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Going 3D – the changing landscape of forest structural complexity

By Alice Rosen and Tommaso Jucker, 23 April 2025

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Forests with complex three-dimensional (3D) structures are home to a disproportionately large fraction of the world's biodiversity. They also capture and store substantial amounts of carbon from the atmosphere, making them a key ally in the fight against climate change. Despite their global importance, forests are facing severe climate-related threats (including fires, drought, and disease) and are being cleared at alarming rates due to logging and agricultural expansion. These disturbances dramatically alter the 3D structure of forests, impacting their ability to safeguard biodiversity and provide valuable ecosystem services. To understand and predict the true impact of these changes, it is crucial that we develop new approaches to accurately measure the 3D structure of forest canopies. Traditional, ground-based methods struggle with this, attempting to describe structural complexity from over-simplified features of their trees. However, with recent advances in LiDAR technology, we can measure complex forest ecosystems in 3D over vast areas. This technology is changing the way we understand structural complexity and what it means for the health of our ecosystems. As these methods continue to improve – becoming more robust and generalisable – they will help us better understand, conserve and restore our globally important forests.

{1}Why complexity matters

{2}As trees grow, jostle for space in the canopy and eventually die, they give rise to incredibly complex three-dimensional (3D) forest structures that have fascinated ecologists for decades [C.G. Jones et al., 1994[1]]. Forests that are more structurally complex not only capture and store more carbon from the atmosphere [C.M. Gough et al., 2019[2]], but also support a much richer and diverse community of organisms that make a living in and below their canopy [J.A. Walter et al., 2021[3]]. Complex 3D structures provide a greater variety of niches for species to exploit and also shape how organisms interact, enabling species to coexist at higher densities [S. Gámez and N.C. Harris, 2022[4]; K.E. Kovalenko et al., 2012[5]; G.A. Langellotto and R.F. Denno, 2004[6]]. It is unsurprising therefore that forest structural complexity is increasingly seen as an important feature of these ecosystems that we should aim to protect and enhance [W.D. Simonson et al., 2014[7]].

{3}A forest's 3D structure is shaped by the pool of tree species that grow in a given region, as well as differences in their ecological strategies. Forests with a diverse mix of tree species generally have a more complex structure than ones that are species-poor [D.C. Zemp et al., 2019[8]; J. Juchheim et al., 2019[9]]. Trees with complementary crown architectures are able to pack their crowns into the available space more efficiently [T. Jucker et al., 2015[10]; H. Pretzsch, 2014[11]]. Light demanding species will extend their crowns to the very top of the canopy, whilst trees that are more tolerant of shade are content to fill the remaining space lower down. Overall, this creates a complex, multi-layered structure that captures more light [J. Sapijanskas et al., 2014[12]; J.W. Atkins et al., 2018[13]] and stores more carbon [M. Dalponte et al., 2019[14]]. This also creates the ideal microclimatic conditions in the understorey for new seedlings to grow, protecting them from extreme changes in temperature and humidity found outside the forest canopy [T. Jucker et al., 2018[15]].

{4}Natural disturbances such as storms, fire and drought also play a key role in shaping the 3D structure of forests [T. Jucker, 2022[16]]. Gaps created after treefalls spark new growth in the understory and preserve a diversity of species with different ecological strategies [A. Muscolo et al., 2014[17]; J. Zhu et al., 2014[18]]. However, the increasing severity of anthropogenic disturbances – including climate change, intensive logging and agricultural expansion – are fundamentally altering the structure of the world's forests, threatening their ability to store carbon and safeguard biodiversity [T. Newbold et al., 2015[19]; A.P. Williams and J.T. Abatzoglou, 2016[20]; D.T. Milodowski et al., 2021[21]]. This has led to growing interest in developing ways to measure and track changes in forest structural complexity over time and

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space in order to guide conservation and restoration efforts [D.C. Zemp et al., 2019[8]; N. Camarretta et al., 2020[22]; D.R.A. Almeida et al., 2019[23]; C. Penone et al., 2019[24]]. But to do this we first need to agree on what we mean by '*structural complexity*', and that is easier said than done.

{5}Defining and measuring structural complexity – not so simple

{6}Structural complexity is multifaceted, which inherently makes it hard to define, but a useful starting point is the '*diversity, density, size, and arrangement of structural elements, as well as the spatial scales over which they occur*' [M. Tokeshi and S. Arakaki, 2012[25]]. Given that this definition incorporates multiple concepts, it is highly unlikely that a single measure would be able to neatly capture every aspect of complexity. This has led to a proliferation of methods used to capture structural complexity and confusion over how to interpret them. At present, there is no widely accepted framework for measuring forest 3D structure. This is only made worse by the fact that numerous terms – including '*habitat architecture'*, '*structural heterogeneity'* and '*structural diversity*' – are all used interchangeably as synonyms of structural complexity [C. McElhinny et al., 2005[26]].

{7}To measure the structural complexity of forests, ecologists have traditionally relied on ground-based measurements requiring little more than a tape measure. These measurements typically focus on a single aspect of forest structure, such as the diameter of tree trunks or their height, rather than their complexity in multiple dimensions. A number of efforts have been made to combine these traditional measures of forest structure into a framework for quantifying structural complexity. Some methods focus on the horizontal arrangement of trees [P.J. Clark and F.C. Evans, 1954[27]; K. Füldner, 1995[28]]; others are concerned with the density and distribution of leaves in the canopy; and others focus instead on the vertical structure of forests [R.H. MacArthur and J.W. MacArthur, 1961[29]] or the diversity of their structural elements [N.L. Lexerød and T. Eid, 2006[30]]. But these approaches that rely on ground-based data to quantify forest structural complexity all suffer from the same fundamental limitation: they attempt to capture something that is inherently 3D without really being able to measure it [E.R. Lines et al., 2022[31]].

{8}Capturing forest structure in 3D – a remote sensing revolution

{9}One increasingly popular solution to the challenge of measuring forest 3D structure has been to turn to remote sensing technologies such as LiDAR [N. Camarretta et al., 2020[22]]. LiDAR scanners work by shooting hundreds of thousands of laser pulses per second towards the canopy and then measuring the time it takes for each of those pulses to return to the sensor. The result is an incredibly detailed 3D 'point cloud' model of the forest canopy. LiDAR

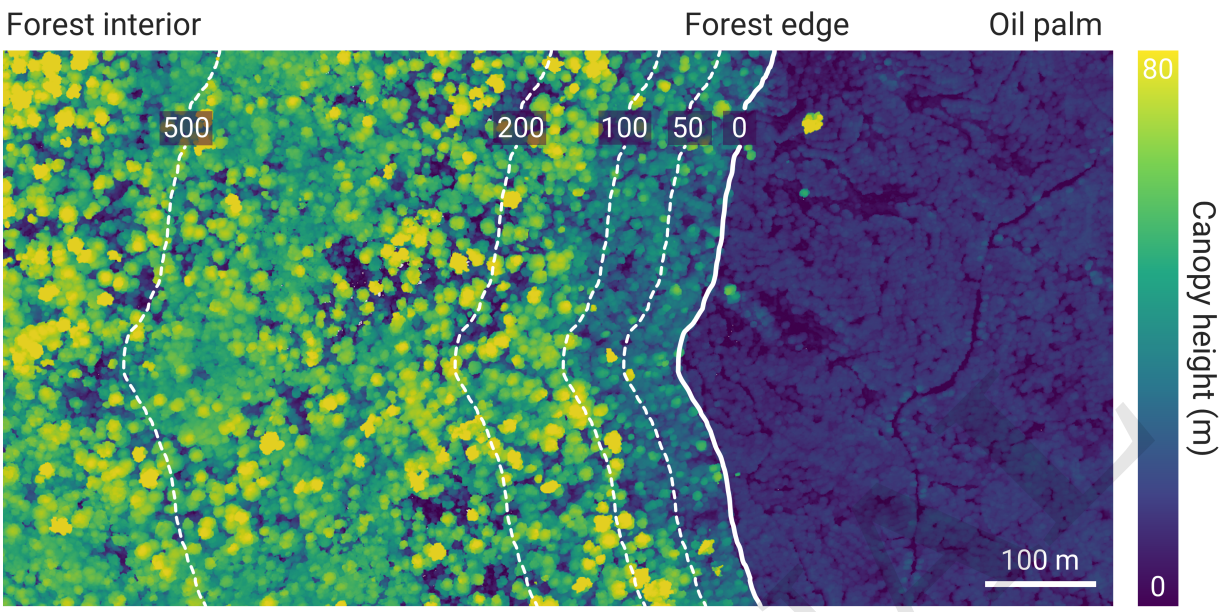
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sensors can be mounted on a range of platforms that allow the measurement of habitats at different scales and from different viewpoints. Operated from the ground, LiDAR can be used to generate highly detailed 3D models of individual trees, right down to the level of fine branches and leaves [K. Calders et al., 2020[32]]. Mounted on aircraft such as an airplane, helicopter or drone, LiDAR allows us to capture the 3D structure of forest canopies across entire landscapes in a way that would simply be impossible from the ground [T. Jucker et al., 2018[15]; E.R. Lines et al., 2022[31]] (Figure 1). And with the recent launch of NASA's Global Ecosystem Dynamics Investigation (GEDI) – a satellite-mounted LiDAR sensor – we are now starting to build the first high-resolution global maps of forest canopy structure from space [F.D. Schneider et al., 2020[33]].

{10}This LiDAR data revolution is leading to a growing interest in the study of forest structural complexity. We are now able to measure classic structural attributes over vastly greater areas thanks to this technology. For instance, foliage height diversity (FHD) has been used by ecologists for decades but is now being mapped from space as part of the GEDI mission [H. Tang et al., 2019[34]]. A growing number of open-source tools are also making the process of extracting ecologically meaningful information from 3D point clouds much more accessible [J.W. Atkins et al., 2022[35]]. As a result, we are starting to build the first picture of how and why structural complexity varies across different forest ecosystems [M. Ehbrecht et al., 2021[36]]. This also extends to ecosystems where tree cover is low (e.g., semi-arid woodlands and savannas) [J. Jucker et al., 2023[37]], thus bridging the gap between open and closed-canopy forests (or better yet 'treescapes'), which for the most part have historically been studied separately. Equipped with this knowledge, we can begin to identify priority areas for conservation [M. Ehbrecht et al., 2021[36]], and develop management practices that help to restore the structural complexity of degraded treescapes [N. Camarretta et al., 2020[22]; C. Penone et al., 2019[24]].

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{12}Figure 1. Example of a 3D canopy height model derived from airborne LiDAR data acquired across a tropical forest landscape in Sabah, Malaysian Borneo. The colour gradient reflects the height of the canopy, ranging from tall forests in yellow to short vegetation and bare ground in blue. Going from left to right, the map shows a sharp transition zone from an old-growth tropical rainforest – where emergent trees exceed 80 m in height – to an oil palm plantation with its characteristic short and uniform canopy. A decrease in forest canopy height is clearly visible in the first 100 m from the boundary of the oil palm plantation. These edge effects can extend hundreds of meters into the forest interior and are linked to increased rates of tree mortality driven by warmer, drier and windier conditions in these transition zones.

{13}But all of this brings into sharp focus the need to think carefully about how we define and measure structural complexity [L.H.L. Loke and R.A. Chisholm, 2022[38]]. In one sense we are no longer constrained by what is practical to measure, so we can focus on metrics that are more ecologically relevant [E.R. Lines et al., 2022[31]]. However, we have also seen a proliferation of metrics, methods and definitions, making it difficult to compare and interpret findings from different studies. Finally, LiDAR is not a panacea. In particular, there are issues with access to data and capacity to analyse them in many of the regions where they are needed most. In tropical forests – home to a large proportion of the world's biodiversity and where LiDAR coverage is lacking [T.R.M. Bakx et al., 2019[39]; R. Valbuena et al., 2020[40]] – the need to understand how structural complexity is impacted by disturbance and how quickly it can recover is more important than ever. Programs that aim to address this unbalance are critical. For instance, the Amazon Biomass Estimation project (EBA) has improved LiDAR coverage across the Brazilian Amazon [R. Dalagnol et al., 2021[41]], opening up new opportunities to measure the structural complexity of these forests like never before.

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{14}Laying the foundations for the future of habitat complexity research

{15}Recent advances in LiDAR technology mean that today we are able to measure the 3D structure of forests at spatial scales and resolutions that were unthinkable even just two decades ago. As interest in habitat complexity research and access to LiDAR data both continue to grow, it is imperative however that we critically assess how best to use these new data sources at our disposal. Importantly, we should strive to develop robust, unambiguous and generalisable methods that are straightforward to interpret and fully capture the 3D structural complexity of different ecosystem types. There is unlikely to be a one-size-fits-all approach, but we should aim to identify measures that have the greatest value for improving our understanding of how ecosystems function and how they support biodiversity. In turn, this could be a promising step towards identifying areas of high conservation value, measuring the impact of habitat disturbance, and improving how we restore habitats following major disturbances.

{16}Bibliography

{17}

[1] C.G. Jones, J.H. Lawton and M. Shachak: Organisms as Ecosystem Engineers, *Oikos*, vol. 69, 130–147, https://doi.org/10.1007/978-1-4612-4018-1_14, 1994.

[2] C.M. Gough, J.W. Atkins, R.T. Fahey and B.S. Hardiman: High rates of primary production in structurally complex forests, *Ecology*, vol. 100, e02864, https://doi.org/10.1002/ecy.2864, 2019.

[3] J.A. Walter, A.E.L. Stovall and J.W. Atkins: Vegetation structural complexity and biodiversity in the Great Smoky Mountains, *Ecosphere*, vol. 12, -, https://doi.org/10.1002/ecs2.3390, 2021.

[4] S. Gámez and N.C. Harris: Conceptualizing the 3D niche and vertical space use, *Trends Ecol Evol*, vol. 37, 953-962, https://doi.org/10.1016/j.tree.2022.06.012, 2022.

[5] K.E. Kovalenko, S.M. Thomaz and D.M. Warfe: Habitat complexity: approaches and future directions, *Hydrobiologia*, vol. 685, 1–17, https://doi.org/10.1007/s10750-011-0974-z, 2012.

[6] G.A. Langellotto and R.F. Denno: Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis, *Oecologia*, vol. 139, 1–10, https://doi.org/0.1007/s00442-004-1497-3, 2004.

[7] W.D. Simonson, H.D. Allen and D.A. Coomes: Applications of airborne lidar for the assessment of animal species diversity, *Methods Ecol Evol*, vol. 5, 719–729, https://doi.org/10.1111/2041-210X.12219, 2014.

[8] D.C. Zemp, M. Ehbrecht, D. Seidel, C. Ammer, D. Craven, J. Erkelenz, B. Irawan, L. Sundawati, D. Hölscher and H. Kreft: Mixed-species tree plantings enhance structural complexity in oil palm plantations, *Agriculture, Ecosystems & Environment*, vol. 283, 106564, https://doi.org//10.1016/j.agee.2019.06.003, 2019.

[9] J. Juchheim, M. Ehbrecht, P. Schall, C. Ammer and D. Seidel: Effect of tree species mixing on stand structural complexity, *Forestry: An International Journal of Forest Research*, vol. 93, 75–83, https://doi.org/10.1093/forestry/cpz046, 2019.

[10] T. Jucker, O. Bouriaud and D.A. Coomes: Crown plasticity enables trees to optimize canopy packing in mixed?species forests, *Functional Ecology*, vol. 29, 1078–1086, https://doi.org/10.1111/1365-2435.12428, 2015.

[11] H. Pretzsch: Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures, *Forest Ecology and Management*, vol. 327, 251–264, https://doi.org/10.1016/j.foreco.2014.04.027, 2014.

[12] J. Sapijanskas, te A. Paquet, C. Potvin, N. Kunert and M. Loreau: Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences, *Ecology*, vol. 95, 2479–2492, https://doi.org/10.1890/13-1366.1, 2014.

[13] J.W. Atkins, R.T. Fahey, B.S. Hardiman and C.M. Gough: Forest Canopy Structural Complexity and Light Absorption Relationships at the Subcontinental Scale, *J Geophys Res Biogeosciences*, vol. 123, 1387–1405, https://doi.org/10.1002/2017JG004256, 2018.

[14] M. Dalponte, T. Jucker, S. Liu, L. Frizzera and D. Gianelle: Characterizing forest carbon dynamics using multi-temporal lidar data, *Remote Sens Environ*, vol. 224, 412–420, https://doi.org/10.1016/j.rse.2019.02.018, 2019.

[15] T. Jucker, S.R. Hardwick, S. Both, D.M.O. Elias, R.M. Ewers, D.T. Milodowski, T. Swinfield and D.A. Coomes: Canopy structure and topography jointly constrain the microclimate of human?modified tropical landscapes, *Global Change Biol*, vol. 24, 5243–5258, https://doi.org/10.1111/gcb.14415, 2018.

[16] T. Jucker: Deciphering the fingerprint of disturbance on the three?dimensional structure of the world's forests, *New Phytol*, vol. 233, 612–617, https://doi.org/10.1111/nph.17729, 2022.

[17] A. Muscolo, S. Bagnato, M. Sidari and R. Mercurio: A review of the roles of forest canopy gaps, *Forestry Res*, vol. 25, 725–736, https://doi.org/10.1007/s11676-014-0521-7, 2014.

NOT FINAL

[18] J. Zhu, D. Lu and W. Zhang: Effects of gaps on regeneration of woody plants: a meta-analysis, *J Forestry Res*, vol. 25, 501–510, https://doi.org/10.1007/s11676-014-0489-3, 2014.

[19] T. Newbold, L.N. Hudson, S.L. Hill, S. Contu, I. Lysenko, R.A. Senior, L. Börger, D.J. Bennett, A. Choimes, B. Collen and co-authors: Global effects of land use on local terrestrial biodiversity, *Nature*, vol. 520, 45-50, https://doi.org/10.1038/nature14324, 2015.

[20] A.P. Williams and J.T. Abatzoglou: Recent Advances and Remaining Uncertainties in Resolving Past and Future Climate Effects on Global Fire Activity, *Curr Clim Change Reports*, vol. 2, 1–14, https://doi.org/10.1007/s40641-016-0031-0, 2016.

[21] D.T. Milodowski, D.A. Coomes, T. Swinfield, T. Jucker, T. Riutta, Y. Malhi, M. Svátek, J. Kvasnica, D.F.R.P. Burslem, R.M. Ewers and co-authors: The impact of logging on vertical canopy structure across a gradient of tropical forest degradation intensity in Borneo, *J Appl Ecol*, vol. 58, 1764-1775, https://doi.org/10.1111/1365-2664.13895, 2021.

[22] N. Camarretta, P.A. Harrison, T. Bailey, B. Potts, A. Lucieer, N. Davidson and M. Hunt: Monitoring forest structure to guide adaptive management of forest restoration: a review of remote sensing approaches, *New Forest*, vol. 51, 573–596, https://doi.org/10.1007/s11056-019-09754-5, 2020.

[23] D.R.A. Almeida, E.N. Broadbent, A.M.A. Zambrano, B.E. Wilkinson, M.E. Ferreira, R. Chazdon, P. Meli, E.B. Gorgens, C.A. Silva, S.C. Stark and co-authors: Monitoring the structure of forest restoration plantations with a drone-lidar system, *International Journal of Applied Earth Observation and Geoinformation*, vol. 79, 192-198, https://doi.org/10.1016/j.jag.2019.03.014, 2019.

[24] C. Penone, E. Allan, S. Soliveres, M.R. Felipe-Lucia, M.M. Gossner, S. Seibold, N.K. Simons, P. Schall, F. van der Plas, P. Manning and co-authors: Specialisation and diversity of multiple trophic groups are promoted by different forest features, *Ecol Lett*, vol. 22, 170–180, https://doi.org/10.1111/ele.13182, 2019.

[25] M. Tokeshi and S. Arakaki: Habitat complexity in aquatic systems: fractals and beyond, *Hydrobiologia*, vol. 685, 27–47, https://doi.org/10.1007/s10750-011-0832-z, 2012.

[26] C. McElhinny, P. Gibbons, C. Brack and J. Bauhus: Forest and woodland stand structural complexity: Its definition and measurement, *Forest Ecol Manag*, vol. 218, 1–24, https://doi.org/10.1016/j.foreco.2005.08.034, 2005.

[27] P.J. Clark and F.C. Evans: Distance to Nearest Neighbor as a Measure of Spatial Relationships in Populations, *Ecology*, vol. 35, 445–453, https://doi.org/10.2307/1931034, 1954.

[28] K. Füldner: Zur Strukturbeschreibung in Mischbeständen, *Forstarchiv*, vol. 66, 235–240, 1995.

[29] R.H. MacArthur and J.W. MacArthur: On Bird Species Diversity, *Ecology*, vol. 42, 594–598, https://doi.org/10.2307/1932254, 1961.

[30] N.L. Lexerød and T. Eid: An evaluation of different diameter diversity indices based on criteria related to forest management planning, *Forest Ecol Manag*, vol. 222, 17–28, https://doi.org/10.1016/J.FORECO.2005.10.046, 2006.

[31] E.R. Lines, F.J. Fischer, H.J.F. Owen and T. Jucker: The shape of trees: Reimagining forest ecology in three dimensions with remote sensing, *J Ecol*, vol. 110, 1730-1745, https://doi.org/10.1111/1365-2745.13944, 2022.

[32] K. Calders, J. Adams, J. Armston, H. Bartholomeus, S. Bauwens, L.P. Bentley, J. Chave, F.M. Danson, M. Demol, M. Disney and co-authors: Terrestrial laser scanning in forest ecology: Expanding the horizon, *Remote Sensing of Environment*, vol. 251, 112102, https://doi.org/10.1016/j.rse.2020.112102, 2020.

[33] F.D. Schneider, A. Ferraz, S. Hancock, L.I. Duncanson, R.O. Dubayah, R.P. Pavlick and D.S. Schimel: Towards mapping the diversity of canopy structure from space with GEDI, *Environ Res Lett*, vol. 15, 115006, https://doi.org/10.1088/1748-9326/ab9e99, 2020.

[34] H. Tang, J. Armston, S. Hancock, S. Marselis, S. Goetz and R. Dubayah: Characterizing global forest canopy cover distribution using spaceborne lidar, *Remote Sensing of Environment*, vol. 231, 111262, https://doi.org/10.1016/j.rse.2019.111262, 2019.

[35] J.W. Atkins, A.E.L. Stovall and C.A. Silva: Open-Source tools in R for forestry and forest ecology, *Forest Ecol Manag*, vol. 503, 119813, https://doi.org/10.1016/j.foreco.2021.119813, 2022.

[36] M. Ehbrecht, D. Seidel, P. Annighöfer and et al.: Global patterns and climatic controls of forest structural complexity, *Nat Commun*, vol. 12, 519, https://doi.org/10.1038/s41467-020-20767-z, 2021.

[37] J. Jucker, C.R. Gosper, G. Wiehl, P.B. Yeoh, N. Raisbeck-Brown, F.J. Fischer, J. Graham, H. Langley, W. Newchurch and and co-authors: Using multi-platform LiDAR to guide the conservation of the world's largest temperate woodland, *Remote Sens Environ*, vol. 296, 113745, https://doi.org/10.1016/j.rse.2023.113745, 2023.

[38] L.H.L. Loke and R.A. Chisholm: Measuring habitat complexity and spatial heterogeneity in ecology, *Ecol Lett*, vol. 25, 2269-2288, https://doi.org/10.1111/ele.14084, 2022.

[39] T.R.M. Bakx, Z. Koma, A.C. Seijmonsbergen and W.D. Kissling: Use and categorization of Light Detection and Ranging vegetation metrics in avian diversity and species distribution research, *Divers Distrib*, vol. 25, 1045–1059, https://doi.org/10.1111/ddi.12915, 2019.

[40] R. Valbuena, B. O'Connor, F. Zellweger, W. Simonson, P. Vihervaara, M. Maltamo, C.A. Silva, D.R.A. Almeida, F. Danks, F. Morsdorf and co-authors: Standardizing Ecosystem Morphological Traits from 3D Information Sources, *Trends Ecol Evol*, vol. 35, 656–667, https://doi.org/10.1016/j.tree.2020.03.006, 2020.

[41] R. Dalagnol, F.H. Wagner, L.S. Galvão and et al.: Large-scale variations in the dynamics of Amazon forest canopy gaps from airborne lidar data and opportunities for tree mortality estimates, *Sci Rep*, vol. 11, 1388, https://doi.org/10.1038/s41598-020-80809-w, 2021.

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