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Community Structure of Corals and Reef Fishes at Multiple Scales

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Distributions of numerical abundance and resource use among species are fundamental aspects of community structure. Here we characterize these patterns for tropical reef fishes and corals across a 10,000-kilometer biodiversity gradient. Numerical abundance and resource-use distributions have similar shapes, but they emerge at markedly different scales. These results are consistent with a controversial null hypothesis regarding community structure, according to which abundance distributions arise from the interplay of multiple stochastic environmental and demographic factors. Our findings underscore the importance of robust conservation strategies that are appropriately scaled to the broad suite of environmental processes that help sustain biodiversity.

Two fundamental aspects of ecosystem structure concern how individuals and resources are partitioned among species (*1*–*5*). Empirically, relative abundances of species approximate either log-series or log-normal distributions. Under the log-series distribution, the number of species is a decreasing function of abundance, with species being most likely to be represented by a single individual (*6*). In contrast, under the log-normal distribution, few species have either very low or very high abundance: On a logarithmic scale, abundance distributions can even exhibit a slight left skew (*7*–*10*). Because the prevalence of extremely rare species differs markedly between these distributions, understanding whether and how communities differ in or shift among these distributions is critically important for predicting consequences of habitat loss and environmental degradation for biodiversity and ecosystem functioning (*11*, *12*).

Several theories have been proposed to account for this variability in shapes of abundance distributions. In particular, niche-based models produce log-series to left-skewed log-normal distributions under different rules for resource allocation (*13*); demographic models can encompass the same range of distributions through changes in rates of dispersal among habitat patches, or the process by which new species originate (*12*, *14*–*17*). Alternatively, a classical null hypothesis asserts that abundance distributions in ecological communities are ubiquitously log-normal (*18*, *19*) and that apparent deviations from this shape arise largely from sampling effects (*7*, *8*, *10*).

Here we examine community structure in scleractinian corals and reef fishes from the family Labridae (wrasses and parrotfishes) at 100 sites arrayed along a 10,000-km transect extending longitudinally from the Central Indo-Pacific global biodiversity hot spot to the comparatively depauperate reefs of French Polynesia (Fig. 1). The rapid, ongoing, and worldwide decline of coral reefs has made it an urgent priority to understand the processes that structure and sustain these ecosystems (*20*–*22*). Scleractinian corals and labrid fishes are principal structure-formers and major consumers, respectively, of coral reefs, so understanding assemblage structure for these groups is particularly relevant to predicting and managing the consequences of biodiversity loss (*22*, *23*). We assess these patterns in local communities from three habitats (reef slope, crest, and flat), using an explicitly hierarchical design that allows us to assess how numerical abundance and resource-use distributions change across three spatial scales: the "local community" scale (tens of meters); the scale of clusters of nearby reefs [here termed the "reef" scale (kilometers)]; and the "metacommunity" scale (tens to hundreds of kilometers) (*24*). We quantify numerical abundance distributions by counts of individual fishes and coral colonies, and we estimate species' population biomass (for fishes) and percentage cover (for corals) as proxies for resource use (fig. S1). To overcome persistent problems with the power of goodness-of-fit and model selection statistics in analyses of abundance distributions (*19*, *25*, *26*), we apply contemporary analytical techniques derived from information theory (*24*).

Numerical abundance and resource-use distributions exhibit markedly different changes in shape with increasing scale, differences that are strikingly parallel in fishes and corals. Fish biomass and coral cover are very closely approximated by log-normal distributions at all scales (Fig. 2 and fig. S2). In contrast, both fishes and corals exhibit a log-series–like distribution of numerical abundance at the local community scale, with decreasing numbers of species in each successive octave (Fig. 3A). However, an alternative hypothesis is that the underlying numerical abundance distribution is log-normal in shape, but that it is truncated because the rarest species have not been sampled (the "veil effect") (*7*, *8*). We find overwhelming support for the latter hypothesis: The truncated log-normal distribution fits the data better than the log-series distribution, with >99% confidence (Fig. 3A and table S1). Further support for a log-normal distribution emerges as data are pooled at the reef and metacommunity scales and subsequently pooled across habitats within metacommunities: The truncated log-normal distribution continues to exhibit excellent fit to the data; the mode of the abundance distribution shifts toward the right; and the distribution becomes less truncated, consistent with the "unveiling" of a log-normal distribution of numerical abundance with increasing sampling effort (Fig. 3B and fig. S3). Moreover, the size of the metacommunity species pool, when estimated from the best-fit log-normal parameters, agrees closely with predictions based on the nonparametric jackknife species richness estimator (Fig. 4).

These results indicate that numerical abundance and resource use both have log-normal distributions, but that these distributions emerge at markedly different scales for both corals and

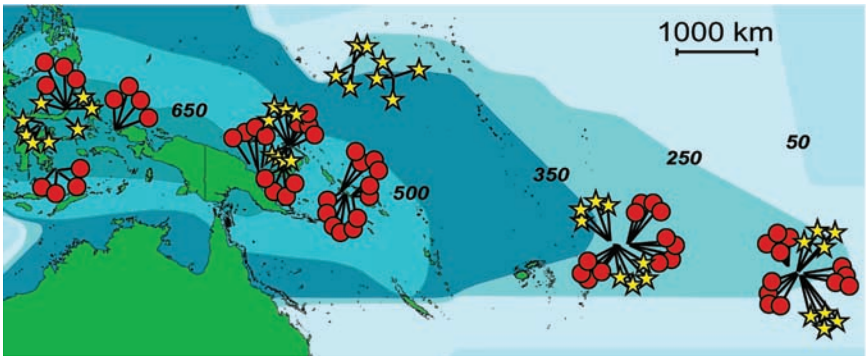

Fig. 1. Locations of study sites. Coral sites are identified with red circles, and fish sites are shown as yellow stars. At each site, three local communities were surveyed, one from each of three habitats (slope, crest, and flat), yielding 180 local communities for corals and 120 for fishes (*24*). Contours of fish species richness are shown and labeled in italics to illustrate the transect's biodiversity gradient; a similar gradient is exhibited by coral species (*29*).

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fishes. Our proxies of resource use are, on average, over 99% unveiled at the scale of local communities (that is, less than 1% of the fitted log-normal distribution is unsampled) (Fig. 2). To unveil numerical abundance distributions to a comparable level, sample sizes approximately two orders of magnitude larger would be required (*24*). This scale discrepancy is inconsistent with arguments based on niche theory, according to which the partitioning of numerical abundance and of resources are equivalent processes (*2*). The strikingly parallel results for corals and fishes also argue against a niche-based explanation. Although corals differ in their performance across habitats (along gradients in light, exposure, turbidity, etc.), their potential for resource partitioning within habitats is likely to be constrained because they compete for a relatively small set of limiting resources. In contrast, niche differences within habitats (such as trophic differentiation) among co-occurring labrid fishes are far more extensive. Species within this family exploit almost every available food resource on coral reefs (*27*); thus, they can partition resources along many more environmental axes than corals can.

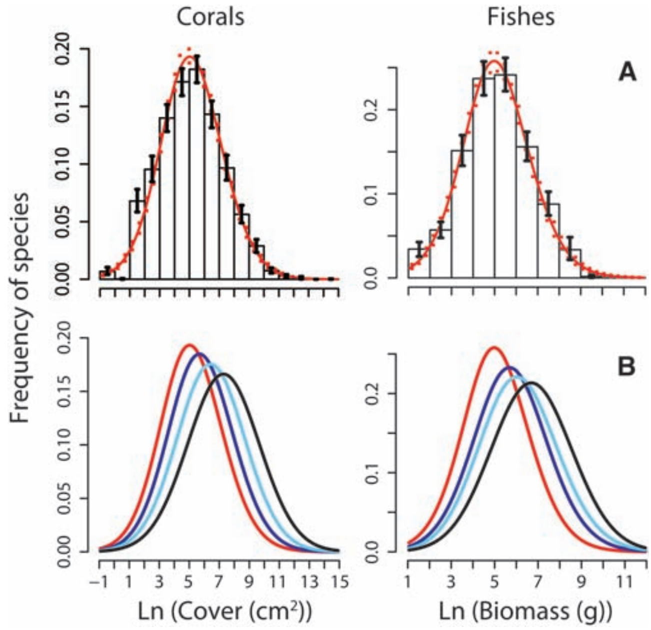

Fig. 2. (**A**) Distributions of resource-use proxies (coral cover and fish biomass) at the local community scale, with best-fit continuous log-normal distributions. Bars represent the mean fraction of observed species in each abundance class. Solid red lines show the mean of best-fit log-normal distributions, normalized for plotting on the same scale as observed frequencies. Black error bars and red dotted lines represent 95% bootstrap confidence limits on observed and predicted means, respectively. (**B**) Consistency in abundance distributions with increasing scale. Best-fit log-normal distributions are plotted for local communities [red line, reproduced from (A)], along with communities pooled at the reef (dark blue line) and metacommunity (light blue line) scales, and finally pooled across habitats at the metacommunity scale (black line).

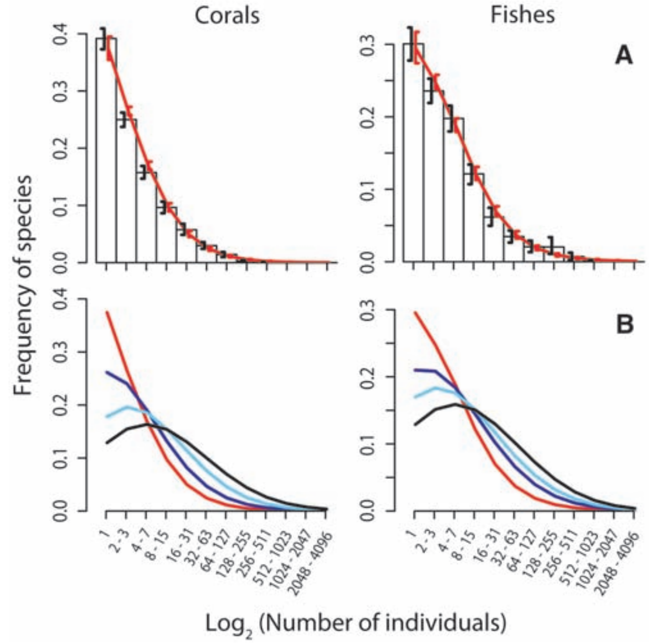

Fig. 3. Numerical abundance distributions for corals and fishes at (**A**) the local community scale, with best-fit Poisson log-normal distributions. These distributions explicitly characterize the veil effect produced by sampling from an underlying log-normal distribution (*24*). Octaves are here plotted as true doubling classes, with each successive octave containing twice as many abundance categories as the preceding one. Bars represent the mean fraction of observed species in each abundance class. Red lines represent the mean of predicted frequencies across local communities, based on independent maximum-likelihood fits of the Poisson log-normal distribution to each local community. Black and red error bars represent 95% bootstrap confidence limits on observed and predicted mean frequencies, respectively. (**B**) Unveiling a log-normal abundance distribution. Best-fit Poisson log-normal distributions are plotted for local communities [red line, reproduced from (A)], communities pooled at the reef (dark blue line) and metacommunity (light blue line) scales, and finally pooled across habitats at the metacommunity scale (black line).

Our study's support for underlying log-normal distributions of numerical abundance is highly consistent with an ecological null hypothesis for community structure that is based on the Central Limit Theorem (CLT): Log-normal abundance distributions arise as a statistical consequence of multiplicative interactions among a large number of stochastic ecological factors that affect population growth (*18*). Resource acquisition is also likely to have a strong multiplicative component, because the capacity to acquire additional resources is likely to scale with resources already acquired (for example, space acquisition in corals will be proportional to space already occupied). Thus, log-normal distributions of resource use are also consistent with this hypothesis. The CLT hypothesis is controversial, and its logic has been criticized (*26*). However, the hypothesis that log-normal abundance distributions are a general consequence of stochastic variation in population growth rates is consistent with demographic theory that explicitly integrates environmental stochasticity with a general form of density-dependent interactions among species (*15*). This contrasts with models that do not incorporate environmental stochasticity and make more specific assumptions about interspecific density-dependence, which tend to predict a broad family of shapes for abundance distributions (*12*, *16*, *17*).

Acceptance of the generality of log-normal abundance distributions has been hindered by the prevalence of deviations from the log-normal in empirical data. Indeed, numerous alternative theories have been proposed in order to account for such deviations (*12*, *13*, *16*, *17*). Although our data exhibit many of these same deviations, our multiscale analysis indicates that they are likely to be caused by sampling effects, rather than biological processes. For resource-use distributions, a hypothesis that left skew is a statistical artifact of pooling samples from multiple locations (*10*) is supported: A slight left skew emerges as local communities are pooled at larger scales (fig. S2). For numerical abundance, the veil effect is supported by the excellent fit of the truncated log-normal distribution to our local community abundance distributions (Fig. 3A and fig. S3), and our multiscale approach uncovers additional evidence for an underlying log-normal distribution of numerical abundance. Specifically, changes in the shape of the distribution with increasing scale (Fig. 3B) match what is expected if a log-normal distribution is being unveiled. Moreover, metacommunity richness levels predicted by the

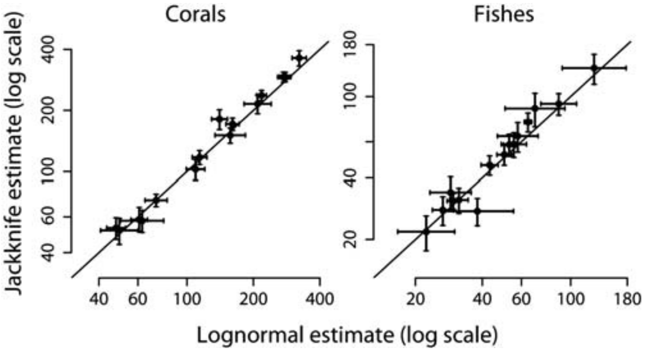

Fig. 4. Comparison of the size of the metacommunity species pool, as predicted by the Poisson log-normal distribution (horizontal axis) and the jackknife estimator (vertical axis), with standard errors (*24*). The diagonal line is the unity line (log-normal estimate = jackknife estimate). Each point corresponds to one habitat type within each metacommunity. The two sets of estimates exhibit excellent fit to the unity line ($r^2 = 0.98$ and 0.94 for corals and fishes, respectively).

log-normal model agree with predictions from the nonparametric jackknife estimator, which makes no assumptions about the form of the underlying distribution of numerical abundance (Fig. 4).

The search for a limited suite of processes that accounts for consistent patterns in species' relative abundances has occupied ecologists for at least a half century (*1*); this search has accelerated as the worsening biodiversity crisis has focused attention on the need to understand how high-diversity communities are structured (*12*, *13*). Our results lend strong support to a classical, but controversial, null hypothesis regarding community structure: The shape of species-abundance distributions arises as a general consequence of environmental stochasticity, through its effects on population dynamics. This finding underscores the importance of robust conservation strategies that adequately encompass the spectrum of environmental variability to which coral reef organisms are exposed. Accordingly, conservation efforts should expand in scale and scope, moving beyond localized protected areas and toward a seascape approach (*28*). Given the accelerating pace of coral reef habitat loss worldwide (*21*), addressing this challenge remains an urgent priority.

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Supporting Online Material
www.sciencemag.org/cgi/content/full/309/5739/1363/DC1
Materials and Methods
Figs. S1 to S3
Table S1
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Global Patterns of Predator Diversity in the Open Oceans

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The open oceans comprise most of the biosphere, yet patterns and trends of species diversity there are enigmatic. Here, we derive worldwide patterns of tuna and billfish diversity over the past 50 years, revealing distinct subtropical "hotspots" that appeared to hold generally for other predators and zooplankton. Diversity was positively correlated with thermal fronts and dissolved oxygen and a nonlinear function of temperature (~25°C optimum). Diversity declined between 10 and 50% in all oceans, a trend that coincided with increased fishing pressure, superimposed on strong El Niño–Southern Oscillation–driven variability across the Pacific. We conclude that predator diversity shows a predictable yet eroding pattern signaling ecosystem-wide changes linked to climate and fishing.

Humans have exploited oceanic predators such as tuna, billfish, sharks, and sea turtles for millennia. Although our knowledge of individual species has rapidly advanced, for example, through sophisticated tagging studies (*1*, *2*), community-wide patterns of abundance and diversity are only beginning to be understood (*3*). This knowledge is timely. Many species have declined, are vulnerable to overfishing, or are threatened by extinction (*4*, *5*), and there is a concern that widespread predator declines can trigger unforeseen ecosystem effects (*6*–*8*). Effective management and conservation in the open oceans will depend on resolving the spatial distribution of multiple species, ecological communities, and fishing effort (*1*, *2*, *9*–*11*). Recent studies performed on a regional scale have indicated that predator species may aggregate at distinct diversity hotspots—areas of high species diversity that may represent important oceanic habitats and hold particular value for biodiversity conservation (*3*, *11*). Yet, global-scale patterns and trends of predator diversity have remained obscure. We investigated the global distribution of predator diversity, how it relates to regional oceanography, and whether diversity has changed over time.

As a first step, we used global 5° by 5° Japanese longlining data from 1990 to 1999 to analyze contemporary patterns of tuna and bill-

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