ECOLOGY

Volatility in coral cover erodes niche structure, but not diversity, in reef fish assemblages

Cheng-Han Tsai[1,2,3]*, Hugh P. A. Sweatman[2], Loïc M. Thibaut[4,5,6], Sean R. Connolly[1,3,7]

The world's coral reefs are experiencing increasing volatility in coral cover, largely because of anthropogenic environmental change, highlighting the need to understand how such volatility will influence the structure and dynamics of reef assemblages. These changes may influence not only richness or evenness but also the temporal stability of species' relative abundances (temporal beta-diversity). Here, we analyzed reef fish assemblage time series from the Great Barrier Reef to show that, overall, 75% of the variance in abundance among species was attributable to persistent differences in species' long-term mean abundances. However, the relative importance of stochastic fluctuations in abundance was higher on reefs that experienced greater volatility in coral cover, whereas it did not vary with drivers of alpha-diversity. These findings imply that increased coral cover volatility decreases temporal stability in relative abundances of fishes, a transformation that is not detectable from static measures of biodiversity.

INTRODUCTION

The world's coral reef ecosystems have been profoundly affected by human activities (1–8). In particular, global warming has markedly increased the frequency and severity of coral bleaching events (6, 9, 10), outbreaks of coral disease (11), and cyclones (12). In addition, land-use change has increased runoff of nutrients and sediments to near-shore coral reefs during major rainfall events (8, 13–16) and may have increased the frequency and intensity of outbreaks of the crown-of-thorns starfish *Acanthaster planci* (17, 18). These types of disturbances lead to episodic coral mortality, and the greater magnitude and frequency of these events decrease both the temporal stability and long-term average of coral cover (6, 8, 16–20). Reef fish assemblages, which play critical roles in reef ecosystem functioning and in the provision of coastal ecosystem services, are also affected by these episodic perturbations in coral cover (14, 21–26). Specifically, before-after studies often show marked changes in the composition of fish assemblages (14, 22) and, less consistently, decreases in fish diversity (14, 25, 27–30). Consequently, increased volatility in coral cover has the potential to influence both the local (i.e., "alpha") diversity of fish assemblages and the turnover in species' relative abundances (i.e., "temporal beta-diversity") (31–33).

The magnitude of temporal turnover in species relative abundances depends on the balance between differences in the long-run average abundances of species and the magnitude of fluctuations that cause relative abundances of species to differ at different points in time. Fundamentally, persistent differences in abundances among species are due to trait-by-environment interactions that cause species with some constellations of traits to be demographically advantaged, relative to other species, in particular habitats (34–39). Conversely, temporal changes in the relative abundances of species are mediated

by stochastic factors. Changes due to chance variation in the fates of individuals (i.e., demographic stochasticity) are independent of species' intrinsic characteristics, such that differences in relative abundance will wax and wane even if species have identical demographic rates, a phenomenon termed "neutral ecological drift" (40, 41). However, fluctuations in environmental conditions (environmental stochasticity) also can cause shifts in species' relative abundances, as trait-by-environment interactions benefit some species in some years, and other species in different years (36, 42–44).

The magnitude of stochastic fluctuations, relative to the magnitude of persistent differences in species' long-run, average abundances, will determine how much assemblage structure can be expected to vary over time (31, 37) and thus represent one way to understand the drivers of biodiversity change on coral reefs. These stochastic and deterministic components reflect a distinct property of communities, relative to static measures of assemblage diversity such as richness or evenness, and their dynamics may be entirely different from those of static metrics (31, 45). Changes in different diversity components (e.g., richness, evenness, and spatial and temporal beta-diversity) likely reflect the operation of different ecological processes (31, 46–49) and have been proposed to respond to different types of disturbances (45, 50). However, measures of temporal turnover in diversity, such as many alpha-diversity metrics, assume that sampled relative abundances (or presences and absences, for presence-absence–based metrics) accurately reflect true relative abundances (37). For species-rich assemblages such as coral reefs, abundances in ecological samples will be dominated by many rare species, whose abundance in (or absence from) a sample may be an extremely noisy estimate of their true abundance in the assemblage.

One theoretical framework for understanding the relative roles of stochastic fluctuations and persistent species differences in structuring communities allows the variance partitioning of relative species abundances (hereafter "VPRSA") into three components using time series of abundance of species (Fig. 1). One component is the variance due to heterogeneity among species in their long-term, equilibrium abundances. This heterogeneity is the consequence of differences in species' demographic or other ecological characteristics such as niche differences that tend to confer higher or lower average abundances in a particular habitat. We term this the "persistent species

¹College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia. ²Australian Institute of Marine Science, Townsville MC, QLD 4810, Australia. ³Australian Research Council Centre of Excellence for Coral Reef Studies, Townsville, QLD 4811, Australia. ⁴School of Mathematics and Statistics, University of New South Wales, Sydney, NSW 2052, Australia. ⁵Centre for Population Genomics, Garvan Institute of Medical Research and UNSW Sydney, Sydney, NSW, Australia. ⁶Centre for Population Genomics, Murdoch Children's Research Institute, Melbourne, VIC, Australia. ⁷Smithsonian Tropical Research Institute, Panama, Republic of Panama.
*Corresponding author. Email: chenghan.tsai@my.jcu.edu.au

differences" component. The second component is the variance due to stochastic fluctuations in species' relative abundances at the population level due to independent and idiosyncratic responses of species' population growth rates to environmental fluctuations, which we term the "stochastic fluctuations" component. The third component is the variance due to additional factors that create overdispersion, such as local aggregation at the spatial scale of sampling (e.g., due to

spatial demographic stochasticity). These variance components can be estimated from the decay in community similarity as a function of time between two sampled species abundance distributions (Fig. 1), and their relative magnitudes determine the long-run expected temporal beta-diversity (i.e., how different should an assemblage at two different time points be, once temporal autocorrelation in relative abundances has decayed away). Assemblage similarity and diversity
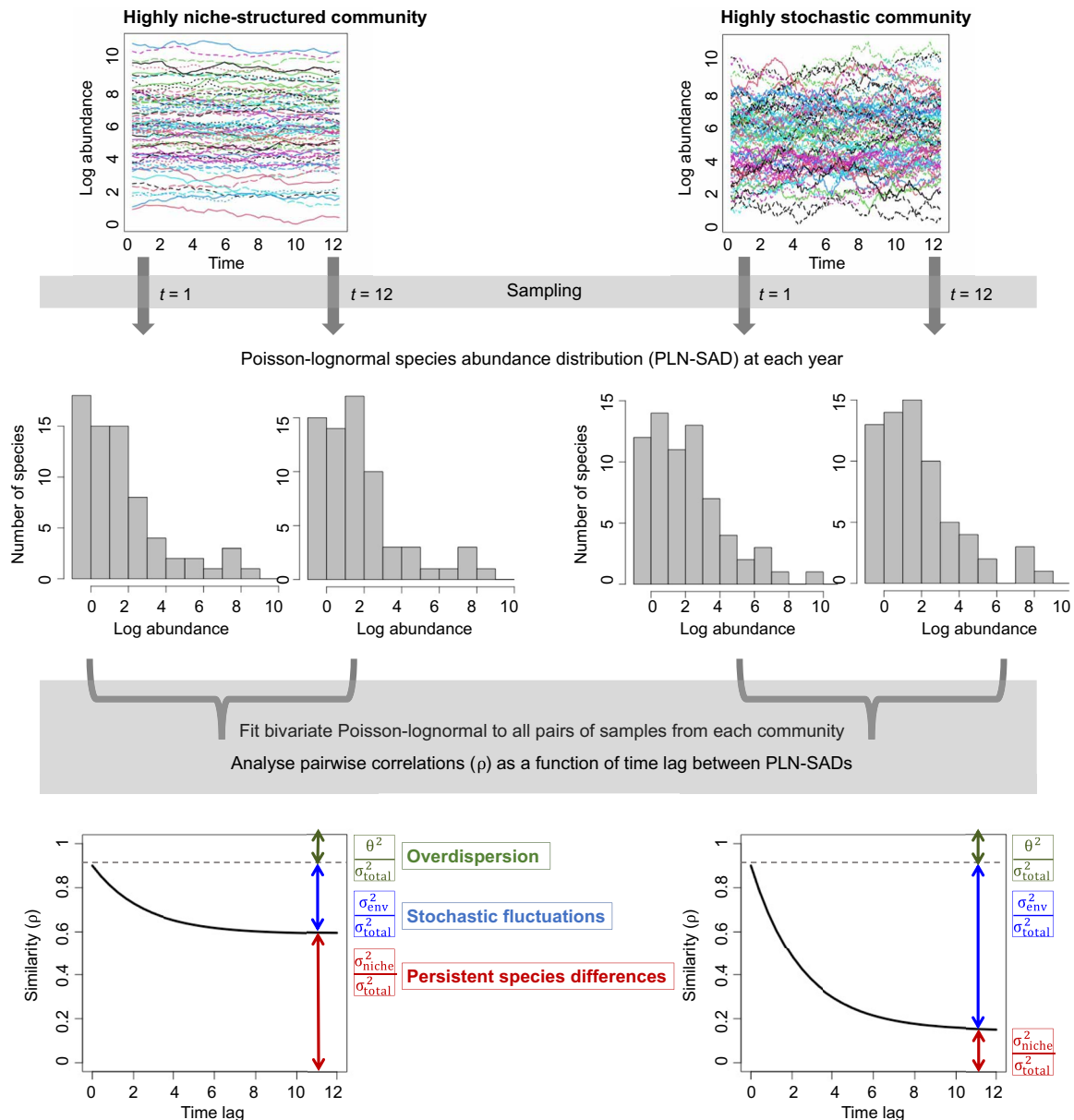
Fig. 1. Conceptual figure illustrating VPRSA. (Top) Color-coded lines represent the log abundances of 80 species in two hypothetical communities over time. Both communities have the same total variance in log abundance. In the "niche-structured" community on the left, species differences in long-term average abundances explain most of the variance in log abundance in the community at any one time (i.e., high community determinism). By contrast, in the "stochastic" community on the right, long-term average abundances of the 80 species are very similar to each other such that the variance in abundance at any one time is driven instead by differences in species' temporal patterns of stochastic fluctuations. The middle panel illustrates sampled species abundance distributions from these communities, which are obtained for each year of the time series. **(Bottom)** Similarity between samples is modeled as a function of time lag between each pair of sampled abundance distributions. The asymptotic similarity is equal to the proportion of variance in species' log abundances that is due to difference in species' long-term mean or equilibrium abundances (red); the distance from this asymptote to the intercept is the proportion due to stochastic fluctuations in relative abundance (blue), and the remainder is the proportion due to overdispersion (green). See Materials and Methods for details of the approach and the theoretical community dynamics model from which it was derived.

in this approach is measured using a sampling model that explicitly accounts for the expected magnitude of sampling error in each year's abundance estimate (*51*), in contrast to other approaches that use sample abundances as a strict proxy for true relative abundances in the community (*33, 37*).

Here, we apply VPRSA to a unique, regional-scale, highly spatially replicated time series of fish species abundances on the Great Barrier Reef (see Materials and Methods). Our first aim is to determine, overall, how much of the variance of relative species abundances of reef fishes is attributable to persistent species differences, versus stochastic fluctuations. Second, we leverage the high degree of spatial replication of the time series to evaluate the potential macroecological-scale drivers of variation in these variance components of relative species abundance, as well as variation in the static diversity measures of richness and evenness more commonly examined in macroecological work. Specifically, we consider the mean and temporal variability in coral cover as our principal explanatory variables (i.e., variables linked to coral cover volatility), but we also consider latitude and cross-shelf position, two macroecological gradients that can serve as proxies for environmental variables known to affect other aspects of fish assemblage structure, such as species richness and composition (fig. S1) (*48, 52–54*). In addition to testing for effects of these environmental variables, we ask whether there is any evidence of additional causal pathways linking richness or evenness with the variance components of relative species abundance.

RESULTS AND DISCUSSION

Our analysis revealed that reef fish communities are structured disproportionately by persistent differences among species, rather than by stochastic fluctuations in population growth rates (Fig. 2E). Specifically, persistent species differences explained a substantially larger proportion of variation in reef fish community structure [75% on average; 95% confidence interval (CI): 72 to 78%], compared to stochastic fluctuations in population growth rates [18% on average (95% CI: 15 to 20%); Fig. 2E]. Only ~7% of the variance was attributable to additional sources of variance, such as demographic and sampling variance (Fig. 2E). Despite the well-documented importance of episodic disturbances in coral reef ecology, our findings showed a high level of persistence in species' commonness or rarity through time. This suggests that ecological traits of species that influence long-term mean abundances, such as traits related to niche size, are disproportionately responsible for the variation in relative species abundances of reef fishes.

A piecewise SEM indicated that the degree of deterministic versus stochastic structure on reefs varied strongly with the mean and temporal variability in coral cover but not latitude or cross-shelf position, whereas the static diversity metrics of richness and evenness varied with latitude and cross-shelf position but not with coral cover variables (Fig. 3 and table S1). Moreover, d-separation tests found no evidence of missing pathways, suggesting the lack of any direct or indirect causal links between the persistent species difference variance component, species richness, or evenness ($P > 0.19$ for all pairwise tests; Fisher's $C = 5.35$; $P = 0.5$ overall). These results were consistent with a model selection approach (table S2). Specifically, reef fish assemblages were less deterministically structured on reefs with more volatile coral cover, especially when mean coral cover was high ($R^2 = 0.39$, $P < 0.001$ for the variance component of persistent species differences and $R^2 = 0.4$, $P < 0.001$ for the variance
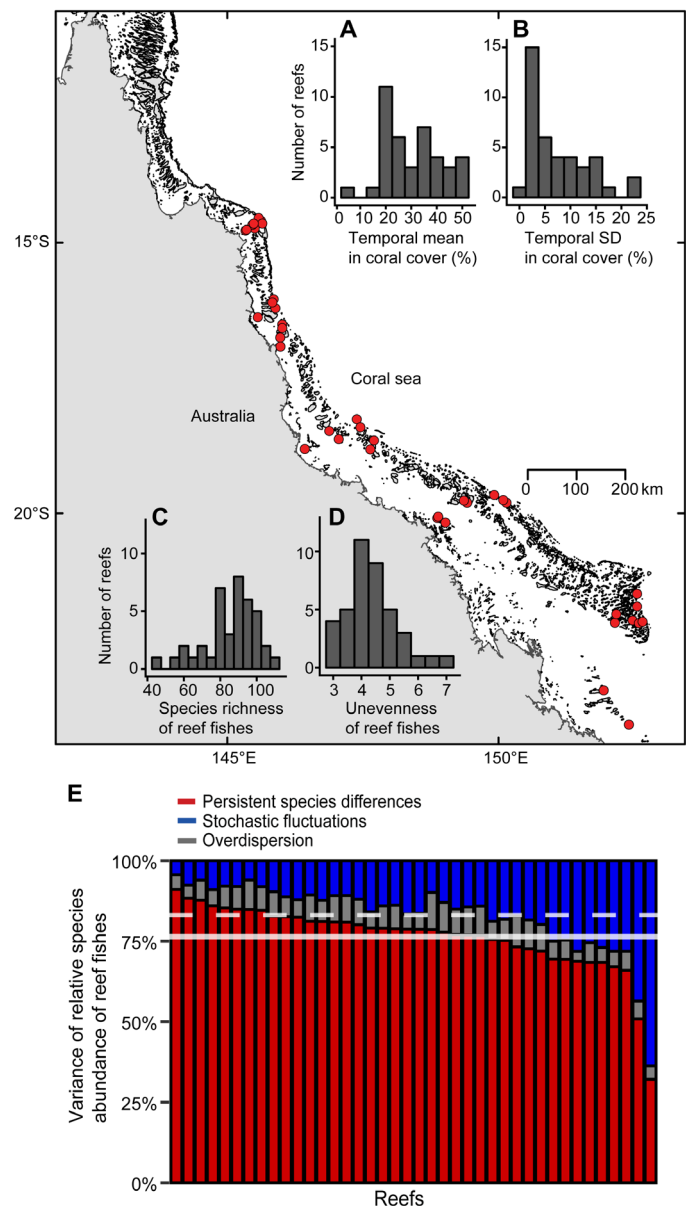
Fig. 2. The map showing coral reefs included in all analyses, along with frequency distributions of explanatory and response variables across the Great Barrier Reef. On the map, red circles show locations of the $n = 40$ reefs used in this study. (**A** and **B**) Explanatory variables related to coral cover fluctuations. Frequency distribution of the temporal mean and SD in living hard coral cover across reefs. (**C** and **D**) Static metrics of reef fish assemblage structure as response variables. Frequency distribution of (time-averaged) species richness and unevenness of reef fish assemblages across reefs. (**E**) Deterministic and stochastic variance components in relative species abundances of reef fishes as response variables. Frequency distribution of the variance in relative species abundances attributable to persistent species differences (red bars; $n = 40$), to stochastic fluctuations in species' growth rates (blue bars; $n = 40$), and to overdispersion effects such as demographic and sampling variance (gray bars; $n = 40$). The solid line indicates the mean value (across reefs) of the variance component due to persistent species differences, and the dashed line separates the remaining variance explained by stochastic fluctuations (the larger portion) and overdispersion (the smaller portion).
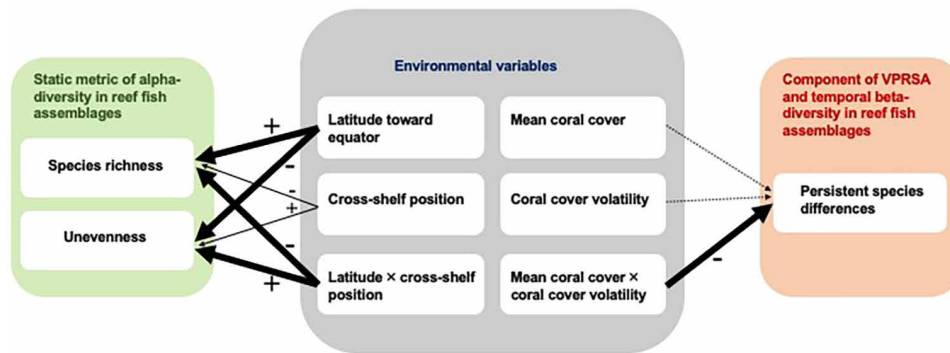
Fig. 3. Structural equation model for persistent species difference variance component, species richness, and unevenness of reef fish assemblages. Solid arrows represent standardized effect estimates, where thick and thin lines represent significance levels of $P < 0.01$ and $P < 0.05$. Dashed arrows represent estimated effects that are not statistically significant. Symbols, plus and minus, indicate the effect direction. Tests of directed separation found no evidence of missing pathways. Model estimates are summarized in table S1.

component of stochastic fluctuations; Fig. 4 and table S2). Conversely, species richness increased, and unevenness decreased (i.e., evenness increased) toward the equator, but the increase in richness and decreases in unevenness were much steeper on the inner shelf than the outer shelf of the Great Barrier Reef (Fig. 5 and table S2). Latitude and cross-shelf position explained almost none of the spatial variation in the variance components of persistent species difference and stochastic fluctuations (table S2) despite the fact that reef fish species composition is known to change quite markedly from inshore to offshore (*53*, *54*), and, in our data, cross-shelf position explained three to four times more variation in community composition than coral cover variables (fig. S2).

We measured richness and evenness using the Poisson-lognormal species abundance model, which fits these reef fish data extremely well (*39*) and is also used in the VPRSA analysis (Fig. 1; Materials and Methods). We choose these metrics because they are both robust to variation in sampling effort. Specifically, they use a sampling model to estimate the richness and evenness of the underlying community from which the data were sampled rather than treating richness and evenness of the sample as strict proxies for the richness and evenness of the community itself. In addition, because evenness is measured as the inverse of the skew of the underlying relative abundance distribution, it can vary independently of species richness (*37*), whereas other evenness metrics are often functions of richness (Materials and Methods). Nevertheless, model selection produced similar results for alternative alpha-diversity metrics, such as the number of observed species, the nonparametric Chao1 estimator, and the Simpson and Shannon-Pielou diversity indices (table S3). Specifically, for the richness estimates, there were strong interactions involving latitude and cross-shelf position and no effects of coral cover variables (fig. S3). Simpson and Shannon-Pielou indices were similar to the unevenness estimates, responding mainly to latitude and cross-shelf position, with an additional detectable but small effect of mean coral cover (tables S3 and S4).

We initially suspected that the large contribution of persistent species differences was a consequence of the presence of multiple functional groups in the reef fish assemblage. However, further analysis of our data indicated that this was not the case. After dividing all fish species into functional/trophic groupings (table S5), we had sufficient species richness in three groups (herbivores, planktivores, and benthic invertivores) to repeat our entire model selection analysis
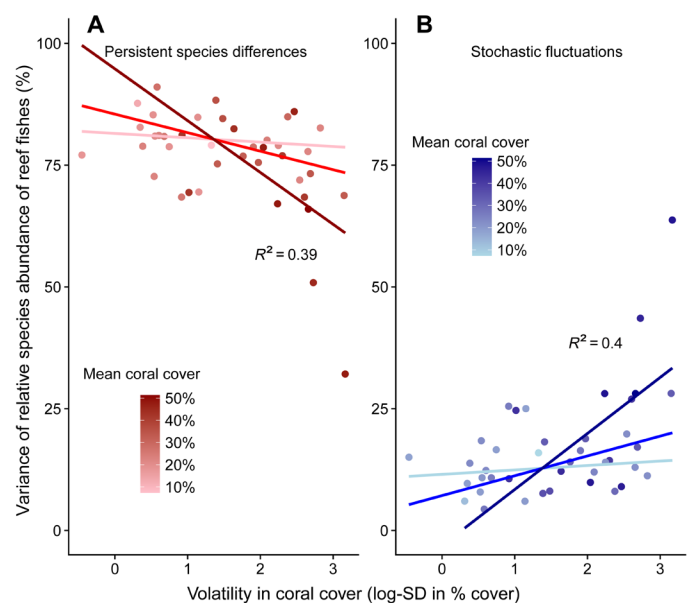
Fig. 4. Persistent species differences and stochastic fluctuation variance components in relative species abundance of reef fishes depend on coral cover volatility and average cover but not on environmental gradients. (**A** and **B**) Relationships between the coral cover variables (log-SD and mean of coral cover) and the relative importance of variance components that underlie patterns of fish species commonness and rarity across reefs. The relationships are plotted using parameter estimates for the lowest-AIC models, with interactive effects of the coral cover volatility and mean coral cover as explanatory variables and variance components of fish assemblage as response variables ($n = 40$ reefs; table S2). To illustrate the interactive relationships, coral cover volatility (log-SD of coral cover) is plotted on the horizontal axis, with points color-coded according to levels of mean coral cover on the corresponding reef. The light-, medium-, and dark-colored lines represent the estimated relationship between the variance component and coral cover volatility for the first (21% cover), median (27% cover), and third (41% cover) quartiles of long-term average coral cover, respectively.

on each group separately (see Materials and Methods). We found that the proportion of variance in abundance attributable to persistent species differences within each of these functional groups was similar to the proportion for the fish fauna as a whole (78, 83, and 75% on average for herbivores, planktivores, and benthic invertivores,
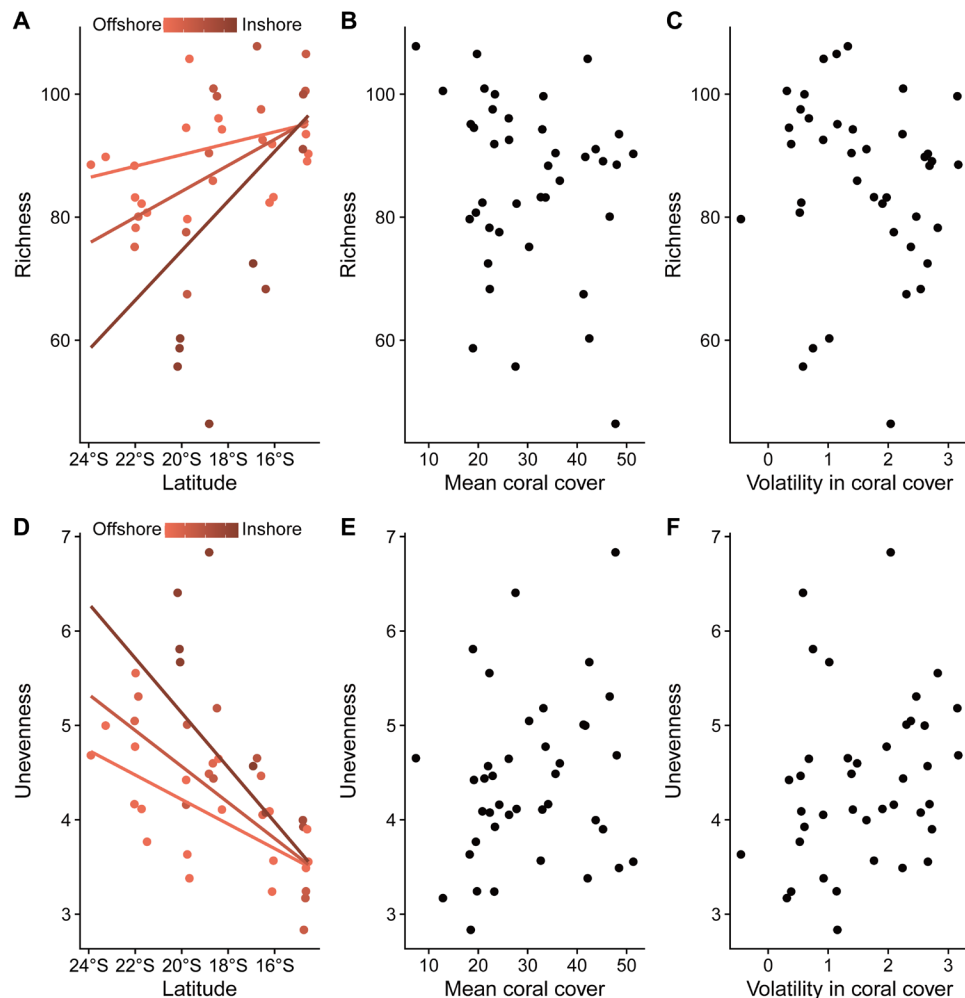
Fig. 5. Alpha-diversity (species richness and unevenness) depend on environmental gradients but not on coral cover variables. (A and **D)** Relationships between fish species richness or unevenness and the interaction of latitude with cross-shelf position. To illustrate the interactive relationships, latitude is plotted on the horizontal axis, with points color-coded according to the cross-shelf position of the corresponding reef. The light-, medium-, and dark-colored lines represent the estimated relationship between the variance component and the first, median, and third quartiles of cross-shelf position, respectively (darker, closer to shore). Fish species richness and unevenness do not depend on mean coral cover (**B** and **E)** nor coral cover volatility (**C** and **F)**, whether in univariate relationships as plotted or in multiple regression (table S2).

respectively; fig. S4 and tables S6 to S8). Moreover, the changes in variance components of relative species abundance within functional groups with coral cover volatility were similar to those found in the analysis of all species, although variance components were most sensitive to coral cover fluctuations for planktivores and herbivores and less sensitive for benthic invertivores (fig. S5 and table S9). This differential sensitivity may arise because many coral reef planktivores are small-bodied and rely for shelter on relatively fast-growing but disturbance-susceptible branching corals that likely contribute disproportionately to coral cover fluctuations. Similarly, herbivores, particularly those that cultivate algal gardens, require coral-free substrate whose availability is closely related to fluctuations in coral cover. Conversely, variance components for benthic invertivores were the least sensitive, implying an ecology in which abundances are less dependent on coral cover fluctuations. With respect to richness and unevenness, as in the original analysis for the fish fauna, latitude and cross-shelf position had interactive effects on richness and unevenness within individual functional groups of fishes (figs. S6 to S8 and table S9).

The large proportion of variance (c. 75%) in relative abundances, both overall and within functional groups, attributable to persistent species differences underscores the importance of interspecific variation in trait-by-environment interactions (i.e., niche differences) as determinants of relative abundance patterns in reef fishes (Fig. 2E and fig. S4). This finding places a clear upper bound on how much of the species abundances can be explained by neutral ecological drift, particularly given that the nondeterministic components of community structure (i.e., stochastic fluctuations and overdispersion) are only partly attributable to such drift. That is, differential fluctuations in abundance can arise not only from demographic stochasticity but also from differences in how species' population growth rates respond to environmental fluctuations. Although the former is clearly a neutral process, the latter implies a type of niche differentiation, differences in how species' demographic rates respond to fluctuating environmental conditions (i.e., an interaction between traits and environmental variables that are fluctuating). Because abundance fluctuations due to demographic stochasticity should be independent of fluctuations in particular environmental variables,

the fact that two-fifths of the variation in the stochastic fluctuations component is explainable in terms of coral cover variables (i.e., temporal volatility and average level in coral cover) suggests that neutral drift likely accounts for only a fraction of the overall stochastic fluctuations. Consequently, our results indicate that patterns of commonness and rarity are strongly driven by niche or other trait differences that tend to make species common or rare on average, and that influences how species' population growth rates respond to temporal fluctuations in their environment.

Our key finding, that two-fifths of the spatial variation in community determinism on reefs spanning 10° of latitude across the Great Barrier Reef can be explained by just two explanatory variables linked to coral cover volatility, highlights the threat from ongoing changes in coral cover dynamics on the world's reefs. Specifically, greater volatility in coral cover, especially on reefs with relatively high cover, is associated with substantially reduced persistence of relative abundance patterns of reef fishes, due to the greater role of stochastic fluctuations in shaping those abundances, and thus higher temporal beta-diversity. This implies, for example, less temporal stability in the performance of the ecosystem functions performed by fish species, particularly given the evidence that some important functions have limited redundancy in reef fishes (55) and that, where redundancy is present, species differ substantially in the efficiency with which key functions are performed (56).

In this reef system, regional variation in coral cover fluctuations over the time frame of our analysis was driven substantially by episodic disturbances, including cyclones, crown-of-thorns starfish outbreaks, and coral bleaching (17, 19, 57). As climate change accelerates, coral bleaching is almost certain to overtake other disturbances as a principal driver of increased coral cover volatility, if this is not already so (6, 9, 10). Our findings suggest that such volatility in coral cover will further erode the temporal stability of relative abundance patterns on coral reefs, with potential implications for the ecosystem functions performed by the community's constituent fish species, most markedly on reefs with the highest average levels of coral cover (Fig. 4 and fig. S5). Moreover, because this erosion in assemblage structure is not reflected in static metrics such as richness, unevenness, and composition (Fig. 5 and fig. S2), reliance on static metrics may not provide sufficient early warning of important changes in the processes structuring coral reef assemblages. This highlights the urgent need for long-term community-level abundance data to identify the onset of ecological degradation (31, 32).

MATERIALS AND METHODS

Reef fish community data and environmental covariates on the Great Barrier Reef

We used data from 40 reefs from the Australian Institute of Marine Science's Long-Term Monitoring Program (LTMP), which has made visual surveys of benthos and fish communities on reefs spanning 10° of latitude on the Great Barrier Reef for more than 20 years (58). The surveys themselves were hierarchically structured: Three sites on the reef slope at a depth of approximately 6 to 9 m were selected, usually on the NE faces of each reef. At each site, five permanently marked 5 m–by–50 m transects were established for censusing larger, noncryptic fishes. Smaller damselfishes, which were counted on 1 m–by–50 m sections of the same transects. Transects were separated by about 10 m. For statistical analyses, we used the fish community data from 1994 to 2004 (11 years) because this was the only

interval during which each reef was surveyed annually (the frequency of surveys changed after the Great Barrier Reef Marine Park was rezoned in 2004) (58).

Our analyses focused on counts of fish identified to species and on percentage cover of living hard coral at each survey reef. Fish species from a prescribed list of species representing 13 families were counted visually. Families were Pomacentridae, Acanthuridae, Serranidae, Lutjanidae, Scaridae, Caesionidae, Chaetodontidae, Labridae, Lethrinidae, Haemulidae, Holocentridae, Siganidae, and Zanclidae. All species examined here were largely noncryptic and easily identified underwater, and thus, cryptic species groups, such as gobies, were excluded. A full list of species observed each year was included in the appendices of each LTMP status report (also see table S5 for species in our analysis) (58). Corals were identified into broad taxonomic and morphological categories, but we considered only total hard coral cover in our analyses. We pooled fish community and coral cover data for each reef, summing abundances over all 15 transects surveyed at each reef. Percentage cover was similarly averaged across transects and sites within reefs. We adopted this approach to reduce stochastic sampling error, thereby obtaining more precise estimates of the community structure statistics that were of interest in this study.

Because the small-sized fish taxa (mainly Pomacentridae) were surveyed in narrower transects than other larger fish taxa, we used subsampling to rescale the abundances of large-sized species to standardize sampling effort. Each fish counted on the wider transects was given a 20% probability of appearing in the subsample (because the small-fish transects covered only 20% of the area of large-fish transects). These subsampled data were used for our analyses.

For each reef, we extracted the temporal average (11-year mean) and SD in coral cover as proxies for disturbance-mediated coral cover fluctuations. We also extracted each reef's latitude and cross-shelf position, where latitude was measured by degrees from the equator, and cross-shelf position was the standardized distance to the nearest continental shelf boundary (i.e., 0 represents the shelf boundary and 1 represents the coast, respectively). We used latitude and cross-shelf position as proxies for major environmental gradients because community structure on the Great Barrier Reef is known to vary strongly along both gradients and because they were strongly correlated with important environmental variables, such as mean and variability in temperature and differences in exposure to terrestrial runoff (fig. S1).

Partitioning variance in relative species abundance: theoretical framework (VPRSA)

We used the partitioning approach of Engen and colleagues (36, 51) to quantify the contribution of deterministic, persistent species differences, relative to that of stochastic fluctuations in driving the total variance in relative species abundances (VRPSA; also see Fig. 1). These variance components can be estimated from the decay of correlation in a community's log abundances over time, i.e., the temporal autocorrelation in relative species abundance

$$\rho_t = (\rho_0 - \rho_\infty) e^{-\delta t} + \rho_\infty \qquad (1)$$

where ρ_t represents the correlation coefficient of log species abundances of a community at time lag t (i.e., it is a measure of community similarity between species' log abundances in two different years). This quantity was modeled as an exponential function of time lag t. That is, for each reef, we estimated the correlation coefficient between

log abundances in all pairs of years and then analyzed how the strength of this correlation decreased as a function of the time elapsed between the two samples (ranging from 1 to 10 years in our analyses). Parameter ρ_∞ represents asymptotic similarity. In the absence of persistent niche structure in long-term average relative abundance (e.g., where all species have the same mean abundance and variation in species abundances is due entirely to their different responses to environmental fluctuations and independent demographic or sampling stochasticity), ρ_∞ would be zero. For a community in which environmental fluctuations play no role, ρ_∞ would be large (and in the absence of demographic or sampling stochasticity, it would tend to unity). Parameter ρ_0 is the intercept (i.e., the expected correlation in species' log abundances for a time lag of zero), and thus $1 - \rho_0$ represents variation that is not captured by the other two components (i.e., overdispersion, including demographic variance and sampling effects due to local aggregation). δ measures the strength of density regulation in the system: It would be larger in assemblages that revert quickly toward their long-term average relative abundances after a disturbance (see Supplementary Text for further explanation of Eq. 1).

The correlation coefficients ρ_t were estimated by fitting the bivariate Poisson-lognormal distribution to all possible pairs of surveys at each site, and these correlation coefficients were then modeled as a function of the amount of time separating the samples following Eq. 1. The estimation assumed that the pairs of surveys were random samples of individuals from two communities whose species abundances followed Poisson-lognormal distributions with correlation coefficient ρ_t. The correlation coefficient therefore represented the true underlying correlation in species' log abundances between the communities at the two sampling times, taking account of the fact that each abundance distribution in the data was an incomplete sample from the community. ρ_t can be conceptualized as a measure of temporal beta-diversity (37). Equation 1 may be justified because the static species abundance distributions of these reef fish assemblages have been shown to be well described by the Poisson-lognormal distribution (39). As a further check, we conducted parametric bootstrap tests (bootstrap $N = 100$ for each fitted bivariate Poisson-lognormal distribution) to verify that the bivariate Poisson-lognormal is an adequate distribution for the LTMP data, and we found that none of our study reefs were statistically distinguishable from this distribution.

After fitting Eq. 1 to the estimates of pairwise correlation coefficients as a function of time lag, variance components of relative species abundance can be obtained as follows

$$\pi_r = \rho_\infty \tag{2}$$

$$\pi_e = \rho_0 - \rho_\infty \tag{3}$$

$$\pi_d = 1 - \rho_0 \tag{4}$$

where π_r represents the proportional variance in relative abundance due to deterministic, persistent differences among species, π_e represents the proportional variance in relative abundance due to species' responses to stochastic fluctuations in population size, and π_d represents the proportional (residual) variance in relative abundance due to overdispersion (demographic or sampling stochasticity).

Stochastic community dynamics model of VPRSA

The variance partitioning approach, VPRSA, described above and in Fig. 1, was explicitly derived from a stochastic theory of community dynamics. This theory characterizes the temporal dynamics of abundance of a community of S species according to the stochastic Ornstein-Ühlenbeck process

$$dX_i = (r_i - \delta X_i)\, dt + \sigma_e\, dW_i \tag{5}$$

$$r_i \sim \mathrm{N}(\mu_r, \sigma_r^2) \tag{6}$$

where X_i represents the abundance of species i on a logarithmic scale, r_i represents the intrinsic population growth rate of species i, δ measures the strength of density dependence, σ_e scales the magnitude of environmental fluctuations in the growth rate (i.e., larger σ_e implies larger fluctuations), and W_i models the fluctuations themselves as a Brownian (Wiener) process. Equation 6 specifies that intrinsic growth rates r_i vary among species according to a normal distribution with mean μ_r and variance σ_r^2. Equation 5 may be interpreted as a continuous-time analog of discrete-time Gompertz-type community dynamics.

Analysis of the model in Eqs. 5 and 6 reveals that each species' abundance fluctuates around a species-specific equilibrium "carrying capacity" ($e^{\frac{r_i}{\delta}}$), and both the carrying capacities and the abundances themselves follow lognormal distributions among species (36, 51). Notably, the stationary distribution of species' abundances remains lognormal, even in the presence of some violations of the model's simplifying assumptions, such as the incorporation of correlations in species' responses to environmental fluctuations, and of interspecific interactions (36, 37). The dynamic model is therefore consistent with the reef fish data in this study whose species abundance distributions are well described as discrete, random samples of individuals from lognormal abundance distributions (i.e., Poisson-lognormal distributions). In addition, previous work suggests that the Gompertz form of density dependence is appropriate for these data (59). For the model in Eqs. 5 and 6, the total variance in relative species abundance on log scale (hereafter σ_{total}^2) can be analytically partitioned into additive components as follows

$$\sigma_{\text{total}}^2 = \frac{\sigma_r^2}{\delta^2} + \frac{\sigma_e^2}{2\delta} + \theta^2 = \sigma_{\text{niche}}^2 + \sigma_{\text{env}}^2 + \theta^2 \tag{7}$$

and thus the proportional variance components π_r, π_e, and π_d (Eqs. 2 to 4) would be equal to $\frac{\sigma_{\text{niche}}^2}{\sigma_{\text{total}}^2}$, $\frac{\sigma_{\text{env}}^2}{\sigma_{\text{total}}^2}$, and $\frac{\theta^2}{\sigma_{\text{total}}^2}$, respectively (also see Fig. 1). Extension of the model in Eq. 5 to explicitly incorporate demographic variance (intrapopulation heterogeneity in demographic rates and demographic stochasticity) suggested that these effects will be principally captured by the θ^2 term of Eq. 7 and thus $\pi_d = 1 - \rho_0$ of Eq. 4, given that, similar to sampling effects, demographic variance will disproportionately affect observed abundances of the rare species. However, to be conservative, our interpretation takes account of the possibility that part of the stochastic fluctuations component of species abundance variance (i.e., $\pi_e = \rho_0 - \rho_\infty$ of Eq. 3) could be due to demographic stochasticity.

Some of the assumptions of the stochastic dynamics model in Eq. 5 are restrictive. Equation 5 assumes that the strength of density regulation and the magnitude of environmentally mediated fluctuations (i.e., variance in population growth rate due to environmental

fluctuations) are the same for all species, and it also assumes that there are neither species interactions nor any covariation in species' responses to environmental fluctuations. All these assumptions might be violated to some degree in our study system. For a community showing Gompertz-type dynamics, the lognormal stationary distribution of abundances is quite robust to these simplifying assumptions. However, to our knowledge, the robustness of variance component estimates has not been investigated previously, so we investigated this in considerable detail in Supplementary Simulation Study.

Estimating richness and unevenness based on VPRSA
We also used the Poisson-lognormal distribution (PLN) to estimate (time-averaged) alpha-diversity measures of richness and unevenness of reef fishes as follows. We fit this distribution to each of the 440 species abundance distributions (40 reefs × 11 years) using the method of maximum likelihood. Fitting this distribution yielded maximum likelihood estimates of the SD of log abundance (hereafter PLN-σ) for the underlying community from which the data are a sample. The skewness of a lognormal distribution is a function of this parameter alone, implying that the skewness (i.e., the unevenness) of abundances in the fish community from which the data are a sample is a monotonically increasing function of PLN-σ (i.e., larger values indicate more uneven communities). In addition, Poisson-lognormal fits can be used to estimate the total number of species in the community, by producing an estimate of the probability that a species is present in the community but not observed in the sample, denoted $\widetilde{P_0}$. An estimate of total community richness is simply the number of observed species divided by $1 - \widetilde{P_0}$. We estimated the PLN-σ^2 parameter (i.e., the variance of the species abundance distribution from which the sample was drawn) for each year using maximum likelihood methods, and then, we calculated the mean of these values across years for each reef as our reef-scale measure of unevenness (averaged PLN-σ^2 here is equivalent to σ^2_{total} in Eq. 7). Similarly, we used the mean of the estimated total community richness across years for each reef as our reef-scale measure of species richness.

There are two important advantages of using PLN-σ as an inverse measure of evenness: First, it is not sensitive to differences in sample completeness that may bias other evenness metrics, and, second, it can vary independently of species richness. These advantages make PLN-σ a particularly useful complement to richness as a diversity metric (37). In this respect, it is unlike other diversity indices, which are explicitly functions of both richness and evenness, making any differential responses of these two diversity components more difficult to disentangle. Nevertheless, to confirm that our findings were not sensitive to specific choice of diversity metrics, we repeated all analyses involving richness and evenness using raw observed richness, the nonparametric Chao1 estimator, and the Simpson and Shannon-Pielou diversity indices.

Parameter estimation for VPRSA
To estimate the three VPRSA components that completely partition the variation in relative abundances of fishes over years for each reef, we fitted a mixed-effects version of Eq. 1 to the LTMP dataset (Supplementary Text). Specifically, we fitted a family of nonlinear mixed-effects models, in which each of the fitted parameters (ρ_∞, ρ_0, and δ in Eq. 1) may be fixed constants for all reefs or they may randomly vary among reefs according to latent lognormal distributions (Supplementary Text). These models were parameterized in Template

Model Builder (TMB) in R. We fitted models with different combinations of the three temporal autocorrelation function parameters of Eq. 1 as fixed versus random, and we ranked model fits by AIC (Akaike information criterion) and bootstrapped AIC (Supplementary Text). We then checked for numerical stability of the model fits (i.e., we confirmed that the model's random effects parameter estimates were valid), and we chose the best-fitting model (by AIC and bootstrapped AIC) that yielded a numerically stable fit as our basis for inference (Supplementary Text). Next, we used the estimates of fixed and reef-level random effects of the best-fitting model to calculate variance components for each reef according to Eqs. 2 to 4.

Predicting among-reef variation in community properties obtained from VPRSA
We used a piecewise structural equation model (piecewise SEM) and ordinary least-squares (OLS) regression to investigate the extent to which variation among reefs in coral cover fluctuations [temporal mean, SD, and coefficient of variation (CV) of coral cover at each reef], latitude, and cross-shelf position may explain variation in reef fish community structure (variance components, species richness, and unevenness). SEM was performed using the R package "piecewiseSEM" (60). We chose latitude and cross-shelf position as our major explanatory variables because many factors that are likely to affect community structure on coral reefs, such as temperature, turbidity, and nutrient loading, vary strongly with one or both of these spatial variables (fig. S1). SD and CV of coral cover were both right-skewed, so they were log-transformed to reduce the heterogeneity of leverage values associated with the different reefs in our analysis [model selection yielded the same best-fitting models when they were untransformed, and R^2 values were higher ($R^2 = 0.55$), making our results conservative with respect to the conclusions drawn]. Log(SD) and log(CV) of coral cover were strongly collinear (Pearson's $r = 0.89$; table S10), and model selection always preferred models using SD rather than CV when analogous models were compared [e.g., AIC favors a multiple regression model with interactive effects of log(SD) and mean coral cover over a model with interactive effects of log(CV) and mean coral cover], so we have not presented results for the models using log(CV). In addition, the persistent species differences and stochastic fluctuation variance components were almost perfectly negatively correlated (Pearson's $r = -0.98$; table S11), so we omitted the stochastic fluctuation variance component from our piecewise SEM. None of the remaining explanatory variables were highly correlated with one another (tables S10 and S11). We used AIC and adjusted R^2 for model comparisons. We chose the parsimonious model with fewer parameters (effects) whenever AIC differences (ΔAIC) among candidates were smaller than 2 because, in these cases, adjusted R^2 favored the simpler models and because the additional variables included in the more complex models tended to have comparatively weak effects. In practice, this affected only model selection for unevenness, where the lowest AIC model included an additive effect of mean coral cover (in addition to a latitude × cross-shelf position interaction) that was small in magnitude and led to a marginally worse adjusted R^2 (table S4).

Last, because the reef-level proportional variance components were estimated from fits of another statistical model, rather than being directly observed, we also performed a sensitivity analysis to test the robustness of our results to parameter uncertainty. Specifically, we estimated the uncertainty in our estimates of variance components by parametric bootstrap, resampling random effects values for the

LTMP's 40 reefs 10,000 times from the variance-covariance matrix of the fitted nonlinear mixed-effects model based on TMB. Then, each bootstrap set of reef-level proportional variance component values was reanalyzed using the OLS regressions repeated on each of the bootstrapped datasets. We evaluated the robustness of our model selection procedure by quantifying the percentage of bootstrapped datasets for which each model was selected as the best model by AIC.

Sensitivity analysis of community properties among functional groups

Reef fish community data were separated into five major functional (trophic) groups: herbivores, planktivores, piscivores, corallivores, and benthic invertivores. These functional groups were classified according to previously published functional classifications of reef fishes, supplemented by communication with experts in the field (table S5). Of these functional groups, only three (i.e., herbivores, planktivores, and benthic invertivores) were sufficiently species-rich to analyze separately. We repeated all the analyses conducted on the overall dataset for each of the groups, as described above. We then compared the distribution of reef-scale estimates of variance components for the three functional groups with each other and with those for the pooled (i.e., across the whole dataset, not separated by functional groups) assemblages to determine whether the magnitudes of the variance components changed markedly when functional groups were considered independently. Formally, these comparisons were made with paired t tests with Bonferroni correction for multiple comparisons.

To examine the potential influence of coral cover variables on variance components of fish relative species abundance within functional groups, we fitted relationships between variance components and coral cover variables using OLS regression. In the full model, temporal mean and log-SD in coral cover and functional group were considered as explanatory variables. AIC was used for model selection, beginning with a model including all main effects and interactions. Effects of latitude, cross-shelf position, and functional group on richness and unevenness were also examined in a similar fashion.

SUPPLEMENTARY MATERIALS

REFERENCES AND NOTES

1. J. B. C. Jackson, M. K. Donovan, K. L. Cramer, V. V Lam, "Status and trends of Caribbean coral reefs" (Global Coral Reef Monitoring Network, IUCN, 2014).
2. S. F. Heron, C. M. Eakin, F. Douvere, K. L. Anderson, J. C. Day, E. Geiger, O. Hoegh-Guldberg, R. Van Hooidonk, T. Hughes, P. Marshall, "Impacts of climate change on World Heritage coral reefs: A first global scientific assessment" (UNESCO World Heritage Centre, 2017).
3. D. Obura, M. Gudka, M. Samoilys, K. Osuka, J. Mbugua, D. A. Keith, S. Porter, R. Roche, R. van Hooidonk, S. Ahamada, A. Araman, J. Karisa, J. Komakoma, J. Madi, I. Ravinia, H. Razafindrainibe, S. Yahya, F. Zivane, Vulnerability to collapse of coral reef ecosystems in the Western Indian Ocean. *Nat. Sustain.* **5**, 104–113 (2022).
4. T. P. Hughes, M. L. Barnes, D. R. Bellwood, J. E. Cinner, G. S. Cumming, J. B. C. Jackson, J. Kleypas, I. A. van de Leemput, J. M. Lough, T. H. Morrison, S. R. Palumbi, E. H. van Nes, M. Scheffer, Coral reefs in the Anthropocene. *Nature* **546**, 82–90 (2017).
5. J. B. C. Jackson, M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–637 (2001).
6. T. P. Hughes, K. D. Anderson, S. R. Connolly, S. F. Heron, J. T. Kerry, J. M. Lough, A. H. Baird, J. K. Baum, M. L. Berumen, T. C. Bridge, D. C. Claar, C. M. Eakin, J. P. Gilmour, N. A. J. Graham, H. Harrison, J.-P. A. Hobbs, A. S. Hoey, M. Hoogenboom, R. J. Lowe, M. T. McCulloch, J. M. Pandolfi, M. Pratchett, V. Schoepf, G. Torda, S. K. Wilson, Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* **359**, 80–83 (2018).
7. P. Houk, R. Camacho, S. Johnson, M. McLean, S. Maxin, J. Anson, E. Joseph, O. Nedlic, M. Luckymis, K. Adams, D. Hess, E. Kabua, A. Yalon, E. Buthung, C. Graham, T. Leberer, B. Taylor, R. van Woesik, The Micronesia challenge: Assessing the relative contribution of stressors on coral reefs to facilitate science-to-management feedback. *PLOS ONE* **10**, e0130823 (2015).
8. K. L. Cramer, J. B. C. Jackson, M. K. Donovan, B. J. Greenstein, C. A. Korpanty, G. M. Cook, J. M. Pandolfi, Widespread loss of Caribbean acroporid corals was underway before coral bleaching and disease outbreaks. *Sci. Adv.* **6**, eaax9395 (2020).
9. T. P. Hughes, J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, M. Beger, D. R. Bellwood, R. Berkelmans, T. C. Bridge, I. R. Butler, M. Byrne, N. E. Cantin, S. Comeau, S. R. Connolly, G. S. Cumming, S. J. Dalton, G. Diaz-Pulido, C. M. Eakin, W. F. Figueira, J. P. Gilmour, H. B. Harrison, S. F. Heron, A. S. Hoey, J.-P. A. Hobbs, M. O. Hoogenboom, E. V. Kennedy, C. Kuo, J. M. Lough, R. J. Lowe, G. Liu, M. T. McCulloch, H. A. Malcolm, M. J. McWilliam, J. M. Pandolfi, R. J. Pears, M. S. Pratchett, V. Schoepf, T. Simpson, W. J. Skirving, B. Sommer, G. Torda, D. R. Wachenfeld, B. L. Willis, S. K. Wilson, Global warming and recurrent mass bleaching of corals. *Nature* **543**, 373–377 (2017).
10. T. P. Hughes, J. T. Kerry, A. H. Baird, S. R. Connolly, A. Dietzel, C. M. Eakin, S. F. Heron, A. S. Hoey, M. O. Hoogenboom, G. Liu, M. J. McWilliam, R. J. Pears, M. S. Pratchett, W. J. Skirving, J. S. Stella, G. Torda, Global warming transforms coral reef assemblages. *Nature* **556**, 492–496 (2018).
11. C. J. Randall, R. van Woesik, Contemporary white-band disease in Caribbean corals driven by climate change. *Nat. Clim. Chang.* **5**, 375–379 (2015).
12. A. J. Cheal, M. A. MacNeil, M. J. Emslie, H. Sweatman, The threat to coral reefs from more intense cyclones under climate change. *Glob. Chang. Biol.* **23**, 1511–1524 (2017).
13. V. Y. Y. Lam, M. Chaloupka, A. Thompson, C. Doropoulos, P. J. Mumby, Acute drivers influence recent inshore Great Barrier Reef dynamics. *Proc. R. Soc. B* **285**, 20182063 (2018).
14. D. H. Williamson, D. M. Ceccarelli, R. D. Evans, G. P. Jones, G. R. Russ, Habitat dynamics, marine reserve status, and the decline and recovery of coral reef fish communities. *Ecol. Evol.* **4**, 337–354 (2014).
15. J. E. Brodie, F. J. Kroon, B. Schaffelke, E. C. Wolanski, S. E. Lewis, M. J. Devlin, I. C. Bohnet, Z. T. Bainbridge, J. Waterhouse, A. M. Davis, Terrestrial pollutant runoff to the Great Barrier Reef: An update of issues, priorities and management responses. *Mar. Pollut. Bull.* **65**, 81–100 (2012).
16. M. A. MacNeil, C. Mellin, S. Matthews, N. H. Wolff, T. R. McClanahan, M. Devlin, C. Drovandi, K. Mengersen, N. A. J. Graham, Water quality mediates resilience on the Great Barrier Reef. *Nat. Ecol. Evol.* **3**, 620–627 (2019).
17. G. De'ath, K. E. Fabricius, H. Sweatman, M. Puotinen, The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 17995–17999 (2012).
18. K. E. Fabricius, K. Okaji, G. De'Ath, Three lines of evidence to link outbreaks of the crown-of-thorns seastar Acanthaster planci to the release of larval food limitation. *Coral Reefs.* **29**, 593–605 (2010).
19. J.-C. Ortiz, N. H. Wolff, K. R. N. Anthony, M. Devlin, S. Lewis, P. J. Mumby, Impaired recovery of the Great Barrier Reef under cumulative stress. *Sci. Adv.* **4**, eaar6127 (2018).
20. J. F. Bruno, E. R. Selig, Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons. *PLOS ONE* **2**, e711 (2007).
21. L. E. Richardson, N. A. J. Graham, M. S. Pratchett, J. G. Eurich, A. S. Hoey, Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Glob. Chang. Biol.* **24**, 3117–3129 (2018).
22. S. K. Wilson, N. A. J. Graham, M. S. Pratchett, G. P. Jones, N. V. C. Polunin, Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? *Glob. Chang. Biol.* **12**, 2220–2234 (2006).
23. G. Strona, P. S. A. Beck, M. Cabeza, S. Fattorini, F. Guilhaumon, F. Micheli, S. Montano, O. Ovaskainen, S. Planes, J. A. Veech, V. Parravicini, Ecological dependencies make remote reef fish communities most vulnerable to coral loss. *Nat. Commun.* **12**, 7282 (2021).
24. R. A. Morais, M. Depczynski, C. Fulton, M. Marnane, P. Narvaez, V. Huertas, S. J. Brandl, D. R. Bellwood, Severe coral loss shifts energetic dynamics on a coral reef. *Funct. Ecol.* **34**, 1507–1518 (2020).
25. N. A. J. Graham, S. K. Wilson, S. Jennings, N. V. C. Polunin, J. A. N. Robinson, J. P. Bijoux, T. M. Daw, Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv. Biol.* **21**, 1291–1300 (2007).
26. G. R. Russ, J. R. Rizzari, R. A. Abesamis, A. C. Alcala, Coral cover a stronger driver of reef fish trophic biomass than fishing. *Ecol. Appl.* **31**, e02224 (2021).
27. S. J. Holbrook, R. J. Schmitt, A. J. Brooks, Resistance and resilience of a coral reef fish community to changes in coral cover. *Mar. Ecol. Prog. Ser.* **371**, 263–271 (2008).
28. S. K. Wilson, A. M. Dolman, A. J. Cheal, M. J. Emslie, M. S. Pratchett, H. P. A. Sweatman, Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs.* **28**, 3–14 (2009).
29. D. R. Bellwood, A. H. Baird, M. Depczynski, A. González-Cabello, A. S. Hoey, C. D. Lefèvre, J. K. Tanner, Coral recovery may not herald the return of fishes on damaged coral reefs. *Oecologia* **170**, 567–573 (2012).

30. S. Wismer, S. B. Tebbett, R. P. Streit, D. R. Bellwood, Young fishes persist despite coral loss on the Great Barrier Reef. *Commun. Biol.* **2**, 456 (2019).

31. M. Dornelas, N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, A. E. Magurran, Assemblage time series reveal biodiversity change but not systematic loss. *Science* **344**, 296–299 (2014).

32. S. A. Blowes, S. R. Supp, L. H. Antão, A. Bates, H. Bruelheide, J. M. Chase, F. Moyes, A. Magurran, B. McGill, I. H. Myers-Smith, M. Winter, A. D. Bjorkman, D. E. Bowler, J. E. K. Byrnes, A. Gonzalez, J. Hines, F. Isbell, H. P. Jones, L. M. Navarro, P. L. Thompson, M. Vellend, C. Waldock, M. Dornelas, The geography of biodiversity change in marine and terrestrial assemblages. *Science* **366**, 339–345 (2019).

33. A. E. Magurran, *Measuring Biological Diversity* (John Wiley & Sons, 2003).

34. A. R. McLean, R. M. May, *Theoretical Ecology: Principles and Applications* (Oxford Univ. Press on Demand, 2007).

35. G. Sugihara, L.-F. Bersier, T. R. E. Southwood, S. L. Pimm, R. M. May, Predicted correspondence between species abundances and dendrograms of niche similarities. *Proc. Natl. Acad. Sci.* **100**, 5246–5251 (2003).

36. R. Lande, S. Engen, B. Saether, *Stochastic Population Dynamics in Ecology and Conservation* (Oxford Univ. Press on Demand, 2003).

37. B. Sæther, S. Engen, V. Grøtan, Species diversity and community similarity in fluctuating environments: Parametric approaches using species abundance distributions. *J. Anim. Ecol.* **82**, 721–738 (2013).

38. M. Bode, S. R. Connolly, J. M. Pandolfi, Species differences drive nonneutral structure in pleistocene coral communities. *Am. Nat.* **180**, 577–588 (2012).

39. S. R. Connolly, M. A. MacNeil, M. J. Caley, N. Knowlton, E. Cripps, M. Hisano, L. M. Thibaut, B. D. Bhattacharya, L. Benedetti-Cecchi, R. E. Brainard, A. Brandt, F. Bulleri, K. E. Ellingsen, S. Kaiser, I. Kröncke, K. Linse, E. Maggi, T. D. O'Hara, L. Plaisance, G. C. B. Poore, S. K. Sarkar, K. K. Satpathy, U. Schückel, A. Williams, R. S. Wilson, Commonness and rarity in the marine biosphere. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 8524–8529 (2014).

40. S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)* (Princeton Univ. Press, 2001).

41. I. Volkov, J. R. Banavar, S. P. Hubbell, A. Maritan, Patterns of relative species abundance in rainforests and coral reefs. *Nature* **450**, 45–49 (2007).

42. T. Fung, J. P. O'Dwyer, K. A. Rahman, C. D. Fletcher, R. A. Chisholm, Reproducing static and dynamic biodiversity patterns in tropical forests: The critical role of environmental variance. *Ecology* **97**, 1207–1217 (2016).

43. S. Engen, E. B. Solbu, B. Sæther, Neutral or non-neutral communities: Temporal dynamics provide the answer. *Oikos* **126**, 318–331 (2017).

44. R. C. Rael, R. D'Andrea, G. Barabás, A. Ostling, Emergent niche structuring leads to increased differences from neutrality in species abundance distributions. *Ecology* **99**, 1633–1643 (2018).

45. H. Hillebrand, B. Blasius, E. T. Borer, J. M. Chase, J. A. Downing, B. K. Eriksson, C. T. Filstrup, W. S. Harpole, D. Hodapp, S. Larsen, Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *J. Appl. Ecol.* **55**, 169–184 (2018).

46. A. E. Magurran, M. Dornelas, F. Moyes, N. J. Gotelli, B. McGill, Rapid biotic homogenization of marine fish assemblages. *Nat. Commun.* **6**, 8405 (2015).

47. J. E. Duffy, J. S. Lefcheck, R. D. Stuart-Smith, S. A. Navarrete, G. J. Edgar, Biodiversity enhances reef fish biomass and resistance to climate change. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 6230–6235 (2016).

48. S. A. Blowes, J. Belmaker, J. M. Chase, Global reef fish richness gradients emerge from divergent and scale-dependent component changes. *Proc. R. Soc. B* **284**, (2017).

49. T. Lamy, P. Legendre, Y. Chancerelle, G. Siu, J. Claudet, Understanding the spatio-temporal response of coral reef fish communities to natural disturbances: Insights from beta-diversity decomposition. *PLOS ONE* **10**, e0138696 (2015).

50. T. J. Matthews, R. J. Whittaker, REVIEW: On the species abundance distribution in applied ecology and biodiversity management. *J. Appl. Ecol.* **52**, 443–454 (2015).

51. S. Engen, R. Lande, T. Walla, P. J. DeVries, Analyzing spatial structure of communities using the two-dimensional Poisson lognormal species abundance model. *Am. Nat.* **160**, 60–73 (2002).

52. C. Mellin, C. J. A. Bradshaw, M. G. Meekan, M. J. Caley, Environmental and spatial predictors of species richness and abundance in coral reef fishes. *Glob. Ecol. Biogeogr.* **19**, 212–222 (2010).

53. A. Cheal, M. Emslie, I. Miller, H. Sweatman, The distribution of herbivorous fishes on the Great Barrier Reef. *Mar. Biol.* **159**, 1143–1154 (2012).

54. A. S. Hoey, S. J. Brandl, D. R. Bellwood, Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: Implications for ecosystem function. *Coral Reefs* **32**, 973–984 (2013).

55. D. R. Bellwood, A. S. Hoey, J. H. Choat, Limited functional redundancy in high diversity systems: Resilience and ecosystem function on coral reefs. *Ecol. Lett.* **6**, 281–285 (2003).

56. D. R. Bellwood, R. P. Streit, S. J. Brandl, S. B. Tebbett, The meaning of the term 'function' in ecology: A coral reef perspective. *Funct. Ecol.* **33**, 948–961 (2019).

57. C. Mellin, M. A. MacNeil, A. J. Cheal, M. J. Emslie, M. J. Caley, Marine protected areas increase resilience among coral reef communities. *Ecol. Lett.* **19**, 629–637 (2016).

58. H. Sweatman, S. Burgess, A. Cheal, G. Coleman, S. Delean, M. Emslie, A. McDonald, I. Miller, K. Osborne, A. Thompson, "Long-term monitoring of the Great Barrier Reef. Status Report Number 7" (2005).

59. L. M. Thibaut, S. R. Connolly, H. Sweatman, Diversity and stability of herbivorous fishes on coral reefs. *Ecology* **93**, 891–901 (2012).

60. J. S. Lefcheck, PIECEWISESEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579 (2016).

61. C. Wager, F. Vaida, G. Kauermann, Model selection for penalized spline smoothing using Akaike information criteria. *Aust. N. Z. J. Stat.* **49**, 173–190 (2007).

62. S. Greven, T. Kneib, On the behaviour of marginal and conditional AIC in linear mixed models. *Biometrika* **97**, 773–789 (2010).

63. S. A. Matthews, C. Mellin, A. MacNeil, S. F. Heron, W. Skirving, M. Puotinen, M. J. Devlin, M. Pratchett, High-resolution characterization of the abiotic environment and disturbance regimes on the Great Barrier Reef, 1985–2017. *Ecology* **100**, e02574 (2019).

64. M. L. Baskett, N. S. Fabina, K. Gross, Response diversity can increase ecological resilience to disturbance in coral reefs. *Am. Nat.* **184**, E16–E31 (2014).

65. R. A. Myers, K. G. Bowen, N. J. Barrowman, Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* **56**, 2404–2419 (1999).

66. G. Gellner, K. S. McCann, Consistent role of weak and strong interactions in high- and low-diversity trophic food webs. *Nat. Commun.* **7**, 1–7 (2016).

67. A. R. Ives, B. Dennis, K. L. Cottingham, S. R. Carpenter, Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.* **73**, 301–330 (2003).