

# Clarifications on habitat complexity: A response to technical note by Madin et al.

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## Abstract

In a critique of our recent review on measuring habitat complexity in ecology, Madin et al. (2023) advocate the use of fractal dimension in ecology and defend their geometric constraint theory of habitat complexity. We explain the flaws in their arguments and highlight points where they misinterpreted our statements.

## KEY WORDS

biodiversity, fractal dimension, geometry, habitat structure, rugosity

Madin et al. (2023; henceforth M2023) have written a Technical Note on our recent review about measuring habitat complexity (Loke & Chisholm, 2022; henceforth L&C2022). They apparently agree with us on several points, but on others they misrepresent what we wrote or provide flawed critiques.

We start with the points of agreement. First, M2023 apparently do not disagree with our statement that widely used methods for measuring fractal dimension ( $D$ ) are biased (see L&C2022 and citations therein). Second, M2023 apparently agree that most biological objects are not true fractals: they write that ‘measures of fractal dimension of natural surfaces change across neighboring scales’. Third, we all agree that in *some* studies measured  $D$  correlates with some biological property. We simply view these correlations with more circumspection than M2023, because of the aforementioned measurement problems. Fourth, we agree with M2023 that ‘Future studies should investigate the simultaneous effects of area and rugosity’, but we emphasise that we did not just ‘allude’ to this, as they

indicate, but rather we recommended it very explicitly (L&C2022).

We now move on to two points on which M2023 misrepresented our statements. First, we did not claim that metrics such as fractal dimension ( $D$ ) and rugosity ( $R$ ) lack clear mathematical definitions: on the contrary, we gave the mathematical definitions. Second, their criticism of our box-counting method for estimating fractal dimension of 3D objects (figures 4–5 of L&C2022) is invalid. The idea that a 2D slice of a fractal embedded in 3D space with fractal dimension  $D$  will have fractal dimension  $D - 1$  goes back to Mandelbrot (1975). Indeed, we were able to recover the correct known values of  $D$  for our synthetic objects using this method (blue points in figure 5 of L&C2022).

We now consider points of genuine disagreement. The first is that M2023 believe that  $D$  is broadly useful in ecology, whereas we are sceptical. The fundamental problem is that, because real biological objects are mostly not close to fractal, estimates of  $D$  will vary depending on the scale of measurement. A single number

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cannot capture the richness of this information: the different estimates across scales actually carry meaning. The prescribed solution of M2023 is to ensure consistency of ‘method, resolution and scales’ to facilitate cross-habitat comparisons of  $D$ . The idea that ecologists will standardise methods across habitats is a dubious prospect, but even if it were achieved, the results would be hard to interpret. For example, estimates of  $D$  at a 10m scale and 0.1m resolution on a coral reef surface and a tropical forest canopy are not comparable in any biologically meaningful way because the constituent organisms live at very different scales. Consistency may be achievable within a study or perhaps within a habitat, but even then continuing to call the metric ‘fractal dimension’ is misleading and sets up the temptation for inappropriate cross-habitat comparisons.

A second point of disagreement concerns the geometric constraint theory of the authors of M2023 (Torres-Pulliza et al., 2020; henceforth TP2020). In L&C2022, we used their theory as an example of confused notions of habitat complexity in ecology. The theory is centred on the finding of a mathematical relationship between rugosity ( $R$ ), fractal dimension ( $D$ ) and height range ( $H$ ) and TP2020 claim that this is ‘a geometric basis for surface habitats that unifies ecosystems and spatial scales’. We agree that  $D$ ,  $H$  and  $R$  are related but see this as a mere mathematical curiosity. In L&C2022, we pointed out various inaccurate and misleading statements in TP2020 (see Appendix S2 in Supporting Information of L&C2022), which M2023 do not rebut. Instead, they make a further dubious statement that ‘the raw relationship is a manifold, and transformations... act to make it a plane’. But they provide no justification for the claim that a cloud of points in three-dimensional  $D$ - $H$ - $R$  space is a manifold, that is, a surface that is locally Euclidean everywhere. The ‘transformations’ to which M2023 refer work only if one uses variables that are not actually  $R$  and  $D$  but approximations of them (see Supporting Information of L&C2022). These technical issues aside, our fundamental problem with TP2020 remains that just because these three surface metrics are highly correlated with one another, there is no reason to think that they capture all aspects of surface variability. More generally, if we measure three properties of some system,  $X$ ,  $Y$  and  $Z$ , and find that  $X$  and  $Y$  explain most of the variation in  $Z$ , this does not imply that we have fully described the system. This is a logical fallacy.

## CONCLUSIONS

We stand by the original conclusions of L&C2022, in particular, that the usefulness of fractal dimension in

ecology is limited. Progress in understanding the complexity of ecological habitats will come from embracing the scale-dependent nature of self-similarity rather than trying to condense it into a single number.

## AUTHOR CONTRIBUTIONS

LL and RC contributed ideas. LL wrote the first draft of the manuscript and RC substantially edited the manuscript.

## PEER REVIEW

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No data were used in this manuscript.

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