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Tansley insight

Deciphering the fingerprint of disturbance on the three-dimensional structure of the world's forests

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Summary

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Key words: airborne laser scanning, canopy gaps, forest dynamics, gap size frequency distributions, individual-based forest models, LiDAR, point pattern analysis, remote sensing.

Canopy gaps and the processes that generate them play an integral role in shaping the structure and dynamics of forests. However, it is only with recent advances in remote sensing technologies such as airborne laser scanning that studying canopy gaps at scale has become a reality. Consequently, we still lack an understanding of how the size distribution and spatial organization of canopy gaps varies among forests ecosystems, nor have we determined whether these emergent properties can be reconciled with existing theories of forest dynamics. Here, I outline a roadmap for integrating remote sensing with field data and individual-based models to build a comprehensive picture of how environmental constraints and disturbance regimes shape the three-dimensional structure of the world's forests.

I. Introduction

When a tree dies in a forest, a gap in the canopy is left in its place – a fingerprint of disturbance. Ecologists have long been fascinated by canopy gaps and the processes that create them, as these disturbance events are the engine that drives forest dynamics. By letting light flood the forest floor, they kick-start a vertical race for space among trees in the understorey (Wright *et al.*, 2003). This process ultimately drives the successional dynamics of forests and shapes the three-dimensional (3D) structure of their canopies, the primary interface between the biosphere and the atmosphere in terms of energy, carbon and water fluxes (Nakamura *et al.*, 2017).

Moreover, gaps provide key insights into how trees partition and fill canopy space (Purves *et al.*, 2008; Jucker *et al.*, 2015; Taubert *et al.*, 2015), which in turn influences how much carbon forests store above ground (Jucker *et al.*, 2018a; Meyer *et al.*, 2018). Consequently, by taking a snapshot of the number, size and spatial arrangement of canopy gaps in forests, we can learn a lot about how environmental constraints and disturbance regimes shape their structure, composition and function.

Traditionally, ecologists have studied the distribution and dynamics of canopy gaps by painstakingly mapping them in the field (Brokaw, 1982). However, because the disturbance events that lead to gap formation are rare and haphazard, locating and accurately measuring gaps from the ground is immensely challenging. Unsurprisingly, in recent years researchers have therefore turned to remote sensing as a way of identifying canopy gaps from above. In particular, airborne laser scanning (ALS, or LiDAR) has

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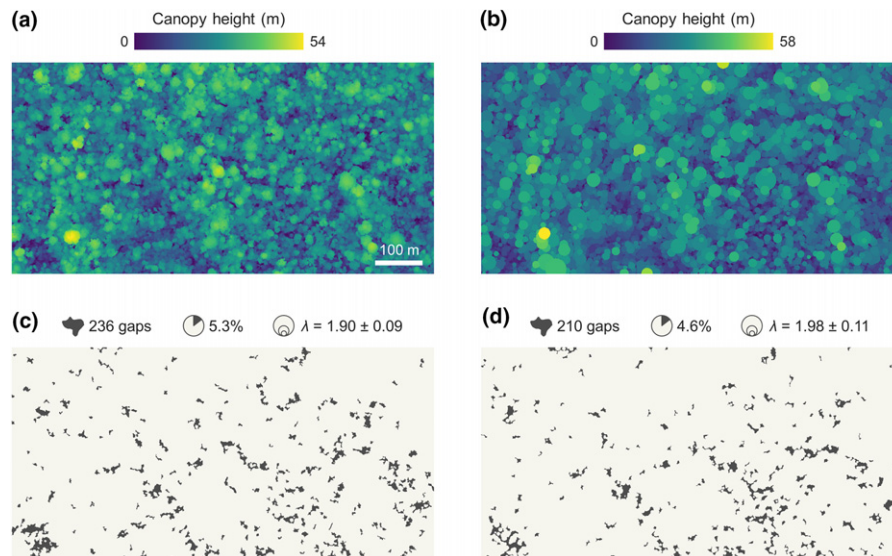


Fig. 1 Making sense of forest canopy gaps using airborne laser scanning (ALS) and individual-based forest simulators. (a) A 1-m-resolution canopy height model (CHM) derived from ALS data acquired over the 50 ha forest dynamics plot at Barro Colorado Island (BCI) in Panama. (b) The CHM was used to map all canopy gaps $\geq 25 \text{ m}^2$ that extend to $\leq 10 \text{ m}$ from the forest floor. A total of 236 gaps were identified, corresponding to a gap fraction of 5.3%. Gap sizes at BCI were observed to follow a power-law distribution with a scaling exponent (λ) of 1.90 ± 0.09 . (c) Observed canopy gaps are compared to those simulated using Canopy Constructor, which combines field inventory and ALS data from the 50 ha plot to generate a virtual CHM of the study site based on a series of allometric and crown packing rules (Fischer *et al.*, 2020). (d) This approach is able to faithfully re-create the number, size and spatial arrangement of canopy gaps observed across BCI. ALS data from BCI are archived on the STRI GIS data portal (<https://stridata-si.opendata.arcgis.com>), while census data from the 50 ha plot are available through Condit *et al.* (2019).

revolutionized our ability to measure canopy gaps at scale (Fig. 1a, b). By using ALS to generate detailed 3D canopy height models of entire landscapes (Jucker *et al.*, 2018b), today we can map the location, size and shape of hundreds of thousands of gaps at any desired height threshold above ground with just a few lines of code (Silva *et al.*, 2019). However, despite growing access to ALS data and numerous studies illustrating its power for studying canopy gaps (Kellner & Asner, 2009; Asner *et al.*, 2013; Goodbody *et al.*, 2020), we continue to miss a global picture of how and why gap size and spatial structure vary across different forest ecosystems and disturbance regimes. Moreover, we have no theoretical framework linking canopy gaps to the types of structural parameters that are routinely measured in the field, such as tree size distributions and above-ground carbon stocks.

To tackle this challenge, here I begin by synthesizing what we have learned from over a decade of using ALS to study canopy gaps, highlighting major milestones and key questions that remain unanswered. I then discuss how individual-based models could provide the key to unlocking how canopy gaps emerge from basic properties of forest communities, such as the size, number and demography of individual trees. In doing so, I outline a framework for reconciling canopy gaps with existing theories of forest dynamics and generating testable hypotheses about why gap size structure and spatial arrangement vary globally.

II. Gap size frequency distributions: emergent pattern or white noise?

Even before ALS became widely available, one feature which had received particular attention is the relationship between the

number and size of gaps in a forest (Fisher *et al.*, 2008). Early efforts to characterize gap size frequency distributions (GSFDs) using ALS led to two key findings. First, like many other emergent patterns in biology, GSFDs tend to follow a power-law distribution, where the frequency of gaps of size x is proportional to: $f(x)x$ (Kellner & Asner, 2009). The scaling exponent of the power-law function (λ) reflects the ratio of large : small gaps, and as a rule of thumb $\lambda < 2$ has been suggested as an indicator of large, frequent disturbances (Asner *et al.*, 2013).

The second – and more surprising – conclusion to emerge from these early studies was that despite strong differences in forest structure, climate and disturbance history, λ appears to converge on a narrow range of values across different sites in the tropics. In one of the first studies of its kind, Kellner & Asner (2009) used ALS data from both Costa Rica and Hawaii to show that λ follows the same U-shaped pattern with canopy height and converges on relatively similar minimum values at multiple sites ($\lambda_{\min} = 1.59\text{--}1.72$, although note that even small changes in λ can correspond to large differences in gap fraction). If similar patterns were found to hold for other sites across the tropics and beyond, it would suggest that disturbance is only of secondary importance in shaping the size structure of forest canopies (Kellner & Asner, 2009). From a practical perspective, it would also mean that GSFDs are of limited use for inferring the processes that shape the structure and function of forests.

However, the idea that GSFDs should be highly conserved is in many ways counterintuitive. Ultimately, canopy gaps are determined by the size distribution, allometry and demography of trees – all of which instead vary substantially among forest types and in relation to climate (Muller-Landau *et al.*, 2006, 2021; Jucker *et al.*,

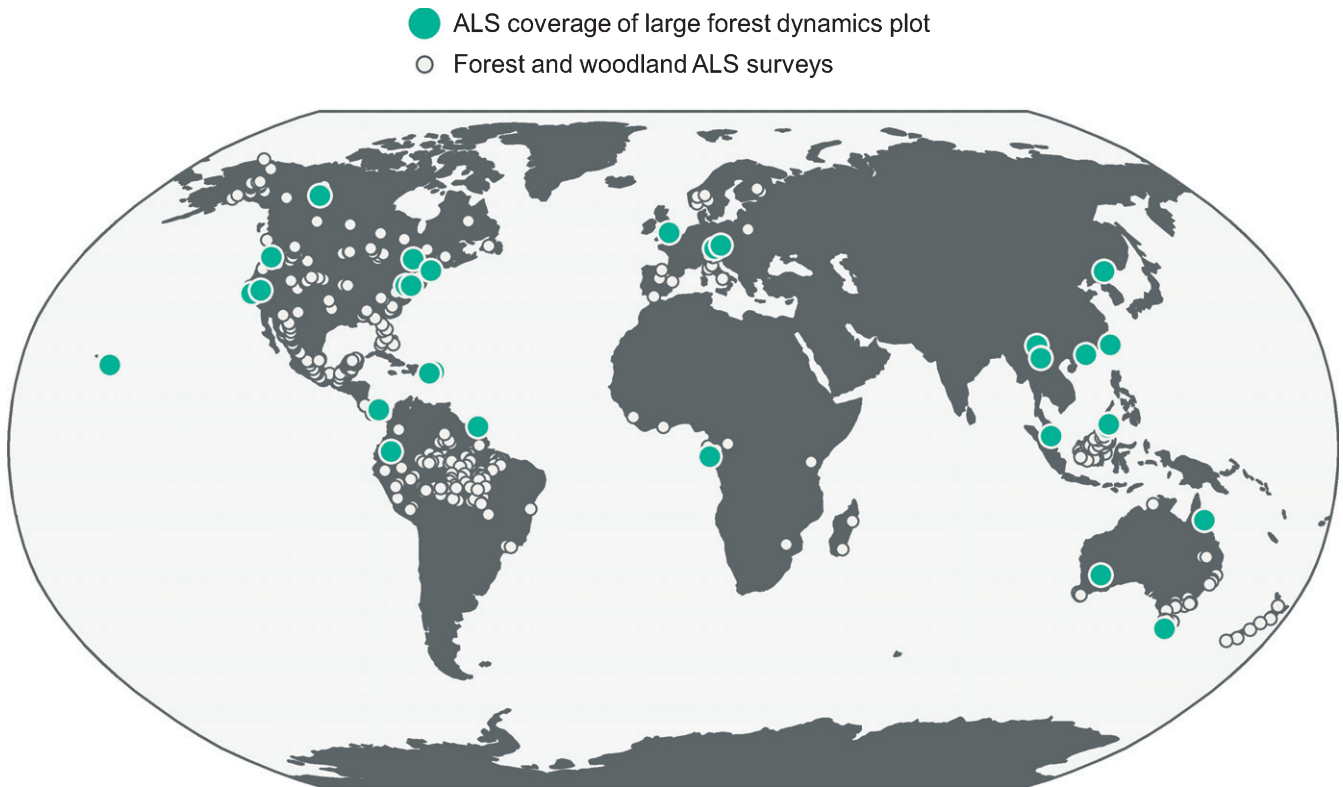


Fig. 2 Global coverage of airborne laser scanning (ALS) surveys of forest and woodland ecosystems. Locations include sites where ALS data have been acquired over forested landscapes (small beige circles), typically covering one or more permanent forest plots. This includes 31 ALS surveys of large forest dynamics plots (5–50 ha; large green circles), most of which are part of the ForestGEO network (<https://forestgeo.si.edu>). Mapped locations were obtained from a combination of published articles and open-access databases, including ALS datasets made available to the public via national research networks such as TERN (<https://portal.tern.org.au>), NEON (<https://data.neonscience.org>) and Brazil's Sustainable Landscapes project (<https://www.paisagenslidar.cnptia.embrapa.br>), through NASA's G-LiHT (<https://gliht.gsfc.nasa.gov>) and CMS programs (<https://carbon.nasa.gov>), and by initiatives such as OpenTopography (<https://opentopography.org>).

2017). It is perhaps unsurprising, therefore, that as ALS data have become increasingly mainstream, a more nuanced and complex picture of GSFs has begun to emerge. First, it appears that at least in certain forest types GSFs are not well captured by a power-law, which tends to overestimate the frequency of large gaps (Wedeux & Coomes, 2015). Even when a power-law is a good fit to the data, λ has been shown to vary considerably among different forest types (Goodbody *et al.*, 2020), as well as within the same landscape due to differences in disturbance (Cushman *et al.*, 2021; Reis *et al.*, 2021), topography and soil fertility (Lobo & Dalling, 2013; Goulamoussene *et al.*, 2017). For example, using ALS data from 650 sites across the Brazilian Amazon, Reis *et al.* (2021) showed that λ ranges between 1.66 and 2.50 across the basin, primarily reflecting underlying gradients in tree mortality, canopy height and human disturbance.

Despite these recent advances, we still lack a complete picture of how GSFs vary across the world's forests, nor do we understand whether they reflect a coherent fingerprint of climate and disturbance. This knowledge gap is not due solely to incomplete geographical coverage, but also reflects the fact that existing studies that have quantified GSFs from ALS are hard to compare due to differences in methodology. For instance, the sampling resolution and spatial coverage of the ALS data can influence the ability to

accurately retrieve gaps (Lobo & Dalling, 2014). More problematic still is the fact that we lack an accepted definition of what constitutes a gap. Both minimum and maximum gap size thresholds vary considerably among studies, as does the height above ground at which gaps are measured (Reis *et al.*, 2021). Finally, there is the enduring issue of how best to estimate power-law exponents (White *et al.*, 2008), a statistical choice which can have a substantial impact on estimates of λ and therefore our understanding of how GSFs vary among forests. Overcoming these challenges will require us to bring together the growing archive of ALS data from forested landscapes worldwide and analyse them within a common methodological framework (Fig. 2).

III. Beyond size structure: spatiotemporal patterns of gap formation and dynamics

Although GSFs dominate the literature when it comes to characterizing forest canopy gaps, they are far from the only tool at our disposal. For instance, one obvious feature that GSFs completely overlook is the spatial arrangement of canopy gaps within a forest – something which is easily retrieved using ALS. Conveniently, this means we can utilize a whole suite of methods developed to analyse spatial point patterns to explore how canopy

gaps are arranged in space, how this varies with spatial scale and what might be driving the spatial patterns we observe (Law *et al.*, 2009). Surprisingly, however, few studies have looked at the spatial distribution of gaps in forests. The handful that have done so suggest that generally gaps tend to be more spatially clustered than one would expect by chance (Silva *et al.*, 2019), particularly those that extend deep into the canopy. Whether spatial clustering is a ubiquitous feature of canopy gaps remains to be tested, but it seems reasonable to expect that the degree of clustering would be influenced by the frequency and mode of disturbance, as well as the subsequent rate of recovery. For example, highly dynamic forests growing on nutrient-rich alluvial soils in the tropics – where a large number of gaps are continuously created and filled – may be characterized by gaps that are less spatially clustered than those on nutrient-depleted soils – where gaps form much less frequently and take longer to close (Jucker *et al.*, 2018b). Similarly, disturbances such as logging may blur underlying spatial patterns as a result of the selective removal of canopy trees.

Another feature of canopy gaps which is not captured by GSFs is their geometry (Halley *et al.*, 2004). Again, while efforts have been made to develop methods to accurately measure the shape and complexity of gaps from remote sensing (Seidel *et al.*, 2015), we know little about if and how gap geometry varies along environmental gradients or in relation to disturbance. In one of the few studies of its kind, Malhi & Román-Cuesta (2008) used very high-resolution satellite imagery to show that lacunarity – a measure of the ‘gappiness’ of a geometric pattern – differs among canopies of Amazonian *terra firme* and swamp forests. More recently, Staver *et al.* (2019) used ALS data to explore spatial patterning of tree clusters in African savannas. They found that the fractal dimension of vegetation clusters increased progressively along a rainfall gradient, whereas other patterns of vegetation structure such as cluster size frequency distributions remained unchanged. A similar approach could be applied to canopy gaps, providing a way to determine what factors constrain the complexity of their shape (e.g. mode of tree death, such as drought, blowdown, lightning or logging) and test whether these attributes can act as early warning signals of regime shifts (Kéfi *et al.*, 2007; Staver *et al.*, 2019).

Finally, growing access to repeat ALS surveys of the same location through time provide an opportunity to study gap dynamics in action, mapping when and where new gaps form, and how quickly they close (Silva *et al.*, 2019; Silvério *et al.*, 2019; Cushman *et al.*, 2021). Using repeat ALS from five sites in the Amazon, Dalagnol *et al.* (2021) showed that gap dynamics are closely correlated to rates of tree mortality derived from plot census data, reflecting broadscale gradients in forest dynamics across the region. Beyond ALS, high-resolution imagery from other remote sensing platforms such as drones and satellites can also be used to track gaps through time, resulting in much richer time-series of canopy dynamics (Dalagnol *et al.*, 2019; Cushman *et al.*, 2021). For instance, Araujo *et al.* (2021) collected monthly drone imagery over 5 years at Barro Colorado Island in Panama and found that treefall events mostly occurred during periods of extreme rainfall accompanied by high winds and lightning – resulting in gap dynamics that are highly spatially and temporally clustered (Fisher *et al.*, 2008; Negrón-Juárez *et al.*, 2010). As our remote sensing

toolbox continues to expand, so too will our ability to detect the fingerprint of different disturbance agents on the structure of forests (Milodowski *et al.*, 2021; Nunes *et al.*, 2021). Just as importantly, these tools will also allow us to monitor how forests recover from disturbance and benchmark the effectiveness of different restoration interventions, such as tree planting (Philipson *et al.*, 2020).

IV. Understanding canopy gaps from first principles using individual-based models

Up to this point I have focused on how ALS and other remote sensing data allow us – for the first time – to fully capture the size structure and spatial organization of forest canopy gaps. However, despite the central role that these technologies have to play in advancing canopy science, they can only take us so far when it comes to linking observed patterns to the processes that generate them. One way to overcome this limitation is using process-based models to simulate what canopy gaps might look like under a range of different scenarios about how individual trees grow, die and compete for space. This is precisely the approach used in early efforts to explore whether tropical forests behave like multifractals, a common feature in nature. For example, using a cellular automaton model known as ‘Forest Game’, which simulates the birth, growth and death of trees in a 2D lattice, Solé & Manrubia (1995) were able to successfully replicate observed GSFs in a Panamanian rainforest.

Since then, substantial progress has been made in developing individual-based models that faithfully replicate key attributes of forest size structure, such as stem diameter distributions and crown packing (Purves *et al.*, 2008; Taubert *et al.*, 2015; Maréchaux & Chave, 2017). One of the main features of these models is that they simulate how individual trees occupy space in three dimensions. This means they can be used to generate virtual canopy height models that can be directly compared to those derived from real-world ALS data (Knapp *et al.*, 2018; Fischer *et al.*, 2019). For instance, Fischer *et al.* (2020) recently developed ‘Canopy Constructor’, a forest simulator which generates ALS-like canopy height models by iteratively placing tree crowns in 3D space following a set of flexible allometric and crown packing rules. Using this approach, Canopy Constructor can accurately replicate the number, size and spatial arrangement of canopy gaps observed from ALS in structurally complex tropical rainforests (Fig. 1c,d).

This makes tools like this ideal for identifying which processes are most important for determining the number, size and spatial arrangement of gaps in a forest. For example, they could be used to simulate how altering the size distribution, demography, allometry, crown plasticity and geometry of individual trees influences emergent properties of the canopy like GSFs. By then comparing simulated GSFs to those observed from ALS, we could determine which combination of processes are key to replicating real-world patterns. Similarly, we could use this approach to simulate how GSFs would be affected by different modes and frequencies of disturbance (e.g. logging, windthrows, fire), as well as generate testable hypotheses about how GSFs might vary along environmental gradients. Finally, this framework would allow us to test whether GSFs can be reconciled with existing theories of forest

size structure and dynamics. Metabolic scaling theory, for instance, makes explicit predictions about tree allometry, tree size distributions and crown spacing (Enquist *et al.*, 2009). However, whether this is consistent with observed GSFDs remains to be tested.


V. Conclusions

Despite decades of research on gap dynamics and recent advances in our ability to study these processes at scale, we are still no closer to deciphering the fingerprint they leave on the 3D structure of forests. As I have discussed here, solving this challenge will require us to borrow ideas, data and methods from a diverse range of fields, including forest ecology, plant demography, remote sensing and computational biology. Specifically, I envisage a two-pronged approach. First, we need to compile ALS data from representative forested landscapes worldwide to determine once and for all how canopy gap size and spatial structure are shaped by environmental constraints and disturbance regimes. Second, in order to link pattern to process, we need to utilize data from global forest plot networks and individual-based models to reveal how emergent properties of forest canopies such as GSFDs emerge from basic rules about how trees grow, die and compete for space. In doing so we have an opportunity to not only solve a long-standing riddle in ecology, but also shed new light on the processes that shape the structure and function of the world's forests.

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References

- Araujo RF, Grubinger S, Celes CHS, Negrón-Juárez R, García M, Dandois J, Muller-Landau H. 2021. Strong temporal variation in treefall and branchfall rates in a tropical forest is explained by rainfall: results from five years of monthly drone data for a 50-ha plot. *Biogeosciences Discussions*. doi: 10.5194/bg-2021-102.
- Asner GP, Kellner JR, Kennedy-Bowdoin T, Knapp DE, Anderson C, Martin RE. 2013. Forest canopy gap distributions in the southern Peruvian Amazon. *PLoS ONE* 8: e60875.
- Brokaw NVL. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14: 158–160.
- Condit R, Perez R, Aguilar S, Lao S, Foster R, Hubbell SP. 2019. Complete data from the Barro Colorado 50-ha plot. *Dryad Digital Repository*. doi: 10.15146/5xc-p-0d46.
- Cushman KC, Burley JT, Imbach B, Saatchi SS, Silva CE, Vargas O, Zraggen C, Kellner JR. 2021. Impact of a tropical forest blowdown on aboveground carbon balance. *Scientific Reports* 11: 11279.
- Dalagnol R, Phillips OL, Gloor E, Galvão LS, Wagner FH, Locks CJ, Aragão LEOC. 2019. Quantifying canopy tree loss and gap recovery in tropical forests under low-intensity logging using VHR satellite imagery and airborne LiDAR. *Remote Sensing* 11: 817.
- Dalagnol R, Wagner FH, Galvão LS, Streher AS, Phillips OL, Gloor E, Pugh TAM, Ometto JPHB, Aragão LEOC. 2021. Large-scale variations in the dynamics of Amazon forest canopy gaps from airborne lidar data and opportunities for tree mortality estimates. *Scientific Reports* 11: 1388.
- Enquist BJ, West GB, Brown JH. 2009. Extensions and evaluations of a general quantitative theory of forest structure and dynamics. *Proceedings of the National Academy of Sciences, USA* 106: 7046–7051.
- Fischer FJ, Labrière N, Vincent G, Hérault B, Alonso A, Memiaghe H, Bissiegou P, Kenfack D, Saatchi S, Chave J. 2020. A simulation method to infer tree allometry and forest structure from airborne laser scanning and forest inventories. *Remote Sensing of Environment* 251: 112056.
- Fischer FJ, Maréchaux I, Chave J. 2019. Improving plant allometry by fusing forest models and remote sensing. *New Phytologist* 223: 1159–1165.
- Fisher JL, Hurtt GC, Thomas RQ, Chambers JQ. 2008. Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecology Letters* 11: 554–563.
- Goodbody TRH, Tompalski P, Coops NC, White JC, Wulder MA, Sanelli M. 2020. Uncovering spatial and ecological variability in gap size frequency distributions in the Canadian boreal forest. *Scientific Reports* 10: 6069.
- Goulamoussene Y, Bedeau C, Descroix L, Linguet L, Hérault B, Goulamoussène Y, Bedeau C, Descroix L, Linguet L, Hérault B. 2017. Environmental control of natural gap size distribution in tropical forests. *Biogeosciences* 14: 353–364.
- Halley JM, Hartley S, Kallimanis AS, Kunin WE, Lennon JJ, Sgardelis SP. 2004. Uses and abuses of fractal methodology in ecology. *Ecology Letters* 7: 254–271.
- Jucker T, Asner GP, Dalponte M, Brodrick PG, Philipson CD, Vaughn NR, Teh YA, Brelsford C, Burslem DFRP, Deere NJ *et al.* 2018a. Estimating aboveground carbon density and its uncertainty in Borneo's structurally complex tropical forests using airborne laser scanning. *Biogeosciences* 15: 3811–3830.
- Jucker T, Bongalov B, Burslem DFRP, Nilus R, Dalponte M, Lewis SL, Phillips OL, Qie L, Coomes DA. 2018b. Topography shapes the structure, composition and function of tropical forest landscapes. *Ecology Letters* 21: 989–1000.
- Jucker T, Bouriaud O, Coomes DA. 2015. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Functional Ecology* 29: 1078–1086.
- Jucker T, Caspersen J, Chave J, Antin C, Barbier N, Bongers F, Dalponte M, van Ewijk KY, Forrester DI, Haeni M *et al.* 2017. Allometric equations for integrating remote sensing imagery into forest monitoring programs. *Global Change Biology* 23: 177–190.
- Kéfi S, Rietkerk M, Alados CL, Pueyo Y, Papanastasiou VP, ElAich A, De Ruiter PC. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature* 449: 213–217.
- Kellner JR, Asner GP. 2009. Convergent structural responses of tropical forests to diverse disturbance regimes. *Ecology Letters* 12: 887–897.
- Knapp N, Huth A, Kugler F, Papathanassiou K, Condit R, Hubbell SP, Fischer R. 2018. Model-assisted estimation of tropical forest biomass change: a comparison of approaches. *Remote Sensing* 10: 1–23.
- Law R, Illian J, Burslem DFRP, Gratzler G, Gunatilleke CVS, Gunatilleke IAUN. 2009. Ecological information from spatial patterns of plants: insights from point process theory. *Journal of Ecology* 97: 616–628.
- Lobo E, Dalling JW. 2013. Effects of topography, soil type and forest age on the frequency and size distribution of canopy gap disturbances in a tropical forest. *Biogeosciences* 10: 6769–6781.
- Lobo E, Dalling JW. 2014. Spatial scale and sampling resolution affect measures of gap disturbance in a lowland tropical forest: implications for understanding forest regeneration and carbon storage. *Proceedings of the Royal Society B: Biological Sciences* 281: 20133218.
- Malhi Y, Román-Cuesta RM. 2008. Analysis of lacunarity and scales of spatial homogeneity in IKONOS images of Amazonian tropical forest canopies. *Remote Sensing of Environment* 112: 2074–2087.
- Maréchaux I, Chave J. 2017. An individual-based forest model to jointly simulate carbon and tree diversity in Amazonia: description and applications. *Ecological Monographs* 87: 632–664.

- Meyer V, Saatchi S, Clark DB, Keller M, Vincent G, Ferraz A, Espírito-Santo F, d'Oliveira MVN, Kaki D, Chave J. 2018. Canopy area of large trees explains aboveground biomass variations across neotropical forest landscapes. *Biogeosciences* 15: 3377–3390.
- Milodowski DT, Coomes DA, Swinfield T, Jucker T, Riutta T, Malhi Y, Svátek M, Kvasnica J, Burslem DFRP, Ewers RM *et al.* 2021. The impact of logging on vertical canopy structure across a gradient of tropical forest degradation intensity in Borneo. *Journal of Applied Ecology* 58: 1764–1775.
- Muller-Landau HC, Condit RS, Harms KE, Marks CO, Thomas SC, Bunyavechewin S, Chuyong G, Co L, Davies S, Foster R *et al.* 2006. Comparing tropical forest tree size distributions with the predictions of metabolic ecology and equilibrium models. *Ecology Letters* 9: 589–602.
- Muller-Landau HC, Cushman KC, Arroyo EE, Martínez Cano I, Anderson-Teixeira KJ, Backiel B. 2021. Patterns and mechanisms of spatial variation in tropical forest productivity, woody residence time, and biomass. *New Phytologist* 229: 3065–3087.
- Nakamura A, Kitching RL, Cao M, Creedy TJ, Fayle TM, Freiberg M, Hewitt CN, Itioka T, Koh LP, Ma K *et al.* 2017. Forests and their canopies: achievements and horizons in canopy science. *Trends in Ecology and Evolution* 32: 438–451.
- Negrón-Juárez RI, Chambers JQ, Guimaraes G, Zeng H, Raupp CFM, Marra DM, Ribeiro GHPM, Saatchi SS, Nelson BW, Higuchi N. 2010. Widespread Amazon forest tree mortality from a single cross-basin squall line event. *Geophysical Research Letters* 37: 16701.
- Nunes MH, Jucker T, Riutta T, Svátek M, Kvasnica J, Rejček M, Matula R, Majalap N, Ewers RM, Swinfield T *et al.* 2021. Recovery of logged forest fragments in a human-modified tropical landscape during the 2015–16 El Niño. *Nature Communications* 12: 1526.
- Philipson CD, Cutler MEJJ, Brodrick PG, Asner GP, Boyd DS, Costa PM, Fiddes J, Foody GM, van der Heijden GMF, Ledo A *et al.* 2020. Active restoration accelerates the carbon recovery of human-modified tropical forests. *Science* 369: 838–841.
- Purves DW, Lichstein JW, Strigul N, Pacala SW. 2008. Predicting and understanding forest dynamics using a simple tractable model. *Proceedings of the National Academy of Sciences, USA* 105: 17018–17022.
- Reis CR, Jackson TD, Bastos Gorgens E, Dalagnol R, Jucker T, Henrique Nunes M, Pierre Ometto J. 2021. Forest structure and degradation drive canopy gap sizes across the Brazilian Amazon. bioRxiv. doi: 10.1101/2021.05.03.442416.
- Seidel D, Ammer C, Puettmann K. 2015. Describing forest canopy gaps efficiently, accurately, and objectively: new prospects through the use of terrestrial laser scanning. *Agricultural and Forest Meteorology* 213: 23–32.
- Silva CA, Valbuena R, Pinagé ER, Mohan M, de Almeida DRA, North Broadbent E, Jaafar WSWM, de Almeida PD, Cardil A, Klauberg C. 2019. ForestGapR: an R Package for forest gap analysis from canopy height models. *Methods in Ecology and Evolution* 10: 1347–1356.
- Silvério DV, Brando PM, Bustamante MMC, Putz FE, Marra DM, Levick SR, Trumbore SE. 2019. Fire, fragmentation, and windstorms: a recipe for tropical forest degradation. *Journal of Ecology* 107: 656–667.
- Solé RV, Manrubia SC. 1995. Self-similarity in rain forests: evidence for a critical state. *Physical Review E* 51: 6250–6253.
- Staver AC, Asner GP, Rodriguez-Iturbe I, Levin SA, Smit IPJ. 2019. Spatial patterning among savanna trees in high resolution, spatially extensive data. *Proceedings of the National Academy of Sciences, USA* 166: 10681–10685.
- Taubert F, Jahn MW, Dobner H-J, Wiegand T, Huth A. 2015. The structure of tropical forests and sphere packings. *Proceedings of the National Academy of Sciences, USA* 112: 15125–15129.
- Wedeux BMM, Coomes DA. 2015. Landscape-scale changes in forest canopy structure across a partially logged tropical peat swamp. *Biogeosciences* 12: 6707–6719.
- White EP, Enquist BJ, Green JL. 2008. On estimating the exponent of power-law frequency distributions. *Ecology* 89: 905–912.
- Wright SJ, Muller-Landau HC, Condit R, Hubbell SP. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84: 3174–3185.



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