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Research Article

Asynchronous population trends stabilize mesopredatory coral reef fish communities in the face of global change

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Biodiversity can underpin stability in communities, allowing them to withstand environmental fluctuations without changes in aggregate properties like total abundance or biomass. We investigated the influence of biodiversity on two crucial population-level mechanisms governing abundance stability in mesopredatory coral reef fishes: 1) 'community asynchrony', where species populations fluctuate inversely over time, and 2) 'species population stability', where highly abundant species with significant community contributions display minimal population fluctuations. Analysing temporal data from 197 reef fish communities across the Indian and Pacific Oceans over a decade, we found that community asynchrony, rather than species population stability, primarily predicted community stability. Functional diversity, not taxonomic diversity, characterized this stability, emphasizing the role of niche differences in stabilizing communities. Heat stress had a significant direct and indirect effect on community stability, while the effect of anthropogenic pressures was weak and site-specific. Our results suggest community attributes such as high functional diversity promote asynchronous population fluctuations, likely by enhancing response diversity, and are vital for stabilizing mesopredatory reef fish communities in the face of global change.

Keywords: biotic interactions, community asynchrony, community stability, response diversity, species population stability

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Introduction

Reliable functioning of ecosystems is essential for achieving many sustainability targets, and understanding the drivers of that reliability remains a key scientific challenge (Anderson et al. 2019). Research on the link between biodiversity and ecosystem stability has expanded considerably in the past three decades, offering insight into how biodiversity influences communities and ecosystem functions such as productivity and biomass generation (van der Plas 2019, Xu et al. 2021). Community stability indicates the extent to which whole-community attributes, for example, total abundance or biomass, resist and recover from environmental change (Tilman and Downing 1994). Two dominant mechanisms have been shown to support this stability (Thibaut and Connolly 2013); first, 'community synchrony' refers to how populations of species within the community are correlated over time (Loreau and de Mazancourt 2013), with stronger negative correlations helping to stabilize community properties (Mcnaughton 1978). Second, 'species population stability' (Doak et al. 1998, Gonzalez and Loreau 2009, Thibaut and Connolly 2013) suggests that community stability may depend on the dominance of species with higher or lower population-level stability. Determining which mechanism prevails in a given ecosystem is challenging (Tsang et al. 2023), as the influence of these mechanisms is shaped by local factors like diversity (McCann 2000), disturbance intensity (Zelnik et al. 2018), and spatial connectivity (Hodapp et al. 2023). As stable communities are more likely to provide predictable ecological functions and services (Worm et al. 2006, Cardinale et al. 2012), understanding the underlying mechanisms is critical in the current times of rapid biodiversity loss.

Diversity in species (taxonomic diversity, TD) and traits (functional diversity, FD) can stabilize community properties by influencing community synchrony and species population stability mechanisms (Craven et al. 2018). For instance. greater TD (specifically, species richness) dampens community synchrony (i.e. enhances community asynchrony) through 'insurance effects' (Ives et al. 2000), i.e. there is increased likelihood of the presence of species with differential responses to disturbances (Yachi and Loreau 1999). Alternatively, it can stabilize communities through 'statistical averaging' or 'portfolio effects', whereby communities composed of many independently fluctuating species are more stable (Tilman 1999, Loreau et al. 2021). Taxonomic diversity can also support species population stability through 'selection effects' which increase the likelihood of the presence of dominant, resistant species which contribute disproportionately to stability (Hallett et al. 2014).

The role of FD is more nuanced: a greater diversity of functions predominantly stabilizes communities through 'compensatory dynamics', due to species opposing responses to environmental drivers (Loreau and de Mazancourt 2013, Loreau et al. 2021). However, biotic interactions driven by functionally distinct species can destabilize individual populations, and their effects on aggregate community stability depend on interaction strength and network structure (Loreau and de Mazancourt 2013). Predator–prey interactions may be stabilizing, whereas competitive and mutualistic interactions can be destabilizing under some network configurations (Allesina and Tang 2012). Conversely, mixtures of antagonistic and mutualistic interaction types can stabilize community dynamics (Mougi and Kondoh 2012).

Despite a wide range of hypotheses for how TD and FD may influence community stability, empirical support for their relative importance, particularly for higher trophic levels, remains uncertain due to research focus on lower trophic level guilds like primary producers and consumers (Jiang et al. 2009, Xu et al. 2021). Higher trophic guilds (secondary or tertiary consumers), typically rich in interactions within and across guilds, including predation, facilitation, and mutualism, remain largely understudied (Loreau et al. 2001, Srednick and Swearer 2024). Further, community stability research has predominantly focused on variation along natural environmental gradients, such as temperature, precipitation, and nutrient enrichment (Hallett et al. 2014). While these environmental drivers often impact communities through synchrony mechanisms, local anthropogenic disturbances like hunting can directly alter the abundance of dominant or keystone species potentially influencing community stability through the species population stability mechanism (Segrestin et al. 2024, White et al. 2024). The combined influence of environmental and anthropogenic drivers is rarely studied in tandem, hindering our understanding of their relative effects. Assessing stability mechanisms in natural ecosystems that account for both environmental and anthropogenic pressures is therefore critical for capturing the complexities of real-world community dynamics.

Coral reefs serve as important model systems to study community stabilizing effects due to their rich TDand FD along substantial natural and anthropogenic gradients (Bellwood and Hughes 2001, Stuart-Smith et al. 2013), uneven species distributions, and wide variety of species interactions (Brandl et al. 2019). Reef fish also play a crucial role in coral reef productivity and functioning and support essential ecosystem services like fisheries (Woodhead et al. 2019). However, the TD and FD of reef fish has been severely impacted over recent decades due to habitat degradation driven by fishing and mass coral-bleaching (D'Agata et al. 2014), with consequences for temporal community stability (Yan et al. 2023). Mesopredatory coral reef fishes from families such as *Serranidae*, *Lutjanidae*, *Lethrinidae*, *Scorpaenidae*, and *Holocentridae* are typically site-attached and strongly dependent on benthic habitat structure, making them particularly vulnerable to both fishing pressure and habitat degradation: fishing reduces their populations directly through targeted or incidental catch; while their life-history traits such as slow growth, late maturity, and higher trophic level further increase their susceptibility to exploitation (Jennings et al. 1999). Habitat loss also affects these fishes by reducing prey availability and accessibility, and limiting access to shelter (Kerry and Bellwood 2015, Hempson et al. 2017, Khan et al. 2017). Further, many mesopredatory fish display high dietary overlap, diet generalization, and foraging plasticity (Farmer

and Wilson 2011, Hempson et al. 2017, Karkarey et al. 2017, Parravicini et al. 2020), suggesting low resource specialization and intense competition for resources. Furthermore, whether temporal changes in mesopredatory fish communities are stabilized by mechanisms such as community asynchrony or by the stability of individual populations may have important trophic implications. For example, a community dominated by a few stable and strongly interacting species may be more prone to destabilization than one composed of fluctuating, weakly interacting species (McCann et al. 1998). The latter may diffuse top–down effects on lower trophic groups, thereby buffering against trophic cascades (McCann et al. 1998, Jiang et al. 2009, Brashares et al. 2010). Despite their importance, the mechanisms underlying mesopredator community stability remain poorly understood.

Here, we aim to determine how biodiversity influences community stability, measured as the inverse of variability in community abundance, within a diverse, multitrophic mesopredatory coral reef fish community facing two major stressors: climate change-related heat stress and anthropogenic pressures like fishing and coastal development (Fig. 1). We quantify long-term population changes over a decade (2010–2021) across 481 species on 197 reefs in 19 locations throughout the Indo-Pacific, spanning gradients of diversity, anthropogenic pressure, and bleaching-induced coral mortality from ocean warming. Our focus is on the stability of community abundance over time to assess 1) how community stability varies across biogeographic regions (western Indian-Pacific Ocean, central Indo-Pacific Ocean, and eastern Indo-Pacific Ocean; Kulbicki et al. 2013), 2) the dominant stabilizing mechanisms (community synchrony versus species population stability) within these regions, 3) the influence of TD and FD on local community stability, and 4) how community stability and these mechanisms respond to a global environmental stressor (heat stress) and local anthropogenic stressors (human impacts including fishing and coastal development; Fig. 1, Table 1).

Material and methods

Reef fish community data

We used time-series fish community data from 197 tropical coral reef sites sampled between 2010 and 2020 in three biogeographic regions: western Indo-Pacific Ocean (Comoros, Mascarenes Lakshadweep Islands, Seychelles), central Indo-Pacific Ocean (Western Australia, Indonesia, New Caledonia), and eastern Pacific Ocean (across Austral, Line, Marquesas, Pitcairn, Society, South Cook and Tuamotu Islands, Samoa and Tonga; Fig. 2A). Reef fish were sampled using belt transects in most regions except Seychelles, where stationary point counts were used (see the Supporting information for additional details on the sampling protocol in different regions and Brandl et al. 2024). Belt transect areas varied from 100 m^2 (50 × 2 m) to 250 m^2 (50 × 5 m) between locations, while point count areas were 153 m^2 (radius 7 m). The two techniques have been shown to give consistent community estimates of reef fish (Samoilys and Carlos 2000), and have been combined successfully in numerous previous large-scale studies (MacNeil et al. 2015, Cinner et al. 2020). Between 4 and 16 replicates (belt/point counts) were sampled annually on each reef. To make fish abundances comparable across methods and sampling areas, all abundances were standardised to a common area of 100 m^2 by first converting counts to densities per m^2 and then multiplying by 100 for each replicate.

To standardize the spatial scale of sampling, transects within 1 km of each other were grouped using hierarchical clustering of site coordinates: pairwise geographic distances were computed with the R 'Geosphere' package (Hijmans 2024; www.r-project.org), and complete-linkage clustering assigned transects within a 1 km threshold, to the same spatial cluster. Within each cluster, species abundances from all transects or point counts sampled up to 17 m depth were averaged at the level of reef zone (lagoon, flat, crest-slope, or NA where reef zone information was unavailable). This produced area-standardised cluster-by-zone community time series (n = 229 sites) for subsequent analyses.

Mesopredatory fishes were defined as small- to medium-sized (i.e. 10–80 cm) secondary consumers belonging to 19 different families (Supporting information). We restricted our sampling to sites with at least three years of monitoring and three species in the community, which is the minimum data requirement for the calculation of FD and community stability metrics in the packages 'mFD' (Magneville et al. 2022) and 'codyn' (Hallett et al. 2016), respectively. A total of 197 sites and 481 species was included in the analysis.

Fish traits

Following Hadj-Hammou et al. (2021) we characterised the trait space for all mesopredatory fish species in each community based on six common functional traits that have been investigated in relation to responding to disturbances (i.e. response traits): dietary guild (Parravicini et al. 2020), body size, water column position, activity, mobility, and social grouping (Supporting information). We used the functional entity approach implemented in the 'mFD' package, in which species are grouped according to identical combinations of trait modalities. Each unique trait combination across dietary guild, body size, water column position, activity, mobility, and social grouping was treated as a distinct functional entity, and all species sharing that trait profile were assigned to the same entity. We conducted a principal coordinates analysis (PCoA) on a distance matrix computed from Gower's distances (Gower 1971) between functional entities. This distance matrix was used in the calculation of FD (below). The first two axes of the functional entities explained 78% variation in fish functional space (Supporting information) and were used in calculation of FD indices. PC1 differentiated species based on body size and mobility as smaller species were positively correlated, while very mobile species and piscivores were negatively correlated with PC1, indicating an axis related to food acquisition. In contrast, PC2 differentiated species based on schooling and the position in the

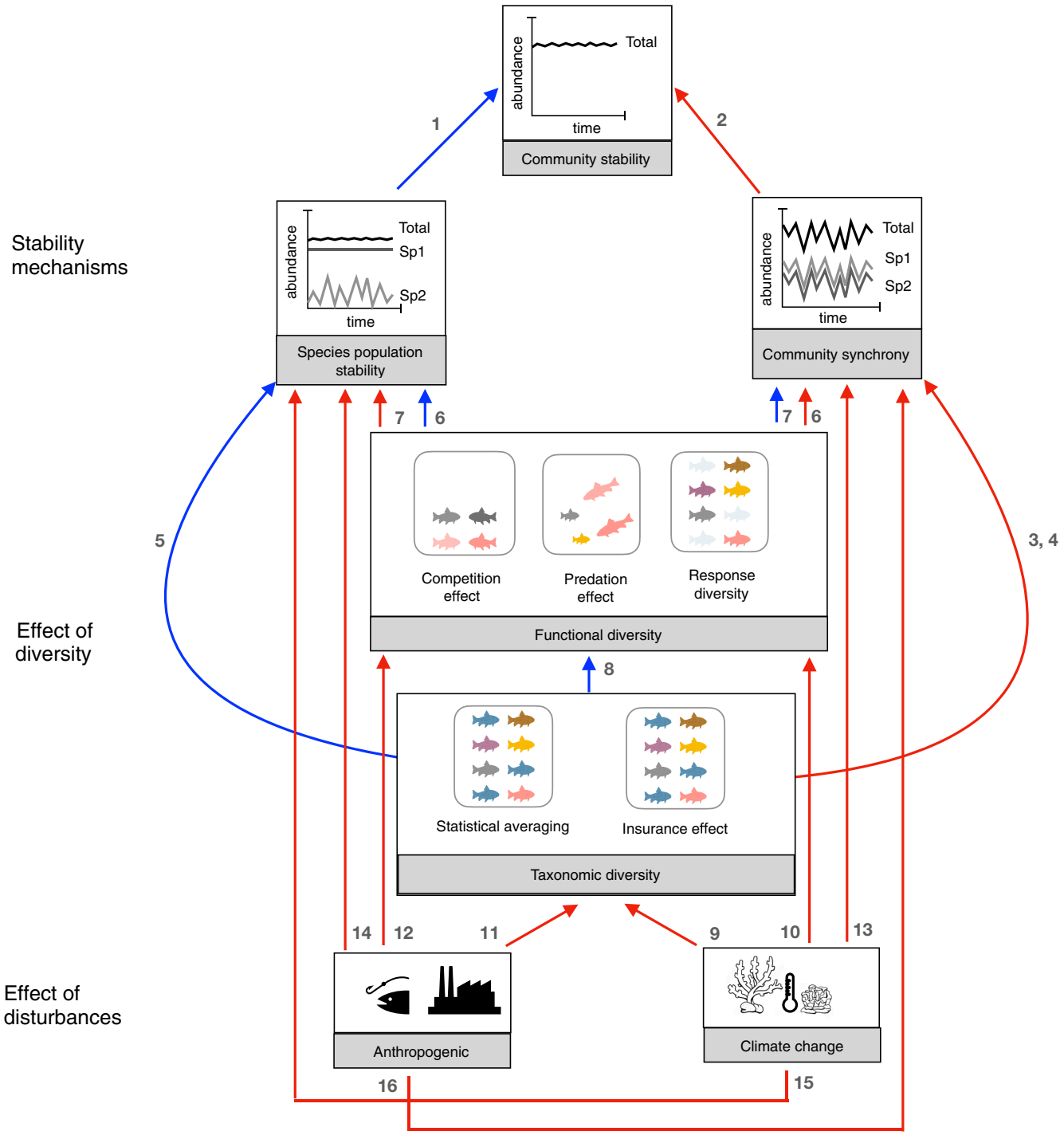

Figure 1. A conceptual model of the effect of stability mechanisms (community synchrony and species population stability), biodiversity (taxonomic and functional), and disturbance (environmental and anthropogenic) on community stability. Numbers correspond to hypothesized mechanisms defined in detail in Table 1. Solid blue arrows represent hypothesized positive effects, and red arrows represent hypothesized negative effects.

water column, representing an axis related to gregariousness and benthic structure dependence (Supporting information). In total, the 481 species were captured within 176 different functional entities.

Biodiversity indices

We used the integrative framework of Chao et al. (2019), based on Hill numbers and distance-based attribute diversity to calculate TD and FD. Hill numbers ('effective

Table 1. Proposed mechanisms and drivers of community abundance stability in mesopredatory coral reef fish (illustrated in Fig. 1).

Driver	Index	Effect on community stability	Mechanisms	Path in Fig. 1
Species population stability	Abundance-weighted average population stability, representing the stability of species' year-to-year fluctuations (Thibaut and Connolly 2013).	Stabilizing	Stable, abundant species contribute disproportionately to aggregate community properties and can therefore increase community stability (Hillebrand and Bennett 2008, Sasaki and Lauenroth 2011, Hallett et al. 2014).	1
Community synchrony	Loreau–de Mazancourt synchrony index, where 0 indicates asynchrony and 1 indicates perfect synchrony (Loreau and de Mazancourt 2008).	Destabilizing	Shared environmental responses, low response diversity, and some interaction structures can increase synchrony. Niche differentiation and compensatory interactions can reduce synchrony (Elmqvist et al. 2003, Thébault and Loreau 2005, Allesina and Tang 2012).	2
Taxonomic diversity, TD	Species richness: Within the integrated Hill–Chao framework, TD is the effective number of equally abundant species. At, it equals species richness because all species are weighted equally (Chao et al. 2021).	Stabilizing	Diversity can stabilize communities through: 1) an insurance effect or 2) statistical averaging of species fluctuations which increases community asynchrony or through a 3) stable-dominant effect which increases species population stability (Doak et al. 1998, Yachi and Loreau 1999, Thibaut and Connolly 2013, Hallett et al. 2014).	3, 4, 5
Functional diversity, FD: response-diversity pathway	Within the integrated Hill–Chao framework, FD is the effective number of equally abundant and functionally equally distinct virtual functional groups at threshold. In this study, emphasizes abundant species and is set to the mean pairwise functional distance (Chao et al. 2019, 2021).	Stabilizing	Functional differences can generate response diversity, resource-use complementarity, and compensatory dynamics, thereby reducing synchrony and buffering community-level fluctuations (Loreau and Hector 2001, Elmqvist et al. 2003, Thibaut and Connolly 2013).	6
Functional diversity, FD	Same FD measure as above.	Can be destabilizing	Functional differences can alter interaction strengths and network structure. Competition and mutualism may destabilize communities under some network configurations, whereas predator–prey interactions may be stabilizing (Thébault and Loreau 2005, Allesina and Tang 2012).	7
Climate change (Heat stress)	Degree heating weeks (DHW) quantifies cumulative thermal stress as the number of weeks sea surface temperature (SST) exceeds the climatological maximum summer temperature by +1°C (Skirving et al. 2020).	Destabilizing	Repeated bleaching and coral loss can filter species and traits, reduce functional redundancy and response diversity, and potentially increase synchrony during subsequent disturbances (Elmqvist et al. 2003, Pratchett et al. 2011, Richardson et al. 2018).	9, 10, 13, 15
Anthropogenic pressure	Human gravity index, combining human population pressure with accessibility or travel time to reefs (Cinner et al. 2018).	Destabilizing	Selective fishing can remove targeted species and trait combinations, reducing functional diversity and response diversity. Changes in dominant species' abundance and biomass can also alter biomass-weighted population stability and aggregate community fluctuations (Martins et al. 2012, D'Agata et al. 2014, Mahaut et al. 2025).	11, 12, 14, 16

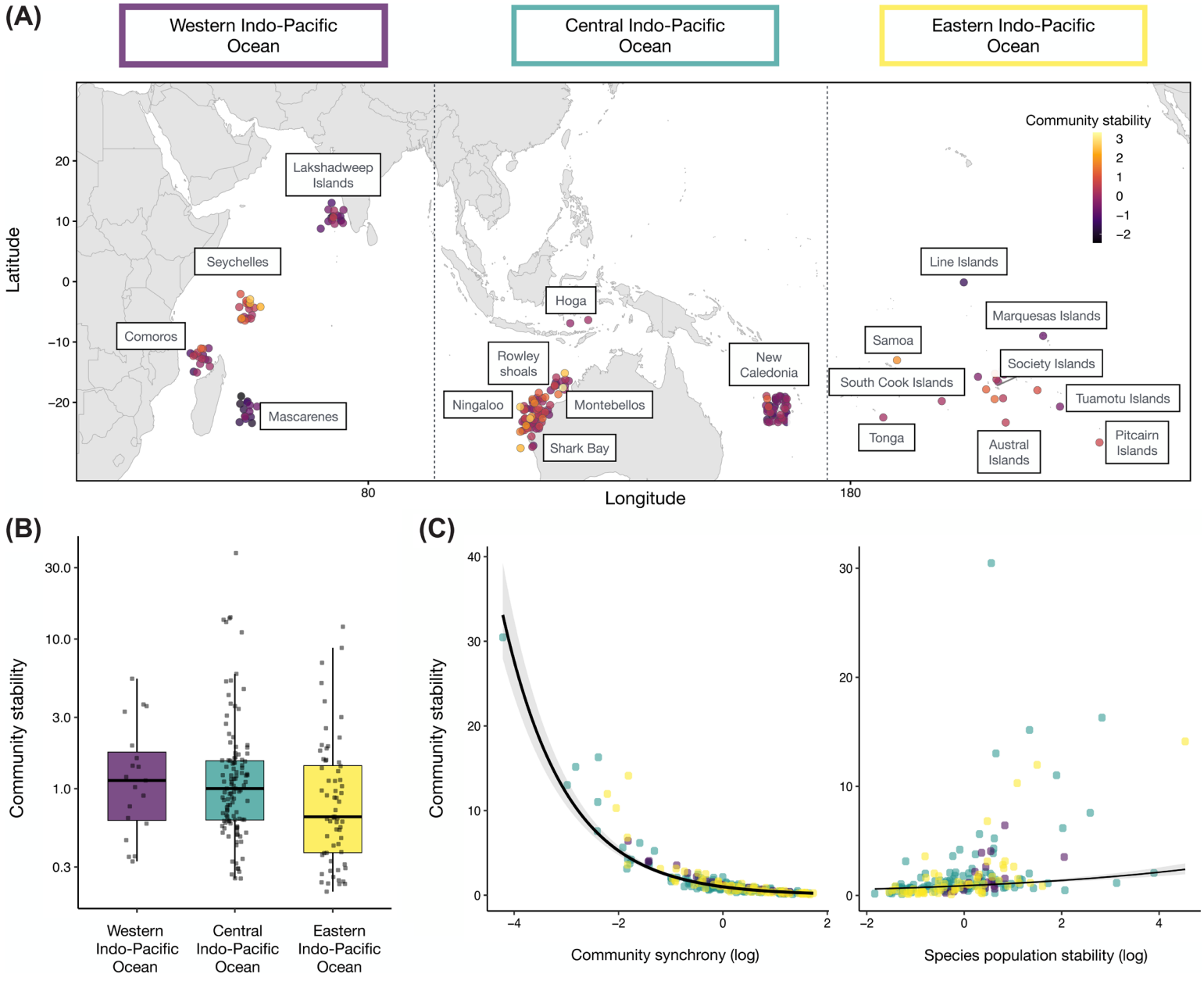

Figure 2. Spatial variation in community stability across coral reef sites. (A) Distribution of 197 coral reef sites and their community stability values across three biogeographic regions: western Indo-Pacific (WIP), central Indo-Pacific (CIP), and eastern Indo-Pacific (EIP). (B) Boxplots of community stability across locations within each biogeographic region. (C) Predicted community stability based on a linear mixed-effects model including community synchrony and species population stability as regulating mechanisms, with zone nested within sites nested within biogeographic region as a random effect. Grey bars indicate 95% confidence intervals. Point colours correspond to biogeographic region: WIP = purple, CIP = teal, and EIP = yellow. [Correction added on September 2, 2026, after first online publication: Figure 2 has been updated in this version.]

number of species') are a family of diversity indices that vary in parameter 'q', which describes the sensitivity of the index to abundance. Thus, Hill numbers when $q = 0$, 1, or 2 correspond to richness, Shannon diversity, and Simpson's diversity, respectively (Chao et al. 2014). The integrative framework includes trait distances (in this case, functional entity distances) based on a similarity matrix and measures TD when the threshold distance between species is set to minimum ($t = 0$), such that each species is its own functional group. When $t > 0$, the framework measures FD. We measured species richness (TD) using this framework with $t = \min$ (distance between species) and $q = 0$. FD was measured with $t = \text{mean}$ (distance between species) and $q = 2$, as this index corresponds to the conventionally used Rao's quadratic entropy index of FD (Chao et al. 2014). From here on we refer to species richness as taxonomic diversity (TD). Biodiversity metrics were calculated at the zone level within clusters for each year and averaged across the years to get a single value per zone-cluster ($n = 197$). All biodiversity indices were calculated using the 'mFD' package (Magneville et al. 2022) in R.

Community metrics

Community stability (μ/σ)

Community stability (μ/σ) was measured by calculating the temporal mean μ of total mesopredator abundance in each site divided by the temporal standard deviation σ (Lehman and Tilman 2000). We then calculated two stability regulatory mechanisms: community synchrony and species population stability.

Community synchrony (φ)

We measured how similarly species fluctuated over time using the community synchrony index, φ (Loreau and de Mazancourt 2013). This index compares how much the total community abundance varies through time with how much the abundance of each species varies on its own. It is calculated as the variance of the total community abundance divided by the square of the sum of each species' standard deviation. The value of φ ranges from 0 to 1, where 0 means species change completely independently of one another (i.e. asynchrony) and 1 means all species fluctuate in perfect unison (i.e. synchrony; Hallett et al. 2016).

Species population stability

Following Thibaut and Connolly (2013), we quantified species population stability as the weighted average of species-specific stabilities (mean abundance divided by standard deviation), with weights proportional to each species' total abundance across samples. All community metrics were calculated in R using the package 'codyn' (Hallett et al. 2016).

Environmental and anthropogenic disturbance data

Environmental stress

We used annual maximum degree heating weeks (DHW) from NOAA's Coral Reef Watch program (https://coralreefwatch.noaa.gov/; Skirving et al. 2020). DHW quantifies cumulative thermal stress as the number of weeks sea surface temperature (SST) exceeds the climatological maximum summer temperature by +1°C DHW. It is a widely used predictor of coral bleaching and disease outbreaks (Hughes et al. 2017, Darling et al. 2019) and fish community composition, both through its effects on coral habitat degradation and direct physiological stress (Magel et al. 2020). DHW values were derived from CoralTemp, at 0.05° spatial resolution (Skirving et al. 2020). For each site, we extracted the maximum DHW values for individual surveyed years using a 100 km buffer around each site and averaged these values for all sites within a cluster to capture thermal stress intensity during the time-series.

Anthropogenic stress

We used the total human gravity index, which estimates human pressure based on population size and travel time to each reef site (Cinner et al. 2018). This index accounts for both local (e.g. coastal development) and market-based pressures (e.g. fishing) and was calculated within a 500 km buffer surrounding each site, reflecting the potential local and regional spatial extent of human influence on reef ecosystems.

Statistical analysis

Relative drivers and mechanisms of community stability

We used piecewise structural equation modelling (pSEMs) to evaluate the effects of the two stability mechanisms (community synchrony and species population stability) and the direct and indirect effects of diversity (TD and FD), environmental (DHW) and anthropogenic stressors (human gravity) on community stability. Piecewise SEMs incorporate multiple linear models into a single causal pathway analysis (Lefcheck 2016), using directional separation tests (d-sep tests), a series of independence claims that statistically identify causal relationships and missing links in a directed acyclic graph (DAG; Shipley 2009). We constructed the piecewise SEMs based on our conceptual framework in Fig. 1. Specifically, we hypothesized that community stability will be negatively and positively related to community synchrony and species population stability, respectively (paths 1 and 2), and that there is an indirect effect of TD and FD on community stability via the two stability mechanisms (paths 3–7). We specified correlated error structures between TD and FD (path 8; Mouillot et al. 2013). We also hypothesized that environmental and anthropogenic pressure indirectly affect community stability through their direct effects on diversity (paths 9–12) and stability mechanisms (paths 13–16). Model specifications for the pSEM included five nested LMEM for community stability, community synchrony, species population stability, TD, and FD.

Before fitting the pSEM, we used intercept-only linear mixed-effects models to partition variation in the five variables among biogeographic region, site, and zone. This analysis was used to identify the spatial scale of sampling that should be accounted for as random effects in subsequent models. Based on this analysis, we included zone nested within sites nested

within biogeographic region as a random effect structure in all the pSEM models (Supporting information).

All variables were standardized and scaled (z-score transformed) to improve interpretability. DHW, human gravity, community synchrony, species population stability, and community stability were log-transformed prior to scaling to reduce skewness. We examined model assumptions graphically, including normality of errors and homogeneity of variances. pSEM was performed using the package 'piecewiseSEM' (Lefcheck 2016). The independence claims of variables were tested using Shipley's test of directed separation (the procedure tests the assumption that all variables are conditionally independent) and Fisher's C statistic to test overall SEM model fit (Supporting information). To assess the robustness of our SEM predictions to site selection, we performed the pSEM multiple times, omitting one site at a time, and compared the resulting changes in the magnitude, significance, and direction of model estimates (Supporting information). We ran all analyses using the statistical software R ver. 4.0 (www.r-project.org).

Results

Community stability, community synchrony, species population stability, and FD varied most strongly among sites within biogeographic regions, with site explaining 10.5, 37.0, 22.2, and 36.2% of total variance, respectively. In contrast, TD was most strongly structured by biogeographic region, which explained 40.0% of total variance. Zone explained little variation for most variables, except for TD, where it accounted for 13.8% of variance (Supporting information).

Community stability varied widely across sites, ranging from 0.46 to 66.65. Within regions, there was considerable among-site variability in community stability (Supporting information). For example, in the central Indo-Pacific Ocean, the highest community stability was recorded in Rowley Shoals, Western Australia (66.65), whereas the lowest value (0.52) was recorded in New Caledonia (Supporting information).

Community stability decreased significantly with community synchrony and increased significantly with species population stability (Fig. 2C). Locations of low community stability were typically characterized by high community synchrony (or low community asynchrony). For example, Mascarenes had the lowest community stability (0.41; Supporting information) and among the highest community synchrony (0.92; Supporting information) in the dataset, while the opposite was true in Rowley shoals, Western Australia which had the lowest community synchrony (0.003) and highest community stability in the dataset (66.65; Supporting information).

Both mechanisms of stability – community synchrony and species population stability – were direct and significant predictors of community stability within our pSEM models ($p < 0.005$, $R_m^2 = 0.95$; Supporting information), which fit the data appropriately (Fisher's $C = 6.937$ with p value $= 0.327$, $df = 6$). Community synchrony played a destabilizing role while species population stability played a stabilizing role (Fig. 3; Supporting information). However, the strength of the effect of community synchrony (−0.825) on community stability was nearly four times greater than the effect of species population stability (0.213, Fig. 3; Supporting information).

D-separation tests did not indicate unsupported direct effects of TD and FD on community stability. Instead, biodiversity effects on community stability were indirect. FD significantly decreased community synchrony ($\beta = -0.374$, $p < 0.001$), while community synchrony had a strong, negative effect on community stability ($\beta = -0.825$, $p < 0.001$), suggesting that FD increased community stability indirectly by promoting asynchronous population dynamics. TD increased species population stability ($\beta = 0.158$, $p = 0.037$), which in turn increased community stability ($\beta = 0.213$, $p < 0.001$). TD was also positively associated with FD ($\beta = 0.303$, $p < 0.001$), suggesting an additional indirect pathway through FD and synchrony.

D-separation tests identified an unmodelled, direct effect of heat stress on community stability which was subsequently included in the final community stability model in the pSEM. Heat stress had a small, but significant direct, negative effect on community stability ($\beta = -0.070$, $p = 0.013$). Heat stress also reduced species population stability ($\beta = -0.232$, $p = 0.040$) and FD ($\beta = -0.300$, $p = 0.009$). In contrast, anthropogenic pressure was not significantly associated with any biodiversity indices or stability mechanisms (all $p > 0.36$), but a site-level sensitivity analysis showed that effects of anthropogenic pressure varied with site inclusion (Supporting information).

Discussion

Our results demonstrate that community synchrony is the primary mechanism driving abundance stability within diverse communities of mesopredatory coral reef fish. The strong stabilizing effect of asynchrony was consistent across biogeographic regions, even in locations with markedly different biodiversity levels and anthropogenic and environmental pressures. FD emerged as a critical driver promoting asynchronous population dynamics, likely enhancing response diversity and buffering the community from environmental and anthropogenic stressors. Our findings highlight the role of biodiversity and disturbances in shaping community dynamics, offering insights for conservation strategies to promote the temporal stability of mesopredatory fish communities in coral reef ecosystems.

Community synchrony versus species population stability as stabilizing mechanisms

Much of our understanding of community stability comes from theoretical and empirical work on synthetic terrestrial communities, which are typically characterized by low species diversity, shaping many of our expectations about diversity–stability relationships (Xu et al. 2021). In such communities, evidence for the role of community asynchrony as a

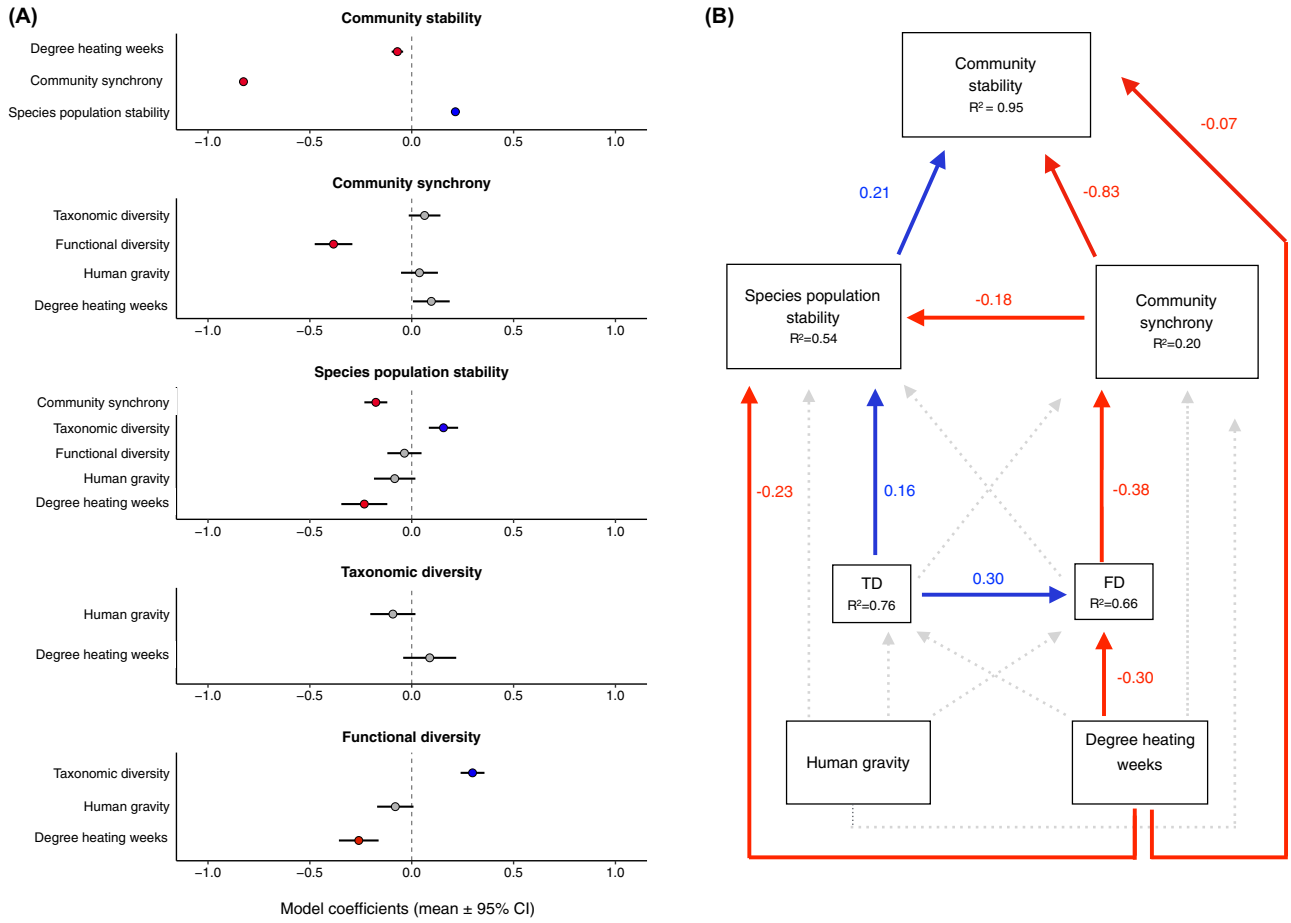

Figure 3. Direct and indirect drivers of community stability estimated using piecewise structural equation modelling: (A) Standardized path coefficients for all relationships included in the piecewise SEM, shown as mean estimates ± 95% confidence intervals. Blue points indicate significant positive effects, and red points indicate significant negative effects; grey points indicate non-significant effects. (B) Final SEM showing hypothesized pathways linking disturbance, biodiversity, and population dynamics to community stability. Solid arrows indicate statistically significant pathways, with blue arrows representing positive effects and red arrows representing negative effects. Dotted grey arrows indicate non-significant pathways. Values along arrows are standardized mean path coefficients. Conditional R^2 values are shown for each response variable, indicating the variance explained by both fixed and random effects (i.e. biogeographic region/site/zone).

stabilizing mechanism is mixed (Houlahan et al. 2007, Gonzalez and Loreau 2009, Valencia et al. 2020), but species population stability, particularly of dominant species, often exerts a strong influence on overall community stability (Roscher et al. 2011, Sasaki and Lauenroth 2011, Hou et al. 2023), likely because environmental variability, competitive effects, and demographic stochasticity can have strong impacts on small population sizes (Loreau and de Mazancourt 2008). Contrastingly, asynchrony frequently emerges as the dominant stabilizing mechanism in aquatic ecosystems (Xu et al. 2021). This is because aquatic systems likely experience high environmental variability and typically support a high diversity of species, with diverse, predominantly weak interactions among them (Shurin et al. 2006). Our findings are consistent with this pattern. Across biodiversity gradients ranging from 8 to 137 fish species and 8 to 75 functional entities per site, community asynchrony had four times the effect on mesopredator abundance stability compared to species-level population stability.

Whether mesopredator communities are stabilized primarily by asynchrony or by species population stability can have important trophic implications. Mesopredators can influence the stability of food webs by increasing per capita prey consumption, facilitating the spread of invasive or opportunistic species, and triggering trophic cascades (Ritchie and Johnson 2009, Britten et al. 2014, Quévreux and Loreau 2022), particularly as apex predators continue to decline globally (Estes et al. 2011). Asynchronous fluctuations in mesopredator populations likely prevent any single species from remaining consistently dominant, potentially spreading predation pressure across a broader range of prey. However, when dominant predators remain abundant over extended periods, they can exert stronger and more selective pressures on prey populations. For example, functionally distinct piscivores such as the introduced peacock grouper *Cephalopholis argus* in Hawaii (Meyer and Dierking 2011, Ruttenberg et al. 2011), the invasive *Pterois volitans* in the western Atlantic (Albins 2015), and various range-expanding

or seasonally migrating mesopredators (Sancho et al. 2000, Beck et al. 2016) illustrate this pattern, where their continued increase in abundance alters prey community composition through their effects on prey abundance and behaviour. In our study, species population stability had a significant but weaker influence on mesopredator dynamics than community synchrony and so we do not expect strong top–down control by mesopredators in these reefs (Casey et al. 2017). However, evidence suggests that the relative importance of stabilizing mechanisms can shift along environmental gradients (Hallett et al. 2014) and is expected to shift further under ongoing trophic downgrading of marine ecosystems driven by anthropogenic and environmental pressures (Baum and Worm 2009). Further, the pSEM also identified a significant negative relationship between community synchrony and species population stability, indicating that sites where populations fluctuated more synchronously also tended to have less stable component populations. This suggests that the two stabilising mechanisms were linked: shared responses to environmental variation may simultaneously increase synchrony and reduce population-level stability. These changes will have important consequences for trophic interactions within fish communities, making it essential to monitor how stabilizing mechanisms change over time on coral reefs.

The effect of biodiversity on community stability

While the dominant stabilizing mechanisms in terrestrial and aquatic systems may differ (Xu et al. 2021), an additional consideration is how species diversity influences these mechanisms. Species diversity (particularly when represented by species richness) is known to increase population asynchrony in both ecosystems, but it tends to decrease species population stability in terrestrial systems and increase it in aquatic ones (Xu et al. 2021). Consistent with this pattern, we found that species diversity had a positive effect on species population stability in mesopredatory reef fish communities. However, species diversity did not directly affect community asynchrony, the dominant stabilising mechanism in our study, whereas FD did.

Community asynchrony can arise through several pathways. It can reflect non-independent species fluctuations driven by differential responses to environmental disturbances or by strong competitive interactions, often described as 'insurance' or 'compensatory' effects, respectively (Yachi and Loreau 1999, Gonzalez and Loreau 2009, Loreau et al. 2021). Alternatively, it can emerge from largely independent, stochastic fluctuations known as 'portfolio effects' (Doak et al. 1998). The significant effect of FD rather than species diversity on synchrony suggests that non-independent (biotic) mechanisms may be important. Although we were unable to determine whether the niche differences we observed primarily reflected species' differential environmental responses or interspecific interactions, environmental responses are generally more influential than competition in generating asynchrony within consumer communities (Thibaut et al. 2012, Tredennick et al. 2017). This pattern may arise because consumer species typically have more distinct ecological requirements than primary producers, resulting in less uniform responses to environmental change. For example, some mesopredators depend heavily on live coral habitat (e.g. hawkfishes; Coker et al. 2015), whereas others, such as peacock groupers, do not (Karkarey et al. 2014). As a result, shifts in coral cover could generate asynchronous population dynamics between coral-dependent and coral-independent species (Wilson et al. 2009), stabilizing community-level abundance. Additionally, mesopredatory fishes likely engage in a range of positive and negative interactions within the guild, like size-structured intra-guild predation (Polis and Holt 1992, Hixon 2015), facilitation (e.g. social such as foraging behaviours seen in groupers; Vontobel et al. 2025), which could further promote asynchrony by creating weak, diffuse trophic links among species. This aligns with the weak-interaction theory, which proposes that diverse natural communities are maintained by a few strong and many weak interactions (Wootton and Emmerson 2005), and those interactions could buffer the effects of strong, potentially synchronous population fluctuations, thereby enhancing community stability (McCann et al. 1998). These stabilizing effects are expected to be stronger in multi-trophic communities such as mesopredatory reef fish, which show intra- and inter-guild predation, than in single-trophic communities (Jiang et al. 2009). Coral reef fish communities are among the most diverse vertebrate assemblages and exhibit extensive life-history, morphological, and behavioural variation that allows species to exploit a wide range of resources (Lieske and Myers 2001). Our results grouped 481 mesopredator species into 176 functional entities, indicating low functional redundancy and high functional complementarity, with an average of only 2.7 species sharing identical trait combinations. This high FD and complementarity could underpin the influence of asynchrony on overall community stability.

The effect of disturbances on community stability

Anthropogenic and environmental disturbances differed in how they affected community stability in our study. Heat stress emerged as a consistent driver of community stability, with both direct and indirect effects in the piecewise SEM. In contrast, anthropogenic pressure, measured as human gravity, did not have significant effects on community stability, community synchrony, species population stability, or biodiversity. However, the leave-one-out sensitivity analysis showed that anthropogenic effects were site-dependent rather than uniformly absent, suggesting that local human impacts may be important but may not be captured consistently by a broad gravity metric across all sites.

Heat stress, measured as DHW, had a significant negative direct effect on community stability, even after accounting for community synchrony and species population stability. Heat stress can influence fish populations both indirectly, through habitat degradation such as loss of shelter and reduced prey following mass bleaching events (Hempson et al. 2017, Pratchett et al. 2017), and directly, by impairing fish physiological performance in environments affecting growth, movement, reproduction, and recruitment to coral

reefs (Johansen et al. 2014, Allan et al. 2015, Pratchett et al. 2017). Such direct effects may generate abrupt, lagged, or nonlinear community responses that are not fully captured by the stabilizing mechanisms originally hypothesized in the model.

In our dataset, nearly 50% of the sites experienced heat stress > 4°C DHW and 25% of the sites experienced heat stress > 8°C DHW, suggesting a high chance of reefs having experienced widespread bleaching and mortality of heat-sensitive corals (Skirving et al. 2020) during the sampling years. Heat stress, and the resulting coral bleaching and loss of structural complexity, can disproportionately affect coral-specialist species while favouring generalists that gain competitive advantages under disturbance (Wilson et al 2009). For example, after repeated mass-bleaching events in the Lakshadweep archipelago, the foraging generalist *Cephalopholis argus* increased in abundance and dominance on repeatedly bleached reefs (Karkarey et al. 2017). Such shifts indicate strong environmental filtering of species assemblages towards traits that confer resilience under chronic disturbance. Consequently, environmental stress likely intensified species gains and losses without necessarily promoting synchrony or asynchrony within the community, but while stabilising the populations of generalist species. This interpretation is consistent with the significant negative effects of heat stress on both functional richness and species population stability observed in our analysis.

By contrast, human gravity did not show significant effects on any model variable, indicating that there was no consistent system-wide relationship between this broad anthropogenic pressure metric and community stability, synchrony, population stability, or biodiversity. However, the leave-one-out sensitivity analysis showed that gravity effects varied with site inclusion. Gravity effects on biodiversity and species population stability were generally negative across site-removal runs, whereas effects on community synchrony were more variable but more often positive than negative (Supporting information). This site contingency is plausible because human pressure can operate through different mechanisms in different reef systems. Studies of regional diversity gradients in human-impacted systems indicate that anthropogenic pressures can strongly shape community stability, often overwhelming any insurance effects of species richness (Hautier et al. 2014). Recent work on Great Barrier Reef fish assemblages (Tsai and Connolly 2025) illustrates this clearly: proximity to the coast, likely reflecting higher sediment and nutrient inputs from human settlements, contributed to species responding more similarly to environmental change, increasing population synchrony and temporally destabilizing communities. In contrast, further away from the coasts where the influence of human settlement pressures declined, volatility in habitat-forming coral cover reduced community stability by intensifying intra-specific density dependence and lowering species population stability. .

Similarly, in remote regions across the eastern Pacific Ocean gravity may also fail to capture the most relevant form of anthropogenic pressure. Export-oriented fisheries predominate in the region which selectively target large, high-value mesopredator species, such as groupers and snappers, for markets in Southeast Asia, especially Hong Kong (Warren-Rhodes et al. 2003). Such distant market hubs, often more than 500 km from sites in the eastern Indo-Pacific, may not be fully captured by the total gravity metric used here. Gravity can be relatively low if nearby human population density is low, yet fishing pressure may still be high if fisheries supply distant markets rather than only local consumers. In such cases, a gravity metric based primarily on nearby human populations may underestimate the true intensity or type of human pressure experienced by reef fish communities. Similarly, fishing, land-based pollution, coastal development, and tourism may affect reef communities through different pathways: fishing may selectively remove particular trophic groups or body sizes, while land-based inputs may affect site-attached, gregarious, or mobile species. These different anthropogenic mechanisms can generate contrasting effects on synchrony, species population stability, and biodiversity among sites.

Together, these results suggest that heat stress acts as a more consistent broad-scale destabilizing force across the study system, whereas anthropogenic pressure is more spatially heterogeneous and dependent on the type of human impact operating at each site. The lack of significant gravity effects in our SEM should therefore not be interpreted as evidence that human pressure is ecologically unimportant. Rather, it suggests that broad gravity-based indices may be too coarse to capture the relevant dimensions of anthropogenic disturbance across diverse reef systems. More specific indicators, such as fishing intensity, market access, gear type, coastal development, sedimentation, nutrient loading, or tourism pressure may be needed to better identify how human impacts shape reef fish community stability.

Conclusion

Using a substantial dataset of time series spanning the Indo-Pacific Ocean, we highlight the generality of community asynchrony in enhancing of community abundance stability in tropical marine systems. Our work suggests that niche differences, rather than species richness per se, are key in determining the stability of mesopredatory coral reef fish. Conserving biodiversity is hailed as an important management goal for all ecosystems facing anthropogenic and environmental changes (Secretariat of the Convention on Biological Diversity 2005). Whether the main mechanism of community stability is driven by diversity effects (community synchrony) or dominant species effects (species population stability) can have important implications for biological conservation. For instance, communities in which diversity effects (community synchrony) prevail, such as found here, could benefit from the management of functional complementarity that would maintain asynchronous population dynamics buffering against disturbances. Alternatively, in communities with strong dominance effects (species

population stability), the conservation of keystone or unique species provides a tangible goal for conservation. This strategy could also be applied through ecosystem restoration, where specific functional groups (example, pioneer species, ecosystem engineers) can be managed strategically. In a world that is increasingly affected by climate change and anthropogenic pressures, community stability for mesopredatory coral reef fish depends on preserving niche differences.

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Author contributions

Rucha Karkarey: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Eva Maire**: Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Validation (supporting); Writing – review and editing (equal). **Nicholas A. J. Graham**: Funding acquisition (supporting); Investigation (supporting); Supervision (supporting); Validation (supporting); Writing – review and editing (equal). **Valeriano Parravicini**: Data curation (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Simon J. Brandl**: Data curation (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Jeremy Carlot**: Data curation (equal); Resources (equal); Visualization (equal); Writing – review and editing (equal). **Mehdi Adjeroud**: Resources (equal); Writing – review and editing (equal). **Rohan Arthur**: Investigation (supporting); Resources (equal); Writing – review and editing (equal). **Teresa Alcoverro**: Investigation (supporting); Resources (equal); Writing – review and editing (equal). **Shaun K. Wilson**: Data curation (equal); Resources (equal); Validation (equal); Writing – review and editing (equal). **Jordan Goetze**: Resources (equal); Writing – review and editing (equal). **Thomas H. Holmes**: Resources (equal); Writing – review and editing (equal). **Julien Wickel**: Resources (equal); Writing – review and editing (equal). **Dan A. Exton**: Resources (equal); Writing – review and editing (equal). **Sally A. Keith**: Conceptualization (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (lead); Validation (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j6q573nmn (Karkarey et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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