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The shape of trees: Reimagining forest ecology in three dimensions with remote sensing

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Abstract

1. How ecologists think about above-ground forest structure and dynamics is fundamentally shaped by the data we can collect. This has historically been limited to what is possible with simple equipment such as a tape measure, which has often led to the three-dimensional complexity of the form of trees being reduced to the diameter of a trunk, and perhaps the height of the tree. While simple and pragmatic, this trunk-centric framework has some obvious limitations, as many of the major processes that influence how trees grow and interact with one another happen up in the canopy. For instance, the structural complexity of individual trees' leaf and branch arrangements and how trees fill canopy space are direct drivers of individual tree and whole-forest productivity and dynamics, but remain poorly studied because they have traditionally been challenging to measure.

2. However, recent advances in remote sensing and data processing are revolutionising our ability to accurately measure tree and forest structure from leaves to landscapes. Not only do we have access to more accurate data on structure, but we also have data spanning a much broader range of spatial, temporal and ecological scales, and new avenues of research that challenge how we understand forests are emerging.

3. *Synthesis*. Here, we review the new opportunities these technologies bring us to measure the physical structure of trees and highlight the technological developments needed to maximise their value to the field of forest ecology. Today, perhaps for the first time, how ecologists choose to study above-ground forest structure and dynamics is limited more by creativity than by what we can measure.

1 | INTRODUCTION

Forest ecology has long relied on a simple measure—the diameter of the trunk of a tree at breast height (dbh)—as a way to summarise individual tree status and performance. This measurement, with its origins in forestry, is non-destructive and quick to take, requiring no special equipment or extensive training, and this ease of use has led dbh to be widely adopted as the key measure of an individual tree in forest ecology. It is used to quantify and predict individual tree demography (Lines et al., 2010; Ruiz-Benito et al., 2013), as a proxy for tree age (Stephenson et al., 2014), to estimate key properties including leaf area, height, crown shape and biomass (Chave et al., 2014;

Lines et al., 2012; Vertessy et al., 1995), to describe the properties of neighbourhoods and whole stands, such as basal area and stem size distributions, and to understand competitive interactions, population dynamics, succession processes and carbon storage (Contreras et al., 2011; Coomes et al., 2014; Purves et al., 2008). Yet, trunk diameter is not a direct measurement of any of these properties and is only one of many dimensions with which we can summarise a tree's size and shape. The widespread reliance on this simple proxy introduces not only errors and biases into quantitative assessments and predictions (Molto et al., 2013), but has also encouraged a trunk-centred view of trees and forests that has shaped the way ecologists have thought about these ecosystems for the better part of a century.

High-resolution remote sensing technologies offer the opportunity to measure the full three-dimensional shape and size of trees and all their component parts—from leaves and leaf arrangement, twigs and branching, to crown morphology, the whole trunk and buttresses (Burt et al., 2021; Jiménez-Brenes et al., 2017; Stovall et al., 2021; Wilkes et al., 2021; Figure 1). While measuring these attributes by hand is possible, this has historically only been done through painstaking and often destructive sampling, resulting in restrictively small sample sizes from a handful of locations, often biased towards small trees (e.g. Bentley et al., 2013). But remote sensing technologies, and crucially the most recently developed analytical tools to process their data, are capable of highly accurate estimates of three-dimensional tree architecture far beyond dbh. Relying on simple trunk measurements to capture the structure of trees and forests is no longer necessary, and a reimagining of individual-based forest ecology away from a dbh-centric framework is possible. We are starting to witness a transition, most notably the use of high-resolution remote sensing for biomass and carbon estimation; for example the direct measurement of individual tree above-ground volume to estimate biomass (Calders et al., 2015) and its upscaling at a landscape level (Asner et al., 2014), but also in the emergence of new avenues of research, including the use of LiDAR to characterise canopy microclimates and wind effects (Jackson et al., 2019; Jucker, Bongalov, et al., 2018; Jucker, Hardwick, et al., 2018; Zellweger et al., 2019). Yet, there remain many areas within forest ecology that could benefit substantially from increased use of three-dimensional data on tree and forest structure. Excitingly, the adoption of these technologies is also driving the development of data-driven forest ecology, and generating new disciplinary interfaces with data science, machine learning and artificial intelligence. Here, we argue for an expansion in the framing of forest ecology beyond the classical trunk-centred view, to capitalise on the ability of remote sensor data to capture the full form of a tree. We argue that doing so, and so bypassing common simplifying assumptions about structure, will open new avenues of research on structural traits, structural dynamics and links between tree structure and the wider biotic and abiotic environment. We discuss how doing so will bring new insights on individuals, whole canopies and ecosystem dynamics, and on the way we explore how some of the classic topics that have captivated forest ecologists for decades can be revisited through the use of three-dimensional remote sensing data. Finally, we discuss the developments needed towards widespread adoption of these approaches and full realisation of the potential of these data within forest ecology.

2 | SENSING THE INDIVIDUAL: MORPHOLOGY, FOLIAGE, CROWNS AND BIOMASS

The advent of ground-based and airborne light detection and ranging (LiDAR) and photogrammetry technologies has made possible direct measurement of the three-dimensional architecture of a tree (Figure 2). Mounted on an aircraft, airborne laser scanning (ALS) can cover large and inaccessible areas, and has been used in a wide variety of ecological studies and across a wide range of forest types to extract individual tree height and crown shape (Aubry-Kientz et al., 2019; Dalponte et al., 2015; Ferraz et al., 2020; Weinstein et al., 2021) and, when combined with optical and hyperspectral imagery, can be used to identify individual species (Deng et al., 2016; Yu et al., 2014) and individual functional traits (Zheng et al., 2021). With their view from above and lack of wide angle beams which can penetrate the sub-canopy, airborne methods to monitor whole-tree shape typically suffer from occlusion, missing fine branching detail and sufficient data to characterise trees below the upper canopy; such problems can be reduced through collection of point cloud data at densities many times higher than what is required for canopy trees (Aubry-Kientz et al., 2019; Hamraz et al., 2017), or scanners are mounted on lower flying unmanned aerial vehicles (UAVs) with more wide angle views (Kuželka et al., 2020) and narrow beam divergence. In contrast, terrestrial laser scanners (TLS), with comparatively much

FIGURE 1 Recent developments in remote sensing technologies and analysis tools offer new ways to conceptualise forest ecology with data from (a) within tree branch and foliage arrangement, to (b) tree–tree interactions and (c) whole-stand properties. Images adapted with permission from (a) Wilkes et al. (2021), (b) Burt et al. (2021) and (c) Calders et al. (2018).

(a) 0.5 m

(b) 15 m

(c) 100 m
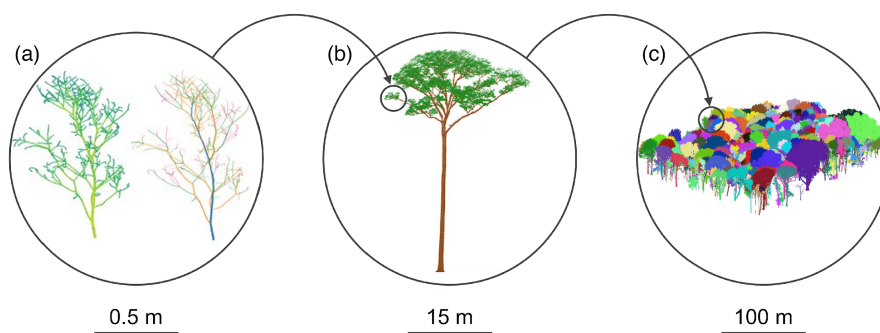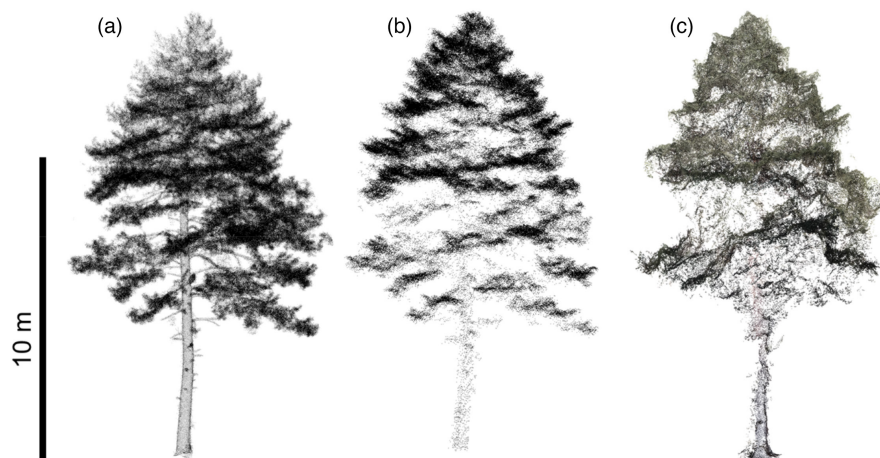
FIGURE 2 Raw point clouds from which structural attributes of a tree may be derived. Data from a single *Pinus sylvestris* in a low-density forest plot in Alto Tajo Natural Park, Spain, surveyed in September 2021 using three different high-resolution remote sensing technologies discussed in this review: (a) a terrestrial laser scanner (Riegl VZ-400i); (b) a UAV LiDAR (Routescene Lidarpod mounted to a DJI M600 Pro UAV) and (c) UAV structure from motion photogrammetry (RGB camera on DJI Mavic Mini UAV). We scanned using TLS (a) from several locations around the tree, generating the highest point density of the three approaches; occlusion effects are evident at the top of the tree and point density is lower. UAV flights (b and c) were conducted at 40 m above surface level, with dense flight lines and high image overlap, and while the top of canopy is well represented for both UAV-borne technologies, occlusion effects mean point density is lower inside the crown and on the trunk.

higher point density and a viewpoint from below, create a rich and highly detailed three-dimensional representation of branch and crown structure (Morsdorf et al., 2018). Much of the earliest work with TLS in forests was focussed on using the technology to improve existing monitoring of structure, including those traditionally taken in ground-based forest inventories (Maas et al., 2008; Thies & Spiecker, 2004; Watt & Donoghue, 2005), or to replace passive instruments to derive gap fraction (Danson et al., 2007).

Tree height and crown area—two morphological metrics that can be obtained from both airborne and terrestrial laser scanning—can improve estimates of large-scale whole-forest properties such as biomass and carbon (though ground measurements of wood properties are still necessary), and allow individual tree monitoring at large scale (Jucker et al., 2017). Tree height can be extracted from ALS data with higher accuracy than in the field (Zolkos et al., 2013), and ALS can provide surface heights at sub-metre resolution (Lee et al., 2010; Lefsky et al., 2005). However, retrieval accuracy can be affected by canopy height and distribution (Hopkinson & Chasmer, 2009), slope of the terrain (Breidenbach et al., 2008), and properties of the sensor including sampling point density (Hyyppä et al., 2000; Roussel et al., 2018) and scanning angle (Qin et al., 2017). Nevertheless, reliable retrievals of stem density, vertical foliage profile (Coops et al., 2007), basal area (Lee & Lucas, 2007) and above-ground biomass measurements (Mascaro et al., 2011; Simonson et al., 2016) have been made using low-density ALS data (e.g. 1–2 points/m²). Crown metrics can be estimated from high point density discrete ALS platforms (~8–20 points m²; Wu et al., 2016), including crown volume (Korhonen et al., 2013), depth (Lee et al., 2010), diameter (Jucker et al., 2017; Morsdorf et al., 2004), cover (Lee & Lucas, 2007), and such data can be used to infer height and crown allometry (Fischer et al., 2020). Full waveform datasets can go a step

further by describing vertical structural complexity (Nie et al., 2017), including understorey characterisation (Hancock et al., 2017) and crown morphology (Lindberg et al., 2012). The inclusion of more individual morphological metrics has been shown to improve whole-forest property estimates; for example, trees vary substantially in their crown mass, and accounting for crown dimensions in allometric models can reduce both uncertainty and bias, particularly for the largest trees which contribute the most to biomass at the plot level (Goodman et al., 2014; Ploton et al., 2016). However, issues of data interpretation persist; Hastings et al. (2020) show that tree size and plot diversity can determine the success of LiDAR-based crown mapping in mixed temperate forests, affecting its applicability in drawing widespread ecological conclusions. Nevertheless, ALS has the major strength in that it can be used to collect data at very large spatial scales, and though it fails to capture smaller trees occluded in the understorey (Donager et al., 2021), this can be addressed with integration of small-scale TLS data within larger ALS surveys to better monitor understorey volume (Liu et al., 2017) and improve biomass calculations (Stovall & Shugart, 2018).

High-resolution remote sensing—including such as may be obtained from sensors on the ground or mounted on drones—offers not only the opportunity to map large numbers of individuals (e.g. to identify single crowns and individual species; Ferraz et al., 2020; Weinstein et al., 2021), but also to quantify many aspects of an individual tree's structure and shape. It is here that the real value of high-resolution remote sensing is evident, demonstrated by developments that use the full three-dimensional data to quantify features that have been impossible to measure without simplifying assumptions, including crown volume (Zheng & Moskal, 2009), vertical profile (Quan et al., 2020) and morphology (Kunz et al., 2019; Owen et al., 2021), above-ground volume and biomass (Brede et al., 2019;

Calders et al., 2015; Disney et al., 2018), and its temporal dynamics (Kaasalainen et al., 2014). TLS data in particular have been used to quantify the properties of crown interiors, including branching size and angle (Lau et al., 2018; Li et al., 2020), fractal space filling (Seidel et al., 2019) and clustering (Béland & Baldocchi, 2020). Observations of crown properties at these fine scales are key to understanding and quantifying fundamental aspects of tree function, such as within crown leaf arrangement to optimise light capture (Valladares & Niinemets, 2007) and reduce it through self-shading (Pearcy et al., 2005), and the impact of three-dimensional crown structural heterogeneity on the light environment of competitors (Kükenbrink et al., 2021). Reconstruction methods such as quantitative structural models (QSMs; see Figure 1a,b) allow the measurement of fine-scale structural details such as twigs, leaves and branches, and how they change through time, from TLS data (Kaasalainen et al., 2014; Raumonen et al., 2013; Wilkes et al., 2021). Furthermore, such data enable new ways to explicitly test theories on crown resource optimisation, light use efficiency and self-shading (Niinemets & Anten, 2009) and pair these to structural-functional plant models (O'Sullivan et al., 2021), leading to new knowledge of structural trade-offs complimentary to well-established leaf and wood economics spectra (Verbeeck et al., 2019). Very high-resolution reconstructions of single trees that reliably preserve fine-scale internal structure may also open new avenues of research to understand the fundamental relationships between genetics, plant morphogenesis and architecture, including testing theories of nested levels of architectural organisation (Barthélémy & Caraglio, 2007), revisiting geometric theories of plant architectural growth (Godin et al., 1999), and improving understanding genetic controls on branching architecture in woody plants (Teichmann & Muhr, 2015).

High-resolution remote sensing can monitor leaf and fine-structural properties relevant to productivity, light environment, structural allocation and stress responses. TLS data can be used to determine leaf angle distributions which drive within-crown light distribution (Stovall et al., 2021; Vicari et al., 2019) and to input into radiative transfer and gas exchange models to predict the spatiotemporal dynamics of forest gas exchange (Damm et al., 2020). Furthermore, dual-wavelength TLS can measure within-crown variation in leaf water, and detect differences between sunlit and shaded leaves (Elsherif et al., 2019). Structural quantification through remote sensing also offers new opportunities to confront widely used allometric theories and geometric assumptions with data (Metz et al., 2013; Owen et al., 2021), to determine understanding of the macroecological drivers of shape branching architecture in plants (Chomicki et al., 2017), to understand the role of abiotic conditions on tree shape, including driving intraspecific variation (Guillén-Escribà et al., 2021) and structural convergence (MacFarlane & Kane, 2017; Martin-Ducup et al., 2020), and the impact of extreme events such as drought on tree shape (Jacobs et al., 2021). High-resolution UAV data can also offer individual structural information, and across larger numbers of trees than TLS. For example UAV-LiDAR can detect phenotypic variation in tree architecture to predict productivity (Camarretta et al., 2020), and produces high enough resolution

information to both discriminate individuals and detect species identity (Apostol et al., 2020). In enabling the quantification of new high-resolution crown morphological metrics at scale, both UAV and TLS allow the expansion of measurement and understanding of multidimensional tree growth, through repeat measurements (Campos et al., 2021; Guerra-Hernández et al., 2017). Though examples are as yet few, such measurements could cast new light on understanding of ontogeny, allocation of resources through changes in leaf distribution and biomass, and fine-scale structural dynamics and plasticity.

3 | SENSING THE THREE-DIMENSIONAL CANOPY: COMPETITION FOR LIGHT, CROWN PLASTICITY AND PACKING

Tree–tree interactions are fundamental to understanding forest ecosystem functions (Trogisch et al., 2021), drive demography and competition (Kunstler et al., 2016; Pacala et al., 1993), and have long formed the basis of simulation models predicting temporal changes in species dominance, stand structure, biomass and carbon (e.g. Coomes et al., 2014; Ménard et al., 2002; Pacala et al., 1996; Purves & Pacala, 2008). Competitive interactions such as asymmetric competition for light are key drivers of forest structure and dynamics (Weiner, 1990), and species' differences in light interception and plasticity create crown complementarity, driving overyielding in diverse plots (Williams et al., 2020). However, tree–tree interactions are typically inferred through strongly simplifying assumptions; for example, the strength of asymmetric competition is typically estimated as some function of density of either taller or larger neighbours (Lines et al., 2012; Lorimer, 1983; Pretzsch & Biber, 2010). These ground measurements provide only a proxy for actual light environments within the canopy as they make simple geometric assumptions about the shape, size and density of tree crowns based on allometry; and the implications of these for understanding competition for light remain poorly understood.

High-resolution remote sensing opens a wide range of opportunities for understanding competition as a driver of ecological dynamics, and for revisiting and refining assumptions. TLS-derived competitive indices have, for example, been shown to outperform those based on traditional standard geometric assumptions to predict growth (Metz et al., 2013). TLS can also quantify the role of competition on crown shape and crown packing, and how these are influenced by shade and drought tolerance (Owen et al., 2021), and disentangle the relative roles of competition and genetics on crown shape (Burkardt et al., 2021). UAV-mounted sensors can quantify structural interactions at much larger scales than is possible through TLS. For example, LiDAR-derived crown properties can predict how neighbourhood competition drives tree growth (Vanderwel et al., 2020), and UAV photogrammetry-derived crowns can be used to determine the relative strength of interspecific vs intraspecific competition on growth (Erfanifard et al., 2021). New insights into how individual shape and competitive interactions affect whole-canopy properties are also emerging; for example, TLS data have

shown how crown shape, branching topology and shade tolerance influence crown position and shading interactions (Martin-Ducup et al., 2021).

Mapping large numbers of individuals, through ALS or UAVs in particular, allows us to ask new questions about the underlying drivers of spatial distribution of trees at scales orders of magnitude larger than ground surveying allows; for example to retrieve stem density (Shang et al., 2019), to demonstrate the regularity of stem clustering patterns across tens of thousands of hectares (Staver et al., 2019), or to map the relationships between crown morphological traits and diversity and elevation (Zheng et al., 2021). Going further, mapping of individual crowns allows us to shift focus from looking at spatial patterning of stems in space (over which each individual tree has little control), to that of crowns (whose positioning can be shifted over a tree's lifetime), uncovering evidence of interspecific variation in crown placement and shyness effects (Disney, 2019; Owen et al., 2021; van der Zee et al., 2021).

4 | SENSING DYNAMICS, DEMOGRAPHY AND ECOSYSTEM FUNCTION

As remote sensors increasingly allow us to map individual trees at large scales in automatic or semi-automatic ways, they are becoming powerful tools to monitor the development of plant populations over time, offering new methods to inform large-scale individual-based forest models. For example, multi-temporal airborne laser scanning has been used to monitor tree migration in transition zones between ecosystems (Næsset & Nelson, 2007), to assess structural dynamics and growth (Duncanson & Dubayah, 2018; Simonson et al., 2016; Yu et al., 2004), to characterise gaps and treefall (Bohlin et al., 2017; White et al., 2018), to detect properties including species identity and size classes for disturbance monitoring (Duncanson & Dubayah, 2018; Levick et al., 2015; Zhao et al., 2018), and to determine individual tree mortality at large scales from crown loss (Aubry-Kientz et al., 2019).

Beyond better monitoring, remote sensing technologies—and the new metrics of structure and competition they reveal—should be capable of generating new knowledge on the causal links between forest structure and demography. The growth and survival of populations is inherently linked to their ability to grow into available space and forage for light (MacFarlane et al., 2011), but growth, mortality and fecundity models usually rely on diameter and/or height to estimate tree performance, even using it to estimate crown properties such as LAI, shading and plasticity (Condit et al., 1998; Lines et al., 2020; Needham et al., 2018; Pacala et al., 1993; Purves et al., 2008). Crown traits have been shown to be good predictors of survival and growth (Kitajima et al., 2005; Smith, 1994; Sterck et al., 2003), and competitive dominance through leaf arrangement and light use (Kitajima et al., 2005). But when the light captured or shaded by individual trees is field assessed for traditional demography studies, this has largely been restricted to classifying trees according to discrete light categories, or using basal-area-derived crowding indices to assess access to space and light and exposure to stressors (Kohyama, 1993; Metcalf et al., 2009; Zambrano et al., 2019). Improved understanding of light and microclimate from remote sensing that can be used to assess the link between structure and vital rates (Stark et al., 2015) may lead to better representation of the impact of small-scale heterogeneity in the abiotic environment, or even direct inclusion of light and microclimate properties, within forest models. For example, three-dimensional foliage distribution obtained from TLS and UAV LiDAR has been used to show trade-offs between light interception and light use efficiency (Onoda et al., 2013), to quantify whole-forest light distribution (Kükenbrink et al., 2021), predict interspecific differences in microclimate (Kong et al., 2016), and model of aerodynamic flow of wind over forest canopies (Floors et al., 2018), and wind and storm damage to trees (Jackson et al., 2019), a leading cause of tree mortality globally (Esquivel-Muelbert et al., 2020; Senf & Seidl, 2021).

Studies using high-resolution remote sensing increasingly show the importance of considering crown complexity and branching to understand how diversity drives forest dynamics. Higher biodiversity promotes more structurally diverse forests, with higher variation in light interception as well as partitioning of space through interspecific variation in crown shape and plasticity, increased light capture and higher biomass accumulation (Fichtner et al., 2018; Jucker et al., 2015; Pretzsch, 2014; Sapijanskas et al., 2014). Furthermore, canopy structural complexity metrics have recently been identified as strong indicators of productivity, outperforming conventional vegetation indices and diversity measures (Gough et al., 2019), but analysis has often been limited by a lack of precise structural data (Dănescu et al., 2016). Both terrestrial and airborne laser scanning provide a wealth of new data that can offer new insights into how plants mix in space (Kamoske et al., 2021; Schneider et al., 2017), and on relationships between diversity and productivity (LaRue et al., 2019). For example, TLS-derived metrics of canopy properties including allocation patterns and internal crown structural complexity show stronger correlations to biodiversity than traditional structural metrics and reveal higher complexity and greater investment towards lateral branch extension in mixed-species forests (Kunz et al., 2019; Walter et al., 2021), leading to new knowledge on the relative importance of functional diversity and morphological plasticity on canopy space optimisation in diverse stands (Hildebrand et al., 2021). TLS has also been used to demonstrate interaction effects (Guimarães-Steinicke et al., 2021; Hildebrand et al., 2021) and the relationships between overyielding and crown complementarity (Guillemot et al., 2020) and diversity in phenological patterns (Lu et al., 2016). Such insights could be used to tease apart structural diversity from other forms of diversity, such as species or functional diversity (Williams et al., 2020), test new theories about how diversity–productivity relationships scale spatially (Gonzalez et al., 2020), and improve understanding on relationships between structural diversity and ecosystem function (LaRue et al., 2019). Combined with ray tracing approaches it will also be possible to directly test species-specific competitive and facilitative shading effects (Kothari et al., 2021), and the relative importance of shade

persistence and structural plasticity as mechanisms driving higher crown packing in mixtures (Williams et al., 2020).

Capturing these processes is key not only to advancing ecological understanding, but also to developing more realistic models that capture the structure and dynamics of forests. Remote sensing technologies such as LiDAR already play an important role in the calibration and up-scaling of forest models (Antonarakis et al., 2014; Fischer et al., 2019; Hurtt et al., 2010; Rödig et al., 2019; Shugart et al., 2015). But they also have the potential to drive the development a completely new generation of forest models that reimagines above-ground forest dynamics from the perspective of tree crowns (Purves et al., 2007). However, these new data streams also pose a challenge for ecological modellers (Fisher et al., 2018), and it remains unclear whether including a representation of three-dimensional complexity in crown architecture and arrangement compared to more traditional measures of competition, such as stand basal area, is worth the increase in model complexity.

5 | SENSING DRIVERS OF CANOPY STRUCTURE AND COMPLEXITY FROM LOCAL TO GLOBAL SCALES

While there is growing interest in developing instruments and data processing pipelines that allow us to use high-resolution remote sensing to study the architecture and growth of individual trees, in ecology their original application was to measure forest structure at a canopy level (Lefsky et al., 1999, 2002). Individual trees aggregate to form canopies, which are a complex emergent property of forests and are the primary interface between the biosphere and the atmosphere for carbon, water and energy exchange. Ecological theories on canopy packing optimisation, and how this is affected by diversity (Coomes et al., 2012; Horn, 1971; Jucker et al., 2015; Purves et al., 2008; Taubert et al., 2015), are influential in quantifying forest biomass dynamics and ecosystem services, but have been developed using geometric assumptions and simple ground data. At a planetary scale, satellite LiDAR instruments such as the Geoscience Laser Altimeter System (GLAS), and more recently the Global Ecosystem Dynamics Investigation (GEDI; Dubayah et al., 2020), have allowed us to capture the first picture of how forest canopy height varies globally (Lang et al., 2022; Simard et al., 2011). Using canopy height observations from GLAS, multiple studies have highlighted the critical role of water availability (measured either as annual rainfall or climatic water deficit) in constraining the distribution of the world's tallest forests (Scheffer et al., 2018; Tao et al., 2016).

However, in addition to these macroscale climatic drivers of forest height, the three-dimensional structure, species composition and diversity of forests vary tremendously within regions and landscapes due to factors unrelated to climate (Gorgens et al., 2019; Jucker, Bongalov, et al., 2018; Jucker, Hardwick, et al., 2018). One key driver of this variation is landscape geomorphology and its influence on local topography and soil chemistry, which LiDAR is particularly well suited to measure (Chadwick & Asner, 2018, 2020; Jucker,

Bongalov, et al., 2018; Jucker, Hardwick, et al., 2018; Muscarella et al., 2020; Walter et al., 2021). Using a combination of airborne LiDAR and hyperspectral imaging, Chadwick and Asner (2018, 2020) showed that, in both the Amazon and Borneo, landscape dynamics linked to erosion, aggrading and soil weathering leave a distinct fingerprint on canopy foliar traits. In turn, these shifts in species composition and diversity along fine-scale topo-edaphic gradients are linked to marked changes in both canopy three-dimensional structure and above-ground carbon stocks in these forests (Jucker, Bongalov, et al., 2018; Jucker, Hardwick, et al., 2018). Moreover, the strength of these topographic effects on canopy structure varies predictably at regional scales due to interactions with climate, with more pronounced differences between forests on steep slopes or ridges and those in valleys in drier environments where soil moisture gradients are most accentuated (Muscarella et al., 2020).

Another key driver of local and regional variation in forest structure, which LiDAR captures the impact of, is disturbance (whether natural or human driven). Canopy gaps, which directly reflect the process of one or more trees dying, have attracted particular attention (Goodbody et al., 2020; Jucker, 2021; Kellner & Asner, 2009). For instance, total gap fraction and gap size frequency distributions have been shown to closely reflect tree mortality rates and reliably detect the effects of selective logging in tropical forests (Dalagnol et al., 2021; Kent et al., 2015; Reis et al., 2021; Wedeux & Coomes, 2015). Beyond gaps, the impacts of logging and habitat fragmentation can also be seen in dramatic changes in the vertical distribution and density of foliage and woody biomass captured by LiDAR (Milodowski et al., 2021), and the spatial and temporal extent of structural change due to habitat fragmentation. A combination of airborne LiDAR and hyperspectral imaging in Borneo has shown that above-ground carbon stocks are >20% lower in the first 100 m from a forest edge, and that these changes are linked to declines in canopy height and shifts in foliar traits related to light capture, growth and longevity such as leaf mass per area and phosphorus content (Ordway & Asner, 2020). Moreover, work using repeat airborne LiDAR acquired before and after the global El Niño event of 2015–2016 has shown that these edge effects can amplify the impacts of drought, as do LiDAR-detectable fine-scale topographic features such as steep slopes and ridges (Leitold et al., 2018; Nunes et al., 2021). A similar before–after approach has been used to quantify the impact of tropical storms on forest biomass stocks and show how biomass losses vary predictably across landscapes with flood risk and exposure to high winds (Cushman et al., 2021; Hall et al., 2020). In the near future, repeat airborne surveys may provide a unique opportunity to study other important but historically overlooked drivers of forest disturbance; for example lightning strikes, which at Barro Colorado Island in Panama have been shown to cause 40% of large tree mortality and 20% of annual gap formation (Gora et al., 2021; Yanoviak et al., 2020).

As access to LiDAR continues to grow, so too do opportunities to leverage these data to advance our understanding of the processes that shape the structure and function of forests at large scales. In particular, we are beginning to see the first real efforts

to bring together high-resolution datasets that capture the full extent to which structural complexity and diversity vary across the world's forests. For example, Ehbrecht et al. (2021) recently used terrestrial LiDAR data from 294 1-ha plots distributed across five biomes to show that canopy structural complexity (quantified using an index based on fractal geometry) is controlled by a combination of broad-scale aridity and rainfall seasonality gradients, soil fertility and water-holding capacity. Equally exciting are the potential to leverage the near-global coverage of GEDI (51.6° north and south of the equator) to capture the diversity of canopy structure from space (Schneider et al., 2020), and potential synergies with other space-borne instruments, such as optical sensors that allow for the mapping of trees at large scales (Brandt et al., 2020), or SAR systems which have been shown to be sensitive to diversity-driven structural variation (Sentinel-1; Bae et al., 2019).

6 | DEVELOPMENTS TOWARDS WIDESPREAD ADOPTION OF REMOTE SENSING IN FOREST ECOLOGY

Many of the technologies described in this review have been shown to be operational within forest monitoring for over a decade, and despite their demonstrated promise, and the wide range of open-source analysis tools available (Atkins et al., 2022), they have not yet become widespread or standard tools within the forest ecological community. Where these data are used, much of the work has reproduced metrics possible from ground measurements (e.g. height), or concentrated on a small number of metrics easily producible from common open-source analysis tools. Obstacles to progress arise for a number of reasons, including complexities in data processing to extract ecologically meaningful information, issues of method comparison and a lack of benchmarking activities, and practical considerations such as high costs associated with data collection, particularly for LiDAR.

Working with three-dimensional data brings unique challenges, so high-resolution remote sensing studies using data processed to individual tree level are often 'proof-of-concept' studies with small sample sizes (<100 trees). A major challenge is the labour-intensive nature of individual tree extraction from point clouds with the most widely used methods still requiring substantial manual processing (Martin-Ducup et al., 2021), leading to many users circumventing automation altogether for a fully manual approach (Guillemot et al., 2020; Kunz et al., 2019). And despite the high-tech nature of sensors, the need to identify the species of scanned trees means hand-drawn stem maps are often still required, bringing additional challenges of stem-matching during post-processing (Guillén-Escribà et al., 2021). The newest deep learning-driven techniques for point cloud classification, tree segmentation, species identification and metric extraction (e.g. Ayrey & Hayes, 2018; Chen et al., 2021; Krisanski et al., 2021; Luo et al., 2021; Xi & Hopkinson, 2021) provide the most promising way forward to increase automation within the processing workflows needed to make use of three-dimensional

data practical at scale. For example, neural network approaches have been used to automate tree crown detection from both RGB aerial imagery (Bosch, 2020; Weinstein et al., 2019), and from aerial LiDAR (Windrim & Bryson, 2020), and to identify species based on whole tree point clouds (Seidel et al., 2021), stem and bark properties (Mizoguchi et al., 2019) and processed, interpretable features (Terryn et al., 2020). The additional inclusion of ecologically realistic information to constrain processing algorithms, including through the use of scaling rules, can further improve performance (Brummer et al., 2021; Tao et al., 2015); however, the need for training data to build these models means that increased data sharing across the community may be needed, as well as adoption of approaches such as transfer learning and data augmentation.

Inevitably, increased access to high-resolution 3D data in the environmental sciences has led to the proliferation of different algorithms for processing the data. While this is essential to move the field forward, many methods exist to calculate the same metrics in different ways, many are tailored to specific sensors, and most methods are developed and tested on small datasets from single forest types with success in processing often dependent on the properties of the ecosystem studied. As a result, approaches may not always be transferable across forest types. For example, species traits and forest structure can determine the success of crown mapping from UAVs (Hastings et al., 2020), and the relative strength of interspecific versus intraspecific variation can complicate automatic identification of species identity (Terryn et al., 2020). Automated approaches are particularly challenging in dense, multi-layered forests where occlusion may be considerable (Aubry-Kientz et al., 2019), though segmenting in simulated leaf-off conditions may improve this, for example using segmentation of leaf and wood points in TLS data through clustering analysis (Ferrara et al., 2018) or supervised learning (Moorthy et al., 2019). Furthermore, different scanners and sampling strategies can lead to highly varying data quality; for example, occlusion effects mean that the number and location of LiDAR scans around a tree strongly influences leaf area retrieval accuracy (Yun et al., 2019), and drones and TLS suffer opposing occlusion effects (Schneider et al., 2019), making them suitable for deriving different metrics. Fine-scale details, even in low-occlusion measurement settings, can be challenging to accurately measure, for example, QSMs have been shown to overestimate small branch diameters (Demol et al., 2022) and taper (Wilkes et al., 2021), so work that explicitly tests the ability of different sensors, sampling strategies and analysis approaches to reliably produce different metrics is invaluable (Boucher et al., 2021; Disney, 2021; Schneider et al., 2019; Wilkes et al., 2017). Navigating the rapidly advancing landscape of developments to identify the best approach is challenging, particularly given the specialist nature of these data. It is clear therefore that in order to advance the adoption of three-dimensional data in forest ecology, improved benchmarking of new methods and improved methodological comparison are sorely needed. New initiatives are opening up access to data collected across a wide range of forest types, including the Global TLS Database (Stovall, 2021), and free airborne LiDAR data across forest sites in the United States

(NEON; Kao et al., 2012) and many European countries (see Ruiz-Benito et al., 2020), bringing new opportunities to demonstrate suitability of methods, and sensor agnostic approaches (Krisanski et al., 2021). Moreover, the cost of sensors and complexity of data acquisition is a barrier to uptake for many, leading to a concentration of work in the best funded universities and institutions. Improved open access to large datasets, particularly when accessible through cloud services with off-site processing, will also improve the number of researchers able to participate in driving forward advances, while improved benchmarking will make clear the effectiveness of different sensors to measure metrics of interest, making infrastructure investment more efficient.

Whilst large-scale initiatives are improving access to data, we still lack a robust common approach to measuring and interpreting forest structural complexity. Instead, an ever-expanding plethora of remote sensing metrics makes comparison across studies, and selection of ones that are ecologically useful and generalisable, extremely challenging. However, there have been attempts to determine the most useful structural properties that can be extracted from high-resolution remote sensing data, including ones which mirror efforts at the individual tree scale by defining a plant structural economic spectrum (Verbeeck et al., 2019), an approach that has huge potential to be expanded towards a whole-plant economics spectrum integrating across leaf, branch, stem and root traits. For instance, terrestrial LiDAR data acquired across multiple sites of the National Ecological Observatory Network (NEON) in the United States were used to identify major canopy structural types using ordination approaches (Fahey et al., 2019). This and similar efforts suggest that there are multiple key axes of canopy structural complexity particularly worth focusing on—including height, height variation, vegetation density and 'gappiness'—and that fractal geometry may hold the key to bringing these together into an overarching framework (Ehbrecht et al., 2021; Fahey et al., 2019; LaRue et al., 2019; Schneider et al., 2020). Large datasets such as these also offer the opportunity to determine the distinctiveness or otherwise of the wide variety of structural complexity metrics proposed in the literature, and to determine distinct axes of variation. Here, there may be opportunities to draw inspiration from other fields in biology that deal with ecosystems that are inherently three-dimensional—such as coral reefs, where theoretical frameworks for describing habitat complexity have been developed (Torres-Pulliza et al., 2020).

There are, of course, many tree and forest properties for which advances from the use of high-resolution remote sensing will provide only partial improvements in estimates, and the measurement of which will continue to need to rely on integration with ground data. An obvious example is above-ground biomass, where accurate volume estimates or improved allometric equations must still be complemented with good wood density data and long-term inventories, particularly in tropical regions (Schepaschenko et al., 2019). While structural properties may hint at individual performance and response to change, many plant traits critical to responses to global change (and all below-ground processes) cannot be sensed with the technologies discussed here. Meaningful transition to increased use of these technologies will only be successful if we build upon existing networks, providing clear links with complementary datasets and robust continuity to the past.

7 | CONCLUSION

The unprecedented detail available from the types of high-resolution remote sensors discussed here makes their adoption inevitable in standard forest ecological research, and will lead beyond improved monitoring to the development of new understanding and theory about the structure and function of trees and forests. These data are beginning to be used to shed new light on classical ecological questions on allocation of resources, competitive interactions, structural optimisation for light capture, and canopy space filling and structural plasticity, but this is just the start of the remote sensing revolution in forest ecology. To enable rapid development, adoption of these data is needed more widely, beyond those groups with access to the resources to collect them, so data sharing with standardised collection methods is needed. Equally, the value of using such data to answer a broad range of ecological questions must be recognised by researchers who have not participated in their collection, and compromise on the particular geographical location of data needs to be traded off against their information content.

Automation of processing workflows is rapidly reducing the time and manual input needed to process point cloud data, and these advances will not only increase pragmatic sample sizes, but will also lower the expertise required to use these data, improving the delivery of information to non-expert end-users. Robust testing of new algorithms is needed, and benchmarking against existing methods should become standard practice, particularly when generating ecological metrics. This could be achieved through reanalysing existing datasets, or the establishment of benchmarking sites with freely available data in plots with contrasting forest structure and diversity. New metrics that describe three-dimensional complexity are needed, and these should be clearly defined, robust to variation in instrument and collection method, and, crucially, demonstrably ecologically interpretable to be useful to a wide range of users.

Here, we find a wide range of exciting uses of these data, and the biggest advances for forest ecology from their use will be made through broad thinking about their potential to take us beyond the framework of a trunk-centred view of forests; many of the studies we have reviewed are pushing this boundary. Proactive and early collaboration between remote sensing scientists and ecologists will lead to the development of new ecologically meaningful metrics far beyond more accurate estimates of properties we can measure with ground data. The value of these data will increase through a series of advances, of course in data availability and technological development, but equally as importantly through creativity of use, leading us to new ways to understand forests.

AUTHORS' CONTRIBUTIONS

E.R.L. and T.J. conceived the idea. E.R.L. led the writing with contributions from all authors.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest. Emily Rebecca Lines and Tommaso Jucker are Associate Editors of *Journal of Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

The review does not use data.

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