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Review

Tansley insights

Improving plant allometry by fusing forest models and remote sensing

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Contents

Summary

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Key words: allometry, Approximate Bayesian Computation, data-model fusion, forest model, LiDAR.

Allometry determines how tree shape and function scale with each other, related through size. Allometric relationships help scale processes from the individual to the global scale and constitute a core component of vegetation models. Allometric relationships have been expected to emerge from optimisation theory, yet this does not suitably predict empirical data. Here we argue that the fusion of high-resolution data, such as those derived from airborne laser scanning, with individual-based forest modelling offers insight into how plant size contributes to large-scale biogeochemical processes. We review the challenges in allometric scaling, how they can be tackled by advances in data-model fusion, and how individual-based models can serve as data integrators for dynamic global vegetation models.

I. Introduction

Forests provide important services to societies globally, sequestering large amounts of carbon, limiting erosion, regulating the water cycle, and providing a habitat for many species. Size, shape and function relationships among plants, or allometries, play a key role in understanding these services. Such relationships encapsulate ontogenetic, ecological and evolutionary constraints (Niklas, 1994) and have been widely used in quantitative tools to aid forest management. How much carbon is stored in the world's forests, for instance, is estimated from forest inventories using allometric models and then scaled up to regional and global scales, based on Earth observation data and modelling (Pan *et al.*, 2011).

Allometries also describe how metabolic functions, such as respiration rates and net primary production, scale with each other. A theory has been developed to infer allometric scaling from evolutionary optimisation principles (Enquist & Niklas, 2002), but this theory does not account for recent advances in plant physiology (Rogers *et al.*, 2017; Scoffoni *et al.*, 2017), and its predictions do not match empirical data well (Muller-Landau *et al.*, 2006; Poorter *et al.*, 2012). Our ability to simulate the vegetation response to environmental change in Dynamic Global Vegetation Models (DGVMs) is, however, directly dependent on the robustness of these scaling relationships. Because DGVMs adopt a coarse-grained description of forests, allometries are often used to link fluxes and pools, but the results do not always correspond to empirical observations (Wolf *et al.*, 2011).

A great opportunity to bring processes and field information into a consistent modelling framework is offered by individual-based models (IBMs) of forest dynamics (DeAngelis & Grimm, 2014). In

IBMs, the forest ecosystem emerges from a combination of individual tree physiological and demographic processes at a scale that is relevant for forest resource management and ecological data assimilation, as in the FORMIND model (Rödig *et al.*, 2017). This approach can be extended to larger scales, either by informing DGVMs through IBMs (for example ED2; Medvigy *et al.*, 2009; LPJ-GUESS, Smith *et al.*, 2014) or by directly scaling them up (SEIB-DGVM, Sato *et al.*, 2007; FORMIND, Fischer *et al.*, 2016). Like DGVMs, forest IBMs often rely on empirical allometric models to predict tree shape and function but, during model calibration, information can also be gained about the allometric models themselves and the processes that shape them.

Proper calibration and validation of forest IBMs should be based on a variety of independent data sources, ranging from forest inventories to eddy-flux data, as recently exemplified with the TROLL model, a physiology-based and fully spatially explicit forest IBM (Maréchaux & Chave, 2017). A promising additional data source is provided by remote sensing. With its ability to generate detailed information over unprecedented scales and at locations that are otherwise hard to access (for example upper canopy layers, remote ecosystems), remote sensing has already had a transformative effect on vegetation modelling (Shugart *et al.*, 2015).

Here, we examine how a fusion of IBMs and airborne laser scanning (ALS), a remote-sensing technology that provides structural information at landscape scale, can be used to improve allometric relationships and better understand the processes that shape them. We argue that by linking forest IBMs with ALS, we can reduce unexplained variation in allometric estimates and extend these to large spatial scales, as displayed in Fig. 1. This is an important step towards increased biological knowledge and improved predictions of ecosystem functioning. It is also a test case for the integration of future remote-sensing sources such as hyperspectral imaging or spaceborne laser scanning.

II. Tree allometry and transferability

When tree size, shape and function relate to each other across scales and environmental conditions, then the measurement of a single dimension can already provide a rough estimate of whole-tree attributes. This factor is particularly relevant when one quantity is more easily measured (for example trunk diameter) than the others (for example metabolic rate or biomass). Empirical studies provide a strong support for generalised allometric relationships. Whole-plant autotrophic respiration, for example, scales predictably with biomass across several orders of magnitude and from boreal to tropical forests (Mori *et al.*, 2010), and general patterns of allocation into aboveground vs belowgound plant organs exist at individual and stand levels globally (Poorter *et al.*, 2012; Chen *et al.*, 2019). Similarly, allometries that relate trunk diameter to tree height, as shown in Fig. 2, can be found across forest types and have been used to supplement height measurements that are error prone and time consuming without optimised protocols (Sullivan *et al.*, 2018).

The notion that a model developed at one site may be valid elsewhere is called transferability (Wenger & Olden, 2012). An important application is exemplified by the calculation of carbon stocks from forest inventories. The product of wood density, trunk cross-sectional area, and tree height turns out the be a good

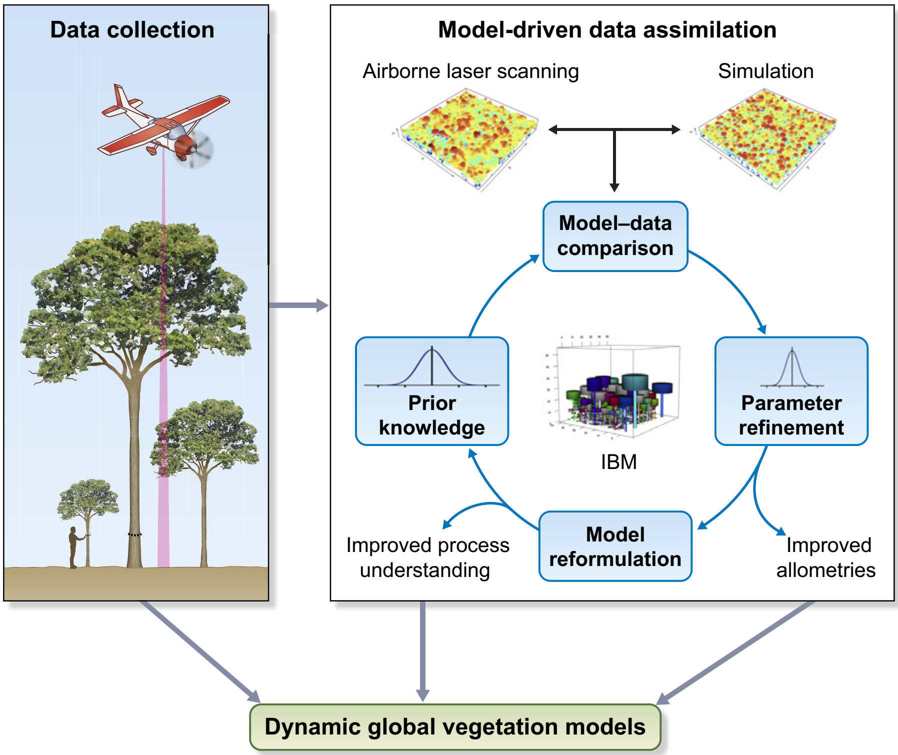

Fig. 1 Individual-based models (IBMs) as data assimilators, in interface with dynamic global vegetation models (DGVMs): application to allometric inference. Ground-based censuses and airborne laser scanning (ALS) provide complementary views on trees and forest canopies. Both techniques can be incorporated into the model–data fusion cycle, as formalised by Approximate Bayesian Computation (ABC). Increasingly diverse data can therefore be used to improve model representation and allometric parameter inference. Such improvement can be a benefit to DGVMs, whose simulations typically reach larger extents than IBMs, but which are currently run at coarse resolution, preventing them from making direct comparisons with data provided at finer spatial resolution.

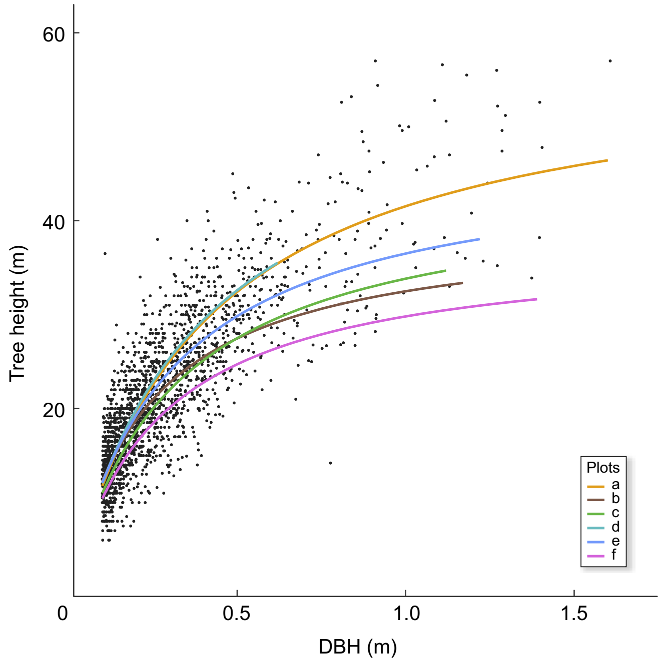

Fig. 2 Empirical allometric relations between tree height and trunk diameter (DBH). Michaelis–Menten type allometric models were fitted with nonlinear least squares and a heteroscedastic error structure at six sites, typical of tropical forests, as follows: (a) Ulu Ulu National Park, Brunei (4.54°N, 115.15°E); (b) Parque Estadual Cristalino, Mato Grosso, Brazil (9.06°S, 55.94°W); (c) Grebo National Forest, southeast Liberia (5.4°N, 7.62°W); (d) Nouragues Ecological Research Station, French Guiana (4.09°N, 52.67°W); (e) Dja Faunal Reserve, Cameroon (1.89°S, 13.22°E); (f) Tambopata National Reserve, Peru (12.84S, 69.29W). Data are from Sullivan *et al.* (2018), and metadata can be accessed on the forestplots.net data portal.

predictor of tree biomass obtained from destructive harvesting (Chave *et al.*, 2014). This holds true across a wide range of values for the predictor variables and broad bioclimatic gradients, from dry forest woodlands to tropical rainforests. Recent work based on an extensive destructive harvest experiment in African tropical forests suggests that relatively simple biomass models are transferable (Fayolle *et al.*, 2018), and could therefore be useful in biomass assessments across the tropics.

However, in most cases, allometries are influenced by environmental factors, both abiotic and biotic, and are not easily transferable. The scaling of tree height with trunk diameter, for example, depends on bioclimatic constraints (Lines *et al.*, 2012; Olson *et al.*, 2018), and tree growth is shaped by interactions with other trees (Coomes *et al.*, 2011; Jucker *et al.*, 2015). Furthermore, allometries typically have a multiplicative error structure. Residual standard deviations for predictions translate into large absolute errors for the biggest individuals and result in inflated uncertainty in the predicted variables.

To quantify variation in scaling of tree shape, remote sensing offers new perspectives. Terrestrial laser scanning (TLS), for example, provides accurate estimates of tree dimensions without requiring destructive harvesting (Momo Takoudjou *et al.*, 2017). It therefore holds great potential for exploring geometric scaling properties in forest trees and their dependence on environmental conditions (Disney, 2019).

III. Condensing the point cloud: allometry from space

Where TLS is a type of remote sensing 'from the ground', airborne LiDAR scanning extends the 3D-mapping capacity of forest and tree structure to the landscape scale. The technology and its application to forest scanning have been developed for over 3 decades (Schreier *et al.*, 1985; Nelson *et al.*, 1988), and studies now commonly cover several 1000 hectares of forest at high point densities, that is high resolution. As a result, individual tree shapes can be measured in open woodlands, allowing researchers to monitor the growth and death of individual plants (Levick & Asner, 2013; Duncanson & Dubayah, 2018). Even more impressively, clustering algorithms have been developed to segment ALS point clouds into individual tree crowns in closed-canopy forests (Ferraz *et al.*, 2016). As tree trunk diameter was recently found to be correlated with the product of tree height and crown size, the segmented crowns can then be used to estimate ground-based measurements (Jucker *et al.*, 2017); this technology is being increasingly used in routine forest monitoring programmes.

Tree-delineation from ALS is not without its problems, however. Trees often have irregular crowns, they may partly overlap, and the sharp light attenuation within dense canopy means that understorey trees are sparsely scanned, rendering the direct retrieval of tree dimensions difficult. IBMs such as TROLL (Maréchaux & Chave, 2017) offer an indirect, yet powerful alternative.

The spatially explicit rendering of treefalls and the competition for light resources introduce ecological constraints on the simulated forest structure, limiting tree density and dimensions across size classes. Instead of translating point clouds back into individual tree dimensions, we can create better fits between virtual and empirical canopies by adjusting vital rates and allometric parameters that can therefore be derived from mechanistic principles – even for trees that are difficult to observe directly from ALS. As TROLL's virtual canopies have a high spatial resolution (m^3), they compare naturally to ALS data and a few statistics are often suffice to link them. For example, Fig. 3 shows the match between top-canopy height obtained by ALS and a TROLL-based reconstruction. In the future it would be critical to extend this approach to other data sources, including TLS and spaceborne missions. Examples are the spaceborne laser scanner GEDI, a LiDAR now on board the International Space Station, and the BIOMASS synthetic aperture radar satellite, scheduled for launch in 2022, that will both provide a radically new view of the world's forests.

Because vegetation models and remote sensing have long proven mutually informative (Sellers *et al.*, 1997), the available approaches for data-model fusion have been well tested. Possibilities include the derivation of tree-level data from ALS for model parameterisation, the comparison of outputs with observed canopies for model validation (Seidl *et al.*, 2012, Fig. 3), and so-called model inversion, in which models are run with a wide range of parameter combinations and systematically compared with remotely derived metrics (Fig. 1). A hybrid between these approaches – partly inverse modelling, partly initialisation – was developed early on and has recently been applied to derive biomass maps across Amazonia using spaceborne LiDAR (Hurtt *et al.*, 2004; Rödig *et al.*, 2017). Moreover, when models

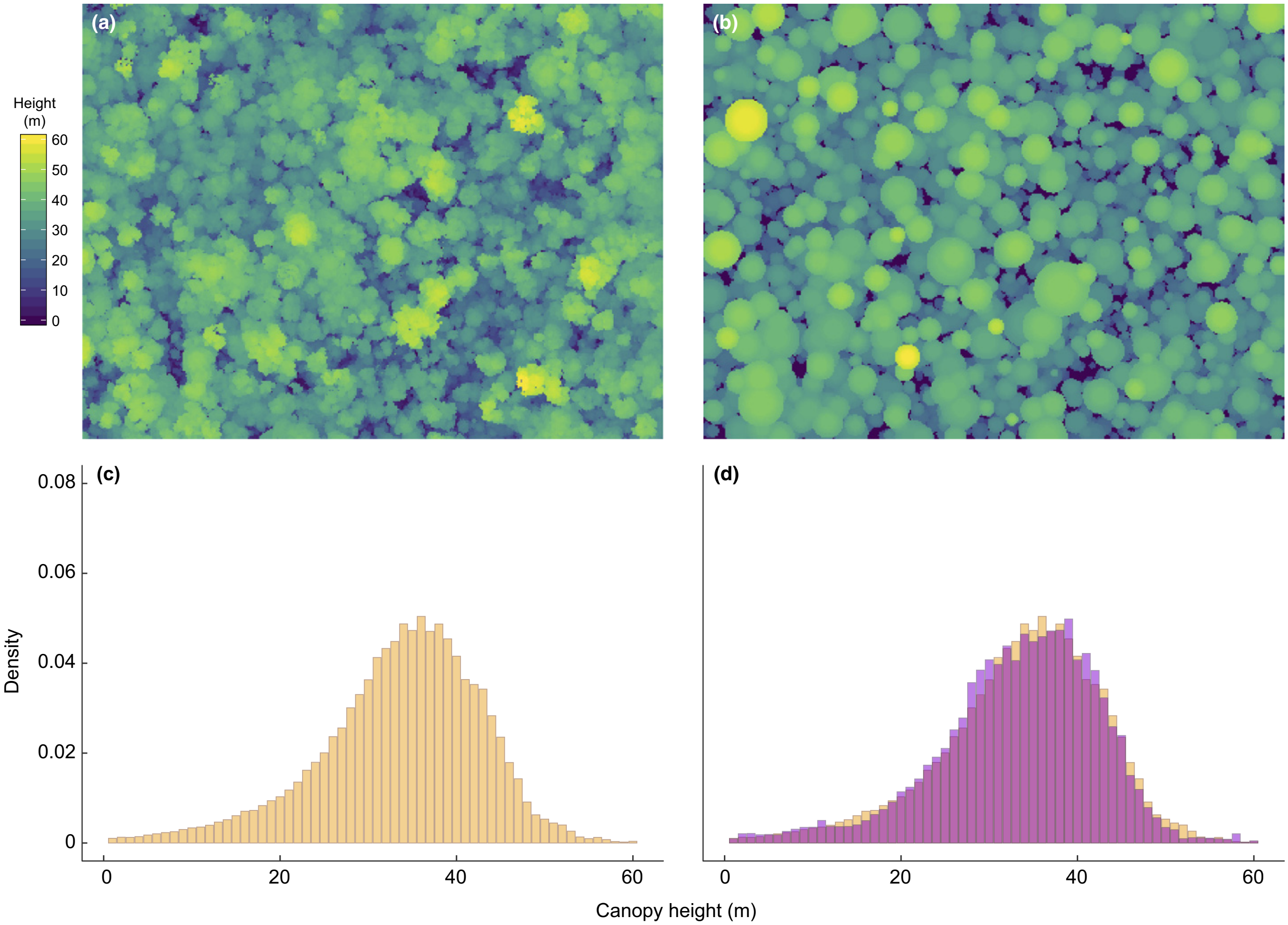

Fig. 3 Comparison of canopies sensed by airborne laser scanning (ALS) and simulated by individual-based models (IBMs). Shown are canopy-height models (height in m across 12 ha, 1-m^2 resolution; (a, b), and the corresponding height distributions (c, d). (a, c) Canopy-height model derived from an ALS campaign at the Nouragues field station, French Guiana, in 2012. (b, d) Canopy-height model as constructed by TROLL, an IBM of forest growth. Input information are a tree inventory, and allometries predicting tree height and crown dimensions from trunk diameter accounting for individual variation around the allometric trend.

provide realistic representations of forest structure, virtual ALS data can be produced and tested before using empirically observed canopies (Fassnacht *et al*., 2018; Knapp *et al*., 2018).

IV. Bayesian merging of data in IBMs

One efficient way to merge data and models is offered by Bayesian approaches such as Approximate Bayesian Computation (ABC), a widespread method in biological and ecological applications (Beaumont, 2010; Hartig *et al*., 2011). Fig. 4 illustrates the inference of crown allometry parameters based on ABC. In qualitative terms, the approach is as follows: large numbers of simulations are performed with variations in crown allometry parameters (the prior in Bayesian statistics), the resulting virtual canopies are then compared with an empirically observed canopy (through statistics such as canopy height; Fig. 3) and, finally, the parameter values of the best-performing simulations are selected (the posterior). Inference on tree allometries is therefore turned into a parameter optimisation problem, and uncertainty around the parameter estimate reflects how informative is the data regarding a particular allometry. In the example given in Fig. 4, the inference is considerably improved by using ALS data in addition to ground data, providing more precise estimates for allometry parameters across diameter-size classes.

When harmonising high-dimensional data, as obtained from ALS and IBMs such as TROLL, some issues emerge. Inferences can be markedly different, depending on how virtual and empirical canopies are compared, and dimension reduction and cross-validation techniques are needed to find an appropriate set of statistics (Csilléry *et al*., 2012; Nunes & Prangle, 2015). But even when summary statistics are well chosen, a pattern (for example a virtual canopy) can be the result of several parameter combinations or ways to represent processes (for example allometries). In this case, inference methods such as ABC are not well posed. This type of uncertainty, usually referred to as 'equifinality' (Luo *et al*., 2009), cannot always be avoided, but it can be mitigated. Additional data sources can help to narrow down the parameter space (Fig. 4). Furthermore, it is desirable to implement mechanistic models over statistical ones, because mechanistic simulations are restricted to a generally smaller universe of possibilities. They therefore

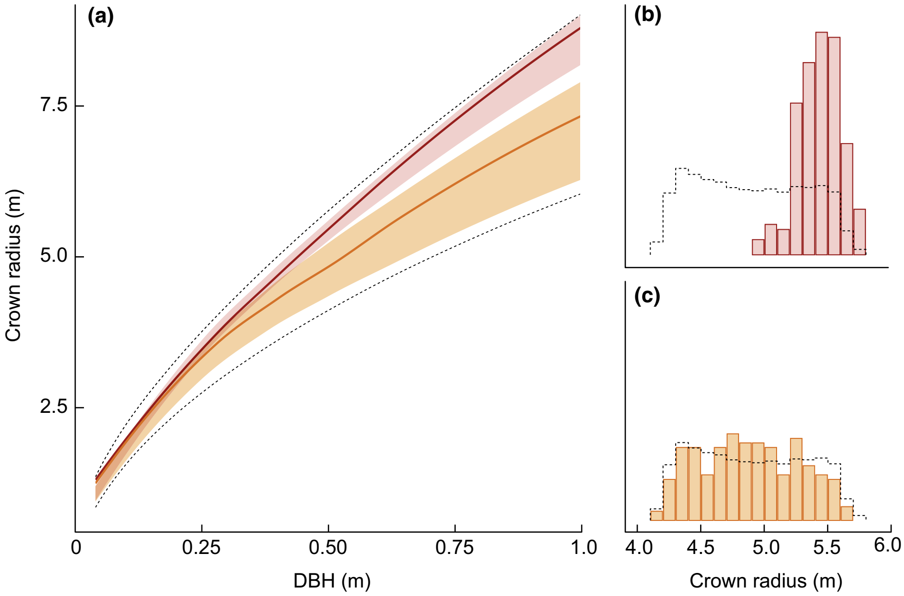

Fig. 4 Crown radius allometries inferred by Approximate Bayesian Computation (ABC) in TROLL. (a) Shape of the crown-radius allometry included in the TROLL model. Two posterior distributions of crown-radius allometry are shown, one constrained by ground data only (orange), the other also constrained by data derived from airborne laser scanning (ALS, red). The thick lines represent the posterior mode, the coloured areas the 70% highest-density intervals, and the dotted lines the extent of the prior distribution. (b, c) Cuts through the allometric distribution at 0.5 m in trunk diameter (DBH), for both simulations, with priors indicated by dotted lines. The addition of ALS data in ABC inference considerably narrows down the crown allometry parameters. The inference is based on 20 000 simulations, with a posterior composed of the best 200 simulations. Summary statistics included tree diameter-size distributions and ALS-derived canopy-height distributions. The overlap between simulated and empirical distributions was quantified and, to determine the posterior, we used the rejection scheme implemented in the R package ABC (Csilléry *et al.*, 2012) with an acceptance rate of 1%.

complement machine-learning techniques that are increasingly popular across science, including forest modelling, but are especially prone to the equifinality problem.

Another approach to narrow down the parameter space for models such as TROLL is the construction of an initial canopy state whose spatial arrangement is consistent with both the mechanistic principles of TROLL and the ALS-derived canopy structure. One method to produce such an initial state consists in sequentially assigning trees to spatial positions such that they receive enough light and that their size matches ALS observations. A space-filling rule is then iterated until all available space in the scene has been filled by trees (Taubert *et al.*, 2015). This initialisation can be useful to explore the range of validity of forest structure parameters (canopy gaps, crown exposure) and, therefore, yields both priors for the IBM and an evaluation of summary statistics. The IBM can then use this information to focus on ecological dynamics and provide distributions for tree trunks, crown dimensions and heights that represent a predictive check on ecological inferences and a new prior for the parameterisation of DGVMs (Fig. 1).

V. Challenges and perspectives

In this paper we argue that the explicit merging of plant allometry, forest observations, and individual-based modelling contributes to a unified vision of forest ecology. A fully spatially explicit IBM, when used for Bayesian data-model fusion, can inform quantities such as crown size and shape that are difficult to measure in dense canopies, but to which spatially explicit models are highly sensitive. The approach also helps to gain an understanding of ecological processes, as it captures the fine-grained structure of forest canopies. It could, therefore, better explain tree regeneration and simulate the dynamics of nontree life forms, including lianas and epiphytes or even canopy-dwelling animals. This challenge is one of the greatest in biodiversity research today (Singer *et al.*, 2016). Further ecological insights can be gained regarding submodels, such as the tree growth equations implemented in gap models (Shugart *et al.*, 2018), or the autotrophic respiration equation (Atkin *et al.*, 2015). The obtained information could then constrain the parameters of physiological models that are usually prescribed in DGVMs (but see Wang *et al.*, 2017), and offer a direct benchmark of upscaling simplifications of canopy structure, such as the perfect plasticity approximation (Purves *et al.*, 2008).

Where the focus of DGVMs has traditionally been on satellite data, forest IBMs have instead been developed for and from ground inventories, with trunk diameters and their growth the main predictors of all simulated ecological processes. The remote-sensing revolution calls, however, for a new paradigm in forest modelling, including new data sets, and new approaches to model building. This mirrors the larger change of direction in global forest research in which remotely sensed metrics are increasingly used to predict ground metrics (Jucker *et al.*, 2017). This also represents a timely challenge because spaceborne missions such as GEDI and BIOMASS will acquire global forest structure datasets, but it is likely that a correct interpretation of these datasets will require an explicit linkage with models (Fisher *et al.*, 2018). Model upscaling raises the question of spatial model transferability. It is crucial to test this by validating the model at places where it has not been calibrated.

The assimilation of global remote-sensing data will be greatly helped by recent advances in computing technology that have shifted the limits of what forest extent can be simulated at tree level (Shugart *et al.*, 2015). For calibration, which requires 1000s of simulations for data-model fusion, computational cost can be reduced by classic assimilation techniques (Hurtt *et al.*, 2004). Future increases in computational power and emulators will further speed up inference (Fer *et al.*, 2018), turning IBMs into Bayesian data integrators that create a common vision of forest functioning and structure and the allometric relationships that link both across scales.

Complementary to this effort is the need to explain allometries from evolutionary optimisation arguments, for plant form (Enquist & Niklas, 2002), plant function (Wolf *et al.*, 2016), and forest structure (Farrior *et al.*, 2016). A better fundamental knowledge on allometric relationships can only improve our confidence in the parameters and simplify model calibration. This can only be achieved if theory is consistent with the known constraints of plant physiology. In return, data-model fusion, as explained here, provides a strong validation for theory.

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