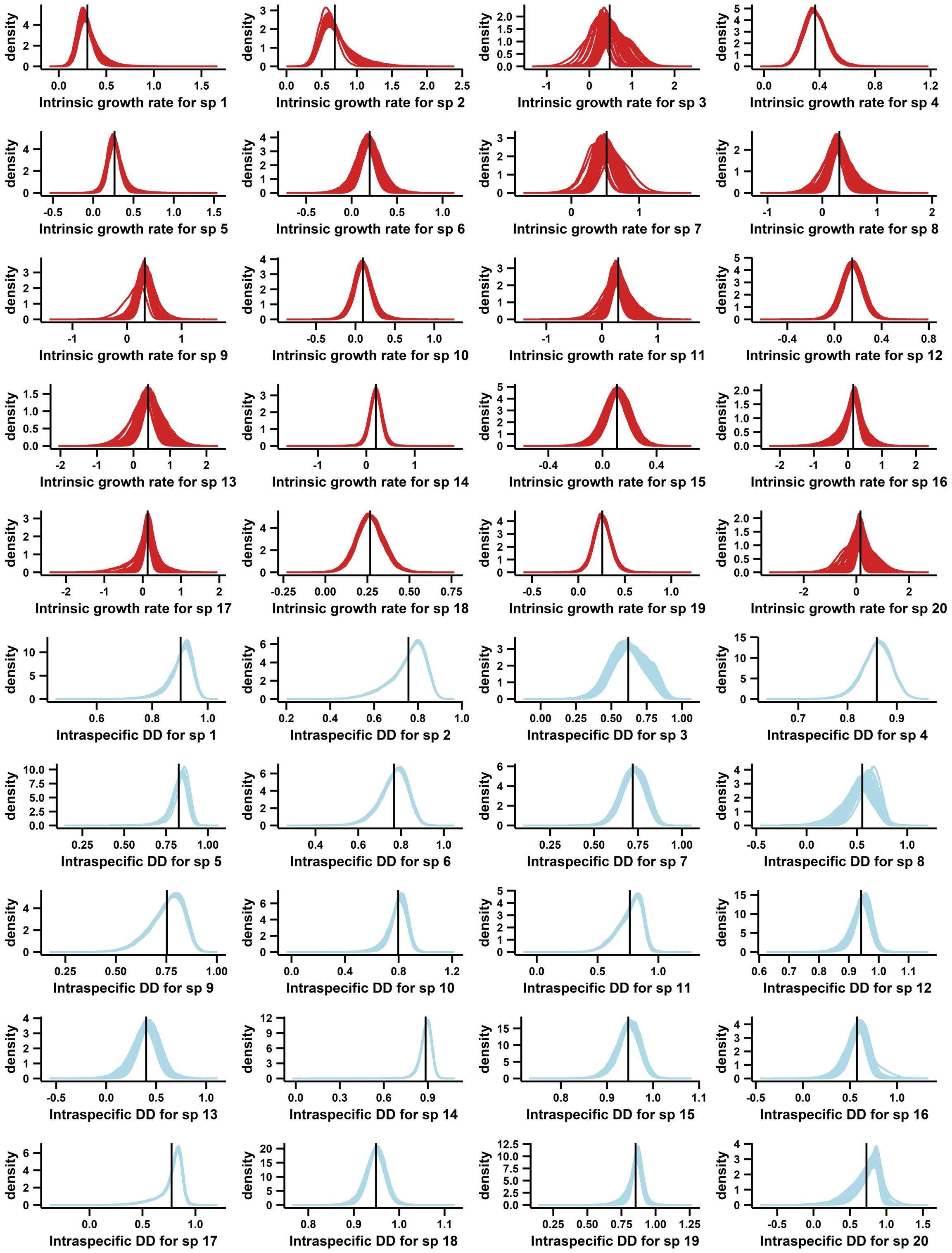

FIGURE 6 Each of the red panels represent a species posterior distribution for the density-independent growth rate parameter across all reefs (41 reefs). Within a panel, one red line represents the posterior distribution of the intrinsic growth rate for one reef (i.e., 41 lines). The black vertical line shows the mean intrinsic growth rate at the species level (mean intrinsic growth rate parameter for the level above). The same is represented in the light blue panels for the intraspecific density-dependent (DD) growth rate parameter.

assemblages exhibited strong evidence of intraspecific density regulation, with detectable conspecific density-dependence for all species. There was, moreover, a high degree (i.e., CV~0.5 or larger) of demographic heterogeneity among species in density-independent and density-dependent components of population growth, as well as in their sensitivity to environmental fluctuations (i.e., the diagonal terms in the variance–covariance matrix Σ). This suggests that species differences in both deterministic (i.e., persistent through time), and stochastic (i.e., responses to environmental fluctuations) components structure patterns of commonness and rarity in fish communities, contrary to biodiversity theory based on approximate ecological equivalence, such as the lottery hypothesis (Sale, 1977, 1978), and Neutral Theory of Biodiversity (Hubbell, 2001). It also suggests more complex interspecific heterogeneity than assumed in at least some tractable alternative theories of biodiversity (Engen & Lande, 1996; Kalyuzhny et al., 2015). Conversely, among-reef variability in both the intraspecific density dependence and intrinsic growth rates was very small, relative to the estimated among-species variation, suggesting that life-history differences among species are more important determinants of demographic variation than geographical variation in environmental conditions.

Our study also demonstrated successful fit of a multivariate community-dynamics model to time series data and accurate estimation of interspecific interactions and covariances in responses to environmental fluctuations even over a decadal time frame (ca. 10 years). We achieved this by leveraging the high degree of spatial replication, along with the dimension-reduction techniques of the regularized horseshoe prior and a latent environmental variable approach. In particular, using the regularized horseshoe prior, in lieu of a discrete mixture modelling approach (Mutshinda et al., 2009), allowed us to use Hamiltonian Monte Carlo and thereby exploit the more extensive model diagnostics available for such models, relative to alternatives such as Gibbs samplers, for which model pathologies can occur without tools to identify them (Betancourt, 2016; Monnahan et al., 2017). These diagnostics, along with our simulation study, indicated that our approach yields robust estimates of community dynamics parameters for species-rich communities, and can do so even for relatively short time series when sufficient replication is available.

Our finding that interspecific interactions were negligible seems at odds with classic and recent studies documenting strong interspecific interactions in nature (Connell, 1961; Krebs et al., 2017; Paine, 1966; Stenseth et al., 1997). In reef fish communities in particular, interspecific interactions have been considered to play a major role in structuring reef fish communities based on both field experiments (Jones, 2005; Robertson, 1996; Shulman, 1985) and observational studies (Ebersole, 1977). However, other reef fish studies have argued that interspecific interactions play a more limited role (Choat & Bellwood, 1985; Mumby & Wabnitz, 2002; Robertson & Sheldon, 1979). A feature of these past reef fish studies is that they have focused on small scales, where particular interactions are frequent, and on response variables whose changes can be measured readily at such scales, such as home range size or location (Jones, 2005). However, such effects may be restricted in time or space, and thus have effects that do not scale up to the population level. For instance, strong heterospecific aggression does not necessarily translate into competitive release at the population level, when dominant competitors are removed (Blowes et al., 2017). Similarly, highly diffuse interactions may likewise lead to negligible population-dynamic effects (e.g., the piscivore in our data, *Plectropomus leopardus* is a generalist feeder that consumes both demersal and water-column species across numerous fish families: St John et al., 2001).

In contrast to interspecific interactions, we found strong evidence for compensatory intraspecific density dependence in fish assemblages, with mean values more than an order of magnitude larger than those estimated for interspecific interactions, and similar in magnitude as earlier estimates for insects, fishes, birds and mammals from analysis of single-population time-series (Thibaut & Connolly, 2020; Figure S8). This finding of much stronger intraspecific than interspecific density dependence is consistent with a recent meta-analysis of pairwise interactions in plant studies (Adler et al., 2018). Similar findings also have been obtained from time series analysis of temperate vertebrate and invertebrate communities (Mutshinda et al., 2009; Ovaskainen, Tikhonov, Dunson, et al., 2017; Sandal et al., 2022). However, it is important to note that our study, like those cited above, focuses on interactions within a particular taxonomic group. Thus, the phenomenology of strong intraspecific against weak interspecific interactions could emerge from the action of species-specific natural enemies from other taxonomic groups, such as parasites and viruses, whose effects could become stronger as species become more abundant. Additionally, our analysis characterizes abundance as a function of abundances in the previous year. Although analysis of individual time series across a broad range of taxa has suggested that lagged density effects are not widespread (Thibaut & Connolly, 2020), the presence of such lagged effects, particularly for species whose abundances fluctuate substantially over short time scales (such that abundance in the previous year is relatively uncorrelated with abundance at the most relevant time lag), could potentially lead to underestimates of the relevant species' density-dependent effects (Thibaut & Connolly, 2020; Ziebarth et al., 2010).

Our finding of large (CV>0.5) and comparable degrees of heterogeneity in temporal average density-independent growth rate (a_i), intraspecific density-dependence (b_{ii}), and sensitivity to environmental fluctuations (σ_{ii}), and substantial variation in pairwise correlations in environmental responses is inconsistent both with the demographic equivalence assumed by neutral theory of biodiversity (Hubbell, 2001), and with the Engen model (Engen et al., 2002; Engen & Lande, 1996), which assumes that interspecific heterogeneity is confined to the mean intrinsic growth rate term. However, the partitioning of variance in species abundances between deterministic and stochastic component, the principal application of this latter theory (Bellier et al., 2022; Engen et al., 2002, 2011; Solbu et al., 2018), appears to be fairly robust, at least for our system, as calculating these component using our full fitted model yields similar variance proportions to a previous application of the Engen model (Tsai et al., 2022; Appendix S8, Figure S9).

There has been considerable debate about the extent to which variation in the strength of conspecific negative density-dependence (CNDD) can explain variances in abundance in tropical forest assemblages. The CNDD has been reported to be stronger for rare species than for common species (Comita et al., 2010; Johnson et al., 2012; LaManna et al., 2017; LaManna et al., 2021; Mangan et al., 2010; but see Detto et al., 2019; Hülsmann et al., 2021), independent of abundance (Chen et al., 2019; Fricke & Wright, 2017), or stronger for common than rare species (Zhu et al., 2015). In our data, more abundant species tend to experience less density-dependence than rarer species, a pattern that remains even when accounting for potential effects of body size (Figure S10; see also Rovere & Fox, 2019; Yenni et al., 2017 for other examples using population time series). However, the relationship is somewhat weak, indicating that the variability in species intraspecific density dependence likely underlies a relatively small proportion of the abundance variation observed in this system.

In contrast to CNDD and species interactions, patterns of covariation in species' responses to environmental fluctuations have received less attention, either theoretically or in previous analyses of community time series (Mutshinda et al., 2009; Ovaskainen, Tikhonov, Dunson, et al., 2017; Sandal et al., 2022). Our finding that a relatively small number of latent variables (as few as two, Figure S5) captures the overall pattern of variances and covariances in response to environmental fluctuations suggests that a relatively small set of common drivers (or multiple drivers whose correlated dynamics produce relatively few important axes of variation) explains much of the environmentally-induced variation in population fluctuations in this system.

Additionally, the weak to moderate correlations in environmental responses indicate a relatively high degree of response diversity (i.e., asynchrony in population fluctuations) in this system, and thus a reasonably strong portfolio effect (Elmqvist et al., 2003; Thibaut & Connolly, 2013; Tilman et al., 1998). Because interspecific interactions were negligible, this heterogeneity in species responses to environmental fluctuations is the overwhelming driver of community asynchrony for fishes on the GBR. However, a more detailed look at our results does reveal that environmentally-mediated correlations between species from the same trophic groups (Table S1) are slightly higher, on average, than those between species from different functional groups (Figure S11a,b). Similarly, more closely related species have slightly more positive environmental correlations than distantly related species (Figure S11c,d, Figure S12 and Appendix S9). Nonetheless, these differences are small and explain little of the overall variation in the structure of the environmental correlation matrix, suggesting that the factors driving these correlations are highly idiosyncratic and not strongly conserved phylogenetically, nor dependent on the nature of a species' trophic role.

Species interactions have been hypothesized to play strong roles in the ecology and evolution of communities, shaping phenomena from equatorward range limits (Darwin, 1964; Paquette et al., 2021), to the latitudinal diversity gradient (Dobzhansky, 1950; Schemske et al., 2009; Zvereva & Kozlov, 2021), to macroevolutionary trends in taxonomic diversity, and ecosystem function (Bush & Payne, 2021; Vermeij, 2019). However, the curse of dimensionality has complicated assessing the role of such interactions at the whole-assemblage level in species-rich ecological communities. Our approach offers a way to confront community-dynamics models with time series from such high-dimensional systems, to rigorously explore the robustness of the models' performance, and to infer the relative importance of such interactions, alongside other factors such as response diversity and other sources of demographic heterogeneity among species. For coral reef fishes, population regulation is driven overwhelmingly by intraspecific density-dependence, whereas interspecific interactions have negligible effects on population-level dynamics, suggesting a high degree of niche differentiation in this assemblage. We hope our work prompts similar analyses in other systems, to more comprehensively assess the factors that drive the dynamics of species abundances in high-diversity systems like coral reefs.

AUTHOR CONTRIBUTIONS

ARM and SRC conceived this study. MJE supervised and provided the LTMP data. ARM performed the modelling work and analysed the model output with help of SRC. ARM and SRC wrote the first draft of the manuscript and MJE contributed substantially to subsequent drafts.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14424.

DATA AVAILABILITY STATEMENT

All the data analysed in this study, as well as the code used to run the analyses are available on Figshare (DOI: https://doi.org/10.6084/m9.figshare.24961575.v1). The simulation code and data are also available on Figshare (DOI: https://doi.org/10.6084/m9.figshare.24962385.v1). For further inquiries about the LTMP data contact Michael Emslie at m.emslie@aims.gov.au.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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