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Research article

Tracking shifts in forest structural complexity through space and time in human-modified tropical landscapes

Alice Rosen^{1,2}, Fabian Jörg Fischer¹, David A. Coomes³, Toby D. Jackson^{1,3}, Gregory P. Asner⁴ and Tommaso Jucker¹  

¹School of Biological Sciences, University of Bristol, Bristol, UK

²Department of Biology, University of Oxford, Oxford, UK

³Department of Plant Sciences and Conservation Research Institute, University of Cambridge, Cambridge, UK

⁴Center for Global Discovery and Conservation Science, Arizona State University, Tempe, AZ, USA

Correspondence: Tommaso Jucker (t.jucker@bristol.ac.uk) and Alice Rosen (alice.rosen@linacre.ox.ac.uk)

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Habitat structural complexity is an emergent property of ecosystems that directly shapes their biodiversity, functioning and resilience to disturbance. Yet despite its importance, we continue to lack consensus on how best to define structural complexity, nor do we have a generalised approach to measure habitat complexity across ecosystems. To bridge this gap, here we adapt a geometric framework developed to quantify the surface complexity of coral reefs and apply it to the canopies of tropical rainforests. Using high-resolution, repeat-acquisition airborne laser scanning data collected over 450 km² of human-modified tropical landscapes in Borneo, we generated 3D canopy height models of forests at varying stages of recovery from logging. We then tested whether the geometric framework of habitat complexity – which characterises 3D surfaces according to their height range, rugosity and fractal dimension – was able to detect how both human and natural disturbances drive variation in canopy structure through space and time across these landscapes. We found that together, these three metrics of surface complexity captured major differences in canopy 3D structure between highly degraded, selectively logged and old-growth forests. Moreover, the three metrics were able to track distinct temporal patterns of structural recovery following logging and wind disturbance. However, in the process we also uncovered several important conceptual and methodological limitations with the geometric framework of habitat complexity. We found that fractal dimension was highly sensitive to small variations in data inputs and was ecologically counteractive (e.g. higher fractal dimension in oil palm plantations than old-growth forests), while rugosity and height range were tightly correlated ($r=0.75$) due to their strong dependency on maximum tree height. Our results suggest that forest structural complexity cannot be summarised using these three descriptors alone, as they overlook key features of canopy vertical and horizontal structure that arise from the way trees fill 3D space.

Keywords: Forest disturbance, LiDAR, logging, recovery, remote sensing, structural complexity



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Introduction

Tropical forests are structurally complex ecosystems that play a crucial role in regulating carbon and water cycling on land (Pan et al. 2011, Malhi 2012, Mitchard 2018, Staal et al. 2020, Smith et al. 2023) and are among the most biodiverse habitats on Earth, accounting for more than two-thirds of terrestrial biodiversity (Gibson et al. 2011, Barlow et al. 2018, Gatti et al. 2022, Pillay et al. 2022). However, the majority of the world's remaining tropical forests have been altered or disturbed in some way, including through logging, habitat fragmentation and degradation, fire and extreme events linked to climate change (Asner et al. 2010, Taubert et al. 2018, Berenguer et al. 2021, Saatchi et al. 2021, Lapola et al. 2023). These human and natural disturbances profoundly alter the three-dimensional (3D) structure of forest canopies (Ordway and Asner 2020, Milodowski et al. 2021, Jucker 2022, Reis et al. 2022, Choi et al. 2023). In doing so they affect the way in which tropical forests sequester and store carbon, cycle nutrients, regulate microclimate and provide habitat for countless organisms (Jucker et al. 2018a, Frenne et al. 2021, Malhi et al. 2022, Heinrich et al. 2023, Mills et al. 2023). Therefore, characterising how disturbance shapes the 3D structure and dynamics of tropical forest canopies is central to understanding its impacts on carbon cycling and biodiversity, as well as building more realistic simulation models of these ecosystems (Taubert et al. 2015, Maréchaux and Chave 2017, Jucker 2022).

Growing access to remote sensing technologies such as airborne laser scanning (ALS, or LiDAR) has revolutionised our ability to map the 3D structure of forest canopies in high detail across broad spatial scales (Kellner and Asner 2009, Jucker et al. 2018b, Valbuena et al. 2020, Jucker 2022, Lines et al. 2022). ALS data are transforming how we study and monitor forests, allowing us to explore how and why forest 3D structure varies across both space (Jucker et al. 2018b, Ordway and Asner 2020, Milodowski et al. 2021, Reis et al. 2022, Jucker et al. 2023) and time (Wedoux et al. 2020, Cushman et al. 2021, Nunes et al. 2021, Choi et al. 2023). However, despite these advances, we continue to lack a clear consensus on what 'structural complexity' actually is and which attributes of 3D canopy structure are most ecologically relevant to measuring it (Valbuena et al. 2020, Ehbrecht et al. 2021, Lines et al. 2022, Atkins et al. 2023a, LaRue et al. 2023). This has led to a proliferation of context-specific canopy structural metrics that can be derived from ALS, without enough effort to consider how these might generalise across different forest ecosystems or drivers of disturbance (Lines et al. 2022, Atkins et al. 2023a, b).

To address this challenge, several efforts have been made to characterise structural complexity from first principles. These theoretical frameworks often start from the idea that biological patterns repeat themselves across scales (e.g. from leaves, to branches, trunks and entire forest stands) in ways that are predictable and quantifiable (Zeide 1991, Enquist et al. 2003, Niklas 2004, Fischer and Jucker 2023). One such example is the geometric theory of surface habitat complexity

developed by Torres-Pulliza et al. (2020), which summarises habitat structural complexity using three surface descriptors – height range, surface rugosity and fractal dimension – and the geometric constraints that link them together (Fig. 1). While originally developed for coral reefs, this geometric framework was designed specifically to be broadly applicable across ecosystems and can be applied to any high-resolution 3D surface model of a habitat, such as those that can be generated from ALS. Since first being proposed, aspects of this theoretical framework have been called into question, particularly around the estimation and ecological relevance of fractal dimension as a measure of structural complexity (Loke and Chisholm 2022, 2023, Fischer and Jucker 2023, Madin et al. 2023). However, no one has yet tested how well this framework is able to characterise the impacts of disturbance on the 3D structure of other structurally complex ecosystems, such as tropical forests. Nor has anyone explored how these three surface descriptors relate to other widely used metrics of canopy structure derived from ALS.

Here, we bring together ALS datasets acquired across a forest disturbance gradient in Malaysian Borneo (Fig. 2), ranging from old-growth rainforests that are home to some of the world's tallest flowering plants, selectively logged forests at varying stages of recovery and oil palm landscapes (Jucker et al. 2018a, Shenkin et al. 2019, Milodowski et al. 2021). Using these unique datasets, we started by rigorously testing the sensitivity of the three structural metrics to the resolution and spatial scale of ALS data. Then, we assessed how height range, rugosity and fractal dimension relate to other widely used metrics of canopy height, density and openness. Next, we used a space-for-time approach to compare the structural complexity of forest landscapes at different stages of recovery following disturbance from logging. This allowed us to determine how well the geometric theory of surface habitats can capture the legacy of these past disturbances on the 3D structure of the canopy. Finally, we used repeat-acquisition ALS data to directly track changes in canopy structural complexity through time. In doing so, we tested the ability of this framework to tease apart the effects of different types of anthropogenic and natural disturbance and recovery processes.

Material and methods

Study region

Our study focuses on several sites in the Malaysian state of Sabah in Borneo (Fig. 2). Sabah has a tropical and largely aseasonal climate, with a mean annual rainfall of approximately 2700 mm year⁻¹ and a mean annual temperature of 26.7 °C (Walsh and Newbery 1999, Kumagai and Porporato 2012). The lowlands of Sabah have been historically covered by tall, structurally complex dipterocarp forests, including the tallest known trees ever recorded in the tropics, which can reach 100 m in height (Shenkin et al. 2019). However, since the early 1970s much of Sabah's forests have either been

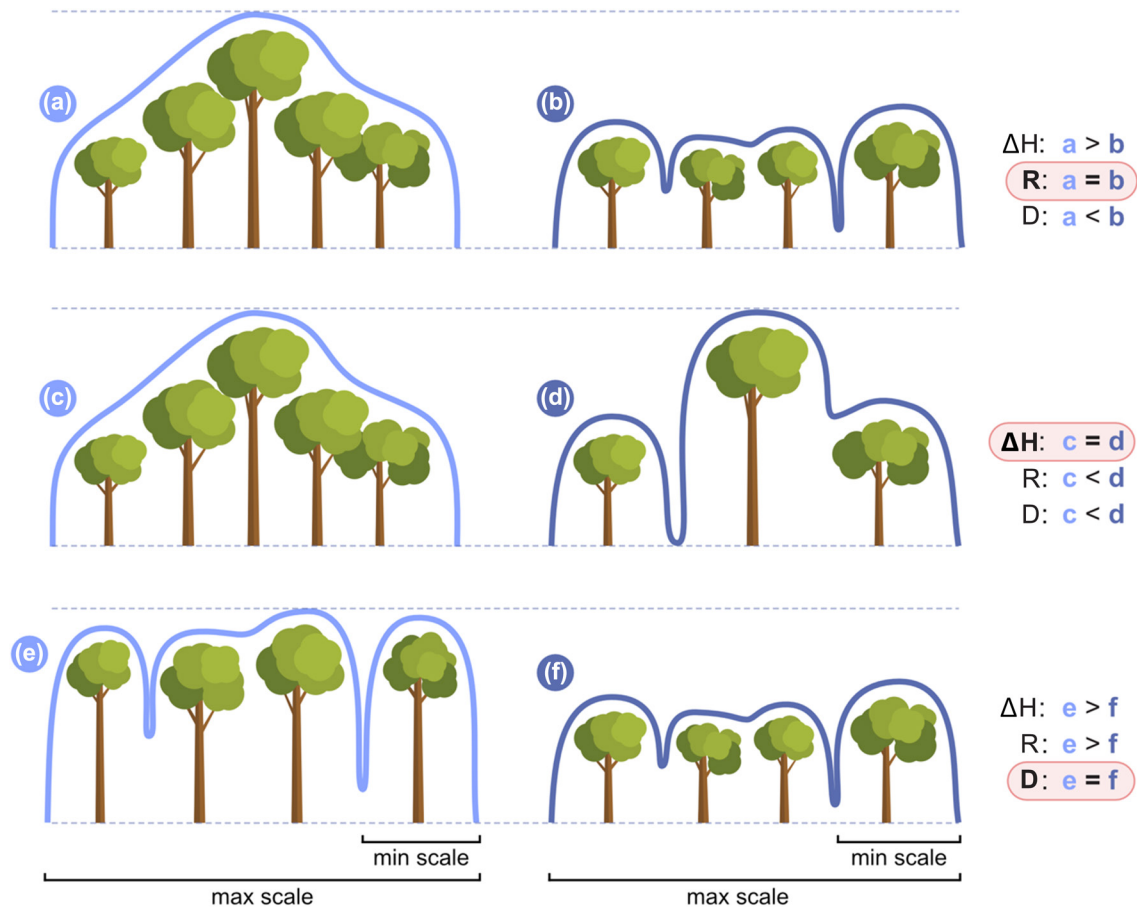


Figure 1. Schematic diagram of the geometric constraints between height range (ΔH), surface rugosity (R) and fractal dimension (D). The blue lines represent a 2D cross-section of a 3D surface. In each row, one metric is kept constant between the two surfaces (outlined in red) to highlight the interaction between the remaining two metrics. In the top row, surfaces (a and b) share the same rugosity (the length of the line is the same), but the fractal dimension of (b) is greater (the surface is more folded over the same distance), meaning that its height range must also be lower. In the middle row, surfaces (c and d) have the same height range, but (d) has a higher fractal dimension and therefore the length of the line has increased, resulting in greater surface rugosity). In the bottom row, surfaces (e and f) have the same fractal dimension, but the greater height range of (e) means that its surface rugosity is also higher.

selectively logged and fragmented or entirely cleared to make way for rubber and oil palm plantations (Reynolds et al. 2011, Bryan et al. 2013, Gaveau et al. 2019).

To capture this broad gradient of forest disturbances, we compiled data from representative sites in Sabah that encompass unlogged old-growth forests, selectively logged forests at different stages of recovery (including ones that have been actively restored) and oil palm landscapes (Fig. 2). Old-growth forests are located at Danum Valley and Maliau Basin conservation areas (Zhang et al. 2023), where no records of commercial tree harvesting exist. Logged forests are mostly found within the Stability of Altered Forest Ecosystems (SAFE) project landscape (Ewers et al. 2011), where we identified both ‘recovering logged forests’ that were selectively logged twice (first in the 1970s and then again in the 1980–1990s) and have since been left to recover, and ‘recently logged forests’ which experienced up to four rounds of logging between the 1970s and 2008. These were contrasted to ‘restored logged forests’ within the Sabah Biodiversity

Experiment (SBE), where selective logging occurred once in the late 1980s and forests have since been actively restored via enrichment tree planting and liana cutting starting in 2002 (Hector et al. 2011). In all cases, the first round of logging removed approximately $113 \text{ m}^3 \text{ ha}^{-1}$ of timber, followed by an additional $37\text{--}66 \text{ m}^3 \text{ ha}^{-1}$ during subsequent rotations (Riutta et al. 2018). In 2014 the basal area of recently logged forests was approximately $10 \text{ m}^2 \text{ ha}^{-1}$, approximately half that of recovering logged forests and only 25–30% of old-growth forests (Riutta et al. 2018). Finally, given the prevalence of oil palm plantations across Sabah, we also included these in our analysis as a comparison to the canopies of natural forests. This includes palm groves at all stages of maturity during the crop’s 25–30 year rotation cycle.

Airborne laser scanning data

ALS data were acquired through multiple surveys conducted in 2013, 2014, 2016 and 2020 (Supporting information).

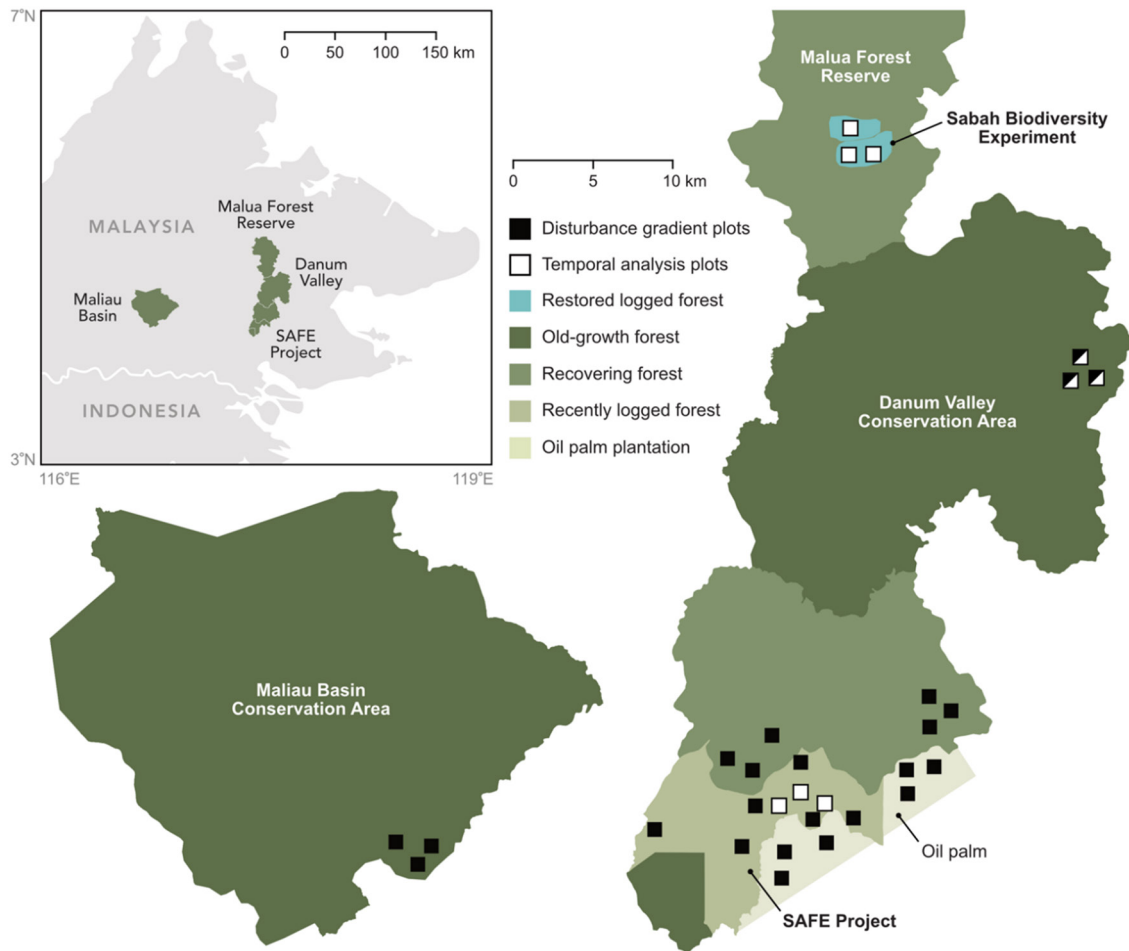


Figure 2. Map of the key study sites where airborne laser scanning (ALS) data were acquired for this study and their location within the state of Sabah in Malaysian Borneo. Black squares indicate the locations of the 24 forest patches (each 800×800 m) used to explore structural complexity across a disturbance gradient. White squares instead correspond to the nine forest patches (each 800×800 m) used in the temporal change analyses. This included three plots known to have been salvaged logged between 2014 and 2016 (within the Stability of Altered Forest Ecosystems (SAFE) project landscape); three previously logged plots that were in a phase of recovery between 2013 and 2020 when the ALS data were acquired (within the Sabah Biodiversity Experiment); and three old-growth plots in Danum Valley known to have been impacted by a windthrow event between 2014 and 2020.

The majority of the analysis is based on ALS data acquired in 2014 by NERC-ARF (<https://nerc-arf-dan.pml.ac.uk/>) at Danum Valley, Maliau Basin and SAFE, which collectively covered ~ 450 km² (Jucker et al. 2018c). Additionally, for the temporal analyses we used ALS data collected in 2013 and 2020 at SBE, and in 2020 at Danum Valley by the Malaysian company Ground Data Solutions, as well as in 2016 at SAFE as part of a wider ALS campaign of Sabah conducted by the Global Airborne Observatory (GAO; Asner et al. 2018).

Point cloud data from each survey were processed using LAStools (<https://rapidlasso.com/lastools>). After classifying the ground returns of the point cloud, a digital elevation model (DEM) was created. We then subtracted the elevations of non-ground points from the DEM to produce a normalised canopy height model (CHM) using a locally adaptive spike-free algorithm (Fischer and Jucker 2023, Fischer et al. 2024). The resolution of the CHMs was 1 m in all cases except for the 2016 data acquired by GAO at SAFE,

which have a resolution of 2 m due to the lower pulse density (approximately 2 pulse m⁻², compared to > 10 pulses m⁻² for all other datasets). All subsequent analyses are based on these CHMs and were conducted in R (ver. 4.1.0; www.r-project.org).

The geometric theory for surface habitats and its application to tropical forest canopies

Torres-Pulliza et al. (2020) developed a geometric theory of surface habitats, which defines the relationship between three structural metrics: height range (ΔH), surface rugosity (R) and fractal dimension (D). The three metrics describe variation in habitat structure across spatial scales, from an entire habitat patch (length L) down to grid cells of a minimum size (L_0) within habitat patches. Together, the three metrics form a surface descriptor that encodes the shape and geometry of a 3D surface based on the following equation:

$$\frac{1}{2} \log_{10}(R^2 - 1) + \log_{10}\left(\frac{L}{L_0}\right)(3 - D) = \log_{10}\left(\frac{\Delta H}{\sqrt{2L_0}}\right) \quad (1)$$

Equation 1 numerically links the three surface descriptors together, such that the value of any one metric can be calculated if the other two are known (see [Torres-Pulliza et al. \(2020\)](#) for details).

For the purposes of our analysis, we chose to set L_0 at 8 m as a compromise between the resolution of the underlying CHMs (1–2 m) and the desire to capture variation in height within individual tree crowns (see below for a sensitivity analysis assessing how the choice of L_0 impacts the estimation of ΔH , R and D). Maximum habitat patch size (L) was set as 800 m to cover at least two orders of magnitude in scale, as required when estimating fractal dimension ([Halley et al. 2004](#)).

Height range

ΔH is the difference between the highest and lowest elevation of the CHM in an entire habitat patch (L). [Torres-Pulliza et al. \(2020\)](#) expressed ΔH as $\log_{10}\left(\frac{\Delta H}{\sqrt{2L_0}}\right)$, which includes a term for the minimum patch size, L_0 . As this parameter will differ depending on the ecosystem and the resolution of the data, we instead use height range calculated on its original scale (in m) throughout this study to improve interpretability.

Surface rugosity

R is defined as the surface area (A) of the entire habitat patch divided by its planar area (L^2): $R = \frac{A}{L^2}$. There are multiple ways to estimate the surface area of a CHM. Here, we replicated the approach of [Torres-Pulliza et al. \(2020\)](#), which sums the area of each grid square at the smallest scale (L_0). This approach provides a lower-bound estimate of rugosity, as it takes the minimum possible surface area given the height range in the grid cell. We compared this approach to an alternative estimate of A derived using the *surfaceArea* function in the ‘sp’ package in R (www.r-project.org). The two measures of rugosity were tightly correlated (Pearson’s correlation coefficient, $r = 0.98$), but R estimates obtained using the *surfaceArea* function were systematically larger (60%) than those derived using the approach of [Torres-Pulliza et al. \(2020\)](#) (Supporting information).

Fractal dimension

Fractals are objects that exhibit self-similar structures across spatial scales, such as lines or surfaces that fold in a predictable way. The extent to which these structures fill space can be described by a fractal dimension (D) that lies between the classical Euclidian dimensions. D is well-defined only if the

underlying objects are or behave like fractals and exhibit scaling across several orders of magnitude, which is rare in ecology ([Halley et al. 2004](#), [Loke and Chisholm 2023](#)). Nonetheless, to assess the theory in its entirety, we calculated D following the approach used by [Torres-Pulliza et al. \(2020\)](#).

Specifically, D was calculated using the variation method ([Dubuc et al. 1987](#)), which quantifies how ΔH varies across spatial scales within a given surface. This involves first dividing a habitat patch (L) into progressively smaller squares of length L_x , where in our case x is a geometric sequence from 8 to 20, 50, 128, 320 and 800 m, with a common ratio of ~ 2.5 . At the smallest scale ($x = 8$ m), $L_x = L_0$ and ΔH is calculated across 10 000 separate patches each 8×8 m in size (64 pixels for a 1 m resolution CHM). At the largest scale ($x = 800$ m), $L_x = L$ and ΔH is calculated across the entire 800×800 m habitat patch (640 000 pixels for a 1 m resolution CHM).

We then calculated the mean ΔH observed at each of these x scales ($\overline{\Delta H_x}$) and regressed it against x on a log–log scale: $\log_{10}(\overline{\Delta H_x}) = \alpha + \beta \times \log_{10}(x)$, where α is the intercept of the regression and β is the slope coefficient. From this, D can then be calculated as $3 - \beta$. When ΔH at the smallest scale (L_0) is similar to that of the entire patch (L), $\beta \rightarrow 0$ and D will be high, reflecting a high degree of space filling across spatial scales. Conversely, the greater the difference between ΔH at L_0 and L , the greater the value of β and therefore the smaller the value of D . Note that a key assumption of the height variation method is that ΔH and x should scale linearly on log–log axes, indicating the relationship between the two is scale invariant ([Loke and Chisholm 2023](#)). A deviation from linear scaling would indicate that a surface is in fact not a true fractal ([Fischer and Jucker 2023](#)).

Testing the robustness of the geometric theory of surface habitats

Some of the assumptions of the geometric theory of surface habitats developed by [Torres-Pulliza et al. \(2020\)](#) have recently been called into question, particularly around the robustness and ecological interpretation of D ([Loke and Chisholm 2022](#)). However, the degree to which ΔH , R and D are sensitive to the scale of observation or the resolution of the underlying data has yet to be explicitly tested, which is critical if these metrics are to be used to compare structural complexity within and across ecosystems using different sources of 3D data.

We therefore devised a number of sensitivity analyses to assess the robustness of ΔH , R and D . First, we selected three large patches (2000×2000 m) of relatively homogeneous habitat in the 2014 CHMs from SAFE and Danum Valley – an old-growth forest, a selectively logged forest and an oil palm plantation – and used these data to test how each metric was impacted by:

- 1) The number of patch divisions across which height variation is calculated (hereafter referred to as the number of

- scales), which we varied from 3 to 10 while keeping the smallest scale (L_0) = 20 m and the largest scale (L) = 2000 m (i.e. 2 orders of magnitude difference).
- 2) The range of scales across which metrics were calculated (i.e. the difference between L_0 and L , which we increased progressively from 1 to 3 orders of magnitude by reducing L_0 from 200 m to 2 m while keeping L = 2000 m and the number of scales = 6).
 - 3) The smallest scale extent, which we varied from L_0 = 2 to 20 m while keeping the number of scales as 6 and the range of scales fixed at 2 orders of magnitude by increasing L from 200 to 2000 m.

Using these same data, we also tested the underlying assumptions of D . Specifically, we visually checked if ΔH_x scaled linearly with x on log–log axes or if instead it deviates from this pattern, which would indicate that canopies are not fractal.

Next, we used the 2014 data from SAFE and Danum Valley, which span a gradient from old-growth forests to oil palm plantations, to quantify how sensitive ΔH , R and D are to specific properties of the CHM. This includes the resolution of the data, for which we compared CHMs generated at 1 m versus 2 m resolution, as well as the presence of extreme height values (e.g. those caused by remnant trees in oil palm landscapes and possible noise in the ALS point cloud data).

Comparing ΔH , R and D with other metrics of canopy structure

To better understand how ΔH , R and D relate not just to each other but also to other widely used metrics of canopy 3D structure, we used the 2014 ALS data from SAFE and Danum Valley to derive a series of measures relating to canopy height, density and openness (Supporting information). Measures of canopy height included mean canopy height, maximum canopy height (99th percentile of the CHM) and the coefficient of variation of canopy height. These height metrics directly reflect variation in aboveground biomass and understory microclimate across human-modified tropical landscapes (Asner and Mascaro 2014, Jucker et al. 2018a). To capture canopy density we calculated the plant area index (PAI), which is a measure of plant area (i.e. leaves, branches and stems) per unit ground area. PAI values derived from ALS have been shown to correlate closely with aboveground woody biomass stocks and productivity in tropical forests (Milodowski et al. 2021, Wiczynski et al. 2022). Finally, to measure canopy openness, we calculated the total gap fraction and the number of gaps in the canopy, which reflect the legacy of past disturbance in these ecosystems (Jucker 2022, Reis et al. 2022, Zhang et al. 2023). Gaps were defined as openings in the canopy that extend to 2 m above the forest floor and that are at least 9 m² in size.

All metrics were calculated at 800 × 800 m scale to match ΔH , R and D . CHMs typically contain a small percentage of missing values (~ 1% in our case), due to things like low ALS scanning densities, atmospheric scattering and the presence

of water bodies. To avoid these having an undue effect on our results, prior to the analysis we removed forest patches where missing values made up > 10% of CHM pixels (4.2% of 800 × 800 m patches). Additionally, we removed seven patches where $\Delta H > 100$ m, as this exceeds the height of the tallest known tree in the region and therefore likely reflects artefacts in the CHM. This left us with 539 habitat patches of 800 × 800 m for the analysis (equivalent to 345 km²).

Characterizing the impacts of logging on canopy structural complexity

To quantify the impacts of logging and forest degradation on canopy structural complexity, we used a space-for-time substitution to compare ΔH , R and D among forest patches subjected to varying degrees of human disturbance. To do this, we began by using the 2014 CHM data to select 24 landscape patches (each 800 × 800 m in size, black squares in Fig. 2) that were representative of the habitat classes described previously: six old-growth forest plots (three at Danum Valley and three at Maliau Basin), six recovering logged forest plots, six recently logged forest plots, as well as six oil palm plantation plots (three each in mature and young oil palm). We then used one-way ANOVAs to compare values of ΔH , R and D between plots in each habitat type.

To complement this targeted approach, we also used the CHMs from SAFE and Danum Valley to explore how ΔH , R and D vary across the broader landscape (539 forest patches described above). Each forest patch was classified as either ‘forest’ (including both old-growth and logged forests) or ‘non-forest’ (including oil palm and heavily degraded scrub vegetation) using an existing habitat map of the study area (Swinfield et al. 2020) and we used t -tests to compare mean values of ΔH , R and D between these two broad habitat classes.

Tracking shifts in canopy structural complexity through time

To capture shorter-term temporal changes in canopy structural complexity driven by both disturbance and recovery processes, we used repeat ALS data acquired at SAFE, SBE and Danum (Fig. 3). The SAFE landscape provided an opportunity to examine the impacts of salvage logging on ΔH , R and D . Between the 2014 and 2016 ALS surveys, portions of the SAFE landscape that had been earmarked for future conversion to oil palm were salvage logged to extract all remaining merchantisable timber prior to establishing the plantations. By comparing ΔH , R and D just before and after salvage logging, we were able to capture the immediate effects of this extreme human disturbance on habitat 3D structure. SBE instead allowed us to test how canopy structural complexity recovers when selectively logged forests are actively restored, which we did by tracking changes in ΔH , R and D between 2013 and 2020 to give a snapshot of forest recovery through this period. Finally, in addition to these human-modified landscapes, we quantified changes in the structural complexity of old-growth forests impacted by natural disturbance.

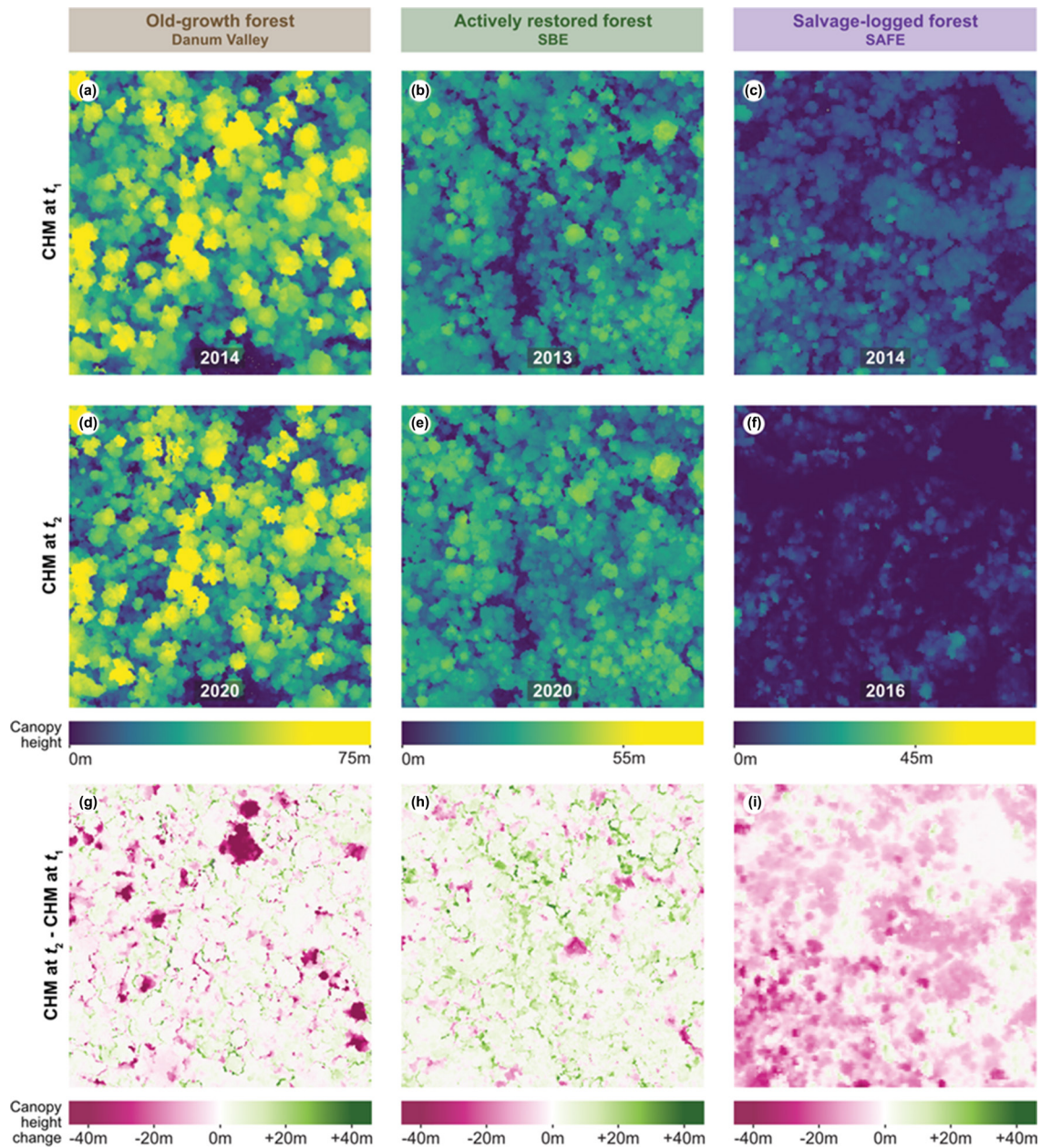


Figure 3. Representative examples of temporal changes in the canopy height models (CHM) of old-growth forests (Danum Valley, left), restored logged forest (Sabah Biodiversity Experiment, middle) and salvage logged forests (Stability of Altered Forest Ecosystems, SAFE project, right). Each tile corresponds to an area 300×300 m in size. The top row of panels shows the CHM at the first time point, while the middle row is the second period (dates indicated in each panel). The bottom row of panels shows the difference in height between the two acquisitions, with pink denoting areas of height loss and green showing areas of height gain.

For this we used the 2014 and 2020 data from Danum Valley to test how ΔH , R and D were impacted by a localised windthrow event that occurred in 2017 and brought down several large, canopy-dominant trees in the area.

Within each of the three sites, we established three 800×800 m plots within the area of overlapping ALS data (white squares in Fig. 2) and used these to calculate changes in ΔH , R and D over time. These small sample sizes are due to the relatively limited degree of overlap between ALS surveys. Because

of this, observed differences between the two time periods were compared in qualitative terms rather than using formal statistical tests. Note also that the 2016 CHM from SAFE was generated at 2 m resolution, instead of 1 m like in all other cases. To ensure ΔH , R and D values were directly comparable between the two surveys, we applied a correction factor to the 2016 data which we developed by comparing 1 m and 2 m resolution CHMs generated using the 2014 data (see the Supporting information and Results section for details).

Results

Robustness of ΔH , R and D

Of the three structural metrics put forward by Torres-Pulliza et al. (2020) in their geometric theory of surface habitats, only ΔH proved robust to changes in the spatial extent and scale across which it was calculated (Fig. 4), as well as the resolution of the CHM (Supporting information). Predictably, we did find that removing extreme height values (top 1%) from the CHM caused ΔH to shrink by 14 m (24%) on average, but relative differences in ΔH among habitat types were unaffected by this (correlation between ΔH before and after the removal of extreme values = 0.93; Supporting information).

By contrast, both R and D varied considerably when we changed the spatial extent and range of scales across which they were calculated (Fig. 4). Specifically, D decreased by 8.8% when we increased the range of scales across which it was calculated from 1 to 3 orders of magnitude (Fig. 4d), and instead increased by 15% when we increased the minimum scale (L_0) from 2 to 20 m (Fig. 4f). Meanwhile, R increased by 35.2% when we increased the range of scales from 1 to 3 orders of magnitude (Fig. 4g) and decreased by 8.4% when we increased L_0 from 4 to 20 m (Fig. 4i). Beyond this ($L_0 > 20$ m), R was severely underestimated, with values approaching 1 (i.e. canopy surface area = ground area; Fig. 4g). These shifts in D and R were observed in all three habitat types (although to a lesser degree in the oil palm landscape

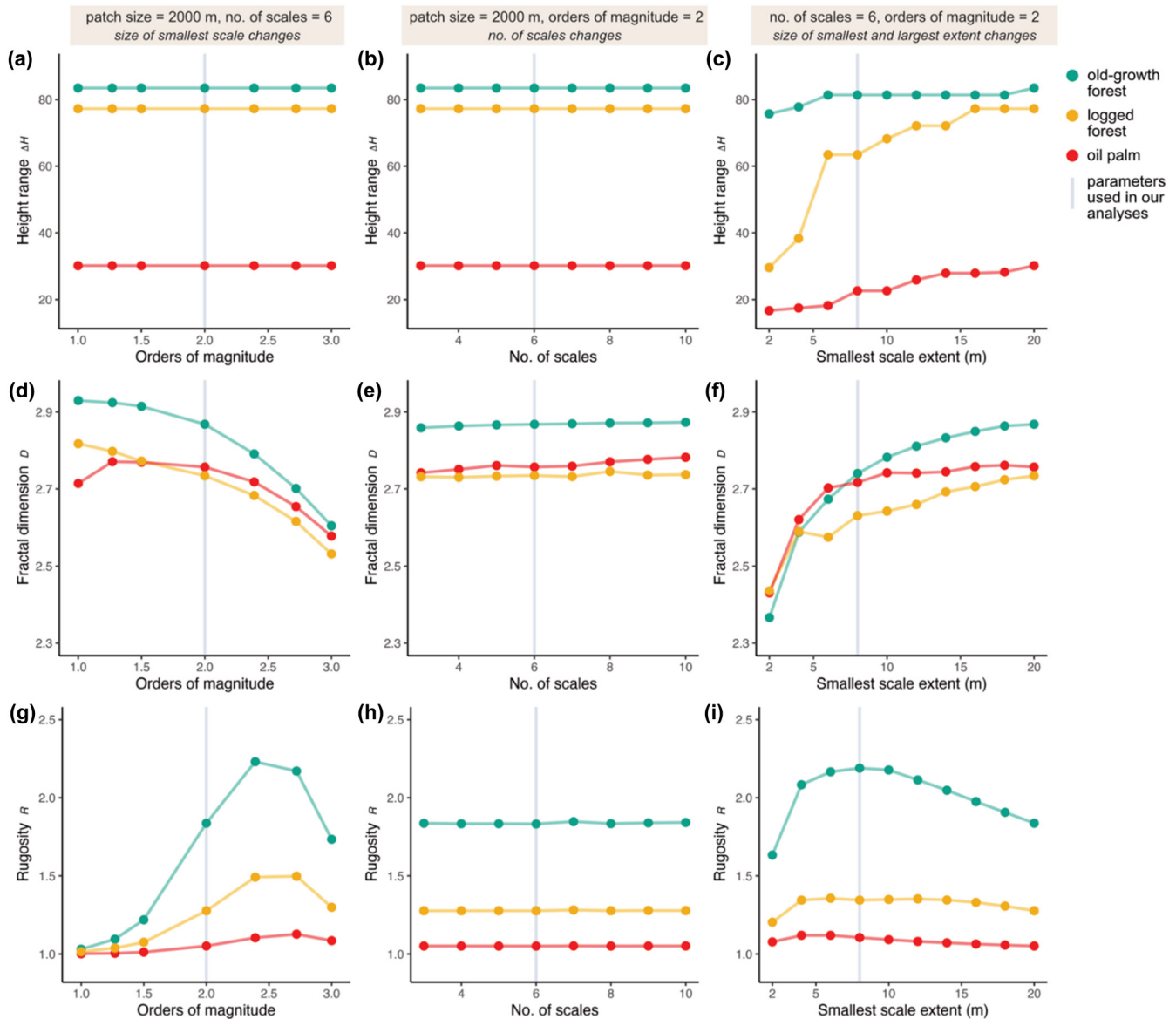


Figure 4. Sensitivity analyses to test the effect of scaling range (orders of magnitude), number of scales and smallest scale linear extent (L_0) on each of the three surface descriptors that make up the geometric theory for surface habitats. Vertical grey lines indicate the parameters used elsewhere in this study.

compared to old-growth and selectively logged forests) and were similar in magnitude to the differences between habitats observed for the default set of parameters used in subsequent analyses (vertical grey lines in Fig. 4).

D was also sensitive to the removal of extreme height values, while R was not. Removing the top 1% of height values caused D to increase by 2.6% on average (Supporting information). However, these shifts were not consistent across habitat, being greatest in recently logged forests (3.9%) and oil palm (3.5%) and then progressively smaller in recovering (2.4%) and old-growth forests (0.6%) – meaning that D estimates calculated before and after the removal of extreme values were only weakly correlated with each other ($r=0.5$, $p=0.01$). To a lesser degree, D was also sensitive to the resolution of the CHM (Supporting information), although in this case D estimates calculated using 1 m and 2 m resolution CHMs were tightly correlated ($r=0.94$). Finally, we also found that ΔH did not scale linearly with x on log-log

scales, especially in old-growth canopies (Supporting information). Instead, ΔH decreased slowly across a broad range of spatial scales (100–2000 m), before then declining rapidly at the smallest scales (20–50 m), indicating that ΔH is not scale invariant and that forest canopies are not true fractals.

Relationship between ΔH , R and D and other metrics of canopy structure

Across the 539 habitat patches at SAFE and Danum Valley that include everything from old-growth forests to oil palm plantations, we found that R was strongly positively correlated with both D ($r=0.66$; Fig. 5a) and ΔH ($r=0.75$; Fig. 5b). By contrast, D and ΔH were only weakly correlated with one another ($r=0.18$; Fig. 5c). When we compared ΔH , R and D to other metrics of canopy structure (Supporting information), we found that ΔH and R increased as forest canopies became taller, as both were strongly positively correlated with

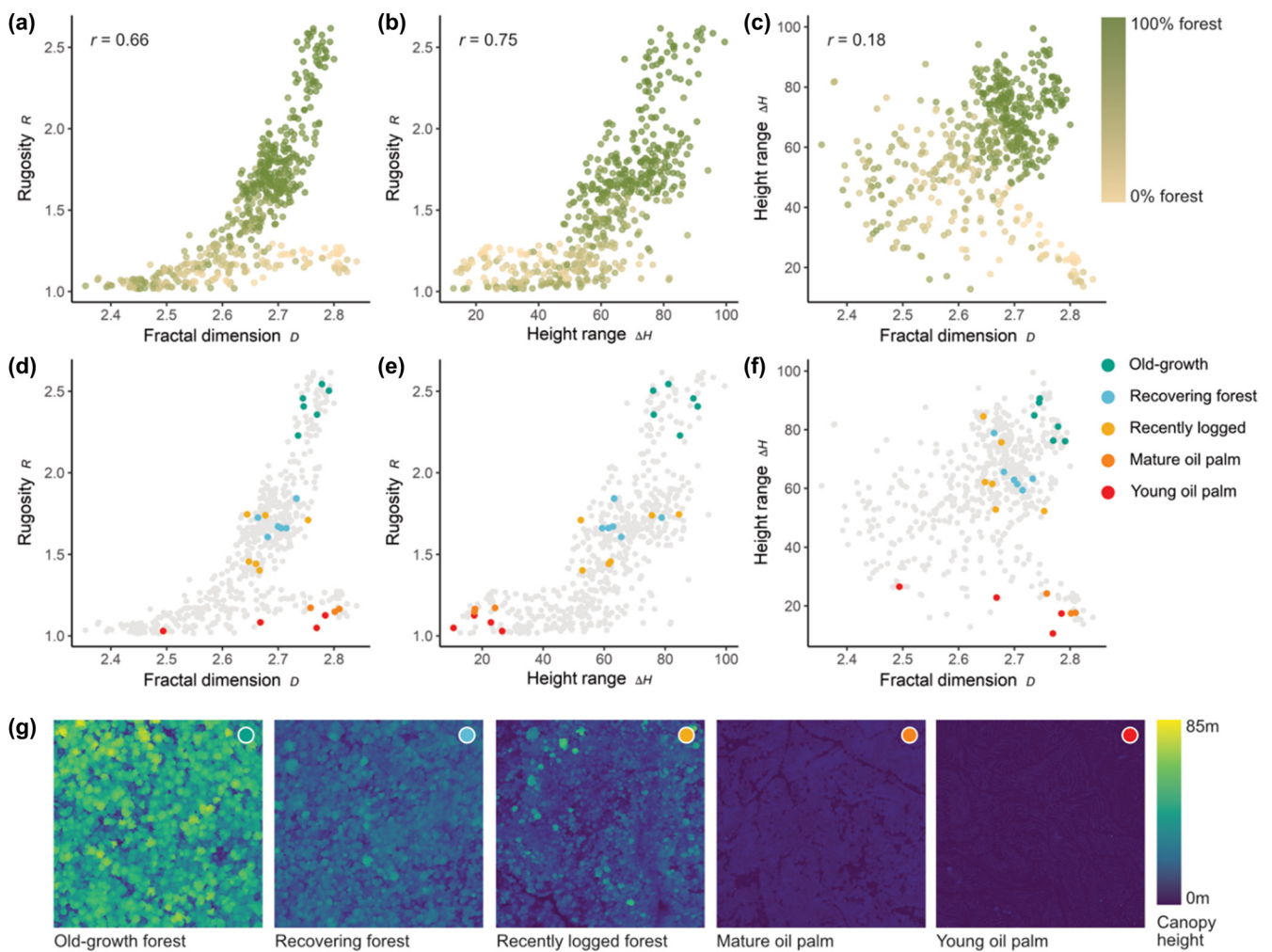


Figure 5. Structural complexity of a tropical forest landscape along a forest disturbance gradient. Pearson's correlation coefficients (r) for the pairwise relationships between each of the three surface descriptors are reported in panels (a)–(c). Points are coloured according to their proportion of forest versus non-forest pixels over a contiguous grid of 800×800 m forest patches ($n=539$) covering a mixed landscape. In panels (d)–(f), plots representing a single category within the disturbance gradient are overlaid onto the mixed landscape points in grey. Canopy height models (g) for each of the forest categories show canopy height captured by airborne laser scanning.

mean canopy height (ΔH : $r=0.70$; R : $r=0.90$) and maximum height (ΔH : $r=0.87$; R : $r=0.91$). The same picture emerged for PAI, which itself was strongly correlated to mean canopy height ($r=0.98$). D was instead strongly negatively associated with both the coefficient of variation of height ($r=-0.85$) and with gap fraction ($r=-0.83$), peaking in forest patches with spatially homogenous canopy height and cover. Meanwhile, none of the above metrics was strongly correlated with the number of canopy gaps ($|r| < 0.40$ in all cases; Supporting information), which emerged as an independent axis of variation of canopy structure.

Characterising the impacts of logging on canopy structural complexity

When calculating ΔH , R and D using our default parameters ($L_0 = 8$ m; range of scales = 2 orders of magnitude; number of scales = 6), we found that together the three metrics were able to tease apart some but not all differences between major habitat classes (Fig. 5d–f). Specifically, we found clear, significant differences in ΔH and R between old-growth forests ($\Delta H=83$ m; $R=2.4$), logged forests ($\Delta H=65$ m; $R=1.6$) and oil palm plantations ($\Delta H=19.5$ m; $R=1.1$), with mean values of both metrics decreasing progressively along this gradient of forest degradation and conversion (Fig. 5e, Supporting information). However, neither metric was able to distinguish between recovering ($\Delta H=65.2$ m; $R=1.7$) and recently logged forests ($\Delta H=64.8$ m; $R=1.6$), nor between young ($\Delta H=19.3$ m; $R=1.1$) and mature oil palm plantations ($\Delta H=19.8$ m; $R=1.2$), despite clearly visible differences in their CHMs (Fig. 5g). D was statistically indistinguishable between any of the habitat classes (Fig. 5d, Supporting information). Mean D values decreased when transitioning from old-growth (2.76) to logged forests (2.69), but then increased again in oil palm plantations (2.73), which also exhibited the greatest range of D estimates (2.49–2.81).

When characterising variation in ΔH , R and D across the broader landscape, we found that both ΔH and R (mean \pm 1SD) were significantly greater in forest ($\Delta H=67.0 \pm 13.9$ m; $R=1.68 \pm 0.37$) than non-forest habitats ($\Delta H=42.0 \pm 15.8$ m; $R=1.16 \pm 0.09$; $p < 0.001$ in both cases; Fig. 5b). D was also marginally higher in forests (2.67 ± 0.08 versus 2.61 ± 0.11), but while this difference was statically significant ($p < 0.001$) we observed almost complete overlap in the range of D values in these two broad habitat classes (Fig. 5c). Moreover, we found that relationships between D and both ΔH and R were notably different in habitat patches classified as forest and non-forest (Fig. 5a–c). In forest patches R and D were tightly coupled, with high D values only found in areas with high R (green points in Fig. 5a). By contrast, in non-forest patches we observed a wide range of D values despite little or no variation in R , which was consistently low (tan points in Fig. 5a). Similarly, in forests we found that D was positively (albeit weakly) correlated with ΔH (green points in Fig. 5c; $r=0.48$, $p < 0.001$), but the opposite was true for non-forest patches (tan points in Fig. 5c; $r=-0.65$, $p < 0.001$).

Tracking shifts in canopy structural complexity through time

When tracking changes in ΔH , R and D over time at SAFE, SBE and Danum Valley, we found clear and distinct directional shifts that reflected the disturbance and recovery processes that characterise each site (Fig. 6). At SAFE, we found that forests subjected to salvage logging showed a shift towards lower values of ΔH , R and D (Fig. 6h–j), consistent with the targeted removal of remnant trees (Fig. 3). At SBE, we instead observed that both R and D increased in unison over the 7-year period of recovery from logging, while ΔH remained constant (Fig. 6e–g). This pattern was driven by a combination of rapid gap closure, progressive canopy height growth and a limited number of new canopy gap openings occurring during this initial regeneration phase (Fig. 3). A similar pattern emerged for old-growth forests at Danum Valley impacted by a windthrow in 2017 (Fig. 6b–d), where the formation of new canopy gaps caused by the mortality of large trees led to an increase in both R and D (Fig. 3).

Discussion

Using a framework initially developed for characterising the surface complexity of coral reefs, we tested whether three structural features of tropical rainforest canopies – their height range, rugosity and fractal dimension – can capture their past disturbance history and predict their subsequent recovery trajectories. We found that together, these three metrics of surface complexity captured major transitions in canopy 3D structure between highly degraded, selectively logged and old-growth forests (Fig. 5). Moreover, they were able to detect distinct temporal patterns of structural change following disturbances from logging and windthrows (Fig. 6). However, we also uncovered several important limitations with the geometric framework of habitat complexity (Fig. 4). Here we explore the key insights gained from applying this framework to a new ecosystem, before charting a way forward for characterising forest structural complexity in a robust and ecologically intuitive way.

Tracking changes in tropical forest canopy structural complexity through space and time

Height range (ΔH) at the patch scale (800×800 m) emerged as a key structural axis separating out habitat types along the disturbance gradient (Fig. 5). At this spatial scale, ΔH is a proxy for maximum tree height ($r=0.87$). This is because forest canopies are ‘porous’ and replete with gaps (Fig. 5g), meaning that if we search over a large enough area (typically > 1 ha; Zhang et al. 2023) the minimum canopy height will always be close to ground level, irrespective of the disturbance history. Given that variation in ΔH can be interpreted in terms of differences in maximum tree height, our results highlight the ‘fast out, slow in’ nature of disturbances such as logging or large windthrows (Chambers et al. 2013,

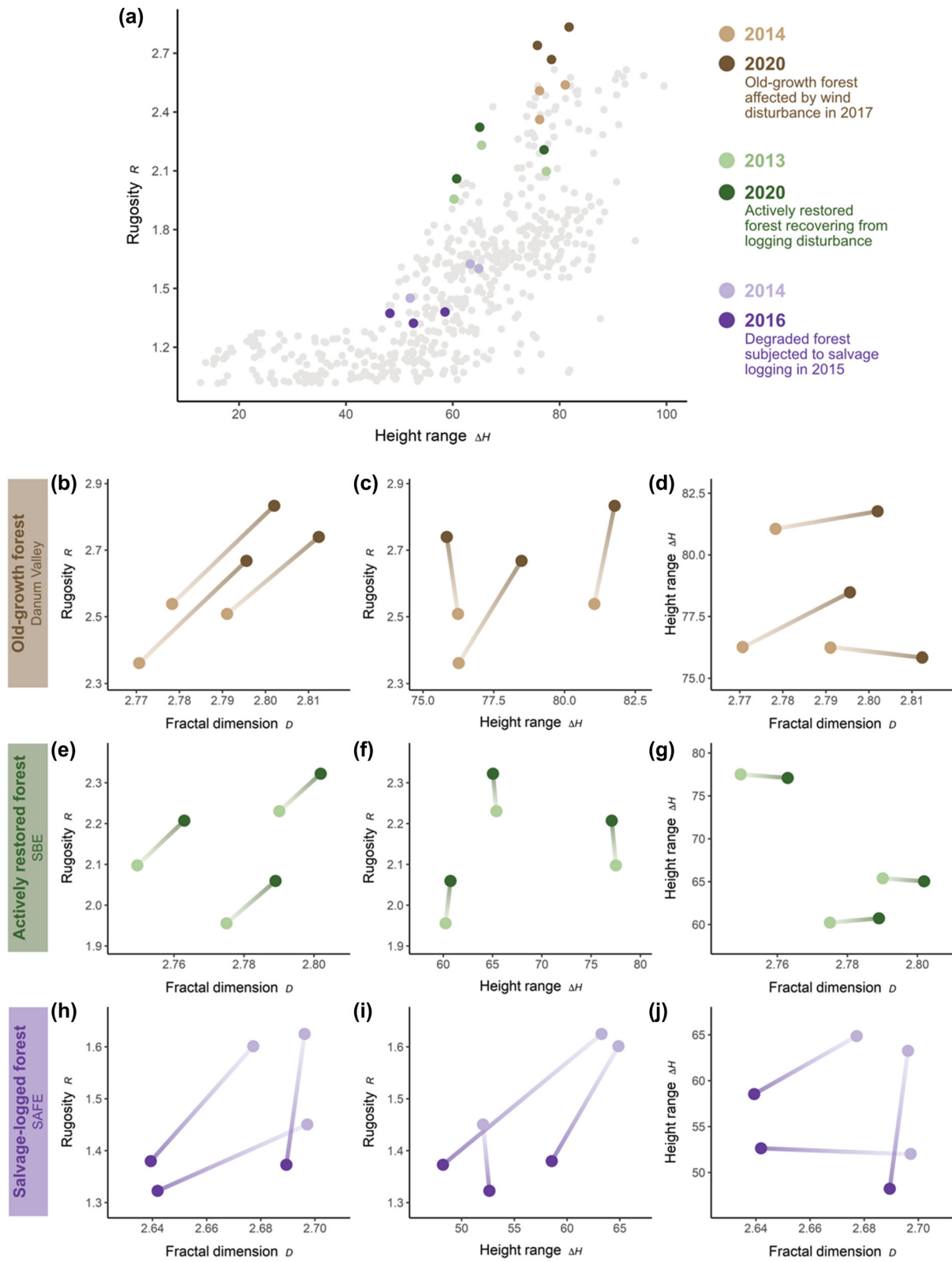


Figure 6. Change in structural complexity over time in wind-disturbed old-growth forest (b–d); in forests recovering from logging (e–g); and in actively logged forests being converted to oil palm plantation (h–j). Time series pairs are plotted in relation to the variation in structural complexity exhibited at the landscape level (a). SAFE, Stability of Altered Forest Ecosystems; SBE, Sabah Biodiversity Experiment.

Lutz et al. 2018, Poorter et al. 2021). By removing the largest trees, these severe disturbances cause an almost instantaneous drop in aboveground biomass, while the subsequent recovery of structural attributes linked to the presence of large trees can take decades or even centuries (Poorter et al. 2021).

The fact that we detected a clear difference in ΔH between old-growth and logged forests at the patch scale illustrates how selective logging removes almost all large trees from the landscape (Fig. 5g). However, we did not find a clear difference in ΔH between recently logged and recovering forests, even though these vary noticeably in both their 3D structure and dynamics (Riutta et al. 2018, Milodowski et al. 2021, Scheeres et al. 2023). The reason for this seems to be in the relatively coarse scale of observation (i.e. 800×800 m): two forest patches could have very different tree size structures, but as long they contain just a handful of remnant large trees and canopy gaps (which is almost inevitable at this scale; see Fig. 5g), they will have very similar ΔH values. However, this finding also points to a more fundamental difference in the way processes like mortality and growth of individuals impact structural complexity metrics such as ΔH in ecosystems like coral reefs and forests. When a coral dies, its skeletal structure becomes a substrate upon which new corals can grow (Bozec et al. 2015). Instead, in forests the maximum height of the canopy is shaped by the environmental conditions in which trees grow (Zhang et al. 2016, Gorgens et al. 2021, Jucker et al. 2022), while tree mortality creates empty space in the form of canopy gaps (Jucker 2022), both of which constrain variation in ΔH across spatial scales (Fischer and Jucker 2023).

This variation in ΔH across spatial scales is what ultimately determines the fractal dimension (D) of the canopy, which emerged as an independent axis of variation in structural complexity from canopy height (Fig. 5c). Our analysis confirmed previous findings that forest canopies are not true fractals beyond the scale of the individual tree (Fischer and Jucker 2023). Nonetheless, exploring how ΔH varies across spatial scales using fractal dimension as an index allowed us to detect major differences in the structure of forest and non-forest habitats (the latter corresponding to highly degraded scrub vegetation and oil palm plantations). In forests, we found that D increased progressively when going from recently logged to old-growth forests. This reflects the fact that in heavily disturbed forests ΔH is much more variable across the landscape due to the scattered presence of remnant large trees (Fig. 5g, Supporting information). This causes a greater difference in mean ΔH between the smallest (8×8 m) and largest scale of observation (800×800 m), which in turn leads to a lower estimate of D.

By contrast, we instead found that fractal dimension increased when transitioning from forest to non-forest habitats, peaking in oil palm plantations. This may seem counter-intuitive if we associate fractal dimension with ‘complexity’, but makes perfect sense if we consider that oil palm plantations consist of an even-aged monoculture planted in a regular grid structure. This inevitably causes ΔH to be very similar across scales (low coefficient of variation in height;

Supporting information), resulting in high values of D. In this regard, D can be thought of as a measure of homogeneity across scales, which may not necessarily conform with our a priori expectations of what constitutes a ‘complex’ ecosystem.

From a temporal perspective, we were able to capture the structural transition between forest and non-forest habitats in areas of the SAFE landscape that were salvage logged prior to conversion to oil palm (Fig. 6). Specifically, salvage logging led to a coordinated decline in height range, rugosity and fractal dimension, shifting what were previously logged forests into a new, highly degraded structural state. By contrast, when we compare the temporal trajectories of restored forests recovering from logging disturbance and old-growth forests impacted by a windthrow event, we observed something unexpected. Specifically, these two very different processes (recovery and disturbance) resulted in the same pattern of change: a coordinated increase in both fractal dimension and rugosity, accompanied by little or no change in height range (Fig. 6).

At SBE, where forests canopies are recovering from logging in the late 1980s, this pattern reflects a general trend toward rapid gap closure, progressive canopy height growth and a limited number of new canopy gap openings occurring during this initial regeneration phase (Zhang et al. 2023; Fig. 3). This led to an overall increase in the height of the canopy (which causes rugosity to increase; Fig. 1), but not in an increase in ΔH over the short term. This is because most of the rapid regrowth occurs within gaps, not in the tall remnant emergent trees. This pattern of gap filling also explains why we observed an increase in fractal dimension over time, as it reduces the spatial variability in ΔH over the landscape caused by logging – slowly erasing the fingerprint of logging disturbance that we observed when comparing recently logged and recovering forests (Fig. 5, Supporting information).

In the old-growth forests of Danum Valley, the opposite process – gap formation following a windthrow event – led to the same pattern of increasing rugosity and fractal dimension. In this system, where maximum canopy height has reached a quasi-equilibrium, the formation of new gaps resulting from the mortality of large emergent trees leads to localised increases in height variation (Fig. 3). This in turn increases both rugosity and fractal dimension (middle panel of Fig. 1). However, at the whole patch scale (800×800 m) ΔH is unaffected by this type of windthrow disturbance, as only some of the emergent trees are brought down, leaving maximum canopy height effectively unchanged. This highlights a major difference in the way natural disturbances impact canopy 3D structure compared to selective logging, which by systematically targeting large trees can reduce ΔH even across large spatial scales (Okuda et al. 2003, Rutishauser et al. 2016, Milodowski et al. 2021).

A general framework for characterising structural complexity across ecosystems: holy grail or poisoned chalice?

If we were to list some of the features that we would want from a set of structural metrics designed to characterise

habitat structural complexity, three key aspects seem particularly important. First, these metrics should be both intuitive to interpret and ecologically meaningful (e.g. ones directly related to habitat diversity and microclimate). Second, they should be complementary to each other, capturing independent facets of ecosystem 3D structure and dynamics. And third, they should be computationally simple and robust to calculate. Together, these features can provide a framework that is widely applicable across ecosystems and data inputs, while also limiting their misuse.

When we assess the geometric theory of surface habitats against these criteria, a number of potential issues emerge. First, our analysis confirmed previous findings that canopy surfaces deviate substantially from fractality (Loke and Chisholm 2022, Fischer and Jucker 2023). This calls into question whether we should be calculating fractal dimension when we know these theoretical assumptions are violated. More generally, it raises the issue of how to interpret values of D from an ecological perspective. In their paper, Torres-Pulliza et al. (2020) interpret D as a measure of niche diversity, and hypothesise that habitats with higher D should harbour greater species diversity. But, as our analysis clearly shows, D is actually a measure of homogeneity in height variation across scales. Consequently, when applied to human-modified tropical forests, D peaked in oil palm plantations – the most highly transformed and least biodiverse habitat considered in our analysis (Malhi et al. 2022, Zemp et al. 2023).

Even more concerning is how sensitive D was to even small changes in the underlying data (e.g. the range of scales across which it was calculated, the smallest scale extent and the removal of extreme CHM values; Fig. 4, Supporting information). The choices we made when calculating D had a major impact on our estimates of fractal dimension, suggesting that values of D are not comparable within and across ecosystems. To avoid the conceptual, theoretical and methodological limitations of D , one could instead calculate a much simpler alternative metric: the percent change in average height variation between the smallest and largest scales (Fischer and Jucker 2023). This has the advantage of being more easily interpretable and overcomes the need to assume scale-invariance, while still capturing how height variation changes across spatial scales (Atkins et al. 2023b). Alternatively, our analysis suggests that the coefficient of variation of the CHM was strongly negatively correlated with D ($r = -0.85$), providing another robust and intuitive solution to measuring spatial heterogeneity of surface heights.

While height range and rugosity were generally less problematic than fractal dimension, they also presented several issues. First, these two metrics are strongly positively correlated and therefore do not capture independent axes of variation in canopy structure (Fig. 5b). This is an inevitable consequence of the way rugosity is calculated, as any increases in canopy height will also increase canopy surface area (Fig. 1). An obvious solution would be to scale rugosity by canopy height, calculating a normalised rumple index (Fischer and Jucker 2023). A second issue is that ΔH calculated at 800×800 m was only of limited use when attempting to characterise

disturbance and recovery processes. This is because only the most severe disturbances (e.g. systematic selective logging and conversion to oil palm) remove all large trees at this scale. A better way to capture differences in canopy height structure at these large scales would be using mean canopy height. Alternatively, if wanting to retain a measure of maximum canopy height, we suggest calculating it at finer spatial grains (e.g. reducing the maximum patch size to 200×200 m led to much clearer differences in ΔH between logged and old-growth forests; Fig. 4c).

Taken together, our findings suggest that ecosystem-specific approaches to characterising habitat structural complexity are likely to prove more fruitful than efforts to draw cross-ecosystem comparison such as those envisioned by Torres-Pulliza et al. (2020). When it comes to characterising the 3D structure of forest canopies using ALS, there are several practical steps one could take to improve robustness and ecological relevance. First, in terms of selecting which structural metrics to use, it is important to be aware that some metrics are considerably more sensitive to ALS acquisition parameters than others. For instance, CHM-derived metrics tend to be much more comparable across ALS platforms than ones calculated directly from point cloud data (Zhang et al. 2024). But even among CHM-derived metrics there can be considerable differences, with metrics designed to measure canopy openness and heterogeneity being more sensitive to features such as point density and scan angle compared to height metrics (Fischer et al. 2024, Zhang et al. 2024). Recent work from dry forests suggests that a combination of mean and maximum height, coefficient of variation of height, gap fraction and normalised rumple index (all calculated from a CHM) are more than sufficient to capture the spectrum of canopy structural types observed across the landscape, while also being computationally robust (Zhang et al. 2024).

Another key aspect to consider is the spatial grain at which metrics are calculated (Atkins et al. 2023b). As discussed previously, metrics such as maximum height may be of limited use in detecting disturbance when calculated at coarse spatial grains (> 4 ha), as these exceed the average size of the disturbance events themselves. Mean canopy height or gap fraction will generally be more informative at these scales, as they are less affected by outliers. However, if we increased the spatial scale too much (> 10 ha), we may miss important underlying gradients in forest structure that unfold over short distances, such as those associated with topography (Jucker et al. 2018b, Muscarella et al. 2020). By contrast, metrics capturing the spatial organization of canopy elements – such as the number and size distribution of gaps – are inherently challenging to quantify robustly at small or intermediate spatial grains (< 50 – 100 ha) due to small sample sizes (Zhang et al. 2023).

Finally, an important but often overlooked component is the CHM itself and the approach used to generate it. Recent work has shown that applying different CHM algorithms to the same ALS data can result in big differences in height estimates (as much as 10 m), and even bigger discrepancies in the retrieval of canopy gaps (Fischer et al. 2024). This presents a real challenge when attempting to combine

and compare CHMs, especially when tracking changes over time and when comparing datasets with large differences in pulse densities. To mitigate these biases, it is important to use CHM algorithms that are stable to difference in ALS data quality, such as the locally adaptive spike-free routine used here (Fischer et al. 2024). We also recommend comparing results derived from multiple different CHM algorithms and reporting sufficient details on which were used.

Forests are more than just their surfaces

Our ability to generate accurate 3D representations of real-world ecosystems has improved dramatically in recent years, leading to a growing interest in developing general approaches for quantifying habitat structural complexity that can be applied across ecosystems and at scale (Calders et al. 2020, Torres-Pulliza et al. 2020, Valbuena et al. 2020, Ehbrecht et al. 2021, LaRue et al. 2023). Surface properties of forest canopies, like those presented here, show great promise for understanding how environmental conditions drive variation in canopy structure (Jucker et al. 2018b, Gorgens et al. 2021), for monitoring disturbance and recovery processes (Ordway and Asner 2020, Reis et al. 2022, Choi et al. 2023) and can even serve as early warning signals of ecosystem change (Veldhuis et al. 2022, Kéfi et al. 2024). However, striving for a general, cross-ecosystem approach to characterising structural complexity might not always be practical or advisable. For instance, there may be features or processes that are unique to a particular ecosystem, and therefore require more tailored solutions. A perfect example is the difference between the hard, mostly filled surface of a coral reef and the highly porous, multi-layered canopy of a forest. In the latter, accounting for the size, number and spatial distribution of empty spaces (gaps) becomes much more important (Jucker 2022, Reis et al. 2022), as does capturing the vertical arrangement of leaves, branches and tree crowns (Milodowski et al. 2021, Scheeres et al. 2023). For instance, two forests could have very similar surface properties (e.g. height, rugosity), but very different approaches to space filling (e.g. different size distribution of individual trees, leaf vertical profiles or total leaf area). When striving for generality we must take care not to miss the subtle but crucial details that can help us understand the processes that shape the structure and dynamics of ecosystems, and how these are responding to global change.

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Author contributions

Alice Rosen: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Fabian Jörg Fischer:** Conceptualization (supporting); Data curation (equal); Formal analysis (supporting); Methodology (equal); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **David Coomes:** Data curation (supporting); Funding acquisition (equal); Writing – review and editing (supporting). **Toby D. Jackson:** Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Gregory P. Asner:** Data curation (supporting); Funding acquisition (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Tommaso Jucker:** Conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Methodology (equal); Supervision (lead); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://datadryad.org/stash/dataset/doi:10.5061/dryad.tmpg4f55v> (Rosen et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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