

Title: Reef fish diversity guarantees productivity

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Abstract: Biodiversity loss on coral reefs may threaten their functioning and services to humanity. However, the impacts of biodiversity change on reef fish productivity, a key function that sustains millions of humans, are not well understood. Here, we compiled a global dataset of coral reef fish surveys to examine whether assemblage biodiversity promotes productivity, in both space and time. Diversity acts as an insurance policy for productivity: although high levels of reef fish productivity can occur at any level of local species richness, we found no diverse assemblages with low productivity. This triangular relationship reconciles the apparent

contradiction of productive monocultures identified in previous studies. Importantly, productivity strongly mirrors species richness trends regardless of initial richness. Implications for conservation and management are clear: reefs that are naturally less diverse can still be productive. Yet human-driven biodiversity declines are likely to translate to productivity declines, impacting ecological productivity and coastal populations.

Main Text

Reef fish production underpins the food security and livelihoods of millions of people worldwide (1–3). Yet we know very little of how reef fish productivity responds to ongoing biodiversity change driven to human activities (4, 5). Impacts from mass bleaching and overexploitation have reshaped fish assemblages on coral reefs (6–9), and continued degradation of reef fish assemblages can result in erosion of the core functions they contribute to— like nutrient cycling (10, 11), biomass production (12, 13), and herbivory (14, 15). Here, with spatially and temporally replicated data from coral reefs throughout the tropics, we focus on reef fish biomass productivity and ask how this function is affected by local biodiversity and its change through time.

Currently, there are critical gaps in our understanding of the functional impacts of biodiversity change. Research conducted largely on temperate plant assemblages points towards a positive effect of biodiversity on ecosystem function (BEF) (16–18) by bolstering resource use efficiency through niche differentiation (i.e. complementarity effect) (19, 20) or by increasing the likelihood of including a high-performing species in an assemblage (i.e. selection effect) (21, 22). Both mechanisms lead to positive diversity-functioning relationships, and have emerged repeatedly in local, regional, and global comparative studies (20, 23–25).

Although BEF effects are often cited as a functional reason for conservation, it is unknown how diversity and ecosystem functioning might be linked as they change through time (26, 27). Studies have rarely investigated biodiversity empirically as a temporal dynamic, sometimes inferring the consequences of biodiversity change from spatial patterns (space-for-time) (28–31). While such patterns can inform ecological theory, biodiversity variability alone cannot replicate the dynamic responses of coexisting, interacting communities of species (32–34) and, as such, does not necessarily capture how ecosystem functioning changes in response to diversity change over time.

Here, we ask whether biodiversity exerts a positive effect on reef fish assemblage productivity in both global spatial patterns and local-scale temporal trends. To link global reef fish diversity with assemblage productivity, we compiled a dataset of 70,836 assemblage surveys from 71 studies that represent all major biogeographical regions for reef fishes (Fig. S1) (35). We defined an assemblage as a group of co-occurring taxa within an ecological community but allowed data sources to vary by taxa criteria (see Methods). The dataset contains observations of 3,258 species in both single-year and time-series surveys collected between 1994–2024 (Table S1). For each individual survey, we quantified assemblage diversity as species richness. Fish productivity here is quantified as a daily rate of biomass production. We used a framework that estimates location-specific growth curves for each species based on the von Bertalanffy Growth Function informed by existing otolith data, species traits known to affect growth, and local sea surface temperature (36; see Methods).

Diversity-productivity links across space

We first explored the global spatial gradient of diversity-productivity links using single-year data in our compiled dataset. We modelled the effect of species richness on reef fish productivity using a directed acyclic graph (DAG) to articulate mechanistic assumptions on causal relationships (Fig. S2; Table S2). DAGs guide model construction to answer causal questions so that only variables involved in the conditional probabilities of the targeted predictor and response relationship are included (see Methods).

Based on our DAGs, we controlled for potential confounding effects from assemblage abundance, level of fishing restriction protection, and human pressure (see Methods; Fig. S2). Human pressure was represented with the human gravity metric, which integrates reef accessibility and human population size (37). We used a standardized categorical index by ProtectedSeas that qualifies fishing restrictions from 1 (no protection) to 5 (maximum protection) (38). The inclusion of assemblage abundance in our mechanistic DAG acknowledges its tightly coupled relationship with species richness and importance in BEF relationships (39–42). We constructed two candidate models depending on the direction of the causal relationship between richness and abundance: *without* abundance as a covariate (if abundance is a consequence of species richness, and hence part of the total effect from richness) and *with* abundance (if abundance causes species richness; , 43, 40) (Fig. S2). We used group-level effects to allow the strength of biodiversity on productivity to vary by biogeographical regions.

We found a strong, positive effect of fish species richness on gross assemblage productivity. The magnitude of this positive effect depends on whether abundance is a numerical consequence of species richness (1.52, 1.26–1.77 95% credible interval (CI); Fig. 1a, S3, Table S3) or whether abundance gives rise to species richness (0.66, 0.52–0.79 CI; Fig. S4, Table S4). Importantly, given the power-law relationship of the model structure, the causal direction between richness and abundance determines whether the richness-productivity relationship is non-saturating (if > 1) or saturating (< 1). However, we cannot reliably interpret the estimated effects of control covariates like abundance, as the model is constructed to quantify only the effect of richness on productivity.

Importantly, our results reveal a triangular pattern (Fig. 1): in the world's least diverse assemblages, productivity is highly variable and spans the full range of possibilities, but in diverse assemblages, productivity varied less and was on average at least two orders of magnitude higher than in low diversity assemblages (Fig. 1a,b). To quantify the triangular pattern, we investigated how the effect of species richness differed for the least and most productive assemblages in a quantile regression (Fig. 1b). We found strong evidence in our model that species richness has the greatest positive effect for the least productive assemblages (1.76 ± 0.07 95% confidence interval). However, the species richness effect was notably smaller but still positive for the most productive assemblages (0.13 ± 0.10 95% confidence interval). Although species richness can incur a numerical response in abundance, we did not find as strong a triangular pattern between abundance and productivity (Fig. S5). We ensured that this was not driven by unequal sampling effort by comparing models constructed with and without low sample completeness records (Figs. S6-7) (44).

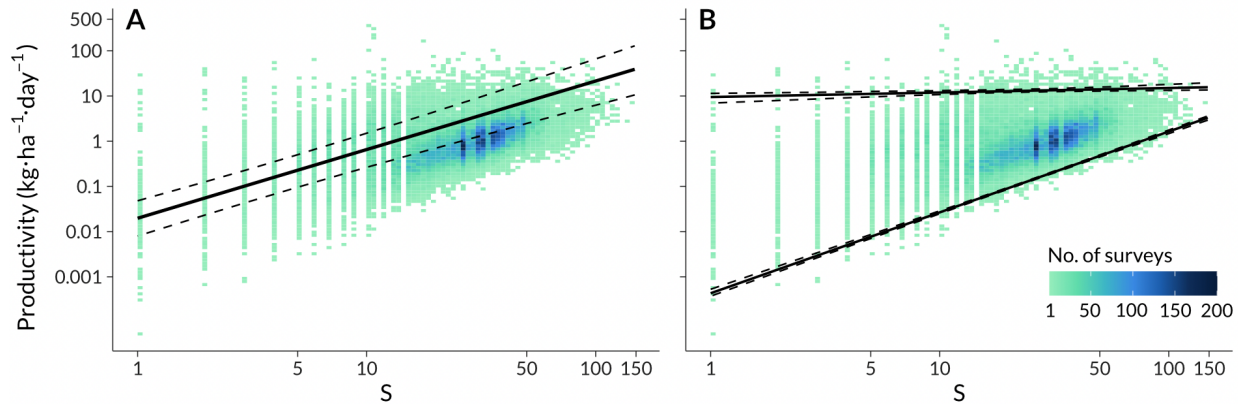


Fig. 1 Spatial patterns in species richness (S) and assemblage productivity links in global reef fish assemblages. Assemblages are represented as a spatial diversity-productivity gradient shaded here by survey count density on a log-log scale ($n = 32418$). We show the partial prediction (solid black line) for the effect of species richness from the spatial model in **A**. Dashed lines represent the 95% credible interval. **B** shows modelled diversity-productivity relationship for the 1st and 99th quantiles, represented by solid lines with 95% confidence intervals indicated by dashed lines.

The BEF relationship was remarkably consistent across biogeographic regions, which can differ almost tenfold in their regional diversity (Fig. S5). Variation based on biogeographical region was driven primarily by productivity differences (random intercept $\sigma = 0.81$, 0.50–1.34 95% CI) rather than in the strength of the species richness effect (random effect $\sigma = 0.27$, 0.17–0.43 95% CI; Figs. S5,6, Table S3). The biogeographic variation in productivity differences could point to ocean basin drivers not accounted for here, such as primary productivity or wider oceanographic conditions affecting fish metabolism (45).

Our estimates of productivity and biodiversity are inferred from assemblage data, so we also compared the modelled relationship with a series of simulated assemblages to ensure that our results here reflect ecological signal rather than methodology choices. By altering assemblage data to flatten the effects of fish length, species identity, or abundance, each model is agnostic to the effects of growth, species richness, and abundance respectively (see Methods). The estimated effect of species richness in our spatial model exceeded that estimated in all agnostic models (Fig. S11), except for the richness-agnostic model simulated with the largest species in each assemblage. Our abundance-agnostic model, where each species only consisted of one individual, was unexpectedly the most similar to our spatial model prediction, where the effect of species richness was 1.36, 1.35–1.38 95% CI (Fig. S11). This abundance-agnostic simulation did not systematically alter the richness-productivity pattern (Fig. S11, S12). Additionally, we conducted a series of sensitivity tests to ensure that productivity patterns were not influenced by method differences in estimating fish lengths (see Methods; Table S5-6, Figs. S13-19). Through these sensitivity analyses, we show that our modelled spatial BEF relationship is robust and not an artefact of our methodological choices.

Diversity-productivity links in temporal trends

Using the time-series subset of the compiled data, we conceptualised diversity-productivity relationships over time by assessing the directionality of trends (Fig. 2a-b). A mechanistic link

between biodiversity and productivity would mean that changes in species richness should be accompanied by concomitant changes in the productivity of the biotic assemblage. We defined a positive relationship if richness and productivity changed in the same direction over time (i.e. both increasing or decreasing), and a negative relationship if they changed in opposite directions (Fig. 2a-b). We then modelled how temporal change in species richness was linked with productivity change using the same approach as before with causal relationships articulated in DAGs. Based on the temporal DAG, we controlled for potential influences from human gravity, abundance change, temperature change, and fishing restriction protection by including them as control covariates (see Methods).

We first quantified the temporal trajectories of both species richness and assemblage productivity for 5,484 time-series by modelling the slope of diversity and productivity on a log-scale with time. We detected a balanced proportion of temporal trends for species richness and assemblage productivity, both centred near zero (mean richness slope = 0.005, mean productivity slope = 0.006) (Fig. 2c). When only comparing temporal trends statistically distinguishable from no change, we found 64% more instances of increases in richness and 30% more in productivity (Fig. 2d). Surprisingly, although there are well-documented concerns of reef degradation and fishing overexploitation (8, 46), declines or increases in either species diversity or assemblage productivity were equally prevalent in the data. This also reflects similar balanced patterns found in global analyses of biodiversity change on local scales (47, 48).

Linking temporal trends in biodiversity and productivity, we found a strong relationship between species richness and productivity change through time. Our model that included species richness, abundance, and temperature change best explained the temporal diversity-productivity patterns in our data. When abundance and temperature changes are accounted for, species richness had a strong, positive effect on assemblage productivity trajectories (0.67, 0.61–0.73 95% CI; Table S7, Fig. S17). Given the large proportion of time-series with temporal trends indistinguishable from zero, we also investigated these temporal links in fluxes in shorter time periods. We still found strong evidence for a positive temporal diversity-productivity relationship when we fitted models on short-term flux trajectories (Figs. S18-19, Table S8).

Although steep temporal trends were rare (Fig. 2c), our analysis reveals a strong link between species richness and productivity in the context of temporal change. If local declines in richness are paired with similar decreases in abundance and temperature, productivity decreases in a similar relative change as richness, regardless of the initial assemblage diversity. All spatial and temporal models found moderate evidence for a slight negative effect from human pressures but weak evidence for a positive effect from fishing restriction protection (0.01, -0.03–0.05). Our results here cannot speak to the effectiveness of marine protected areas, but rather their effect in the model's causal structure can be sufficiently explained through changes in species richness and/or assemblage abundance. Theoretical advances have suggested that diversity-productivity relationships should not be as strong and widely variable on local scales and only detectable on global scales (49, 50). However, by analysing local scale temporal changes across a global extent, we find strong links between biodiversity and productivity as both change through time.

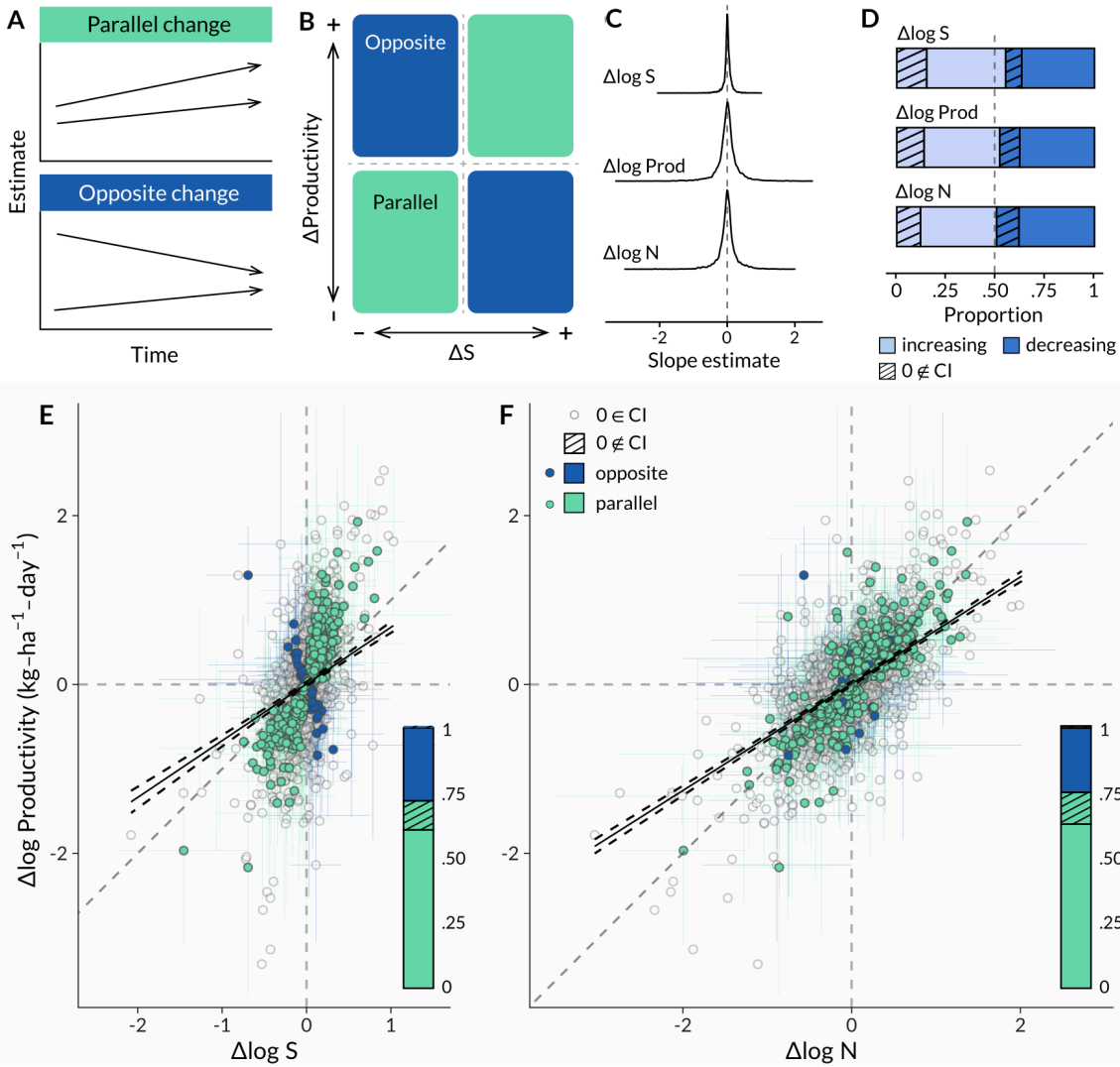


Fig. 2 Temporal models showing the links between assemblage productivity change ($\Delta \log \text{Prod}$) and species richness change through time ($\Delta \log S$). We conceptualise diversity-productivity relationships in temporal change as shown in A. Temporal trends of richness and productivity moving in the same or parallel directions indicate positive diversity-productivity relationships, while opposite change trends indicate negative relationships (A). A pairwise visualisation of trajectories across multiple time-series would look like B, where positive and negative BEF relationships are distinguished by quadrants. The frequency of diversity and productivity trends estimated for time-series ($n = 5484$) are shown in C and D. D shows these trends binned by their overall directions, and whether slope estimates are distinguishable from zero (confidence intervals do not overlap 0, $0 \notin \text{CI}$). E shows partial predictions from the temporal model for species richness change ($\Delta \log S$), while F shows the same for abundance change ($\Delta \log N$). The diagonal grey dashed line indicates where $\Delta \log S$ or $\Delta \log N = \Delta \log \text{Prod}$. The partial predictions are shown by a black solid line with the 95% credible interval as a black dashed line. Each circle represents a pair of temporal trend estimates for a time-series. Circles that are filled with colour indicate that both trajectory estimates do not have confidence intervals that overlap 0. Grey circles indicate trajectory estimates that are more uncertain ($0 \in \text{CI}$).

Species richness is an important predictor of productivity for local assemblages, but it is not the only influential driver of spatial patterns. The spatial gradient analysis revealed less diverse assemblages could still achieve high productivity, suggesting that species identities may be an important determinant of productivity (51, 52). However, these types of functionally dominant, highly productive species are not easily predicted (51). Within our productivity framework based on the von Bertalanffy Growth Function (53; see Methods), the most productive species in an assemblage combines high abundance and high per capita productivity, which typically consists of young individuals of large species (13, 36, 39). This may be why global analyses of reef fish functions have found substantial spatial variation in the identity of functionally dominant species (51). Our spatial models support arguments from both sides of the BEF debate by showing that diversity drives a large-scale pattern of higher productivity but other influences like species identity are still at play (54–57).

Our analysis also reveals two patterns that signal to potential upper bounds in the biodiversity-productivity relationship. First, our data and quantile regression for the most productive assemblages suggest a conserved upper productivity bound. Reef fish assemblage growth is dependent on and likely limited by benthic and pelagic sources of primary productivity (58, 59), which typically do not exceed 1000-2000 g C m⁻² annually on coral reefs (60, 61). While externally supplied plankton has been observed to increase the energetic bounds of coral reefs (62), pelagic sources of primary production on coral reefs are not yet well quantified. Reef fish productivity will be limited to some upper bound that will also reflect metabolic limits on individual growth, which have been found to scale with assemblage composition, and trophic structure constraints among others (59, 63). We also recognise that our method of estimating productivity independently for each species based on species traits cannot account for competition, facilitation, or nutrient availability (64, 65), and realised *in situ* productivity in some assemblages may differ from these estimates. Second, in comparing our observed data with model predictions, productivity tends not to increase as predicted when assemblages comprise of more than 75 species (Fig. S10). More data from highly diverse assemblages can help determine whether this pattern extends into even higher species richness extremes.

Biodiversity change is often missing from studies seeking to demonstrate diversity-functioning relationships to support conservation efforts. By addressing this gap with observed assemblage changes combined with extensive single-year surveys across the global tropics, our analyses collectively show that biodiversity promotes productivity in both spatial patterns and temporal changes. Across space, species richness acts as insurance for a highly productive bottom line. Diverse reefs will not exhibit low levels of productivity, even though high levels of reef fish productivity can and do occur across the species richness range. Biodiversity change, when paired with similar changes in abundance and temperature, drives a similar proportional change in productivity, regardless of where an assemblage is located on the global diversity-productivity gradient (Figs. 2, 3). This pattern also clarifies an ongoing debate on biodiversity-functioning relationships, demonstrating that a triangular relationship can explain two seemingly contradictory outcomes where productive assemblages can be diverse or not (66, 67).

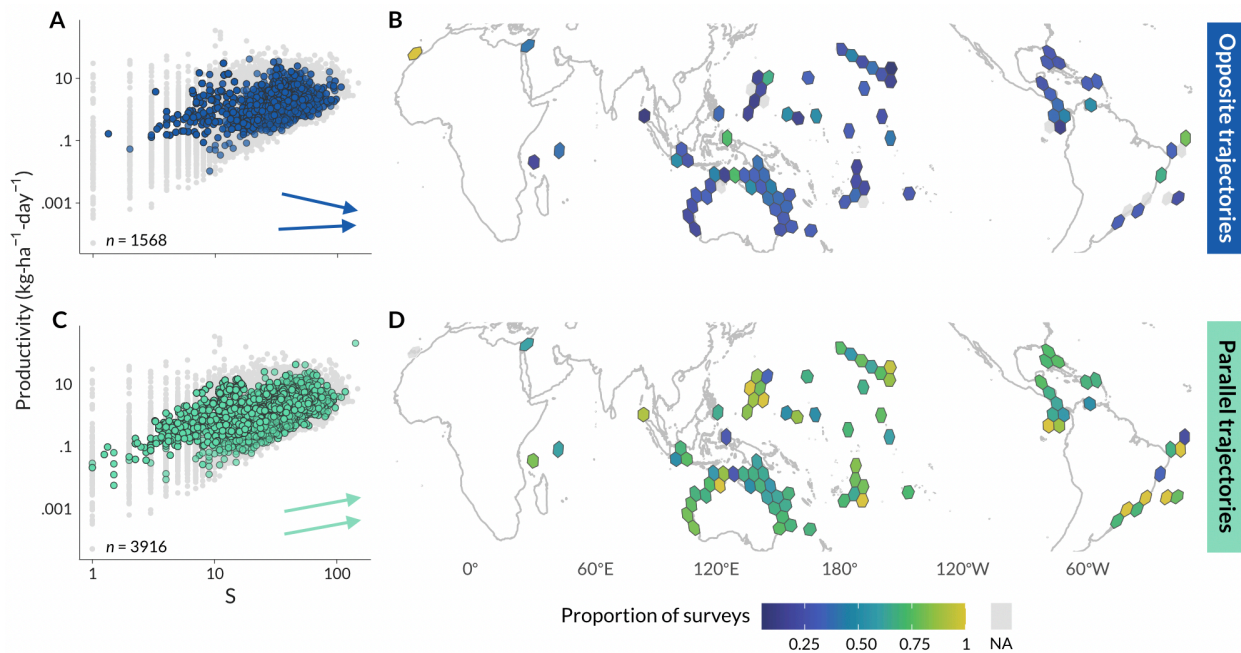


Fig. 3 The spatial pattern of temporal biodiversity-productivity links. The distribution of time-series (coloured circles) on the biodiversity-productivity gradient (light grey circles) are shown on the left, split by time-series where diversity and productivity are parallel (C, D) or opposite trajectories (A, B). For each time-series, they are shown on the species richness-productivity gradient by their mean species richness and productivity through time (A, C). The geographic distributions of temporal diversity-productivity relationships are shown as heatmaps in B and D, where hexagonal cells are coloured by their relative proportion of opposite or parallel trajectories.

By focusing on a global picture of local change in diversity and productivity, we highlight the potential for local biodiversity conservation action to maintain productive, functioning reef fish assemblages and coral reef ecosystems. BEF research has long been motivated by both theory and conservation and served as evidence that biodiversity loss is a key contributor to the degradation of ecosystem functioning (68). This has been and remains a core basis of global governance efforts to prevent further biodiversity declines and loss of ecosystem functioning, like IPBES (69) and the Kunming-Montreal Global Biodiversity Framework (70). BEF links fundamentally operate at the local scale arising from interacting, coexisting species (71), and are consequently strongest at that scale. Global patterns are valuable for coordinating biodiversity priorities (72, 73), but meeting the challenge of global biodiversity goals, especially those that relate to ecosystem functions, needs to remain locally applicable. This is especially applicable for coastal populations where reef fisheries are a primary nutrient source (1) but also declining in its capacity to provide food (74). Human activities are undoubtedly reshaping biotic assemblages and reefs (75–77). Even without widespread steep declines in global reef fishes, current temporal trends show that productivity will mirror biodiversity change. Preventing further declines of biodiversity would benefit both reefs and the people who rely upon them.

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Data, code, and materials availability: The data compiled for this study and its underlying
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Supplementary Materials

Materials and Methods

1070 Figs. S1 to S19

Tables S1 to S8



Supplementary Materials for

Reef fish diversity guarantees productivity

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References

Methods

We compiled reef fish assemblage survey data containing both abundance and length observations sourced through scientific literature, public data repositories, and data request communications. We ensured that data applied a consistent methodology with a broad enough scope to capture an assemblage (as opposed to targeted species) where most individuals were identified to the species level. Because our research question focuses on taxonomic diversity rather than individual species identities, we conserved uncertain species identifications that used open nomenclature or internal working names distinguishable from other species (e.g. *Genus unknown1* or *Genus cf. species*). Our dataset consists of 70,840 surveys from 71 studies conducted between 1994-2024 across the global tropics and subtropics on reef fishes (Table S1). The majority of surveys used underwater visual census methods in belt transects or stationary point counts, but data collected with anaesthetic clove oil stations (4 studies) and diver operated stereo-video surveys (2 studies) are also represented.

To accommodate the myriad of survey methods and spatiotemporal sampling designs in our dataset, we standardised our data into a common hierarchy of:

1. **Biogeographic province**, namely Western Indian, Central Indo-Pacific, Central Pacific, Tropical Eastern Pacific, Western Atlantic, or Eastern Atlantic (35),
2. **Study**, a collection of surveys conducted with a consistently applied method,
3. **Location**, a collection of surveys conducted within an area measuring 0.04 km² or smaller (see below),
4. **Sampling event**, the smallest independent survey unit conducted at a time and location (e.g. a transect, point count).

We partitioned studies with more than one survey location by a grid of 0.04 km² hexagonal cells (200 m * 200 m). This spatial standardisation ensures that data of varying spatial extents (single location to multi-region studies) and precision (ranging from permanent locations to random sampling within reef areas) are structured in an ecologically relevant scale, especially when accounting for spatial non-independence in modelling. For time-series studies, one grid cell can contain multiple habitats, which can have a strong local effect on assemblage structure and should be accounted for as best as possible in global syntheses (78). If more detailed informal survey site labels were provided by data contributors to define separate locations or habitats within a grid cell, we used those in conjunction with gridding to define the spatial dimension of a time-series (e.g. grid1_site1 and grid1_site2).

32 studies in our dataset were conducted over multiple years. For these time-series data, we conducted sample-based rarefaction so that each survey year has a consistent number of sampling events. This is especially important as species diversity measures are highly sensitive to sampling effort (79, 80). We calculated the minimum number of sampling events across years for each time-series, then randomly drew sampling events each year to match that minimum. A time-series hereafter refers to multiple years of rarefied sampling events within a grid cell location belonging to a study. Our final standardised dataset consists of 5,484 time-series and 32,418 single-year sampling events on 3,258 reef fish species.

Trait-based estimates of productivity

We use the modelling framework described by Morais and Bellwood (36) to estimate reef fish assemblage growth and productivity from observational survey data. This framework is based on the special integrated von Bertalanffy Growth Function (81), which describes the

asymptotic growth of a fish individual or population in length (L) throughout their lifespan (t) (Equation 1). The parameter K determines the rate at which fish reach their theoretical maximum length (L_{∞}). Because the von Bertalanffy Growth Function is traditionally applied within populations, Morais and Bellwood (36, 52) derived a standardised $K_{\max}$ in reference to a species maximum recorded length ($L_{\max}$) to allow for generalised comparisons across populations (52).

Equation 1
$$L_t = L_{\infty}(1 - e^{-K(t-t_0)})$$

Length-age von Bertalanffy growth parameters can be estimated from sufficient sampling using otolith dating or mark-recapture techniques. However, parameters obtained through direct sampling are tied to the specific sampling location and its temperature regimes. $K_{\max}$ can be relatively robustly imputed or predicted for species and locations without direct sampling using species maximum body size, sea surface temperature, and traits such as reef residence, water column position, diet/trophic guild, and maximum observed length (52). We compiled reef residence and position traits from Floeter et al. (82). Diet and trophic guild traits were obtained from phylogenetic extrapolations by Parravicini et al. (83). Species without information in any of these sources were manually classified based on ecological and diet information found in FishBase (84). We extracted all maximum length records and Bayesian length-weight parameters from FishBase as well. For low taxonomic resolution records, we used the genus or family mean values for maximum length and growth parameters, and most common values for diet and position traits. We prioritised matching trait values based on the closest species relative for taxa with poor information completeness or no information, which were typically due to open nomenclature, hybrids, or recently described species. If that was not available, we then downgraded the taxon to a genus or family-level record for trait matching purposes. Any records less resolved than family level were omitted. Finally, we obtained mean SST values corresponding to each sampling event (a unique combination of location and time) in our dataset from the NOAA Optimum Interpolation Sea Surface Temperature v2.1 data layer (85). Because a minority of our sampling event coordinates were outside the NOAA marine boundaries, we matched sampling events to the nearest neighbour SST 0.25° grid cell. We used a monthly resolution where possible, but for studies in which sampling dates only specified years, we assigned annual mean values.

We predicted $K_{\max}$ values using extreme gradient boosted regression trees (XGBoost). Regression trees are predictive unsupervised machine learning models that estimate a series of binary rules or relationships (“trees”) to describe links between predictor and response values (86). Boosting increases a model’s predictive power by additively iterating the tree building, focusing on areas of poor prediction fit with each iteration (86). We trained and predicted from an XGBoost model over 1000 iterations based on the optimum model, compiled training data, and tuning parameters from Morais and Bellwood (36, 52). The training data consisted of $K_{\max}$ values derived from otolith or mark-recapture data with the aforementioned species traits (36). We modified the training data by incorporating trophic guilds informed by phylogenetic relationships and gut content analyses (36). We specified a gamma log-link error distribution for the learning task parameters given that $K_{\max}$ values should be non-negative.

To obtain $K_{\max}$ values for our species at each given location, we generated predictions from the trained XGBoost model over 1000 iterations based on the model structure established by Morais and Bellwood (52). $K_{\max}$ was predicted from sampling event SST and species-level

traits of species maximum lengths ($L_{\max}$), diet, reef residence, and water column position. Due to the size of our predictor data for each species-location ($n = 1230764$), we generated predictions in batches of 20000 data points to avoid reaching computational memory limits. We ensured that generating predictions in batches did not meaningfully differ from one computationally intensive prediction by holding XGBoost training data and parameters constant and implemented consistent reproducible practices in iterations (i.e. `set.seed` functions in R) across batches. 95% prediction intervals were obtained from the 2.5th and 97.5th quantiles over the 1000 iterations. We then applied the predicted $K_{\max}$ values in the integrated von Bertalanffy growth function to observed fish assemblage length data, resulting in body size growth over one day at $t = 1$ for each individual. Estimated length increases were then converted to biomass using published Bayesian length-weight parameters from FishBase (84, 87). We scaled gross biomass growth by the survey area for each sampling event, resulting in an aggregated measure of gross assemblage productivity in $\text{kg}\cdot\text{ha}^{-1}\cdot\text{day}^{-1}$. This estimate of assemblage productivity serves as a snapshot of the instantaneous growth of fishes at the time of observation without any assumptions regarding mortality or later survivorship. We also did so as any true assemblage mortality would be reflected in our time-series data in abundance and species richness trends.

Assemblage species diversity

We used observed species richness (S) as our metric of species diversity. We chose species richness as a metric of biodiversity instead of other abundance-weighted metrics to avoid potential confounding effects of abundance, given that it is already incorporated in productivity estimates.

Directed acyclic graphs (DAGs) for predictor selection

We used DAGs to determine the predictor structure of our models *a priori* (Figs. S2, S16). We chose to use DAGs for their utility in identifying potential cofounders and articulating explicit assumptions about interconnected model variables (88–90). DAGs visually articulate assumptions about relationships between variables of interest and related variables within a system. DAGs share similarities with structural equation model visualisations, where arrows denote a unidirectional, direct causal relationship between two independent variables ($X \rightarrow Y$, where X has a causal effect upon Y) and a chain of causal relationships are known as causal paths. We ensured that all causal paths were unidirectional and acyclic. Importantly, all relationships included within a DAG are based on existing literature. Because DAGs must remain acyclic, we created an alternative DAG where variables exhibit two-way relationships or where there is no literature consensus yet on the directionality of relationships. Specifically, this applied to the relationship between species richness (S) and assemblage abundance (N), one DAG where richness causes abundance ($S \rightarrow N$) and vice versa ($N \rightarrow S$). We constructed three DAGs: two for the spatial pattern of species diversity and assemblage productivity (Fig. S2) and the third relating to diversity and productivity temporal change (Fig. S16, Table S2).

Because we aim to model the direct relationship between diversity and productivity, it is important to ensure that the estimated effect of diversity does not include any other causal effects at play. We used our DAG to identify whether there were any confounding variables (i.e. a variable with direct effects *on* both diversity and productivity) or collider variables (i.e. a variable directly *affected by* both diversity and productivity) that needed to be accounted for. Applying the backdoor criterion *sensu* Pearl (88) can control for such confounders or colliders by specifically including them as predictors (named as control covariates) to “block” all noncausal pathways between a predictor and response variable. Across all DAGs, we

identified human pressure as a confounding variable acting upon both diversity and productivity with the aid of R package dagitty (89). We used total human gravity as a proxy measure for human pressures including fishing, which represents the cumulative interaction between reefs to their surrounding human populations (91). The human gravity metric also decays with travel time so that proximity and accessibility is also accounted for. Human gravity is a spatial layer at a resolution of 10 km * 10 km, which is relevant to the operational spatial extent of artisanal and commercial fishing fleets (92). In spatial DAGs, area-based protection from fishing exploitation was also identified as a necessary control covariate. We used data from the ProtectedSeas Navigator database on area-based fishing restriction protections (93). Fishing restriction protections were qualified from 1 to 5, in which 1 means no restriction and 5 as maximum no-take restrictions (38). Restrictions were matched both spatially and temporally to our reef fish assemblage data, so that restrictions only applied to years after designation of protection.

Spatial patterns of diversity-productivity links

To understand whether species richness is linked with reef fish assemblage productivity on a global spatial gradient, we worked with single-year survey data from our dataset as it is the most spatially representative and would not have issues with temporal autocorrelation. Two models were constructed based on the DAGs depending on the direction of the causal relationship between richness and abundance: without abundance if species richness acts on abundance and with abundance vice versa.

We fitted two Bayesian hierarchical mixed effects models with a Gamma-distributed errors and log-link function (Equations 2,3). In accordance with our DAG, we modelled gross assemblage productivity (Prod) for a given sampling event i as a function of fixed effects of species richness (S) with a control for human gravity (Grav) (Equations 2,3). We also anticipated the strength of the species richness effect to vary geographically, so we allowed the species richness effect and intercept to vary by biogeographical regions (group-level slope β_{2g} and group-level intercept β_{0g}). Additionally, we included group-level intercepts for each study a , location b , and human gravity grid cell m to account for non-independence due to shared methodological limitations, observer effects, and/or spatial proximity. Intercepts for location are nested within study, indicated by β_{0ab} . Our data exploration revealed a potential power law/log-log relationship, and so we elected to specify log transformation within the model for richness and human gravity. Human gravity is also offset by its minimum to avoid non-real values in log-transformation. We provided weakly regularising priors to the global and group-level intercepts and hypothesis assumptions of a positive effect from richness and negative effect from human gravity.

Equation 2

$$\begin{aligned} \text{Prod}_{iab} &\sim \text{Gamma}(\mu_{iab}, \text{shape}) \\ \log(\mu_{iab}) &= (\beta_1 + \beta_{2g}) \log(S_{iab}) + (\beta_3 + \beta_{4r}) \log(\text{Grav}_m + \text{Grav}_{\min}) + \beta_5 \text{Notake} + (\beta_0 + \beta_{0a} + \beta_{0ab} + \beta_{0m} + \beta_{0g} + \beta_{0r}) \\ \text{shape} &\sim \text{Gamma}(0.01, 0.01) \\ \beta_0 &\sim T(3, 0.1, 2.5) \\ \beta_1 &\sim N(0.1, 3) \\ \beta_{2g} &\sim N(0, \sigma_{2g}) \\ \sigma_{2g} &\sim T(3, 0, 2.5) \\ \beta_3 &\sim N(-0.1, 3) \\ \beta_{4r} &\sim N(0, \sigma_{4r}) \\ \sigma_{4r} &\sim T(3, 0, 2.5) \\ \beta_5 &\sim N(0, 3) \\ \sigma_a &\sim T(3, 0, 2.5) \\ \sigma_b &\sim T(3, 0, 2.5) \\ \sigma_m &\sim T(3, 0, 2.5) \\ \sigma_g &\sim T(3, 0, 2.5) \end{aligned}$$

Equation 3

$$\begin{aligned} \text{Prod}_{iab} &\sim \text{Gamma}(\mu_{iab}, \text{shape}) \\ \log(\mu_{iab}) &= (\beta_1 + \beta_{2g}) \log(S_{iab}) + (\beta_3 + \beta_{4r}) \log(\text{Grav}_m + \text{Grav}_{\min}) + \beta_5 \text{Notake} + \beta_6 N + (\beta_0 + \beta_{0a} + \beta_{0ab} + \beta_{0m} + \beta_{0g} + \beta_{0r}) \\ \text{shape} &\sim \text{Gamma}(0.01, 0.01) \\ \beta_0 &\sim T(3, 0.1, 2.5) \\ \beta_1 &\sim N(0.1, 3) \\ \beta_{2g} &\sim N(0, \sigma_{2g}) \\ \sigma_{2g} &\sim T(3, 0, 2.5) \\ \beta_3 &\sim N(-0.1, 3) \\ \beta_{4r} &\sim N(0, \sigma_{4r}) \\ \sigma_{4r} &\sim T(3, 0, 2.5) \\ \beta_5 &\sim N(0, 3) \\ \beta_6 &\sim N(0.1, 3) \\ \sigma_a &\sim T(3, 0, 2.5) \\ \sigma_b &\sim T(3, 0, 2.5) \\ \sigma_m &\sim T(3, 0, 2.5) \\ \sigma_g &\sim T(3, 0, 2.5) \end{aligned}$$

In our data exploration, we also noted that our single-year survey data exhibited a triangular pattern of variance in which productivity varied less with increasing richness. To understand how the diversity-productivity relationship effect varied in the least to most productive assemblages, we also fitted a frequentist quantile regression to estimate species richness slopes for the 1%, 50%, and 99% quantiles (Equation 4).

Equation 4

$$\begin{aligned} \log(\text{Prod}_{iab}) &\sim \log(S_{iab}) + \log(\text{Grav}_m + \text{Grav}_{\min}) + \varepsilon \\ \varepsilon &\sim N(0, \sigma) \end{aligned}$$

Simulated assemblage models

Because our productivity and richness variables originate from the same underlying assemblage data on observed species, there can also be an intrinsic relationship between the two variables due to our methodological choices. Namely, in a theoretical assemblage productivity and species richness would be mathematically equivalent if all species exhibited a total population productivity of 1 kg/ha/day (although extremely unlikely to occur in reality). Furthermore, the number of species can influence the range of assemblage productivity because key growth parameters like $K_{\max}$ and $L_{\max}$ are all species-level parameters. An increased number of species will affect the possible ranges of these species traits. Based on this understanding of our productivity modelling framework, species richness could influence the range and minima of productivity. We anticipate this mathematical relationship will influence the spatial model most as it uses observed values as opposed to the proportional change values in the temporal models. We fitted three types of simulated assemblage models to aid interpretation of an ecological signal apart from these intrinsic mathematical links: growth agnostic, abundance agnostic, and species agnostic models. For all of the following models, we simulated assemblage data where we hold one variable constant, recalculate assemblage productivity, and fitted models described in Equation 2, where productivity is replaced by the productivity estimate from simulated data.

Table 1 Summaries of null data simulations for each null model

Model	Variable changed	Description of null data simulation
Growth agnostic	Length	Individual lengths = $0.9999 * L_{\max}$
Species agnostic, minimum	Species	All species in assemblage as the species with smallest $L_{\max}$
Species agnostic, maximum	Species	All species in assemblage as the species with greatest $L_{\max}$
Abundance agnostic	Abundance	All species abundances = 1

We fitted the growth agnostic model where all individuals were at a productivity value approaching 0. To estimate productivity approaching 0, we kept our observed assemblage abundances the same but transformed lengths to 0.9999 of the species $L_{\max}$, as productivity approaches 0 at $L_{\max}$. We estimated gross assemblage productivity with these transformed lengths as described above, generating $Prod_0$. We then refitted the model described in Equation 2 using $Prod_0$ as the response variable, resulting in our length agnostic model.

We fitted two species agnostic models assuming if all individuals in an assemblage belonged to one singular, extreme species in productivity. Because body size is the single greatest driver of growth in fish (52), we simulated the data for this assemblage by changing all species identities to the largest and smallest species of the assemblage, determined by $L_{\max}$. We scaled all individual lengths to match the simulated $L_{\max}$, preserving the relative size structure of each species population. We did so by obtaining each individual's length relative to its original $L_{\max}$, then scaled that by the extreme species $L_{\max}$. We estimated gross assemblage productivity as described above, using the extreme species traits and estimated $K_{\max}$ for the assemblage, resulting in $Prod_{\text{spmin}}$ and $Prod_{\text{spmax}}$. We then fitted the model described in Equation 2 using $Prod_{\text{spmin}}$ and $Prod_{\text{spmax}}$ as response variables.

To simulate abundance agnostic data, we simply assumed the abundance for all species to equal 1. We recalculated productivity without any abundance scaling at the species level before aggregating to assemblage productivity.

Diversity-productivity links in temporal change

To understand diversity-productivity relationships under the context of temporal change, we first estimated temporal trends for assemblage productivity and species richness for each time-series. We fitted frequentist generalised linear models for each variable per time-series s with log-linked Gamma distributed errors. The resulting estimated β_1 coefficients for Year_{tba} are then later referred to as ΔProd_s and ΔS_s , respectively.

Equation 5

$$\text{Prod}_{iba} \sim \text{Gamma}(\mu_{iba}, \alpha)$$

$$\log(\mu_{iba}) = \beta_1 \text{Year}_{iba} + \beta_0$$

Equation 6

$$S_{iba} \sim \text{Gamma}(\mu_{iba}, \alpha)$$

$$\log(\mu_{iba}) = \beta_1 \text{Year}_{iba} + \beta_0$$

We assessed the links in diversity-productivity trajectories both qualitatively and quantitatively. To qualitatively characterise diversity and productivity trajectories as parallel or opposing, we binned each time-series (full time-series) or time-series year (adjacent years) by the directions of their temporal change, parallel where the trajectories are both positive or negative, and opposing where trajectories move in opposite directions. We also classified time-series by the certainty of their diversity and productivity trajectories, i.e. whether both trajectory estimates overlap 0 in their confidence intervals.

To quantitatively investigate the link between productivity and diversity change, we modelled productivity change as a function of species richness change (Equation 7). Each data point in this model refers to a time-series i belonging to study a at location b . This includes control covariates of change in assemblage abundance (ΔN), change in sea surface temperature (ΔSST), level of no-take restriction protection, and the number of years in a time-series with no-take designation (MPAYears). Again, we obtained spatial and temporal data on no-take restrictions from the ProtectedSeas Navigator database (38, 93). We estimated temporal trajectories using frequentist generalized linear models (Equations 8-9). We used Gamma distributed errors with a log-link for assemblage abundance and Gaussian distributed errors for sea surface temperature. Sea surface temperature data is at a 0.25° resolution matched to sampling events at the lowest available temporal resolution provided by the assemblage data. Moving forward, the corresponding β_1 coefficient estimates are referred to as ΔN_{iba} and ΔSST_{iba} .

Similar to the spatial model, we included log-transformations in the model formula and included group-level intercepts for study (σ_a), location (σ_b), and gravity grid cell (σ_m) with weakly regularising priors (Equation 6). We specified similar priors to our fixed effects that reflect our hypotheses about a positive effect from richness and a negative effect from human gravity.

Equation 7

$$\Delta \text{Prod}_{tba} \sim N(\mu_{iba}, \sigma)$$

$$\mu_{iba} = \beta_1 \Delta S_{iba} + \beta_2 \log(\text{Grav}_m + \text{Grav}_{\min}) + \beta_3 \Delta N_{iba} + \beta_4 \Delta \text{SST}_{iba} + \beta_5 \text{No-take}_{iba} + \beta_5 \text{MPAYears}_{iba} + \beta_0 + \beta_{0a} + \beta_{0b} + \beta_{0m}$$

$$\beta_1 \sim N(0.1, 3)$$

$$\beta_2 \sim N(-0.1, 3)$$

$$\beta_3 \sim N(0.1, 3)$$

$$\beta_4 \sim N(0.1, 3)$$

$$\beta_0 \sim T(3, 0.1, 2.5)$$

$$\sigma_a \sim T(3, 0, 2.5)$$

$$\sigma_b \sim T(3, 0, 2.5)$$

$$\sigma_m \sim T(3, 0, 2.5)$$

Equation 8

$$N_{iba} \sim \text{Gamma}(\mu_{iba}, \alpha)$$

$$\log(\mu_{iba}) = \beta_1 \text{Year}_{iba} + \beta_0$$

Equation 9

$$\text{SST}_{iba} \sim N(\mu_{iba}, \sigma)$$

$$\mu_{iba} = \beta_1 \text{Year}_{iba} + \beta_0$$

We also fitted an alternative temporal model based on short-term temporal trajectories. Our time-series data varies widely in temporal scope with time-series spanning 2 to 29 years. In longer time-series, year to year fluxes in richness or productivity are not as influential to the overall estimated temporal trend. Hence, the length of time-series may influence the estimated effects of the temporal model. To account for a potential effect in time-series length, we conducted an alternate temporal analysis based on adjacent year temporal trends. We calculated short-term temporal trends of richness and productivity using log-ratios between adjacent observation years. The resulting log ratios are then later referred to as $\Delta \text{Prod}_{\text{flux}}$ and ΔS_{flux} , respectively. We then fitted an adjacent year model with the same structure as shown in Equation 10 with $\Delta \text{Prod}_{\text{flux},t}$ and $\Delta S_{\text{flux},t}$.

All Bayesian models were fitted using the R brms package (94–96) which implements multilevel Bayesian models with Stan programming language. The package estimates posterior distributions for the model parameters using the Hamiltonian Monte Carlo algorithm. For each model in our statistical analyses, we specified fitting using 4 chains. Spatial models were fitted with 5000 iterations per chain including 2500 initial burn-in sampling iterations, totalling 10,000 sample draws for resulting posterior distributions. Temporal models were fitted with 8000 iterations per chain with 4000 burn-in iterations, totalling 16,000 sample draws for posterior distributions. We determined model convergence by ensuring $\hat{R} = 1.00$ for all estimated parameters. Model performance was also assessed by checking bulk effective sample sizes, tail effective sample sizes, leave-one-out cross-validation, and visual assessments of MCMC traceplots.

Length binning effects on productivity

Nine studies recorded fish lengths in binned classes. Because productivity is estimated from length observations, we conducted a sensitivity analysis on the potential effect of length binning on a subset of our data. We selected a subset of 2000 unbinned length records and applied an artificial binning used by many of our studies: 5 cm bins for individuals ≤ 10 cm, 10 cm bins where length is between 10-100 cm, and 50 cm bins above 100 cm. The resulting lengths would reflect the midpoint of the length class, e.g. 7.5 cm for a bin of 5–10 cm. We first assessed the effect of binning on productivity estimates by modelling binned productivity as a function of productivity from the original estimated lengths ($\text{Prod}_{\text{actual}}$). We fitted a generalised linear model using Gamma distributed errors and a log link function.

Equation 11

$$\text{Prod}_{\text{bin}} \sim \text{Gamma}(\mu_i, \text{shape})$$

$$\mu_i = \exp(\chi_{iba}\beta_0)$$

$$\log(\mu_i) = \beta_1 \log(\text{Prod}_{\text{actual}})$$

We then explored the drivers of productivity differences due to binning ($\Delta\text{Prod}_{\text{bin}} = |\text{Prod}_{\text{bin}} - \text{Prod}_{\text{actual}}|$), using absolute values of differences because we were not concerned with the direction of differences but rather the magnitude. We modelled the influence of individual body size (L_i), species body size (L_{max}), change in length due to binning ($\Delta L_{\text{bin}} = L_{\text{bin}} - L_i$), and size of an individual relative to its species size (L_i / L_{max}) as drivers of $\Delta\text{Prod}_{\text{bin}}$. We fitted a global generalised linear regression model with all these predictors using Gamma distributed errors and a log link function due to the zero-bounded continuous nature of the difference data. To determine the ideal predictor structure, we used automated dredging with corrected Akaike information criterion (AICc) rankings to select a model that explains patterns in productivity differences best.

Equation 12

$$\Delta\text{Prod}_{\text{bin}} \sim \text{Gamma}(\mu_i, \text{shape})$$

$$\log(\mu_i) = \beta_0 + \beta_1 L_{\text{max}} + \beta_2 L_i + \beta_3 (L_i / L_{\text{max}}) + \beta_4 (\Delta L_{\text{bin}})$$

Sample completeness sensitivity comparison

Because this study synthesises data collected using a variety of methods over variable spatial grains, species richness can be highly sensitive to incomplete sampling or smaller survey areas (80). To ensure that our spatial model was not driven by sampling artefacts or methodological differences, we reconstructed the spatial model without low completeness samples in our dataset. We determined sample coverage as established by Chao and Jost (44) by adapting an implementation found in the iNEXT package (97). Sample completeness is bounded between 0 and 1, where 1 indicates maximum completeness. The median sample completeness for our data was 0.95 with 75% of the data with a minimum of 0.89 completeness. We fitted the model with filtered data following the same predictor and error structure outlined in Equation 2 using frequentist generalised linear mixed modelling. We then quantified the influence of low sample completeness data by comparing model coefficient estimates between the original and filtered model.

Data processing and statistical analyses were performed in R 4.3.3 (98). Code and data for replicating data compilation, processing, and analysis can be found at GitHub (data compilation: https://github.com/cherfychow/macro_reef_fish, analysis: <https://github.com/cherfychow/producDiv>). We used the following R packages (Table 2): dggirdR for spatial gridding, sf for spatial data manipulation, iNEXT for calculating sample

coverage and completeness, rfishprod for modelling reef fish growth parameters and somatic growth, rfishbase to query and extract species traits from the FishBase database, xgboost for boosted regression trees in imputing fish $K_{\max}$ parameters, tidync to interact and manipulate sea surface temperature netCDF data, lubridate to handle time and date data, brms for Bayesian hierarchical modelling, including model diagnostics and comparisons, quantreg for quantile regression analysis, lme4 for generalised linear models, and tidybayes to extract posterior distributions from fitted Bayesian models. We used dplyr, tidytable, stringr, and readr for general data wrangling and manipulation. Data visualisation was done with the ggplot2, patchwork, ggdist, and rnaturalearth packages. The versions used are listed in Table 2.

Table 2 R packages used for data processing and analysis.

Package	Version	Citation	Package	Version	Citation
brms	2.22.0	(94–96)	readr	2.1.5	(99)
dggridR	3.1.0	(100)	rfishbase	5.0.0	(101)
dplyr	1.1.4	(102)	rfishprod	0.0.3	(36, 52)
ggdist	3.3.2	(103, 104)	rnaturalearth	1.0.1	(105)
ggplot2	3.5.2	(106)	sf	1.0.16	(107, 108)
iNEXT	3.0.1	(97, 109, 110)	stringr	1.5.1	(111)
lme4	1.1.37	(112)	tidybayes	3.0.7	(113)
lubridate	1.9.4	(114)	tidync	0.3.0	(115)
patchwork	1.3.1	(116)	tidytable	0.11.2	(117)
quantreg	6.1	(118)	xgboost	1.7.7.1	(119)

Supplementary tables and figures

Table S1 Studies used in the data compilation and their sources. We also indicate the inclusion of each study in the resulting data subset for single-year (1 yr) and time-series (2+ yr) analyses determined by spatial gridding. Data without a reference are not previously associated with another source or publication and provided directly for this paper.

Study identifier	Title	1 yr	2+ yr	Ref.
001_dyiigurra_macro	Long-term UVC fish surveys of Dyiigurra, Great Barrier Reef		X	nil
011_quimbayo_timefish_scuba	TimeFISH: Fish assemblages in a 15-year monitoring program– no-take zone scuba surveys	X	X	(120, 121)
011_quimbayo_timefish_snorkel	TimeFISH: Fish assemblages in a 15-year monitoring program– snorkel surveys	X		(120, 121)
012_alzate_gorgona	Community data on coral and rocky reef fish, Gorgona, Colombia	X		(122)
014_andradibrown_utila	Data from: Reef Fish Community Biomass and Trophic Structure Changes across Shallow to Upper-Mesophotic Reefs in the Mesoamerican Barrier Reef, Caribbean	X		(123)
017_brandl_uacryptic	Extreme environmental conditions reduce coral reef fish biodiversity and productivity	X		(124, 125)
020_noaa_micronesia	NOAA coral reef monitoring fish data from sites across Micronesia from 2009-09-29 to 2015-09-25, MPA sites	X	X	(126)
021_noaa_pacificstrs	NOAA National Coral Reef Monitoring Program: Stratified random surveys (StRS) of reef fish	X	X	(127)
022_noaa_puertorico	Puerto Rico Long-Term Coral Reef Monitoring Program Database Compilation	X	X	(128)
025_friedlander_costarica	Nearshore marine biodiversity of Osa Peninsula, Costa Rica	X		(129, 130)
027_friedlander_palau	Size, age, and habitat determine effectiveness of Palau’s Marine Protected Areas	X		(131, 132)
028_caribbean_cuba	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Caribbean	X		(133, 134)
028_eastern_atlantic_cverde	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Eastern Atlantic Cabo Verde	X		(133, 134)
028_eastern_atlantic_stome	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Eastern Atlantic São Tomé	X		(133, 134)
028_mexico	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Mexico	X		(133, 134)
028_clipperton_alan_2017	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Clipperton	X		(133, 134)
028_cocos	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Cocos Islands	X		(133, 134)
028_curacao	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Curacao	X		(133, 134)

Study identifier	Title	1 yr	2+ yr	Ref.
028_easter_salaz	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Rapa Nui and Isla Salaz y Gomez	X		(133, 134)
028_hawaii	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Hawai'i	X		(133, 134)
028_loyalty	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Loyalty Islands, New Caledonia	X		(133, 134)
028_mozambique_alan_2017	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Mozambique	X		(133, 134)
028_pitcairn	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Pitcairn Islands	X		(133, 134)
028_revillagigedo_alan_2017	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Revillagigedo Islands, Mexico	X		(133, 134)
028_seychelles_alan_2017	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Seychelles	X		(133, 134)
028_agreen_palau	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Palau	X		(133, 134)
028_agreen_raja_ampat_2012	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Raja Ampat, Indonesia	X		(133, 134)
028_agreen_samoa	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Samoa	X		(133, 134)
028_agreen_solomon_2008	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Solomon Islands	X		(133, 134)
028_fiji_biomass_2013a	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Fiji	X		(133, 134)
028_flores_1993_michel	Body size, reef area, and temperature predict global reef-fish species richness across spatial scales: Flores Sea	X		(133, 134)
031_crane_ulithi	Atoll-scale patterns in coral reef community structure: Human signatures on Ulithi Atoll, Micronesia		X	(135, 136)
032_carvalho_indonesia	Data from: Fishing and habitat condition differentially affect size spectra slopes of coral reef fishes	X		(9)
033_jennings_fiji	Size-spectra as indicators of the effects of fishing on coral reef fish assemblages	X		(137)
036_noaa_sefsc	NOAA Southeast Fisheries Science Center Reef Visual Census (RVC) dataset	X	X	(138, 139)
051_usvi_termp	US Virgin Islands Territorial Coral Reef Monitoring Program (TCRMP) Fish Census		X	(140)
052_noaa_pacificramp2000	Pacific Reef Assessment and Monitoring Program: Rapid Ecological Assessments of Fish Large-Area Stationary Point Count Surveys (SPC) at Coral Reef Sites across the Pacific Ocean from 2000 to 2007	X	X	(141)

Study identifier	Title	1 yr	2+ yr	Ref.
054_RLS	IMOS - National Reef Monitoring Network Sub-Facility - Global reef fish abundance and biomass	X	X	(142–145)
060_smallhornwest_tonga	Benthic and reef fish surveys from the Kingdom of Tonga in 2017-2024 (375 sites)	X	X	nil
072_alvarezfilip_cozumel	Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs	x		(146)
093_debrauwer_lucipara	Lucipara - Banda Sea	X		(147)
104_brandl_crypticflux_belize	Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning- Belize	X		(10, 148)
104_brandl_crypticflux_lizard	Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning- Lizard Island	X		(10, 148)
104_brandl_crypticflux_moorea	Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning- Moorea	X		(10, 148)
110_brandl_farms_hawaii	Data from: Using standardized fish-specific autonomous reef monitoring structures (FARMS) to quantify cryptobenthic fish communities- Kaneohe Bay, Hawaii	X		(149, 150)
110_brandl_farms_panama	Data from: Using standardized fish-specific autonomous reef monitoring structures (FARMS) to quantify cryptobenthic fish communities- Bocas del Toro, Panama	X		(149, 150)
110_brandl_farms_saudi	Data from: Using standardized fish-specific autonomous reef monitoring structures (FARMS) to quantify cryptobenthic fish communities- Saudi Arabia	X		(149, 150)
113_alzate_malpelo_RLS	Malpelo Island, Colombia reef fish surveys - Reef Life Survey method	X		nil
113_alzate_malpelo_SIMAC	Malpelo Island, Colombia reef fish surveys - SIMAC method	X		(151)
114_gavrielbelmaker_aqaba	Reef fish belt-transects surveys in the Israeli Gulf of Aqaba	X	X	nil
122_SIFkoester_aldabra	Reef fish abundance, size and biomass from Aldabra Atoll (Seychelles) between 2014 and 2021 collected by the Seychelles Islands Foundation		X	(152)
127_philippines_liloan	Sampling-event dataset of short-term monitoring of Poblacion and Kadurong Reefs in Liloan, Cebu, Philippines	X		(153)
129_reefSYN_alcatrazes	ReefSYN Standardized datasets of Brazilian reef diversity in space and time - Dataset X: Alcatrazes monitoring	X	X	(154, 155)
129_reefSYN_arraial	ReefSYN Standardized datasets of Brazilian reef diversity in space and time - Dataset III: Arraial do Cabo (Rio de Janeiro) monitoring	X	X	(155, 156)
129_reefSYN_brazilian	ReefSYN Standardized datasets of Brazilian reef diversity in space and time - Dataset I: Fish communities from the Brazilian province	X	X	(155, 157)
129_reefSYN_oceanic	Long-term Ecological Monitoring Research Brazilian Oceanic Islands (reef fish)	X	X	(155, 158)
129_reefSYN_trindade	ReefSYN Standardized datasets of Brazilian reef diversity in space and time - Dataset V: Fish assemblages from Trindade and Martin Vaz		X	(155, 159, 160)
130_protectWPS_philippines	ProtectWPS Philippines reef fish monitoring	X	X	nil

Study identifier	Title	1 yr	2+ yr	Ref.
131_bluealliance_pemba	Blue Alliance Fish Visual Census Pemba, Tanzania	X		nil
131_bluealliance_philippines	Blue Alliance Fish Visual Census Philippines	X		nil
133_hadjhammou_SERF_belt	Global patterns and drivers of fish reproductive potential on coral reefs— belt surveys		X	(161, 162)
133_hadjhammou_SERF_point	Global patterns and drivers of fish reproductive potential on coral reefs— point count surveys	X		(161, 162)
134_richardson_lirs	Mass coral bleaching causes biotic homogenization of reef fish assemblages		X	(7, 163)
135_emslie_gbraims_method1	Australian Institute of Marine Science (AIMS) Long-term Monitoring Program: Visual Census Fish Data	X	X	(164)
135_emslie_gbraims_method2	Australian Institute of Marine Science (AIMS) Long-term Monitoring Program: Visual Census Fish Data		X	(164)
136_noaa_crcp_usvi	NOAA Coral Reef Conservation Program US Virgin Islands, 2017-2023	X	X	(165)
BT45_moorea_lter	MCR LTER: Coral Reef: Long-term Population and Community Dynamics: Fishes, ongoing since 2005		X	(166, 167)
BT640_opwall_utili	Operation Wallacea reef fish surveys at Utila, Honduras	X	X	(123, 167)
BT692_grahamwilson_seychelles	Changing role of coral reef marine reserves in a warming climate		X	(167–169)
BT436_hoey_karimunjawa	Karimunjawa WCS fish survey	X	X	(167)
BT437_hoey_aceh	Aceh WCS long-term fish survey		X	(167)
BT437_hoey_aceh_single	Aceh WCS fish survey- single year	X		(167)

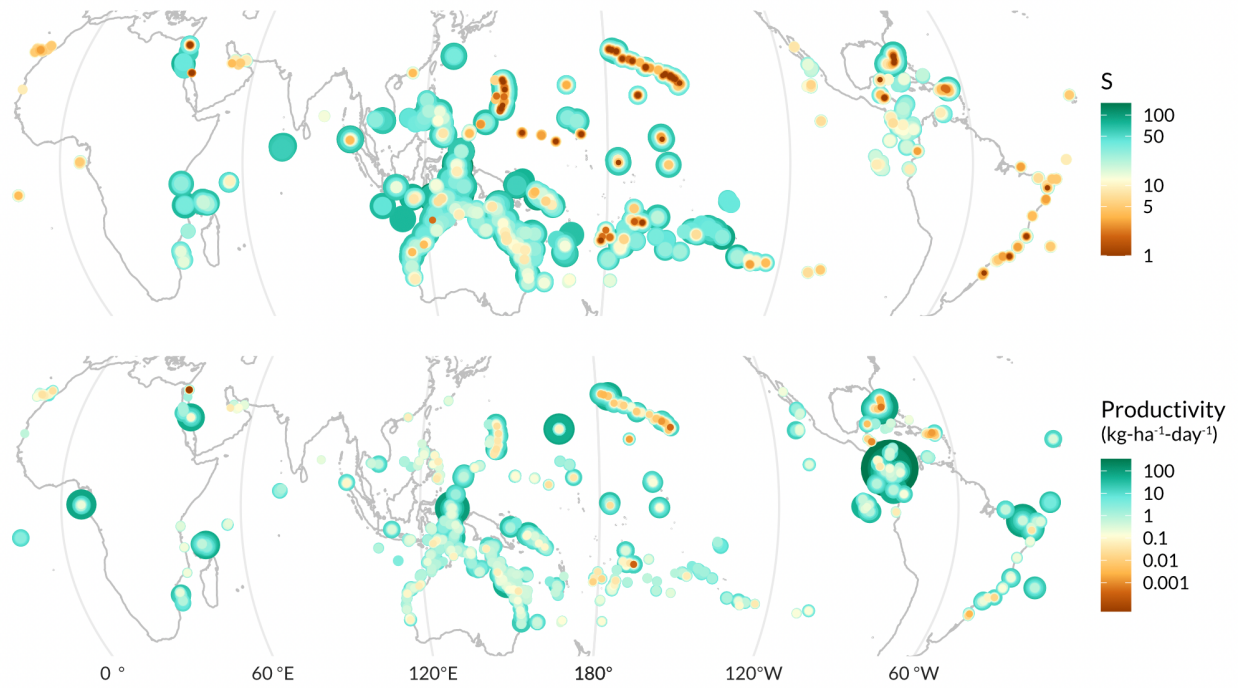


Figure S1. Geographic distribution of the compiled dataset consisting of both single-year and time-series data. Each circle represents a unique survey location, shaded by species richness (S) on the top panel and productivity on the bottom panel. For time-series, mean values over time are shown.

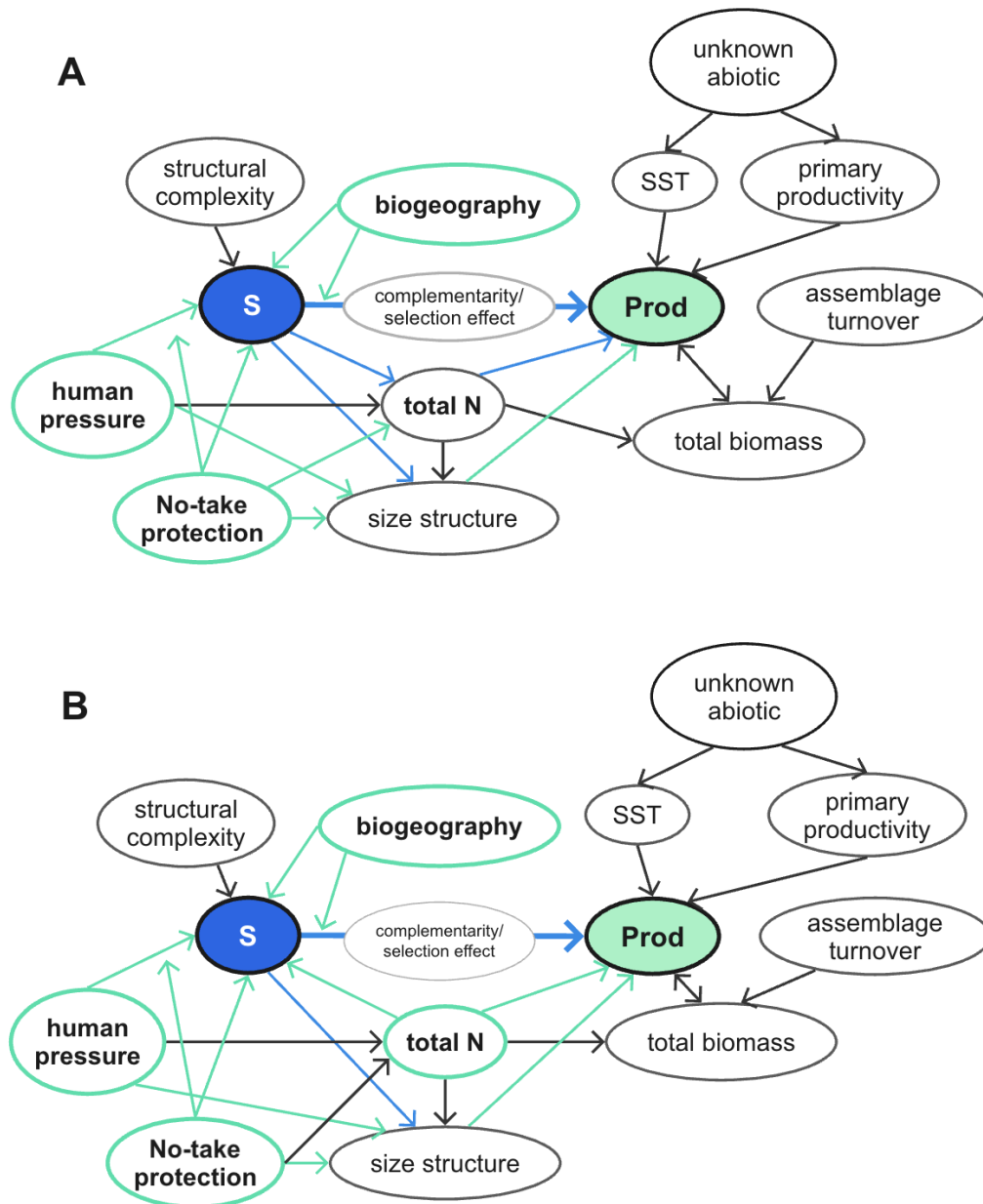


Fig. S2 Graphical causal diagrams that show explicit assumptions about variables involved in diversity links with productivity across space. Each oval is an independent variable, whether observed or unobserved. Arrows signify directional causal relationships between variables. We highlight species richness (S, filled blue) as our primary explanatory variable in question and assemblage productivity (Prod, filled green) as our target response variable. Causal relationships that link species richness with productivity are highlighted in blue arrows. Confounding and collider variables that need to be included as covariates are highlighted by green outlines with green arrows to show their biasing paths. Diagram A and B differ in the directionality of the link between species richness and assemblage abundance (total N). If abundance causes richness, it's included as a covariate (B). Vice versa, if abundance is a result of richness, it is included as part of the total effect of richness on productivity (A).

Table S2 Supporting rationale and sources in each of the directed arrows in our graphical causal diagrams.

Hypothesised relationship	Rationale	Source
Species richness (S) → Productivity (Prod) via niche complementarity, competition, and/or facilitation, $\Delta S \rightarrow \Delta \text{Prod}$	Positive biodiversity-ecosystem functioning relationships. Diversity fosters resource partitioning, maximising efficient energy acquisition and somatic growth.	(41, 170–172)
S → Abundance (total N), $\Delta S \rightarrow \Delta N$	The minimum total abundance must be equivalent to the number of species. Tightly coupled with richness in assemblage structure.	(40, 41, 173)
Total N → Prod	Total abundance is mathematically integrated into how assemblage productivity is calculated from individual productivity.	
Structural complexity → S	More structurally complex habitats result in greater reef fish diversity by increasing available habitat and space	(174, 175)
Biogeography → S	Species diversity of reef fishes varies by biogeographical region.	(35, 176)
SST → Productivity, $\Delta \text{SST} \rightarrow \Delta \text{Prod}$	Ambient temperature will affect the metabolism of ectotherms like reef fishes	(52, 177, 178)
Primary productivity → (fish) productivity	Trophic webs and hence energy acquisition of an assemblage are limited by an ecosystem's primary productivity	(179, 180)
Human pressure → S, total N, ΔN , No-take protection → S, total N, ΔN	Fishing exploitation and local pollution results in declines of assemblage diversity and abundance. No-take protections mitigate these effects from fishing exploitation.	(6, 181, 182)
Total N → total biomass	Total abundance is mathematically integrated into how total biomass is calculated	(41)
Prod → total biomass	Stored biomass comes from somatic growth. They are metabolically linked	(36, 41)
Assemblage turnover → total biomass	Higher rates of assemblage turnover result in less storage of biomass from production.	(183, 184)
Human pressure → size structure, No-take protection → size structure	Fishing exploitation is often size-selective and alters the size structure of fish assemblages, resulting in fewer large-bodied species. No-take protections mitigate these effects from fishing exploitation.	(185–187)
Total N → size structure	Size spectra are a good metric for assemblage size structure and incorporate relationships between abundance and body size	(187)
Size structure → Prod, size structure → ΔProd	Body size is the greatest determinant of growth in reef fish. At the assemblage scale, size structure would influence total assemblage productivity.	(52)
S → size structure	Assemblage composition and diversity can drive assemblage size structure and body size patterns	(76)
Range shifts → immigration, local extinction, emigration		(188)
Immigration, local extinction, emigration → ΔN , ΔS		(189–191)
Climate → ΔSST gamma → range shifts	Range shifts are driven by changes in regional climate and temperature	
Climate change → ΔSST local, ΔSST gamma	Climate change can cause marine heatwaves that affect reef ecosystems	(192, 193)

Table S3 Bayesian generalised linear mixed model fitting results to explore diversity-productivity links and their spatial patterns. The model predictors are species richness (S), human gravity, biogeographic region level variation of species richness (S|biogeo). We denote group-level intercepts as (1|group), where the estimates shown represent the σ parameters. We show the expected value for coefficient estimates, 95% credible intervals, R-hat values, standard effective sample size (ESS), and tail ESS for each predictor.

Predictor	Estimate	95% CI		R-hat	Std ESS	Tail ESS
log(S)	1.52	1.26	1.77	1.00	3354	4072
log(human gravity)	-0.04	-0.06	-0.03	1.00	3801	3247
(S biogeo)	0.28	0.13	0.60	1.00	3931	4901
(1 biogeo)	0.89	0.40	1.96	1.00	4671	5039
(1 gravity cell)	0.26	0.23	0.28	1.00	2059	3954
(1 location:study)	0.48	0.47	0.49	1.00	3727	6457
(1 study)	1.43	1.18	1.73	1.00	1862	3421
Intercept	-3.66	-4.57	-2.77	1.00	1965	4087

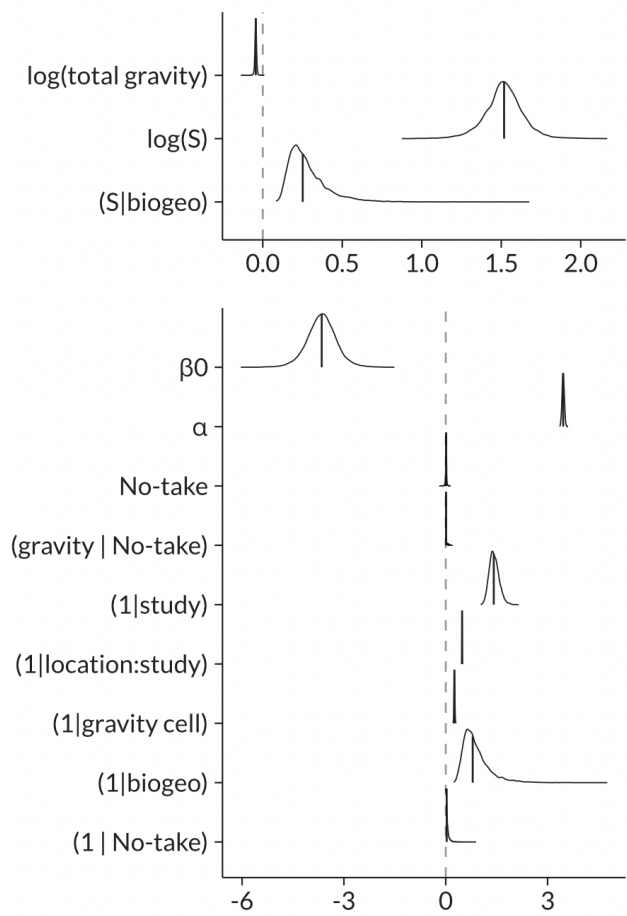


Fig. S3 Posterior distributions for coefficient estimates in the spatial diversity-productivity model. Species richness is shown as S, model intercept as β_0 , Gamma error distribution shape parameter as α , and group-level intercepts denoted by (1|variable). For label simplicity, logged predictors are not indicated in group-level labels. The distribution median is marked by a line.

Table S4 Bayesian generalised linear mixed model fitting results for an alternate spatial model. The model predictors are species richness (S), total assemblage abundance (N), human gravity, biogeographic region level variation of species richness (S|biogeo). We denote group-level intercepts as (1|group), where the estimates shown represent the σ parameters. We show the expected value for coefficient estimates, 95% credible intervals, R-hat values, standard effective sample size (ESS), and tail ESS for each predictor.

Predictor	Estimate	95% CI		R-hat	Std ESS	Tail ESS
log(S)	0.66	0.52	0.79	1.00	2428	2999
log(N)	0.64	0.63	0.65	1.00	6169	7226
log(human gravity)	-0.04	-0.05	-0.02	1.00	2641	2670
No-take restriction	0.01	-0.02	0.03	1.00	1924	1945
(S biogeo)	0.14	0.07	0.30	1.00	2781	4059
(1 biogeo)	0.33	0.11	0.81	1.00	2779	3950
(1 gravity cell)	0.24	0.22	0.26	1.00	1512	3051
(1 location:study)	0.42	0.42	0.43	1.00	2796	5243
(1 study)	1.49	1.22	1.81	1.00	950	1848
Intercept	-4.52	-5.03	-4.01	1.00	551	1429

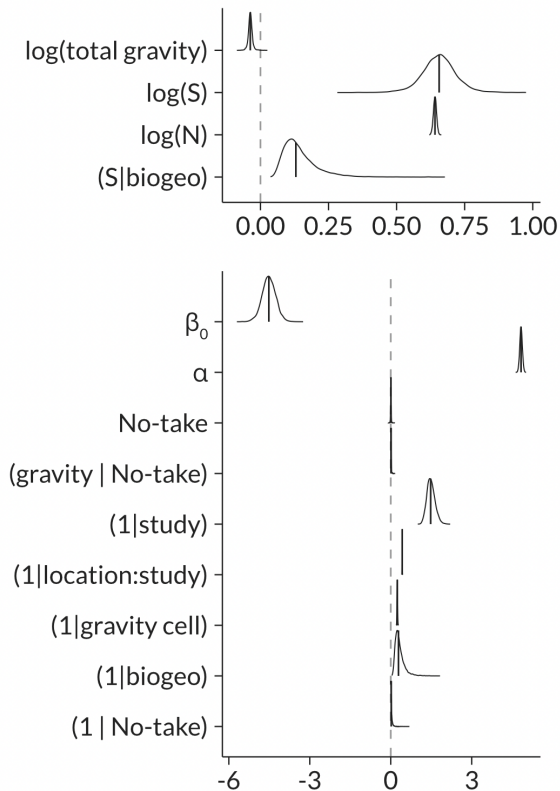


Fig. S4 Posterior distributions for coefficient estimates in the spatial diversity-productivity model in which abundance causes species richness. Species richness is shown as S, model intercept as β_0 , Gamma error distribution shape parameter as α , and group-level intercepts denoted by (1|variable). For label simplicity, logged predictors are not indicated in group-level labels. The distribution median is marked by a line.

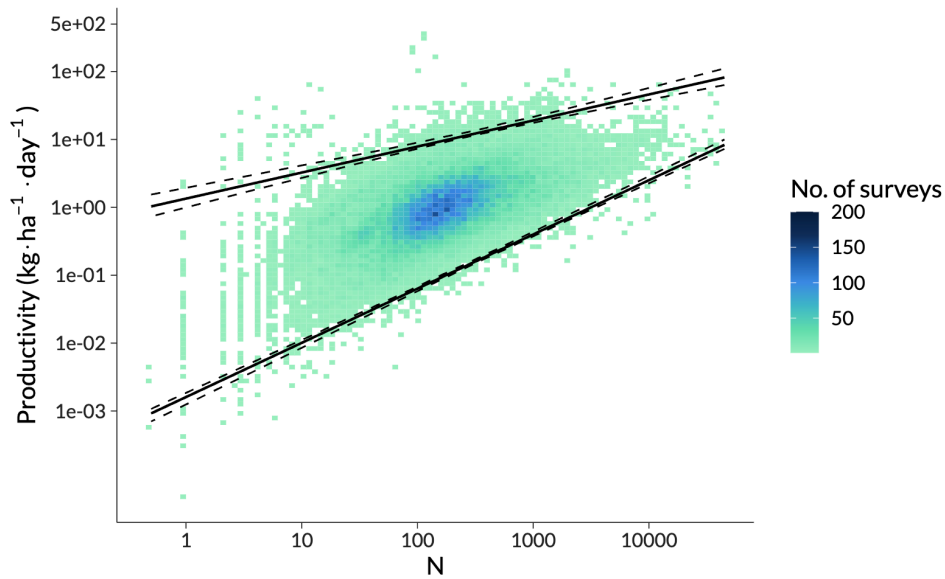


Figure S5. Quantile regression model results on the relationship between assemblage abundance (N) and reef fish gross assemblage productivity. The partial predictions for assemblage abundance are shown in black solid lines at 1% and 99% quantiles. 95% confidence intervals are shown as dashed lines.

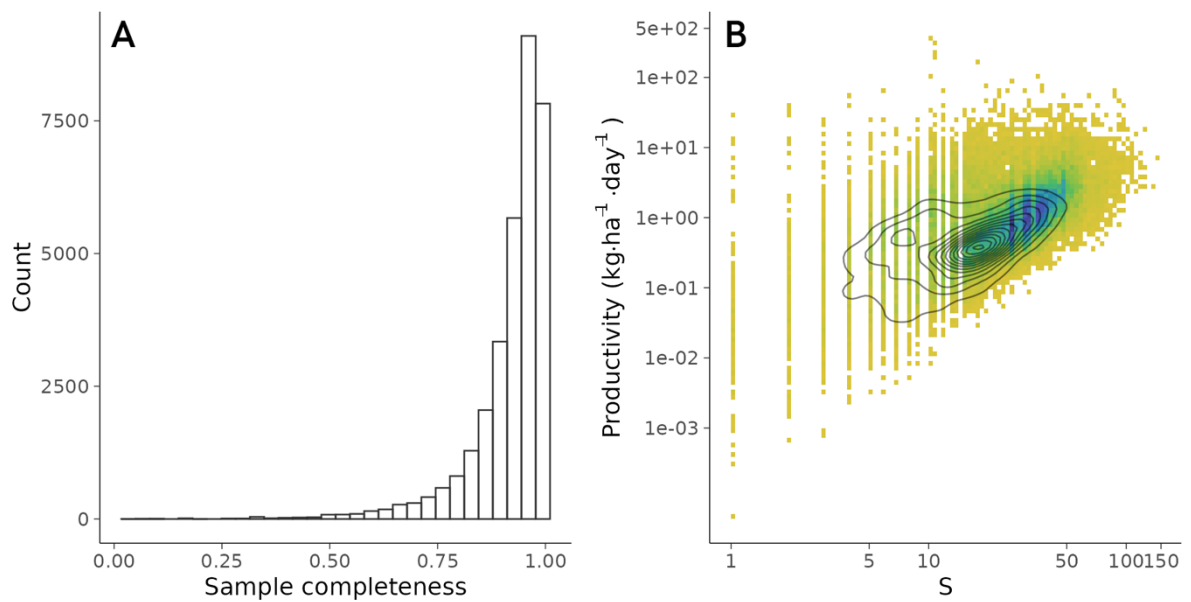


Fig. S6 Completeness of single-year data used in spatial modelling. Panel A shows the distribution of sample completeness in the study data. Panel B highlights where low completeness samples (line contours) are located in the diversity-productivity gradient of the dataset (pixels).

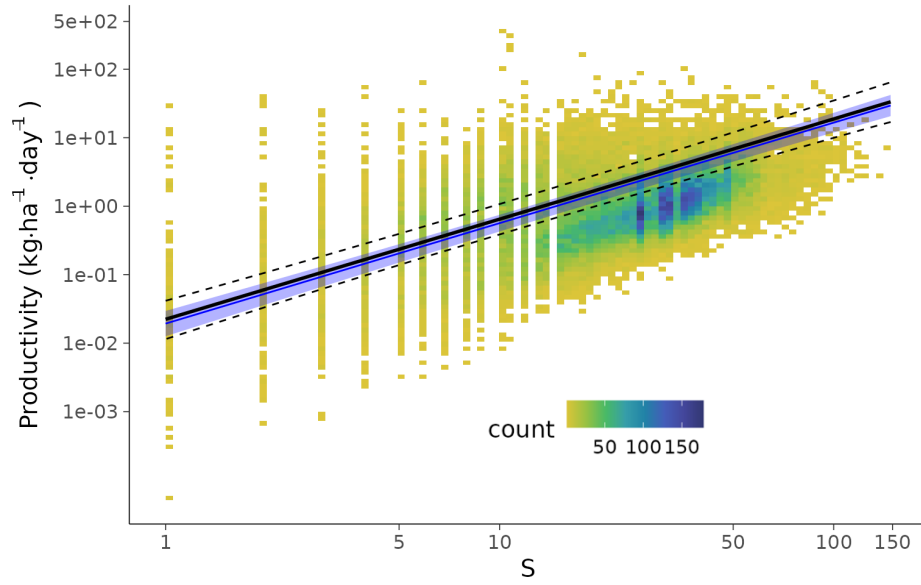


Fig. S7 Comparing the effect of sample completeness on the fit of a spatial diversity-productivity model. The black line with 95% credible intervals as dashed lines shows predictions from the model containing the full dataset. The blue line with 95% confidence intervals as a blue ribbon shows predictions from the model containing only complete samples (≥ 0.80).

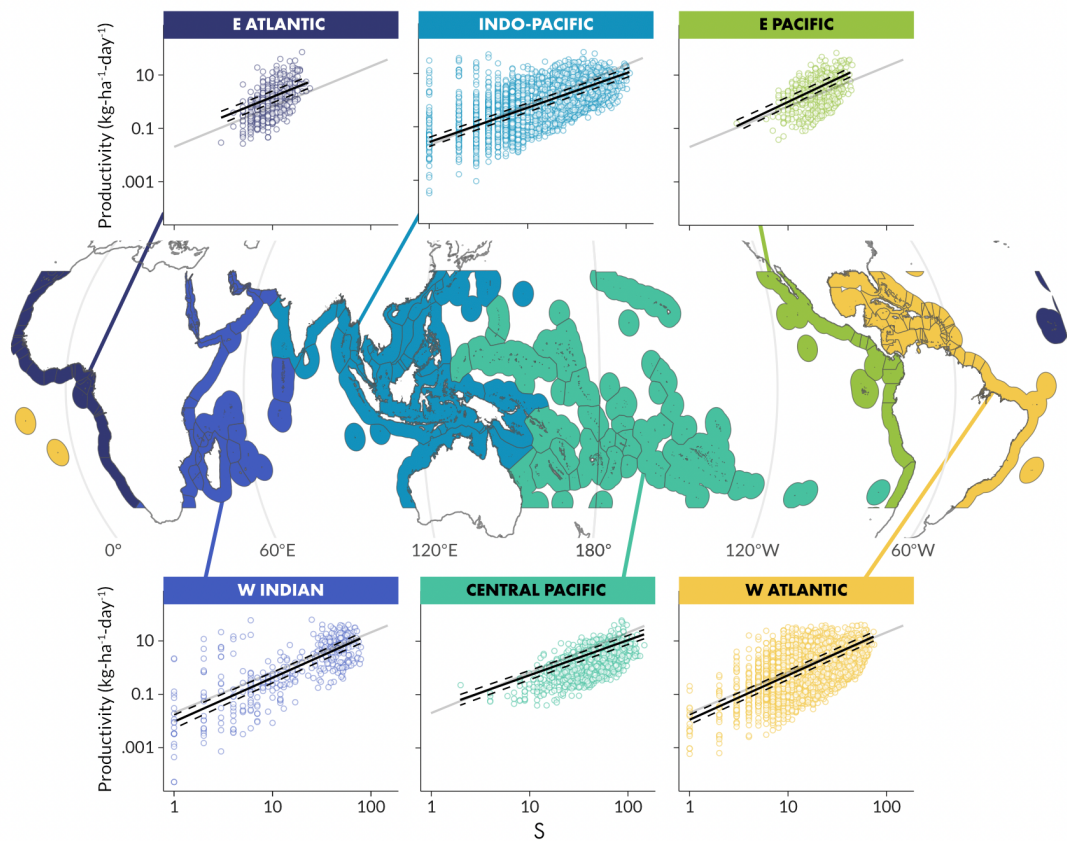


Fig. S8 Biogeographic patterns of the diversity-productivity relationship with partial predictions for each biogeographical region: Western Indian, Indo-Pacific, Central Pacific, Eastern Pacific, Western Atlantic, and Eastern Atlantic. The region-level partial effects of species richness are shown as black lines with the 95% credible interval indicated by dashed lines. The overall effect of species richness (without region-level intercepts or slopes) is shown in grey for reference.

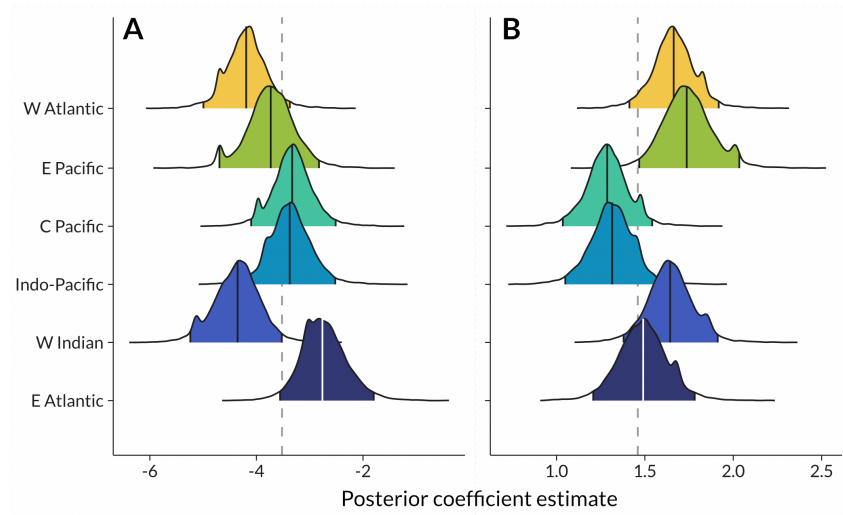


Fig. S9 Posterior distributions for group-level/random intercepts (β_0 , A) and species richness effects ($\log(S)$, B) by biogeographical region, Eastern Atlantic, Western Indian, Indo-Pacific, Central Pacific, Eastern Pacific, and Western Atlantic. The central 95% of the distributions are delineated by colour fill with the median indicated by lines. Grey dashed lines represent the model estimates for the fixed intercept and species richness effect.

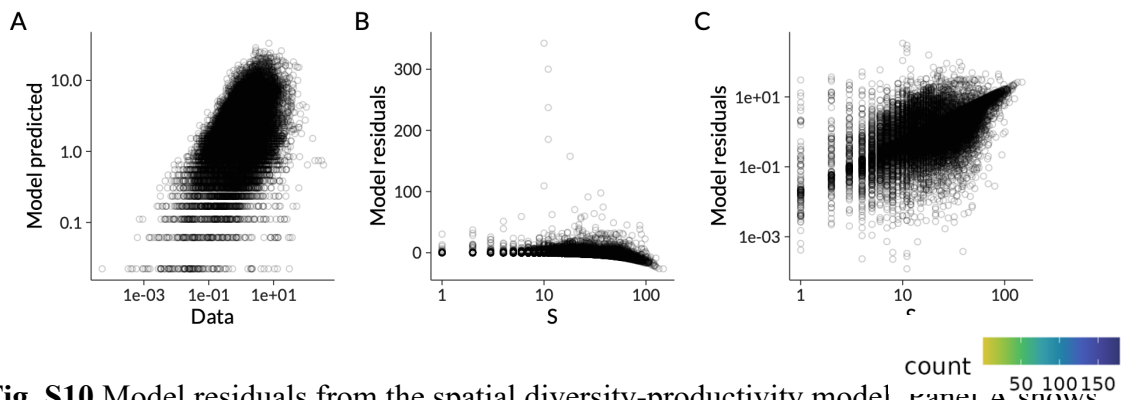


Fig. S10 Model residuals from the spatial diversity-productivity model. Panel A shows productivity data against the model prediction values. Panel B shows the spread of model residuals along the species richness gradient, and the absolute values of these residuals are shown on a log-log scale in panel C.

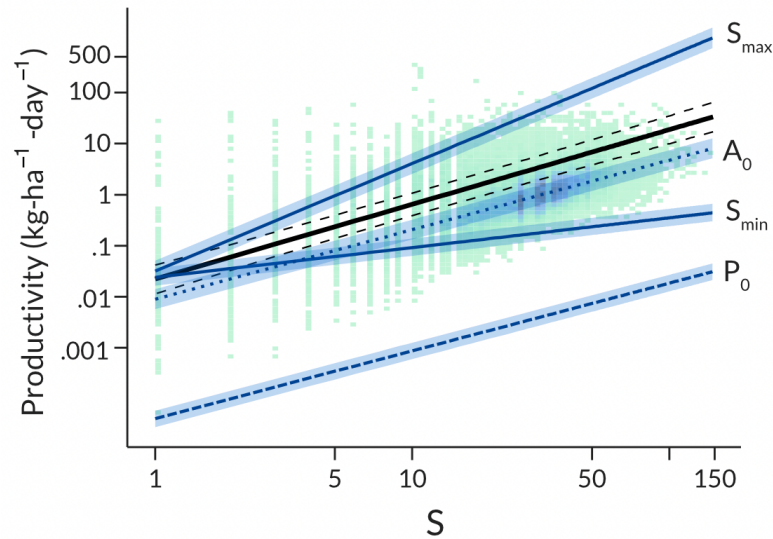


Figure S11. Null models which serve as reference baselines are shown in panel C as blue lines: null species with maximum size ($S_{\max}$, solid), null abundance (A_0 , dotted), null species with minimum size ($S_{\min}$, solid), and null productivity (P_0 , dashed). 95% credible intervals are shown as shaded blue ribbons. The partial prediction from the spatial hierarchical model is shown in black for comparison.

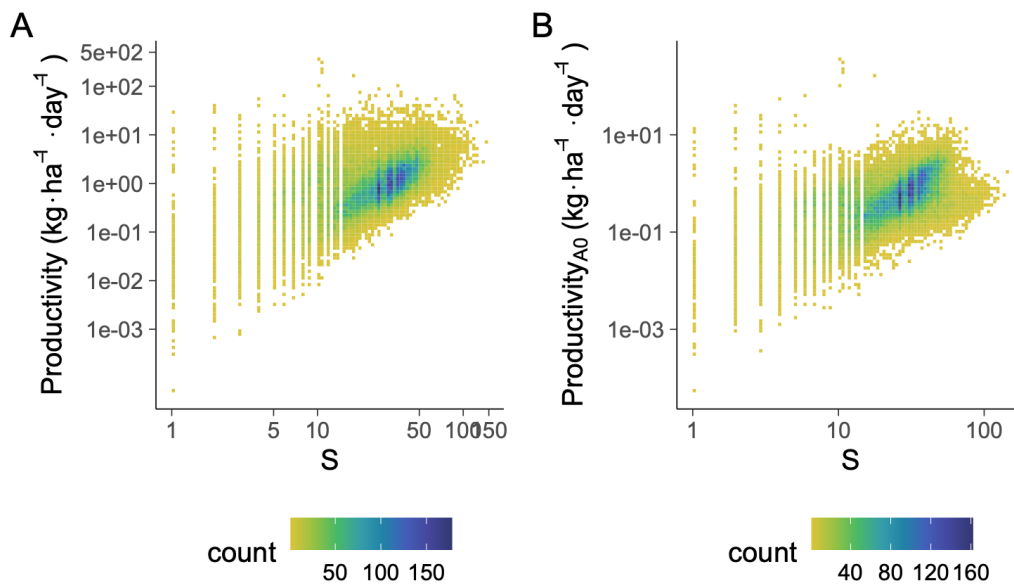


Fig. S12 Comparing the effect of altering abundance on assemblage productivity estimates. Panel A shows the original data of assemblage species richness with productivity. Panel B shows the simulated assemblage productivity if all species only consisted of one individual (abundance = 1).

Table S5 Generalised linear model fitting results to link fish individual productivity estimates when length is estimated to the nearest cm (actual) and when length is estimated in size

classes (bin). We show coefficient estimates, standard errors, and p -values for each predictor and overall model percent deviance and root mean squared error.

Predictor	Estimate	$\pm$ S.E.	p -value
$\log(\text{Prod}_{\text{actual}})$	0.921	± 0.013	< 0.001
Intercept	-0.684	± 0.121	< 0.001
Percent deviance	87.5%		
Nagelkerke's R^2	0.968		

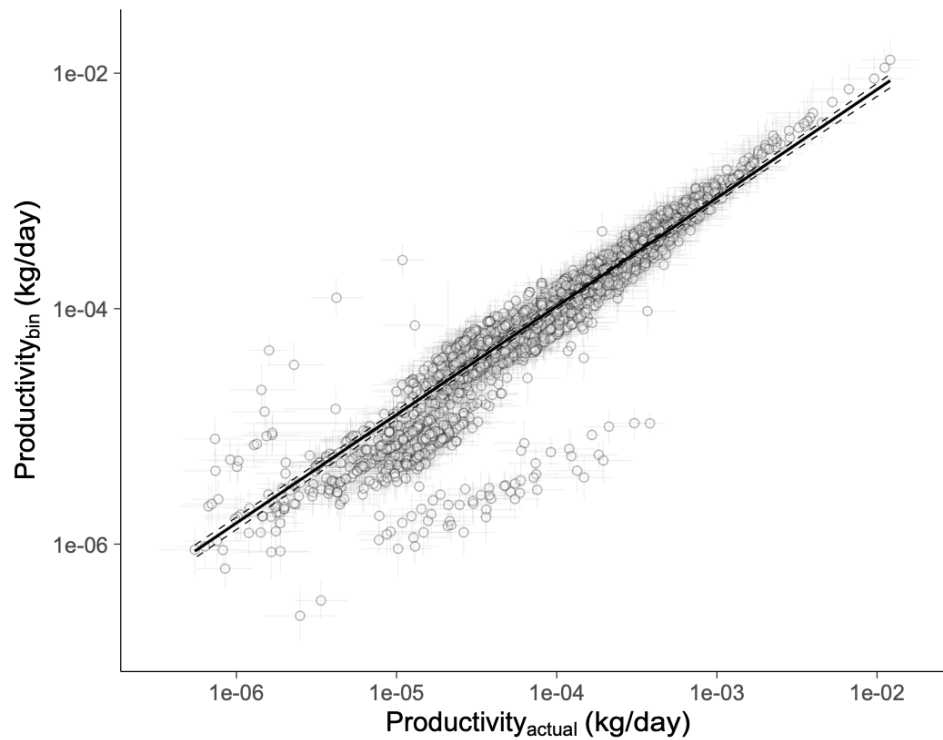


Fig. S13 Effects of length binning on productivity estimates at the individual-level. The relationship between productivity estimated from in situ length observations ($\text{Productivity}_{\text{actual}}$) and productivity estimated from the middle value of size class bins ($\text{Productivity}_{\text{bin}}$). The predicted fit from a generalized linear model between actual and binned productivity is shown as a black line with the 95% confidence interval as a dashed line.

Table S6 Generalised linear model fitting results to explore influences on length-binning induced productivity differences. The model predictors are differences in length (ΔLength), species body size (L_{max}), and the individual body size relative to their species size ($\text{Length}/L_{\text{max}}$). We show coefficient estimates, standard errors, and p -values for each predictor and overall model percent deviance and root mean squared error.

Predictor	Estimate	$\pm$ S.E.	p -value
$\log(\Delta\text{Length})$	0.946	± 0.022	< 0.001
$\log(L_{\text{max}})$	1.046	± 0.028	< 0.001
$\text{Length}/L_{\text{max}}$	0.733	± 0.092	< 0.001
Intercept	-15.102	± 0.109	< 0.001
Percent deviance	70.2%		
Nagelkerke's R^2	0.877		

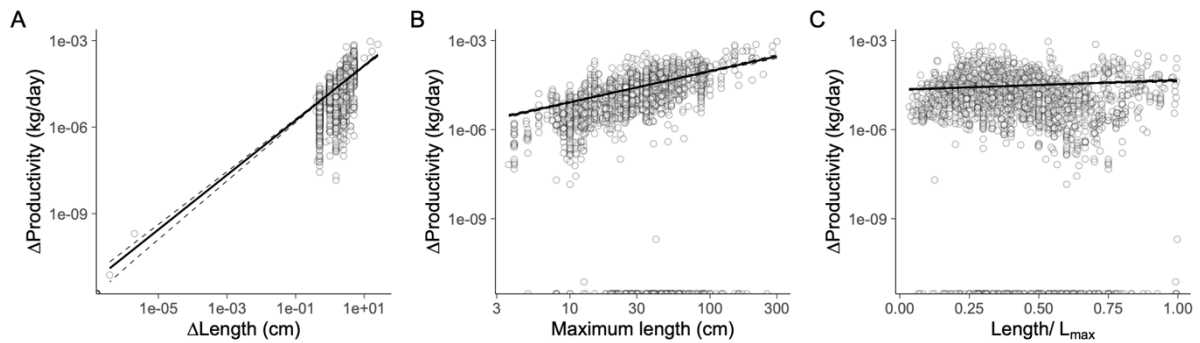


Fig. S14 We show how length binning driven error in productivity (calculated as $|\text{actual productivity} - \text{binned productivity}|$) increase proportionally binning length differences (ΔLength , panel A) and species body size (panel B), but there is no pattern with length relative to species maximum length ($\text{Length}/L_{\text{max}}$; panel C). Partial predictions from our generalized linear regression model are shown as black lines with the 95% confidence interval as a dashed line.

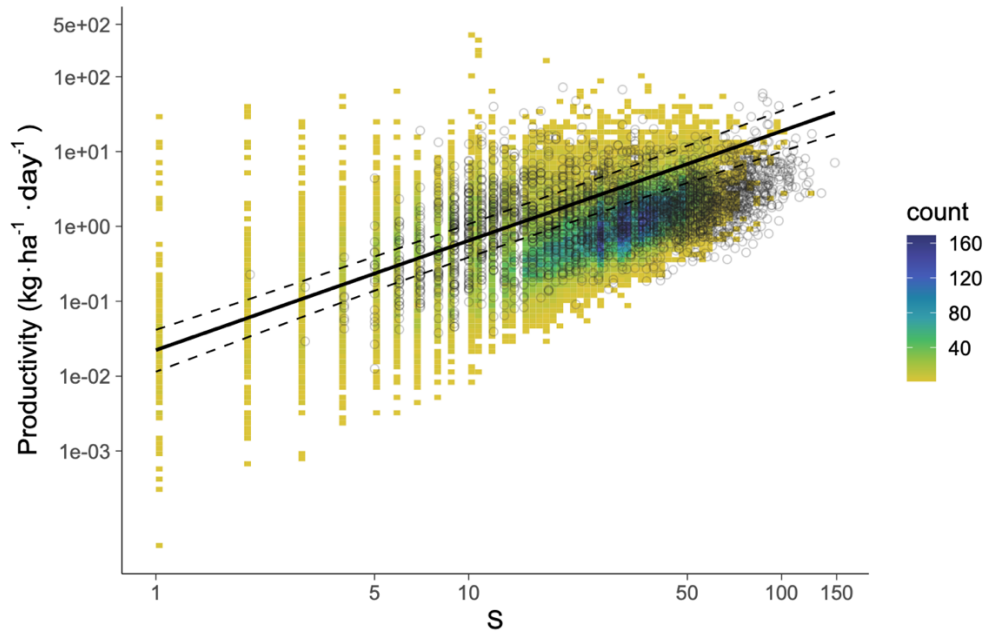


Fig. S15 Spatial single-year data disaggregated by length estimation method type. The data underlying the spatial diversity-productivity model is shown split, where filled pixels represent data with length estimated to the nearest cm ($n = 28857$) and grey circles as data estimated by size class bins ($n = 3561$). Some of the most diverse assemblages are surveyed using size class bins but the fitted model is still largely informed by non-binned length data.

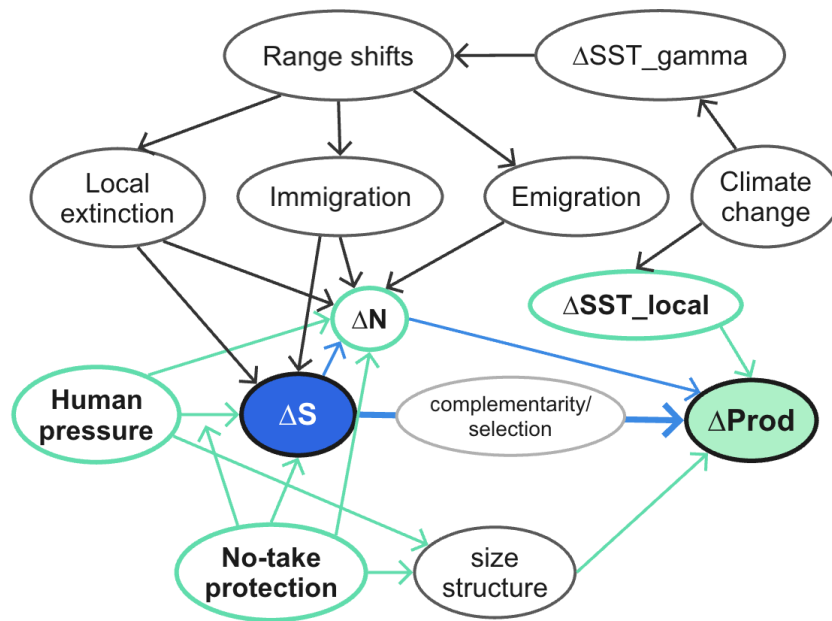


Fig. S16 Graphical causal diagram that shows explicit assumptions about variables involved in diversity links with productivity in temporal change. Each oval is an independent variable, whether observed or unobserved. Arrows signify directional causal relationships between variables. We highlight species richness change (ΔS , filled blue) as our primary explanatory variable in question and assemblage productivity change (ΔProd , filled green) as our target response variable. Causal relationships that link species richness with productivity are highlighted in blue arrows. Confounding and collider variables that need to be included as covariates are highlighted by green outlines.

Table S7 Bayesian generalised linear mixed model fitting results on the spatiotemporal patterns of diversity-productivity links. The model predictors are species richness change ($\Delta\log(S)$), assemblage abundance change ($\Delta\log(N)$), sea surface temperature change (ΔSST), and human gravity. We denote group-level intercepts as (1|group), where the estimates shown represent the σ parameters. We show the expected value for coefficient estimates, 95% credible intervals, R-hat values, standard effective sample size (ESS), and tail ESS for each predictor.

Predictor	Estimate	95% CI		R-hat	Std ESS	Tail ESS
$\Delta\log(S)$	0.67	0.61	0.73	1.00	2056	760
$\Delta\log(N)$	0.63	0.61	0.66	1.00	3295	6810
$\log(\text{human gravity})$	0.00	0.00	0.00	1.00	1935	677
ΔSST	0.66	0.33	0.97	1.00	5999	8640
MPA duration	0.00	0.00	0.00	1.00	5003	8133
No-take restriction	0.00	-0.01	0.00	1.00	4807	5434
(gravity no-take)	0.00	0.00	0.00	1.00	1369	692
(1 gravity cell)	0.06	0.05	0.07	1.00	1040	1379
(1 location:study)	0.22	0.21	0.23	1.00	395	790
(1 study)	0.04	0.02	0.07	1.00	2953	6355
Intercept	0.01	-0.01	-0.04	1.00	4957	5863

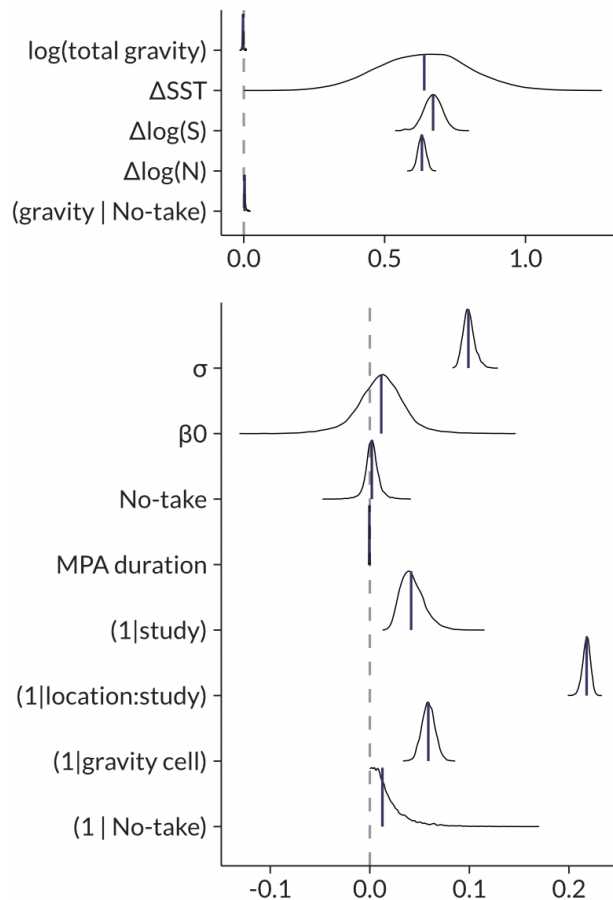


Fig. S17 Posterior distributions for coefficient estimates in the spatiotemporal diversity-productivity model. Sea surface temperature is shown as SST, species richness as S, assemblage abundance as N, Gaussian error distribution parameter as σ , intercept as β_0 , and group-level intercepts as (1|variable). The distribution median is marked by a line.

Table S8 Bayesian generalised linear mixed model fitting results on the alternate spatiotemporal model. The model is fitted to temporal data over shorter time scales, specifically adjacent years. Predictors are species richness change ($\Delta\log_2(S)$) and human gravity. We denote group-level intercepts as (1|group), where the estimates shown represent the σ parameters. We show the expected value for coefficient estimates, 95% credible intervals, R-hat values, standard effective sample size (ESS), and tail ESS for each predictor.

Predictor	Estimate	95% CI		R-hat	Std ESS	Tail ESS
$\Delta\log_2(S)$	0.40	0.38	0.42	1.00	22287	6932
log(human gravity)	0.00	0.00	0.00	1.00	13947	8827
(1 gravity cell)	0.01	0.00	0.02	1.00	5351	5295
(1 location:study)	0.01	0.00	0.02	1.00	6495	4883
(1 study)	0.02	0.00	0.04	1.00	3203	4851
Intercept	0.01	0.00	0.03	1.00	9250	7639

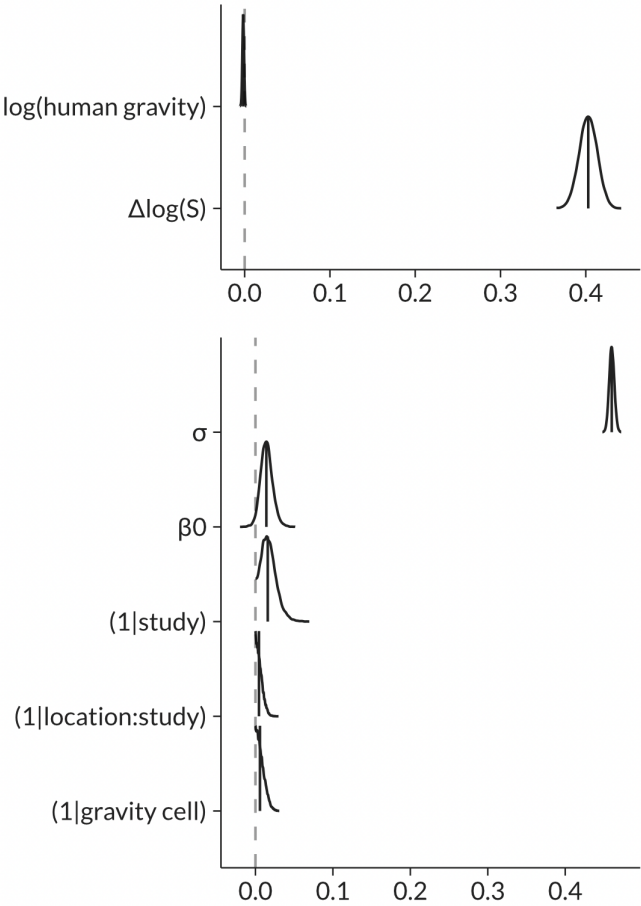


Fig. S18 Posterior distributions for coefficient estimates in the alternate spatiotemporal diversity-productivity model. Species richness change is shown as $\Delta\log(S)$, Gaussian error distribution parameter as σ , intercept as β_0 , and group-level intercepts as (1|variable). The distribution median is marked by a line.

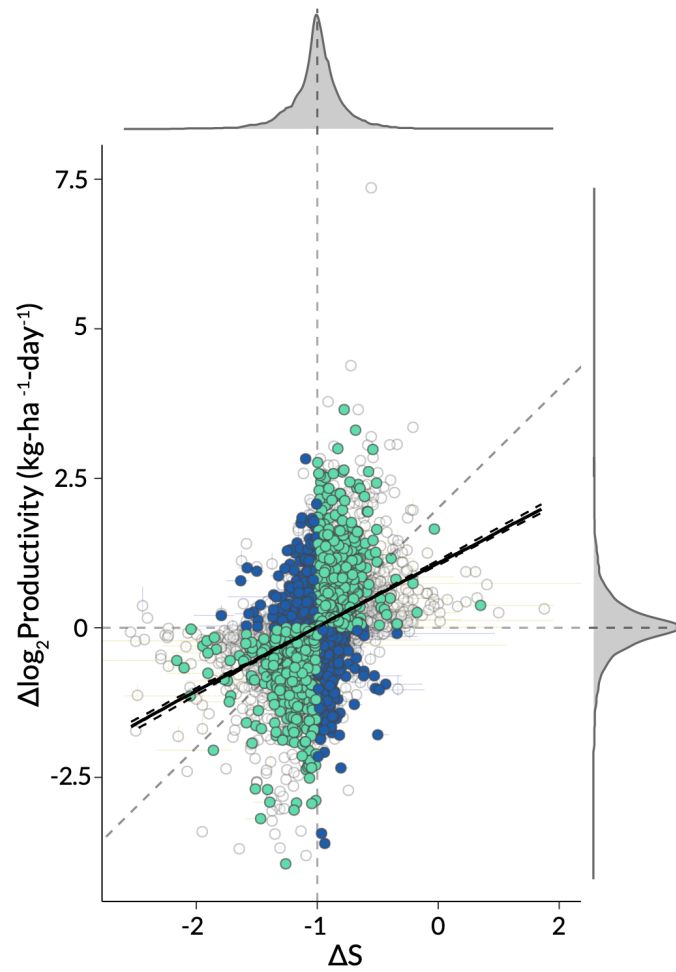


Fig. S19 Partial predictions for an alternate temporal model fitted to temporal trend data measured over adjacent years within a time-series ($n = 15115$). The partial prediction is shown for the effect of species richness, without group-level effects and where human gravity was held at its mean value. The model prediction is represented as a black line with the 95% credible interval shown as a black dashed line. Each data point represents a pair of temporal trajectories. Filled points represent temporal trend estimates that do not contain 0 in its 95% confidence interval. Green points represent parallel trajectories and a positive diversity-productivity link, while blue represents opposite trajectories, i.e. a negative link.