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Review

Terrestrial laser scanning in forest ecology: Expanding the horizon

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ABSTRACT

Terrestrial laser scanning (TLS) was introduced for basic forest measurements, such as tree height and diameter, in the early 2000s. Recent advances in sensor and algorithm development have allowed us to assess in situ 3D forest structure explicitly and revolutionised the way we monitor and quantify ecosystem structure and function. Here, we provide an interdisciplinary focus to explore current developments in TLS to measure and monitor forest structure. We argue that TLS data will play a critical role in understanding fundamental ecological questions about tree size and shape, allometric scaling, metabolic function and plasticity of form. Furthermore, these new developments enable new applications such as radiative transfer modelling with realistic virtual forests, monitoring of urban forests and larger scale ecosystem monitoring through long-range scanning. Finally, we discuss upscaling of TLS data through data fusion with unmanned aerial vehicles, airborne and spaceborne data, as well as the essential role of TLS in validation of spaceborne missions that monitor ecosystem structure.

1. Introduction

Prior to the availability of laser scanning, explicit 3D forest structure was often represented qualitatively. These representations were often only two dimensional such as the hand-drawn tropical forest tree archetypes (Hallé et al., 1978; Specht, 1970). New developments in terrestrial laser scanning (TLS) provide unprecedented three-dimensional in situ information of trees and forests (Malhi et al., 2018). This 3D information is argued to play a key role in monitoring and understanding how terrestrial ecosystems are functioning and physically changing due to climate change (Calders et al., 2020; Verbeeck et al., 2019).

The potential of TLS for forest monitoring was first demonstrated in published literature since the early 2000s (Hopkinson et al., 2004; Jupp et al., 2009; Lovell et al., 2003; Strahler et al., 2008). Applications initially focused on measuring traditional structural metrics that are used in forestry such as height and diameter at breast height (DBH), but eventually evolved to whole-tree volumetric assessment to improve

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estimates of aboveground biomass (Calders et al., 2015a; Gonzalez de Tanago et al., 2018; Momo Takoudjou et al., 2018). Current applications also include individual modelling of branch architecture (Lau et al., 2018), habitat assessment (Ashcroft et al., 2014) or quantifying fuel loads (Chen et al., 2016; Hudak et al., 2009; Loudermilk et al., 2009). Vertical profiles of forest structure from TLS (Palace et al., 2016) can characterise successional vegetation types (Cuni-Sanchez et al., 2016) and show potential for global ecology and biodiversity studies (Valbuena et al., 2020) when combined with large footprint spaceborne LiDAR missions, such as GEDI (Global Ecosystem Dynamics Investigation) (Marselis et al., 2018).

Here, we provide an interdisciplinary view on essential method development and technological advances in TLS in forest ecology. These new developments are set to revolutionise the way in which we observe and monitor changes in tree and forest structure and functioning. We review and identify state-of-the-art methods for a range of ecological applications, and reflect on their bottlenecks and current issues. We aim to set an agenda for increased uptake of TLS to support and improve our understanding and dynamic modelling of forest ecosystems in a changing climate. Within this context, we first discuss critical sensor and algorithm development and their role in forest measurements. We then reflect on new opportunities that these in situ 3D data are creating, including research on tree form and function, input for radiative transfer modelling, monitoring of urban trees and long-range scanning of large areas. Finally, we will discuss the upscaling of fundamental ecological understanding through TLS data and links to large-area or global remote sensing products.

2. Advances in instrument technology and data processing

2.1. Advancing TLS technology enables sensor-specific applications

While the basic premise for collecting 3D data is similar across TLS instruments, distinct ranging methods have emerged: time-of-flight (TOF) and phase-shift (PS) sensors (Kahlmann et al., 2006; Wehr and Lohr, 1999). They differ primarily by a balance of cost and signal-to-noise ratio (SNR). TOF sensors emit a discrete outgoing laser pulse, measuring the amount of time required to intercept an object and return to the scanner. Using the constant speed of light in vacuum (299,792,458 m s^{-1}) and the laser pulse travel time divided by two, distance is estimated. PS sensors operate using a similar concept, but emit a continuous signal, modulating frequency and amplitude to produce a unique outgoing signal. The incoming signal is compared with the outgoing signal and out-of-phase regions are translated into range estimates. PS sensors tend to be quick, relatively inexpensive, lightweight, and have low beam divergence that produces extremely high-resolution data, but rarely sense multiple returns, have lower SNR, lower maximum range, and increased ranging artifacts compared to TOF sensors (Newnham et al., 2012). The latter is especially true in complex vegetation, where multiple beam interceptions occur, substantially increasing range ambiguity in single return systems. Despite TOF sensors generally being heavier and more expensive, their consistent, high-quality data they collect make them the current "gold-standard" TLS (Fig. 1) for a range of vegetation applications (Newnham et al., 2012). For all TLS instruments, the effective range of measurements is limited by surface reflectance, which can be estimated directly from instrument specifications with the radar equation. For example, at an approximate leaf reflectance of 20%, long-range TOF scanners can reliably collect measurements at ~150 m distance, while other laser scanning technologies are effectively limited to a range of ~30–40 m. Beam divergence affects the resolution of fine branches and leaves in the TLS data, so should be carefully considered, depending on forest type and the specific application of TLS data.

Due to cost, speed of acquisition, weight, and SNR, specific sensors and approaches may be ideal, depending on the application. In order from least to most expensive, we evaluate [a] short-range TOF, [b] mid-range TOF, [c] long-range PS, [d] long-range TOF, and [e] mid-range dual wavelength, highlighting relevant forest ecology applications and avenues for sensor improvement in an operational context. Table 1 gives a non-exhaustive overview of commonly used commercial and non-commercial TLS instruments in vegetation monitoring.

Short-range TOF TLS systems may provide an affordable option for high-quality TLS data, at the expense of limited range and/or durability. The canopy biomass lidar (CBL) is a non-commercial multiple-return low-range (< 40 m) TLS built for durability (e.g. covered rotating mirror and IP68 weatherproof) and fast acquisition time (Paynter et al., 2016, 2018, 2019). Due to range limitations, the CBL is ideal for quickly characterising short forests and the under- and mid-story of forests using a metaproperty approach (Paynter et al., 2018). The Leica BLK360 – a less durable (e.g. exposed rotating mirror and non-waterproof) mid-range (60 m) TOF TLS is a lower-cost commercial option that offers a cost-effective alternative for quantifying forest structure in detail, with initial observations showing high-quality point clouds with lower noise than PS TLS units in a similar price bracket (Disney et al., 2019). However, increased range and durability would be needed to enable use in taller stature forests and more challenging field conditions.

PS TLS instruments are generally cheaper, lighter, and capture high-resolution data effective in low to mid complexity or leaf-off forests. Due to their light weight (~5 kg), PS TLS are ideal in difficult terrain or secluded field sites, where heavier scanners are more cumbersome when traveling long distances on foot. Scan noise is highest in coniferous and dense broadleaf forests (Newnham et al., 2012) since PS technology has greater ranging ambiguity when intercepting multiple objects within the footprint of a single laser beam. Filtering and modelling algorithms specific to PS TLS focus on reducing ranging errors by excluding low return intensity and inconsistent range estimates by directly filtering outliers at the scan grid-level. Appropriate filtering of PS data enables accurate and precise biomass estimates of trunk, branch, and needles (~3–15% RMSE for whole-tree biomass) in coniferous trees (Stovall et al., 2017). In leaf-off hardwood forests, phase-shift sensors can help develop non-destructive allometric models (Stovall et al., 2018), reducing uncertainty in calibration and validation of global aboveground biomass missions (Stovall and Shugart, 2018). Given the low cost of PS instruments, noise reduction (e.g. more advanced grid filtering or post-processing k-nearest neighbor and outlier removal) would be the main requirement to substantially improve the applicability of these instruments in more complex forests.

Long-range (> 300 m) TOF TLS systems are widely recognized as the best option for measuring forest structure and tree architecture in a range of forest types with the highest spatial detail (Newnham et al., 2015). TLS instruments in this category, e.g. RIEGL VZ400(i) or Leica ScanStation P40, are ideal for capturing forest structure for several reasons. First, high-powered TOF instruments have superior SNR, providing more accurate return positions with less noise (Newnham et al., 2012). This, coupled with over 1 MHz pulse rate, the ability to detect multiple returns per laser pulse, and near-automatic registration, increases measurement density and reduces occlusion (Calders et al., 2014). The tight manufacturer specifications in high-end instruments also improve instrument comparability (Calders et al., 2017) and global consistency in TLS products (Duncanson et al., 2019).

The spectral information from TLS return intensity can be leveraged to estimate biochemical properties and separate leaves from wood. Eitel et al. (2010) and Zhu et al. (2015) used the intensity of a typical single-wavelength commercial TLS instrument to estimate biochemical parameters (chlorophyll and water content, respectively). However, this approach can be challenging as this requires adjusting for incidence angle and partial intercepted laser beams and needs further research in more complex and larger canopies. An evaluation of the radiometric calibration of three same make and model (RIEGL VZ-400) scanners showed that radiometric calibrations are instrument specific and that absolute bias is greater for high reflectance returns (Calders et al.,

Fig. 1. 3D complexity of a Simple Notophyll Vine Forest (Robson Creek, Australia) captured using a time-of-flight RIEGL VZ-400 instrument. Left panel: The colours represent the distance from the scanner. Right panel: Derived plant area volume density as a function of canopy height derived for the same scan using (Calders et al., 2015b). This estimated structural metric tells us how the volume of leaf and branch material is distributed with height in the canopy and its integral is the plant area index.

Table 1
Examples of TLS instruments used to assess forest structure.

Major Instrument Categories	Short-range TOF + large beam divergence	Mid-range TOF + medium beam divergence	Long-range PS + small beam divergence	Long-range TOF + medium beam divergence + low noise	Mid-range Dual Wavelength + medium beam divergence
Cost	$	$	$$	$$$	$$$
Ideal Forest conditions	+Sparse/simple forests + Remote areas	+Sparse/simple forests + Remote areas	+ Leaf-off or structurally simple forest stands + Remote areas	+ Best in tall/dense forests	+ Accessible, structurally simple forest stands
Optimal Forestry Applications	+ Rapid assessment + Robust + Cost-effective forest structural metrics	+ Rapid assessment + Cost-effective forest structural metrics	+ Finely resolving small branches	+ Finely resolving small branches + Potential for full waveform applications	+ Leaf-wood separation + Biochemical properties + Improved vertical foliage distribution + Potential for full waveform applications
Example Instrument	UMB CBL (SICK Lidar; non-commercial)	Leica BLK360	FARO Focus^{3D} X 330	RIEGL-VZ400i	SALCA (non-commercial)
Ranging method	TOF	TOF	PS	TOF	TOF
# returns	1st + 2nd	Single	Single	Multiple	Full waveform
Wavelength [nm]	905	830	1550	1550	1545.4 & 1063.4
Maximum Range [m]	40	0.6 - 60	0.6 - 330	1.5 – 250 (high speed) 0.5 – 800 (long range)	100 m
Samples/sec	11,000	360,000	122,000- 976,000	42,000– 500,000	5,000
Beam Divergence [mrad]	15	0.4	0.19	0.35	0.56
Weight [kg]	3.9	1	5.2	9.7	17
Temperature range [deg C]	-30 to 50	5 to 40	5 to 40	0 to 40	5 to 30
References	Paynter et al. (2018, 2016)	Disney et al. (2019)	Liang et al. (2015); Pyörälä et al. (2018)	Bienert et al. (2018); Tian et al. (2019)	Danson et al. (2018); Schofield et al. (2016)

2017). Users are therefore recommended to carry out a radiometric calibration before including reflectance information in TLS analysis (Calders et al., 2017; Hartzell et al., 2015). Including intensity-based features through multispectral TLS could enhance leaf-wood classification and additionally allow measurement of biochemistry and health to reveal the 3D distribution of canopy physiological features (Danson et al., 2014, 2018; Douglas et al., 2015; Elsherif et al., 2019b; Gaulton et al., 2013; Junttila et al., 2019). However, multispectral TLS remains experimental with research instruments such as SALCA (Danson et al., 2018; Schofield et al., 2016), DWEL (Douglas et al., 2015; Li et al., 2016, 2018) or hyperspectral TLS (Hakala et al., 2012). The use of two or more individual single-wavelength TLS systems operating at different wavelengths (but with similar technical specifications) has been shown to be successful for detecting differences in leaf water content or tree health (Elsherif et al., 2019a; Junttila et al., 2019), but is complicated by the need for careful radiometric calibration and beam alignment. Such approaches also introduce significant logistical challenges in field application as multiple scans are required, especially if conditions are windy or change between scans.

Other terrestrial laser scanning instruments offer atypical acquisition strategies (transecting, handheld mobile, and multi-spectral) that enable unique perspectives of forest structure and function. Portable canopy LiDAR (PCL) is an upward facing pulsed TOF that collects transects of vertical forest structure and can help capture structure-function relationships through canopy metrics (Atkins et al., 2018a, 2018b; Parker et al., 2004), but the instrument has yet to be widely adopted. Handheld mobile laser scanning (MLS) continuously acquires data while carried by the operator thereby reducing understory occlusion (Bauwens et al., 2016) but until recently had a limited range (Cabo et al., 2018) and large beam divergence compared to stationary TLS systems. New MLS instruments now offer an increased range up to 100 m (ZEB Horizon) and recent developments in MLS (Hyyppä et al., 2020) are promising, but require further testing in structurally complex forests.

Overall, the diversity of TLS systems available has produced a range of novel measurement approaches, useful for characterising forest structure in 3D. Each system can effectively be deployed in a range of scenarios highlighted in Table 1, but, at a given price point and set of specifications, certain instruments excel at specific tasks. Granted, we recognise many instruments can be used to collect similar 3D structure information, especially if the limitations of each instrument are considered and mitigated with appropriate acquisition strategies (e.g. reducing occlusion, higher density scan spacing, etc.; Wilkes et al. (2017)). Reliable automation with weatherproof designs will make high frequency seasonal TLS collections possible for phenological studies and change detection (Culvenor et al., 2014). Price is a major barrier for adopting TLS technology into forest ecology, but instruments with acceptable specifications are becoming available at much lower price points. At present, commercial TLS units and onboard detection and filtering algorithms are not optimised for capturing vegetation structure. Now, major technological advances specific to forest ecology must address the issue of more reliably sensing "soft" surfaces (e.g. leaves) with lower beam divergence and greater sensitivity to low reflectance surfaces.

2.2. Towards algorithms for automated TLS data processing

The past two decades have seen significant progress in the development of near-automated processing pipelines for extracting different forest structural attributes from TLS data. However, most TLS approaches in forest ecology often still rely on some time-demanding manual steps for data analysis. The need to advance and automate algorithms for deriving structural features from 3D data is equally important as sensor advancement for the broader uptake of TLS in forest monitoring.

2.2.1. Current approaches

Methods for analysing TLS data from forests can be broadly classified into two main categories: (1) gap probability methods and (2) geometrical modelling (Newnham et al., 2015). Pulse-based or voxel-based gap probability methods are used to estimate plant area index (PAI, Fig. 1) or leaf area index (LAI) of forest stands, whereas geometrical modelling allows for explicit reconstruction of individual tree structure.

2.2.1.1. Gap probability methods. LAI quantifies the area of leaf material per unit area in an ecosystem, and critically contributes to the characterisation of Earth's climate (Asner et al., 2003; Calders et al., 2015b; Jonckheere et al., 2004). It is important to note that TLS can essentially only estimate PAI or WAI (wood area index) in forests (Calders et al., 2018b). Gap probability estimates are the basis for deriving PAI and the vertically resolved plant area volume density (PAVD) based on a form of the Beer-Lambert's law (Calders et al., 2014; Jupp et al., 2009; Pimont et al., 2018; Zhu et al., 2018b):

$$P_{gap}(\theta, z) = e^{-G(\theta)\, PAI(z)/\cos(\theta)} \tag{1}$$

z is the height above terrain and where z_{max} is the height of the canopy and θ is the zenith angle of the laser pulse. $P_{gap}(\theta, z)$ is the vertically resolved gap probability and $G(\theta)$ is the foliage orientation function, which equals the projection of a unit area of plant constituents on a plane perpendicular to the direction θ, averaged over elements of all orientations (Ross, 1981).

From a single scan, pulse-based methods (Calders et al., 2014; Jupp et al., 2009) approximate vertically resolved gap probability, $P_{gap}(\overline{\theta}, z)$as

$$P_{gap}(\overline{\theta}, z) = 1 - \frac{\Sigma w_i (z_i < z, \overline{\theta})}{N(\overline{\theta})}, \text{ where } w = 1/n_s \tag{2}$$

$\overline{\theta}$ is defined as the mid-point of the finite zenith angle interval used to aggregate laser pulses. The numerator in Eq. (2) gives the number of laser returns that are below z and $N(\overline{\theta})$ is the total number of outgoing laser pulses for the zenith angle interval. For a specific emitted laser pulse each return equates to a beam area interception of $1/n_s$, where n_s is the number of total returns for that emitted laser pulse. This approach is implemented in the open source python library *pylidar* (www.pylidar.org).

Alternatively, several voxel-based methods to estimate PAI are available (Pimont et al., 2018). These include ray-tracing methods based on contact frequency approach (Béland et al., 2011) and methods based on Beer-Lambert's law (Béland et al., 2014b; Grau et al., 2017; Hosoi and Omasa, 2006). Voxelising TLS data is not trivial especially when we deviate from the theoretical assumptions that TLS instruments emit an infinite number of infinitely small laser pulses through any given voxel (Pimont et al., 2018). In reality, beam divergence and the finite number of laser pulses entering any given voxel due to angular scanning resolution and occlusion results in voxels with varying point density. This will influence the choice of right voxel size (Pimont et al., 2018).

Whereas both pulse-based and voxel-based approaches have their own set of problems related to theoretical assumptions that cannot be met in measured TLS data, there are some issues common to both of them. First, to calculate LAI we need robust algorithms to distinguish between leaf and woody points. We have recently seen an increase in the number of leaf-wood separation methods from TLS data based on both intensity (Béland et al., 2014b) and geometric properties of the points in 3D space (Béland et al., 2014a; Belton et al., 2013; Boni Vicari et al., 2019a; Krishna Moorthy et al., 2019b; Wang et al., 2018; Yun et al., 2016; Zhu et al., 2018a). Methods based on geometric properties of the points are more robust than intensity-based methods as they are independent of the TLS instrument. However, most of these methods are developed and tested only on temperate forests (except for Boni Vicari et al. (2019a) and Krishna Moorthy et al. (2019b)) and do not provide sufficient detail to reproduce or benchmark the results of different methods. Second, both pulse-based and voxel-based approaches make theoretical assumptions about the foliage distribution, which are not always valid in reality. Leaf angle distributions (LADs) influence the incoming radiation regime within the canopy and are an important parameter in estimating vertical LAI profiles (Ross, 1981; Wilson, 1959). LAD is often ignored in ecological models due to the difficulty in quantifying this parameter. Recent studies have succeeded in estimating LAD at individual tree level from TLS data (Boni Vicari et al., 2019b; Itakura and Hosoi, 2019; Kuusk, 2020; Liu et al., 2019) enabling reliable estimation of LAI and vertical LAI profiles from TLS. Irrespective of some of the still prevalent issues in estimating PAI from TLS data and the difficulty to measuring true PAI, recent studies have demonstrated that TLS provides a more stable estimate of PAI when compared to other ground-based sensors such digital hemispherical photography (DHP) as it is independent of the illumination conditions (Calders et al., 2018b; Hancock et al., 2014).

2.2.1.2. Geometrical modelling. Geometrical modelling approaches exploit the full 3D structure of the TLS data and generally require single trees to be segmented from co-registered point clouds. Multiple single scans can be co-registered using high reflectivity targets that act as tie-points between different scan locations (Wilkes et al., 2017). Work on reflector-less registration algorithms is promising (Kelbe et al., 2016) and a new range of commercial scanners (Leica BLK360 and RIEGL VZi-series, see Section 2.1) provide onboard registration without the need for targets. Currently, we recommend more testing (i.e. quantifying the effect of ecosystems, instrument characteristics and sampling design) before using this in an operational context. A uniform point density is recommended to provide consistent point cloud quality throughout the plot. This may require downsampling the point cloud (e.g. using voxel grid filtering, Burt et al. (2019)) or scanning an area larger than the plot (Wilkes et al., 2017).

In the past decade a range of methods have been developed to extract trees (Burt et al., 2019; Raumonen et al., 2015; Trochta et al., 2017; Yrttimaa et al., 2019a), lianas (Krishna Moorthy et al., 2019a, 2020) or downed dead wood (Yrttimaa et al., 2019b) from plot-level TLS data in a (semi-)automated manner. Most tree segmentation methods follow a bottom-up approach by first identifying the potential stem bases and subsequently growing the identified stems into branches and twigs to reconstruct full tree crowns iteratively. For example, *3D FOREST* (Trochta et al., 2017) first divides the whole point cloud into horizontal slices and further divides each of these slices into clusters based on user-defined parameters (e.g. cluster size and maximum distance between two points to belong in the same cluster). Each of the clusters are treated as a potential tree and are merged vertically with the closest clusters from other slices based on the angle and distance

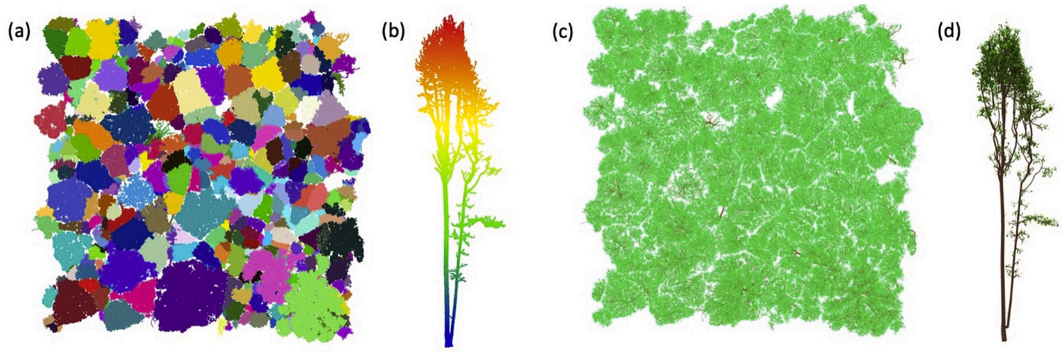

Fig. 2. Conversion of a segmented point cloud (Burt et al., 2019) from terrestrial laser scanning to a virtual forest for radiative transfer modelling, example of 1 ha Wytham Woods (Calders et al., 2018a). (a) & (c) give a view from above of the 3D point cloud and 3D model respectively. (b) & (d) give a side view of a single tree point cloud and its corresponding model (branches + leaves) respectively.

between the centroids of the clusters. *Treeseg* (Burt et al., 2019) follows a slightly different approach by first detecting the stem points closer to the ground instead of treating every cluster as a possible tree. The tree is then further extracted using generic point cloud processing techniques including Euclidean clustering, principal component analysis, region-based segmentation, shape fitting and connectivity testing. Fig. 2(a-b) shows a segmented point cloud using *treeseg*. These methods usually require manual assistance and quality control to correct omission or commission errors in the segmented point clouds. Generally, more manual intervention is required in complex ecosystems, such as tropical rainforest, where multiple crowns can interact with each other.

Once the trees are extracted, the tree point cloud can be modelled using quantitative structure modelling (QSM) algorithms. However, leaf-wood separation might be required first for leaf-on point cloud data. Current state-of-the-art leaf-wood separation algorithms are mostly based on machine learning (ML) and computer vision (CV) approaches (Béland et al., 2014a; Belton et al., 2013; Boni Vicari et al., 2019a; Krishna Moorthy et al., 2019b; Wang et al., 2018, 2020a; Yun et al., 2016; Zhu et al., 2018a). Classical ML algorithms such as random forests and Gaussian mixture models (GMM) were trained on manually labelled point clouds from specific forest types with features based on eigenvectors and eigenvalues that describe the local geometric properties of the points in 3D space. Given that the training data points for a model come from a handful of forest types, further testing of these algorithms is advised. Unsupervised approaches are preferred over supervised ML approaches considering the difficulty in acquiring manually labelled data points (Wang et al., 2020a).

Tree structural metrics related to branching architecture can be derived through skeletonising methods that derive a graph with geometric information of the vertices and edges from the point cloud (Bucksch and Lindenbergh, 2008). Based on QSM algorithms such as *TreeQSM* (Calders et al., 2015a; Raumonen et al., 2013) or *simpletree* (Hackenberg et al., 2015) that both fit cylinders, the tree volume as well as 3D structural metrics and their topology can be estimated. The quality of the QSM depends on the quality of the point cloud data and quantifying uncertainty of QSMs remains challenging. Whereas the QSM cylinder fitting approach might work for most trees (Akerblom et al., 2015), it might fail for buttressed trees in tropical forests (Disney et al., 2018) and mesh-based models are advised (Liski et al., 2014; Morel et al., 2018). Open source initiatives such as *computree* (Othmani et al., 2013) and *3D FOREST* (Trochta et al., 2017) have integrated the point cloud processing workflow in a GUI.

2.2.2. *The potential of deep learning for TLS data processing*

Deep learning differs from classic ML algorithms in how features are extracted from data. In classical ML, features are handcrafted by humans and then fed into classification algorithms, whereas in deep learning, the algorithm learns the features by itself from the data (Goodfellow et al., 2016).

While object detection, classification and segmentation in 2D images have moved away from classical ML to deep learning (Toshev and Szegedy, 2014), segmentation of 3D data is still predominantly based on classical CV and ML algorithms. The first set of deep learning networks for 3D data projected the 3D point clouds into 2D images from multiple viewpoints and used 2D convolutional neural networks (Rehush et al., 2018; Su et al., 2015). Deep learning for 3D point clouds has made considerable progress and evolved from converting point clouds to voxels (Xi et al., 2018; Zhou and Tuzel, 2018) or octrees (Riegler et al., 2017) to working directly on 3D point clouds (Qi et al., 2017a, 2017b). Furthermore, a recent deep learning based network called BranchNet has been trained to specifically extract structural information from branch-like structures (Halupka et al., 2019).

Deep learning techniques can potentially automate the processing pipeline for extracting various features from 3D data of forests. This includes, but is not limited to, segmenting individual tree stems and branches (Xi et al., 2018) to extracting detailed branch structural information (Halupka et al., 2019). However, challenges still need to be overcome. The main success of deep learning in 2D image segmentation is the availability of a large number of images to train and benchmark these networks. Reference datasets of 3D tree architecture that would be useful for training and benchmarking the algorithms are currently lacking. This is not surprising considering the difficulty in creating reference datasets. Open access to these already available reference datasets with well-described metadata and uncertainties would facilitate deep learning approaches for TLS. With the increasing amount of TLS data being collected across the world, deep learning based algorithms have the potential to revolutionise the field (Arel et al., 2010) and could fuel the automation of some of the existing manually intensive tasks of extracting features from the 3D data.

3. Forest measurement and management

Key observation variables in forest monitoring and management are DBH, tree height, basal area per hectare, stand growing stock volume, and aboveground biomass (AGB). In order to generate these attributes, individual trees need to first be identified providing an attribute of tree count. Henning and Radtke (2006), Maas et al. (2008) and Liang et al. (2012), to name a few, presented methods for identifying tree stems from TLS point clouds whereas Donager et al. (2018) compared point densities and Liang et al. (2018) compared a variety of methods in tree detection. Both Donager et al. (2018) and Liang et al. (2018) concluded that increasing forest density increased the challenge of correctly detecting all trees within the area of interest. Reliable tree count estimates from TLS have implications for the reliability of data fusion and upscaling applications (see Section 4).

Circle or cylinder fitting have most commonly been used for deriving DBH estimates from TLS (Liang et al., 2018). Nevertheless, both circle and cylinder fitting assume circularity of tree stems, which is a rather optimistic assumption (Saarinen et al., 2014; Stovall et al., 2017) and could further be enhanced as TLS data enables modelling of more complex primitives (Akerblom et al., 2015) or convex hull (Stovall et al., 2017). TLS estimates of tree height from co-registered point clouds (Wilkes et al., 2017) have been obtained as a difference between the highest and lowest points of tree point clouds (Calders et al., 2015a; Saarinen et al., 2017) or as the value of 99.9th percentile of height (Stovall et al., 2017). Several studies have reported underestimates for TLS-based tree height (reviewed by Liang et al., 2016, Liang et al., 2018), although accurate height measurements have also been reported when compared with destructively felled trees (Calders et al., 2015a; Stovall et al., 2017). These different observations in the accuracy of estimating tree height can be attributed to differences in sensors and fieldwork setup (see Section 2.1). A combination of TLS with 3D observations above canopy can be used to enhance tree height estimates (Schneider et al., 2019; Yrttimaa et al., 2020). However, this approach warrants more research in the future, especially within more complex forest ecosystems. Additionally, scan design (i.e. number and location of scans) as well as scanner technology (i.e. time-of-flight vs phase-shift, single return vs multiple returns) should more thoroughly be investigated in order to better understand effects of each component on tree height accuracy.

Both stem volume and AGB are traditionally indirectly estimated using allometric models with field measurements such as DBH and tree height as predictors (Chave et al., 2005; Henry et al., 2011; Zianis et al., 2005). Current TLS approaches reduce allometry-related uncertainty through direct estimates of woody volume from point clouds (Gonzalez de Tanago et al., 2018; Kankare et al., 2013; Yu et al., 2013), which can be converted to AGB using wood specific gravity (WSG) information. For carbon stock assessments, proper error accounting is crucial, especially for large trees for which current allometric models are most uncertain (Case and Hall, 2008; Chave et al., 2014; Réjou-Méchain et al., 2019). Conversion of volume into AGB through WSG adds uncertainties to AGB estimates, caused by the high spatial, intra-specific and intra-individual variability of WSG, and the occurrence of hollow stems, which cannot be detected by TLS. Often it is impossible to sample each scanned tree for WSG, hence approximative values are sourced from species-specific or plot WSG averages. This requires the availability of sufficient WSG data coupled to correct species identifications. Åkerblom et al. (2017) showed that tree species recognition with QSMs is feasible in low-diversity boreal forests. For more species diverse forests, tree species classification performance greatly depends on the targeted application and exhibits a trade-off between sensitivity and specificity (Terryn et al., 2020). Ideally, a whole-tree or volume-weighted WSG is used as a conversion factor. Discrepancies between a database WSG value, or a partial WSG measurement (e.g. increment coring at breast height) and whole-tree WSG can contribute to bias in TLS-derived AGB estimates (Sagang et al., 2018; Wassenberg et al., 2015). Efforts to derive whole-tree WSG from a partial WSG measurement have been developed to some extent (Bastin et al., 2015; Momo Takoudjou et al., 2020; Wassenberg et al., 2015). Other solutions to mitigate WSG related uncertainties, such as novel WSG sampling methods, are discussed in (Réjou-Méchain et al., 2019).

The increased accuracy of direct volume and derived AGB estimates with TLS data is poised to improve the quality of carbon stock assessments through permanent sample plots, supersites or national forest inventory (Liang et al., 2016). Alternatively, TLS can be used to include information about crown structure into allometric models to better distinguish the heteroscedasticity of tree size-to-mass allometry (Goodman et al., 2014; Kankare et al., 2013; Lau et al., 2019a; Ploton et al., 2016). Whereas existing pantropical tree allometric models are transferable across tropical forest types (Chave et al., 2014), more complex models, including additional geometric plant features from TLS, may show a better performance locally. However, they are expected to be less transferable, due to the differences in site-specific tree allocation patterns across environmental gradients. We recommend that it is essential to carefully evaluate (potential) empirical models that use TLS data to estimate AGB as well as tree allocation patterns in different ecoregions to better understand forest dynamics and especially suitability of tree allometric models across forest types.

Crown structure is difficult to measure automatically and objectively with traditional forest measurement devices but can be extracted from TLS data (Kankare et al., 2013; Lau et al., 2019a; Srinivasan et al., 2015). For instance, Seidel et al. (2011) and Metz et al. (2013) have presented a variety of attributes derived from TLS point clouds characterising crown size and shape (e.g., crown height, projection area, volume, asymmetry) using a convex hull of points in a plane at various heights as well as a 3D convex hull for calculating crown surface area. Literature on the accuracy of TLS-based crown attributes is not extensive (Fleck et al., 2011; Seidel et al., 2015). Fleck et al. (2011) compared the reliability of crown area estimates from TLS with the area of eight-point crown projections measured in the field and obtained R^2 of 0.96 and RMSE of 6.5 m^2 whereas Seidel et al. (2015) reported correlations from 0.5 to 0.7 between crown attributes measured with traditional means (e.g. clinometer, densiometer, measuring tape) and derived from TLS. However, in dense forests where crowns interweave, reliably obtaining crown attributes from TLS point clouds is similarly challenging to field measurements. This requires further methodological development, which can also contribute to automatically and reliably segmenting individual trees (see Section 2.2.1.2).

Taper curves provide diameters along a stem and it has been utilised for obtaining stem volume, especially in Scandinavia. Measuring diameters from the upper part of a stem (i.e. within crown), especially for conifers, can be challenging from TLS point clouds. A spline function (i.e. a proxy for taper curve) can be used in completing the diameter measurements from the occluded part of the stem (Saarinen et al., 2017, 2019). This approach can also be used for buttressed trees, with the overall shape of the stem being estimated from the upper well-scanned part downwards with the use of a taper curve (Bauwens, S. et al., unpublished).

These new developments in forest measurement and new structural metrics from TLS are relevant to forest management. For example, TLS provides new information on how structural crown properties vary in mixed and pure stands (Barbeito et al., 2017; Bayer et al., 2013; Hajek et al., 2015; Kunz et al., 2019) as well as how canopy gaps impact crown shape (Hess et al., 2018; Seidel et al., 2016). Detailed information about the taper curve (Pitkänen et al., 2019; Saarinen et al., 2017) provides information on log geometry and wood quality (Pyörälä et al., 2019a). Future improvements of forestry volume tables will be possible by repeated TLS measurements to gain new insights into growth (Mengesha et al., 2015; Sheppard et al., 2016), changes in stem taper (Luoma et al., 2019) and biomass (Kaasalainen et al., 2014; Srinivasan et al., 2014). Repeated TLS data acquisition requires careful planning for ensuring point clouds with comparable quality. Co-registering of multiple point clouds from different time points should result in a similar level of quality. Furthermore, scan design and geometry should provide comparable information on the same trees, crowns, and branches for reliably assessing possible changes and their magnitude. An example of intensive temporal resolution of a TLS time series for which these challenges were minimized was presented by Puttonen et al. (2019) who demonstrated circadian movements of tree branches during a 14.5 h measurement period.

Silvicultural practices affect growing conditions (i.e. light, temperature, water, nutrients) of individual trees and thus, forest structure and tree growth (Eriksson, 2006; Juodvalkis et al., 2005; Mäkinen and Isomäki, 2004; Nilsson, 2010; Río et al., 2017; Valinger et al., 2019). Since TLS can provide a variety of structural attributes of trees as well as their relationship (e.g. spatial distribution or crown competition), which have traditionally been demanding or impossible to measure, TLS can expand our understanding about the effects of silviculture. TLS has already been used in investigating effects of silviculture practices on structural diversity through space filling (Juchheim et al., 2017a), competition and tree structure (i.e. stem and crown attributes) (Georgi et al., 2018; Juchheim et al., 2017b). Additionally, TLS has shown its potential in providing information on how species composition affects tree architecture (Barbeito et al., 2017; Bayer et al., 2013; Juchheim et al., 2020; Krůček et al., 2019; Metz et al., 2013). However, the majority of studies on the effects of silviculture have been concentrating on deciduous trees, especially European beech (*Fagus sylvatica* L.) in central Europe. Therefore, we encourage the use of TLS also for conifers and in boreal forests where forest management and silviculture have long traditions to understand the potential of TLS in various forest environments (Saarinen et al., 2020).

In addition to forest management, TLS can be used in mapping and measuring downed dead wood (Yrttimaa et al., 2019b) - an important attribute for biodiversity-, classifying defoliation (Huo et al., 2019), characterising tree health (Junttila et al., 2019), and natural sway frequencies (Jackson et al., 2019) related to tree architecture and tree-wind dynamics. Understory vegetation, obtained by TLS, can be related to regeneration or forest structural complexity (Willim et al., 2019). Microstructure (i.e. vegetation canopy and topography at cm to m scales, Maguire et al. (2019)) has been shown to affect photosynthetic functioning in forest-tundra ecotone with TLS, and a relationship between rainfall interception and LAI was demonstrated by (Yang et al., 2019). Finally, TLS has enabled assessing forest surface fuel loads (Chen et al., 2017; Wallace et al., 2016) and it is expected to enhance forest fuel hazard assessments as well as planning ecological and risk mitigation strategies.

4. New opportunities with terrestrial laser scanning

Beyond the applications of TLS in the fields of forest measurement and management there is a wide range of new application areas where tree architectural information, at a range of scales, may provide the key to new scientific insights (Disney, 2019). For example at the finest spatial scales, TLS can provide direct measurements of tree canopy components like branch size, position and orientation, all of which are impractical to measure manually. These measurements can provide fundamental new insights into the scaling of branches. Furthermore, this feeds into reconstruction of virtual trees that can be scaled up to represent complete forest stands (Calders et al., 2018a). These virtual forest models can in turn be used to improve the accuracy of the retrieval of forest biophysical properties from radiative transfer models (RTMs) when coupled with Earth Observation (EO) data. New applications are rapidly developing to characterise and quantify the biophysical properties of urban trees (Baines et al., 2020). Recent research has illustrated the magnitude of the contribution of such trees to carbon storage and other ecosystem services (Wilkes et al., 2018). A final example of new insights arises through the opportunity to obtain accurate repeated measurements with TLS to detect landscape-scale ecosystem changes (Singh et al., 2020). Long-range TLS measurements may be limited in terms of spatial resolution at kilometer scales but recent research has highlighted the power of long-range measurements for ecosystem change detection. These four examples are explored in more detail next. This review focuses on forest ecosystems, but it is worth mentioning that TLS data is increasingly used in horticultural tree crops for assessing tree structure (Decuyper et al., 2018; Fernández-Sarría et al., 2019; Moorthy et al., 2011) and advancing the development of monitoring with remote sensing platforms (Wu et al., 2020a, 2020b).

4.1. Metabolic scaling theory

Measurements resulting from TLS can provide precise and detailed information on tree structure that can help answer fundamental questions about tree size and shape, allometric scaling, metabolic function and plasticity of form (Disney, 2019). Importantly, detailed TLS measurements of branch architecture can test not only the predictions, but also the assumptions, of how tree structure and metabolism scale with size (Metabolic Scaling Theory, MST, West et al. (1997) and Savage et al. (2010)). Testing these assumptions holds large implications for the use and potential revision of MST predictions related to the scaling of plant growth (Enquist et al., 2007) and to linking forest structure and productivity (Enquist et al., 2009; Fyllas et al., 2017; West et al., 2009). For example, this theory assumes that branch radii and branch lengths follow a scaling relationship, but testing this assumption accurately would require felling trees and measuring the size of branch segments by hand, a prohibitively time consuming task for large trees (Bentley et al., 2013). As such, Lau et al., 2018 proposed a method to use TLS to quantify fine scale branch architecture. A proof of concept from nine sampled trees in Guyana was deemed successful to test branch scaling predictions of MST (Lau et al., 2019b).

Furthermore, TLS can measure the quantitative architectural metric path fraction. This quantity is the ratio of the mean path length (from tree base to branch tip) to maximum path length (Smith et al., 2014), and it relates to tree hydraulic efficiency. Relatively little research has been devoted to the reconstruction of fine scale branching architecture, and the estimation of the metric path fraction thus remains challenging for trees (Lau et al., 2018). Occlusion and wind effects while scanning have been well established to be problematic (Seidel et al., 2012; Vaaja et al., 2016; Wilkes et al., 2017), but are even more so when fine branches need to be estimated. In addition, scanning to the level of precision needed to estimate small branches requires instruments with small beam divergence, extremely high-resolution scans, and a small scan position grid (~10 m) (Wilkes et al., 2017), which are time consuming to acquire. Recent developments in measuring small fine-scale branches include the use of optical photogrammetry to potentially refine TLS size estimates for small fine-scale branches towards the tips of trees (Wilkes et al., 2019); and the development of modified QSMs that combine leaf and wood processing (Boni Vicari et al., 2019a; Krishna Moorthy et al., 2019b; Wang et al., 2020a) or allow data co-registration and volume enclosure to be considered as part of the same process (Wang, 2020).

4.2. Virtual tree models for radiative transfer models

Radiative Transfer Models (RTMs) are an integral tool within Earth Observation (EO) of forests, as they enhance our ability to monitor and understand the linkages between light emitted or reflected (i.e. an EO observed signal), forest structure and biochemistry. Representing forest structure in RTMs can range from 1D horizontally homogeneous layers to fully geometrically explicit 3D models, where the latter can facilitate the calibration and validation of EO data, better uncertainty quantification and algorithm development.

Previously, 3D virtual forests were reconstructed using softwares such as *OnyxTree* (www.onyxtree.com), *xfrog* (Lintermann and Deussen, 1999) or *arboro* (Weber and Penn, 1995), which requires parameterisation from field inventory data, airborne LiDAR, or parametric modelling of plant growth and topology. However, numerous gaps in information based on traditional inventory data exist, which can (potentially) be addressed by TLS, including: shoot/leaf shape and dimensions (curl, size) (Åkerblom et al., 2018; Zhu et al., 2018b), shoot/leaf orientation (Boni Vicari et al., 2019b), foliage distribution in crowns (Martin-Ducup et al., 2018), crown shapes (Côté et al., 2009) and the wooden skeleton including branching angles and density (Calders et al., 2018a; Raumonen et al., 2013). Fig. 2(c-d) shows an example of a fully explicit structural model derived from TLS where the woody components are modelled by QSMs and leaves are added with the *FaNNI* algorithm (Åkerblom et al., 2018) through LAI estimates from TLS.

Despite these advancements, a number of challenges still remain, particularly in providing a fully explicit representation of individual leaves/shoots and/or tree crowns (for example recent work by Wang et al. (2020b) demonstrated promising results on the use of TLS to extract photon recollision probability at the crown level, allowing delineation of tree crown structures), understory structure and woody content (live and dead) (Lau et al. (2018)). Along with these challenges, further considerations need to be taken into account when using TLS measurements for RT modelling. The collection of ground-based data concurrently with TLS is necessary for RT modelling, including the scattering directionality of the forest elements (leaves/shoots, wood, understory and background bidirectional reflectance distribution function) and illumination, as well as in situ measurements of EO data products (e.g. LAI, Fraction of Absorbed Photosynthetically Active Radiation or biochemical constituents) to validate reconstructed virtual forests and simulated EO measurements of forest structure and function (Calders et al., 2018a; Cifuentes et al., 2018; Widlowski et al., 2014). Site selection is also important, specifically if TLS measurements are used to characterise calibration and validation networks, such as the Terrestrial Ecosystem Research Network (TERN) (Karan et al., 2016), the National Ecological Observatory Network (NEON) (Kao et al., 2012), and the Integrated Carbon Observation System (ICOS) (Gielen et al., 2018) to name but a few. Both larger sites, and consistent measurements over time are needed, in order to represent the spatial heterogeneity (Morsdorf et al., 2020) and temporal evolution (Calders et al., 2018a) of forests as seen by a remote sensing sensor. Finally, data fusion of TLS with hyper- or multi-spectral remote sensing data can improve sampling of the distribution of canopy spectral properties to better parameterise the spectral information input into RTMs, as well as providing additional data sources for validation of the RTMs, for example Schneider et al. (2014) reconstructed a virtual forest based on ALS- and TLS-derived voxel grids of PAI, and showed good agreement between simulated and measured hyperspectral data from the APEX airborne imaging spectrometer (Schaepman et al., 2015). Addressing such challenges can improve realistic radiative transfer modelling of forests and help provide a better understanding of the interaction between forest structure and EO derived parameters.

4.3. Trees outside of forests

TLS has been applied to quantify the structure of trees outside of forests as well, for example in commercial orchards (Murray et al., 2020; Wu et al., 2020a) and as discussed below in urban forests. The ecosystem services offered by urban forests are now recognized for making our ever expanding cities more habitable for city dwellers in the face of changing climate. The structure of urban trees and forests can be highly variable due to context, management and planting strategies which often deviate from natural forests. This can lead to structural outliers (e.g. very tall or open grown) and may give insight into the limits of growth for particular species (Disney, 2019). TLS allows for capturing variability in tree morphology when compared to traditional measurement techniques; this includes capturing environmental context (e.g. tree spacing, buildings, etc.). TLS datasets can therefore be used to derive new allometric models specifically for quantifying the volume of urban trees, for example, to estimate AGB (Lefsky and McHale, 2008; Wilkes et al., 2018). Further, TLS is an excellent way to digitise, study and monitor exceptional or unusual trees which are often found in cities (Fig. 3).

The use of TLS in urban forestry is not yet operational, and still requires method development especially for trees outside of forests. However, TLS datasets have been used to train predictive models of urban forest structure. When combined with airborne and satellite remote sensing data (Baines et al., 2020; Tanhuanpää et al., 2019), this can identify patterns in urban forest structure and allow monitoring of highly dynamic forests through time. A barrier to operational adoption of TLS for urban forest inventory could be cost and the time taken to acquire data. However, cities are some of the most surveilled areas on earth and offer opportunities to supplement TLS with new 3D measurements, e.g. Structure-from-Motion (SfM) from airborne aerial imagery or LiDAR sensors on (driverless) cars. Further, citizen science projects (e.g. Treezilla) could also be used as additional training data or validation for remote sensing derived urban forest structure or deep learning approaches.

4.4. Long-range scanning

Most progress in ecological TLS research has taken place in forested ecosystems, where the laser ranging distance of an instrument is seldom a limiting factor for long-range TOF instruments. Line-of-sight is typically limited to < 100 m in temperate, boreal and tropical forests (Calders et al., 2014), and avoiding excessive occlusion requires multiscan setups with 10 or 20 m grid spacing (Wilkes et al., 2017). In these forests there is little benefit to be gained by investing in laser systems that can range accurately over distances longer than 1 km. As such, the spatial extent of TLS data acquisitions is typically restricted to < 1 ha in scale (Beland et al., 2019), limiting their suitability for monitoring hillslope and landscape scale dynamics. Outside of forestry research however, much progress has been made in developing long-ranging TOF TLS instruments (> 2000 m) for applications in glaciology, geomorphology, archeology, and mining engineering (Fischer et al., 2016; Gabbud et al., 2015; Lercari, 2016). Long-range scanning offers potential to complement the TLS methodologies that have been developed in forests so far, but their suitability for ecological studies will vary as a function of the habitat type and landscape terrain features.

The utility of long-range scanning to inform ecological questions, such as vegetation response to disturbances, has only recently been explored (Singh et al., 2018), and provides an avenue for obtaining high-resolution 3D data at hillslope scales (Singh et al., 2020). Long-range TLS is suited to open landscapes with uninterrupted line-of-sight for hundreds of meters (Fig. 4). These criteria can be met in many savanna and shrub-land ecosystems around the globe, especially if the TLS instrument can be elevated to positions above the tree canopy and the topography is relatively flat. A key consideration of long-distance scanning is the beam divergence of the laser. For example, the RIEGL VZ-2000 has a beam divergence of 0.35 mrad, which translates to a footprint spot size of 0.04 m at 100 m distance, and 0.7 m at 1000 m. Explicitly testing how beam divergence and incidence angle affect the characterisation of vegetation canopies are key areas of ongoing research, which will lead to better quantification of how error propagates with distance from the scanning position. These advances will allow for broader scale 3D mapping that can capture the structure and dynamics of heterogeneous systems, which are difficult to represent through traditional plot- or transect-based scanning approaches.

5. Towards global ecosystem understanding

Local measurements are useful for key challenges such as carbon balance or long-term forest monitoring only if they can be scaled up to the ecosystem, landscape, and regional scale. The extensive TLS data collection efforts across diverse forest ecosystems are increasingly being coupled and augmented with airborne and spaceborne LiDAR characterisation of vegetation structure. This facilitates appropriate scaling from individual trees to local plot measurements to regional estimates. TLS data is expected to play a crucial role in helping revise and extend ecological scaling theories related to tree form and function to help determine the ecological and evolutionary drivers (Magney et al., 2014). This could then further relate branch architecture traits to leaf and wood properties at the whole tree level (Verbeeck et al., 2019). However, when we aim for upscaling to stand and landscape level, there is a practical limit to the amount of resources that can be allocated to the collection of TLS data over larger areas (> 1 ha). We should question if the high point density and level of detail acquired with TLS is always required for studies at larger spatial scales. In this context, it is useful to consider the potential of other laser scanning platforms (spaceborne, airborne, Unmanned Aerial Vehicles - UAV), and evaluate

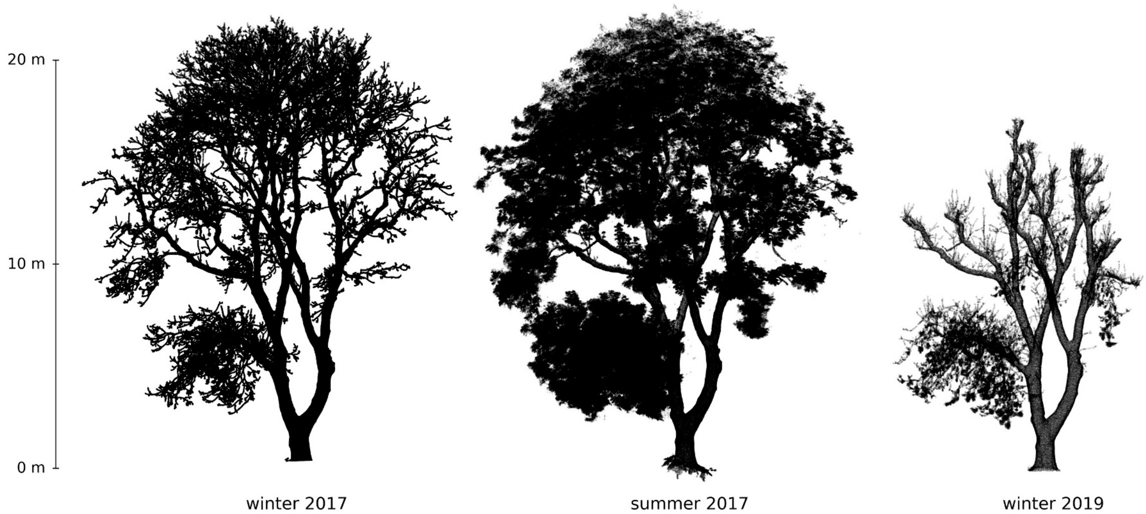

Fig. 3. TLS data of the Hardy tree, situated in the grounds of St Pancras Old church in London (51.5350° N, 0.1302° W). This Ash tree (*Fraxinus excelsior* L.) is notable for the many gravestones sitting leaf-like in around the base of the tree, that were supposedly placed there by the author Thomas Hardy in the 1860s during his time working as a clerk on the rapid expansion of the railway system. The tree is senescing and is being actively managed by Camden Council (compare summer 2017 and winter 2019). The tree has been scanned three times with a RIEGL VZ-400 to monitor how tree structure changes over time. An interactive 3D model can be viewed at https://skfb.ly/6GVBK.

the added value of fusing data from these platforms with TLS data.

Unmanned Aerial Vehicles equipped with laser scanners (UAV-LS) have been explored as a possible solution to speed up the scanning process, in order to cover larger areas and still allow analyses comparable to those from TLS (Brede et al., 2017; Liang et al., 2019; Wallace et al., 2014b). There are currently multiple commercial UAV systems available, with a large variation in data quality. Recent UAV-LS systems have produced point clouds with densities of around 50 (Wallace et al., 2012), 1500 (Gottfried et al., 2015; Jaakkola et al., 2010) and 4000 points per m^2 (Brede et al., 2017). Compared to traditional Airborne Laser Scanning (ALS), UAV-LS demonstrates significantly higher point density at lower cost and with higher flexibility, but with significantly smaller spatial coverage. The choice for ALS or UAV-LS mainly depends on the size of the study area and application. Fig. 5 demonstrates different point densities for ALS, UAV-LS and TLS along a 150 m transect in a tropical savanna.

UAV-LS has been successfully used for a number of forestry related applications. These applications include: tree height estimation and localisation (Wallace et al., 2014b), tree detection and segmentation (Balsi et al., 2018; Wallace et al., 2014a), DBH estimation (Brede et al., 2017; Wieser et al., 2017), Canopy Height Model (CHM) generation, LAI estimation, AGB estimation via allometric equations based on tree height and crown area (Guo et al., 2017), and tree parameter estimation from tree reconstruction algorithms (Brede et al., 2019). We emphasise again that QSMs only estimate volume and conversion to AGB through wood specific gravity will introduce additional uncertainties (see Section 3). A comparison between the TLS and UAV-LS systems from RIEGL show that for more open forest types (temperate beech forest or

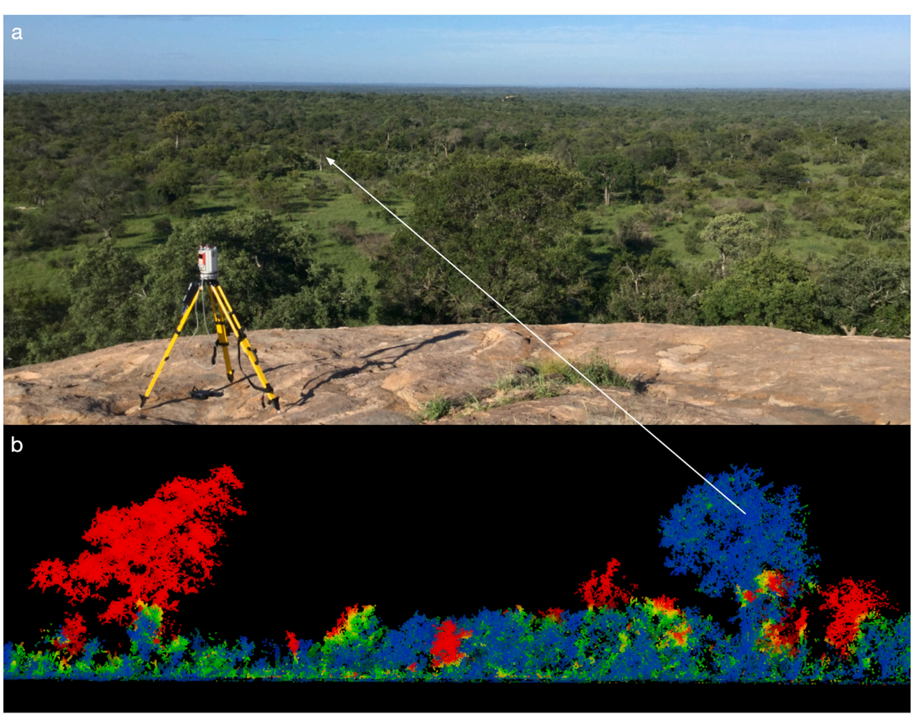

Fig. 4. Long-range scanning. Panel (a) shows the RIEGL VZ-2000 setup on a topographic vantage point in southern Kruger National Park, South Africa. Panel (b) shows the point cloud difference for a cross-section (2015–2016). Blue points are unchanged, red points are not present anymore (e.g. red tree on the left has been toppled, mostly likely by an elephant). Yellow/green also indicates vegetation loss, but at a small magnitude of less than 0.2 m (e.g. defoliation). No growth was detected in this example due to extreme drought conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

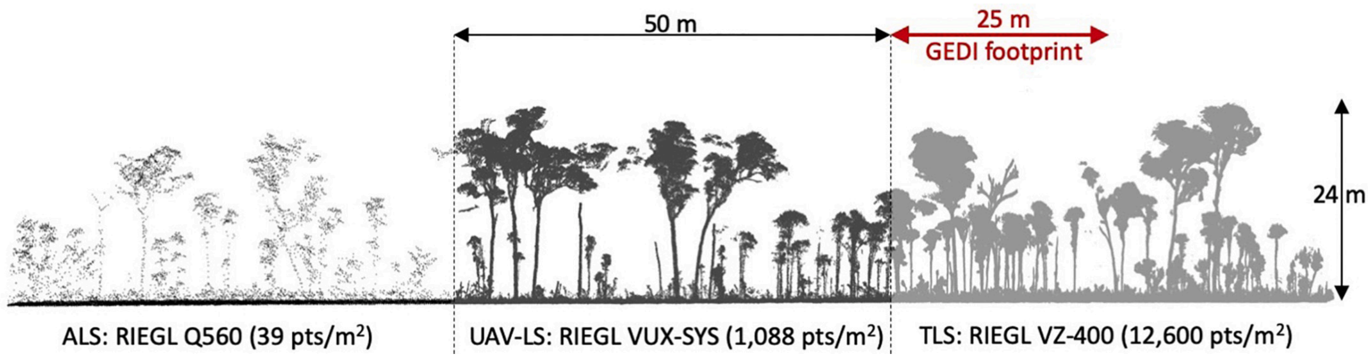

Fig. 5. LiDAR data at the tropical savanna Litchfield TERN supersite in Australia. The LiDAR cross section is 150 m long and 10 m wide constructed from three sections of 50 m × 10 m (from left to right: ALS, UAV-LS, TLS). All point cloud data is downsampled to 0.02 m voxels to give a fair comparison of point density. ALS data was collected through TERN in June 2013, TLS data collected in August 2018 and UAV-LS data collected in September 2018. For scale, we show the footprint size of a NASA Global Ecosystem Dynamics Investigation (GEDI) laser footprint.

savannah woodlands), the UAV-LS data of the RIEGL RiCOPTER equipped with a VUX-SYS has a lower point density and distribution than the RIEGL VZ-400 TLS data. However, the two datasets are geometrically still very comparable and QSM algorithms can successfully be applied on the UAV-LS data (Brede et al., 2017, 2019). Other UAV-LS systems on the market yield a lower point density and data quality, which may limit possibilities to reconstruct the tree structure. Schneider et al. (2019) found that generally 71% of a canopy up to 25 m above ground may be occluded in a temperate forest when observed with UAV-LS. In more dense forest types (e.g. tropical rainforest or coniferous forest) the above-canopy viewpoint of the UAV-LS limits capturing the full tree structure. To overcome this, critical future research will include developing methods to: (a) upscale fine-scale structure over larger areas by fusion of TLS and UAV-LS to benefit studies where forest dynamics are high and occur at a limited spatial scale (< 100 ha); and then (b) further extrapolating this to regional scales (> 100 ha) by fusion of UAV-LS and ALS data (Boucher, 2019; Pyörälä et al., 2019b). Fusion of LiDAR data from terrestrial with different platforms and the use of fused point clouds has only been marginally explored in forest ecology (Paris et al., 2015; Shenkin et al., 2019; Wilkes et al., 2018). Co-registration of multi-source point clouds will be critical, but can be achieved if enough in common objects are present to act as tie-points (Calders et al., 2014). Particularly in dense forests, fusion of TLS with above-canopy LiDAR (e.g. UAV-LS, Schneider et al. (2019)) can significantly reduce occlusion.

We are presently in a new era of spaceborne active remote sensing, with three missions having accuracy requirements linked to their AGB data products. These missions include two Synthetic Aperture Radar (SAR) instruments – ESA BIOMASS (https://earth.esa.int/eogateway/missions/biomass) at P-band (Quegan et al., 2019; Toan et al., 2011) and NASA/ISRO NISAR (https://nisar.jpl.nasa.gov/) at L-band (Rosen et al., 2015) – and the NASA Global Ecosystem Dynamics Investigation (GEDI, https://gedi.umd.edu/) LiDAR on the International Space Station (Dubayah et al., 2020). The NASA GEDI LiDAR mission was launched on December 5th 2018 and started scientific data collection on April 19th 2019 (Dubayah et al., 2020). GEDI will collect global scale measurements of vertical canopy structure for two years using eight ground tracks (600 m spacing across track) composed of ~25 m laser footprints (60 m spacing along track). Each of these spaceborne missions have calibration and validation programs and TLS and UAV-LS contribute to these efforts (Duncanson et al., 2019). Fig. 6 shows two examples of GEDI waveforms and derived elevation and height metrics from the TERN Litchfield SuperSite, where the footprint size is larger than individual trees. An illustration of the scale of these individual GEDI footprint measurements relative to the detailed 3D information in the ALS, UAV-LS and TLS point clouds is shown in Fig. 5. Building on the findings of Blair and Hofton (1999), recent work has developed methods for simulation of GEDI waveforms from ALS and UAV-LS point clouds and collocation of these simulations with on-orbit measurements from GEDI (Hancock et al., 2019). These methods may be extended for simulation of waveforms from TLS point clouds (Hancock et al., 2017), enabling simulated spaceborne measurements to be directly linked with the forest structure measurements described in Section 3.

TLS and UAV-LS present unique opportunities to improve the accuracy of forthcoming AGB maps from these spaceborne missions and also provide more insight into their uncertainties. Disney et al. (2019) outlined the following key areas where TLS would contribute:

- Improvements of the existing allometric models through increased sample sizes and reduction in allometric bias through incorporating more near-direct measurements of large tree volume and stem diameter (Burt et al., 2020; Stovall et al., 2018; Vorster et al., 2020). This is likely to reduce the uncertainty of estimates compared with allometric methods that underpin all current spaceborne AGB estimates (Stovall and Shugart, 2018).
- Development and testing of EO retrieval using 3D RTMs (Calders et al., 2018a) (see also Section 4.2). A key problem of validating EO-derived products is the difficulty of making direct measurements of the desired biophysical properties (Disney, 2016). New TLS-derived structure for RTM allows for integration of much more realistic and detailed 3D surface structure into retrieval and testing processing chains (Calders et al., 2018a).
- Quantifying uncertainty in retrieved AGB estimates through pre-launch modelling and calibration, and post-launch validation at the plot scale (Réjou-Méchain et al., 2019).
- Providing a link between measurements made at the tree and plot scale, from forestry, UAV-LS, ALS, and spaceborne platforms (Kellner et al., 2019).

The Committee on Earth Observation Satellites (CEOS) Land Product Validation (LPV) focus area for AGB has developed a protocol for best practices in the validation and comparison of AGB map products (Duncanson et al., 2019). This protocol has outlined key uncertainties and knowledge gaps, and synthesized recommendations to advance TLS and UAV-LS from a research technology to one that is used more routinely in the calibration and validation programs of spaceborne biomass missions and the establishment of biomass supersites (Chave et al., 2019). Protocols for data product quality assessment and quality control, metadata and attribution are also required to see TLS data products reach a similar level of maturity as comparable protocols for forest mensuration and ALS in large area forest plot monitoring networks. Existing networks (e.g. TERN) have made substantial

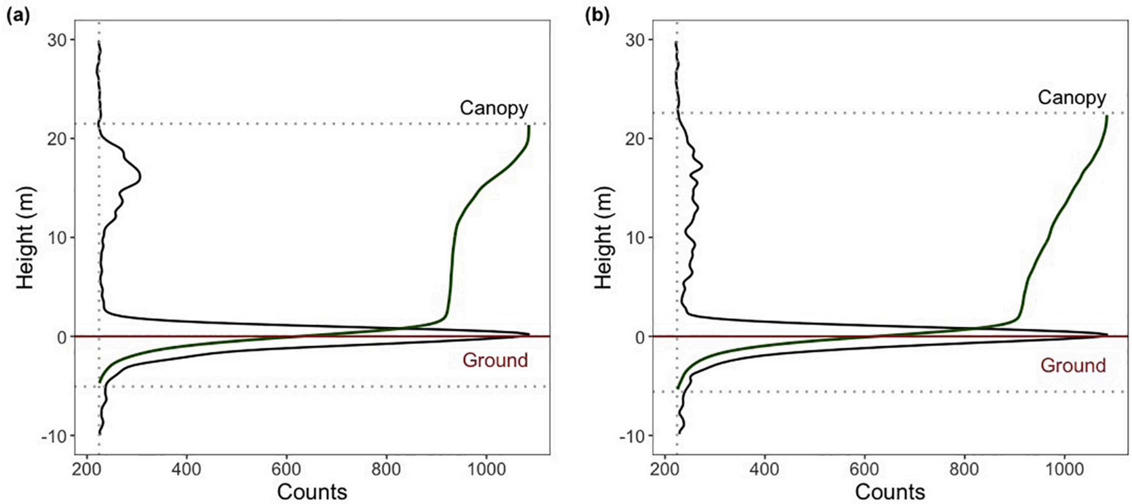

Fig. 6. Two GEDI waveform examples at the tropical savanna Litchfield TERN supersite in Australia. The plots show the vertical profile of digitizer counts for a single shot, which has a footprint diameter of nominally 25 m (see Fig. 5 for a spatial reference). The elevation of the lowest mode ("ground") and highest reflecting return ("canopy") are derived from the waveform and available in the GEDI Level 2A product (Dubayah et al., 2020). The green line indicates the cumulative digitizer counts between the elevation of the lowest and highest return. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

progress towards standardization of acquisition protocols and are collecting new plot scale measurements contemporaneous with GEDI.

6. Conclusions and outlook

TLS, along with other developments in 3D imaging, has already provided a step change in our ability to measure tree structure in detailed 3D, from the individual to the canopy-scale. As the interest in, and use of TLS for forest ecology has increased, a number of new challenges are arising in order to make the best use of existing and new data and tools. TLS opens a realm of untapped research questions and applications that call for the most detailed and accurate 3D information on canopy structure possible. Key to this is the need to develop more robust, automated and flexible 3D canopy structure reconstruction methods. This is particularly true for very tall (> 60 m), dense tropical forests and for TLS data with correspondingly greater variation in point density from low to high in the canopy, laser beam spot size, and occlusion. Current 3D reconstruction approaches have generally been developed to work best on good quality (i.e. no noise and even point density) TLS point clouds, for single trees. This means that the more time and resources that are put into data collection, registration, prefiltering and then fine-tuning the reconstruction, the better the results with these existing approaches. To advance cost-effective data collection, consensus needs to be reached over what constitutes 'optimal' data; and how we objectively assess occlusion and point cloud quality. As we collect more data across a wider range of forested ecosystems, with different systems and under different conditions, the need for more rapid automated methods increases. 3D structure methods should ideally require little-to-no manual input and be agnostic to the specifics of TLS system, data collection or ecosystem. A key additional benefit of fully-automated approaches is to drastically lower the barrier to entry to the use of the data. Moreover, as 3D reconstruction approaches could benefit from deep learning approaches (see Section 2.2), it should be possible to learn from every reconstruction so that each new branch, tree or forest reconstruction is approached with the inbuilt expertise of all previous reconstructions. We want to avoid constraining reconstructions to exist in an echo chamber - *'if you liked that tree, you'll like this one'* - as that is the best way to filter out diversity and miss the unusual, which ecological systems have a habit of throwing up. This is especially true for urban trees, which have a highly variable structural complexity.

Finding ways to reconstruct 3D structures that better incorporate probability in both process and outcome, should tell us significantly more about the organisms and systems we are trying to measure. Ongoing work in graphics on incorporating semantic info to assess and infill occlusion for image reconstruction (Li et al., 2020) can potentially be applied to point clouds (Miao et al., 2020; Shu et al., 2019). A key part of this needs to be validation and benchmarking. A diversity of approaches to deriving structural information is vital, but this means that we also need objective ways to decide which approaches work best, and why. This is an area where the sheer difficulty of collecting detailed and direct 3D structural measurements, makes validation of indirect methods like TLS or SfM so difficult. On the other hand, this difficulty is also the reason why indirect methods are so attractive. In conclusion, high quality validation data, tools and frameworks are needed to underpin our ability to extract higher detail information from very accurate 3D data. There is ample opportunity to learn from other communities here who have used model intercomparison exercises to rapidly develop fields such as radiative transfer modelling of the atmosphere and in vegetation (Widlowski et al., 2015) or filtering algorithms for digital elevation models from airborne laser scanning (Sithole and Vosselman, 2003).

New ecological insight arising from 3D measurements is leading us to ask new and harder questions of our data. For example, TLS data can be used to develop a structural economic spectrum to understand how woody plants arrange themselves along a few descriptive axis of structural traits (Verbeeck et al., 2019). TLS has increasingly been used to support interdisciplinary research such as understanding habitat requirements of mammals (Stobo-Wilson et al., 2020), monitoring butterfly populations (Hristov et al., 2019) or modelling leaf-deposition of atmospheric particles in urban environments (Hofman et al., 2014, 2016). Addressing new, often more complex, research questions leads to greater appreciation of both the limitations but also the potential. When we think about ways to improve the extraction of 3D canopy structure information from TLS, two aspects should be considered. The first is time; high resolution temporal monitoring of 3D structure via repeated TLS scanning has the potential to deliver unique time-varying 4D data of canopy structural dynamics. This is common-place in the spectral domain, but arguably the structural domain provides as much, if not more, information. Developing ways to combine high time and space resolution 3D data with spectral information, will open up new ways to analyse the relationships between structure and function, trait-based analysis and more. This will require new methods to enable routine collection and merging of these data with special attention to quantifying occlusions and point cloud quality, but the rapid development of TLS systems and methods is already heralding a new era in 4D measurement.

The second consideration is integration across spatial scales, as well as with other measurements. UAV-LS is becoming increasingly common, as is the development of low-range-low-cost LiDAR systems that could be deployed on mobile platforms and/or in large numbers simultaneously within a forest system. We need to be thinking about algorithms and data collection approaches that make the integration of these data as seamless as possible. Various studies have already combined UAV, TLS, and ALS in one combination or another, but currently these approaches are highly manually-intensive and typically require downsampling or aggregation to some lower resolution or point density than the native systems are capable of. This translates into new questions as how do we avoid losing information like this and does it really matter? We believe that currently there is no one-size-fits all approach, and that searching for one is a mistake. We should accept that some applications will prioritise different data collection approaches (e.g. single scans vs high density scanning) and require different levels of detail of the derived structural parameters (e.g. total tree AGB vs. diameter and angles of higher order branches). Another aspect to consider is the inclusion of other data sources or data fusion. For example, SfM is developing as rapidly as TLS methods, if not more so. New TLS approaches ought to be very open to integration with SfM to make the most of all the new tools at our disposal. This requires thinking about tools and software that will make this possible, which in turn needs ecologists with training in these methods and how to develop them.

One way to potentially accelerate this development is by bringing in expertise from across domains. If we can define our problems in forest ecology more generally, so that they are attractive for other communities (e.g. remote sensing, physics, engineering, computer science and ML etc.) then there is clearly the potential for more rapid advancement than solely by trying to turn forest ecologists into computer scientists. These are issues that will be central to the next generation of *'4D ecologists'* and the insights they will provide in forest ecology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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