Structural complexity shapes the global distribution of ecosystems and people

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Abstract: The three-dimensional structure of land- and seascapes, links biotic and abiotic processes to shape how organisms use their environments. Much effort has been dedicated to understanding this relationship between structural complexity and biodiversity. However, tailored, system-specific approaches to quantifying structural complexity preclude cross-system comparisons. Expanding a geometric framework developed for quantifying the structural complexity of local-scale surface environments, we generate high-resolution, global maps of the key complexity measures of height range, rugosity, and fractal dimension. We illustrate how patterns in these complexity attributes across the globe reflect the distribution of ecosystems, land cover types, and the presence of people. Using these tools to understand how structural complexity determines the arrangement of natural and socio-ecosystems, we can better predict their responses to ongoing global change.

Main Text:

The physical structure of natural environments sets the stage on which ecological, geological, and climatic processes shape global biodiversity and socio-ecosystems (*1*, *2*). Climatic regimes are a major determinant of global species richness trends (*3*). However, abiotic topography modulates the spatio-temporal configuration of climate systems, thereby mediating local climate exposure, resource availability, and resource access (*4–6*). For instance, the structural complexity of natural landscapes influences the taxonomic and functional diversity of the forest ecosystems they support (*7*). Indeed, some conservation approaches, such as *Conserving Nature's Stage*, a global initiative aimed at incorporating landscape features in conservation planning (*8*), argue that protecting the enduring physical structure of natural habitats is a more effective use of conservation resources than safeguarding more transitory biotic assemblages (*9–13*). The structure of natural environments also contributes to human wellbeing, provides key cultural benefits, and supports agricultural diversification (*2*, *14*). Despite this ecological and socioeconomic value, the term complexity is poorly defined, prompting a lack of consensus for how it is quantified and measured (*15*, *16*). As a result, insight into the role of structural complexity in determining the configuration of natural systems is typically tailored to specific organisms or ecosystems such as terrestrial mammals, inshore reef fish, rocky reefs and mussel beds (*17–20*). Identifying scalable metrics applicable across systems is thus essential for quantifying the general effect of structural complexity in shaping ecological systems across the globe.

Interwoven with long established theory linking changes in area to patterns in species diversity (e.g. (*21–23*)), increases in structural complexity are hypothesised to promote biodiversity (*24*). More structurally complex environments are thought to accommodate a greater diversity of available habitat types and, therefore, support higher species richness (*25*, *26*). Yet, the relationship between complexity and habitat diversity is scale dependent with the greater habitat variety brought about by enhanced complexity likely reducing the size of available habitats (the area-heterogeneity trade-off) (*27*). Thus, increasing structural complexity can also reduce population sizes and increase the likelihood of local extirpation (*28–31*). The importance of evaluating the nuanced effects of structural complexity on the assembly of biological systems has given rise to concepts such as *geodiversity* (*11*). An abiotic analogue of the term biodiversity, geodiversity combines measures of the richness of structural features (e.g. sediment types and landforms) and processes (e.g. riverbed erosion) comprising different environments (*32*). By synthesising the chemical, geological, and physical features comprising natural environments, geodiversity offers a proxy measure of habitat diversity that has been associated with the maintenance of ecosystem function and functional diversity (*33*, *34*). However, for identifying mechanistic drivers, there is a tension between synthesising the characteristics of underlying abiotic variables and evaluating their individual attributes. To establish the association between abiotic structure and the functioning of biotic systems, we must disentangle how the structural complexity of global landscapes influences the natural assemblages they can support (*33*, *35*).

Here, we present a quantitative global-scale assessment of structural complexity patterns using a geometric framework originally developed to quantify the structural complexity of coral

reef ecosystems (*36*) and forest canopies (*7*, *37*). Complementing efforts to classify global ecosystem types (*5*) and map the distribution of land use practices (*38*) and human occupancy (*39*), we evaluate how ecosystem and land cover classifications correspond with global patterns in the structural complexity attributes of *height range* (*ΔH*), *rugosity,* (*R*) and *fractal dimension* (*D*). Describing the shape of surfaces, *ΔH* captures the variation between maximum and minimum elevation, *R* represents a measure of true surface area, and *D* details the shape-filling capacity of a surface (*i.e.*, increases in *D* correspond with an increase in contortion) (*40*, *41*). Specifically, we set out to test two key hypotheses. Firstly, (H1) we expect that similar ecosystem types will exhibit similar structural attributes, with structural characteristics refining local climate exposures and thus driving the establishment of similar biotic communities (*42*, *43*). Secondly, (H2) we hypothesise that human activities will be concentrated in less complex environments, since anthropogenic pressures are often attributed to simplifying natural landscapes (*44–46*). Overall, we demonstrate the value of using geometric descriptors of structural complexity to detect effects of abiotic structure influencing the global configuration of ecosystems, land use, and socio-ecosystems.

Results

Quantifying global complexity patterns

Using a global terrain model sourced from the General Bathymetric Chart of the Oceans (GEBCO) (*47*) we derived estimates of height range (*ΔH*), rugosity (*R*), and fractal dimension (*D*) for the Earth's surface at a resolution of 1.87 km, reflecting ~185 million grid cells. Across the globe, we report that estimates of *ΔH* and *R* align with patterns of topographic relief (Fig. 1A & B). Higher *ΔH* and *R* estimates have been shown to reflect rougher benthic surfaces in both rocky intertidal and coral reef environments (*36*, *48*). At the global scale, this relationship is maintained, with higher *ΔH* and *R* estimates corresponding with regions characterised by frequent tectonic activity such as the Himalayan, Andean, and Mid- Atlantic mountain ranges, and the Pacific Ring of Fire (a high density of plate boundaries around the coastal Pacific region associated with increased volcanic and tectonic activity (*49*)). However, unlike *ΔH*, *R* also provides a representation of the space made available by increasing roughness and offers insight into finer-scale variation across surface gradients (*1*, *36*). Indeed, focusing on selected locations within the Amazon, the Mariana Trench, and the Sahara Desert (Fig. 1) illustrates how it is possible to distinguish the topographically complex canyon at the entrance to the Mariana Trench and the topographic channels associated with the Amazon River and Saharan sand dunes using just their associated rugosity values.

Areas of high fractal dimension (*D*) occur in the arctic tundras of North America and Siberia, the Amazonian and Patagonian regions of South America, and in central Africa (Fig 1C). A notable difference between the fractal properties of marine and terrestrial environments is also evident, with the global seabed typically having lower fractal dimension than the terrestrial landscape (Fig. 1C; see Appendix S2 for further details). Fractal dimension relates to the intricacy of a surface, relative to its elevation, with higher *D* suggesting increased convolution (*36*).

Accordingly, differences between the fractal dimension of terrestrial and marine landscapes are consistent with the prominence of sedimentation throughout deep sea habitats (*50*), which, in areas of low tectonic activity and high sediment influx, likely buries bathymetric lows and the more intricate features of marine landscapes (*51*). Geometric constraints ensure that the intricacy of a surface comes at the expense of its topographic complexity; such that increases in D correspond with declines in ΔH and R (when either R or ΔH are held constant) (*36*) (Appendix S1). Characterised by regions of geologically younger and less rugged terrain, rainforest river basins such as the Amazon are therefore capable of possessing high fractal dimension (Fig. 1). Alternatively, when viewed through the lens of its fractal dimension, the main canyon of the Mariana Trench almost disappears, as its surface complexity is small relative to its associated large changes in elevation (Fig. 1). Intriguingly, with higher fractal dimension often associated with an increase in habitat diversity and resource partitioning (*7*, *25*, *52*, *53*), perhaps it is not coincidental that highly diverse rainforest ecosystems are affiliated with environments characterised by higher fractal dimension, allowing for greater habitat variety, and lower elevational changes, minimising the development of topographic barriers.

Structural complexity across ecosystems and land cover types

The geometric attributes of differing environments position global ecosystem types along a spectrum of structural complexity (Fig. 2). To delineate the structural signatures associated with differing global ecosystems we quantified R and D across the distributions of different IUCN ecosystem functional groups (EFGs; *sensu* (*5*)). Despite rugosity and fractal dimension estimates varying considerably across global EFGs, we highlight an association between particular complexity signatures and particular ecosystem types (*H1*) (Figs. 2A, S4 & S5). Marine ecosystems stand out as being characterised by a higher prevalence of less fractal and less rugose environments (Fig. 2A). Meanwhile, whilst transitional coastal ecosystems possess the lower rugosities of their fully marine counterparts (*54*), they exhibit higher fractal dimension (Fig 2A). Across the terrestrial realm, Polar and Alpine landscapes and forest and woodland ecosystems are typically more rugose environments, whilst desert and grassland ecosystems have lower height variation. Wetland ecosystems also comprise lower height variation but possess very high fractal dimension. Our spectrum of ecosystem complexities also illustrates how, irrespective of their associated realm, anthropogenically-modified habitats are associated with lower rugosities compared to corresponding natural environments (Fig. 2A).

Cross-system similarities in ecosystem complexities offer insights into the causal mechanisms and processes involved in generating and maintaining different ecosystem types. Coastal and freshwater ecosystems typically possess comparatively high fractal dimension (Fig. 2B). One exception to this pattern are permanent salt lakes (e.g. the Atacama Desert), which display low structural complexity compared to freshwater ecosystems, and instead possess similar geometric attributes to sclerophyll desert ecosystems (Fig 2B). Both permanent salt lakes and sclerophyll deserts are found in semi-arid plains (*55*, *56*), the key difference between them being the proximity of salt lake catchments to sources of periodic water inflow (*57*). Cross-system

similarities in ecosystem complexities are also evident between permanent marshlands and river deltas (Fig. 2B). Aside from the association of river deltas with saline conditions, these ecosystem types are largely indistinguishable and possess the shared characteristics of a high deposition of silt and clay-based sediments, constant or periodic inundation, and high turbidity (*58*). Indeed, permanent marshlands and river deltas are often components of the same environments (e.g. the Okavango Delta). We also demonstrate similar attributes of rugosity and fractal dimension across oceanic temperate rainforests and polar tundra ecosystems (Fig 2B). Presently, these ecosystems support very different biological communities due to their differing climate exposures. However, during the mid-Cretaceous (the Turonian–Santonian age, circa 92 to 83 million years ago), when a far warmer global climate maintained polar temperatures > 14ºC (*59*), the structural complexity associated with contemporary polar tundra ecosystems supported diverse oceanic temperate rainforests (*60*). Together these highlighted examples evidence the mediatory role structural complexity plays in delineating global ecosystems through time and space.

We illustrate how patterns in rugosity and height range correlate with patterns in the recently established measure of geodiversity (Fig. 3), which represents the combined richness of geological, geomorphological and hydrological features comprising different environments. However, fractal dimension and geodiversity exhibit no apparent relationship (Fig. 3), suggesting that they are orthogonal descriptors of environments. To further distinguish the mechanisms through which the structure of natural environments modulates the biotic assemblages they support, we compared the different but complementary perspectives of structural complexity and geodiversity across the terrestrial landscape. Aligning global maps of terrestrial geodiversity with our global maps of structural complexity, we observed how environments comprising a greater richness of different geological and hydrological features typically have a more rugged topography (Fig 3A & B). Alternatively, geodiversity and fractal dimension offer different perspectives on the structural regimes of natural environments (Fig 3C). Although increases in both geodiversity and fractal dimension have been reported to increase biodiversity (*25*, *61–63*), often their effects on diversity are complex and non-linear (*64*). Consequently, it would be worthwhile exploring how the interaction between a system's abiotic richness and its fractal dimension mediates resource availability and how organisms exploit them.

Finally, our evaluation of global structural complexity patterns continually emphasises evidence in support of our hypothesis that (*H2*) human societies are typically associated with more lowland environments with reduced elevational variation (Figs. 4). We quantified the rugosity and fractal dimension patterns associated with the global distributions of different land cover classifications obtained from the Copernicus Climate Change Service (C3S) land cover survey (*38*). Although clustering rugosity and fractal dimension estimates by associated land cover categories represents a coarse filter, it is apparent how land cover corresponding with increased human modification (*i.e.*, urban and cropland environments) are associated with lower estimates in both *R* and *D*, compared to more 'natural' land cover (Fig. 4A). Our findings also suggest that human occupancy, but not density, is strongly associated with the structural complexity of natural environments. By overlaying gridded human population densities sourced from NASA (*39*) onto

our maps of global complexity patterns we evaluated how human population densities worldwide correspond with patterns in ΔH, R, and D. Specifically, the likelihood of observing human population counts > 0 decreases with increasing ΔH, R, and D (Fig 4B). However, we only observe a directional association between fractal dimension and human population density, with the density of human populations decreasing with increasing fractal dimension (Fig 4B[iii]).

Discussion

We demonstrate here that using geometric measures to quantify cross-system patterns in global structural complexity can inform our understanding of the processes through which structural complexity delineates abiotic and biotic regimes. Understanding the drivers of biodiversity, and how natural communities respond to ongoing global change, requires an appreciation for the intrinsic association between biodiversity and abiotic structural complexity (*65*). Colonisation, extinction, and speciation are fundamental drivers of global patterns in species richness (*66*, *67*), and are acutely linked to the structural shape of global landscapes over time (*6*). Moreover, landscape morphology and structure mediate whether, how, and when, organisms can access available resources (*6*). Indeed, by shaping dispersal pathways and niche partitioning trends, historic shifts in landscape structure are thought to have influenced the contemporary arrangement of global biodiversity more so than prevailing climatic regimes (*65*, *68–70*).

Emphasising the value of considering both climatic regimes and structural complexity, our findings offer numerous quantitative insights supporting the notion that the interaction between structural complexity and climate shapes biodiversity (*1*). Increases in the fractal dimension of natural landscapes correspond to increasing habitat diversity, thereby supporting species coexistence through enhanced resource partitioning (*52*, *71*, *72*). Increases in fractal dimension could, therefore, be expected to increase speciation by fostering elevated rates of diversification. Indeed, we have shown how the Amazonian Basin, considered amongst the planet's most biodiverse ecosystems (*73*, *74*), is an environment dominated by the fractal dimension of its complexity signature. Nevertheless, the complexity signature of the Sahara Desert, a comparatively more inhospitable environment, is similarly dominated by its fractal dimension. Yet rather than weaken the argument that structural complexity plays a role in configuring biodiversity, this scenario elevates the importance of considering the interaction between local climate regimes and abiotic structural complexity (*4*). Moreover, alongside illustrating similarities across the structural regimes associated with ecosystems supporting similar biotic communities, we highlight how the association between biodiversity and structural complexity is not static through time. The biotic components of natural ecosystems are typically more transient through time than their geological counterparts (*2*). Despite being associated with similar structural regimes, oceanic temperate rainforests and the polar tundra represent very different ecosystems. Yet, the historical biotic communities associated with polar tundra ecosystems under a warmer climate were similar to the contemporary biotic communities of oceanic temperate rainforests. Likewise, although presently comparatively species poor, under differing past climate regimes, the Sahara Desert

supported vibrant grassland communities (*75*, *76*). Overall, these examples highlight the key underlying role of abiotic structural complexity in shaping global biodiversity over time.

The relationship between species diversity and area has long been central to our understanding of biodiversity theory (*77*), yet environmental context underpins how the relationship actually manifests (*78*, *79*). Applying our quantification of structural complexity to the assessment of avian species-area relationships observed across global island systems highlights the nuanced insights structural measures can offer into the mechanisms mediating the configuration of global species and functional diversity patterns (Box 1). Area is important for providing the space necessary for species to coexist (*24*, *67*, *80*). Whether changes in available area constitute increases or decreases in rugosity, height range, or fractal dimension will determine whether these changes actually benefit or limit species diversity. Using the geometric measures of structural complexity it is possible to quantify and detect the mechanisms (e.g. changes in habitat diversity, niche size and/or species isolation) through which changes in area influence the configuration of biotic communities. Accordingly, using these measures we can reconcile understanding of the nuanced effects of area on species diversity patterns across ecosystems and taxa.

Human presence is negatively correlated with increasing landscape complexity. Beyond its effects on biodiversity, the complexity of natural landscapes is known to have profound impacts on multiple aspects of human society and its development (e.g. tourism, agriculture, mobility, and wellbeing) (*2*, *14*). For instance, with mountain ranges and high alpine regions typically associated with a reduction in the space and arable land needed for agriculture and food production, the development of human settlements has often gravitated towards flatter, more lowland environments (*81*). Accordingly, environments exposed to the greatest levels of anthropogenic pressure and exploitation are those that typically possess reduced structural complexity. However, this association is unlikely to be solely due to the selective bias of humans having historically selected less complex environments for development (*14*, *82*). Instead, increased anthropogenic pressure being associated with reduced structural complexity is also indicative of human activities simplifying natural landscapes through the active removal of geometric and compositional structure (*44–46*, *83*, *84*). While we are unable to distinguish between cause and effect with our static layers, the two processes are not mutually exclusive, and both instances are likely true across the global landscape.

Conclusions

Our global-scale assessment suggests that geometric structural complexity plays a substantial role in mediating the configuration of natural and anthropogenic communities. Having long appreciated the association between diversity and area (*7*, *77*), a recent focus of ecological research has been to quantify the mechanistic drivers linking biodiversity and the physical structure of natural environments (*10*, *33*, *66*). Nature also does not exist in a vacuum, with the majority of global ecosystems facing some form of anthropogenic pressure (*85–87*). How we interact with and use our local environment is mediated by patterns in their structural complexities. So, too, is how these

natural environments respond to our activities. The use of geometric theory to quantify and isolate patterns in the structural complexity of global environments can provide continuous quantitative variables for delineating ecotones based on their shared structural characteristics. Moreover, we have demonstrated the value of including measures of geometric structural complexity within assessments into the drivers of spatial biodiversity patterns. Overall, our approach offers insight into the future configuration of global biodiversity by serving as a basis for evaluating how structural complexity helps to shape biotic communities, and how this association will be influenced by anthropogenic pressures and ongoing global change.

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Data and materials availability: All the R scripts used in developing these maps and implementing all analyses discussed throughout this manuscript have been uploaded to a public repository on GitHub (https://github.com/CantJ/Global-Geometric-Complexity). This code repository and the global maps of structural complexity presented in this manuscript have also been archived open access on Zenodo (https://doi.org/10.5281/zenodo.18153610).

Supplementary Materials:

Materials and Methods [2028 words]

Supplementary Text

Figs. S1 to S6

Tables S1 to S3

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Figures & Tables

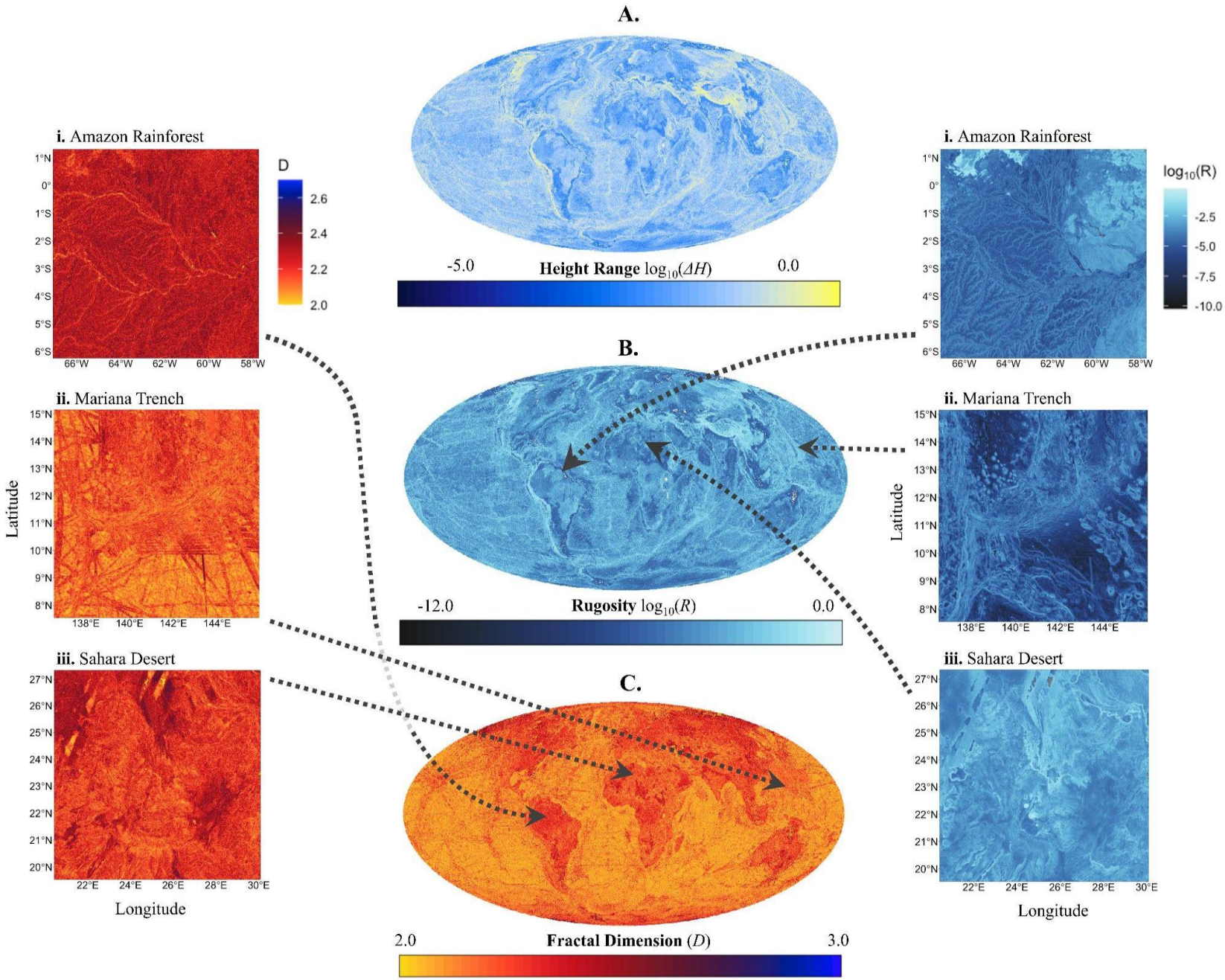
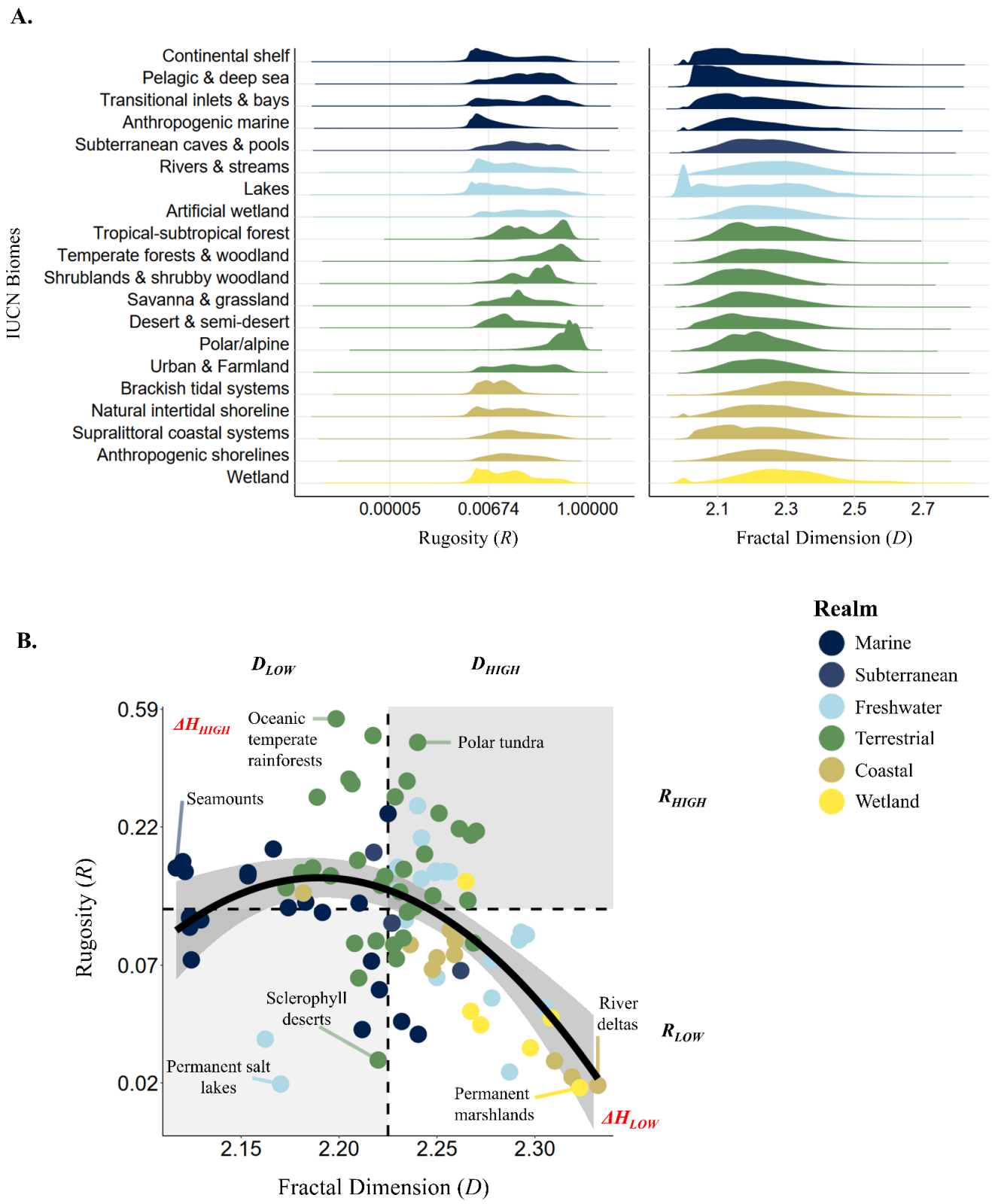


Fig. 1. Global patterns in geometric structural complexity. High resolution maps (1.87 × 1.87 km) depicting variation in the structural complexity measures of (A) Height Range (ΔH), (B) Rugosity (R), and (C) Fractal Dimension (D), across all terrestrial and marine environments. Global maps are displayed in a global Mollweide equal area projection and comprise ~146 million estimates of ΔH, R, and D, with white pixels reflecting missing or omitted entries. Comparing measures of fractal dimension and rugosity can offer differing insights into the complexity characteristics of natural environments, with the close-up panels highlighting the fractal dimension (*left*) and rugosity (*right*) of the (i) Amazonian Basin, (ii) Mariana Trench, and (iii) Sahara Desert. Each panel shows a representative 935 × 935 km section of the selected locations and is displayed in a WGS84 projection.


A.
IUCN Biomes
Continental shelf
Pelagic & deep sea
Transitional inlets & bays
Anthropogenic marine
Subterranean caves & pools
Rivers & streams
Lakes
Artificial wetland
Tropical-subtropical forest
Temperate forests & woodland
Shrublands & shrubby woodland
Savanna & grassland
Desert & semi-desert
Polar/alpine
Urban & Farmland
Brackish tidal systems
Natural intertidal shoreline
Supralittoral coastal systems
Anthropogenic shorelines
Wetland
0.00005
0.00674
1.00000
Rugosity (R)
2.1
2.3
2.5
2.7
Fractal Dimension (D)
B.
D_LOW
D_HIGH
ΔH_HIGH
Oceanic temperate rainforests
Polar tundra
Seamounts
R_HIGH
Sclerophyll deserts
River deltas
R_LOW
Permanent salt lakes
Permanent marshlands
ΔH_LOW
0.59
0.22
0.07
0.02
Rugosity (R)
2.15
2.20
2.25
2.30
Fractal Dimension (D)
Realm
Marine
Subterranean
Freshwater
Terrestrial
Coastal
Wetland

660

Fig. 2. The relative structural characteristics of differing environments delineates the differing complexity regimes underlying ecosystems worldwide. (A) Ridgeline plots illustrating the distribution of rugosity (*R*) and fractal dimension (*D*) values associated with ecosystem types across different IUCN biome classifications (see Figs. S4 & S5 for a within biome breakdown of rugosities and fractal dimension across ecosystem types). Global distributions of different biomes and ecosystem types obtained from the IUCN function-based ecosystem typology (*5*). Fill colour used to delineate the realm types associated with each biome class. **(B)** Mean fractal dimension and rugosity estimates derived for differing ecosystem types. Point colouring used to cluster ecosystem types based on their associated realms, with panel colouring used to highlight regions of comparatively high and low rugosity and/or fractal dimension. Red inset text highlights the corresponding pattern in height range (ΔH) across this parameter space, with representative ecosystem types shown for reference. Fit line shows modelled relationship between mean ecosystem rugosity and fractal dimension estimates (r^2: 0.26 [95% CI. 0.13, 0.38]) with error displayed as 95% CI.

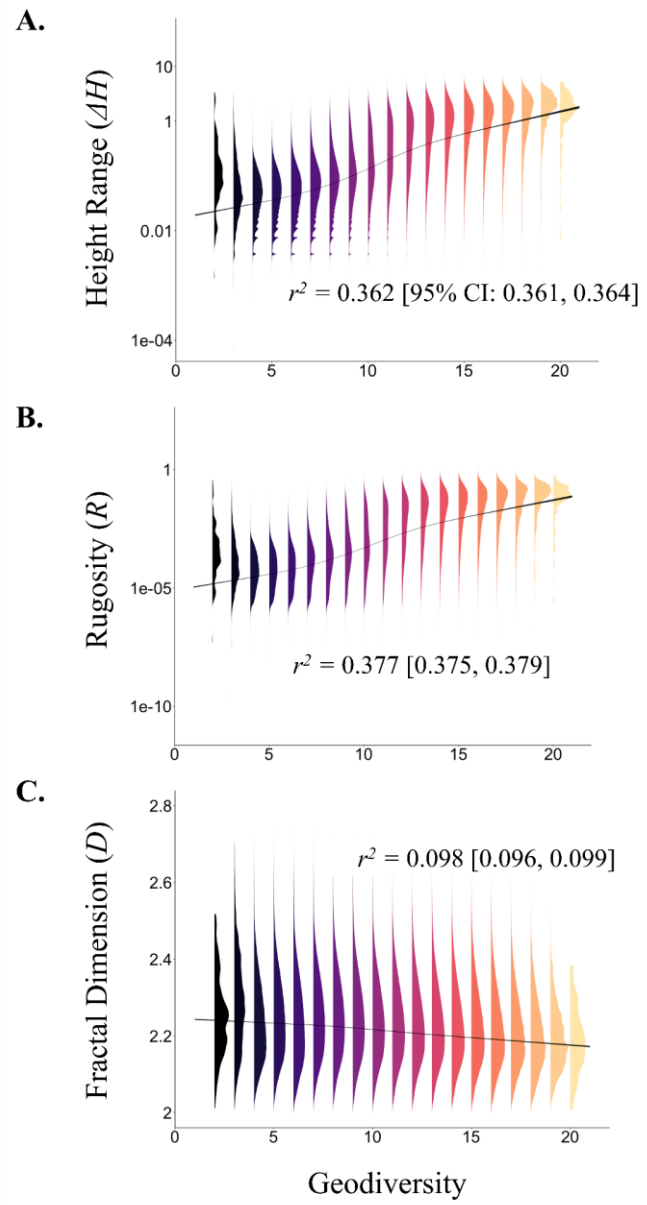


Fig. 3. Comparing the geometry and structural richness of natural environments allows for disentangling the mechanisms through which structural complexity mediates the configuration of global biodiversity. The alignment of the structural complexity measures of **(A)** Height Range (*ΔH*), **(B)** Rugosity (*R*), and **(C)** Fractal Dimension (*D*) with estimates of geodiversity (geology, geomorphology and hydrology combined). Geodiversity estimates were extracted from a high resolution (1.87 × 1.87 km) global map depicting patterns in the richness of structural features comprising an environment (*88*). The solid line across each plot represents the predicted relationship between each geodiversity and each complexity measure, with the thickness of the line corresponding with the 95% confidence intervals.

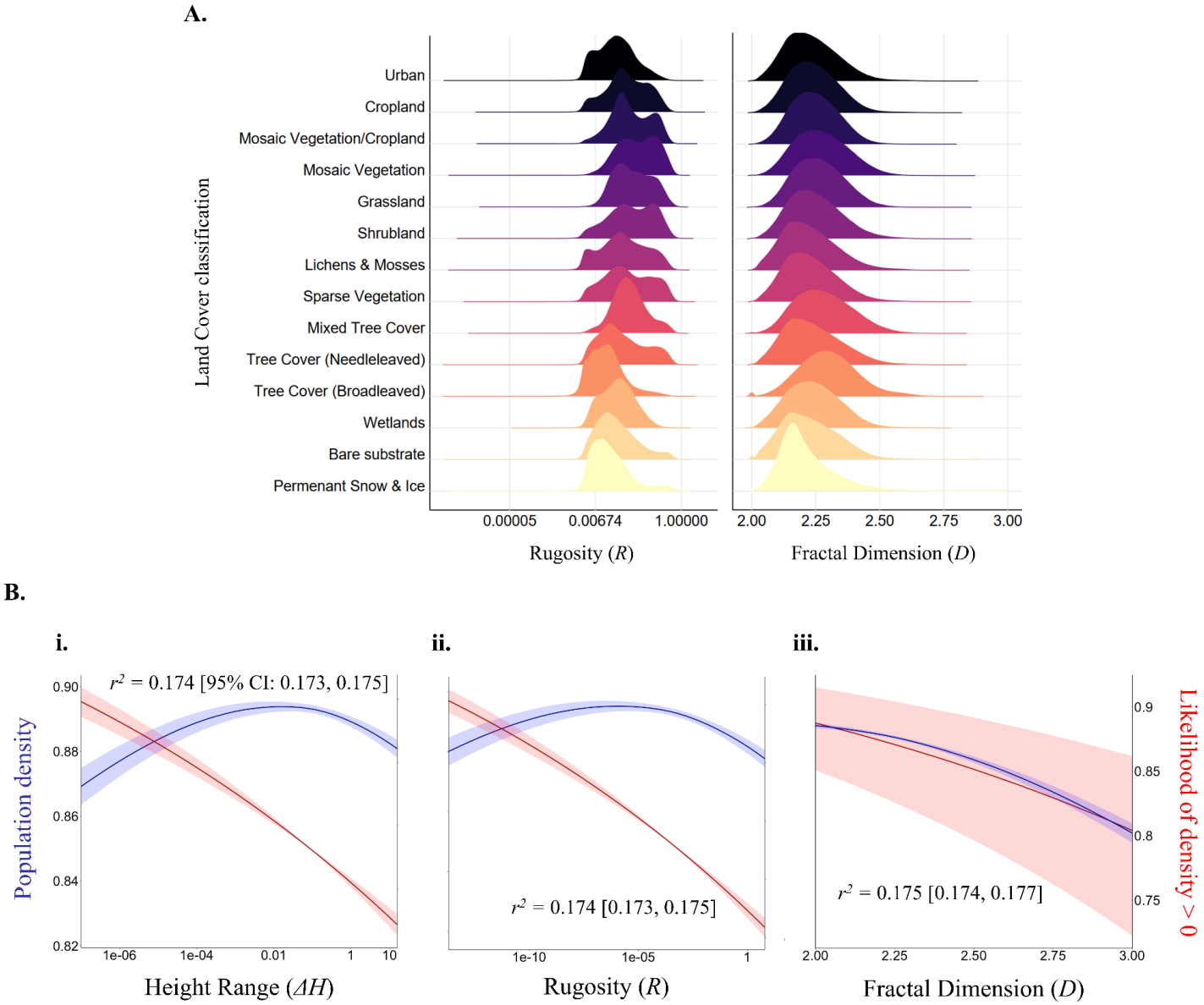


Fig. 4. Global patterns in structural complexity influence how humans interact with and use natural environments worldwide. (A) Ridgeline plots illustrating the distribution of rugosity (*R*) and fractal dimension (*D*) estimates associated with different land cover classifications. Land cover categories and their spatial distributions obtained from the Copernicus Climate Change Service (C3S) land cover survey (*38*). **(B)** The alignment of the structural complexity measures of **(i)** Height Range (*ΔH*), **(ii)** Rugosity (*R*), and **(iii)** Fractal Dimension (*D*) with patterns in human population density. Human population density patterns were sourced from the Gridded Population of the World (*39*), with each plot showing the predicted relationships (including 95% CI) derived from two-part hurdle models separately exploring patterns in the probability of greater than zero population densities (red) and recorded population count densities (blue). Population density estimates were transformed using a power transformation ($y^{0.05}$).

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Box 1. ***Case-study: Disentangling drivers of island biodiversity***

To demonstrate how metrics of structural complexity can help us understand the intrinsic association between biodiversity and abiotic habitat structure, we separately modelled the relationships between the complexity variables of height range (ΔH), rugosity (R), and fractal dimension (D), and measures of native (*i.e.*, non-introduced) island bird species and functional richness. Consistent with established theory, island area has a positive effect on both island bird species richness (Fig. 5A) and functional richness (Fig. S6A). Underlying this effect of island area, however, we evidence how the effects of structural complexity on species and functional richness patterns contribute to the multifaceted and heterogeneous relationship between species diversity and area. Overall, we illustrate that whilst increases in island rugosity and height range have little effect on bird species richness, they have a positive effect on functional diversity (Fig. 5B). Alternatively, fractal dimension has an overall negative effect on bird species richness but little effect on bird functional richness (Fig. 5B). Yet, these overall effects mask important non-linear relationships between structural complexity and species diversity. Large elevational gradients (*i.e.*, high R and/or ΔH), such as those associated with mountainous regions, generate geographical barriers and support high habitat and climatic heterogeneity, thus promoting high rates of speciation and diversification (*6*, *69*, *89*). Areas of high elevational complexity also support high endemism due to the specialisation required for inhabiting their associated ecosystems (*90*, *91*). Hence, at lower levels of rugosity and height range, increases in these complexity measures correlate with slight increases in island bird species richness (Fig. 5C[i & ii]) and large increases in island bird functional richness (Fig. S6B & C). However, this positive effect of rugosity and height range tapers off as complexity increases. Alongside a potential reduction in available niche space, the specialisation needed to initially access and colonise island systems coupled with the specialisation needed to tolerate the climate regimes associated with areas of high elevational and topographical complexity (*92*) may explain why, beyond a particular threshold, increases in ΔH and R diminish the effect of area on bird diversity. Meanwhile, at lower levels, changes in fractal dimension have little effect on either island bird species or functional richness (Fig. 5C[iii] & S6D). However, at higher levels, increases in island fractal dimension have a negative effect on island bird species and functional diversity. Higher fractal dimension across natural landscapes is attributed with promoting speciation through diversification by increasing habitat diversity and enabling more effective resource partitioning (*52*, *71*, *72*). However, the increased habitat diversity associated with higher fractal dimension likely reduces the availability of realised niche space; eliciting an increase in local extirpation rates (*27*). Our assessment here focused on avian fauna whose distributions are more defined by coarse-scale topographic features than fine-scale patterns in the shape of surface environments (*93*). However, the patterns we highlight here testament the necessity for continued exploration into the relationship between structural complexity and species diversity across taxa, as the necessary data becomes available.

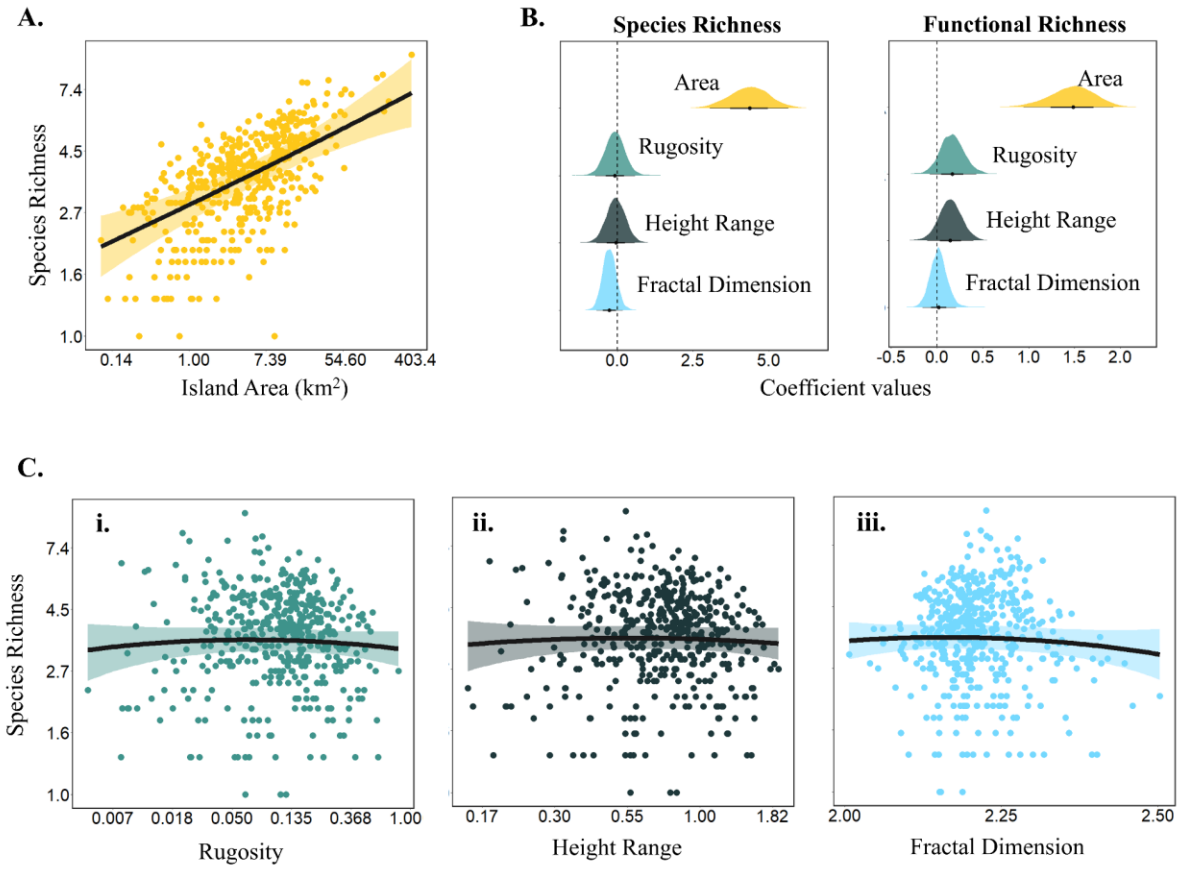

Fig. 5. Habitat structural complexity influences how changes in available space influence biotic configurations. (A) The conditional effect of Island area (km^2) on island bird species richness when accounting for the nested effect of archipelago and the fixed effects of island latitude, distance to nearest mainland, and human population density (r^2 = 0.844 [95% CI: 0.829, 0.857]). **(B)** Posterior distributions of the first polynomial slope coefficients extracted from models evaluating the effects of island area, rugosity, height range, and fractal dimension, on island bird species and functional richness. **(C)** The conditional effects of **(i)** rugosity (R), **(ii)** height range (ΔH), and **(iii)** fractal dimension (D) on island bird species richness (r^2: R = 0.795 [0.775, 0.811]; ΔH = 0.794 [0.775, 0.810]; D = 0.795 [0.776, 0.812]). All models account for the nested effects of archipelago and the fixed effect of island area, island latitude, distance to nearest mainland, and human population density. Error displayed as 95% CI across all panels.