Supplementary Materials for

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

Cheng-Han Tsai et al.

Corresponding author: Cheng-Han Tsai, chenghan.tsai@my.jcu.edu.au

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This PDF file includes:

- Supplementary Text
- Figs. S1 to S9
- Tables S1 to S12
- Supplementary Simulation Study
- References
Supplementary Text:

To choose the optimal mixed-effects structure (with reefs as random effects) for fitting the autocorrelation function (i.e., eq. 1 in Materials and Methods), we first confirmed numerical stability of the random-effect estimates (to verify that we had a valid model), by fitting the models using both importance sampling and the Laplace approximation, both implemented in Template Model Builder (TMB) in R. Then, for those models that produced stable, valid parameter estimates, we used model selection by AIC to choose the best model (Table S1). To confirm our model selection results, we also calculated marginal AIC, a statistic that uses penalized marginal likelihood by bootstrap resampling (5000 bootstrap replicates in our case). This statistic has been proposed as a more robust model selection statistic than AIC for models that have a common fixed effect structure but differ in their random effects (62, 63).

The model with random effects on all three parameters ($\rho_\infty$, $\rho_0$, and $\delta$) was highly numerically unstable, as shown by the poor agreement between random effects estimates produced by importance sampling and the Laplace approximation ($R^2<0.5$ to the unity line for all three parameters) (Fig. S9 A-C). For comparison, our estimated best model, which contains random effects on $\rho_\infty$ and $\rho_0$ but not $\delta$, was numerically stable, shown by virtually identical random effects estimates produced by the two fitting approaches ($R^2>0.95$ in every case) (Fig. S9 D-E). Of all possible combinations of random effects structures, only models including a random effect of $\rho_\infty$ were numerically stable, and all numerically stable models produced very similar parameter estimates (Table S1). We therefore used the fixed and random effect estimates from our best-fitting model of all models producing numerically stable fits in all subsequent analyses throughout this study.
Figs. S1 to S9:

Fig. S1 Latitude and cross-shelf position covary with oceanographic environmental conditions on the Great Barrier Reef. Pairwise Pearson correlations are presented in color scale (n=40 reefs). ‘Nitrate_mean’, ‘Phosphate_mean’, ‘DO_mean’, ‘Chla_mean’, and ‘SST_mean’ represent long-term average of nitrate, phosphate, dissolved oxygen, chlorophyll-a, and sea surface temperature, respectively. Similarly, variables with ‘_SR’ and ‘_min’ attached represent averaged seasonal range and long-term minimum of the variables, respectively. ‘Latitude’ value increases towards the equator. ‘ShelfPosition’ value increases towards the coast.
The Oceanographic environmental data on the Great Barrier Reef were taken from Matthews et al. 2019 (64), and were refined to the same timeframe employed in our analyses.
Fig. S2 Reef fish community composition explained by environmental variables employed in our analyses. Redundancy analysis (RDA) constrained by environmental variables was used for the multivariate ordination plot. Open circles represent fish assemblages on coral reefs (n=40 reefs), and vectors represent major environmental variables, where ‘Shelf’, ‘MeanC’, ‘Log_sdC’ and ‘Latitude’ represents shelf position, average coral cover, coral cover volatility and latitude, respectively. On the right-hand side, the inertia (overall variance) is decomposed into RDA variance components explained by environmental variables in percentage. Reef fish community matrices among reefs are averaged over time and standardized prior to analysis. The RDA presented here uses abundance-weighted species composition, but the pattern is consistent with another RDA computed using only presence-absence data (not shown).
**Fig. S3** Interactive effect of latitude and cross-shelf position on raw observed richness and nonparametric Chao1 estimator. Fitted relationships are from best-fitting OLS regression models (Table S3).
Fig. S4 Estimated VPRSA variance components of reef fish functional groups. Points and horizontal lines represent the median and the 1st and 3rd quartiles of estimates (n=40 reefs). Red represents estimated variance component due to persistent species differences. Blue represents estimated variance component due to stochastic fluctuations. Grey represents estimated variance component due to overdispersion (demographic and sampling variance).
Fig. S5 Relationship between coral cover dynamics and VPRSA variance components of fish functional groups, compared to those of pooled assemblage. (A-C) Herbivores. (D-F) Planktivores. (G-I) Benthic invertivores. The relationships are plotted using the best fitting (lowest-AIC) OLS regression models, with interactive effects of the mean and log-standard deviation of coral cover as explanatory variables, and with variance components of reef fish functional groups as response variables (n=40 reefs; Table S9). The red band represents the 95% confidence intervals of the variance components attributable to persistent species differences, while the blue band represents the 95% confidence intervals of the variance components attributable to stochastic fluctuations. For comparison, the grey bands represent the variance components for the original model, with functional groups pooled as a whole. To illustrate the interactive relationships, the 1st (21% cover), median (27% cover), and 3rd (41% cover) quartiles of mean coral cover are fixed in panels (A-C), (D-F), and (G-I) respectively, and the relationship between the log-standard deviation of coral cover and variance component values plotted for the corresponding value of mean coral cover.
Fig. S6 Richness and unevenness of reef fish functional groups on the Great Barrier Reef, compared to those of pooled assemblage. Estimates are obtained from Poisson-lognormal (PLN) fits (see Materials and Methods). Points and horizontal lines represent the median and the 1st and 3rd quartiles of estimates (n=40 reefs). (A) Estimated species richness of functional groups, and (B) estimated unevenness of functional groups.
Fig. S7 **Richness of reef fish functional groups depend on interactive effect of latitude and cross-shelf position, but not on coral cover variables.** Relationship between PLN-species richness (time-averaged) of reef fish functional groups and the interaction of latitude with cross-shelf position. (A-C) Herbivores. (D-F) Planktivores. (G-I) Benthic invertivores. Darker grey bands are the 95% confidence intervals predicted from the best fitting (lowest-AIC) models for PLN-richness \((n=40 \text{ reefs}; \text{Table S9})\), compared to those of the pooled assemblage (lighter grey bands). To better illustrate the interactive relationships, the 1st, median, and 3rd quartiles of cross-shelf positions are fixed in panels (A-C), (D-F), and (G-I), respectively, and the relationship between species richness as a function of latitude show for the corresponding value of cross-shelf position. Note that cross-shelf position value increases towards the coast.
Fig. S8 Unevenness of reef fish functional groups depend on interactive effect of latitude and cross-shelf position, but not on coral cover variables. Relationship between PLN-unevenness (time-averaged) of reef fish functional groups and the interaction of latitude with cross-shelf position. (A-C) Herbivores. (D-F) Planktivores. (G-I) Benthic invertivores. Darker grey bands are the 95% confidence intervals predicted from the best fitting (lowest-AIC) models for PLN-unevenness (n=40 reefs; Table S9), compared to those of the pooled assemblage (lighter grey bands). To better illustrate the interactive relationships, the 1st, median, and 3rd quartiles of cross-shelf positions are fixed in panels (A-C), (D-F), and (G-I), respectively, and the relationship between unevenness as a function of latitude show for the corresponding value of cross-shelf position. Note that cross-shelf position value increases towards the coast.
Fig. S9 Relationship between random-effect parameters estimated from Laplace approximation and importance sampling in the full random effects model versus the lowest-AIC random effects model. In the full model (A-C), the density dependence parameter δ is assumed to be a random-effect parameter in addition to the other two parameters of eq. 1 in Materials and Methods. By contrast, in the best model (D-E), density dependence parameter δ is a fixed effect while keeping the other two parameters of eq. 1 as random effects. The red line represents a 1:1 relationship where estimates from both methods of Laplace approximation and importance sampling converge to the same values. The strong departures from the red line in panels (A-C) indicate numerical instability of the estimated values for this model and illustrate why we excluded this model from our model selection procedure (Table S12).
Tables S1 to S12:

Table S1 Structural equation model (SEM) for persistence species differences, richness, and unevenness of reef fish assemblages. For response variables, ‘Persistent species difference’ represents the persistent, deterministic variance component in relative species abundance patterns, ‘Richness’ represents Poisson-lognormal estimated richness, and ‘Unevenness’ represents Poisson-lognormal estimated unevenness. For explanatory variables, ‘mC’ and ‘log(sdC)’ represents the average coral cover and coral cover volatility (log-transformed standard deviation in coral cover). ‘Lat’ and ‘Shelf’ represents latitude and cross-shelf position. Cross symbol represents an interaction effect. ‘Std. estimate’ represents the standardized estimate, where * indicates $P < 0.05$ and ** indicates $P < 0.01$. Tests of directed separation found no evidence of missing pathways.

| Response variable                  | Explanatory variable | Std. estimate | $P$ value |
|-----------------------------------|----------------------|---------------|-----------|
| Persistent species differences    | mC                   | 0.698         | 0.056     |
| Persistent species differences    | log(sdC)             | 0.794         | 0.075     |
| Persistent species differences    | Lat                  | 0.022         | 0.964     |
| Persistent species differences    | Shelf                | -0.346        | 0.774     |
| Persistent species differences    | log(sdC)×mC          | -1.873 **     | 0.006     |
| Persistent species differences    | Lat×Shelf            | -0.322        | 0.812     |
| Richness                          | mC                   | -0.082        | 0.784     |
| Richness                          | log(sdC)             | 0.138         | 0.706     |
| Richness                          | Lat                  | 1.544 **      | 0.001     |
| Richness                          | Shelf                | -2.152 *      | 0.04      |
| Richness                          | log(sdC)×mC          | -0.15         | 0.783     |
| Richness                          | Lat×Shelf            | -3.143 **     | 0.009     |
| Unevenness                        | mC                   | 0.038         | 0.875     |
| Unevenness                        | log(sdC)             | 0.015         | 0.96      |
| Unevenness                        | Lat                  | -1.594 **     | 0.001     |
| Unevenness                        | Shelf                | 1.875 *       | 0.028     |
| Unevenness                        | log(sdC)×mC          | 0.1           | 0.819     |
| Unevenness                        | Lat×Shelf            | 2.819 **      | 0.004     |
Table S2 Ordinary least squares (OLS) regression models for VPRSA variance components, richness, and unevenness of reef fish assemblages. For explanatory variables, ‘mC’ and ‘log(sdC)’ represents the mean coral cover and coral cover volatility (log-transformed standard deviation in annual coral cover fluctuations), respectively. ‘Lat’ and ‘Shelf’ represents latitude and cross-shelf position (the value increases towards the coast), respectively. ‘Intercept’ represents the regression model that contains only an intercept. Cross symbols indicate models that include main effects and interactions, whereas plus symbols denote models including only main effects (i.e., additive effects of the explanatory variables). The analyses of the variance component due to overdispersion (e.g., demographic and sampling variance) are not presented, because their magnitudes are negligible compared to those of other variance components as per Fig. 2E.

| Response variable | Explanatory variable | adjR\(^2\) | AIC | ΔAIC |
|-------------------|----------------------|------------|-----|------|
| Persistent species differences | log(sdC)×mC | 0.39 | -80.93 | 0 |
| | log(sdC)×mC+Lat×Shelf | 0.34 | -75.66 | 5.27 |
| | log(sdC) | 0.19 | -71.64 | 9.29 |
| | mC | 0.16 | -70.28 | 10.65 |
| | log(sdC)+Lat×Shelf | 0.19 | -68.83 | 12.1 |
| | mC+Lat×Shelf | 0.12 | -65.59 | 15.34 |
| | Intercept | 0 | -64.2 | 16.73 |
| | Shelf | 0 | -63.78 | 17.15 |
| | Lat | 0 | -62.24 | 18.69 |
| | Lat×Shelf | 0 | -59.87 | 21.06 |
| Stochastic fluctuations | log(sdC)×mC | 0.4 | -77.47 | 0 |
| | log(sdC)×mC+Lat×Shelf | 0.35 | -71.96 | 5.51 |
| | log(sdC) | 0.19 | -67.43 | 10.04 |
| | mC | 0.16 | -65.91 | 11.56 |
| | log(sdC)+Lat×Shelf | 0.18 | -64.39 | 13.08 |
| | mC+Lat×Shelf | 0.12 | -61.05 | 16.42 |
| | Intercept | 0 | -59.85 | 17.62 |
| | Shelf | 0 | -59.4 | 18.07 |
| | Lat | 0 | -57.97 | 19.5 |
|                      | Lat×Shelf             | 0   | -55.55 | 21.92 |
|----------------------|-----------------------|-----|--------|-------|
| Richness             | Lat×Shelf             | 0.55| 299.34 | 0     |
|                      | mC+Lat×Shelf          | 0.55| 299.83 | 0.49  |
|                      | log(sdC)+Lat×Shelf    | 0.54| 301.18 | 1.84  |
|                      | log(sdC)×mC+Lat×Shelf | 0.54| 303.61 | 4.27  |
|                      | Shelf                 | 0.24| 318.69 | 19.35 |
|                      | Lat                   | 0.1 | 325.51 | 26.17 |
|                      | Intercept             | 0.  | 328.96 | 29.62 |
|                      | mC                    | 0.01| 329.39 | 30.05 |
|                      | log(sdC)              | 0.03| 330.47 | 31.13 |
|                      | log(sdC)×mC           | 0.02| 332.25 | 32.91 |
|                      |                       |     |        |       |
| Unevenness           | mC+Lat×Shelf          | 0.7 | 60.45  | 0     |
|                      | log(sdC)+Lat×Shelf    | 0.7 | 60.58  | 0.13  |
|                      | Lat×Shelf             | 0.71| 60.78  | 0.33  |
|                      | log(sdC)×mC+Lat×Shelf | 0.69| 63.8   | 3.35  |
|                      | Lat                   | 0.27| 94.14  | 33.69 |
|                      | Shelf                 | 0.22| 96.93  | 36.48 |
|                      | log(sdC)              | 0.03| 105.65 | 45.2  |
|                      | Intercept             | 0   | 106.03 | 45.58 |
|                      | mC                    | 0.02| 106.16 | 45.71 |
|                      | log(sdC)×mC           | 0.02| 107.83 | 47.38 |
Table S3 Best-fitting (lowest-AIC and ΔAIC<2) regression models for explaining static alpha-diversity metrics. Model selection procedure, candidate explanatory variables, and alternative models considered as in Table S2.

| Response variable       | Best explanatory variable | adj$R^2$ | ΔAIC |
|------------------------|---------------------------|----------|------|
| Observed richness      | Lat×Shelf                 | 0.64     | 0    |
| Chao1 richness         | Lat×Shelf                 | 0.64     | 0    |
| Simpson index          | Lat+Shelf+mC              | 0.36     | 0    |
| Simpson index          | Lat×Shelf+mC              | 0.36     | 0.96 |
| Shannon-Pielou index   | Lat+Shelf+mC              | 0.38     | 0    |
| Shannon-Pielou index   | Lat×Shelf+mC              | 0.37     | 0.65 |
Table S4 Effect size comparison for AIC-similar (ΔAIC<2) models of unevenness. Variables are standardized prior to estimating effect size. Model structure for predicting (PLN-) unevenness presented as in Table S2 and S3. ** indicates $P<0.01$.

| Model                        | Intercept | Lat  | Shelf | Lat×Shelf | mC   | log(sdC) |
|------------------------------|-----------|------|-------|-----------|------|----------|
| Unevenness~Lat×Shelf         | 0.05      | -0.73** | 0.59** | -0.38**   | NA   | NA       |
| Unevenness~Lat×Shelf+mC      | 0.05      | -0.71** | 0.6**  | -0.34**   | 0.13 | NA       |
| Unevenness~Lat×Shelf+log(sdC)| 0.05      | -0.71** | 0.59** | -0.4**    | NA   | 0.12     |
### Table S5: Classifications of functional/trophic groups of coral reef fishes on the Great Barrier Reef.

| Species name                      | Functional/ trophic group |
|-----------------------------------|---------------------------|
| Acanthochromis polyacanthus       | Planktivore               |
| Acanthurus albipectoralis         | Planktivore               |
| Acanthurus auranticavus           | Herbivore                 |
| Acanthurus bariene                | Herbivore                 |
| Acanthurus blochii                | Herbivore                 |
| Acanthurus dussumieri             | Herbivore                 |
| Acanthurus grammoptilus           | Herbivore                 |
| Acanthurus lineatus               | Herbivore                 |
| Acanthurus maculiceps             | Herbivore                 |
| Acanthurus mata                   | Planktivore               |
| Acanthurus nigricans              | Herbivore                 |
| Acanthurus nigricauda             | Herbivore                 |
| Acanthurus nigrofuscus            | Herbivore                 |
| Acanthurus nigroris               | Herbivore                 |
| Acanthurus olivaceus              | Herbivore                 |
| Acanthurus pyroferus              | Herbivore                 |
| Acanthurus spp                    | Herbivore                 |
| Acanthurus thompsoni              | Planktivore               |
| Acanthurus triostegus             | Herbivore                 |
| Acanthurus xanhtopterus           | Herbivore                 |
| Amblyglyphidodon aureus           | Planktivore               |
| Amblyglyphidodon curacao          | Planktivore               |
| Amblyglyphidodon leucogaster      | Planktivore               |
| Amphiprion akindynos              | Planktivore               |
| Amphiprion chrysopterus           | Planktivore               |
| Amphiprion clarkii                | Planktivore               |
| Amphiprion melanopus              | Planktivore               |
| Amphiprion percula                | Planktivore               |
Amphiprion perideraion  Herbivore
Anyperodon leucogrammicus  Piscivore
Aprion virescens  Piscivore
Bolbometopon muricatum  Herbivore
Caesio caerulaurea  Planktivore
Caesio cuning  Planktivore
Calotomus carolinus  Herbivore
Cephalopholis argus  Piscivore
Cephalopholis boenak  Piscivore
Cephalopholis cyanostigma  Piscivore
Cephalopholis microprion  Piscivore
Cephalopholis miniata  Piscivore
Cephalopholis urodeta  Piscivore
Cetoscarus bicolor  Herbivore
Chaetodon aureofasciatus  Corallivore
Chaetodon auriga  Benthic invertebrate feeder
Chaetodon baronessa  Corallivore
Chaetodon bennetti  Corallivore
Chaetodon citrinellus  Benthic invertebrate feeder
Chaetodon ephippium  Benthic invertebrate feeder
Chaetodon flavirostris  Corallivore
Chaetodon kleinii  Benthic invertebrate feeder
Chaetodon lineolatus  Benthic invertebrate feeder
Chaetodon lunula  Benthic invertebrate feeder
Chaetodon melannotus  Benthic invertebrate feeder
Chaetodon mertensii  Benthic invertebrate feeder
Chaetodon meyeri  Corallivore
Chaetodon ornatissimus  Corallivore
Chaetodon oxycephalus  Corallivore
Chaetodon pelewensis  Corallivore
Chaetodon plebeius  Corallivore
*Chaetodon punctatofasciatus*  Corallivore
*Chaetodon rafflesii*  Benthic invertebrate feeder
*Chaetodon rainfordi*  Herbivore
*Chaetodon reticulatus*  Corallivore
*Chaetodon speculum*  Corallivore
*Chaetodon trifascialis*  Corallivore
*Chaetodon trifasciatus*  Corallivore
*Chaetodon ulietensis*  Corallivore
*Chaetodon unimaculatus*  Corallivore
*Chaetodon vagabundus*  Corallivore
*Cheilinus fasciatus*  Benthic invertebrate feeder
*Cheilinus undulatus*  Benthic invertebrate feeder
*Cheiloprion labiatus*  Corallivore
*Chelmon rostratus*  Benthic invertebrate feeder
*Chlorurus bleekeri*  Herbivore
*Chlorurus japonensis*  Herbivore
*Chlorurus microrhinos*  Herbivore
*Chlorurus sordidus*  Herbivore
*Choerodon fasciatus*  Benthic invertebrate feeder
*Chromis acares*  Planktivore
*Chromis agilis*  Planktivore
*Chromis amboinensis*  Planktivore
*Chromis atripectoralis*  Planktivore
*Chromis atripes*  Planktivore
*Chromis chrysura*  Planktivore
*Chromis flavomaculata*  Planktivore
*Chromis iomelas*  Planktivore
*Chromis lepidolepis*  Planktivore
*Chromis lineata*  Planktivore
*Chromis margaritifer*  Planktivore
*Chromis nitida*  Planktivore
Chromis retrofasciata   Planktivore
Chromis ternatensis    Planktivore
Chromis vanderbilti    Planktivore
Chromis viridis        Planktivore
Chromis weberi         Planktivore
Chromis xanthochira    Planktivore
Chromis xanthura       Planktivore
Chrysiptera biocellata Herbivore
Chrysiptera flavipinnis Planktivore
Chrysiptera rex        Planktivore
Chrysiptera rollandi   Planktivore
Chrysiptera talboti    Planktivore
Coris gaimard          Benthic invertebrate feeder
Cromileptes altivelis  Piscivore
Ctenochaetus binotatus  Herbivore
Ctenochaetus spp       Herbivore
Dascyllus aruanus      Planktivore
Dascyllus melanurus    Planktivore
Dascyllus reticulatus  Planktivore
Dascyllus trimaculatus Planktivore
Dischistodus melanotus Herbivore
Dischistodus perspicillatus Herbivore
Dischistodus prosopotaenia Herbivore
Dischistodus pseudochrysopoecilus Herbivore
Epibulus insidiator    Benthic invertebrate feeder
Epinephelus cyanopodus Piscivore
Epinephelus fasciatus  Benthic invertebrate feeder
Epinephelus fuscoguttatus Piscivore
Epinephelus merra      Benthic invertebrate feeder
Epinephelus ongus      Benthic invertebrate feeder
Epinephelus quoyanus   Benthic invertebrate feeder
Forcipiger flavissimus  Benthic invertebrate feeder
Forcipiger longirostris  Benthic invertebrate feeder
Gnathodentex aureolineatus  Benthic invertebrate feeder
Gomphosus varius  Benthic invertebrate feeder
Gymnocranius spp  Benthic invertebrate feeder
Halichoeres hortulanus  Benthic invertebrate feeder
Hemiglyphidodon plagiometopon  Herbivore
Hemigymnus fasciatus  Benthic invertebrate feeder
Hemigymnus melapterus  Benthic invertebrate feeder
Hemitaurichthys polyplepis  Planktivore
Hipposcarus longiceps  Herbivore
Lethrinus atkinsoni  Benthic invertebrate feeder
Lethrinus erythracanthus  Benthic invertebrate feeder
Lethrinus harak  Benthic invertebrate feeder
Lethrinus laticaudis  Benthic invertebrate feeder
Lethrinus lentjan  Benthic invertebrate feeder
Lethrinus miniatus  Benthic invertebrate feeder
Lethrinus nebulosus  Benthic invertebrate feeder
Lethrinus obsoletus  Benthic invertebrate feeder
Lethrinus olivaceus  Piscivore
Lethrinus ornatus  Benthic invertebrate feeder
Lethrinus rubrioperculatus  Benthic invertebrate feeder
Lethrinus semicinctus  Benthic invertebrate feeder
Lethrinus xanthonchilus  Benthic invertebrate feeder
Lutjanus adetii  Piscivore
Lutjanus argentimaculatus  Piscivore
Lutjanus biguttatus  Piscivore
Lutjanus bohar  Piscivore
Lutjanus boutton  Piscivore
Lutjanus carponotatus  Piscivore
Lutjanus fulviflammus  Piscivore
| Species                     | Feeding Type                  |
|-----------------------------|-------------------------------|
| Lutjanus fulvus             | Piscivore                     |
| Lutjanus gibbus             | Piscivore                     |
| Lutjanus kasmira            | Piscivore                     |
| Lutjanus lemniscatus        | Piscivore                     |
| Lutjanus lutjanus           | Piscivore                     |
| Lutjanus monostigma         | Piscivore                     |
| Lutjanus quinquelineatus     | Piscivore                     |
| Lutjanus rivulatus          | Piscivore                     |
| Lutjanus russellii          | Benthic invertebrate feeder   |
| Lutjanus sebae              | Piscivore                     |
| Lutjanus semicinctus        | Piscivore                     |
| Lutjanus vitta              | Piscivore                     |
| Macolor spp                 | Planktivore                   |
| Monotaxis grandoculis       | Benthic invertebrate feeder   |
| Naso lituratus              | Herbivore                     |
| Naso tuberosus              | Herbivore                     |
| Naso unicornis              | Herbivore                     |
| Neoglyphidodon melas        | Benthic invertebrate feeder   |
| Neoglyphidodon nigroris     | Herbivore                     |
| Neoglyphidodon polyacanthus | Planktivore                   |
| Neopomacentrus azysron      | Planktivore                   |
| Neopomacentrus bankieri     | Planktivore                   |
| Neopomacentrus cyanomos     | Planktivore                   |
| Paracanthurus hepatus       | Planktivore                   |
| Plectroglyphidodon dickii   | Benthic invertebrate feeder   |
| Plectroglyphidodon johnstonianus | Herbivore            |
| Plectroglyphidodon lacrymatus| Herbivore                     |
| Plectropomus areolatus      | Piscivore                     |
| Plectropomus laevis         | Piscivore                     |
| Plectropomus leopardus      | Piscivore                     |
| Plectropomus maculatus      | Piscivore                     |
Pomacentrus adelus  Herbivore
Pomacentrus amboinensis  Herbivore
Pomacentrus australis  Herbivore
Pomacentrus bankanensis  Herbivore
Pomacentrus brachialis  Planktivore
Pomacentrus chrysurus  Herbivore
Pomacentrus coelestis  Planktivore
Pomacentrus grammorhynchus  Herbivore
Pomacentrus imitator  Planktivore
Pomacentrus lepidogenys  Planktivore
Pomacentrus moluccensis  Planktivore
Pomacentrus nagasakiensis  Planktivore
Pomacentrus nigromarginatus  Planktivore
Pomacentrus philippinus  Planktivore
Pomacentrus reidi  Planktivore
Pomacentrus tripunctatus  Herbivore
Pomacentrus vaiuli  Benthic invertebrate feeder
Pomacentrus wardi  Herbivore
Premnas richardsoni  Planktivore
Pomadasys taeniatus  Benthic invertebrate feeder
Premnas biaculeatus  Planktivore
Sargocentron spiniferum  Benthic invertebrate feeder
Scarus altipinnis  Herbivore
Scarus chameleon  Herbivore
Scarus dimidiatu  Herbivore
Scarus flavipectoralis  Herbivore
Scarus forsteni  Herbivore
Scarus frenatus  Herbivore
Scarus ghobban  Herbivore
Scarus globiceps  Herbivore
Scarus longipinnis  Herbivore
| Species                        | Diet                          |
|-------------------------------|-------------------------------|
| Scarus niger                  | Herbivore                     |
| Scarus oviceps                | Herbivore                     |
| Scarus psittacus              | Herbivore                     |
| Scarus rivulatus              | Herbivore                     |
| Scarus rubrovio latceus       | Herbivore                     |
| Scarus schlegeli              | Herbivore                     |
| Scarus spinus                 | Herbivore                     |
| Scarus spp                    | Herbivore                     |
| Siganus argenteus             | Herbivore                     |
| Siganus corallinus            | Herbivore                     |
| Siganus doliatus              | Herbivore                     |
| Siganus fuscescens            | Herbivore                     |
| Siganus javus                 | Herbivore                     |
| Siganus lineatus              | Herbivore                     |
| Siganus puellus               | Herbivore                     |
| Siganus punctatissimus        | Herbivore                     |
| Siganus punctatus             | Herbivore                     |
| Siganus spinus                | Herbivore                     |
| Siganus vulpinus              | Herbivore                     |
| Stegastes apicalis            | Herbivore                     |
| Stegastes fasciolatus         | Herbivore                     |
| Stegastes gascoynei           | Herbivore                     |
| Stegastes nigricans           | Herbivore                     |
| Variola albimarginata         | Piscivore                     |
| Variola louti                 | Piscivore                     |
| Zanclus cornutus              | Benthic invertebrate feeder   |
| Zebrasoma scopas              | Herbivore                     |
| Zebrasoma veliferum           | Herbivore                     |
**Table S6** Results of paired $t$-tests for differences between variance components of persistent species differences of fish functional groups. The direction of the estimated mean difference is presented as row subtracted by column. Thus, for example, -1.8%, in the herbivore row and planktivore column, indicates that the species differences explained 1.8% less variation for herbivores than it did for planktivores. * indicates $P < 0.05$ and ** indicates $P < 0.01$ after Bonferroni correction of $P$ values.

|               | Herbivore | Planktivore | Benthicinvertivore |
|---------------|-----------|-------------|-------------------|
| Herbivore     | NA        | -1.8%       | 1.9%              |
| Planktivore   | NA        | NA          | 3.7%              |
| Benthicinvertivore | NA | NA          | NA                |
Table S7 Results of paired $t$-test for differences between variance components of stochastic fluctuations of fish functional groups. The direction of the estimated mean difference is presented as in Table S6. * indicates $P < 0.05$ and ** indicates $P < 0.01$ after Bonferroni correction of $P$ values.

|                | Herbivore | Planktivore | Benthicinvertivore |
|----------------|-----------|-------------|--------------------|
| Herbivore      | NA        | -4.2%       | -11.2%**           |
| Planktivore    | NA        | NA          | -7%*               |
| Benthicinvertivore | NA        | NA          | NA                 |
Table S8 Results of paired $t$-test for difference between variance components of overdispersion of fish functional groups. The direction of the estimated mean difference is presented as in Table S6. * indicates $P < 0.05$ and ** indicates $P < 0.01$ after Bonferroni correction of $P$ values.

|          | Herbivore | Planktivore | Benthicinvertivore |
|----------|-----------|-------------|--------------------|
| Herbivore| NA        | 6.1%**      | 8.8%**             |
| Planktivore| NA     | NA          | 2.6%**             |
| Benthicinvertivore| NA | NA | NA |
Table S9 OLS regression models for VPRSA variance components, richness, and unevenness of reef fish functional groups. For explanatory variables, ‘mC’ and ‘log(sdC)’ represents the mean coral cover and coral cover volatility (log-transformed standard deviation in annual coral cover fluctuations), respectively. ‘Lat’ and ‘Shelf’ represents latitude and cross-shelf position (the value increases towards the coast), respectively. ‘TG’ represents the identity of functional group as a categorical variable. Cross and plus symbols represent interactive and additive effects, respectively. The analyses of the variance component of overdispersion are not presented, because their magnitude is negligible compared to that of other variance components as per Fig. S4.

| Response variable                  | Explanatory variable | adjR² | AIC    | ΔAIC |
|-----------------------------------|----------------------|-------|--------|------|
| Persistent species differences    | log(sdC)×mC×TG       | 0.15  | -168.2 | 0    |
|                                   | log(sdC)×TG          | 0.07  | -161.9 | 6.3  |
|                                   | Shelf×TG             | 0.05  | -160.5 | 7.7  |
|                                   | mC×TG                | 0.05  | -159.8 | 8.4  |
|                                   | TG                   | 0     | -157.1 | 11.1 |
|                                   | Lat×Shelf×TG         | 0.05  | -155.7 | 12.5 |
|                                   | Lat×TG               | 0     | -154.5 | 13.7 |
| Stochastic fluctuations           | log(sdC)×mC×TG       | 0.26  | -176.1 | 0    |
|                                   | log(sdC)×TG          | 0.16  | -165.1 | 11   |
|                                   | Shelf×TG             | 0.15  | -164.9 | 11.2 |
|                                   | mC×TG                | 0.15  | -164.8 | 11.3 |
|                                   | TG                   | 0.11  | -162.4 | 13.7 |
|                                   | Lat×Shelf×TG         | 0.16  | -160.2 | 15.9 |
|                                   | Lat×TG               | 0.11  | -159.3 | 16.8 |
| Richness                          | Lat×Shelf×TG         | 0.84  | 673.4  | 0    |
|                                   | Shelf×TG             | 0.77  | 708.5  | 35.1 |
|                                   | Lat×TG               | 0.74  | 724.3  | 50.9 |
|                                   | mC×TG                | 0.74  | 725.7  | 52.3 |
|                                   | TG                   | 0.73  | 727.1  | 53.7 |
|                                   | log(sdC)×mC×TG       | 0.74  | 730.9  | 57.5 |
|                                   | log(sdC)×TG          | 0.72  | 731.4  | 58   |
| Unevenness          | Lat×TG  | 0.75 | 414.8 | 0  |
|---------------------|---------|------|-------|----|
| Lat×Shelf×TG        | 0.74    | 425.2| 10.4  |   |
| log(sdC)×TG         | 0.72    | 428.6| 13.8  |   |
| log(sdC)×mC×TG      | 0.7     | 438.4| 23.6  |   |
| mC×TG               | 0.69    | 441.4| 26.6  |   |
| TG                  | 0.66    | 448  | 33.2  |   |
| Shelf×TG            | 0.65    | 453.7| 38.9  |   |
Table S10 Pearson correlations between explanatory variables. ‘mC’, ‘log(sdC)’, and ‘log(cvC)’ represents the long-term (11-yr) average, log-standard deviation, and log-coefficient of variation of annual coral cover fluctuations, respectively. ‘Lat’ and ‘Shelf’ represents the latitude and cross-shelf position, respectively. Symbol * indicates $P<0.05$.

|       | log(sdC) | mC  | log(cvC) | Lat  | Shelf |
|-------|----------|-----|----------|------|-------|
| log(sdC) | 0.53     | 0.89* | -0.24    | -0.04 |       |
| mC      | 0.12     |      | -0.16    | -0.12 |       |
| log(cvC) |         |      |          | -0.18 | 0.07  |
| Lat     |         |      |          |       | 0.15  |
| Shelf   |         |      |          |       |       |
Table S11 Pearson correlations between static diversity metrics and variance components of relative species abundance and temporal beta-diversity. ‘Richness’ and ‘Unevenness’ represents time-averaged richness and unevenness from Poisson-lognormal (PLN) fits of reef fish relative species abundances, respectively. $\pi_r$, $\pi_e$ and $\pi_d$ (as eqs 2-4 in Materials and Methods) represents the proportional variance in relative abundances of reef fishes explained by persistent species differences, stochastic fluctuations, and overdispersion (demographic and sampling variance), respectively. Symbol * indicates $P<0.05$.

|          | Richness | Unevenness | $\pi_r$ | $\pi_e$ | $\pi_d$ |
|----------|----------|------------|---------|---------|---------|
| Richness | -0.67*   | -0.08      | 0.11    | -0.17   |         |
| Unevenness |         | 0.09       | -0.07   | -0.08   |         |
| $\pi_r$   |         |            | -0.98*  | 0.23    |         |
| $\pi_e$   |         |            |         | -0.39*  |         |
| $\pi_d$   |         |            |         |         |         |
Table S12 Model selection of auto-correlation function (eq. 1 in Materials and Methods) for VPRSA. $\rho_\infty$, $\rho_0$, and $\delta$ indicate either the fixed-effect parameter estimate (where the corresponding “SD(.)” column is NA), or the estimated mean of the random-effect distribution, for the parameters of the autocorrelation function eq. 1 in Materials and Methods, respectively. SD(.) is the estimated standard deviations of the random-effect distribution for the corresponding parameter. SDtotal is the estimated residual standard error. 95% confidence intervals are enclosed in square brackets. Random effects are modelled as following lognormal distributions because normally distributed random effects yielded numerically unstable fits. Note that, with respect to all possible combinations of fixed and random-effect model structure of eq. 1., only the results of numerically stable models are reported. AIC represents Akaike information criteria. Bootstrapped marginal-AIC values are consistent with AIC (not shown for simplicity).

| Fixed effect | Random effect | $\rho_\infty$     | $\rho_0$      | $\delta$    | SD ($\rho_\infty$) | SD ($\rho_0$) | SDtotal | AIC     |
|--------------|---------------|------------------|---------------|-------------|-------------------|---------------|---------|---------|
| $\rho_\infty$, $\rho_0$, $\delta$ | $\rho_\infty$, $\rho_0$ | 0.75 [0.72, 0.78] | 0.93 [0.92, 0.94] | 0.09 [0.08, 0.11] | 0.18 [0.15, 0.22] | 0.02 [0.02, 0.03] | 0.05 [0.047, 0.051] | -6844.62 |
| $\rho_\infty$, $\rho_0$, $\delta$ | $\rho_\infty$ | 0.75 [0.73, 0.78] | 0.93 [0.93, 0.94] | 0.09 [0.08, 0.11] | 0.16 [0.13, 0.2] | NA | 0.05 [0.049, 0.051] | -6803.06 |
| $\rho_\infty$, $\rho_0$, $\delta$ | NA | 0.76 [0.7, 0.82] | 0.93 [0.93, 0.94] | 0.09 [0.05, 0.15] | NA | NA | 0.06 [0.059, 0.061] | -6096.7 |
Supplementary Simulation Study:

Our analyses of the reef fish data use the variance partitioning of relative species abundance (hereafter VPRSA) method (Fig. 1 and Materials and Methods). However, the underlying community dynamics model from which VPRSA is derived (eqs. 5-6 in Materials and Methods) makes some important simplifying assumptions that may commonly be violated in real communities, including the data analyzed in this paper. It is important to evaluate whether inferences about proportional variance components are sensitive to those assumptions. Specifically, we wish to determine whether estimates produced by the VPRSA method, when applied to simulated data that violate model assumptions, still produce variance component estimates that reflect the relative contribution of “persistent species differences” versus “stochastic fluctuations” to overall variation in species abundances.

Simplifying assumptions of this model include the following: (i) species’ intrinsic growth rates vary according to a normal distribution, (ii) the strength of intra-specific density dependence is the same for all species and for all inter-specific interactions to be negligible, and (iii) the responses of species’ intrinsic growth rates to environmental fluctuations (environmental variance) are assumed to be independent and equal in magnitude (i.e., they fluctuate from year to year with the same variance, and, because of the log-scaling of abundance in this model, this implies that fluctuations in population growth have a variance that is proportional to the mean). Samples from communities whose abundances follow these assumptions generate a static species-abundance pattern that follows a Poisson-lognormal distribution, consistent with what is commonly observed in data (39) and allow derivation of the autocorrelation function that we used in the main text (eq. 1 in Materials and Methods) to partition the variance in relative species log-abundances into components.

Some of these assumptions are likely to be more reasonable than others. For instance, the assumption of Gompertz-type density dependence is consistent with many previous studies, which have found that this model characterizes the functional form of density dependence well and performs better than, or as well as, other forms such as the Ricker or Logistic form (60, 65). More specifically, in a previous study of reef fish functional group dynamics on the Great Barrier Reef (60), Gompertz-type density dependence was found to fit data better than other forms of
density dependence. Another assumption is the normal distribution of intrinsic growth rates. Because of the log-scaling of species abundances in eq. 5 in Materials and Methods, this implies a lognormal distribution of geometric growth factors. A strongly right-skewed distribution of this quantity, such as a lognormal, is consistent with the few studies of variation in population growth at the assemblage-level, which show that most species are relatively slow growing, with a long tail of a few fast-growing species (66).

In contrast, the assumptions of equal strength of density dependence, and equal proportional magnitude of environmentally induced fluctuations in abundance, seem unlikely to hold in nature. Between these extremes, the assumptions that interspecific interactions are negligible, and that species respond independently to environmental fluctuations, are common in biodiversity models, but controversial. For instance, there is some evidence that between-species interactions tend to be weak, particularly for high-diversity systems (67), and species’ responses to fluctuations tend to be relatively independent on average (60, 65). As noted above, the lognormal shape of the static species abundance distribution has been shown previously to be robust to violation of these assumptions (36, 37). But whether variance components estimated from the temporal evolution of such species-abundance distributions are equally robust is unknown. For instance, the deterministic “persistent species difference” component captures the proportional variance in log-abundance due to species differences in equilibrium abundance, but this will no longer be directly proportional to variance in intrinsic growth rates (as in the $\sigma^2_{niche}$ term of eq. 7 in Materials and Methods) when species interactions or among-species heterogeneity in density dependence is present.

In this Supplementary Simulation Study, we simulate different scenarios of community dynamics to test the robustness of variance components estimated from VPRSA to violations of assumptions. Specifically, we conduct VPRSA analysis on simulated community dynamics data that systematically violate model assumptions of VPRSA, and we compare estimated variance components with approximate “true” variance components based on the analytical solutions and known underlying parameters of the simulated communities. R code for simulations and fits is available at https://github.com/TsaiCH/simsEngenVPRSA. Our objective here is not to comprehensively examine the statistical performance of the estimates from this method, but
rather to verify that any biases in the estimates produced when the model’s assumptions were violated do not compromise the conclusions drawn about the reef fish community data (LTMP; Materials and Methods) in the main text. For that reason, we focus on simulated data that share key features of the LTMP data, specifically with respect to species richness, number and length of replicate time series, and parameter values.

Community dynamics model

We use state-space models that incorporate different assumptions about community dynamics to produce simulated data, which we then analyze using the VPRSA approach applied in the main text. This allows us to evaluate the robustness of VPRSA estimates to violation of the assumptions of the community dynamics model from which it was derived. The R code for simulations of community dynamics, and VPRSA estimation, is available and open access at https://github.com/TsaiCH/simsEngenVPRSA.

First, we simulate the abundance dynamics of species \( i = 1 \ldots S \) in a community according to the discrete-time multivariate Gompertz model (68):

\[
N_{i,t+1} = N_{i,t} \exp \left[ a_i + (b_{ii} - 1) \log N_{i,t} - \sum_{j \neq i} b_{ij} \log N_{j,t} \right] + e_{i,t} + \epsilon_{i,t} \quad \text{(eq. 8)}
\]

where \( N_{i,t} \) is the abundance of species \( i \) at time \( t \), \( a_i \) is the species-specific intrinsic growth rate, and \( b_{ii} \) and \( b_{ij} \) are coefficients related to intra- and inter-species density dependence, respectively. \( b_{ii} - 1 \) is the strength of intra-specific density-dependence, while larger values of \( b_{ij} \) indicate stronger inter-specific interactions. Here, we constrain these values to be between 0 and 1, consistent with parameter estimates from Gompertz model fits to individual population time series (61), as well as the parameter estimates from our analyses here. (Note that \( b_{ii} < 0 \) represents strongly over-compensatory interactions, where increases in \( N_i \) produce decreases in \( N_{i,t+1} \), whereas \( b_{ii}=1 \) indicates density-independent dynamics). Additionally, the species-specific intrinsic growth rates (\( a_i \)) are assumed to vary among species according to a normal distribution.
More formally, let $\log N_t = X_t$ and take the natural logarithm of both sides of eq. 8 in order to facilitate expressing the Gompertz-type community dynamics in matrix form. By doing so, the community dynamics model becomes an order-one multivariate autoregressive model (MAR) with two components of process noise as follows:

\[
X_{t+1} = A + BX_t + D_t + E_t \quad (eq. 9)
\]

\[
E_t \sim MVN(O, \Sigma) \quad (eq. 10)
\]

\[
D_t \sim MVN(O, \Lambda) \quad (eq. 11)
\]

where $X_t$ is a vector containing log abundance for each species at time $t$, $A$ is a vector containing species-specific intrinsic growth rates ($a_i$), and $B$ is the interaction matrix where the diagonal ($b_{ii}$) and off-diagonals ($b_{ij}$) are coefficients related to intra- and inter-specific density dependence (keeping in mind that the intra-specific density-dependence is $b_{ii} - 1$, whereas the intra-specific density dependence is $b_{ij}$). $E_t$ is a vector of random variables containing species’ responses to environmental fluctuations (i.e., the perturbations to the intrinsic growth rate due to environmental stochasticity) and follows a multivariate normal distribution ($MVN$) with zero means and variance-covariance matrix $\Sigma$ in eq. 10. $D_t$ is a vector of random variables representing perturbations due to demographic stochasticity. These quantities also follow a multivariate normal distribution ($MVN$) with zero means and variance matrix $\Lambda$ (by definition, the covariances of this matrix are all zero). Because less abundant species are more prone to demographic stochasticity than abundant species, we follow previous work and model the demographic variances in log-abundance (the diagonal of $\Lambda$ in eq. 11) as inversely proportional to the square root of species abundance ($36$). That is, the diagonal elements of $\Lambda$ follow:
Finally, let $\lambda$ represent a vector containing the expected relative species abundance in a random sample of the species-abundance distribution, such that:

$$
\lambda_t = c \exp(X_t)
$$

where $c$ is a measure of sampling intensity. Hence the (simulated) sampled species abundances $Y_t$ will be a Poisson sample of $\lambda_t$:

$$
Y_t \sim \text{Poisson}(\lambda_t)
$$

The final model of community dynamics represents a discrete-time multivariate state-space model with normally distributed equilibrium log-abundances, normally distributed process noise, and Poisson-distributed observation error. We therefore model the sampled abundance values $y_t$ as following a Poisson-lognormal distribution (36, 37, 39).

**Simulating empirically constrained community dynamics data**

Simulated data were constrained to have similar numbers of locations ("reefs"), time series lengths, species richness, and numbers of individuals as per the LTMP data analyzed in the main text. Specifically, we generated 100 simulated data sets, each of which consisted of 40 simulated time series ("reefs") sampled annually for 11 years, to correspond to the time series for the 40 annually sampled reefs in the LTMP. For each reef, “true” total species richness was fixed at $S=100$ in all simulations. The level of “true” total richness used in simulations is close to the upper bound of estimated total richness at the reef scale in the LTMP (cf. Fig. 2 in the main text). Then, for each year at each reef, we simulated a Poisson random sample with a mean of 1500 individuals (i.e., the sampling intensity $c$ was set so that the sum of the Poisson mean abundance across all species was equal to 1500), since this was close to the median sample size in the LTMP. If any simulated samples had fewer than 40 observed species (i.e., species with sampled
abundance greater than zero), that sample was discarded, and a new random sample was taken from the community for that reef and year. This threshold of 40 observed species was used to prevent unrealistically low representation of the community (in the LTMP data, no reefs had fewer than 40 observed species in any year). Simulations where this occurred were extremely rare (approximately 2% of simulations), so it is unlikely that this culling process has affected our conclusions.

For each simulated data set, the communities on all reefs were specified to have the same community dynamics parameters for eqs. 9-11, except for the strength of environmental stochasticity (i.e., \( \sigma_e \) in eq. 5 in Materials and Methods, and the diagonal \([\sigma_e^2]\) of \( \Sigma \) in eq. 10). This last quantity was varied systematically, in order to produce a data set in which the relative importance of deterministic species differences versus environmental stochasticity varied widely among reefs, which could then be used to evaluate how well VPRSA resolved these differences. Specifically, the environmental variance term (i.e., \( \sigma_e^2 \)) was varied from 0.025 to 0.5 in equal sized increments across the simulated reefs (e.g., one reef had \( \sigma_e^2 = 0.025 \), another had \( \sigma_e^2 = 0.0372 \), and so on up to \( \sigma_e^2 = 0.5 \)). This created a true distribution of variance components among reefs that was uniform and extended almost all the way to zero. For the effect of persistent species differences (cf. eqs. 5-6 and eq. 9), the species-specific intrinsic growth rates were modelled as varying among species according to a normal distribution with mean \( \mu_i = 1.5 \) and standard deviation \( \sigma_i = 0.25 \), based on a meta-analysis of global fishery stock assessments (10).

Demographic stochasticity was simulated as process noise (\( D_t \)), where the demographic variances (the diagonal of \( \Lambda \) in eq. 11) were scaled by the value \( \sigma_d^2 = 0.5 \). Other parameter values varied among simulation scenarios, as specified below.

Scenarios of simulated community dynamics data

We simulated five scenarios of community dynamics, which are constrained as described above, to test the robustness of variance components (i.e., the relative importance of deterministic versus stochastic factors in eq. 7 in Materials and Methods) estimated by VPRSA. The values of \( \sigma_e^2 \) and \( \sigma_d^2 \) specified above were used for all simulations, and the additional parameters specified in scenarios (i)-(v) below were chosen so that the simulations produced
frequency distributions of \( \widehat{\sigma^2_{tot}} \) (variance of log-abundance in the communities), and sample completeness (measured as the fraction of the species pool observed at each site in each year) that were similar to those produced when the Poisson-lognormal was fitted to the LTMP data (Simulation Study Fig. 1). In addition, to ensure a stationary distribution of population sizes (i.e., all species coexisting), the complex norm of eigenvalues of interaction matrix \( B \) was constrained to be less than the unit circle (one for the real part). This constrained the overall strength of interspecific competition in scenario (iii) (i.e., if interactions were too strong, species would be unable to coexist).

The details of parameters and scenarios of simulated community data are as follows:

(i) **Baseline:** These simulations were run to conform with the assumptions of the stochastic community-dynamic theory from which VPRSA was derived. Specifically, intra-specific density dependence was the same for all species \( (b_{ii} = b) \), the interaction matrix \( B \) contained no inter-specific density dependence (i.e., the off-diagonals of \( B \) were zero in eq. 9) and responses to environmental fluctuations were independent and equal in variance (i.e., the off-diagonals of \( \Sigma \) were zero in eq. 10, and the variances were all equal to the reef-specific values of \( \sigma^2_e \) specified above: \( \sigma^2_{e,ii} = \sigma^2_e \)). In these simulations, we set \( b = 0.84 \) (i.e., the “strength of density dependence” was \( 1 - 0.84 = 0.16 \)), as this is consistent with the estimate of this parameter from the real data.

(ii) **Varied intra-specific interactions (varIntra):** This scenario introduces between-species variation in intra-specific density dependence. Specifically, values on the diagonal of \( B \) in eq. 9 were drawn from a normal distribution with mean 1.8 and standard deviation 0.4, and then inverse-logit transformed to yield values between 0 and 1. This produces random coefficients of the diagonal of \( B \) with mean values close to 0.84 (i.e., \( E[b_{ii}] \approx 0.84 \), implying average strength of density-dependence \( 1 - E[b_{ii}] \approx 0.16 \)), and standard deviations close to 0.06, implying a coefficient of variation of density-dependent strength of about 0.37. Because equilibrium abundance is \( \exp \left( \frac{T_i}{b_{ii}} \right) \), this approach produced unrealistically large variance in the total variance of log-abundance, \( \sigma^2_{tot} \). Therefore, the diagonal elements of \( B \) were
reordered to increase with species’ intrinsic growth rates (i.e., elements of vector $A$ in eq. 9), so that species with strong density dependence also had high intrinsic growth rates. This yielded more realistic variances of log-abundance (see below).

(iii) *Inter-specific interactions (varInter)*: This scenario introduces diffuse inter-specific density dependence by drawing the off-diagonals of $B$ from a uniform distribution between 0 and 0.002 (mean=0.001). This yielded an average summed effect of interspecific interactions (across the other 99 species in the community) that was approximately 60% the strength of intra-specific density-dependence (i.e., $0.001 \times 99 \approx 0.6 \times 0.16$). All other parameter values were the same as in the *Baseline* simulation. Mean interaction strength values slightly above those employed here (0.001-0.003) tended to produce distributions of observed richness values that differed notably from the data (lower observed richness levels, and more strongly right-skewed abundance distributions). Moreover, mean interaction strengths above about 0.003 tended to produce assemblages lacking a stable coexistence equilibrium.

(iv) *Unequal environmental variances (varEnv)*: This scenario introduces heterogeneity among species in sensitivity to environmental fluctuations. Specifically, species-specific environmental variances (the diagonal of $\Sigma$ in eq. 10) were drawn from a uniform distribution between 0 and 2 (mean=1), and then multiplied by the reef-specific $\sigma^2_e$ term, as specified above. This ensured that the average value of environmental variance ranged from 0.025 to 0.5, as in the *Baseline* scenario, and thus continued to yield realistic $\sigma^2_{tot}$ values. All other parameter values were as in the *Baseline* scenario.

(v) *Unequal environmental covariances (varcovEnv)*: This scenario introduces covariance in species’ responses to environmental fluctuations. Specifically, we generated a lower-triangular matrix $L$ whose elements were drawn from a normal distribution with mean 0 and standard deviation 0.25. We then produced a covariance matrix $\Sigma = LL^T$. The elements of $\Sigma$ were subsequently standardized by the mean of the diagonal elements, and then the entire matrix multiplied by the reef-specific environmental variance term $\sigma^2_e$. This yielded a matrix of unequal variances and covariances among species, whose correlation coefficients ranged from -0.5 to 0.5, with mean 0, and with the mean of the diagonal elements equal to the reef-
specific value $\sigma^2$ (and thus comparable in average magnitude of environmental variability to the other scenarios).

**Estimating VPRSA from simulated community dynamics data**

We tested the robustness of statistical inferences drawn from VPRSA by analyzing the simulated data described above. Following the approach used with the real data, we used the R package “poilog” to fit the bivariate Poisson-lognormal distributions to paired assemblage at different time lags, and then analyzed the correlation coefficients for all of these pairs as functions of the time elapsed between them, to estimate the three parameters ($\rho_0$, $\rho_\infty$, and $\delta$) of the autocorrelation function of eq. 1 in Materials and Methods for all 40 reefs simultaneously using the nonlinear mixed-effects modelling approach employed in the main text analysis. Consistent with our main text analysis, we included random effects on $\rho_0^{\text{R}}$ and $\rho_\infty^{\text{R}}$ but not $\delta$ to avoid numerical instability of parameter estimates (Supplementary Text). From these estimates, we calculated the proportion of the total variance of log-abundance attributable to persistent species differences ($\pi_r$), responses to environmental fluctuations ($\pi_e$), and demographic and sampling variance (overdispersion, $\pi_d$), as in the original analysis.

**Testing the robustness of statistical inferences drawn from VPRSA**

Once we had our reef-level variance component estimates, we then assessed the robustness of estimated proportional variance components to violations of model assumptions (scenarios ii through iv). For these simulations, we used average values of density dependence and environmental variance and covariance parameters (across species) for computing “expected” proportional variances (i.e., according to eq. 7 in Materials and Methods) in scenarios of varied intra- and inter-specific interactions (scenarios ii and iii) and environmental variances and covariances (scenarios iv and v). Thus, for example, for the case of variable intra-specific density dependence, we compared the variance components obtained from analysis of the simulated data with the theoretical expectation under the assumption that all species exhibited the average level of density dependence (i.e., the averaged $\delta$ to substitute $\delta$ in eq. 7 in Materials and Methods) for that simulation. Our goal is to determine whether the proportional variance estimates produced by applying the VPRSA method, to simulated data that violate the model
assumptions, produce estimates that are consistent with the overall relative importance of persistent species differences versus stochastic fluctuations in those simulated data.

In addition, we calculated, analytically, an alternative measure of theoretical expected proportional variances to take more explicit account of between-species heterogeneity, species interactions, and covariances in response to environmental fluctuations (termed the “Robust” predictions, below). We did this by exploiting general analytical solutions (68) for the environmental variance and variance in equilibrium abundance for the discrete time, stochastic, multivariate Gompertz model as follows:

\[ \nu_r = \text{var} \left( \log \hat{N} \right) = \text{var} \left[ (I - B)^{-1} A \right] \]  
(eq. 15)

\[ \nu_e = \bar{V}_e = \text{avg} \left[ \text{diag} \left[ (I - B \otimes B)^{-1} \text{vec} \left( \Sigma \right) \right] \right] \]  
(eq. 16)

\[ P_{\text{niche}} = \frac{\nu_r}{\nu_r + \nu_e} \]  
(eq. 17)

\[ P_{\text{env}} = \frac{\nu_e}{\nu_r + \nu_e} \]  
(eq. 18)

where \( \nu_r \) is the among-species variance of equilibrium population sizes (on a logarithmic scale), and \( \nu_e \) represents the average species-level variance of log-abundance due to environmental stochasticity. In eq. 15, \( \log \hat{N} \) represents the species’ abundances at stationary or equilibrium states, “var” represents the variance operator, \( B \) is the interaction matrix (as per eq. 9), \( A \) is a vector of intrinsic growth rates (as per eq. 9). In eq. 16, \( \bar{V}_e \) is the average of the diagonal of the environmental variance-covariance matrix at stationary states, “avg” represents the arithmetic mean function, and “diag” and “vec” are the diagonal and vectorization operators. The symbol \( \otimes \) represents the Kronecker or tensor product. From equations 17-18, the two variance components are generalized to account for heterogeneity in intra-specific and inter-specific density dependences through the interaction matrix \( B \), as well as heterogeneity in environmental variances and covariances through the environmental variance-covariance matrix \( \Sigma \).

Importantly, under the assumptions of the Baseline scenario, the approximate measures of \( \nu_r \) and \( \nu_e \) above (eqs. 15-18) collapse to discrete-time analogous of Engen and colleagues’
functional forms of \( \pi_r \) and \( \pi_e \) (cf. \( \sigma_{\text{niche}}^2 \) and \( \sigma_{\text{env}}^2 \) in eq. 7 where the density-dependent parameter \( \delta \equiv 1 - b_{ij} \)). However, once species interactions or heterogeneity in density-dependence are incorporated (e.g., scenarios ii and iii), \( \sigma_r^2 \) would cease to be directly proportional to the variance in species’ equilibrium log-abundances, so we would expect this modified version of \( \nu_r \) (eq. 15) to better measure the relative importance of persistent niche structure than \( \sigma_{\text{niche}}^2 \) from the original theory (eq. 7). Similarly, in the presence of environmental covariances or heterogeneity in environmental variances among species (e.g., scenarios iv and v), the functional relationship between \( \sigma_{\text{env}}^2 \) in eq. 7 and the overall contribution of environmentally mediated population fluctuations to variance in species-abundances may also break down, rendering eq. 16 a more robust measure. Consequently, for scenarios (ii)-(v), we test estimated variance components from our fits against theoretical variance components calculated according to both the original theory (eq. 7), and the generalized forms above (eqs. 15-18). However, as noted above, the model from which these generalized forms are derived (eqs. 15-16) omits demographic stochasticity; thus, if the contribution of \( \theta^2 \) in eq. 7 is non-negligible, then analytically calculated proportional variance components from eqs. 17-18 will be biased. Consequently, to maximize the comparability of these quantities \( \nu_r \) and \( \nu_e \) with the original VPRSA forms (\( \pi_r \) and \( \pi_e \) in eqs. 2-3, and \( \sigma_{\text{niche}}^2 \) and \( \sigma_{\text{env}}^2 \) in eq. 7), we normalized the variance components as follows:

\[
\check{\nu}_r = \frac{\nu_r}{\nu_r + \nu_e} \equiv \frac{\nu_r}{\sigma_{\text{tot}}^2 - \nu_d} \\
\check{\nu}_e = \frac{\nu_e}{\nu_r + \nu_e} \equiv \frac{\nu_e}{\sigma_{\text{tot}}^2 - \nu_d}
\]

(eq. 19) (eq. 20)

As expected, estimated variance components from data simulated according to our “baseline” scenario were highly consistent with the theoretical expectation. In Simulation Study Fig. 2, each point represents variance component estimates for one reef in one simulation. The colored line represents the theoretical expectation for the variance component due to persistent species differences (red), and environmental variance (blue), and overdispersion (demographic and sampling variance) (green). The black line is a smoothed fit to the simulated data. Thus, the discrepancy between the black line and the corresponding color line represents the difference between the underlying trend in the simulated data, versus the theoretical expectation according to the original theoretical model. For this baseline scenario, there is a slight tendency to
overestimate, by a few percentage points on average, the contribution of persistent species
differences relative to stochastic fluctuations, particularly when the contribution of stochastic
fluctuations is large. This discrepancy is not markedly increased by the incorporation of species
interactions, interspecific variation in sensitivity to environmental fluctuations, or covariation
between species in fluctuations, but is slightly larger in the presence of variation in intra-specific
density-dependence (Simulation Study Fig. 3).

Our “robust approach” seems to better capture the behavior of the variance components
than the original theory (Simulation Study Fig. 4, Simulation Study Fig. 5). Specifically, the
central tendency of the variance component estimates aligns much more closely with the
variance components predicted by the more general theoretical model given by eqs. 15-18 than it
does to the predictions of the original theory (Simulation Study Fig. 4, Simulation Study Fig. 5).
To understand this, it is important to note that, conceptually, the variance attributable to
“persistent species differences” is the variance in deterministic equilibrium population sizes (on a
logarithmic scale). In Engen et al.’s (2002) (51) original model, as in the baseline scenario, this
is equal to \( \sigma^2_c / \delta^2 \) in eq. 7 (cf. \( \rho_c \) in eq. 1). However, when there is heterogeneity among species
in intra-specific density dependence (i.e., the “varIntra” scenario; Simulation Study Fig. 4A-B)
or species interactions (i.e., the “varInter” scenario; Simulation Study Fig. 4C-D), or when there
are different species responses to environmental fluctuations (i.e., the “varEnv” and “varcovEnv”
scenario; Simulation Study Fig. 5), this is no longer true, and thus the original analytical
expectation (eq. 7) itself may be less representative of the true variance components of relative
species abundance. In this context, it is encouraging that the VPRSA estimates produced by
analysis of the autocorrelation function (eq.1) align well with the “robust” formulation that takes
the additional heterogeneity among species into account with the appropriate multivariate
Gompertz expressions (eqs. 15-18) (Simulation Study Fig. 4 and Simulation Study Fig. 5). In
other words, the estimated proportional variance component for persistent species differences
appears to provide a robust estimate of the relative amount of the variance in species’ log-
abundances that is due to variance in their long-term equilibrium values, relative to the variance
due to stochastic fluctuations. Notably, the modified expressions (eqs. 15-18) also perform better
in the baseline scenario (i.e., when species differ only in intrinsic growth rates), compared to the
original analytical expressions (eq. 7) (Simulation Study Fig. 6), which suggests that some of the
discrepancy may be due to the discrete-time nature of the simulations (since the original theoretical model was developed for continuous-time dynamics, whereas the theoretical model underpinning our “robust approach” is formulated in discrete time).

These supplementary simulation results suggest that proportional variance estimates from VPRSA provide robust information about the relative importance of persistent species differences (i.e., community determinism) versus stochastic fluctuations in shaping patterns of commonness and rarity among species, even when key simplifying assumptions about community dynamics made by the original theory are violated. We conclude that VPRSA may be much broadly applicable and “empirical” than previously realized, particularly when the variance component due to persistent species differences is conceptualized as representing the “proportional” variance in species abundances due to differences in their long-term mean abundances (as in our derivations from the more general theory), rather than specifically to differences in their intrinsic growth rates (as in the original theory used to derive the variance components). Of course, our simulation study cannot be a comprehensive exploration of the robustness of this approach to all possible assumption violations. However, the robustness that we have identified suggests that VPRSA is more robust than one might have assumed, given the original model of community dynamics that inspired it (36, 37, 51).
Simulation Study Figs. 1 to 6:

Simulation Study Fig. 1 (A) Density distribution of estimated overall variance of Poisson-lognormal species-abundance distributions. (B) Density distribution of sample completeness measured as the ratio of observed (sampled) species richness to estimated species richness from Poisson-lognormal fits. Curves are probability density distributions from empirical and simulated data. Red curves represent the empirical LTMP data. Green curves (light green, intermediate, and dark green) are ‘baseline’, ‘varcovEnv’, and ‘varEnv’ scenarios, respectively. Light- and dark-gray curves are ‘varIntra’ and ‘varInter’ scenarios, respectively.
**Simulation Study Fig. 2** Relationships between “true” environmental variance and VPRSA-estimated variance components. Red, blue, and green colors represent the VPRSA-estimated proportional variance due to persistent species differences, stochastic fluctuations, and overdispersion, respectively. Each point, irrespective of color, represents one simulated time series for one spatial replicate (reef) (i.e., for each color, n = 40 spatial replicates with varied environmental variance × 100 simulations = 400 points). All community dynamics data (points) are simulated from the baseline scenario. Red, blue, and green lines represent the kernel smoothing of proportional variance estimates, respectively, obtained using local polynomial regression fitting. Black lines represent the analytical predictions of Engen et al. 2002 (eq. 7 in Materials and Methods) using the true parameters from the simulations.
Simulation Study Fig. 3 Relationships between “true” environmental variance and estimates of variance components under different community dynamics scenarios. Red, blue, and green colors represent the proportional variance components due to persistent species differences, stochastic fluctuations, and overdispersion. Colored (red, blue, and green) lines represent the kernel smoothing of proportional variance estimates, respectively, obtained using local polynomial regression fitting. Black lines represent the analytical prediction of Engen et al. 2002 (eq. 7 in Materials and Methods) using the true parameters from the simulations. (A) The “varIntra” scenario, which includes species differences in intra-specific density dependence. (B) The
“varInter” scenario, which includes species differences in inter-specific density dependence. (C) The “varEnv” scenario, which includes species differences in the magnitude of environmental variance. (D) The “varcovEnv” scenario, in which species’ responses to environmental fluctuations covary.
Simulation Study Fig. 4 Relationships between variance estimate of persistent species differences and its analytical prediction. The black line is the unity line indicating perfect agreement between VPRSA estimates and analytical predictions. The red line is a quantile regression through the median of the VPRSA estimates of variance components of persistent species differences. (A, C) The relationship between VPRSA estimates and the original analytical prediction of Engen et al. 2002 (eq. 7 in Materials and Methods), and (B, D) the relationship between VPRSA estimates and the generalized analytical prediction from the discrete-time multivariate Gompertz model (eqs. 15-18) under the (A, B) “varIntra” and (C, D) “varInter” community dynamics scenarios.
Simulation Study Fig. 5 Relationships between variance estimate of persistent species differences and its analytical prediction. The black line is the unity line indicating perfect agreement between VPRSA estimates and analytical predictions. The red line is a quantile regression through the median of the VPRSA estimates of variance components of persistent species differences. (A, C) The relationship between VPRSA estimates and the original analytical prediction of Engen et al. 2002 (eq. 7 in Materials and Methods), and (B, D) the relationship between VPRSA estimates and the generalized analytical prediction from the discrete-time multivariate Gompertz model (eqs. 15-18) under the (A, B) “varEnv” and (C, D) “varcovEnv” community dynamics scenarios.
Simulation Study Fig. 6 Relationships between variance estimate of persistent species differences and its analytical prediction under baseline scenario. The black line is the unity line indicating perfect agreement between VPRSA estimates and analytical predictions. The red line is a quantile regression through the median of the VPRSA estimates of variance components of persistent species differences. (A) The relationship between VPRSA estimates and the original analytical prediction of Engen et al. 2002 (eq. 7 in Materials and Methods), and (B) the relationship between VPRSA estimates and the generalized analytical prediction from the discrete-time multivariate Gompertz model (eqs. 15-18).
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