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Testing biodiversity theory using species richness of reef-building corals across a depth gradient

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Natural environmental gradients encompass systematic variation in abiotic factors that can be exploited to test competing explanations of biodiversity patterns. The *species–energy* (SE) hypothesis attempts to explain species richness gradients as a function of energy availability. However, limited empirical support for SE is often attributed to idiosyncratic, local-scale processes distorting the underlying SE relationship. Meanwhile, studies are also often confounded by factors such as sampling biases, dispersal boundaries and unclear definitions of energy availability. Here, we used spatially structured observations of 8460 colonies of photo-symbiotic reef-building corals and a null-model to test whether energy can explain observed coral species richness over depth. Species richness was left-skewed, hump-shaped and unrelated to energy availability. While local-scale processes were evident, their influence on species richness was insufficient to reconcile observations with model predictions. Therefore, energy availability, either in isolation or in combination with local deterministic processes, was unable to explain coral species richness across depth. Our results demonstrate that local-scale processes do not necessarily explain deviations in species richness from theoretical models, and that the use of idiosyncratic small-scale factors to explain large-scale ecological patterns requires the utmost caution.

1. Background

Despite decades of research and more than 100 proposed explanations [1,2], the processes that generate and maintain species richness gradients remain poorly understood [2–5]. An important contributor to this lack of understanding is the paucity of species abundance data with sufficient coverage and resolution to identify underlying patterns and thereby help distinguish between competing possible causes [4–6]. Ecosystem-specific differences in interspecific responses to environmental factors further limit our ability to separate general ecological processes from local-scale idiosyncratic effects [7]. Moreover, differences in dispersal boundaries [8], area effects [3,9], sampling bias [2,10] and the proportion of gradients sampled [5] have all contributed to a lack of consensus regarding the processes that generate and maintain species richness gradients.

The *species–energy* (SE) hypothesis proposes that species richness gradients can be explained by spatial variability in energy availability, predicting a monotonic decline in richness with decreasing energy [11]. Theoretically, more energy allows more individuals to coexist, thereby allowing more species to maintain large enough populations to avoid local extinction via demographic stochasticity. Despite many empirical studies, however, there is still little agreement on the importance of SE in structuring ecological communities in nature, although controlled experiments have demonstrated the potential [12]. Instead of a monotonic pattern of species richness declining with energy availability, field studies often report lower richness where energy levels are greatest [2,6,13–15]. Potentially confounding these patterns further, species richness across a gradient can be strongly influenced by the scale at which it is measured [3,16,17], an important consideration because most empirical studies of this nature occur at small scales. Limited support for SE in empirical studies at local scales is often attributed to disproportionately strong local-scale community assembly processes occurring at the high-energy region of the domain, thereby modifying the shapes of species richness curves from monotonic to a hump-shaped unimodal pattern [18–20]. While the inclusion of local modifying factors can help explain a lack of support for theoretical predictions, the role of deterministic community assembly processes in species richness gradients remains contentious [21–24].

One way to resolve this issue is to test the predictions of the SE hypothesis using a diverse biological community where all individuals occur along a geographically short but clearly defined energy gradient. Doing so helps remove confounding factors such as area effects and dispersal boundaries, the identity of the limiting energetic resource and incomplete sampling of the full gradient. Coral reefs provide such an opportunity because light declines exponentially with depth, and is also the primary limiting energetic resource for photo-symbiotic reef-building corals: light provides corals with the vast majority of their energy requirements via photosynthesis [25,26], and the influence of energy availability on coral community composition is well understood [27,28]. Although some corals can supplement their energetic budget with heterotrophic feeding [29], light availability is closely linked to the physiological process of calcification [30,31] and heterotrophy cannot replace the photosynthetic acquisition of energy. Moreover, photo-symbiotic reef-building corals occur over a relatively short depth range because light irradiance at a depth of only 60 m is typically only approximately 1% of surface irradiance even in clear tropical waters. Consequently, virtually the entire gradient can be sampled, thereby minimizing any potential effects of sampling a truncated energy distribution [32].

Coral community assembly may also be influenced by local-scale processes, such as competitive interactions and environmental disturbance [33,34]. Predictable changes in the energetic and environmental conditions over depth are thought to influence the intensity and nature of these processes over this gradient [35,36], making coral reefs an ideal model ecosystem to test the effects of local processes on species richness [28,35–37]. Specifically, the hump-shaped pattern commonly observed in empirical studies is typically attributed to deterministic community assembly processes being strongest at the shallowest sites, where the energetic resource is also most abundant [18,20,35,36]. For example, shallow-water corals are disproportionately exposed to the damaging effect of wave energy, which declines rapidly with depth [38,39]. High disturbance frequency might, therefore, select for a limited subset of species that could coexist at shallow sites, resulting in decreased species richness. Specifically, consistently high wave energy should select for species either capable of withstanding hydrodynamic forces, or that can rapidly recover following disturbance [33,35,37]. Conversely, higher levels of the energetic resource are thought to promote increased growth, which in turn promotes competitive interactions, and ultimately accelerated rates of competitive exclusion [20]. These processes underpin the *hump-backed model* (HBM), which seeks to explain hump-shaped species richness patterns often observed along a productivity gradient [18–20]. In both cases, species richness would be suppressed by deterministic processes at a local scale, but are reliant on these processes being disproportionately more influential only in the shallowest sites. However, support for these ideas remains scarce, primarily owing to the difficulty of obtaining suitable data to test them [24].

Here, we census photo-symbiotic reef-building corals over a depth range of 0–45 m, encompassing 98% of the light gradient, to test predictions of the SE hypothesis of a monotonic decline in species richness over depth. We then use the nested spatial structure of these data and a null-model approach to estimate the influence of local-scale community assembly processes over depth.

2. Methods

(a) Field surveys

Coral surveys were conducted between April 2015 and November 2016 on six reefs in Kimbe Bay, Papua New Guinea, located in the Indo-Australasian Archipelago (IAA) centre of coral diversity [40]. Corals were censused using vertical point count transects [41], spanning nine separate depth bins at 5 m intervals from the surface (i.e. 0–5 m) to 45 m (40–45 m). At each reef, at least nine up-slope point count transect surveys were conducted, with at least one count station completed in each depth bin. Count stations consisted of 12 coral colonies ranging outwards from a randomly selected central colony via the nearest neighbour. At least 144 colonies (mean = 177) were recorded and identified to species in each depth bin, at each of six reefs (total $n = 8460$ colonies, 705 count stations, more than 864 colonies/depth bin). For full methodology, see the electronic supplementary material.

(b) Species richness analysis

To correct for sampling effort [10], species richness estimates for each depth bin were generated using species accumulation curves. Curves were generated using the function 'specaccum' within the package 'vegan' in R [42,43]. Each curve was re-assembled 999 times randomly with replacement to capture the possible variation in species richness, before being subsampled at 70 counts (840 individual colonies). This sample size allowed species estimates to be compared without requiring extrapolation of the accumulation curves beyond the empirical data. The resulting 8991 data points were retained, and the mean of each depth was taken to represent the empirical species richness.

Species–energy model. Light irradiance was used to estimate available photosynthetic energy for use in the SE model. At each reef, light intensity was recorded at 5 m intervals along the depth gradient using an Odyssey submersible photosynthetic irradiance recording system logger [44]. Levels were recorded during November 2015, at 12.00, and each estimate was the mean of at least three estimates of irradiance recorded a
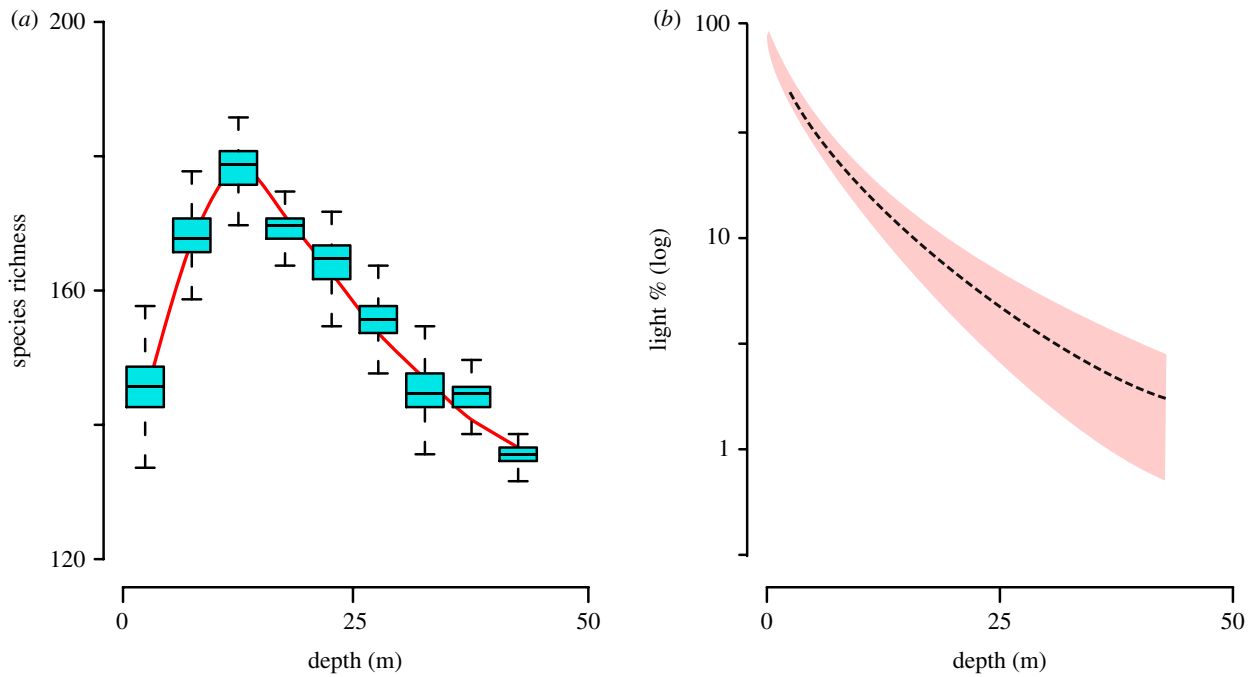
Figure 1. *Species–energy model* (SE) predictions versus observed data. Species richness showed a skewed hump-shaped pattern, peaking in the 10–15 m depth bin (*a*). This pattern was not consistent with the predictions of the SE model using light (*b*). Blue box plots (*a*) represent quartiles of the 999 estimates of species richness at 840 individuals at each depth bin; the red line shows the trend in mean values. Dashed line shows the change in light with depth (*b*), with red shading representing the variation between sites. (Online version in colour.)

minimum of 30 s apart and expressed as a percentage of the surface light level at each reef. These values were used to estimate a standard light attenuation curve over depth for the study location. The predictor value of energy in the SE model was then calculated as the percentage of surface irradiation available at each depth. A one-factor general linear model was used to test the capacity of light irradiance to predict the mean estimated species richness over depth.

Local assembly processes. We used a null-model to generate expected values of local species richness for any given species pool, which we compared with observed species richness. Negative deviations from the null expectation indicate the strength of local-scale deterministic processes, and how the influence of these processes changes over the depth gradient. This approach enabled examination of the influence of local-scale processes on species richness in isolation from larger-scale processes [24,45]. For each of the nine depth bins, a species pool was assembled consisting of all species recorded, and the relative abundance of each species. Null assemblages were then generated at each depth by selecting 12 individuals from the available species pool, with the selection probability reflecting its abundance. At each depth bin, 10 000 virtual count stations of 12 colonies were assembled, and the mean species richness per count extracted. Empirical values were compared with null expectations at each depth, and the discrepancy between the two values was taken as a measure of the intensity of local-scale deterministic community assembly processes.

3. Results and discussion

Observed species richness showed a left-skewed hump, peaking at the 10–15 m depth bin (figure 1*a*), a result not predicted by the SE model (figure 1*b*, SE: $r^2 < 0.01$). Over the full depth gradient, there was little support for the monotonic decline in richness predicted by the SE model, primarily because the model was unable to predict the observed low species richness in the shallow high-energy section of the domain (figure 2*a*). This discrepancy could be accounted for if

deterministic community assembly processes were disproportionately stronger only in the shallowest sites, as theorized by the HBM (figure 2*b*). Species richness at the count station scale was significantly lower than expected at all depths (figure 2*c*), indicating that species are strongly influenced by local-scale community assembly processes. However, the influence of these processes was not significantly stronger in the shallow depths (figure 2*c*). Therefore, deterministic processes are unable to account for the mismatch between the SE prediction and the observed data.

Declines in species richness in high-energy sections of domains have been observed in many ecosystems [2,6,13–15] and although the suggestion that the pattern is universal is not new [46], what creates and maintains such patterns remains unsubstantiated [15,20,21]. Explanations of observed species richness patterns as functions of SE and HBM generally require *post hoc* modifications through the invocation of idiosyncratic additional factors to reconcile these observations with theoretical predictions [7,23,47,48]. Often, the processes underpinning these *post hoc* modification are poorly understood, making clear mechanistic predictions difficult. For example, competitive interactions are thought to strongly influence the structure and richness of a coral community by affecting the physiological fitness of individual coral colonies [20,35–37]. However, the real-world impact of competition on key demographic traits (such as growth rate) is insignificant, or more complex than anticipated [49]. In the absence of clear and testable mechanistic predictions, deviations from empirical observations are uninformative for testing these theories [21,50–52]. The persistence of these theories is impeding the development of alternative hypotheses to explain patterns of biodiversity [21,22,50].

The challenge of explaining the commonly observed pattern of lower species richness at the highest energy portions of a gradient was first discussed in the early 1990s [15,46]. Potential explanations include the combined effects of
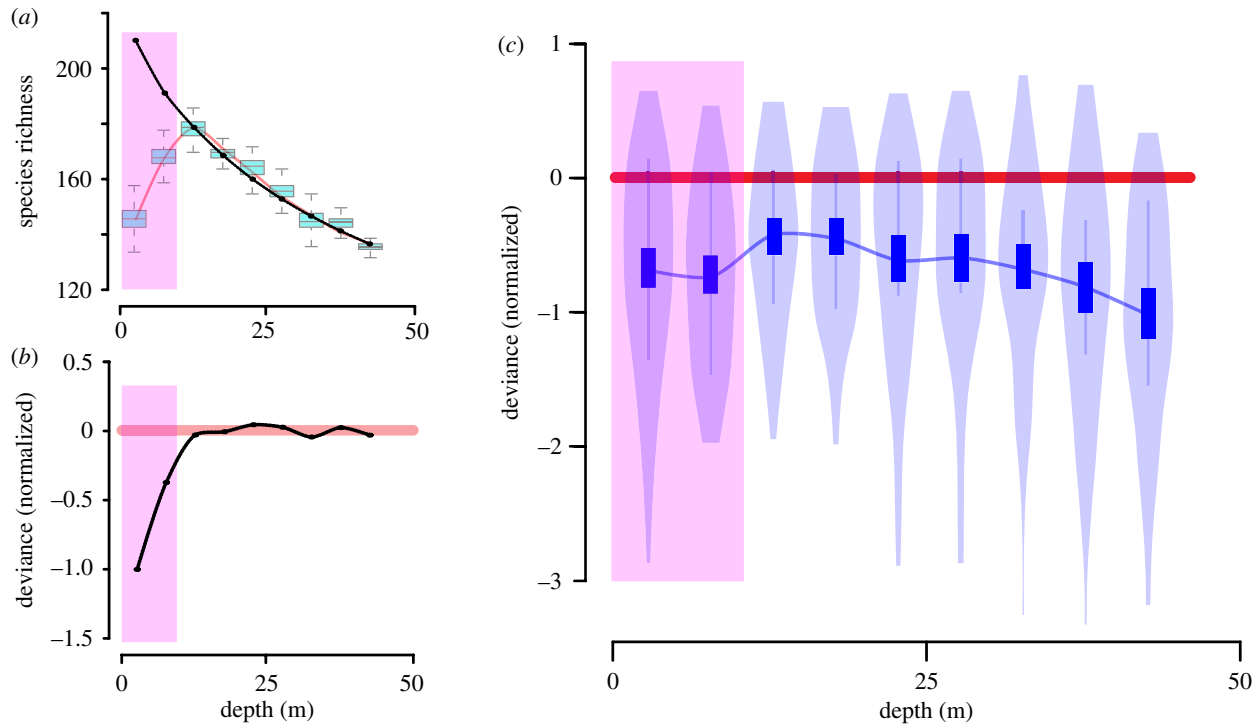
Figure 2. Influence of local-scale community assembly processes. To fit the observed data to the SE prediction (black line), species richness must be disproportionately reduced at depths below 10 m (*a*). Count-scale species richness must therefore negatively deviate from the null expectation at the shallowest depths (*b*). Although species richness within counts is lower than null expectations at all depths (*c*), the trend is unable to reconcile the observed species richness with the SE prediction (*b,c*). Model fit predictions for the SE are represented in black (*a*), and deviance of predicted count station richness versus observed means are normalized to between 0 and −1 for both predicted (*b*) and empirical (*c*) values. Null values are shown as a red bar (*b,c*). Pink polygons overlay the depths where deviance must be significantly greater than at other depths to meet the SE prediction. Frequency distributions of all count-scale richness values are shown in pale blue (*c*), while 95% confidence intervals of the mean are represented by solid blue bars, and quartiles by fine blue lines.

multiple energetic factors [53], scale effects [17] and local disturbance regimes [18,20,35]. Consequently, discerning the relative effects of such processes has proven difficult. By using observations free of the common factors that can confound such studies, we show that the species richness gradient in reef corals over depth is not predicted by the SE hypothesis. We also find no support for the contention that lower species richness at the high-energy end of the gradient is due to local deterministic processes such as increased disturbance frequency or competitive exclusion. Instead, we propose that future studies should focus on generating theoretically sound mechanistic predictions that can be tested across multiple spatial scales. While other authors have made similar suggestions [21,50–52], our results further highlight the need to robustly test predictions of theoretical models, rather than relying on *post hoc* explanations of poorly fitting models to help us understand important and widespread patterns in nature.

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