Habitat complexity defines global biological and societal landscapes

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Summary

The three-dimensional structure of land- and seascapes sits at the boundary of biotic and abiotic geographies, linking geological processes to the configuration of localised weather patterns and oceanographic regimes and determines whether, and how, organisms access and use available resources[1–3]. Evaluating the relationship between habitat complexity and biodiversity has long been a prominent feature of ecological research[4,5]. However, inconsistencies in approaches used in defining and quantifying habitat complexity have so far precluded cross-system comparisons[6,7], preventing synthetic assessments into the ecological and evolutionary role of habitat complexity. Here we expand a framework developed for quantifying the structural complexity of coral reef environments[8] to present a scalable solution for estimating the complexity of terrestrial and aquatic habitats globally. We present high-resolution (1.87 × 1.87 km pixel size) maps detailing global patterns in the geometric complexity measures of height range, rugosity, and fractal dimension, and illustrate how key differences in these characteristics across marine and terrestrial landscapes serve to delineate the configuration of different biomes and anthromes. Overall, this work refines understanding for the mechanisms through which habitat complexity defines the global configuration of society and nature and offers a platform for exploring these interactions at varying spatial scales.

Main

The physical structure of natural environments sets the stage onto which ecological, geological, and climatic processes shape global biodiversity, human civilisation, and their interactions[7,9]. Indeed, whilst climatic regimes are a major determinant of global species richness trends[10], abiotic structure coordinates the spatio-temporal configuration of climate systems, thereby mediating climate exposure and resource availability and access[1,11]. Topographical and geological patterns also influence the taxonomic and functional diversity of forest ecosystems, subsequently underpinning their localised provision of biotic complexity and niche variety[5]. Moreover, the shape of natural habitats provides a wealth of green, blue and white spaces that support physical and mental wellbeing and agricultural diversification, thus supporting human health and socioeconomic development[9,12]. Understanding global patterns in habitat structure is key to safeguarding biodiversity, ensuring the sustainable use of natural resources, maintaining human livelihoods and public health, and for conserving earth's unique and diverse natural heritage[13–15].

Our growing appreciation for the role of structural habitat complexity (henceforth habitat complexity) in the development of natural and anthropogenic systems is accelerating calls for greater insight into the mechanisms interfacing abiotic and biotic systems[16–18]. Conservation initiatives, such as *Conserving Nature's Stage*, argue that the successful conservation of biodiversity relies upon protecting the enduring landscape features upon which it exists[19,20]. Access to the diversity of habitats necessary for maintaining genetic diversity is also considered amongst the legal Rights of Nature[21]. In light of continual land-use change, climatic change, and unmet conservation targets, the UN's sustainable development goals (SDG's) reflect the need for humanity's use of global resources to not undermine our biotic life-support system[22,23]. However, despite habitat complexity being a prominent feature of ecological research, the term itself is poorly defined, prompting a lack of consensus for how it

should be quantified and measured[6,24]. As a result, existing insight into the underlying role of

habitat complexity in determining the configuration of natural systems is fragmented across

isolated systems and often evaluated using incomparable approaches[2].

Here, we provide a comprehensive, quantitative assessment of global habitat

complexity patterns using a geometric framework established for quantifying the structural

complexity of coral reef environments[8]. Complementing recent efforts to classify global

ecosystem types[11], we use this approach to demonstrate how ecosystems are aligned along a

complexity gradient based on their relative geometric attributes, in turn offering insight into

the link between the processes driving the formation of abiotic habitats and their subsequent

association with distinct biological assemblages. We also illustrate mechanistic signals across

the association between habitat geometry and socioeconomic drivers, highlighting the link

between socio-economic development and global habitat structure. Consequently, this work

represents a unified approach for evaluating the role of habitat complexity in (1) mediating the

configuration of society and nature, (2) influencing the success of conservation efforts, and (3)

can be used to monitor the success of ongoing sustainable development targets.

98
Assessing habitat complexity across ecosystems

Heterogeneity in habitat structure (*i.e.*, its complexity) is assumed to be important for

maintaining biodiversity[25]. This assertion forms a key component of the theory of Island

Biogeography, with more structurally complex environments thought to accommodate a

greater diversity of available niche space and, therefore, support higher species richness[26,27].

However, this assumption is contradicted by the area-heterogeneity trade-off concept, which

predicts that the greater niche variety brought about by enhanced habitat complexity, likely

reduces realised niche space, thereby reducing population sizes and increasing the likelihood

of local extirpation[28]. How these two ecological processes interact holds the key for evaluating

and forecasting localised patterns of biodiversity change in response to climate shifts, habitat

fragmentation, and ecological restoration.

To assess global-scale patterns in habitat complexity we quantified the complexities of

global land- and seascapes, using the geometric measures of, *height range* (ΔH), *rugosity,* (R)

and *fractal dimension* (D; Fig. 1). To produce these global maps of structural habitat

complexity, we applied a geometric framework originally established for quantifying coral reef

structure[8], to a global elevation model sourced from the General Bathymetric Chart of the

Oceans (GEBCO)[29]. As measures of geometric complexity, ΔH captures the variation between

the maximum and minimum elevation of a surface, R describes the true surface area of the

surface, and D details the shape filling capacity of a surface (increases in D correspond with an

increase in the convolution of a surface)[30].

Global patterns in our measures of ΔH, R, and D, reveal key variation across the habitat

complexity regimes of different marine and terrestrial environments. First, the greatest height

range and highest rugosity environments are associated with the Himalayan, Andean, and Mid-

Atlantic mountain ranges (Fig. 1b & c). Second, dense areas of higher fractal dimension are

visible in the arctic tundras of North America and Siberia, the Amazonian and Patagonian

regions of South America, and pockets of north central Africa (Fig 1a). Third, a clear difference

emerges between the fractal nature of marine and terrestrial environments (Fig. 1a), with the

marine landscape characterised by more extensive regions of low fractal dimension.

At a more local scale, isolating the relative fractal dimension and rugosity regimes of

selected locations within the Amazonian Basin (AB; Fig. 2a), the Mariana Trench (MT; Fig.

2b), and the Sahara Desert (SD; Fig. 2c), demonstrates how habitat rugosities align with local

elevation patterns. In comparison with the other locations, the Mariana Trench is characterised

by a high density of more rugose environments (mean R: AB = 0.001, MT = 0.020, SD <

0.001). Meanwhile, the contours associated with the river channels spanning the Amazon River

basin are visible across its rugosity regime (Fig 2a). However, unlike estimates of rugosity, the

fractal dimension of surface habitats does not conform with their more obvious structural

features, offering a very different perspective of natural landscapes. When viewed through the

lens of its fractal dimension, the main channel of the Mariana Trench almost disappears (Fig.

2b). Alternatively, the Sahara Desert and the Amazon river basin, are characterised by regions

of higher fractal dimension, corresponding with their less rugged terrains (Fig. 2). Higher

fractal dimension is often associated with an increase in niche diversity, and therefore species

richness[31–33]. Perhaps it is not surprising then, that the Amazonian Basin, considered amongst

the most biodiverse ecosystems, is underpinned by dense regions of higher fractal dimension

(mean D: AB = 2.29, MT = 2.15, SD = 2.22). However, that the Sahara Desert, a comparatively

more inhospitable environment, also maintains regions of higher fractal dimension, emphasises

that it is the interaction between each of an ecosystem's individual attributes of structural

complexity and their local climate regime that defines their associated biodiversity[1].

The mechanistic drivers of a global complexity gradient

The relative rugosity and fractal dimension characteristics of natural environments positions

ecosystems along a gradient of habitat complexity (Fig. 3) and can be used to explore the

mechanisms through which environmental structures mediate biodiversity and socio-economic

development (Fig. 4). Recently, the IUCN established a function-based ecosystem typology

classification (FET) aimed at supporting the development of ecosystem management and

restoration initiatives while enhancing our ability to predict the response of ecosystem

functioning to ongoing global change[11]. These ecosystem classes align along a gradient

defined by their rugosity and fractal dimension characteristics (Fig. 3a; r^2 = 0.172 [95% CI:

0.058, 0.292]), highlighting the role played by the geometric complexity of environments in

delineating abiotic and biotic regimes to underpin the diversity of earth's natural heritage. Aside

from the clear distinction between the complexities of marine and terrestrial ecosystem types,

this gradient reveals how, across all realms, ecosystems of similar classifications maintain

comparable complexity regimes (*i.e.*, wetland environments are all characterised by higher

fractal dimension and low rugosities; Fig. 3a). This pattern does not mean that habitat

complexity is the driving force underpinning global biodiversity patterns. However, it again

emphasises how by interacting with local climate factors, the geometric structure of natural

environments can preserve and perpetuate the spatial distributions of particular ecosystem

states. For instance, despite possessing similar ratios of rugosity and fractal dimension, oceanic

temperate rainforests and polar alpine cliff ecosystems support different biological

communities due to their differing climate exposures. Yet, during the mid-Cretaceous (92 to

83 million years ago), under a far warmer global climate, the habitat structure associated with

contemporary polar alpine cliff ecosystems supported diverse oceanic temperate rainforests[34].

Habitat morphology and topography influence whether, how, and when, organisms can

access available resources[3]. The FET framework includes the presence of geomorphic features

(the categorisation of topographic reliefs and slope aspects as visible structural features[35]) as a

classification criteria[11]. With our measures of height range, rugosity and fractal dimension

extracted from topographical records, it is not surprising that ecosystem types fall along a

complexity gradient. However, the FET framework includes geomorphic indices as indirect

modulators of resource access[11]. Here, the alignment of ecosystem types along a complexity

gradient attests to a much more direct association between the structural composition of natural

habitats and the configuration of global biodiversity.

The importance of evaluating the direct association between habitat complexity and

biological assembly has given rise to novel ecological concepts such as *geodiversity*[14]. Akin to

an abiotic analogue of the term biodiversity, geodiversity combines measures of the richness

of structural features and processes comprising different environments[36]. Geodiversity offers a

measure of niche diversity that has been illustrated to support the maintenance of ecosystem

function and functional diversity[18]. However, assessments of geodiversity overlook how the

structural elements that comprise different environments subsequently shape those

environments[37]. Indeed, measures of geometric structure offer a differing perspective regarding

the heterogeneity regimes imposed by different environments, compared to geodiversity (Fig.

4a). While rugosity, height range and geodiversity explain similar trends in the structural

heterogeneity of natural environments (r^2: $\Delta H = 0.3619$ [0.3603, 0.3634], $R = 0.3766$ [0.3751,

0.3782]), patterns in fractal dimension and geodiversity are unrelated across the terrestrial

landscape ($r^2 = 0.0978$ [0.0964, 0.0992]). Measures of fractal dimension and geodiversity can

therefore offer independent perspectives into how the structural complexity of natural

ecosystems mediates the configuration of global biodiversity; emphasising the importance of

including various measures of structural heterogeneity within assessments aimed at informing

conservation action and ecosystem management[38].

The complexity of landscapes also has profound impacts on multiple aspects of human

society (*e.g.*, tourism, agriculture, mobility, and wellbeing)[9,12]. Patterns across the structural

complexities of natural habitats reveals insight into how geometric structure influences the way

human society uses natural environments, but also into how this usage impacts upon the

underlying structure of those environments (Fig 3b). The arrangement of global land-use types

based on their rugosity and fractal dimension aligns somewhat with the same gradient observed

across the complexities of different ecosystem types. However, land-use types corresponding

with increased human modification (*i.e.*, urban and cropland environments) display reduced

complexities (R and D) when compared to more 'natural' land-use types (Fig. 3b). This pattern

may arise from human activity diminishing the complexity of natural environments and/ or by

humans selecting less complex environments for development[12,24]. Whilst we are unable to

distinguish between cause and effect with static layers, both instances are likely true across the

global landscape.

A similar cyclical relationship between human society and habitat complexity is evident

across the associations between our measures of ΔH, R, and D, and global human population

density (Fig. 4b). With mountain ranges and high alpine regions (areas associated with high

estimates of ΔH and R) 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[39]. Accordingly, human population densities are

negatively correlated with our global measures of height range and rugosity (Fig 4b; r^2: ΔH =

0.1738 [0.1725, 0.1750], R = 0.1741 [0.1729, 0.1754]). Intriguingly, human population

densities are also negatively associated with fractal dimension (Fig. 4b; r^2 = 0.1754 [0.1741,

0.1767]). The surface descriptors of height range, rugosity, and fractal dimension are

constrained in such a way that it is extremely rare for natural surfaces to exhibit low estimates

of all three measures[8]. Thus, human population densities being associated with environments

that exhibit low ΔH, R, and D may be indicative that anthropogenic activity simplifies the

geometric, compositional, and configurational structure of natural landscapes[40–42].

223
Future research

Our global-scale assessment of geometric habitat structure emphasises the role of habitat

complexity in mediating the configuration of natural and anthropogenic communities. Having

long appreciated the association between diversity and area, a recent focus of ecological

research has been devoted to quantifying the mechanistic drivers linking biodiversity and area.

Naturally, it is not changes in area *per-se* that determine trends in species richness but the

changes in environmental structure it entails. Colonisation, extinction, and speciation are

fundamental drivers of species richness patterns[43], and are acutely linked to the structural shape

of the landscape[3]. Through the shaping of dispersal pathways and niche partitioning, prehistoric

shifts in landscape topography have defined the contemporary arrangement of global biodiversity more so than prevailing climatic regimes[44]. Thus, forecasting how natural communities will respond to ongoing global change requires the evaluation of the intrinsic association between biodiversity and abiotic habitat structure. Moreover, nature does not exist in pristine isolation, with the majority of global ecosystems facing some form of direct anthropogenic pressure[45–47]. How we interact with and utilse our local environment is also mediated by patterns in habitat complexity. So too is how these natural environments respond to exploitation. We have demonstrated how the same geometric theory offers informative and relevant insights into the mechanisms through which habitat structure underpins the configuration of global biomes and anthromes. Having illustrated the applicability of our approach at the global-scale, the methodology through which we scaled-up the geometric assessment of surface habitats is sufficiently flexible for accommodating assessments of habitat complexity at varying resolutions across local, regional, and continental terrains. Thus our approach here opens up avenues for addressing how the distribution of topographical boundaries and microhabitats configures the nuanced processes of speciation, diversification, isolation, and connectivity[31,33], and how these processes will interact with anthropogenic pressures and ongoing global change.

Methods

Briefly, our study comprised the following sequence of steps: generating global maps of selected complexity indices; evaluating ecosystem and land-use associated complexity characteristics; and quantifying the association between habitat complexity and additional abiotic and biotic mechanisms. All spatial analyses were carried out using R[48] and QGIS[49].

Generating global complexity maps

We estimated global patterns in height range (ΔH), rugosity (R), and fractal dimension (D)

using the GEBCO 2023 global ocean and land terrain model (including ice surface elevation)[29].

Initially merging the corresponding raster tiles downloaded from GEBCO

(https://www.gebco.net/) to produce a 15 arc-second resolution (EPSG: 4326, WGS84) global

map of surface elevation in metres, we reprojected this elevation model (henceforth digital

elevation model [DEM]) to an equal-area Mollweide projection (EPSG: 54009) at a resolution

of 187 m (L_0). From this DEM, using the associated functions contained in the *habtools*

package[50] we then extracted estimates of ΔH, R, and D, at a scale of 1870 m (L; one order of

magnitude greater than L_0). Briefly, this extraction involved separating our DEM file into

longitudinal tiles each corresponding with a longitudinal distance equal to L (equivalent to 10

pixel columns). Using multicore processing, implemented using the *foreach* and *doParallel*

packages[51,52], we iteratively processed each longitudinal tile to extract estimates of ΔH (the

difference between the maximum and minimum elevation of a surface), R (the surface area of

a surface), and D (calculated using the associations between ΔH, R, and D in the geometric

plane equation from Torres-Pulliza *et al.*[8] [equation 1]) for each latitudinal band (each band

corresponded with 10 rows, equivalent to a distance of L, resulting in a series of $L \times L$ pixels):

274
$$D = 3 - \frac{\log\left(\frac{\Delta H}{\sqrt{2} L_0 \sqrt{R^2 - 1}}\right)}{\log\left(\frac{L}{L_0}\right)} \tag{1}$$

Next, we carried out data cleaning, omitting all estimates that, (1) violated geometric

theory for surface habitats ($\Delta H < 0$; $R < 1$; $2 > D > 3$; 85,183 entries, 0.046% of initial sample)

and, (2) corresponded with non-fractal (flat) pixel cells ($\Delta H = 0$, $R = 1$ & $D = 2$; 435,225 entries,

0.233% of initial sample). We omitted non-fractal cells on the basis that, at a scale of 1870m,

perfectly flat landscapes do not exist and instead represent artefacts present in the original

elevation model[53], or accuracy errors introduced during model reprojection. Prior to collating

our estimates for each complexity measure into separate spatial raster files we transformed all

ΔH and R estimates according to their expression in the geometric plane equation[8], such that

rugosity is expressed as $R^2 - 1$ and height range is expressed as $\frac{\Delta H}{\sqrt{2}L_0}$.

Comparing ecosystem and land use type complexities

We evaluated patterns across our estimates of R and D associated with differing ecosystem and

land use classifications. Carrying out this assessment involved assigning each pixel across our

complexity maps to particular ecosystem and land-use types. Firstly, we used the IUCN

ecosystem typology classification framework[11] to define our ecosystem types and their spatial

distributions across the global landscape[54] (all distribution maps were reprojected to a

Mollweide projection). Next we quantified spatial patterns in land-use categories using a

satellite derived global land cover map sourced from the Copernicus Climate Change Service

(C3S)[55]. From the C3S data portal, we sourced an .nc file comprising different global land

cover variables derived from satellite surveys carried out during 2022. From this file we

extracted the associated land cover class layer using the *raster* package[56], which we then

reprojected to a Mollweide projection (EPSG: 54009) at a resolution of 1870m (L), all whilst

ensuring the finalised map extent corresponded with that of our DEM. For the assessment of

both ecosystem and land-use associated complexities we overlayed the corresponding spatial

files detailing the spatial distributions of selected ecosystem and land use types (Tables S1 &

S2) onto our global complexity maps to isolate the values of R and D associated with each

ecosystem and land use category. Using the *brms* package[57], we performed polynomial

Bayesian regression to evaluate the relationship between mean R and D estimates across

ecosystem types. We opted for this non-linear format following 'leave-one-out' cross-

validation model comparisons between non-linear and linear formats. For this analysis we

implemented a single model consisting of 20 Markov Chains, each comprising 5000 iterations

(including 1000 warm-up iterations).

Evaluating associated mechanisms

Focusing on the terrestrial landscape, we evaluated how our estimates of ΔH, R, and D

correspond with two established drivers of global biotic and abiotic regimes: geodiversity (G),

and human population density (PD). We sourced geodiversity estimates from a global map of

terrestrial geodiversity developed during an assessment of geodiversity representation across

UNESCO geoparks[58] (EPSG: 54009). Originally, sourced at a resolution of 250m, this global

map was reprojected to a resolution of 1870m (L) and to an extent equal to that of our global

complexity rasters. Meanwhile, we obtained global data on human population densities from

the Gridded Population of the World[59]. We downloaded a map of the global population density

recorded in 2020 at a 30 arc-second resolution (EPSG: 4326) which we subsequently

reprojected to a 1870m resolution in a Mollweide projection. Aligning corresponding pixel

values across these spatial maps, then allowed for extracting corresponding estimates for ΔH,

R, D, G, and PD, from which we retained the pixel cells with complete entries for all variables

(~38 million pixels). Following data omission, we used the *terra* package[61] to test each of our

geometric complexity variables (ΔH, R, and D) for spatial autocorrelation, by computing

Moran's I statistic for each measure (I: $\Delta H = 0.883$; $R = 0.805$; $D = 0.476$, assuming a Queen's

case nearest neighbour matrix, *i.e.*, all adjacent cells including diagonals). Lastly, we

transformed our population density variable for normality. This transformation took the form

of a power transformation ($y^{0.05}$) applied only to non-zero entries.

We analysed the pairwise relationships between each of our geometric variables (ΔH,

R and D) and G, using generalised additive models (GAMs) and Monte-Carlo resampling. To

assess each pairwise relationship we implemented our GAMs using the *mgcv* package[60],

repeating each pairwise comparison 1000 times on a randomly selected sub-sample of 1000

data points (0.0026% sample), each time computing the associated model's r^2 value and

predicted relationship. We fitted all models to a gaussian distribution, with geodiversity set as

the predictor variable, and with a fixed spatial smoothing term included (defined by the

covariates of latitude and longitude) to account for the spatial autocorrelation evident across

our complexity variables. ($I > 0$).

Also implemented using Monte-Carlo resampling, we analysed the pairwise

relationships between each of our geometric variables and PD, using hurdle models

implemented via a Bayesian framework in $brms$. Using this hurdle approach allowed us to

separately model the probability of zero population density as a function of geometric

complexity, and the relationship between non-zero population densities and geometric

complexity. We repeated each pairwise hurdle model 1000 times on a randomly selected sub-

sample of 1000 data points, each time retaining the model's r^2 value, predicted non-zero

relationship, and its hurdle coefficients (probability of being zero). We modelled the

relationship between complexity and non-zero population density using a gamma distribution,

and again, included a fixed spatial smoothing term to account for spatial autocorrelation across

our complexity variables.

347
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References

1.   Coelho, M. T. P. *et al.* The geography of climate and the global patterns of species

diversity. *Nature* **622**, 537–544 (2023).

2.   Kovalenko, K. E., Thomaz, S. M. & Warfe, D. M. Habitat complexity: Approaches

and future directions. *Hydrobiologia* **685**, 1–17 (2012).

3.   Badgley, C. *et al.* Biodiversity and Topographic Complexity: Modern and

Geohistorical Perspectives. *Trends Ecol. Evol.* **32**, 211–226 (2017).

4.　　　MacArthur, R. H. & MacArthur, J. W. On Bird Species Diversity. *Ecology* **42**, 594–

598 (1961).

5.　　　Ehbrecht, M. *et al.* Global patterns and climatic controls of forest structural

complexity. *Nat. Commun.* **12**, 519 (2021).

6.　　　Loke, L. H. L. & Chisholm, R. A. Measuring habitat complexity and spatial

heterogeneity in ecology. *Ecol. Lett.* **25**, 2269–2288 (2022).

7.　　　Madin, J. S. *et al.* A word on habitat complexity. *Ecol. Lett.* **26**, 1021–1024 (2023).

8.　　　Torres-Pulliza, D. *et al.* A geometric basis for surface habitat complexity and

biodiversity. *Nat. Ecol. Evol.* **4**, 1495–1501 (2020).

9.　　　Alahuhta, J. *et al.* Acknowledging geodiversity in safeguarding biodiversity and

human health. *Lancet Planet Health* **6**, 987–92 (2022).

10.　　Pecl, G., Araujo, M. B., Bell, J. D., Blanchard, J. & Bonebrake, T. C. Biodiversity

redistribution under climate change: Impacts on ecosystems and human well-being

Publication Details. *Science* **355**, 1–9 (2017).

11.　　Keith, D. A. *et al.* A function-based typology for Earth's ecosystems. *Nature* **610**,

513–518 (2022).

12.　　Nelson, K. S. & Burchfield, E. K. Landscape complexity and US crop production.

Nat. Food **2**, 330–338 (2021).

13.　　Schrodt, F. *et al.* To advance sustainable stewardship, we must document not only

biodiversity but geodiversity. *PNAS* **116**, 16155–16158 (2019).

14.　　Schrodt, F. *et al.* The status and future of essential geodiversity variables. *Philos.*

Trans. R. Soc. A **382**, 1–18 (2024).

15.　　Knudson, C., Kay, K. & Fisher, S. Appraising geodiversity and cultural diversity

approaches to building resilience through conservation. *Nat. Clim. Change* **8**, 678–685

(2018).

16. Zarnetske, P. L. *et al.* Towards connecting biodiversity and geodiversity across scales

with satellite remote sensing. *Glob. Ecol. Biogeogr.* **28**, 548–556 (2019).

17. Zarnetske, P. L. *et al.* The Interplay Between Landscape Structure and Biotic

Interactions. *Curr. Landsc. Ecol. Rep.* **2**, 12–29 (2017).

18. Vernham, G. *et al.* Understanding trait diversity: the role of geodiversity. *Trends*

Ecol. Evol. (2023) doi:10.1016/j.tree.2023.02.010.

19. Beier, P., Hunter, M. L. & Anderson, M. Special Section: Conserving Nature's Stage.

Conserv. Biol. **29**, 613–617 (2015).

20. Lawler, J. J. *et al.* The theory behind, and the challenges of, conserving nature's stage

in a time of rapid change. *Conserv. Biol.* **29**, 618–629 (2015).

21. Epstein, Y., Ellison, A. M., Echeverría, H. & Abbott, J. K. Science and the legal

rights of nature. *Science* **380**, eadf4155 (2023).

22. Steffen, W. *et al.* Planetary boundaries: Guiding human development on a changing

planet. *Science* **347**, 1259855 (2015).

23. Reyers, B. & Selig, E. R. Global targets that reveal the social–ecological

interdependencies of sustainable development. *Nat. Ecol. Evol.* **4**, 1011–1019 (2020).

24. Green, D. G., Klomp, N., Rimmington, G. & Sadedin, S. *Complexity in Landscape*

Ecology. vol. 4 (Springer, The Netherlands, 2006).

25. Tews, J. *et al.* Animal species diversity driven by habitat heterogeneity/diversity: The

importance of keystone structures. *J. Biogeogr.* **31**, 79–92 (2004).

26. MacArthur, R. H. & Wilson, E. O. *The Theory of Island Biogeography*. (Princeton

University Press, 1967).

27. Stein, A., Gerstner, K. & Kreft, H. Environmental heterogeneity as a universal driver

of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* **17**, 866–880 (2014).

28. Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M. & Kadmon, R. Area–

heterogeneity tradeoff and the diversity of ecological communities. *Proc. Natl. Acad. Sci.*

109, 17495–17500 (2012).

29. GEBCO Compilation Group. GEBCO 2023 Grid. (2023).

30. Warfe, D. M., Barmuta, L. A. & Wotherspoon, S. Quantifying Habitat Structure:

Surface Convolution and Living Space for Species in Complex Environments. *Oikos* **117**,

1764–1773 (2008).

31. Johnson, M. P., Frost, N. J., Mosley, M. W. J., Roberts, M. F. & Hawkins, S. J. The

area-independent effects of habitat complexity on biodiversity vary between regions. *Ecol.*

Lett. **6**, 126–132 (2003).

32. Gámez, S. & Harris, N. C. Conceptualizing the 3D niche and vertical space use.

Trends Ecol. Evol. **37**, 953–962 (2022).

33. Tokeshi, M. & Arakaki, S. Habitat complexity in aquatic systems: fractals and

beyond. *Hydrobiologia* **685**, 27–47 (2012).

34. Klages, J. P. *et al.* Temperate rainforests near the South Pole during peak Cretaceous

warmth. *Nature* **580**, 81–86 (2020).

35. Harris, P. T., Macmillan-Lawler, M., Rupp, J. & Baker, E. K. Geomorphology of the

Oceans. *Mar. Geol.* **352**, 4–24 (2014).

36. Gray, M. *Geodiversity: Valuing and Conserving Abiotic Nature*. (Wiley-Blackwell,

2013).

37. Hjort, J. *et al.* Towards a taxonomy of geodiversity. *Philos. Trans. R. Soc. A* **382**, 1–

14 (2024).

38. Tukiainen, H., Bailey, J. J., Field, R., Kangas, K. & Hjort, J. Combining geodiversity

with climate and topography to account for threatened species richness. *Conserv. Biol.* **31**,

364–375 (2017).

39.   Shi, T., Li, X., Xin, L. & Xu, X. The spatial distribution of farmland abandonment

and its influential factors at the township level: A case study in the mountainous area of

China. *Land Use Policy* **70**, 510–520 (2018).

40.   Fahrig, L. *et al.* Functional landscape heterogeneity and animal biodiversity in

agricultural landscapes. *Ecol. Lett.* **14**, 101–112 (2011).

41.   Meehan, T. D., Werling, B. P., Landis, D. A. & Gratton, C. Agricultural landscape

simplification and insecticide use in the Midwestern United States. *Proc. Natl. Acad. Sci.*

108, 11500–11505 (2011).

42.   Wang, T., Belle, I. & Hassler, U. Modelling of Singapore's topographic

transformation based on DEMs. *Geomorphology* **231**, 367–375 (2015).

43.   Valente, L. *et al.* A simple dynamic model explains the diversity of island birds

worldwide. *Nature* **579**, 92–96 (2020).

44.   Igea, J. & Tanentzap, A. J. Global topographic uplift has elevated speciation in

mammals and birds over the last 3 million years. *Nat. Ecol. Evol.* **5**, 1530–1535 (2021).

45.   Ellis, E. C. *et al.* People have shaped most of terrestrial nature for at least 12,000

years. *Proc. Natl. Acad. Sci.* **118**, e2023483118 (2021).

46.   Sullivan, A. P., Bird, D. W. & Perry, G. H. Human behaviour as a long-term

ecological driver of non-human evolution. *Nat. Ecol. Evol.* **1**, 1–11 (2017).

47.   Flores, B. M. & Levis, C. Human-food feedback in tropical forests. *Science* **372**,

1146–1147 (2021).

48.   R Core Team. R: A language and environment for statistical computing. R Foundation

for Statistical Computing (2022).

49.   QGIS.org. QGIS Geographic Information System. QGIS Association (2023).

50.   Madin, J. & Schiettekatte, N. habtools: Tools and Metrics for 3D Surfaces and

Objects. (2024).

51.   Microsoft Corporation & Weston, S. doParallel: Foreach Parallel Adaptor for the

'parallel' Package. (2022).

52.   Microsoft Corporation & Weston, S. foreach: Provides Foreach Looping Construct.

(2022).

53.   Smith, B. & Sandwell, D. Accuracy and resolution of shuttle radar topography

mission data. *Geophys. Res. Lett.* **30**, (2003).

54.   Keith, D. A., Ferrer-Paris, J. R., Nicholson, E. & Kingsford, R. T. Indicative

distribution maps for Ecosystem Functional Groups - Level 3 of IUCN Global Ecosystem

Typology. (2023) doi:10.5281/zenodo.10081251.

55.   Copernicus Climate Change Service. Land cover classification gridded maps from

1992 to present derived from satellite observation. (2019).

56.   Hijmans, R. J. raster: Geographic data analysis and modeling. (2020).

57.   Bürkner, P. brms: An R Package for Bayesian Multilevel Models Using Stan. *J. Stat.*

Softw. **80**, 1–28 (2017).

58.   Polman, E. M. N., Seijmonsbergen, A. C., Versteegh, H. & Kissling, W. D. Global

geodiversity components are not equally represented in UNESCO Global Geoparks. *Philos.*

Trans. R. Soc. A **382**, 1–18 (2024).

59.   Center for International Earth Science Information Network (CIESIN). Gridded

Population of the World, Version 4 (GPWv4): Population Count, Revision 11. (2018).

60.   Wood, S. N. *Generalized Additive Models*. (Chapman and Hall/CRC, New York,

2017). doi:10.1201/9781315370279.

61.   Hijmans, R. J. terra: Spatial Data Analysis. (2023).

 Figures & Tables

 Figure 1. Global patterns in structural habitat complexity. High resolution maps (1.87 ×

 1.87 km) depicting patterns in the geometric complexity measures of **(a)** Fractal Dimension

 (*D*), **(b)** Rugosity (*R*), and **(c)** Height Range (*ΔH*), across all terrestrial and marine

 environments. Each map is displayed in a global Mollweide equal area projection and

 comprises ~146 million estimates of *ΔH*, *R*, and *D*, with white pixels reflecting missing or

 omitted entries.

 Figure 2. The relative complexity characteristics of differing global environments offer

 insight into the differing structural regimes underlying different ecosystems. Comparisons

 of the fractal dimension (*D*) and rugosity (*R*, displayed following log10 transformation)

 patterns across the **(a)** Amazonian Basin, **(b)** Mariana Trench, and **(c)** Sahara Desert. Each map

 displays a 935 × 935 km section of selected locations and are displayed in a global Mollweide

 equal area projection, with latitude and longitude in metres. Inset photographs (obtained from

 www.freepik.com) offer a visualisation of how the landscapes associated with the Amazon

 Rainforest and the Sahara desert translate into their associated complexity regimes.

 Figure 3. The rugosity and fractal dimension characteristics of natural environments

 situate differing ecosystem types along a complexity gradient and offer insight into the

 relationship between habitat structure and the anthropogenic use and change of local

 environments. (a) Ecosystems (categorised using the IUCN function-based ecosystem

 typology[11]) can be arranged along a complexity gradient based on their mean fractal dimension

 (*D*) and rugosity (*R*) characteristics. Solid line represents the predicted relationship between

 ecosystem estimates of *R* and *D*, with the shaded region identifying the 95% confidence

 intervals of these predictions. Dashed lines highlighting the position of selected ecosystem

 classifications. **(b)** Comparing the mean rugosity and fractal dimension characteristics of

differing land cover classifications. Land cover categories and their spatial distributions obtained from the Copernicus Climate Change Service (C3S) land cover survey[55]. Solid line represents the relationship between land use type estimates of R and D predicted using our Bayesian model parameterised using ecosystem type estimates of R and D. Dashed lines highlighting the three primary human modified land cover types within the C3S classification.

Figure 4. Evaluating the association of geological, climatic, and societal patterns with geometric habitat structure highlights mechanisms through which habitat complexity refines the global configuration of society and nature. The association between each of the structural complexity measures of Height Range (ΔH), Rugosity (R), and Fractal Dimension (D), and global **(a)** geodiversity, and **(b)** human population density. 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[58]. 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. Human population density patterns were sourced from the Gridded Population of the World[59], with each plot showing the predicted relationships (including 95% CI) derived from two-part hurdle models separately exploring patterns in the probability of zero population densities (red) and population count densities (blue). Population density estimates were transformed using a power transformation ($y^{0.05}$).

533 **Figure 1**

542   **Figure 2**

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a. Ecosystem types

b. Land use

     Figure 4