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

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TER, AHB, and TCLB conceived the research, TER collected the data, and analysed the data with input from SAK, MJC, and CR. TER led the writing of the manuscript with contributions from all authors.

1 **Title: Testing biodiversity theory using species richness of reef-building corals**

2 **across a depth gradient**

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Abstract: 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 species-

energy relationship. Meanwhile, studies are also often confounded by factors such as

sampling biases, dispersal boundaries, and unclear definitions of energy availability.

Here, we use spatially-structured observations of 8,460 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, neither energy availability in isolation, nor in combination

with local deterministic processes were able 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.

Background

Despite decades of research and more than 100 proposed explanations[1, 2], the

processes that generate and maintain species richness gradients remain poorly

50 understood[2-5]. An important contributor to this lack of understanding is the paucity

51 of species abundance data with sufficient coverage and resolution to identify

52 underlying patterns and thereby help distinguish between competing possible

53 causes[4-6]. Ecosystem-specific differences in interspecific responses to

54 environmental factors further limits our ability to separate general ecological

55 processes from local-scale idiosyncratic effects[7]. Moreover, differences in dispersal

56 boundaries[8], area effects[3, 9], sampling bias[2, 10], and the proportion of gradients

57 sampled[5] have all contributed to a lack of consensus regarding the processes that

58 generate and maintain species richness gradients.

59   The *Species Energy* hypothesis (*SE*) proposes that species richness gradients

60 can be explained by spatial variability in energy availability, predicting a monotonic

61 decline in richness with decreasing energy[11]. Theoretically, more energy allows

62 more individuals to co-exist, thereby allowing more species to maintain large enough

63 populations to avoid local extinction via demographic stochasticity. Despite many

64 empirical studies, however, there is still little agreement on the importance of *SE* in

65 structuring ecological communities in nature, although controlled experiments have

66 demonstrated the potential[12]. Instead of a monotonic pattern of species richness

67 declining with energy availability, field studies often report lower richness where

68 energy levels are greatest [2, 6, 13-15]. Potentially confounding these patterns further,

69 species richness across gradients can be strongly influenced by the scale at which they

70 are measured [3, 16, 17], an important consideration because most empirical studies

71 of this nature occur at small scales. Limited support for *SE* in empirical studies at

72 local scales is often attributed to disproportionately strong local-scale community

73 assembly processes occurring at the high energy region of the domain, thereby

74 modifying the shapes of species richness curves from monotonic to a hump-shaped

75   unimodal pattern[18-20]. While the inclusion of local modifying factors can help

76   explain a lack of support for theoretical predictions, the role of deterministic

77   community assembly processes in species richness gradients remains contentious[21-

78   24].

79   One way to resolve this issue is to test the predictions of the *SE* hypothesis

80   using a diverse biological community where all individuals occur along a

81   geographically short but clearly-defined energy gradient. Doing so helps remove

82   confounding factors such as area effects and dispersal boundaries, the identity of the

83   limiting energetic resource, and incomplete sampling of the full gradient. Coral reefs

84   provide such an opportunity because light declines exponentially with depth, and is

85   also the primary limiting energetic resource for photo-symbiotic reef-building corals:

86   light provides corals with the vast majority of their energy requirements via

87   photosynthesis[25, 26], and the influence of energy availability on coral community

88   composition is well understood[27, 28]. Although some corals can supplement their

89   energetic budget with heterotrophic feeding [29], light availability is closely linked to

90   the physiological process of calcification [30, 31], and heterotrophy cannot replace

91   the photosynthetic acquisition of energy. Moreover, photo-symbiotic reef-building

92   corals occur over a relatively short depth range because light irradiance at a depth of

93   only 60 m is typically only ~1% of surface irradiance even in clear tropical waters.

94   Consequently, virtually the entire gradient can be sampled, thereby minimising any

95   potential effects of sampling a truncated energy distribution[32].

96   Coral community assembly may also be influenced by local-scale processes,

97   such as competitive interactions and environmental disturbance[33, 34]. Predictable

98   changes in the energetic and environmental conditions over depth are thought to

99   influence the intensity and nature of these processes over this gradient[35, 36],

100   making coral reefs an ideal model ecosystem to test the effects of local-processes on

101   species richness [28, 35-37]. Specifically, the hump-shaped pattern commonly

102   observed in empirical studies is typically attributed to deterministic community

103   assembly processes being strongest at the shallowest sites, where the energetic

104   resource is also most abundant[18, 20, 35, 36]. For example, shallow-water corals are

105   disproportionately exposed to the damaging effect of wave energy, which declines

106   rapidly with depth[38, 39]. High disturbance frequency might therefore select for a

107   limited subset of species that could co-exist at shallow sites, resulting in decreased

108   species richness. Specifically, consistently high wave energy should select for species

109   capable of either withstanding hydrodynamic forces, or which can rapidly recovery

110   following disturbance[33, 35, 37]. Conversely, higher levels of the energetic resource

111   are thought to promote increased growth, which in turn promotes competitive

112   interactions, and ultimately accelerated rates of competitive exclusion[20]. These

113   processes underpin the *Hump-Backed Model* (*HBM*), which seeks to explain hump-

114   shaped species richness patterns often observed along a productivity gradient [18-20].

115   In both cases, species richness would be supressed by deterministic processes at a

116   local scale, but are reliant on these processes being disproportionately more influential

117   only in the shallowest sites. However, support for these ideas remains scarce,

118   primarily due to the difficulty of obtaining suitable data to test them[24].

119   Here, we census photo-symbiotic reef-building corals over a depth range of 0

120   to 45 m, encompassing 98% of the light gradient, to test predictions of the *SE*

121   hypothesis of a monotonic decline in species richness over depth. We then use the

122   nested spatial structure of these data and a null-model approach to estimate the

123   influence of local-scale community assembly processes over depth.

124

125   **Methods**

126   *Field Surveys*

127   Coral surveys were conducted between April 2015 and November 2016 on six reefs in

128   Kimbe Bay, Papua New Guinea, located in the Indo-Australasian Archipelago (IAA)

129   centre of coral diversity[40]. Corals were censused using vertical point count

130   transects[41], spanning nine separate depth bins at five metre intervals from the

131   surface (i.e. 0-5 m) to 45 metres (40-45 m). At each reef, at least nine up-slope point

132   count transect surveys were conducted, with at least one count station completed in

133   each depth bin. Count stations consisted of twelve coral colonies ranging outwards

134   from a randomly selected central colony via the nearest neighbour. At least 144

135   colonies (mean = 177) were recorded and identified to species in each depth bin, at

136   each of the six reefs (total n = 8,460 colonies, 705 count stations, > 864

137   colonies/depth bin). For full methodology, see electronic supplementary material.

138   *Species Richness Analysis*

139   To correct for sampling effort[10], species richness estimates for each depth

140   bin were generated using species accumulation curves. Curves were generated using

141   the function 'specaccum' within the package 'Vegan' in R[42, 43]. Each curve was

142   re-assembled 999 times randomly with replacement to capture the possible variation

143   in species richness, before being subsampled at 70 counts (840 individual colonies).

144   This sample size allowed species estimates to be compared without requiring

145   extrapolation of the accumulation curves beyond the empirical data. The resulting

146   8,991 data points were retained, and the mean of each depth taken to represent the

147   empirical species richness.

148   *Species Energy Model:* Light irradiance was used to estimate available photosynthetic

149   energy for use in the *SE* model. At each reef, light intensity was recorded at 5 metre

150   intervals along the depth gradient using an Odyssey submersible photosynthetic

151   irradiance recording system logger[44]. Levels were recorded during November 2015,

152   at 1200 hours, and each estimate was the mean of at least 3 estimates of irradiance

153   recorded a minimum of 30 seconds apart and expressed as a percentage of the surface

154   light level at each reef. These values were used to estimate a standard light attenuation

155   curve over depth for the study location. The predictor value of energy in the *SE* model

156   was then calculated as the percentage of surface irradiation available at each depth. A

157   one factor general linear model was used to test the capacity of light irradiance to

158   predict the mean estimated species richness over depth.

159   *Local Assembly Processes:* We used a null model to generate expected values of local

160   species richness for any given species pool which we compared to observed species

161   richness. Negative deviations from the null expectation indicate the strength of local

162   scale deterministic processes, and how the influence of these processes change over

163   the depth gradient. This approach enabled examination of the influence of local-scale

164   processes on species richness in isolation from larger-scale processes[24, 45]. For

165   each of the nine depth bins, a species pool was assembled consisting of all species

166   recorded, and the relative abundance of each species. Null assemblages were then

167   generated at each depth by selecting 12 individuals from the available species pool,

168   with the selection probability reflecting its abundance. At each depth bin, 10,000

169   virtual count stations of 12 colonies were assembled, and the mean species richness

170   per count extracted. Empirical values were compared to null expectations at each

171   depth, and the discrepancy between the two values was taken as a measure of the

172   intensity of local-scale deterministic community assembly processes.

173

174   **Results and Discussion**

175   Observed species richness showed a left-skewed hump, peaking at the 12.5 m

176   depth bin (Fig. 1a), a result not predicted by the *SE* model (Fig. 1b, *SE*: r^2 = <0.01).

177   Over the full depth gradient, there was little support for the monotonic decline in

178   richness predicted by the *SE* model, primarily because the model was unable to

179   predict the observed low species richness in the shallow high-energy section of the

180   domain (Fig. 2a). This discrepancy could be accounted for if deterministic community

181   assembly processes were disproportionately stronger only in the shallowest sites, as

182   theorised by the *HBM* (Fig. 2b). Species richness at the count station scale was

183   significantly lower than expected at all depths (Fig. 2c), indicating that species are

184   strongly influenced by local-scale community assembly processes. However, the

185   influence of these processes was not significantly stronger in the shallow depths (Fig.

186   2c). Therefore, deterministic processes are unable to account for the mismatch

187   between the *SE* prediction and the observed data.

188   Declines in species richness in high energy sections of domains have been

189   observed in many ecosystems[2, 6, 13-15] and although the suggestion that the pattern

190   is universal is not new[46], what creates and maintains such patterns remains

191   unsubstantiated[15, 20, 21]. Explanations of observed species richness patterns as

192   functions of *SE* and *HBM* generally require post-hoc modifications through the

193   invocation of idiosyncratic additional factors to reconcile these observations with

194   theoretical predictions[7, 23, 47, 48]. Often, the processes underpinning these post-

195   hoc modification are poorly understood, making clear mechanistic predictions

196   difficult. For example, competitive interactions are thought to strongly influence the

197   structure and richness of a coral community by affecting the physiological fitness of

198   individual coral colonies[20, 35-37]. However, the real-world impact of competition

199   on key demographic traits (such as growth rate) is insignificant, or more complex than

200   anticipated[49]. In the absence of clear and testable mechanistic predictions,

201   deviations from empirical observations are uninformative for testing these

202   theories[21, 50-52]. The persistence of these theories is impeding the development of

203   alternative hypotheses to explain patterns of biodiversity [21, 22, 50].

204   The challenge of explaining the commonly-observed pattern of lower species

205   richness at the highest energy portions of a gradient was first discussed in the early

206   1990s[15, 46]. Potential explanations include the combined effects of multiple

207   energetic factors[53], scale effects[17], and local disturbance regimes[18, 20, 35].

208   Consequently, discerning the relative effects of such processes has proven difficult.

209   By using observations free of the common factors that can confound such studies, we

210   show that the species richness gradient in reef corals over depth is not predicted by

211   the *SE* hypothesis. We also find no support for the contention that lower species

212   richness at the high-energy end of the gradient is due to local deterministic processes

213   such as increased disturbance frequency or competitive exclusion. Instead, we

214   propose that future studies should focus on generating theoretically sound mechanistic

215   predictions which can be tested across multiple spatial scales. While other authors

216   have made similar suggestions[21, 50-52], our results further highlight the need to

217   robustly test predictions of theoretical models, rather than relying on post-hoc

218   explanations of poorly-fitting models to help us understand important and widespread

219   patterns in nature.

220

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226   TER, AHB, and TCLB conceived the research, TER collected the data, and analysed

227   the data with input from SAK, MJC, and CR. TER led the writing of the manuscript

228   with contributions from all authors. **Competing interests:** Authors declare no

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230   validate the study are available in the supplementary materials.

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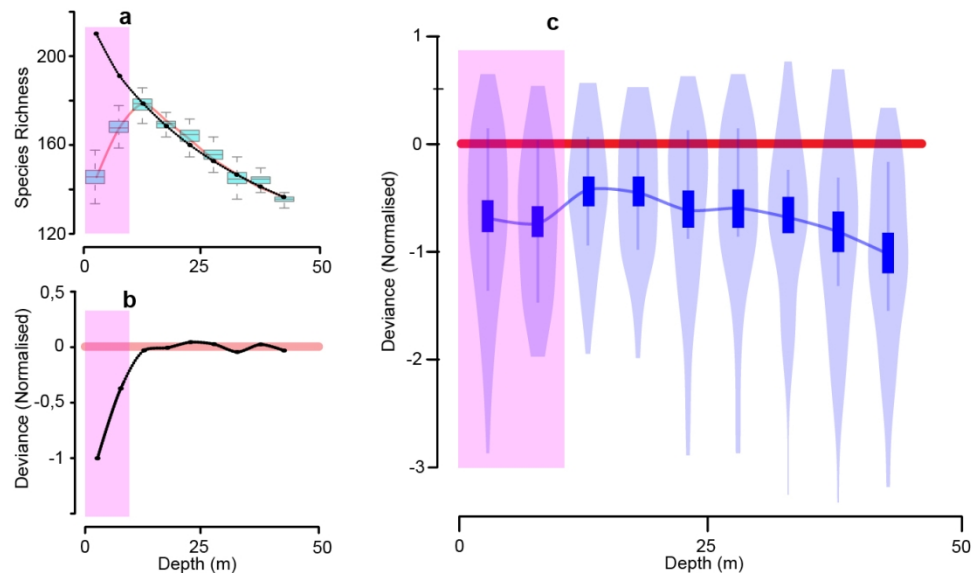
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Figure 2: Influence of local-scale community assembly processes. To fit the observed data to the SE prediction (black line), species richness must be disproportionately reduced at depths below 10 m (a). Count-scale species richness must therefore negatively 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 normalised 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.

120x70mm (300 x 300 DPI)