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Environmental Gradients Linked to Human Impacts, Not Species Richness, Drive Regional Variation in Community Stability in Coral Reef Fishes

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ABSTRACT

The stabilising effect of biodiversity on aggregate community properties is well-established experimentally, but its importance in naturally assembled communities at larger scales requires considering its covariation with other biotic and abiotic factors. Here, we examine the diversity–stability relationship in a 27-year coral reef fish time series at 39 reefs spanning 10° latitude on Australia's Great Barrier Reef. We find that an apparent relationship between species richness and synchrony of population fluctuations is driven by these two variables' covariation with proximity to coastal influences. Additionally, coral cover volatility destabilises fish assemblages by increasing average population variability but not synchrony, an effect mediated by changes in the intensity of density regulation in the fish community. Our findings indicate that these two environmental factors, both of which are strongly influenced by anthropogenic activity, impact community stability more than diversity does, but by distinct pathways reflecting different underlying community-dynamic processes.

1 | Introduction

Diversity can impact a range of forms of community stability, including resilience, resistance, persistence and robustness (Donohue et al. 2013, 2016). In recent decades, attention has focused particularly on how diversity can mitigate the temporal variability of aggregate community properties (typically measured as the coefficient of variation in total community abundance, with 'community stability' being the inverse of community variability) (Gross et al. 2014; Tilman 1999; Xu et al. 2021). Experimental studies generally indicate that species richness reduces community variability (i.e., there is a positive diversity–stability relationship [DSR]) (Campbell, Murphy, and Romanuk 2011; Gross et al. 2014; Xu et al. 2021). This phenomenon is commonly attributed to the 'portfolio effect', wherein diversity confers stability due to partial averaging-out of individual species fluctuations (Schindler, Armstrong, and Reed 2015; Thibaut and Connolly 2013; Zhao et al. 2022). The consensus that species richness generally reduces temporal variation in total community abundance, the

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concept of stability on which we focus here, has spurred advocacy for protection of diversity to ensure stability in provisioning of ecosystem goods and services (Cardinale et al. 2012; Pettersen et al. 2022).

In contrast to experiments, investigations of DSRs along natural diversity gradients have yielded less consistent outcomes (Houlahan et al. 2018; van der Plas 2019; Valencia et al. 2020; Wisnoski et al. 2023). While positive DSRs are common, naturally assembled communities often exhibit non-significant DSRs (Houlahan et al. 2018; van der Plas 2019), and a noteworthy minority of DSRs may be inverted (Houlahan et al. 2018; Tredennick, Adler, and Adler 2017; Wisnoski et al. 2023). Evidence for positive DSRs along natural richness gradients is particularly sparse for marine systems. In a recent meta-analysis of 73 studies along richness gradients (Xu et al. 2021), only seven were aquatic, of which three were marine (excluding brackish rock pools). Of these marine studies, one focused on spatial rather than temporal variability (Mouillot, George-Nascimento, and Poulin 2005). The remaining two produced divergent results; one reported a positive DSR (Lamy et al. 2020), and the other a negative DSR (Valdivia and Molis 2009). Within marine systems, studies often concentrate on the mesoscale (~ hundreds of km^2 or less; see, e.g., datasets in Wisnoski et al. 2023). For larger-scale studies, researchers have tended to focus on stability in species composition, or short-term proxies for stability in community abundance (Mellin et al. 2016, 2019; Yan et al. 2023; Yeager, Gouhier, and Hughes 2020), rather than stability of community abundance itself.

Theoretically, community stability depends not only on asynchrony of population fluctuations but also on the average temporal variability of a community's constituent populations, with the average being weighted by relative abundance (hereafter, 'average population variability') (Loreau 2010; Thibaut and Connolly 2013). While synchrony tends to decrease with increased diversity, average population variability may vary positively or negatively with diversity (Thibaut and Connolly 2013; Xu et al. 2021). Consequently, DSRs can be positive or negative, depending on whether and how diversity covaries with evenness in abundance, species interaction strengths and species' responses to environmental fluctuations (Loreau and de Mazancourt 2008, 2013; Thibaut and Connolly 2013; Tredennick, Adler, and Adler 2017). In natural systems, diversity often covaries with environmental gradients that may independently influence community stability, such as habitat degradation (Blüthgen et al. 2016), habitat stability (Lamy et al. 2020) and precipitation variability (García-Palacios et al. 2018; Hallett et al. 2014; Valencia et al. 2020).

From a process-oriented perspective, community stability depends on density-dependent interactions and stochastic variation in species' population growth rates (Hughes and Roughgarden 2000; Loreau and de Mazancourt 2013). Stochastic fluctuations in species' population growth rates can increase average population variability; however, if those growth rate fluctuations are not too positively correlated among species, then they can promote stability via reduced interspecific synchrony (de Mazancourt et al. 2013; Thibaut, Connolly, and Sweatman 2012; Tredennick et al. 2017). Similarly, compensatory interactions and density-dependent feedbacks can promote asynchronous dynamics: a challenging year for one competitor may boost the per-capita population growth rate of the other via competitive release, enhancing stability (Hughes and Roughgarden 2000; Ives and Hughes 2002). However, process-oriented approaches face limitations in species-rich assemblages, because the number of parameters needed to estimate interaction terms and environmental covariances increases quadratically with species richness. To better link statistical components of stability—synchrony and population variability—to community-dynamic processes, tractable methods are needed for quantifying compensatory interactions and species' differential responses to stochastic fluctuations.

Here, we test for a positive DSR in species-rich coral reef fish assemblages, using a 27-year time series at 39 reefs on the Great Barrier Reef, spanning 10° latitude, a cross-shelf gradient in exposure to human-influenced coastal processes, and substantial among-reef variation in the frequency and intensity of episodic disturbances. We evaluate the relative importance of community stability's constituent components, species synchrony and average population variability, as proximate drivers of variation in community stability, and we determine whether and how those stability components vary with species richness, and with environmental variables known to affect reef fish community structure and dynamics. Moreover, to better understand the relationships that these analyses reveal in the context of community-dynamic processes, we consider how community stability components covary with other community properties. Specifically, we consider evenness in abundance, and two parameters derived from a theoretical model of community dynamics that can be tractably confronted with species-rich community time series (Engen et al. 2002): the relative importance of stochastic fluctuations in population growth rates and the aggregate strength of density regulation in the community.

2 | Materials and Methods

2.1 | Long-Term Community and Environmental Data on Coral Reefs

We analysed data from the Australian Institute of Marine Science's Long-Term Monitoring Program (LTMP) on the Great Barrier Reef, spanning 1995 to 2021 (Figure 1a). Of 41 reefs surveyed annually from 1995 to 2005, 39 were subsequently surveyed every other year until 2021, yielding 19 years of observations spanning 27 years on each reef. Surveys encompassed three sites on the reef slope of each reef at 6–9 m depth. Five permanent 5 m-by-50 m marked transects at each reef site were used for censusing larger, noncryptic fishes, while damselfishes and other smaller fishes were surveyed on 1 m-by-50 m sections of the same transects. In total, nine fish families (Pomacentridae, Acanthuridae, Serranidae, Lutjanidae, Chaetodontidae, Labridae, Lethrinidae, Siganidae and Zanclidae), excluding cryptic species (which represent 0%–3% of the species in these families, and cannot be counted accurately using visual transects: Brandl et al. 2018), were surveyed, along with benthic cover composition. See Sweatman et al. (2005) and Emslie et al. (2020) for further methodological details.

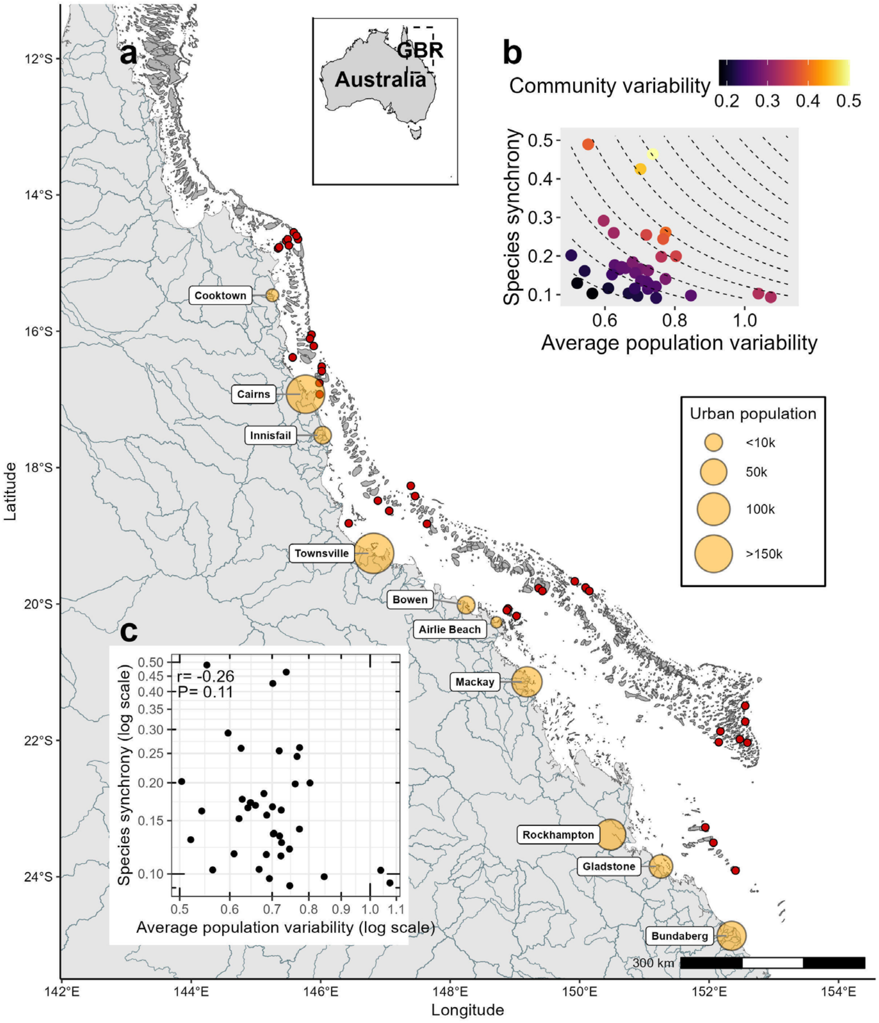

FIGURE 1 | (a) Map of the Great Barrier Reef showing the locations of reefs included in the study, with rivers in the GBR watershed and populated cities/towns overlaid. The cities/towns are represented by light blue circles sized according to the number of inhabitants, and reef locations are indicated by red points. Waterways are depicted in light blue. (b) Spatial variation of fish community variability, colour-coded as determined by species synchrony and average population variability. Dashed lines denote contours of identical community variability values. Each point represents a reef. (c) The relationship between species synchrony and average population variability on log–log scale. *r* denotes the correlation coefficient, and *p* the *p*-value. Spatial data were accessed via a client interface for the Australian Institute of Marine Science Data Platform API (Barneche et al. 2021).

2.2 | Quantifying Community Stability and Portfolio-Effect Components

We quantify temporal variability in reef fish communities using the coefficient of variation (CV) of total abundance, denoted by $\mathrm{CV_c}$, an inverse measure of stability in total community abundance. Following Thibaut and Connolly (2013), we decompose community variability ($\mathrm{CV_c}$) into two components: (i) *species synchrony*, the degree of correlation in abundance fluctuations among different species, and (ii) *average population variability*, a weighted average of the species' coefficients of variation of abundance:

$$\mathrm{CV_c} = \sqrt{\varphi} \times \mathrm{CV_s} \tag{1}$$

where φ and $\mathrm{CV_s}$ represent the synchrony index and the average population variability, respectively. The synchrony index is as follows:

$$\varphi = \frac{\sum_{ij}\sigma_{ij}^2}{\left(\sum_i \sigma_{ii}\right)^2} \tag{2}$$

where σ_{ii} and σ_{ij} represent the square roots of the elements of the variance–covariance matrix for temporal fluctuations in species-abundance observations. The numerator represents the variance of total community abundance, while the denominator represents the maximum possible total variance for a community with the same constituent species variances, but with perfectly positive correlations in abundance fluctuations among species. ϕ varies between zero (constant total community abundance) and one (perfectly positively correlated fluctuations among all species). Average population variability is as follows:

$$\mathrm{CV_s} = \sum_i \left(\frac{\mu_i}{\sum_j \mu_j}\right)\left(\frac{\sigma_i}{\mu_i}\right) \tag{3}$$

where σ_i and μ_i represent the temporal standard deviation and mean abundance of species i, respectively. The term in the first set of brackets represents the relative abundance of species i, while the term in the second set of brackets corresponds to the coefficient of variation of abundance of species i.

Because small-bodied fishes (mostly Pomacentrids) were counted on transects only one-fifth the width of the transects used to count all other fish families, we subsampled the fish counted on the large transects, giving each individual a 20% chance of appearing in the subsampled transect. We repeated this subsampling 100 times and averaged over these subsamples to obtain estimates of CV_c, CV_s and ϕ. To confirm that 100 replicates were sufficient for robust estimates, we divided the replicates into 10 subgroups of 10 replicates each, calculated each reef's mean CV_c, CV_s and ϕ across replicates within subgroups, and compared these estimates across subgroups. Mean correlation coefficients for these comparisons exceeded 0.99 for all three metrics, indicating that 100 replicates were more than sufficient to ensure robust estimates of these quantities.

2.2.1 | Estimating Community Parameters

To quantify the roles of species' differential responses to environmental fluctuations and density regulation at the community scale, we estimate variance components of relative species abundance derived from a theoretical model of community dynamics (Engen et al. 2002; also see Appendix S1). In doing so, we extend an earlier analysis (Tsai et al. 2022) by considering a 27-year time span (rather than just 11 years of annual sampling), and by leveraging this additional time span to resolve among-reef differences in the aggregate strength of density regulation at the community level (assumed constant in our previous work). Briefly, the community-dynamics parameters are estimated from the temporal decay of autocorrelation in a community's log-abundances over time:

$$\rho_t = \left(\rho_0 - \rho_\infty\right)e^{-\delta t} + \rho_\infty \tag{4}$$

ρ_t is the estimated correlation coefficient of log species-abundances at time lag t (years), which is an exponential function of time lag. ρ_∞ is asymptotic similarity. It increases as persistent demographic differences become more important, relative to environmentally mediated fluctuations, such that relative abundances become more consistent over time. ρ_0 is the intercept, reflecting the expected cross-correlation in species' log-abundances for replicate samples taken that the same time, such that $1 - \rho_0$ accounts for the variation not explained by either persistent species differences or environmental stochasticity (i.e., accounting for effects of spatial demographic stochasticity and overdispersion: Engen, Aagaard, and Bongard 2011). δ represents the strength of density regulation, with larger values indicating assemblages that rapidly return to their long-term average relative abundances following a disturbance.

Using Equation (4), the variance components of relative species-abundance are as follows:

$$\pi_r = \rho_\infty \tag{5a}$$

$$\pi_e = \rho_0 - \rho_\infty \tag{5b}$$

$$\pi_d = 1 - \rho_0 \tag{5c}$$

π_r is the proportional variance in relative (log-)abundance attributed to deterministic, persistent differences among species, π_e is the proportional variance in relative abundance stemming from species' differential responses to stochastic fluctuations in population size, and π_d is the proportional variance in relative abundance due to overdispersion or demographic stochasticity (Engen et al. 2002; Engen, Aagaard, and Bongard 2011). To quantify the relative importance of species' differential responses to environmental stochasticity versus persistent differences in species' mean abundances in structuring species' relative abundances, we introduce the 'Community Determinism Index' (hereafter CDI):

$$\text{CDI} = \log\left(\frac{\pi_r}{\pi_e}\right) \tag{6}$$

CDI ranges from negative to positive infinity, from completely stochastic (all species have the same mean abundance, and variation in abundances is due entirely to stochastic fluctuations), to completely deterministic (species' relative abundances are maintained perfectly consistently through time), respectively. We prefer CDI over absolute variance component magnitudes to avoid statistical confounding with the estimated total variance in log-abundance, σ^2_total, which represents evenness (see below). See Appendix S1 for further theoretical background.

To estimate density regulation (δ) and CDI, we first estimate the pairwise correlations in community log-abundances between pairs of years, and we analyse the decay in these correlation coefficients as a function of the time lag between the years being compared for each of the 39 reefs. To estimate the between-year correlation coefficients, ρ_t, we fit the bivariate Poisson-lognormal distribution (PLN) to all survey pairs at each site, with a modification to the likelihood to account for the fact that Pomacentridae were counted on transects one-fifth the width of the transects used to count all other fish families (Appendix S2). This obviates the need to subsample and thereby reduce sample sizes, as in previous work (Connolly et al. 2014; Connolly, Hughes, and Bellwood 2017; Tsai et al. 2022). We then analyse the pairwise estimated correlation coefficients with a nonlinear mixed-effects version of Equation (4), with reefs as random effects on each parameter using Template Model Builder (TMB) in R (Kristensen et al. 2016), to estimate δ, ρ_∞ and ρ_0 for each reef (Table S1; Figure S1). We then calculated CDI from ρ_∞ and ρ_0 using Equations (5) and (6).

Because prior work shows that the Poisson-lognormal distribution provides an excellent fit to these data (Connolly, Hughes, and Bellwood 2017; Tsai et al. 2022), we also use this distribution to estimate species richness and evenness. Specifically, for each year, we estimate the total number of species in the community, accounting for the estimated proportion of species that were present in the community but not observed in that year, and, for evenness, we use the estimated variance of log-abundance of the community from which the sample was drawn, $\widehat{\sigma^2}$, which varies inversely with evenness. We then average these values across years to obtain richness and evenness for each reef. To further confirm the robustness of our results, we repeated our analyses using the cumulative number of observed species through time at each reef as a measure of richness and Pielou's J as a measure of unevenness. See Appendix S2 for further details.

2.2.2 | Explaining Variation in Community Stability

We employ piecewise structural equation models (pSEMs; Lefcheck 2016) to assess the factors explaining variation in community stability of reef fishes on the Great Barrier Reef. We first use a simple pSEM to test whether richness stabilises communities. The pSEM comprises two layers: in the first layer, community variability (CV_c) is modelled as a linear function of species synchrony (φ) and average population variability (CV_s) on a logarithmic scale. In the second layer, φ and CV_s are modelled as separate functions of species richness. Because φ and CV_s perfectly partition community variability on a log scale, it follows that geographical variation in CV_c arises from either variation in φ, variation in CV_s or both. Thus, modelling the potentially different effects of diversity on φ and CV_s helps reveal which component(s) drive any DSR which may be apparent in the data.

To assess whether community stability is instead (or additionally) explained by environmental factors extrinsic to the fish assemblage, we used a second pSEM to model community stability (via synchrony and average population variability) as functions of latitude, distance from the coast, mean coral cover and variability in coral cover, and we examine evenness alongside richness. In this pSEM, we also model diversity as functions of our environmental variables, in order to determine (i) whether any environmental variables have direct effects on φ or CV_s, or if their effects are mediated by richness or evenness (e.g., the environmental factor affects richness, which in turn affects φ or CV_s, *sensu* Lamy et al. 2020), and (ii) whether the inclusion of these environmental factors alters the estimated effect of richness on φ or CV_s.

To understand how community stability may depend on community-dynamics parameters, we followed a similar process in a third pSEM to test for effects of the strength of density regulation (δ) and the community determinism index (CDI). Specifically, we treated these two variables as we treated richness in the above analysis.

Finally, we constructed a synthetic pSEM including richness, evenness and our community-dynamics parameters, to determine whether any of the effects identified in the 'diversity' and 'community dynamics' pSEMs above changed when they were incorporated in the same model. Because this model included a large number of estimated effects, we also used model selection to test whether a model with only a subset of the estimated effects provided a better fit to the data.

See Appendix S3 for further details and rationale for the structure of our pSEMs, the use of such models to test hypotheses about causal structure, a summary of model checks performed and descriptions of the model selection procedure as well as additional analyses to assess the robustness of our findings.

3 | Results

We found substantial geographic variation in both synchrony and average population variability (Figure 1). Among-reef variation in community variability (the inverse of stability) was driven by variation in both average population variability and species synchrony, with synchrony exhibiting a stronger effect (Figure 2). A diversity–stability relationship was mediated by a tendency for synchrony to be lower on more species-rich reefs, whereas there was no significant relationship between diversity and average population variability (Figure 2).

However, the pSEM with environmental factors indicated that the effect of richness on synchrony was not directly causal; rather, on reefs closer to the coast, fish communities exhibited greater synchrony, destabilising communities, and they were also more species-poor (Figure S2). That is, the direct effect of richness on synchrony was non-significant and much smaller once proximity to the coast was accounted for (cf. Figure 2 and Figure S2; Table S2). Additionally, latitude indirectly influenced synchrony via evenness: more equatorial reefs had greater evenness, which in turn reduced synchrony (Figure S2; Table S2). Conversely, on reefs with high coral cover volatility, reefs were destabilised because the constituent populations were more variable, but neither more nor less synchronous (Figure S2; Table S2). These effect sizes of proximity to the coast, unevenness and coral cover volatility were substantial and similar in magnitude for both effects: a one standard deviation change in distance from the coast, evenness or coral cover volatility, produced an approximately half-standard deviation change in either species synchrony or average population variability.

In our pSEM analysis incorporating effects of the community-dynamics parameters, we identified a relationship between (weighted) average population variability and the aggregate strength of density regulation in the community, δ, whereas there was no detectable effect of CDI (Table S3). This model exhibited statistically detectable lack of fit to the data (Table 1), probably due to statistical covariance between δ and CDI, which were estimated from the same statistical model. Eliminating CDI from the model (which neither significantly explained, nor was significantly explained by, any other variables in the analysis) resulted in a pSEM that fit the data adequately (Figure S3; Table 1), and whose significant effects and approximate effect magnitudes recapitulated those from the analysis with both δ and CDI (Table S3). Specifically, for both models, the intensity of density regulation mediated the effect of coral cover volatility on average population variability (Figure S3; Table S3). That is, the direct effect of coral cover volatility on average population variability from the diversity analysis (Figure S2) became non-significant and declined substantially in magnitude. Instead, increasing coral volatility amplified community density regulation, which in turn significantly increased average population variability (Figure S3; Table S3). Effect sizes were relatively large, with one standard deviation changes in coral cover volatility producing a two-thirds standard deviation change in density regulation, and a half-standard deviation effect of density regulation on average population variability (Figure S3; Table S3). As in the pSEM with diversity metrics, reefs more distant from the coast were also stabilised via reduced synchrony (Figure S3; Table S3).

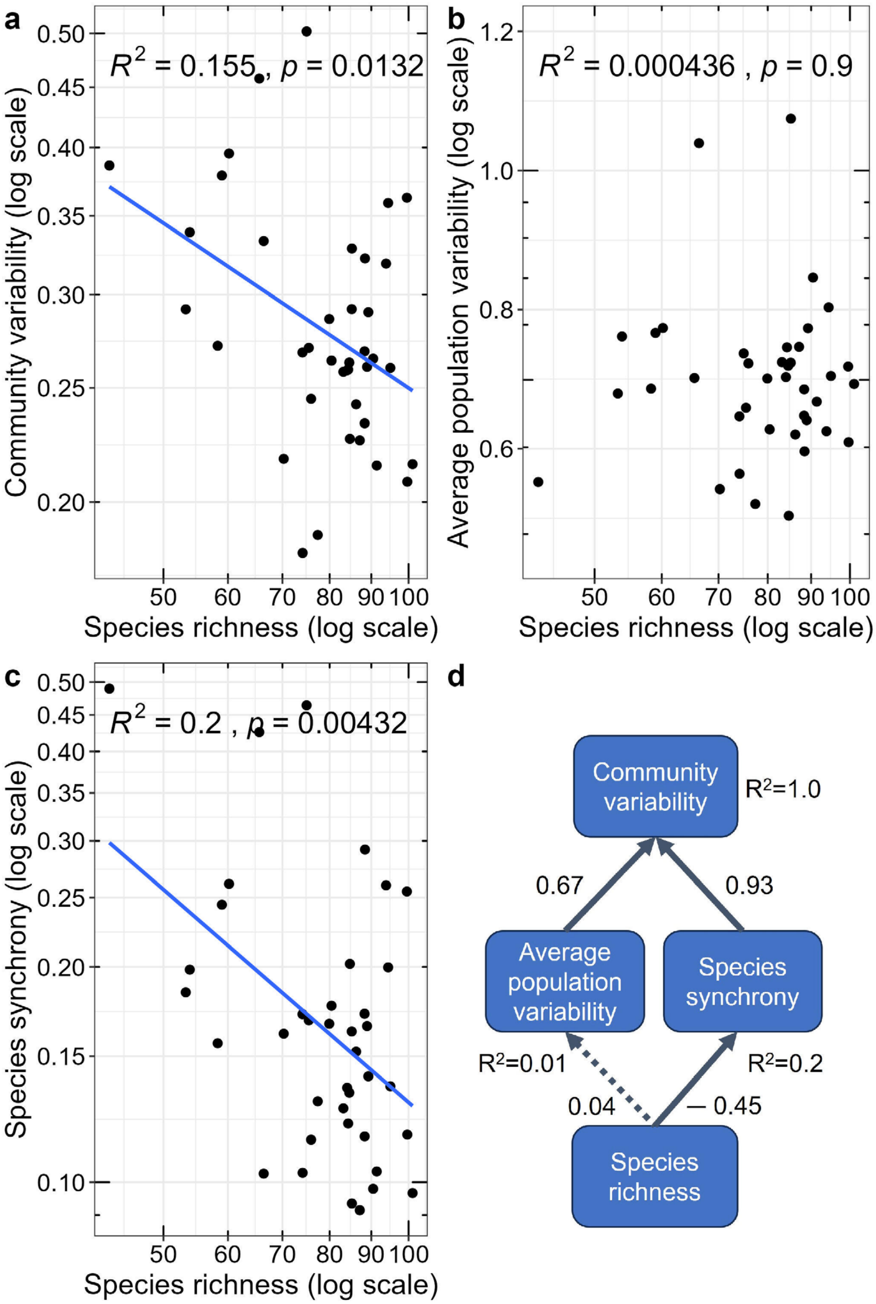

FIGURE 2 | The diversity–stability relationship of fish communities along natural species richness gradients on the Great Barrier Reef. (a) Community variability as a function of species richness. (b) Average population variability as a function of species richness. (c) Species synchrony as a function of species richness. R^2 for panels (a)–(c) are from OLS regressions. (d) Piecewise structural equation model (pSEM) illustrating the effects of species richness on community variability. Significant relationships are indicated by solid arrows and non-significant relationships by dotted arrows. Effect sizes in (d) are standardised; thus, an effect size of −0.48 indicates that an increase of one standard deviation in the explanatory variable produces a decrease of 0.48 of a standard deviation in the response variable.

Further analysis indicated that the effects identified in the above analyses were robust, except for that of evenness. A full synthetic pSEM including richness, evenness and δ, produced very similar effects to those apparent in the component pSEMs (compare Tables S2 and S3 with Table S4), and it fitted the data adequately (Table 1). The optimal synthetic model by AICc included all significant effects from the full model, except for evenness: evenness stabilised communities by reducing population variability, rather than reducing synchrony as in the preceding analyses (Figure 3). All four variables (CDI, δ, richness and evenness) could not be included in the same model without the number of estimated effects exceeding the number of observations; however, when we used CDI in place of density regulation, it did not affect, nor was it affected by, any other variables in the analysis (Table S4).

All of the statistically significant effects (direct or indirect) on synchrony or average population variability in the baseline analyses remained statistically significant when we used observed richness and Pielou's J as our alternative richness and evenness metrics,

TABLE 1 | Goodness-of-fit tests for pSEMs. The chi-squared statistic, *p*-value and degrees of freedom correspond to a likelihood ratio test of the given model against a 'saturated' model, where missing paths from the candidate SEM are estimated (Shipley and Douma 2020). The d-separation-based test is based on a null distribution for the sum of the *p*-values testing the adequacy of the implied independence claims in the pSEM topology ('Fisher's *C*'; Shipley 2013).

	Versus saturated model			d-separation-based test		
Model	χ^2	***p***	**df**	**Fisher's *C***	***p***	**df**
Diversity SEM	5.835	0.054	2	8.002	0.088	4
Community-dynamics SEM	7.605	0.022	2	9.95	0.041	4
Excluding CDI	1.321	0.25	1	2.397	0.302	2
Full Synthetic SEM	7.75	0.101	4	11.357	0.182	8
Optimal Synthetic SEM	26.787	0.083	18	39.262	0.326	36

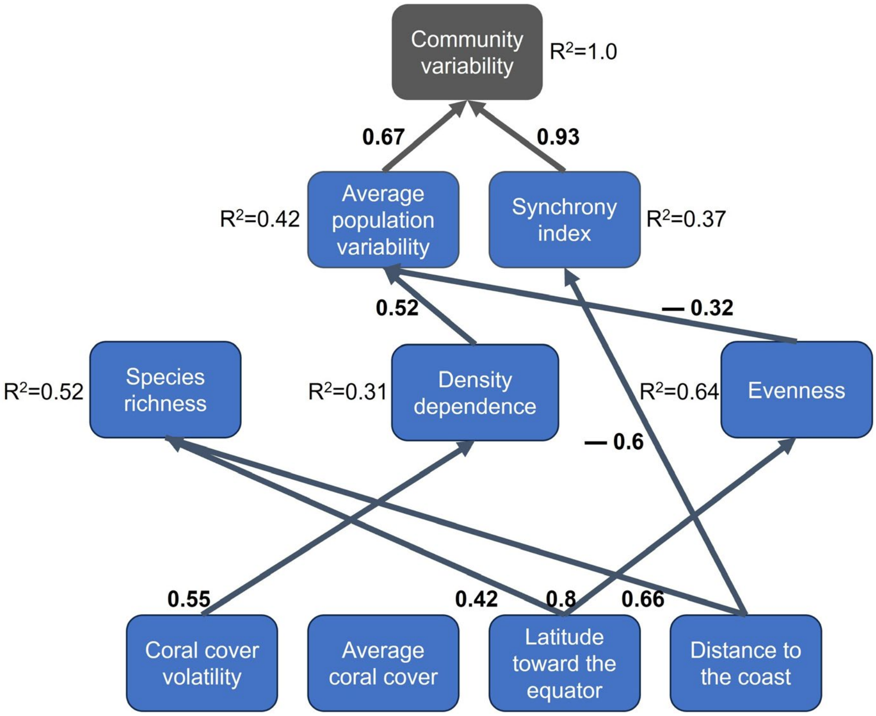

FIGURE 3 | Optimal synthetic pSEM combining species richness, evenness and the strength of density regulation in the community, as selected by d-sep AIC (Shipley 2013). Relationships included in the model indicated by solid arrows (all of which were statistically significant). Standardised effect sizes are shown for each relationship. See Table 1 for global goodness-of-fit statistics and Table S4 for parameter estimates with *p*-values. In this model, no interactive statistical effects were included (see Appendix S4 for alternative models tested, including with interactions among explanatory variables). Additionally, because synchrony and average population CV explain 100% of the community CV by mathematical identity, community CV was not included in the pSEM analysis (and hence is depicted in grey), but standardised effect sizes are shown to facilitate calculation of net effects on community variability (see Appendix S3 for further explanation).

respectively, except for the effect of evenness on population variability in the optimal synthetic model, which was not present (instead, evenness reduced synchrony, as in the other pSEMs including evenness: Appendix S4; Tables S5 and S6). However, all synthetic models with alternative diversity metrics exhibited significant lack of fit to the data (Appendix S4; Table S7). Lastly, the contribution of stochastic effects other than those induced by environmental fluctuations (e.g., due to observation error or demographic stochasticity) likely made only a small contribution to the regional variation in community stability (Appendix S5).

4 | Discussion

There is a relationship between diversity and stability on the Great Barrier Reef. Reefs with higher richness are associated with less synchronous population fluctuations, consistent with studies in other systems that have found richness to be more strongly associated with synchrony than with average population variability (Gross et al. 2014; Hautier et al. 2014; Zhao et al. 2022). However, the effects of richness do not appear to be causal: both richness and synchrony vary with proximity to the coast, and once this environmental factor is accounted for, the statistical dependence of synchrony on richness disappears (Figure 3). Conversely, average population variability is independent of richness, but is higher on reefs exhibiting greater volatility in coral cover (Figure S2), a relationship mediated by an effect of coral cover volatility on the strength of density regulation in the fish community (Figure 3). These strong effects of proximity to the coast and coral cover variability are striking, as both reflect anthropogenic impacts (De'ath et al. 2012; Hughes et al. 2018; Roff et al. 2013), and they are highly robust, appearing in pSEMs with and without community-dynamics parameters, in our optimal synthetic model, and in our pSEMs using alternative richness and evenness metrics (Figure 3; Figure S2; Tables S4 and S6). In contrast to the evidence for the above effects, evidence for a stabilising effect of evenness via synchrony was present, but weaker: the effect was missing from the optimal synthetic model, and present in most, but not all, of our robustness checks (Appendix S4).

Our study system differs from most previously studied systems along natural diversity gradients in three key ways, each of which could potentially explain the lack of a causal relationship between richness and community stability. Firstly, the Great Barrier Reef is vast, spanning ~350,000 km^2. This extent contrasts with the local- to mesoscale scope that is typical of DSR studies [see, e.g., the meta-analysis by Xu et al. (2021) and data sets in Houlahan et al. (2018) and Wisnoski et al. (2023)]. Thus, our reefs may span comparatively large gradients in environmental conditions, which can drive changes in both richness and stability, overwhelming any direct effects of richness on stability (Valencia et al. 2020). Secondly, our study is among the few marine studies that directly examine temporal variability in an aggregate community property; however, we see no reason why marine systems would be less sensitive to the stabilising effects of diversity than terrestrial or freshwater systems. Thirdly, most studies of DSRs compare communities across low to intermediate richness (typically less than 20 species, rarely higher) (Houlahan et al. 2018; Xu et al. 2021), whereas the species richness values in our study are well above this range (~40–100 species). This could explain the lack of a strong independent richness effect on synchrony, since on statistical grounds one would expect synchrony to decline asymptotically as richness increases (Thibaut and Connolly 2013). In contrast, evenness varied among reefs from a low of $\hat{\sigma} \approx 2.7$ to a high of $\hat{\sigma} \approx 1.8$ (recall $\hat{\sigma}$ varies negatively with evenness), which can produce similar magnitude effects on synchrony in communities of both low (~10) and high (>50) richness (e.g., fig. 5a in Thibaut and Connolly 2013). This may explain the somewhat stronger evidence for effects of evenness than richness in our study.

Our finding that proximity to coastal influences and coral cover volatility destabilise reef fish communities aligns with the hypothesis that strong direct effects of environmental gradients on community stability may swamp diversity effects (Blüthgen et al. 2016; Hautier et al. 2014, 2020). Previous work along natural species richness gradients showed that community stability decreases with increased land use intensity across forests and grasslands at regional scales (Blüthgen et al. 2016) and with nutrient enrichment in grasslands (Hautier et al. 2014, 2020), leading to synchronous population fluctuations and obscuring or eliminating richness effects. This parallels our finding that marine fish assemblages on nearshore reefs, exposed to sediment runoff and nutrient enrichment, are less stable due to greater population synchrony than offshore reefs. The significant increase in coastal development near the Great Barrier Reef over the last 150 years has profoundly impacted sediment and nutrient influx, and coral assemblage structure (D'Olivo and McCulloch 2022; Roff et al. 2013). If pulses of sediment and nutrient input have broadly negative effects across fish species, this would increase synchrony.

Similar to habitat degradation and nutrient enrichment gradients, our finding that volatility in the foundational taxon of our system (corals) destabilises communities echoes a previous finding in kelp ecosystems, where kelp cover volatility reduced stability in understory algal and invertebrate communities (Lamy et al. 2020). However, in kelp forests, stable kelp cover promotes understory diversity, which in turn stabilises the understory community via effects on both synchrony and average population variability (Lamy et al. 2020). In contrast, in our study, coral cover volatility is independent of synchrony, and coral volatility's effect on stability is mediated by average population variability, independently of coral cover's effect on species richness (Figure 3). Unlike coastal development that is linked to spatial gradients in the influence of terrestrial nutrients and sediment, high volatility in coral cover is directly provoked by spatially heterogeneous disturbance regimes, such as cyclones, coral bleaching and crown-of-thorns seastar outbreaks (Dietzel et al. 2021), which tends to produce a diverse range of responses from reef fishes at local scales (Wilson et al. 2006). Consequently, an increased amplitude or frequency of coral cover volatility may be more likely to elevate average population variability without substantially altering synchrony.

Theoretical studies of diversity and stability have explored processes influenced by community-dynamics parameters, particularly compensatory interactions and covarying responses to environmental fluctuations (Hughes and Roughgarden 2000; Ives et al. 2003; Ives and Hughes 2002; Loreau and de Mazancourt 2008, 2013; Tredennick, Adler, and Adler 2017). As noted earlier, this theoretical framework has seen limited application in empirical DSR studies of speciose assemblages, due to challenges associated with calibrating community-dynamics parameters in systems with many species. We addressed this challenge by employing a theoretical model of community dynamics to estimate the aggregate strength of density regulation and the relative importance of species' differential responses to environmental fluctuations (Engen et al. 2002; Tsai et al. 2022). This approach facilitated the connection between DSRs and community-dynamic processes without requiring explicit estimation of species-by-species interaction terms or pairwise covariances in responses to environmental fluctuations.

We expected that our application of this framework to the reef fish data would reveal that the relative importance of environmental fluctuations drives patterns in species synchrony, in line with previous findings suggesting a predominant role for species' differential responses to environmental fluctuations in mediating DSRs in low-richness assemblages (e.g., Tredennick et al. 2017). However, CDI has no statistically significant effect on community stability in our analysis, possibly because it is estimated from fluctuations in abundances on a logarithmic scale (Engen et al. 2002; Engen, Aagaard, and Bongard 2011), whereas synchrony is disproportionately affected by fluctuations in abundances of the most abundant species (Thibaut and Connolly 2013). If the temporal correlations of the most abundant species' fluctuations differ from average values for the assemblage as a whole, then CDI may not capture the temporal variability of total community abundance well. However, we did find that stronger density regulation was destabilising. Although theoretical work has indicated this latter possibility (e.g., Loreau and de Mazancourt 2008), the mechanism appears different. In earlier theoretical work, stronger interspecific competition increases synchrony (Loreau and de Mazancourt 2008, 2013), whereas we find that density dependence destabilises communities via average population variability. This apparent discrepancy is likely explained by the predominantly intra-specific nature of density regulation in our system (Ruiz-Moreno, Emslie, and Connolly 2024; Thibaut, Connolly, and Sweatman 2012). One potential mechanism for a destabilising effect of density regulation is that stronger density dependence induces cycles or chaos (Loreau and de Mazancourt 2013); however, density dependence in this system is only weakly compensatory (Ruiz-Moreno, Emslie, and Connolly 2024). While far from values that would induce population cycling, simulations from a discrete-time version of the community-dynamics model employed here indicate that even increases in density dependence from very small values can increase temporal variability in population size (Solbu et al. 2022), consistent with the destabilising effect of density regulation on average population variability in our study.

Our findings highlight two pathways by which anthropogenic impacts can influence community stability. Where such impacts induce environmental fluctuations that have similar effects across species, species fluctuations will be more positively correlated, increasing synchrony and destabilising communities. Conversely, where human impacts amplify or increase the frequency of fluctuations that affect species in different ways, they may increase average population variability without changing synchrony substantially. Our findings suggest that proximity to the coast, by exposing reefs to increased sediment and nutrient levels, is an instance of the former type of destabilisation, whereas increased coral cover volatility is an instance of the latter. The parallel between our findings and those of other studies of diversity gradients over regional spatial scales in systems heavily impacted by anthropogenic activity (Blüthgen et al. 2016; Hautier et al. 2014, 2020) suggests that regional gradients in anthropogenic impacts may have dramatic effects on community stability and the underlying community-dynamic processes that give rise to it. Such effects may swamp any direct effects of species richness on community stability, particularly in highly speciose systems where, on statistical grounds, one might expect DSRs to be less pronounced. These findings suggest that alleviating such anthropogenically influenced environmental impacts directly, rather than trying to maintain richness in the face of such impacts, may be more effective for enhancing community stability and its components in species-rich systems such as coral reefs.

Author Contributions

Both authors devised the research programme, interpreted results and wrote the manuscript. C.-H.T. led the Poisson-lognormal and community-dynamics analyses, and S.R.C. led the SEM analyses.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are available in Zenodo at https://zenodo.org/records/13826659.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.