A geometric basis for surface habitat complexity and biodiversity

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Abstract

Structurally complex habitats tend to contain more species and higher total abundances than simple habitats. This ecological paradigm is grounded in first principles: species richness scales with area, and surface area and niche density increase with three-dimensional complexity. Here we present a geometric basis for surface habitats that unifies ecosystems and spatial scales. The theory is framed by fundamental geometric constraints among three structure descriptors—surface height, rugosity and fractal dimension—and explains 98% of surface variation in a structurally complex test system: coral reefs. We then show how coral

biodiversity metrics vary over the theoretical structure descriptor plane, demonstrating the value of the new theory for predicting the consequences of natural and human modifications of surface structure.

One Sentence Summary

Surface habitats fall upon a plane of geometric possibilities that mediate biodiversity.

Main text

Most habitats on the planet are surface habitats—from the abyssal trenches to the tops of mountains, from coral reefs to the tundra. These habitats exhibit a broad range of structural complexities, from relatively simple, planar surfaces to highly complex three-dimensional structures. Currently, human and natural disturbances are changing the complexity of habitats faster than at any time in history (*1*, *2*). Therefore, understanding and predicting the effects of habitat complexity changes on biodiversity is of paramount importance (*3*). However, empirical relationships between commonly-used descriptors of structural complexity and biodiversity are variable, often weak or contrary to expectation (*4-8*). Moreover, there are no standards in how structural complexity is quantified, precluding general patterns in the relationship between structure and diversity from being identified. We therefore propose a new geometric basis for surface habitats that integrates and standardises existing surface descriptors (*6*, *8*).

The geometric basis arises from quantifying the distribution of surface area in habitat surfaces. In theory, species richness scales with surface area according to a power law (*9*). Island biogeography theory articulates that this relationship arises out of extinction and colonization, as larger areas provide larger targets for species to colonize and a greater variety of habitats allowing species to coexist (*10*). Our geometric theory builds on these ideas by exploring the notion that habitat surfaces with the same total surface (and hence rugosity) can exhibit a range of different forms (Fig. 1). Total surface area is the integration of component areas at the smallest scale (i.e., resolution), but it does not explain how these surfaces fold and fill the three-dimensional spaces they occupy. Rather, fractal dimension quantifies space-filling at different scales (*11*). Space-filling promotes species co-existence by dividing surface area into a greater variety of microhabitats and niches (e.g., high and low irradiance; small and large spaces; fast and slow flow) (*12*). This variety of niches allows species to coexist (e.g. different competitors, or predator and prey [*13*]) and therefore enhances biodiversity (*14*, *15*). There is a fundamental geometric constraint between surface rugosity and fractal dimension: for a given surface rugosity, an increase in fractal dimension will result in a reduction of the surface's mean height (Fig. 1). As the basis for a geometric theory, we derived the trade-off between surface

rugosity (R), fractal dimension (D) and surface height range (ΔH) as (see Supplementary Methods for mathematical derivation):

$$\frac{1}{2} log(R^2 - 1) + log\left(\frac{L}{L_0}\right)(3 - D) = log\left(\frac{\Delta H}{\sqrt{2}L_0}\right) \qquad \text{Eq. 1}$$

Where L is the surface extent and L_0 is the resolution (i.e., the smallest scale of observation). R and D are both dimensionless, with $R \geq 1$ and $2 \leq D \leq 3$; ΔH is dimensionless when standardised by resolution L_0, with $\frac{\Delta H}{\sqrt{2}L_0} \geq 0$. When rugosity is expressed as R^2-1 (with R^2-1 ≥ 0) and height range as $\frac{\Delta H}{\sqrt{2}L_0}$, Eq. 1 is a plane equation. Moreover, it is clear than any one of the surface descriptors can easily be expressed in terms of the other two, highlighting that any of the three variables is required, but not sufficient alone, to describe the structural complexity of a surface habitat.

To test the theory, we examined associations among surface rugosity, fractal dimension and height range across coral reef habitat patches. Coral reefs are ideal ecosystems for testing a theory of surface habitats, because they are structurally complex surface habitats constructed in large part by the reef-building scleractinian corals that, in turn, live upon the habitat (i.e., corals are autogenic ecosystem engineers [*16*]). Structural complexity affects biodiversity in general (*17*) and of coral reefs in particular (*18*). We estimated surface rugosity (as the *log* of R^2-1), fractal dimension (D) and height range (as the *log* of $\frac{\Delta H}{\sqrt{2}L_0}$) for 591 reef patches of 4 m^2 at 21 reef sites encircling Lizard Island on the Great Barrier Reef, Australia (see Supplementary Methods). Analyses of the structure of these patches reveal that while rugosity, fractal dimension and surface height range are not independent, they have substantial independent variation (r^2 for pairwise relationships between variables ranging between 3% and 30%, Fig. 2A-C). However, when framed together, the three variables formed the surface descriptor plane that captured 98% of the variation in D (Fig. 2D). The remaining 2% of the variation can be explained by the model assuming perfectly fractal surfaces (Eq. S2), while the digital representation of natural reef patches often deviated from statistical self-similarity (Fig. S3B).

The observation that the structure of nearly all measured reef patches fell upon a plane delineated by three simple surface descriptors highlights the fundamental geometric constraints of surface habitats. All three descriptors are essential for capturing structural complexity because they explain different elements of surface geometry: height range captures large scale variation, rugosity captures small scale variation, and fractal dimension captures topographic entropy when transitioning from large to small scales (Fig. S1A).

Different reef locations, with different ecological and environmental histories, occupied different regions on the surface descriptor plane (Fig. 3). For example, one site that was stripped of living coral during back-to-back tropical cyclones (*19*) largely occupied the region of the plane where rugosity, fractal dimension and surface height range are all low (Fig. 3A); that is, the patches at this site were closest to a theoretical flat surface. Another site also impacted by the cyclones but left littered with dead coral branches, had similar levels of rugosity and height range, but fractal dimension was relatively high (Fig. 3B). In contrast, a site containing several large colonies of living branching coral had patches with the highest fractal dimension and rugosity, yet the height range of these patches was low (Fig. 3C) reflecting the approximately uniform height of living branching corals in shallow waters where water depth and tidal range constrains colony growth. Meanwhile, a site containing large hemispherical *Porites* corals had patches with large height ranges and high rugosity but lower fractal dimension (Fig. 3D).

Finally, to connect the geometric variables to biodiversity, we examined how species richness and abundance varied across the surface descriptor plane. Strong ecological feedbacks occur between coral reef habitat structure and coral biodiversity. Coral reef structures are largely created by corals, but their structure is mechanistically affected by environmental conditions such as tidal range, currents, storm impacts and wave exposure. For instance, coral larvae are poor swimmers and are more likely to settle in reef patches with small-scale complexity, because they get entrapped by micro-eddies (*20*). At the same time, more intricate coral structures (with higher fractal dimension, *D*) are more likely to be damaged or uprooted during

storms that flatten reef patches (*21*, *22*). Species-area theory predicts that species richness and abundances should be highest in patches with the greatest surface area (i.e., highest rugosity) (*9*). We predicted that higher fractal dimension would also enhance species richness and abundance, because of niche diversity (i.e., increases in surface area at different scales), and that this effect would be additional to overall surface area. The surface descriptor plane allows estimating the combined effects of not just area, but also niche differentiation associated with fractal dimension and depth range (*8*, *12*).

We examined geometric-biodiversity coupling for a large plot, containing 261 of the 4 m^2 reef patches, in which 9,264 coral colonies of 171 species were recorded (see Supplementary Methods). Contrary to expectation, we found that coral species richness and abundance peaked in reef patches with intermediate surface rugosities (Fig. 4A, B and table S2). Richness and abundance also tended to be associated with patches with higher fractal dimension and smaller height range. (The consistency of patterns for both species richness and abundance was not surprising, because the two biodiversity metrics are strongly associated in our data.) The explanatory power of reef geometry on both biodiversity metrics was more than 40% (Table S1)—10 to 15% higher than any surface descriptor alone. The geometric plane explaining this much variation in biodiversity is striking, given the number of other, non-geometric processes that govern coral biodiversity, including environmental filtering, dispersal and species interactions (*23*). Because corals are autogenic ecosystem engineers, reciprocal causality is likely to strengthen and shape geometric-biodiversity coupling. For instance, high rugosity is often generated by large hemispherical corals (e.g., Fig. 3D) that reduce the number of individuals, and hence species, per area. Subsequently, geometric-biodiversity coupling may be weaker for other surface-associated taxa, such as fishes and invertebrates, and should be tested. Nonetheless, our findings have implications for resilience following disturbances and for restoration efforts that aim to maximise biodiversity, specifically identifying the reef structural characteristics that should be maintained (or built) to maximize biodiversity.

A general, scale-independent geometric basis for surface habitats provides a much-needed way to quantify habitat complexity across ecosystems and spatial scales. The importance of surface complexity as a determinant of habitat condition, biodiversity, and ecosystem function is well recognised (*24*), yet different metrics are typically used for different ecosystems, or different taxa within the same ecosystem (*8*). The general approach we propose is applicable across surface habitats in both marine and terrestrial environments, allowing formal comparisons examining whether geometric-biodiversity couplings differ among systems in terms of both pattern and strength. The surface descriptor plane uncovered here clearly defines the fundamental geometric constraints acting to shape surface habitats, and consequently how changes in surface geometry affect biodiversity. As powerful ecosystem engineers, humans are modifying the planet, through the structures we destroy, as well as those we construct. Typically, human-modified structures differ significantly in their geometry from nature-built structures. Determining biodiversity, conservation, and recovery rates through habitat complexity measures is paramount in the Anthropocene. The approach we propose here allows for predictions of the biodiversity consequences of these structural changes across land and seascapes.

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Author contributions

The study was conceptualized by JSM, DTP, MD and OP. All authors curated the data. JSM and OP developed the theory and JSM ran the analyses. JSM, DTP and OP developed the software

pipeline for data and produced the visualizations. The investigation was led by JSM, DTP, MD and OP. JSM and MD lead and fund the broader project, with additional field robotics resources from OP and SW. JSM wrote the first draft of the paper and all authors reviewed at least one draft.

Competing interests

Authors declare no competing interests.

Data and materials availability

Source data and code for data preparation, statistical analyses and figures are available at https://github.com/jmadin/surface_geometry (currently private until published; but access can be granted if requested for reviewing purposes).

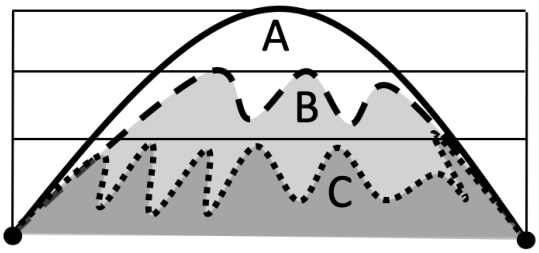


Fig. 1. Increasing fractal dimension (i.e., space filling) while keeping surface rugosity constant results in a decline in a surface's mean height range. A two-dimensional representation of three hypothetical surface habitats with the same surface rugosities (**A**, **B** and **C**). That is, the lengths of the lines **A**, **B** and **C** are the same and occur over the same planar extent (black points). However, line **A** fills less of its two-dimensional space (black rectangle) than does line **C**, and therefore has a lower fractal dimension.

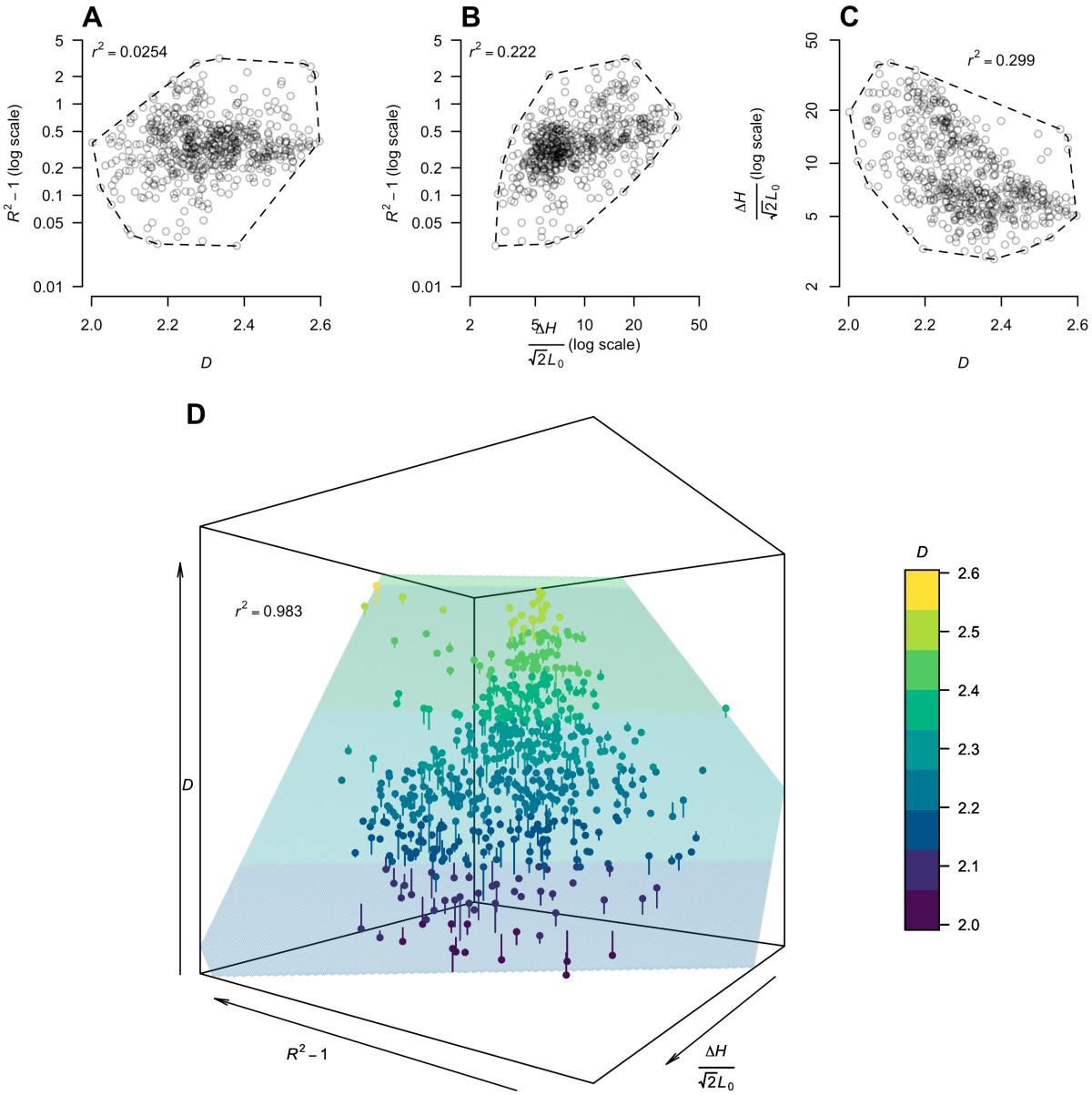


Fig. 2. Comparison of the geometric theory with field data. Relationships between the descriptors that frame the geometric theory for *n*=595 reef patches: (**A**) surface rugosity (as R^2-1); (**B**) fractal dimension *D*; and (**C**) surface height range (as $\frac{\Delta H}{\sqrt{2}L_0}$). Coefficients of determination (r^2) show the variance explained in the y-axis variable by the x-axis variable. (**D**) When combined the three descriptors explain more than 98% of the variation in fractal dimension *D*. Field data are points, and the surface descriptor plane is coloured by fractal dimension.

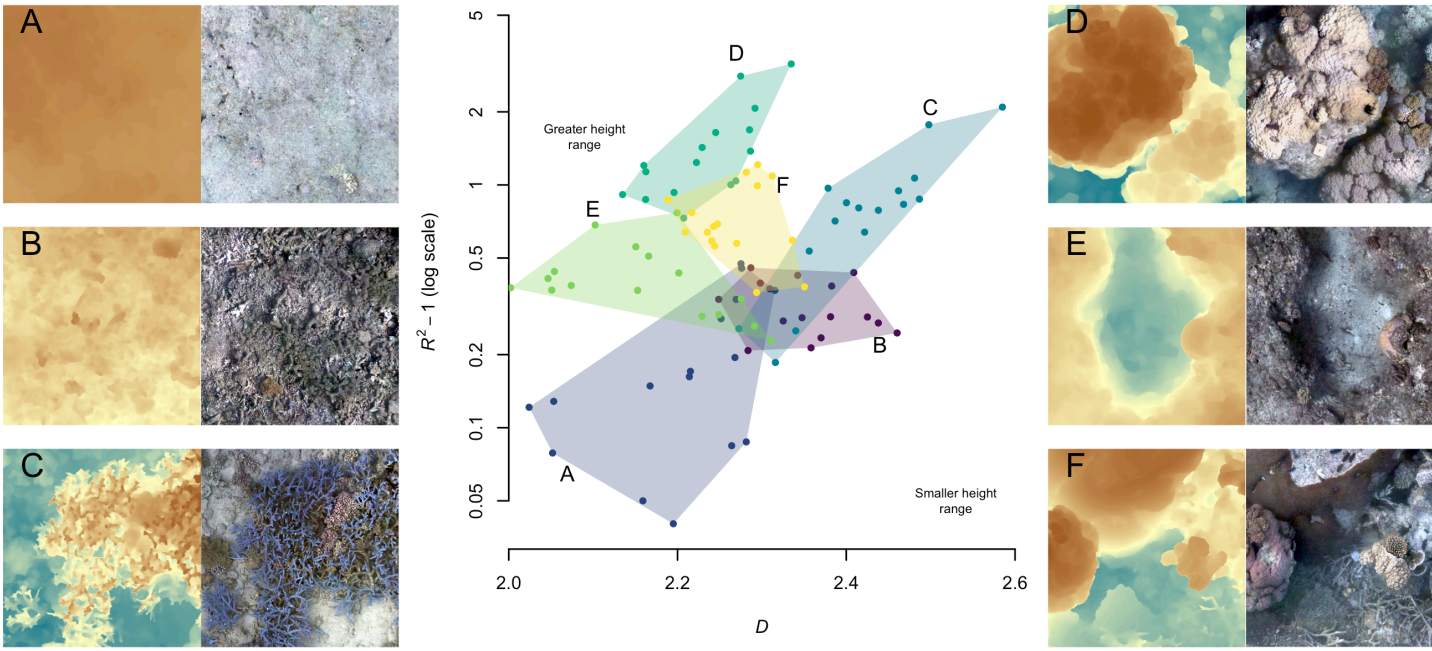
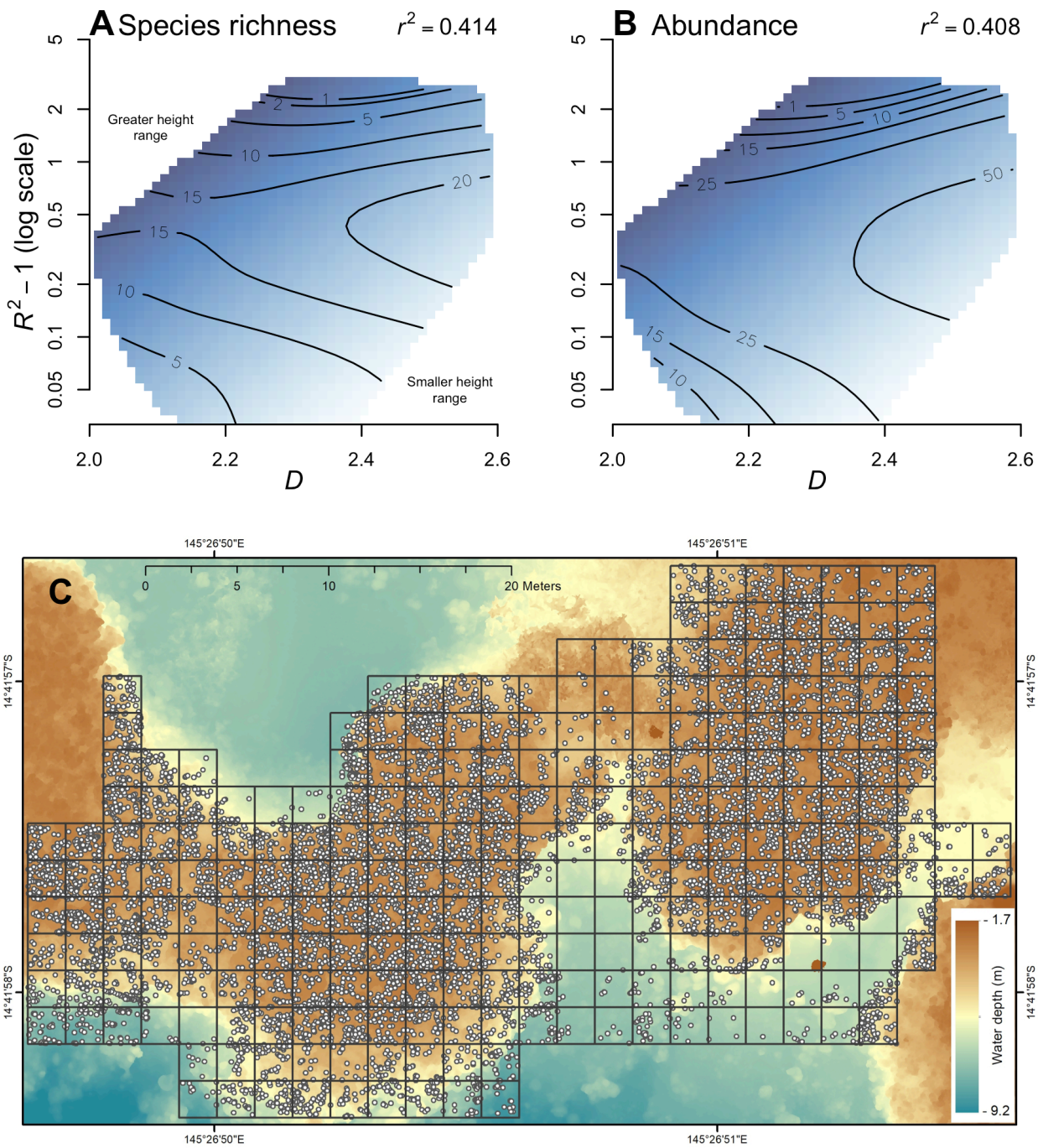


Fig. 3. The geometric diversity of coral reef habitats. Reef patches (*n*=16) from a subset of six sites are superimposed onto a two-dimensional representation of the surface descriptor plane (colour used here to delineate sites). (**A**) North Reef; (**B**) Osprey; (**C**) Lagoon-2; (**D**) Resort; (**E**) South Island; and (**F**) Horseshoe. The corresponding DEMs and orthographic mosaics show selected patches at each site to help visualise geometric differences. Patch height range is greater in the top left corner and decreases towards the bottom right corner.



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296 **Fig. 4.** Geometric-biodiversity coupling of coral reef habitats. Predicted coral species (**A**)
297 richness and (**B**) abundance within reef patches as contours and plotted upon the surface
298 descriptor plane, where the colour-scale shows the gradient of height range according to Eq. 1.
299 Prediction contours are from general additive models (Table S2). (**C**) A digital elevation model of

the large plot with contiguous reef patch delineations (black squares) and the 9,264 coral colony annotations (white points) capturing 171 species.