A word on habitat complexity

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Authorship

JM, MA and NS developed the initial concept. MA and NS performed analyses. JM wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Data availability statement

No new data were used in this manuscript. The code for analyses and figures is available at: https://github.com/jmadinlab/TechnicalNoteComplexity

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Abstract

In their recent synopsis, Loke and Chisholm (2022) present an overview of habitat complexity metrics for ecologists. They provide a review and some sound advice. However, we found several of their analyses and opinions misleading. This technical note provides a different perspective on the complexity metrics assessed.

Main text

Ecologists have long grappled with the concept of habitat complexity. Loke & Chisholm (2022, hereafter L&C) suggest that there is “no consensus over the definition of complexity or how to measure it” (Abstract). While habitat complexity includes multiple components, L&C largely focus on structural complexity, and on rugosity and fractal dimension in particular. Contrary to L&C, we argue that structural complexity metrics such as these have clear geometric definitions and simple, dimensionless mathematical underpinnings. Moreover, as long as ecologists are consistent about the method, resolution, and scales, these metrics provide a quantitative approach to compare habitats.

L&C present three arguments against the use of fractal dimension in ecology: 1) natural surfaces are not full fractals; 2) methods for estimating fractal dimension are prone to biases; and 3) the biological significance of fractal dimension is unclear. First, almost everything in ecology is scale-dependent and ecologists are well-aware that measures of fractal dimension of natural surfaces change across neighboring scales (Martin-Garin et al. 2007; Plotze et al., 2005, Florindo et al. 2012). Rather than being a hindrance, these changes provide useful information about how a 3D habitat is perceived by organisms at different scales, and how ecosystem engineers build habitat complexity. How an ecologist chooses to summarize a collection of slope estimates when calculating fractal dimension will depend upon the question being addressed and the data at hand.

Second, with regard to their argument about estimation biases, L&C present an example that conflates 2D (i.e. box-counting) and 3D (i.e. variation) methods for estimating fractal dimension (Fig. 5 in L&C). They create a Brownian surface of an approximate fractal dimension to test both methods and conclude the box-counting method is superior. Notably, the box-counting method was conducted by extracting the middle contour of this surface as a binary 2D bitmap, thereby ignoring the third dimension. This is a misleading comparison, primarily because box counting cannot be applied to real world 3D surfaces (L&C's first argument, above) as results will vary depending on the contour selected. Appropriate comparisons would have been provided using cube-counting (the 3D equivalent of box-counting, Zawada et al. 2019) or other existing techniques for 3D surfaces (Fukunaga et al. 2019, Florindo et al. 2012, Tricot, 1995, Reichert et al. 2017). Regardless of the estimation method, as long as it is consistent (method, resolution, and scales), comparisons in space and time are valid.

Third, L&C question the biological relevance of fractal dimension (page 5; L&C). Yet, in their own review, they list several studies that found consistent correlations between fractal dimension and species diversity (Table S1.1; L&C). In addition, fractal dimension can be strongly associated with the size structure of biological communities—habitats with higher fractal dimension have a higher proportion of smaller-sized organisms (Morse et al. 1985; Ackerman and Bellwood 2003). Body size distributions are a main determinant of energy flux (Gillooly et al. 2001), and have fundamental implications for multiple ecosystem functions (Yvon-Durocher & Allen 2012). Hence, dismissing the role of habitat fractal dimension in shaping biological communities seems premature.

In addition to the arguments raised against fractal dimension, L&C go on to suggest that rugosity is confounded with area effects and suggest that area alone explains much of any biodiversity patterns observed. Rugosity is indeed, per definition, driven by surface area. However, a flat surface of a given surface area is fundamentally different from a surface that has the same surface area squeezed into a smaller planar area (Torres-Pulliza et al. 2020; Fig. 1). Surfaces with a higher rugosity theoretically can provide more niches and thus host more species and body sizes. Future studies should investigate the simultaneous effects of area and rugosity, as alluded to by L&C (pg. 12). We present such an analysis here (Fig. 1, Supplementary Methods), which shows the number of coral species found in a given area of reef depends significantly on rugosity.

Finally, L&C's criticism of the geometric constraint presented in Torres-Pulliza et al. (2020) is flawed. Regardless of how you calculate rugosity, fractal dimension and height range, the tight relationship remains; even when using L&C's own simulated data (Fig. 2, Supplementary Methods). We note that the raw relationship is a surface, and transformations in Eq. 1 in Torres-Pulliza et al. (2020) act to make it a plane. Although the mathematics behind the geometric constraint proposed in Torres-Pulliza et al. (2020) can undoubtedly be improved, the constraint is consistent across large geographic scales and habitats (Asbury et al. 2023). It is important to recognize and understand constraints among structural complexity metrics when addressing ecological questions. They tell us, for example, what metric value combinations are geometrically impossible, and so greatly help us make sense of habitat complexity.

Conclusion

We advocate encouraging rather than diminishing the use of structural complexity metrics. Habitat complexity provides the potential for ecological patterns and processes to occur; it does not determine them. Structural complexity metrics have geometric underpinnings, are well-defined mathematically, and are more reliable than most ecological metrics. Fractal dimension offers an excellent way to approximate how habitat surfaces fill space at different scales, and has important ecological implications. Finally, Torres-Pulliza et al. (2020) highlights an important geometric constraint that does not disappear when using different methods for calculating complexity metrics, and provides a useful, standardized framework for ecologists to build upon.

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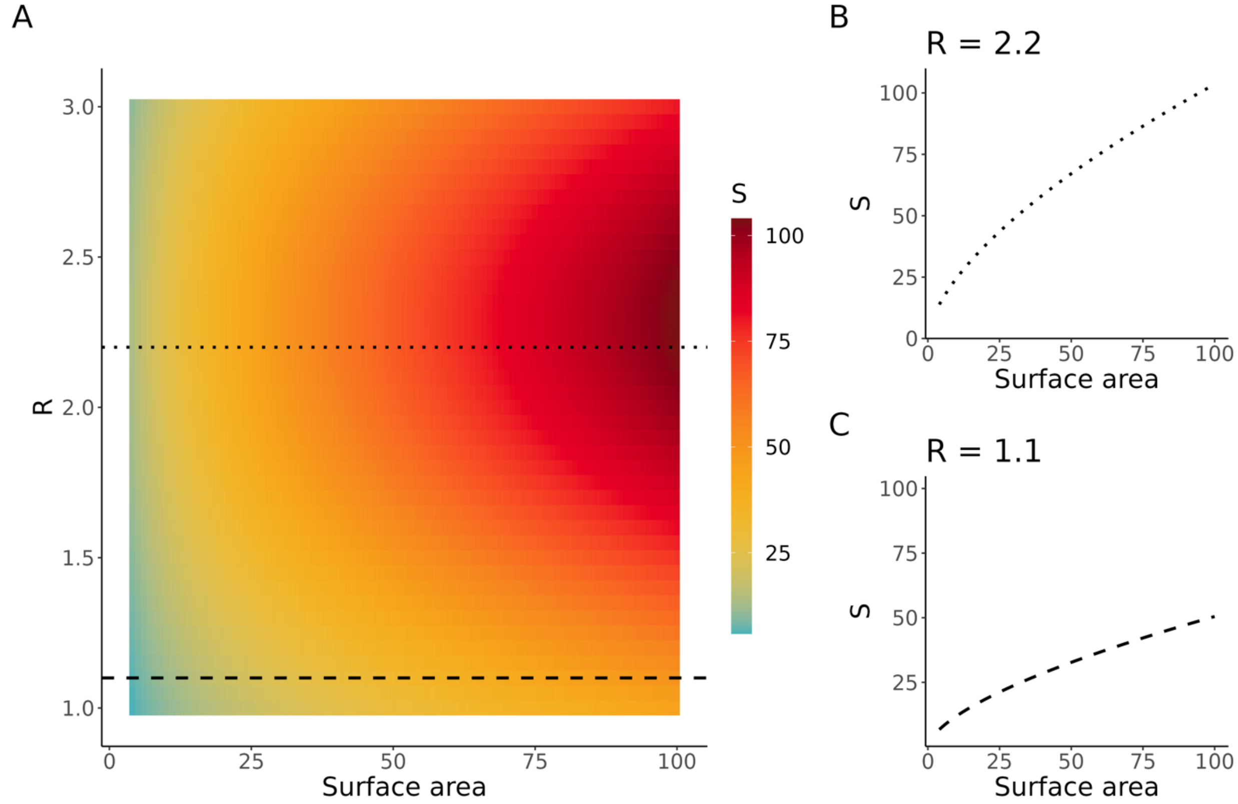

Figure 1. (A) Predicted coral species richness in relation to surface area and rugosity for reef plots of different sizes ranging from 4 to 100 m^2 at Lizard Island, Great Barrier Reef. Fractal dimension is fixed at D=2.5 (see Supplementary Methods). Dotted and dashed lines show how species richness increases with surface area (B) more rapidly on surfaces with higher rugosity than (C) flatter surfaces, respectively.

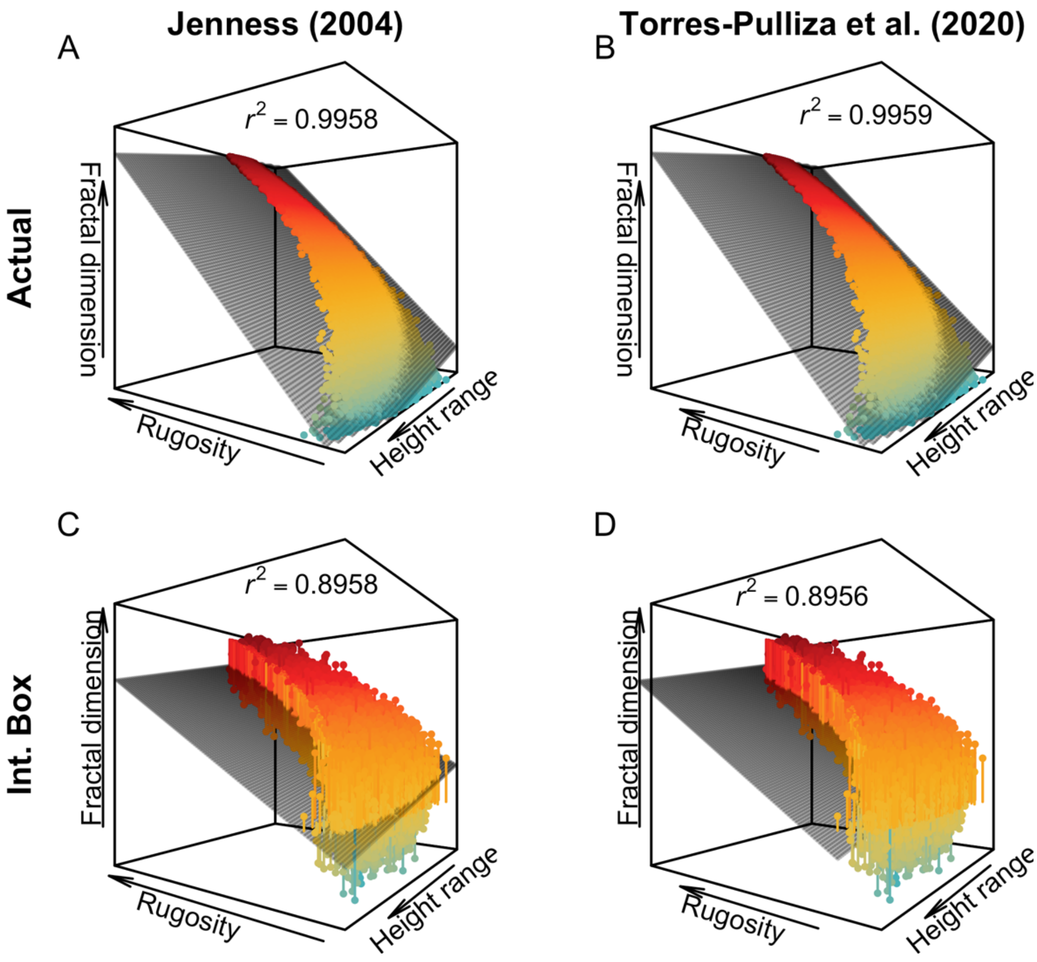

Figure 2. Data from L&C simulated fractal surfaces showing the relationship among rugosity, fractal dimension and height range. Rugosity was calculated in two different ways (panel columns, respectively): DEM rugosity, in which we use the *surfaceArea* function (Jenness 2004), and height range rugosity, in which we use surface area method from Torres-Pulliza et al. (2020). Fractal dimension are the actual values simulated and those estimated using L&C's intermediate box count method (panel rows, respectively). Height range is the distance between the lowest and highest point in the defined area. r-square values were estimated by comparing fractal dimension data to fractal dimension calculated from the respective plane equation.

Supplementary Methods

Species area and rugosity

Using the coral diversity dataset presented in Torres-Pulliza et al. 2020, we investigated the effects of surface area, rugosity, and fractal dimension. The data presented in their manuscript includes species richness of Scleractinia corals for 2x2m squares on a reef patch in the Northern Great Barrier Reef. For each square, the fractal dimension and rugosity are also provided. Torres-Pulliza et al. (2020) showed that both complexity metrics had an effect on richness. We built upon their analysis by adding surface area as a dependent variable. We increased the range of planar area by grouping the 2x2m patches. Specifically, we then obtained 252 patches of 4 m^2 planar area, 52 patches of 16 m^2 planar area, 18 patches of 36 m^2, and 7 patches of 64 m^2. For all the grouped patches larger than 4 m^2, we then approximated fractal dimension (D) and rugosity (R) by taking the average. We estimated surface area (SA) for all patches by multiplying planar area by rugosity. We also calculated the total species richness (S) for each patch. We then performed a Bayesian linear regression using Stan and brms (Bürkner 2017):

$\log(S) \sim \mathrm{normal}(mu, sigma)$,

$mu = b_0 + b_1 \log(SA) + b_2 R + b_3 R^2 + b_4 D$,

where b_0 is the intercept, b_1, b_2, b_3, and b_4 are the fixed effects of log(SA), R, R^2, and D, respectively. mu the average fitted values, sigma the residual error, S = species richness, SA = surface area, R = rugosity, and D = fractal dimension, mu represents the average predicted log-transformed S, and sigma is the residual error. We used uninformative priors for all fixed effects and a weakly informative prior for sigma (i.e. sigma ~ student_t(3, 0, 2.5)). We verified the fit by checking Rhat values and the posterior predictive plot.

We log-transformed S and SA to respect the theoretical relationship between area and species richness. We also allowed a quadratic relationship between species richness and rugosity following previous findings (Torres-Pulliza et al. 2020). We found a confident effect for all variables. Parameter estimates were -3.72 (95% CI: -5.18 ;-2.27), 2.36 (1.73; 3.01), -0.52 (-0.65; -0.39), 0.64 (0.55; 0.72), 1.11 (0.61; 1.60), and 0.57 (0.53; 0.62) for b_0, b_1, b_2, b_3, b_4, and sigma, respectively, and the Bayesian R-squared was 0.53 (0.47; 0.57).

In conclusion, we demonstrate that rugosity remains an important determinant for coral diversity when incorporating surface area in the analysis. Furthermore, we confirm the previously-found effect of fractal dimension on coral diversity.

Geometric plane

We used methods from Loke et al. (2022) to simulate surfaces with known fractal dimension and calculate metrics. Fractal dimension was the actual dimension simulated (Fig. 2A and B) and as estimated by L&C's intermediate box counting method (Fig. 2C and D). Rugosity was estimated using two different methods: DEM rugosity, in which we use the *surfaceArea* function (Jenness 2004); and height range rugosity, in which we use surface area method from Torres-Pulliza et al. (2020). Height range was calculated the same way in all comparisons: the distance between the lowest and highest point in the simulate surface. We apply the transformations to rugosity, height range, and fractal dimension as per Equation 1 in Torres-Pulliza et al. (2020), which act to make the manifold relationship into a plane. We fit a plane model using least squares relative to the fractal dimension axis (i.e., the linear regression: $F \sim R + H$) and present the r^2 value to give an indication of goodness of fit.

In conclusion, we demonstrate that regardless of the method to calculate surface area (for rugosity), the three metrics of structural complexity are geometrically constrained, for both actual and estimated fractal dimensions.

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