L	1	
Using terrestrial laser scanning to constrain forest ecosystem structure and functions in the Ecosystem Demography model (ED2.2)		(Formatted: English (UK)
Authors		
Félicien Meunier <sup>1</sup> , Sruthi M. Krishna Moorthy <sup>1</sup> , Marc Peaucelle <sup>1</sup> , Kim Calders <sup>1</sup> , Louise Terryn <sup>1</sup> , Wim	e	Deleted: ,
Verbruggen <sup>1</sup> , Chang Liu <sup>1</sup> , Ninni Saarinen <sup>2,3</sup> , Niall Origo <sup>4</sup> , Joanne Nightingale <sup>4</sup> , Mathias Disney <sup>5,6</sup> ,		Formatted: English (UK)
Yadvinder Malhi <sup>7</sup> , and Hans Verbeeck <sup>1</sup>		<sup>1</sup> Deleted:
		Formatted: English (UK)
Affiliations		
<sup>1</sup> CAVElab - Computational and Applied Vegetation Ecology, Department of Environment, Ghent University, Ghent, Belgium		
<sup>2</sup> Department of Forest Sciences, University of Helsinki, Finland		Deleted:
		Formatted: English (UK)
<sup>3</sup> School of Forest Sciences, University of Eastern Finland, Finland		
<sup>4</sup> NPL - Climate and Earth Observation (CEO) group, National Physical Laboratory		
<sup>5</sup> UCL Department of Geography, Gower Street, London WC1E 6BT, UK		
<sup>6</sup> NERC National Centre for Earth Observation (NCEO), UCL Geography, Gower Street, London, WC1E 6BT, UK		
<sup>7</sup> Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK		
*now at INRAE, Université de Bordeaux, UMR 1391 ISPA, 33140 Villenave-d'Ornon, France		
Potential journal		Deleted: journals
Geoscientific Model Development		Deleted: (IF = 5.2) $\rightarrow$ Accept "development and
		technical papers describing new
		calibration/parameterization/sensitivity"
		Deleted: Other possible options: Ecological applications (IF = 4.2) Geophysical research letters (IF = 4.6) Journal of Advances in Modeling Earth Systems (IF = 4.3)
	1	Formatted: Footer
•		

l

#### Abstract

Terrestrial Biosphere Models (TBMs) are invaluable tools for studying plant-atmosphere interactions at multiple spatial and temporal scales, as well as how global change impacts ecosystems. Yet, TBM projections suffer from large uncertainties that limit their usefulness. Forest structure drives a significant part of TBM uncertainty as it regulates key processes such as the transfer of carbon, energy, and water between the land and the atmosphere, but remains challenging to observe and reliably represent. The poor representation of forest structure in TBMs might actually result in simulations that reproduce observed land fluxes, but that fail to capture carbon pools, forest composition, and demography. Recent advances in Terrestrial Laser Scanning (TLS) offer new opportunities to capture the three-dimensional structure of the ecosystem and to transfer this information to TBMs in order to increase their accuracy. In this study, we quantified the impacts of prescribing initial conditions (tree size distribution), constraining key model parameters with observations, as well as imposing structural observations of individual trees (namely tree height, leaf area, woody biomass, and crown area) derived from TLS into the state-of-the-art Ecosystem Demography model (ED2.2) at a temperate forest site, (Wytham Woods, UK). We assessed the relative contribution of initial conditions, model structure, and parameters to the overall output uncertainty by running ensemble simulations with multiple model configurations. We show that forest demography and ecosystem functions as modelled by ED2.2 are sensitive to the imposed initial state, the model parameters, and the choice of key model processes. In particular, we show that:

- parameter uncertainty drove the overall model uncertainty with a mean contribution of 63% to the overall variance of simulated gross primary production;
- model uncertainty on the gross primary production was reduced fourfold when both TLS and trait data were integrated into the model configuration;
- <u>land fluxes and ecosystem composition could be simultaneously and accurately simulated with</u> <u>physically realistic parameters when appropriate constraints were applied to critical parameters</u> <u>and processes.</u>

We conclude that integrating TLS\_data can inform TBMs on the most adequate model structure, constrain critical parameters, and prescribe representative initial conditions. Our study also confirms the need for simultaneous observations of plant traits, structure and state variables if we seek to improve the robustness of TBMs and reduce their overall uncertainties.

## Keywords

Ecosystem Demography model version 2.2 (ED2.2), Terrestrial Laser Scanning, Sensitivity analysis, Terrestrial Biosphere Model, Temperate forest ecosystems, Forest structure

	Deleted: Modeling (TBM) is an
	Deleted: approach
	Deleted: the
	Deleted: on
< //	<b>Deleted:</b> A large part of this uncertainty arises from the empirical allometric (size-to-mass) relationships that are used to represent forest structure in TBMs.
$\langle \rangle$	Deleted: actually
$\langle \rangle$	Deleted: large
$\langle \rangle \rangle$	Deleted: measure
$\mathbb{N}$	Deleted: results
	Deleted: models
	Deleted: are able to
$\left( \right) $	Deleted: which
	Deleted: realistically represent
//	Deleted: techniques
$\left( \right)$	Deleted: a huge opportunity
$\mathbb{N}$	Deleted: integrating
Ŵ	Deleted: .
	Deleted: model sensitivity to
$\left\{ \right\}$	Deleted: allometric
	Deleted: , and canopy representation
())	Deleted: changing them in turn from default
	Deleted: to site-specific, TLS-derived values.
	Deleted: productivity
$\langle \rangle \rangle$	Deleted: structural
	Deleted: way canopy is represented
())	Deleted: imposed openness
$\langle \rangle \rangle$	Deleted: canopy dramatically influenced
	Deleted: potential vegetation,
11	Deleted: optimal
	Deleted: leaf area, and the vertical distribution of light in the forest, as simulated by ED2.2;
	Formatted: Space After: 10 pt, Outline numbered + Level: 1 + Numbering Style: Bullet + Aligned at: 0.63 cm + Indent at: 1.27 cm
	Deleted: <#>TLS-derived allometric parameters increased simulated leaf area index and aboveground biomass by 57 and 75%, respectively;¶ the choice of model structure and allometric coefficient both significantly impacted the optimal set of parameters necessary to reproduce eddy covariance flux data. ¶
	Deleted: <#>vegetation structure information derived from

#### Introduction

Terrestrial biosphere models (TBMs) are key tools to understand the ecosystem response to anthropogenic disturbances and climate change (Medvigy and Moorcroft 2012; McGuire et al. 2001). Nowadays they are intensively used, as is or embedded in Earth system models, to study plant-atmosphere interactions and predict the future of ecosystems facing global change (*e.g.*, Poulter et al. 2010). Yet, the usefulness of TBMs <u>is</u> currently limited by the large uncertainties in their projections which originate from different sources (Lin et al. 2011).

Forest structure has long been recognized as a critical component to understand forest dynamics (Hurtt et al. 2010). It influences the climatically important fluxes of carbon, energy, and water (Bonan 2008). Yet, its realistic representation is, challenging and an urgent priority in the development of next-generation TBMs (Fisher et al. 2018). The representation of the forest structure within TBMs is associated with three sources of uncertainty: model structure, model initialisation, and model parameter uncertainty.

The model structure entails by definition all the processes included in a model, how they are implemented, and all the underlying assumptions (Bonan 2019). Model structure complexity varies among TBMs and also depends on the user configuration choices: different formulations of the same process can co-exist within a TBM. This complexity results from the necessary compromise between an accurate representation of reality on the one hand and the computational demand and observational requirements on the other (Shiklomanov et al. 2020). Model intercomparison studies have demonstrated that discrepancies in the representation of key processes such as forest structure (Fisher et al. 2018) or photosynthesis (Rogers et al. 2017) lead to significant uncertainties in the projections of critical variables such as the overall land carbon sequestration capacity (Friedlingstein et al. 2014; Lovenduski and Bonan 2017; Friedlingstein et al. 2006).

The <u>initialisation</u> uncertainty reflects the error made when determining the initial conditions of the modelled ecosystem. Several approaches exist for <u>initialising</u> TBMs, the most common of which is probably to start runs from near-bare ground conditions, force the simulations with relevant climate-forcings, and wait for the model to reach an equilibrium state, the so-called potential vegetation (Antonarakis et al. 2011). Yet, such a spin-up approach does not guarantee reliable initial demography, carbon pools, or ecosystem structure. Alternatively, forest inventories can be used to prescribe the initial composition of the ecosystem (Medvigy et al. 2009). The derivation of the initial states of critical variables, such as the aboveground biomass or the total leaf area from the plant size distribution, then relies on model default allometries which are often derived from other, potentially non-representative site-specific data.

Parameter uncertainty arises <u>among other things</u> from the necessary simplification of the natural complexity into a coherent <u>list of model parameters</u>, the uncertainty in the measurements used to calibrate the model, or the methods used to upscale local measurements to scales on which TBMs operate (Zaehle et al. 2005). Previous sensitivity analyses have underlined the critical importance of parameter uncertainty for the projections of ecosystem demography and productivity (Dietze et al. 2014;

 Deleted: are

 Deleted: complex,

 Deleted: the

 Deleted: the

 Deleted: the initialization

 Deleted: the

 Deleted: the

 Deleted: the

 Deleted: the

 Deleted: the

 Deleted: the

 Deleted: the

Deleted: e.g.

Deleted: structure

Massoud et al. 2019; Raczka et al. 2018; Wramneby et al. 2008). In a recent comparative study, parameter uncertainty was even shown to dominate the overall model uncertainty over process uncertainty (Shiklomanov et al. 2020). Among model parameters, allometric coefficients scale the shape and mass of the plants or of its components with their size (Chave et al. 2014). Not surprisingly, multiple TBMs were shown to be sensitive to such allometric parameters (Collalti et al. 2019; Cano et al. 2020; Esprey et al. 2004). Parameter uncertainty can be reduced by constraining the range of variation of model parameters through the assimilation of different sources of observations or via model optimization (LeBauer et al. 2013). In the past, TBMs have often been calibrated with eddy covariance data (Fer et al. 2018; Rezende et al. 2016; Collalti et al. 2016). While this approach ensures that the model correctly reproduces the short timescale (diurnal/seasonal) dynamics of land fluxes, it does not ensure an accurate representation of forest structure and carbon pools. This is especially true because forest structure-related parameters can present a low sensitivity to those observations (LeBauer et al. 2013; Richardson et al. 2010), and the equifinality in TBMs (Luo et al. 2009) can lead to acceptable land fluxes with a poor representation of ecosystem structure (i.e. fluxes can be reproduced from an almost infinite range of structural possibilities, some of which will be much more likely than would be others).

Among the different sources of observations used to reduce model uncertainties, remote sensing from various platforms (terrestrial, air- and space borne) has increasingly been used to monitor and understand terrestrial ecosystems (Jones and Vaughan 2010). LiDAR (Light Detection And Ranging) data in particular have been used in the past to initialise forest biomass and constrain predictions of TBMS (Thomas et al. 2008; Hurtt et al. 2019). The recent revolution in Terrestrial Laser Scanning (TLS, also called terrestrial LiDAR) provides new opportunities for constraining TBMs, and reducing the uncertainties related to the vegetation structure representation (Fischer et al. 2019). The ability of TLS to measure the distance to reflecting surfaces was initially used in ecological studies to measure simple metrics like DBH and tree heights (Maas et al. 2008; Hopkinson et al. 2011). Since then, TLS methods have rapidly evolved to derive more complex metrics, such as the vertical profiles of the forest structure (Jupp et al. 2009; Calders et al. 2018) and whole-tree volumetric assessments (Fan et al. 2020), leading to an accurate determination of forest structure across various forest types (Calders et al. 2015; Tanago et al. 2018; Takoudjou et al. 2018; Ehbrecht et al. 2017; Stiers et al. 2018; Saarinen et al. 2021.). Today, the ability of TLS to accurately represent the 3D structure of forests via quantitative structure modelling (QSM), see Raumonen et al. (2013) and Hackenberg et al. (2015) represents a unique opportunity to improve our understanding of forest ecosystems under changing climates (Calders et al. 2020). In particular, TLS snapshots of vegetation ecosystems could simultaneously provide important state variables to initialise TBMs, strong constraints to some critical allometric parameters, and help determine the most appropriate model structure for some key processes.

In this study, we <u>evaluated the relative contribution of different sources of uncertainty (parameters, processes, initial conditions) to the overall uncertainty of multiple simulated outputs of a specific TBM, namely the Ecosystem Demography model version 2 (ED2.2). We also explored the benefits of constraining vegetation structure related parameters and processes using TLS on the model</u>

Deleted: drive

Deleted: large

Deleted: that

Deleted:

Deleted: vegetation Deleted: (Jones and Vaughan 2010)

Deleted: representation

-(	Deleted: or
-(	Deleted: (
Y	Deleted: ;
Y	Deleted: huge
-(	Deleted: initialize

Deleted: quantified the sensitivity

 Deleted: ), to
 Deleted: by varying the initial state of
 Formatted: Footer

performance and output variability. To do so, we ran ED2.2 simulation ensembles for a temperate forest in the UK considering different initial states for the modelled ecosystem, and varying multiple model, parameters and process settings with or without TLS constraints. In other words, we assessed: (i) the relative importance of the model structure, initialisation, and parameter uncertainties in the ED2.2 model representation of a temperate forest; (ii) the potential added value of TLS data for vegetation modelling, To the best of our knowledge, this study is the first attempt to <u>fuse</u> TLS data and a TBM.

**Deleted:** and the model allometric parameters that control the structural representation of the canopy within the...

**Deleted:** . More specifically, we investigated the benefits of integrating TLS measurements of forest structure on the simulated demography and productivity, as well as on the model calibration when using flux tower data. We were particularly interested to

Deleted: assess

Deleted: initialization

Deleted: in

Deleted: quantify

Deleted: (as, to

Deleted: couple

**Deleted:** ); and (iii) determine if equifinal ecosystem simulations could be discriminated from a structural point of view...

# Material and Methods Study site and data

#### Study site

Wytham Woods is a mixed deciduous forest, predominantly broadleaved, covering approximately 40 ha. It is located 5 km northwest of Oxford in southern England (Thomas et al. 2011). Owned by Oxford University, Wytham Woods has been part of the UK Environmental Change Network (ECN) and of the Smithsonian Global Earth Observatory (SIGEO) <u>network</u> since 1992 and 2008, respectively, and has hosted numerous ecological studies (Savill et al. 2010). The site is classified as an ancient semi-natural woodland (Hall et al. 2001), which means that the site has been continuously covered by trees through recorded history (since at least 1600), occasionally managed, and experienced <u>minimal</u> intervention (*i.e.* no silvicultural management) since WWII (Fenn et al. 2015). Over the 1993-2008 time period, the site was <u>characterised</u> by a mean annual temperature of 10°C and a mean annual precipitation of 726 mm (Butt et al. 2009). The <u>area we simulate in this</u> study <u>is</u> a 1.4 ha forest plot nested within the 18 ha long-term monitoring site part of the ForestGEO global network of forest inventory plots. This 140 <u>m</u> × 100 m area has a local SW-coordinate (0, 100) and local NE-coordinate (140, 200) boundary. The local origin coordinate (0,0) was <u>located</u> with a differential GPS <u>at</u> Lat 51.7750579 <u>and</u> Lon -1.33904729.

#### Field inventory and Terrestrial Laser Scanning data

The studied plot was inventoried during the summer of 2016. All trees were located, measured, and identified at the species level. The plot is largely dominated by sycamore (*Acer pseudoplatanus*, 65<u>.3</u>% of the <u>815</u> inventoried trees in the 1.4 ha plot, see Table 1, Figure 1 and Supplementary Figure S1), ash (*Fraxinus excelsior*, 10<u>.3% of the stems</u>), and hazel (*Corylus avellana*, 8<u>.2% of the stems</u>). Oaks (*Quercus robur*) represent a limited fraction of the woody stems (4<u>.3</u>%) but disproportionately contribute (23<u>.4</u>%) to the total basal area as they mostly consist of large trees (Table 1 and Figure 1). From the inventory, tree DBH is 24.4 cm on average (DBH median is 19.8 cm), and ranges from 2.9 cm to 141.2 cm.

Three-dimensional forest structure data were collected using a RIEGL VZ-400 terrestrial laser scanner (RIEGL Laser Measurement Systems GmbH) in leaf-on (June and July 2015) and leaf-off (December 2015 and January 2016) conditions (Calders et al. 2018). The RIEGL instrument uses on-board waveform processing and records multiple return LiDAR data, which improves vertical sampling (Lovell et al. 2003; Calders et al. 2014). Individual trees were extracted using *treeseg* (Burt, et al. 2019), and their structure modelled with *TreeQSM* (Raumonen et al. 2013) with the leaf-off TLS point cloud. Leaves were then added to the individual tree branches using both the leaf-off and -on TLS datasets with the <u>FaNNI algorithm (Åkerblom et al. 2018)</u>. Doing so, TLS allowed retrieving of individual tree height, aboveground woody biomass (modelled through estimates of volume combined with species-specific wood density), and leaf area. In addition, the individual trees. For more details, a complete description of the TLS data collection and forest stand reconstruction is available in Calders et al. (2018).

Deleted: . This classification Deleted: minimum Deleted: characterized Deleted: took place on

Deleted: Network

(	Deleted: measured	Ĵ
-(	Deleted: and located	2
)(	Deleted: ,	2

Deleted: 821
Deleted: and
Deleted: %),
Deleted: %).
Deleted: (BA)
Deleted: The mean (resp. median)
Deleted: (resp.
Deleted: )
Deleted: , ranging

Deleted:

#### Flux tower data and species traits

Stand-scale carbon and water fluxes have been occasionally measured in Wytham Woods using the eddy covariance technique. We <u>digitised</u> the most recent (to our knowledge) data collection of  $CO_2$  fluxes that was reported by Thomas et al. (2011) for the period May 2007<sub>E</sub>April 2009. To do so, we <u>digitised</u> the weekly mean values of ecosystem gross primary productivity (GPP), ecosystem respiration (R<sub>ecol.</sub> and net ecosystem productivity (NEP) from Figure 6 of the aforementioned reference using the Plot digitizer software (v.2.6.8, <u>http://plotdigitizer.sourceforge.net/</u>). For a more detailed description of the eddy covariance data (including the data frequency of the original data, and the data quality filtering), we refer the readers to the original publication by Thomas et al. (2011).

In addition, we extracted all existing records of specific leaf area (SLA) and maximum rate of carboxylation ( $V_{c.max}$ ) for the five most important species in Wytham woods (*Acer pseudoplatanus*, *Corylus avellana, Crataegus monogyna, Fraxinus excelsior*, and *Quercus robur*) from the TRY database (Kattge et al. 2020), see Table 1 (the complete list of references from which the data originate is available in supplementary section 1). Individual traits were converted into ED2.2 units (m<sup>2</sup> kgc<sup>-1</sup> for SLA with a fixed leaf carbon content of 0.5 and µmolc m<sup>-2</sup> s<sup>-1</sup> for  $V_{c.max}$ ).  $V_{c.max}$  data were also rescaled to the ED2.2 reference temperature (15°C) using the model default value for the temperature coefficient Q10. Following Asner et al. (2017), we calculated the community-weighted mean (CWM) and community-weighted standard deviation (CWSD) for both traits based on the species composition and species-level average values, using species basal area as weights:

$$CWM = \frac{\sum_{i=1}^{N} w_i \cdot x_i}{\sum_{i=1}^{N} w_i}$$

Equation (1)

 $\frac{\sum_{i=1}^{N} w_i \cdot (x_i - CWM)^2}{(N-1) \sum_{i=1}^{N} w_i}$ CWSD = 1

Equation (2)

where N is the total number of species for which data was available in TRY for <u>each</u> trait  $\underline{x}, \underline{x}_i$  is the mean trait value for species  $\underline{i}$ , and  $\underline{w}_i$  is the species weight (here the basal area of species  $\underline{j}$ ).

Flux tower data were used as a validation dataset while the TRY data were used to constrain parameters of the TBM used in this study and described just below.

#### Model

#### The terrestrial biosphere model ED2.2

ED2.2 is a terrestrial biosphere model that can simulate the vegetation dynamics of a wide range of ecosystems from boreal to tropical forests (Longo et al. 2019). It is a cohort-based, spatially implicit model that approximates the <u>behaviour</u> of an individual-based, spatially distributed vegetation model through a system of size- and age-structured partial differential equations (Moorcroft et al. 2001). ED2.2 integrates modules of plant growth, mortality, phenology, disturbance, hydrology, and soil biogeochemistry to predict *e.g.*, the demography, the succession, and the dynamics of water and carbon within the simulated ecosystem.

Deleted: digitized
Deleted: flux
Deleted: (2011)
Deleted: between
Deleted: and
Deleted: digitized
Deleted: )

Deleted: V<sub>cmax</sub>

Deleted: used	
Deleted: Appendix).	
Deleted: constant	
Deleted: Vomax), Vomax	

1	$CWM = \frac{\sum_{i=1}^{N} w_i \cdot x_i}{\sum_{i=1}^{N} w_i \cdot x_i}$
/ \	<b>Deleted:</b> $\sum_{i=1}^{i} w_i$
(	Formatted Table
A	$CWSD = \sqrt{\frac{\sum_{i=1}^{N} w_i \cdot (x_i - CWM)^2}{(N-1)\sum_{i=1}^{N} w_i}}$ Deleted:
(	Formatted Table
1	Deleted: N
(	Deleted: x
1	Deleted: $x_i$
$\square$	Deleted: i
///X	Deleted: $w_i$
(())	Deleted: its
(///)	Deleted: ,
	Deleted: total
	Deleted: i
	Deleted: Those trait
11/1	Deleted: not
	Deleted: calibrate nor validate the model as such but simply simply compared with the optimized
(	Deleted: after calibration (see
$\langle  $	Deleted: ).
Ì	Deleted: behavior
Å	Formatted: Footer

In ED2.2, the inter- and intra-specific diversity is represented by a set of plant functional types (PFTs) that differ by their leaf physiology, phenology, growth and allocation strategies, mortality, and sensitivity to environmental conditions. (D. Medvigy et al. 2009). The trees inventoried in Wytham Woods were classified as <u>either mid- or late</u>-successional temperate deciduous trees. (see below for the reasoning of the mapping). These PFTs are cold-deciduous, *i.e.* leaf phenology is prognosed by the accumulation of growing degree-days (growing season) and chilling days (senescing season) (Longo et al. 2019). A comprehensive model description, including photosynthesis, allometries, radiative transfer, and phenology, is available in Longo et al. (2019).

#### The ED2.2 model is available at https://doi.org/10.5281/zenodo.3365659.

#### Model initialisation and forcings

In this study, the ED2.2 model was initialised using i) near-bare ground (NBG) initial conditions (i.e. seedlings only), ii) the field inventory, or iii) the TLS-reconstructed size distribution. In the latter two configurations, the 1.4 ha site was initially divided into 35 square patches of 20 x 20 m. These three types of initial conditions are referred to below as NBG, Census, and TLS respectively. Simulations were run for multiple years using the local forcing data of the corresponding years of the CRU-NCEP reanalysis dataset (Viovy 2018). Simulations were run for either five years (Census and TLS configurations) or the approximate age since the last large-scale disturbance (100 years, NBG configuration), see Table 5. Soil texture was set according to the dominant soil type, based on site-level observation (Butt et al. 2009).

#### Allometries and model parameters

In ED2.2, the carbon made available from net assimilation is partitioned at the cohort level into the different plant pools according to DBH-dependent allometries (Longo et al. 2019). In other words, plant cohorts allocate the carbon assimilated through photosynthesis to living tissues (i.e. fine roots, sapwood, leaves, seeds), the non-structural storage pool, and the dead tissues (i.e. coarse roots, and aboveground woody biomass) depending on (i) a set of allometries and (ii) whether the plant carbon balance and environmental conditions are <u>favourable</u> for growth. In ED2.2, aboveground woody biomass, height, leaf biomass, and crown area are scaled through DBH-dependent allometries (Table 3). The ED2.2 default allometric models and parameters are defined according to Medvigy et al. (2009) for the leaf biomass and height, Dietze et al. (2008) for the crown area, and Albani et al. (2006) for the aboveground woody biomass,

To estimate the relative contribution of the parameter uncertainty to the variability of the model outputs, we used parameter distributions from previous ED2.2 parameter uncertainty studies (Dietze et al. 2014; Shiklomanov et al. 2020; Raczka et al. 2018; Viskari et al. 2019). We only targeted those parameters that were shown to significantly contribute to the overall parameter uncertainties in the aforementioned studies (Table 4) and set the rest to their ED2.2 default values for all simulations. For SLA and V<sub>c.max</sub> in particular, we defined two types of parameter distributions: either relatively wide priors as in the previous sensitivity analyses listed above (Table 4) or constrained posteriors generated by the trait meta-analysis

# Deleted: . All

Deleted: . This PFT is

Deleted: during the extended growing and

Deleted: , respectively

**Moved down [1]:** By default in ED2.2, plant canopies are represented as infinitely thin flat crowns (a.k.a.

Deleted: complete shading) that virtually occupy the entire horizontal space of the patch in which the cohort is located. In an alternative configuration, cohorts are stacked on top of each other but have finite radius and hence tallest plants only partially shade the underlying cohorts. A comprehensive model description (including photosynthesis, radiative transfer, and phenology) is available in Longo et al. (2019).¶

Deleted: default

Formatted: Normal

Deleted: -derived allometries

Deleted: favorable	
Deleted: As such in	
Deleted: 2	
Deleted:	

Deleted: We compared those default allometric parameterization with site-specific, TLS-derived ones. To do so. we fitted the individual plant metrics (height, crown area, aboveground woody biomass, and leaf area) vs DBH relationships derived from TLS using the ED2.2 default set of equations (Table 2). More specifically, the parameters of the four allometric equations of the ED2.2 model were optimized with the 'nlsLM' function of the minpack.Im R package (Elzhov et al. 2016) for the height and the 'Im' function of the 'stats' R package applied to the log-transformation of the allometric power equations for the crown area, the leaf biomass, and the aboveground woody biomass. To convert the leaf area obtained from TLS into leaf biomass, we used the CWM of SLA. Model initialization and forcings

In this study, the ED2.2 model was initialized using i) near-bare ground initial conditions (i.e. seedlings only), ii) the DBH distribution available through the field inventory, or iii) the TLS-reconstructed size distribution. In the latter two configurations, the 1.4 ha site was initially divided into 35 square patches of  $20 \times 20$  m that were allowed to fuse along the simulation. Simulations were run for multiple years using the corresponding years of the CRU-NCEP reanalysis forcing dataset (Viovy 2018).

of the Predictive Ecosystem Analyzer (PEcAn) run with the existing data in TRY, see (LeBauer et al. 2013; Meunier et al. 2021). Those distributions are referred to below as without or with TRY-constraints, respectively. The uncertainty of the allometric coefficients was determined either by the range of variation of those parameters in the ED2.2 model for hardwood tree PFTs (NBG and Census configurations) or by the posterior distributions of these parameters generated when fitting the TLS data (see below).

#### Model configurations

To assess the importance of the model structure uncertainty, we targeted processes that were shown to induce significant variability in the model outputs in previous studies (Shiklomanov et al. 2020). In detail, we ran the model with multiple combinations of the following configurations: (i) closed canopies versus crowns of finite radii; (ii) two-stream versus multiple-scatter canopy radiative transfer models (RTMs); (iii) static versus plastic (varying with available light level) SLA and V<sub>c.max</sub>; and (iv) a single versus two plant functional types (Table 2).

By default in ED2.2, plant canopies are represented as infinitely thin flat crowns (a.k.a. complete shading or closed canopy) that virtually occupy the entire horizontal space of the patch in which the cohort is located. In an alternative configuration, cohorts are still stacked on top of each other but have a finite radius and hence tallest plants only partially shade the underlying cohorts. In other words, the crown sub-model of ED2.2 determines the nature of the light competition between cohorts. Closed canopies have been shown to dramatically suppress competition from sub-dominant PFTs and typically result in unrealistically homogeneous patches (Fisher et al. 2015) while understorey cohorts receive more incoming diffuse and direct light if finite crowns are simulated.

The second sub-model we investigated was the choice of RTM. In both options (two-stream and multiscatter), the full vertical radiation profile within each patch is resolved as a function of the canopy structure (e.g. leaf and wood area, clumping) and the environmental conditions (e.g. incident solar radiation, solar angle) following the approach of CLM 4.5 (Oleson et al. 2013). Both RTMs differ in the numerical resolution of the radiative transfers. By default (two-stream), the special multi-canopy solution of the two-stream approximation for vegetation canopies (Sellers 1985) is used as described in Longo et al. (2019) while the multiple-scatter is derived from first principles by Zhao and Qualls (2005) to address the long-known issues and biases of the two-stream model (Wang 2003). The multiple-scatter configuration increases diffuse light levels in the understorey as compared to the default two-stream approach (Shiklomanov et al. 2020).

The third sub-model that we evaluated is related to trait plasticity. By default (static), all cohorts of a given PFT share the same set of parameters which do not evolve over time, in contradiction with well-documented intra-specific variability of plant traits with environmental conditions (e.g. Keenan and Niinemets 2016). In the alternative configuration (plastic), cohort SLA and V<sub>c.max</sub> respectively decrease and increase with light availability, following empirical relationships from the tropics (Lloyd et al. 2010).

(Moved (insertion) [1]

Finally, we also evaluated the impact of simulating one or multiple PFTs by either classifying all trees in the Wytham Woods inventory as belonging to the mid-successional hardwood tree PFT of ED2.2 ( $N_{PFT} = 1$ ) or according to a classification similar to the one of Dietze and Moorcroft (2011), ( $N_{PFT} = 2$ ), supplemented by a clustering analysis of the allometric relationships derived from the TLS data (see below).

### Analyses

Impact of TLS data on model allometries and initial conditions

We first compared the model default allometries with <u>site-specific ones constrained from the TLS data</u>. To do so, we fitted the individual plant metrics (height, crown area, aboveground woody biomass, and leaf area) versus DBH relationships derived from TLS with the set of equations used in ED2.2 (Table 2). More specifically, we fitted the parameters of the four allometries of ED2.2 using a Bayesian approach and the brms package of R (Bürkner 2017). To convert the leaf area obtained from TLS into leaf biomass, we used the CWM of SLA. We evaluated the quality of fit of the allometric models by computing the root-mean-square deviations (RMSD, van Breugel et al. 2011) normalised by the observed mean and the Watanabe information criterion (WAIC) for all four allometric models (height, crown area, aboveground woody biomass, leaf biomass). We fitted all allometric models using multiple possible species-to-PFT classifications and only retained the classifications that minimised the WAIC for the configurations N<sub>PFT</sub> = 1 and N<sub>PFT</sub> > 1<sub>e</sub>

To assess the relative importance of TLS for the model initialisation, we compared the tree size distributions obtained from the field inventory and the TLS data and computed the absolute and relative differences between both DBH distributions (ground-truthing of TLS).

### Ensemble runs

For each type of initial conditions (NBG, Census, and TLS), we ran ensembles of 500 simulations with parameters randomly sampled from the parameter distributions (Table 4) and with process configuration randomly selected from the different options (Table 5). Each ensemble was equally split between runs with (250) and without (250) TRY constraints on SLA and V<sub>c.max</sub>. The same parameter samples and process configurations were used for all three types of initial conditions, and with and without TRY restrictions on SLA and V<sub>c.max</sub> to allow independently evaluating the impact of the initial conditions, TRYand TLS-constraints at specific parameter values.

#### Sensitivity analyses and variance decomposition

Einally, we assessed which processes and parameters contributed the most to the overall model variance by performing a sensitivity and a variance decomposition analysis following Dietze et al. (2014) and Lebauer et al. (2013). This analysis allows predicting the fraction of the variance in target output variables attributable to individual parameters and processes (or "partial variance"). We chose as target output variables the ecosystem GPP during the most productive month (June) or over the leaf-on season (May-October), the total leaf area index (LAI) and the understorey photosynthetically active radiation (PAR) in leaf-on conditions, as well as the aboveground woody biomass at the end of the

Deleted: To achieve the overarching objective of this study, we designed three different main analyses that explore the sensitivity of the model to TLS data. Those analyses aim to compare the potential vegetation, the forest structure and its functioning, as well as the model calibration between the default model configuration and when the model is informed by TLS data. The overall workflow of this study together with the three main analyses are schematically represented in Figure 2.¶

Deleted: the site-specific ones derived from the TLS data. To do so, we evaluated the quality of fit of both allometric models by computing the corresponding mean relative errors (van Breugel et al. 2011) for all four considered allometric metrics. To assess the relative importance of TLS for the model initialization, we compared the tree size distributions obtained from the field inventory and from the TLS data using a linear model and by computing the absolute and relative differences between both DBH distributions

#### Formatted: Highlight

Deleted: Sensitivity of the potential vegetation to TLS data (Analysis I)

vegetation, we compared uncalibrated simulations, initialized from near-bare ground (NBG) conditions and run for 100 years, which approximately corresponds to the latest large-scale disturbance (Analysis I). We specifically considered three model configurations: the model default (NBG-Default), the finite crown (NBG-FC), and one constrained with TLS data (NBG-TLS). NBG-Default represents the most traditional version of ED2.2. It uses the model default coefficients for all allometric equations and the default infinite size representation of tree crowns. NBG-FC is identical to NBG-Default, except for the finite crown (FC) representation.

simulation. For the NBG configuration, we also decomposed the variance of the total stem density (which is prescribed in the other two configurations). Parameters included in the variance decomposition analyses were re-classified as belonging to one of these three categories: allometric parameters. TRY-constrainable parameters (SLA and V<sub>c.max</sub>), and others. All five years of the Census and TLS configurations were kept for analysis while only the last five years of the NBG runs were considered. Note that the variance partitioning algorithm that we used only attributes to the parameters and processes their direct effect: interactions are not accounted for in the variance decomposition.

All analyses presented in this study were performed using R 3.6 (R Core Team, 2019). Code and supporting data (including initialization and setting files) for reproducing the results presented below are publicly available in Zenodo and have the permanent DOI 10.5281/zenodo.6363617.

#### Results

# Impact of TLS data on model allometries and initial conditions

TLS-extracted and field inventory DBHs were very well correlated ( $R^2 = 0.98$ , slope of the inventory vs TLS linear model = 0.998, see supplementary Figure S4), The mean (resp. median) relative difference between the TLS and field inventory DBHs was -0.2% (resp. -1.7%), see Supplementary Figure S5. The minimum and maximum absolute differences in DBH were -13.8 and 32.9 cm, respectively; the minimum and maximum relative differences were -42 and 101%, respectively (Supplementary Figure S5). The total tree basal area from the inventory was 36.8 cm<sup>2</sup> m<sup>-2</sup> while the total tree basal area obtained from TLS tree reconstruction was 36.2 cm<sup>2</sup> m<sup>-2</sup>.

Individual tree measurements from QSMs applied to the TLS point cloud could all be <u>satisfactorily</u> represented by <u>the</u> ED2.2 allometric equations <u>and a single PFT</u> (Figure <u>2</u>). R<sup>2</sup> of the allometric models for the individual aboveground woody biomass, height, crown area, and leaf biomass respectively reached 0.95, 0.83, 0.67, and 0.77. The <u>normalised RMSD</u> changed from <u>18.3</u> to <u>16.9</u>% (height), from <u>85.1</u> to <u>75.7</u>% (crown area), from <u>146.1</u> to <u>95.0%</u> (woody biomass), and from <u>151</u>% to <u>83.5</u>% (leaf biomass) when switched from ED2.2 default allometries for the mid-successional hardwood tree PFT to TLS-derived, site-specific ones <u>(Table 3)</u>.

Over the DBH range in Wytham Woods, TLS-derived <u>allometries</u> led to systematically larger allocations to aboveground woody biomass (+73% on average, up to +177% for the smallest tree) and leaf biomass (+75% on average), and smaller tree height (-1.9 m on average) as compared to ED2.2 defaults (Figure 2). Individual crown areas derived from TLS measurements varied between 0.2 and 465.4 m<sup>2</sup>, with a mean of 26 m<sup>2</sup>. As compared to the TLS-calibrated <u>allometries</u>, default model <u>coefficients</u> predicted larger crown areas for trees with DBH < 64 cm (-22% on average), and smaller crown areas for trees with DBH < 64 cm (-22% on average), and smaller crown areas for trees with DBH  $\geq$  64 cm (+17% on average), see Figure 2. The latter category (DBH  $\geq$  64 cm) comprised 30 trees (3.7% of the total) and contributed to 30.7% of the total basal area and 24.9% of the total leaf

#### area.

Increasing the number of PFTs only slightly improved the goodness of fit of all four allometric models. The best species-to-PFT mapping according to the literature-informed minimization of the Watanabe information criterion was to classify *Acer pseudoplatanus* as belonging to the late-successional hardwood PFT and the rest of the tree species as belonging to the mid-successional hardwood PFT (Table 1, Supplementary Figures S2 and S3). Using this classification, the normalised RMSD of the allometric models decreased from 16.9 to 16.8% (height), 75.7 to 71.1% (crown area), 95.0 to 77.9% (aboveground woody biomass), and 83.5 to 73.9% (leaf biomass). This mapping resulted in larger crown areas and larger carbon allocation to woody and leaf tissues for small (DBH < 50 cm) trees of the mid-successional tree PFT and taller late-successional trees across all DBHs (+1.16 m on average). Deleted: Finite crowns are expected to increase light availability for short cohorts by reducing the light intercepted by the tallest ones (Dietze et al. 2008). Finally, NBG-TLS was configured according to the allometric coefficients fitted to the TLS data for the individual plant height, the leaf biomass, the aboveground woody biomass, and the crown area. Table 4 summarizes all model configurations used in this study alongside with their most important features. To evaluate the impact of the model structure and TLS derived allometries, we compared the size distribution of the potential vegetations as simulated by ED2.2 for the three model configurations with the inventory data. *Short-term model sensitivity to TLS-derived allometries (Analysis II)* 

To quantify the impact of TLS-derived allometries on ED2.2 outputs at short-time scales, we ran a batch of sixteen uncalibrated sensitivity analysis (SA) simulations prescribed with field inventory data (Analysis II). In those simulations, we progressively incorporated the allometric parameters optimized from the TLS data, by changing a single or a combination of allometric equations from the default set of relationships. We then compared the relative changes of some of the most relevant model outputs (i.e., the ecosystem GPP, the total leaf area index (LAI), the understorey photosynthetically active radiation (PAR), and the aboveground woody biomass) between the sensitivity analysis runs and a reference one that used all default allometric parameters. In this analysis, we calculated those relative changes as the direct or the indirect impact of each allometric equation. The direct impact corresponds to the effect of changing a single allometric equation from the default model parameterization while the indirect impact reflects (....[1])

Moved (insertion	n) [2]
Deleted: satisfac	ctory
Deleted: 3	
Deleted: mean r	elative errors
Deleted: -46.9	
Deleted: 1.42%	(woody biomass), from 14.7 to -4.8
Deleted: 109.0	
Deleted: 9.1	
Deleted: -26.8	
Deleted: 2.8	
Deleted: .	
Deleted: allomet	tric coefficients
Deleted: 3	
Deleted: allomet	try
Deleted: parame	eters
Deleted: ).	
Deleted: .	
Deleted: TLS-de well correlated (	erived and field inventory DBHs were (R² = 0.98, RMSE = 2.3 cm, slope (

#### Ensembles runs

Regardless of the TRY constraints and the model configurations, the model ensembles could reproduce, both the amplitude and the seasonality of the gross ecosystem productivity, as observed by the eddy covariance flux tower, with a maximum GPP in June and a leaf-off season with close-to-zero GPP in <u>December-February</u> (Figure 3). R' of observed vs simulated mean of the monthly GPP was larger than 0.93 for all configurations (NBG, Census, TLS) while the RMSE varied between 1,2 (NBG), 1.3 (TLS) and 1.9 (Census) µmol m<sup>-2</sup> s<sup>-1</sup>, much lower than the mean and standard deviation of the two years of observational data of GPP (5.5 and 4.7 µmol m<sup>-2</sup> s<sup>-1</sup>, respectively). Because we only simulated fully deciduous tree PFTs, model ensembles underestimated GPP during winter: simulated ecosystem LAI and hence ecosystem gross productivity dropped to almost zero in <u>December-February</u> (Supplementary Figure 36) while measured ecosystem productivity was non-null during the same period (Figure 3), driven by evergreen understory plants such as shrubs that were not included in our simulations.

The variability of the simulated GPP was critically influenced by the model configuration and the application of constraints on SLA and V<sub>c.max</sub> (Figure 3). The standard deviation of the ensemble runs for the simulated GPP was not unexpectedly the largest for the configuration with the least information on the ecosystem (the NBG configuration without TRY constraints), and reached 6.33 µmol m<sup>-2</sup> s<sup>-1</sup> for June (Figure 3). More than 23% of the runs in the NBG configuration without TRY constraints led to unvegetated conditions (LAI < 0.1 m<sup>2</sup> m<sup>-2</sup>, all year long, see Supplementary Figure S6) after 100 years of simulations while about 5% of the runs simulated unrealistically dense tree covers (LAI > 10 m<sup>2</sup> m<sup>-2</sup> when the tree covers reaches its maximum). Combined with the uncertainty of the photosynthetic parameters, the LAI variability explained the extreme variability of the ecosystem's gross productivity. The confidence interval of the simulated ecosystem GPP in June for the NBG configuration without TRY constraints (0 - 19.8 µmol m<sup>-2</sup> s<sup>-1</sup>) was almost twice as large as the observed GPP at that moment (13.2 µmol m<sup>-2</sup> s<sup>-1</sup>). The predicted variability of the ecosystem LAI and GPP was on the contrary very low for the TLS configuration with TRY constraints: 3.79 ± 0.50 m<sup>2</sup> m<sup>-2</sup> for the ensemble mean (± one standard deviation) of the ecosystem LAI (Supplementary Figure S6), 9.86 ± 2.89 µmol m<sup>-2</sup> s<sup>-1</sup> for the ensemble mean (± one standard deviation) of the ecosystem GPP (Figure 3), both during leaf-on conditions, which compared well with independent observations (Table 6). The confidence interval of the simulated ecosystem GPP in June for the TLS configuration with TRY constraints was significantly reduced (11.8 - 17.6 µmol m<sup>-2</sup> s<sup>-1</sup>) and much closer to the confidence interval of the observations (11.5 - 14.6 µmol m<sup>-2</sup> <sup>2</sup> s<sup>-1</sup>).

Prescribing realistic initial conditions reduced the variability of the simulated outputs (ensemble standard deviation of GPP in June for the Census configuration without TRY constraints was 4.83 µmol  $m^2 s^{-1}$ ), just like imposing the TLS-constrained allometries (ensemble standard deviation of GPP in June for the TLS configuration without TRY constraints was 3.78 µmol  $m^2 s^{-1}$ ). However, for the ecosystem productivity constraining SLA and V<sub>c.max</sub> was even more critical: ensemble standard deviation of GPP in June for the Census and TLS configurations with TRY constraints decreased to

Moved up [2]: The mean (resp. median) relative difference between the TLS and field inventory DBHs was -0.2% (resp.

Deleted: -1.7%). The minimum and maximum difference in DBH reached -13.8 and 32.9 cm, respectively (Supplementary Figure S2).¶ Sensitivity of the potential vegetation to TLS data

#### (Analysis I) None of the unprescribed simulations (NBG-Default,

NBG-FC and NBG-TLS) captured the size distribution observed through the inventory (Figure 6). While the infinite crown configuration (NBG-Default) generated large trees (DBH > 70 cm), yet smaller than the observations (the biggest tree cohort in the NBG-Default reached 74.4 cm in DBH while the biggest tree based on the field inventory had a DBH of 127.4 cm), it systematically underestimated the density of small (DBH < 50 cm) trees, by 46% on average. The opposite trend could be observed for both configurations with finite crowns (NBG-FC and NBG-TLS), with a smaller density of large trees when allometric coefficients were derived from TLS data (NBG-TLS). When starting from near-bare ground conditions, model structure (NBG-FC vs NBG-Default, +53% on average) had a bigger impact on the tree size distribution than the allometric coefficients (NBG-TLS vs NBG-FC, -7% on average), see Figure 4.¶

# Short-term model sensitivity to TLS-derived allometries (Analysis II)

Direct and indirect impacts of TLS-derived allometries were well correlated for every model output considered (the slope of the linear model of all indirect vs all  $d(\dots, [3])$ 

<b>Deleted:</b> 6). The posterior ensemble runs from calibrated configurations (IC-Default, IC-FC, and IC-TLS) we $( [4])$
Deleted: modelled
Deleted: reached
Deleted: 94
Deleted: three
Deleted: Figure 6A
Deleted: 0.
Deleted: (IC-Default
Deleted: 0.3 (IC-TLS
Deleted: one
Deleted: PFT, the
Deleted: the
Deleted: assimilation
Deleted: down
Deleted: from January to March
Deleted: 6B) due to understorey
Deleted: (

Deleted: shrub

Deleted: simulated here).

Deleted: Despite the similarities in simulated GPP, those runs resulted in very different parameter posterior (... [5]) Formatted: Footer <u>1.99 and 1.54 µmol m<sup>-2</sup> s<sup>-1</sup>, respectively (Figure 3 and Figure 4 where the pie radius is proportional to the variance of ecosystem GPP).</u>

## Variance decomposition and sensitivity analyses

The variance of the ecosystem GPP was dominantly driven by the parameter uncertainty regardless of the configuration and the application of TRY constraints (Figure 4). Together, TRY-constrainable parameters, allometric coefficients, and the other ED2.2 parameters included in the sensitivity analysis, contributed on average to 63% of the total variance of GPP in June. On average, processes only accounted for 11% of the overall variance of GPP with a maximum (resp. minimum) for the TLS configuration with TRY constraints with 20% (resp. for the NBG without TRY constraints with 5%). Constraining SLA and V<sub>c.max</sub> with TRY datasets dramatically decreased the relative contribution of these two parameters to the overall variance: moving from uninformed priors to posteriors generated by the trait meta-analysis of PEcAn made the sum of their partial variances drop from a majority (57% on average for all three configurations) to a small contribution (7% on average for all three configurations), their share being mainly replaced by unconstrained parameters which increased from 6% to 50% on average across all configurations (Figure 4), especially the Quant. Eff., the Clumping and the Growth resp. parameters (Figure 5).

The variance decomposition of the simulated ecosystem LAI and aboveground biomass led to very similar results, yet with a larger contribution of allometries (average contribution of 6 and 20% for LAI and AGB, to be compared with the mean contribution of 3% for GPP) and hence a stronger impact of TLS-constraints on those output variables (Figure 5 and Supplementary Figures S7-S8). Processes (especially the choice of the RTM) played a stronger role for the available light in the understorey (on average 40% of the total variance), especially in runs with prescribed initial conditions (on average 56% of the total variance, see Supplementary Figure S9). Due to compensatory effects (Supplementary Figure S2), the number of simulated PFTs had a limited impact on all of the considered model outputs: N<sub>PFT</sub> only contributed to 3% of the variance of ecosystem GPP, 2% of the variance of LAI and PAR, and 1% of the variance of AGB.

#### **Ecosystem structure and functions**

Despite similar seasonal cycles of ecosystem productivity (Figure 3), ensemble means exhibited very contrasted ecosystem structure (Figures 6-7). None of the unprescribed simulations (NBG configuration) could capture the size distribution observed through the inventory (Figure 6). Small-size stem (especially DBH < 50 cm) densities were underestimated while large tree (DBH > 100 cm) densities were overestimated in the vegetated simulations (LAI > 0.1 m<sup>2</sup> m<sup>-2</sup>) of the NBG configuration with or without TRY constraints. Switching from closed canopy to finite crowns systematically increased the density of small (DBH < 50 cm) trees, by 73% on average; just like constraining SLA and V<sub>c.max</sub> with TRY data. While the ecosystem LAI of the NBG configuration with closed canopies compared well with independent observations from the literature (3.83 ± 1.94 versus the range of 3.6 - 4.1 m<sup>2</sup> m<sup>-2</sup> observed in Wytham Woods, Table 6), the vertical arrangement of the leaves significantly differed from what was observed by TLS and imposed in the TLS configuration (Figure 7), as a result of the differences in tree size distribution (Figure 6).

Despite lower total leaf areas, the infinitely wide crown configuration (closed canopies, Table 6) made the forest more opaque to the incoming solar radiation than the <u>finite crowns</u>. Across all configurations, the PAR available in the <u>understory</u> decreased by <u>15%</u> throughout the <u>year while</u> the ecosystem <u>LAI</u> decreased by <u>18%</u> when closed canopies were simulated (Table <u>6</u>). For near bare-ground configurations, the LAI of the potential vegetation simulated <u>was 23% lower</u> with infinite crowns, <u>and</u> <u>16</u>% less PAR reached the understorey.

As the soil received more radiation when finite crowns were simulated, it was warmer and as a result, heterotrophic (and ecosystem respiration, see Table 6) increased (+,25% on average) when switching from infinite to finite crowns. Forest carbon stocks also diverged between configurations: driven by higher allocations to leaf and aboveground woody biomass (Figure 2), aboveground carbon storage was larger (+,74% on average) in TLS-derived runs than when default allometries were applied (Table 6). Aboveground woody biomass from configurations starting from near bare-ground conditions was systematically underestimated compared to the TLS estimates (11.4 kgc m<sup>-2</sup> on average for the NBG configuration, versus 24.5 kgc m<sup>-2</sup> on average for the TLS configuration). However, the larger allocation to woody biomass induced by the use of TLS-derived allometries mostly did not impact any other model outputs (Figure 5) as that carbon pool is inert and does not influence a lot of processes downstream (e.g. more woody biomass does not translate into exacerbated light interception). Leaf biomass allometry derived from TLS both reduced the simulated LAI and ecosystem GPP to more realistic values and constrained its variability (Figure 3, Table 6, and Supplementary Figure S6).

None of the simulation/configurations <u>could</u> accurately <u>represent</u> all features of Wytham woods. <u>The</u> model <u>simulations</u> starting from near bare-ground conditions <u>failed to capture the vertical distribution of</u> leaves (Figure 6) and the tree size distribution (Figure 7): the model simulations prescribed with the inventory overestimated the ecosystem GPP (Table 6): and the model simulations from the three configurations all overestimated the net ecosystem productivity (NEP), due to an overestimation of GPP (Census) and/or an underestimation of the ecosystem respiration (Census, NBG, and TLS), see Table <u>6. Model simulations</u> underestimated R<sub>eco</sub> on average by <u>17% leading to unrealistic NEP predictions</u>, which illustrates the need for <u>constraining or optimising</u> autotrophic and heterotrophic respiration parameters <u>along with the photosynthetic and allometric parameters</u> to align those with observational data.

	Deleted: crowpo
-	Deleted: Clowins
	Deleted: IC-Delault
	Deleted: (IC-FC and IC-TLS):
$\langle $	Deleted: understorey
	Deleted: 14%. When comparing prescribed model configurations with finite crown areas (IC-FC and IC-TLS),
	Deleted: smaller carbon allocation to leaves imposed by ED2.2 default allometries (Figure 3) was compensated by
	Deleted: larger calibrated values of SLA (Figure 7) resulting in a similar total
	Deleted: leaf area
	Deleted: 5) and its vertical distribution (Figure 8) after calibration. Similarly
	Deleted: from near bare-ground configurations was 32% higher
	Deleted: but at the same time 14
	Deleted: (Table 5).
	Deleted: ) largely
	Deleted: 26
	Deleted: closed
	Deleted: (Table 5).
	Deleted: ,
	Deleted: much
	Deleted: 70
	Deleted: (NBG-TLS and IC-TLS)
	Deleted: 5). Estimates of aboveground
	Deleted: were also contrasted but
	Deleted: lower than
	Deleted: 23.9
	Deleted: IC-TLS
	Deleted: , see
11	Deleted: 5).
	Deleted: Alone, allometric coefficients were responsible for a large variability for all investigated variables: the range of variation in SA runs (Analysis II) was as large and even sometimes larger than in all simulations from Analyses I and III combined (Table 5). Yet, none
	Deleted: represented
	Deleted: All
	Deleted: configurations
	Deleted: , $R_{eco}$ , and NEP, on average by 26%, $30\%$ [6]
	Deleted: 19% and hence overestimated
	Deleted: by 256%, illustrating
	Deleted: optimizing
Å	Formatted: Footer
1	

#### Discussion

### The relative weight of the different sources of uncertainty

The different model configurations tested in this study led to contrasting predictions of vegetation states. Depending on the chosen model outputs, the relative weights of the sources of uncertainty considerably varied. Near bare-ground simulations generated potential vegetations that significantly differed in their demography from observations (Figure 4) while prescribing initial tree size distribution was not a guarantee for accurately reproducing observed land fluxes (Figure 3, Table 6). The finite crown area representation also had a substantial impact on the model outputs. In particular, limiting the crown radius to finite values promoted smaller plants in the understorey (Figure 6), increased the simulated LAI (Table 6) and profoundly modified the vertical distribution of Jight in the canopy (Figure 8 and Table 6). Carbon pools also considerably diverged between model configurations, especially when TLS-derived allometries were taken into account (Table 6).

However, in general, it was the parameter uncertainty that dominated the overall model uncertainty (Figure 3. Supplementary Figure S7 and S8), just like it was previously observed for ED2.2 simulations of temperate forests (Shiklomanov et al. 2020). The parameters that dominated the variance depended on the use of TRY and/or TLS constraints. When observations were available, uncertainty was transferred to other unconstrained parameters while the overall variance was reduced, like in previous similar studies (Meunier et al. 2021), which supports the process of progressively integrating observations of most sensitive parameters until the model variance is reduced to satisfactorily levels in an efficient data-model fusion loop (Dietze et al. 2014).

Although parameter uncertainty was larger in magnitude than process uncertainty, crown size representation and the choice of RTMs appear to drive a significant part of the model process uncertainty and should be paid more attention to in future analyses, Especially, because the implementation and the sensitivity of the radiative transfer processes are currently overlooked in ED2.2 like other vegetation models (Fisher et al. 2018; Viskari et al. 2019).

#### The added value of TLS for vegetation modelling

The quantitative information that remote sensing generates at unprecedented spatial and temporal scales can serve the purpose to reduce uncertainties in TBM projections. It has already been shown that airborne laser scanning (ALS) combined with an individual-based forest model could offer new insights into the contribution of plant size to ecosystem functioning (Fischer et al. 2019). Similarly, ALS and synthetic-aperture Radar have successfully been applied to prescribe the initial structure and composition of tropical forests (Antonarakis et al. 2011; Antonarakis et al. Moorcroft 2014; Longo et al. 2020), and LiDAR data have been coupled to allometric models to estimate carbon stocks and fluxes at large scale (Hurtt et al. 2019; Thomas et al. 2008). Yet, our study is the first attempt to fuse TLS data and TBMs. As compared to ALS, TLS offers a few significant advantages, as well as some drawbacks, that are important to remember. Airborne techniques allow for wall-to-wall coverage characterising 3D forest structure at the regional scale, whereas TLS offers far more detailed information but only at the local (up to a few ha) scale. However, TLS is capable of estimating the volume of individual trees

Deleted: very

Deleted: and	
Deleted: 5), as a result of the configuration-specific choice of allometries and model structure related to canopy	
<b>Deleted:</b> when using both near bare-ground and prescribed initial conditions.	
Deleted: to	
Deleted: detriment of the largest ones	
Deleted: 4), made	
Deleted: closer to the expected value	
Deleted: 5),	
Deleted: leaves and	
Deleted: 5) Crown	

	Deleted: appears
	Deleted: large
	Deleted: of variance decomposition
(	Deleted: in
	<b>Deleted:</b> Carbon pools also considerably diverged between model configurations, especially when TLS- derived allometries were taken into account (Table 5). Not surprisingly, leaf and aboveground woody biomass allometries had the largest impact on the corresponding carbon pools (Figure 5).
Ì	Formatted: Font: Italic
	Deleted: also
	Deleted: .
	Deleted: illustrates

١	Denetu. mustates
(	Deleted: couple
-(	Deleted: characterizing

# Deleted: Yet

<u>directly</u>, instead of relying on <u>allometries</u> that require calibration and thus field measurements. In addition, it can accurately capture the entire size distribution (DBH and height) of the sample plot while smaller trees can easily be missed with airborne surveys (Wang et al. 2016) leading to incorrect demography, especially in dense forests.

Because TLS data are complementary to the datasets that are frequently used for model calibration (e.g. eddy covariance data), they can <u>contribute</u> in a collective effort towards realistic representations of ecosystems in TBMs. TLS has the potential to fill important <u>parameter</u> and process gaps and in doing so, to help reduce the uncertainties in vegetation model simulations. The steep increase in the amount of available forest TLS data over the past decade (Calders et al. 2020) makes its coupling with TBMs even more timely. As demonstrated in this study, TLS observation can ensure a more adequate model structure, constrain model allometric parameters and prescribe representative initial conditions. <u>Yet</u>, only a combination of constraints on both allometries (using TLS data) and photosynthetic parameters (thanks to TRY data) could satisfactorily reduce the model uncertainties to its lowest level, which supports the integration of multiple data sources into TBMs for more realistic simulations (Peylin et al. 2016). Such fusion of a TBM and multiple data streams allowed us to accurately simulate both ecosystem productivity and ecosystem community composition with physically realistic parameters, which was previously highlighted as a challenge for dynamic vegetation models (Shiklomanov et al. 2020; Fisher et al. 2010).

#### Model equifinality

Some runs from all three configurations (prescribed or not with initial size distributions) could reproduce the seasonal cycle of GPP observed by the flux tower (Figure 3). However, those 'optimal' simulations were very different from the forest structure point of view (Table 6, Figures 6-7). This situation illustrates the low identifiability of numerous TBM parameters and the need for multiple simultaneous constraints and observations. While aboveground carbon storage is critical to estimate forest sink strength and the overall carbon storage capacity of the ecosystem (Keeling and Phillips 2007), it has a limited impact on simulated land fluxes (GPP in particular, see Figure 5) that are often used to calibrate TBMs. The parameters controlling land fluxes, namely those controlling ecosystem LAI (Williams and Torn 2015; Wei et al. 2013) and those related to photosynthesis (Figure 5), are also confounded, echoing observed trade-offs of the Leaf Economic Spectrum (Wright et al. 2004; Peaucelle et al. 2019). TLS has the potential to discriminate equifinal model simulations with similar land fluxes but contrasting structure. On-site trait measurements (Figure 3) could further help avoid those risks of equifinality (Babst et al. 2020; Peaucelle et al. 2019).

#### Study limitations

<u>Our findings come with several important</u> limitations. First, the eddy covariance flux data (2007-2009) preceded the observation of the forest structure (TLS and field inventory occurred <u>over the</u> 2015-2016 <u>period</u>) by almost a decade. The forest composition and demography might have changed in the <u>meanwhile</u>, which reduces the confidence of the <u>validation with eddy covariance data (Figure 3)</u>. This is even more true as one <u>realises</u> that the <u>validation</u> dataset is rather limited in size and information content (two very similar seasonal cycles of GPP). Yet, <u>in this study</u> we were more interested in the

Deleted: directy

Deleted: allometric equations

# Deleted: participate

Deleted: data

Deleted: Even though we limited our analysis to a single PFT, hundreds of plant traits can still be calibrated in a vegetation model like ED2.2. Therefore, it is not surprising that multiple sets of parameters can lead to equifinal states. Yet, it is striking to see how critical parameters like SLA and V<sub>cmax</sub> can end up being so different after calibration when the crown representation or default model allometries changed. All

# Deleted: conditions

\)(	Deleted: accurately simulate
Ì	Deleted: after calibration
1	Deleted: 6
(	Deleted: vegetation states
V(	Deleted: 5, Figure 8
Ì	Deleted: perfectly
Y,	Deleted: ,
Ì	Deleted: highly
7	Deleted: 7
Л	Deleted: As for any study, the present one has
λ	Deleted: in
4	<b>Deleted:</b> posterior distributions resulting from the calibration
Д	Deleted: realizes
1	Deleted: calibration
1	Deleted: here

variance decomposition for different model configurations (Figures 3-4) than the actual goodness of fit of every single configuration. GPP is not directly observed but rather a derived (modelled) quantity as opposed to the net ecosystem exchange of carbon and the latent heat flux of water that are directly measured. We could not access water flux raw data nor were they reported in publications that we knew of. GPP uncertainties were also not quantified in the original publication of Thomas et al. (2011). While NEP values were reported, validating the model simulations with those values would have biassed our analyses as we could not constrain respiration parameters with data. Mismatches between different data sources and/or the low availability of good-quality data are recurrent issues in vegetation modelling exercises. Despite multiple initiatives to standardise high quality data such as Fluxnet (Baldocchi et al. 2001), we emphasise here the need for concomitant observations in experimental and observational plots.

Second, the comparison between the potential vegetations as simulated by ED2.2 and the field inventory data are also imperfect as Wytham Woods is a managed forest that has been frequently coppiced and pollarded. <u>Disturbance</u> history experienced by the ecosystem is mostly unknown, preventing us from reproducing the current forest demography by the model.

Einally, the ecosystem growth form complexity was neglected in this study. We only simulated tree PFTs while shrubs and grass species also coexist in Wytham Woods. Integrating this ecological complexity would not have brought additional information or robustness regarding the objectives of our study on the variance decomposition while increasing the dimensionality and complexity of the problem. Future research should investigate whether the main findings highlighted in this study hold with other PFTs, across other sites and biomes, or even in other vegetation models (Dokoohaki et al. 2021).

Deleted: differences of posterior distributions Deleted: their

Deleted: shapes. In addition, an imperfect match

#### Deleted: of data

Deleted: cruel situations that faced any

**Deleted:** modeller at least once. We dare to say that as of today, it remains more the rule than the exception, despite very valuable

Deleted: standardize

Deleted: (Baldocchi et al. 2001)).

Deleted: Without a better knowledge of the disturbance Deleted: (which

Deleted: ), a perfect reproduction of

Deleted: would only be obtained by compensation processes. Finally, the actual forest composition complexity was completely neglected in this study: we only simulated one PFT while several tree, shrub, and grass species coexist in Wytham Woods. However, integrating this ecological complexity could only have decreased the parameter identifiability while increasing the methodological complexity of this study.

#### Conclusion

Vegetation models are important tools to predict the fate of ecosystems in a changing climate but are often used as <u>black-box</u> tools due to their complexity. They have been designed to realistically, represent the ecosystem that they simulate, but often fail to do so primarily because of considerable parameter uncertainties as well as process and <u>initialisation</u> errors. Even for the state-of-the-art process-based terrestrial biosphere models, not all parameters can be constrained with data: some cannot be observed in the field, require calibration, or the appropriate observational trait data may be missing. In addition, model <u>initialisation</u> and the choice of model structure necessarily <u>lead</u> to additional uncertainties. We demonstrate in this study that TLS has the potential to provide initial condition estimates and to constrain some critical vegetation model parameters (allometries) and processes (crown representation). <u>Combined with trait-based constraints on a few key parameters, TLS was able to define a model configuration that could reproduce both the ecosystem productivity and the plant community composition of the simulated site with physically realistic parameters, as well as considerably reduce model uncertainties.</u>

#### Deleted: too

Deleted: blackbox
Deleted: intrinsically
Deleted: and accurately
Formatted: Font: Not Italic
Deleted: initialization

Deleted: Model calibration can simultaneously lead to satisfactory runs from a fitness perspective while giving unrealistic optimal parameter sets.

# Deleted: initialization Deleted: leads

Deleted: Hence, TLS data can help reduce the initialization, model structure and parameter uncertainties. By informing TBMs, TLS can help discriminate realistic states from 'right for the wrong reasons' equifinal vegetation model states

#### Acknowledgements/Funding

This research was funded by BELSPO (Belgian Science Policy Office) in the frame of the STEREO III programme - project 3D-FOREST (SR/02/355). The computational resources and services used in this work were provided by the VSC (Flemish Supercomputer Center), funded by the Research Foundation - Flanders (FWO) and the Flemish Government - department EWI. During the preparation of this manuscript, F.M. was funded by the FWO as a junior postdoc and is thankful to this organisation for its financial support (FWO grant nº 1214720N). N.S. was funded by the Academy of Finland (project number 315079). K.C was funded by the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement Nº 835398. M.P. was funded by the FWO (grant No. G018319N) and the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No. 891369. The TLS fieldwork was funded through the Metrology for Earth Observation and Climate project (MetEOC-2), grant number ENV55 within the European Metrology Research Programme (EMRP). The EMRP is jointly funded by the EMRP participating countries within EURAMET and the European Union. Funds for purchase of the UCL RIEGL VZ-400 instrument was provided by the UK NERC National Centre for Earth Observation (NCEO). The census of the forest plot was supported by an ERC Advanced Investigator Grant to Y.M. (GEM-TRAIT, grant number 321131), We are grateful to the whole PEcAn group and the ED2 team for helpful discussions and support related to the functioning of PEcAn and ED2.

Formatted: Heading 1

### Deleted: organization

Deleted:

Deleted:

Formatted: Font color: Auto

-Page Break-

#### **Tables**

Table 1: Mean ( $\pm$  one standard deviation) of <u>plant</u> traits (Specific Leaf Area or SLA, and maximum rate of carboxylation or  $V_{Cmax}$ ) available in the TRY database for each of the five dominant species in Wytham woods, and their local prevalence (in terms of individual density and basal area). <u>Missing traits were unavailable in TRY</u>. The table also summarises the abundance of those five dominant species in the 1.4 ha plot in terms of absolute and relative density and basal area, as well as the PFT mapping when more than one PFT were simulated ( $N_{PFT} > 1$ ). The community weighted means (CWM) and standard deviations (CWSD) were obtained using the basal areas as weights.

Deleted: V<sub>cmax</sub>

Ap = Acer pseudoplatanus, Ca = Corylus avellana, Cm = Crataegus monogyna, Fe = Fraxinus excelsior, and Qr = Quercus robur. The colours of the different species in the first row of the Table are consistent with Figures 1 and  $\frac{2}{2}$ .

Deleted: Missing traits were unavailable in TRY when we consulted it. Total number of inventoried trees = 821, total basal area =  $50.71 \text{ m}^2$  for the 1.4 plot.

Page Break le 2: List of allometries modified in this study, ED2.2 ault and TLS-derived allometric coefficients. DBH =

meter at Breast Height (cm).

	with Fig	ures 1 and 2.					Deleted: 3			
Trait		Ар	Са	Cm	Fe	Qr	Others	CWM (± C	WSD)	
SLA (m² k	gc <sup>-1</sup> )	-	34.7 (± 36.1)	62.8 (± 65.5)	-	22.9 (± 23.9)	-	25.1 (± 1.5	5)	
<mark>↓/<sub>c.max</sub></mark> (µmo	um <sup>-2</sup> s <sup>-1</sup> )	31.9 (± 16.1)	<u></u>	··· <u>·</u> ·····	39.7 (± 18.0)	31.1 (± 18.8)	<u>-</u>	32.6 (± 0.9	ə) De	leted: V <sub>cmax</sub>
<u>PFT</u> (if N <sub>P</sub>	<sub>FT</sub> > 1)	<u>LH<sup>(1)</sup></u>	<u>MH<sup>(1)</sup></u>	MH	MH	MH	<u>MH</u>			
State	e variable							<u>Total</u>		
Dens (-)	iity	532	67	24	84	35	73	<u>815</u>	De	leted: 79
Relat (%)	ive density	<u>65.3</u>	<u>8.2</u>	<u>2.9</u>	<u>10.3</u>	<u>4.3</u>	<u>9.0</u>	<u>100</u>		
Basa	l area (m²)	31.59	0.48	0.24	5.96	11.87	0.57	<u>50.71</u>		
Relat basal (%)	<u>ive</u> I area	<u>62.3</u>	<u>0.9</u>	<u>0.5</u>	<u>11.8</u>	<u>23.4</u>	<u>1.1</u>	<u>100</u>		
4	_ <sup>(1)</sup> MH = №	lid successional	Hardwood trees.	LH = Late succe	essional Hardwoo	od trees			eted	• ¶

								Moved (insertion) [3]	
							/	Formatted	[8
								Formatted Table	[9
								Deleted: Allometry	
abla 2: Liet c	of varving process	os incl	uded in the	model ensembles in order to evaluat	o tho r	nodel		Deleted: Equation	
tructural unce	rtainty as well as the	heir dif	ferent possib	le configurations. Adapted from Shikle	omanov	et al.		Deleted: Default	
<u>020.</u>							II/	Deleted: TLS	
Desses				Description				Formatted	(
Process				Description	Ж			Deleted: Parameter	(]11
				Choice of the crown representation in				Deleted Cells	(112)
Crown model				the canopy radiation model and in the turbulence scheme			$(\chi)$	Deleted Cells	[12
								Deleted Cells	
Closed				Crowns are evenly spread throughout	<b>v</b>	<b>•</b>	•	Formatted	
Closed				on the top of each other.				Manual dama [4]: 0.27	(110
								Moved down [4]: 0.37	( [16
Finite_				Cohorts have a finite radius and are stacked on the top of each other		<b>X</b>		Deleted: Height, h (m)	( [15
				(Dietze et al. 2008)				<b>Deleted:</b> $CA = CA_1 \cdot DBH^{CA_2}$	
Dedictive tree	oformodol					-		Split Cells	[21
(RTM)	Ister model			Choice of the canopy radiation model					
								Deleted Cells	( [23]
<u>Two-strea</u>	<u>am</u>			Two-stream approximation (Oleson et a	l. 2013;	Sellers	1985	Deleted: 2.49	
Multi-scat	tter			Multiple-scatter approximation (Zhao an	d Quall	s 2005)		Deleted Cells	[24
								Deleted: 0.63	
Trait plasticity	L			Choice of including plant trait variation with the local environment				Deleted Cells	([25
								Split Cells	(117
False			SLA and V <sub>c.max</sub> are constant				Formatted	([17]	
<b>T</b>				$\frac{SLA \text{ and } V_{c,max}}{shading}$ respectively increases and decreases with shading			rith	Formatted Table	( [18
True								$\frac{1}{2} \frac{1}{2} \frac{1}$	( [19
Plant function	al diversity							Example d	
(NPFT)	<u>la aversity</u>			Number of PFTs included in the simulat	ion			Formatied	(  20
				All short success and short for the success of				Formatted	( [22
		<b>u</b>	4	All plant species are classified as mid-si deciduous trees	uccessi	onal ten	iperat	Formatted	( [28
								Deleted: CA <sub>2</sub>	
<u>2</u>				Plant species are mapped into two PFT	s accord	ling to T	able	Deleted: 0.81	
								Deleted: 1.14	
								Formatted	( [27
								Formatted	( [26
								Formatted	
								<b>Deleted:</b> $B_l = B_{l1} \cdot DBH^{B_{l2}}$	
								Deleted: 0.048	
								Deleted: 0.081	
								Formattad	
								Formatted	30
								Pormatieu	(  31
								Deleted: Leal biomass, <i>B</i> <sub>l</sub> (kg)	
								Formatted	( [32
								Formatted	[33
								Deleted Cells	[34
								Formatted Table	( [35
								Deleted Cells	[36
								Deleted Cells Deleted: B <sub>l2</sub>	( [36
								Deleted Cells Deleted: B <sub>12</sub> Deleted Cells	( [36
								Deleted Cells Deleted: B <sub>12</sub> Deleted Cells Deleted: 1.46	( [36

Formatted

Formatted Formatted Formatted Formatted

Deleted: .46

... [39]

(... [40]) (... [41]) (... [42]) (... [7])

1

Table 3: <u>List of al</u> (for one or multip	lometries modified in this s le simulated PFTs). The corr	esponding curves	are plotted in F	ved allor igure 2.	netric co	petficier	<u>nts</u> /
		Paramet er	ED2.2	default		<u>JLS</u>	
Allometry	Equation <sup>(1)</sup>				<u>Npft =</u>	NPF	T= <b>1</b>
			<u>MH<sup>(2)</sup></u>	<u>LH<sup>(2)</sup></u>	<u>MH</u>	<u>MH</u>	LH
Heght, h (m)	$\underline{h} = h_{ref} + h_1 \cdot [1 - exp(DBH \cdot$	h <sub>ref</sub>	<del>_1</del> _3	<u>.1.3</u>	<b>3</b> 2	<u>_3.2</u>	-2.8
x		- <u>h-</u>	<u>25</u> 2	23,4	26.2	25:4	26
		<u>h_2</u>	<u>-0.05</u>	<u>-0.054</u>	<u>-0.074</u>	<u>-</u> 0.074	<u>-0.0</u>
Aboveground woody biomass, Bd	$\underline{B_d} = B_{d1} \cdot DBH^{B_{d2}}$	$\underline{B_{d1}}$	<u>0.16</u>	<u>0.24</u>	<u>0.37</u>	0.67	<u>0.2</u> :
<u>(kg)</u>		$\underline{B_{d2}}$	<u>2.46</u>	<u>2.25</u>	2.29	<u>2.13</u>	2.42
	$\underline{CA} = CA_1 \cdot DBH^{CA_2}$	$\underline{CA_1}$	<u>2.49</u>	<u>2.49</u>	<u>0.6</u>	<u>1.4</u>	<u>0.3</u>
		$\underline{CA_2}$	<u>0.81</u>	<u>0.81</u>	<u>1.15</u>	<u>0.95</u>	<u>1.33</u>
Last biomass B. (kg)	$B_{l} = B_{l1} \cdot DBH^{B_{l2}}$	$\underline{B_{l1}}$	<u>0.048</u>	<u>0.017</u>	0.065	0.095	<u>0.01</u> 5
Lean Divillass, D/ (NY)	$\underline{p_l - p_{ll} \cdot p_{ll}}$	$\underline{B_{l2}}$	<u>1.46</u>	<u>1.73</u>	<u>1.48</u>	<u>1.22</u>	<u>1.69</u>

10DBH = Diameter at Breast Height (cm) 20MH = Mid successional Hardwood trees, LH = Late successional Hardwood trees

I

Deleted: Model prior distributions,is	st of allor [44]
Formatted	( [47]
Deleted: Prior(a,b)	
Deleted Cells	[48]
Deleted: Posterior median	
Formatted	( [49]
Formatted	( [50]
Formatted	( [51]
Deleted: IC-FC	
Inserted Cells	( [45]
Inserted Cells	( [46]
Deleted: IC-Default	
Merged Cells	[52]
Formatted	([53]
Deleted: IC-TLS	([11]
Formatted	[55]
Formatted	(156)
Formatted	( [50]
Deleted: unif(5.60)	([54]
Merged Cells	[60]
Formatted	( [00]
Deleted: 17.5	([01]
Formatted	
	( [62]
Formatted	( [5/]
Delotod: -2 s-1	( [58]
Deleted: 12	
Deleteu: 15	
Polated: 16.7	( [65]
Deleted: 16.7	
Formatted	( [66]
Inserted Cens	( [67]
Pormatted	( [59]
Deleted: 47	
Formatted	( [63]
Inserted Cells	( [64]
Deleted: SLA	( [68]
Formatted	( [69]
Deleted: unif(5,70)	
Formatted	( [70]
Deleted: 24	
Formatted	( [72]
Deleted: 14	
Formatted	( [73]
Deleted:	
Formatted	( [74]
Deleted: 39.8	
Formatted	( [75]
Inserted Cells	( [76]
Formatted	( [77]
Deleted: 9	
Formatted	( [78]
Inserted Cells	( [71]
Moved (insertion) [4]	
Moved (insertion) [5]	
Deleted:Page Break	[79]
Formatted	( [43]

		Deleted: Configuration	
	1	Merged Cells	[83]
		Formatted	( [84])
		Inserted Cells	[85]
orior		Inserted Cells	( [86])
as it		Formatted	( [81])
over		Inserted Cells	
		Formatted	
	177.	Deleted: Analysis III	([0_])
	117.	Inserted Cells	[02]
<u>e</u> /	$\mathbb{V}_{-}$	Inserted Cells	( [92])
~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~		Formatted	
	1/1	Deletede Anelusia I	( [91])
		Merged Cells	( [89])
		Formatted	( [88])
		Deleted: Analysis II	
		Formatted	[90]
•		Deleted: NBG-Default	
		Formatted	( [95])
		Förmatted	[96]
		Deleted: NBG-FC	
		Deleted: NBG-TLS	
		Snlit Cells	[04]
		Formetted	[94]
		Politica Co	<u> </u>
		Deleted: SA	
		Deleted: IC-Default	
		Deleted: IC-FC	)
4		Deleted: IC-TLS	
		Deleted Cells	( [103])
<u> </u>		Formatted	( [101])
		Formatted	( [97])
		Formatted	
		Formatted	
		Formatted	
		Deleted: ¶	([100])
		Moved up [3]: Process	
		Formatted	
		Deleted. Initial conditions	([104])
		Deleted: Near-bare ground	
		Formatted	( [106])
		Deleted: Near-bare ground	
•		Formatted	( [107])
		Deleted: Near-bare ground	
		Deleted: Inventory	
		Formatted	([109])
		Deleted: Inventory	
		Deleted: TLS	
		Deleted: TIS	
		Deleted Cells	
		Esumetted	
-		Formatied	([105])
		Formatted	( [108])
		Formatted	( [110])
		rormatted	( [112])
		Formatted	( [113])
		Deleted: Crown representation	)
		Deleted: Infinitely wide	)
		Formatted	( [115])
		Deleted: Finite radius	
		Deleted: Infinitely wide	
		Formatted	[12]
		Deleted: Finite radius	( [121])
		Delated: Einite radius	
		Deleted: Finite radius	

Table 4: Description of the ED2.2 parameters varied in this stuy, their unit, and the definition of their p used to evaluate the model parameter uncertainty. "Source code name" is the name of the parameter a appears in the ED2.2 source code. When trait plasticity is enabled, both SLA and  $V_{c.max}$  may change of time and for different cohorts of the same PFT.

				1			1	<u> </u>	Forr
		,Description	<u>Unit</u>	Prior				]///	Dele
Pai nar	r <u>ameter</u> ne				(0)	. (0)	Source code name	<b>*//</b> //	Inse
		x	x	Function	<b>a</b> <sup>(2)</sup>	•• <b>b</b> <sup>(2)</sup> ••••			Inse
									For
<u>Wa</u>	ter cond.	Soil-plant hydraulic	m <sup>2</sup> (kg <sub>C,root</sub> ) <sup>-1</sup> yr <sup>-</sup>	<u>Inorm</u>	<b>1</b> 0	3.5	water conduct		Dele
		conductance	<b>`</b>		<u>10.</u>		ance		Mer
Gr	with resp	Fraction of assimilation lost	Linitess (0-1)	beta	4.0	72	growth resp. fa		For
	warresp.	to growth respiration			6	¥4	ctor.		Dele
Md	rt C bal	C balance ratio at which	Unitlass	aamma	1.4	0.05	mort?		For
		mortality rapidly increases	Dimess		7	8.	<u>+110122</u>		Dele
V-		Maximum rate of CO <sub>2</sub>	umole m <sup>-2</sup> s <sup>-1</sup>	weibull	17	80	Vm0		For
<u>v c.</u> r	nax	carboxylation at 15°C					<b>W</b> 1115		Föri
		(baseline)							Dele
Lea	af resp.	Leaf dark respiration at	<u>µmol<sub>C</sub> m<sup>-2</sup> s<sup>-1</sup></u>	gamma	<u>1.5</u>	<u>0.4</u>	<u>Rd0</u>		Dele
ļ		<u>15°C</u>							Spli
Ro	ot:leaf	Ratio of fine root to leaf	Unitless	Inorm	0.2	<u>0.6</u>	a		For
		biomass			<u>1</u>				Dele
<u>SL</u>	<u>4</u>	Specific leaf area	<u>m² (kg<sub>C,leaf</sub>)<sup>-1</sup></u>	gamma	5.1	0.23	<u>SLA</u>		Dele
		(baseline)			<u>3</u>				Dele
Clu	mping.	Canopy clumping factor	Unitless (0-1)	<u>beta</u>	3	1.5	clumping facto	<b>•</b>	Dele
				-			<u> </u>		Dele
Qu	ant. eff.	Fraction of absorbed light	mol CO <sub>2</sub> (mol	weibull	3.3	<u>0.08</u>	quantum_efficiency		For
		used for CO <sub>2</sub> fixation	photon) <sup>-1</sup>		<u>2</u>				For
Ret	1. (VIS)	Leaf reflectance in the	Unitless (0-1)	<u>beta</u>	<u>10.</u>	157	leaf reflect vis		For
		visible range (400-700 nm)			1				For
Ret	1. (NIR)	Leaf reflectance in the	Unitless (0-1)	beta	35	<u>56</u>	leaf reflect nir		Fori
		NIR <sup>(3)</sup> range (700-2500							Dele
		<u>nm)</u>							Mov
Sto	matal	Slope between leaf	<u>Unitless</u>	Inorm	<u>2.3</u>	<u>1</u>	stomatal_slope		For
<u>slo</u>	<u>De</u>	assimilation and stomatal conductance (Leuning)							Dele
$\vdash$		( <u>9</u> )							Dele
Min	<u>i. height</u>	Minimum height for plant reproduction	<u>m</u>	<u>gamma</u>	<u>1.5</u>	<u>0.2</u>	repro_min_h		For

<sup>(1)</sup>Inorm = log-normal distribution <sup>(2)</sup>The values a and b define the parameters of the prior distributions (LeBauer et al., 2013). <sup>(3)</sup>NIR = near-infrared

I

Table 5	5: Summary of <u>the model o</u>	configurations used in this st	tudy and the underlying mod	el settings.			
			Configuration name				
		NBG	<u>Census</u>	<u>TLS</u>			
	Initial conditions	Near-bare ground	Inventory	TLS			
	Allometric parameters	Unconstrained	<u>Unconstrained</u>	TLS-constra	<u>iined</u>		
	Run length (years)	<u>100</u>	<u>5</u>	<u>5</u>			
Sottingo	Crown model	Closed or finite	Closed or finite	Finite			
<u>Settings</u>	RTM	Two-stream or multi-scatter					
	Trait plasticity	True or false					
	<u>N<sub>PFT</sub></u>		<u>1 or 2</u>				
	Ensemble size		<u>500</u>				

I

<u>Table 6: Summary of</u> most important state variables in all <u>three</u> model configurations and how they compare with observational datasets, including flux tower data of ecosystem respiration and net ecosystem productivity. <u>Those numbers take</u> into account the full <u>five</u> years of simulation for the prescribed model configurations (<u>Census and TLS</u>), and the last <u>five</u> years of simulation for the near bareground conditions (NBG), and the two years of eddy covariance <u>observational data</u>. For the observations of LAI in the leaf-on season, we provide a range of variation.

LAI = Leaf Area Index, AGB = Aboveground Biomass, GPP = Gross Primary Production, NEP = Net Ecosystem Productivity, PAR = Photosynthetically Active Radiation

	Uni ts	Configuration									Observations				
Ī			NBG <u>Cens</u>					isus ŢLS						1	
	<b>.</b>	Clos ed can opie s	F P	<u>inite</u> rowns	<u>Clo</u> canc	sed opies	<u>Fini</u> crov	<u>ite</u> vns		<u>Fini</u> crow	ite vns			<b>.</b>	
LAI	m <mark>2</mark> m-2	<u>3.83</u> <u>±</u> 1 <u>.94</u>	47	<u>2 ± 3.67</u>	4 <u>71</u>	<u>± 1.28</u>	\$ <u>75 ±</u>	<u>: 2.74</u>	<u>3.79</u> ± 0 <u>50</u>		r		3	:64 <u>1<sup>(3)</sup></u>	
AGB	kg <sub>G</sub> m <sup>-2</sup>	<u>11.9</u> <u>±</u> <u>7.4</u>	10. <u>8</u> ±6 <u>8</u>	<b>XX</b>	<u>16</u> .4		<u>17</u> .1 :	± <u>4.7</u>		24.5 <u>+</u>	<u>+ 2.5</u>				
GPP( <u>1</u> )	μm ol m <sup>-2</sup> s <sup>-1</sup>	<u>9.55</u> <u>±</u> <u>4.34</u>	<u>9,81</u> <u>±</u> <u>4.70</u>	<b>.</b>	<u>10.</u>	<u>90 ±</u> 91	<u>11:8</u> <u>0±</u> -2 <u>95</u>			9 <u>86±</u>	<u>-2.89</u>		9.	.8±3 <b>,</b> ₄ <sup>(2)</sup>	
Ecos yste m respi ratio n	μm ol m <sup>-2</sup> s <sup>-1</sup>	<u>4.51</u> ± <u>2.04</u>	4:6	<u>4±2.24</u>	<del>4.56</del> -	<u>+ 1,16</u>	4.78 ±	:1,15	3 <u>98</u> <u>±</u> <u>1.17</u>	<b>x</b>			5.	.3±2. <mark>2</mark> (2)	
NEP	μm ol m <sup>-2</sup> s <sup>-1</sup>	1 <mark>53</mark> ±	1,6	<u>3</u> ±0, <u>89</u>	<u>2:32 -</u>	<u>± 1.05</u>	<u>2:68 ±</u>	: <u>0:42</u>	<u>2.26</u> ± 1,02	•			0.	.3 ± 2.9 <sup>(2)</sup>	
PAR reac hing the grou nd	μm ol m <sup>-2</sup> s <sup>-1</sup>	<u>78.6</u> ± <u>93.2</u>	<u></u>	<u>9-±-95:4</u>	<u>44.8</u> ± - <u>34.7</u> -	X			¥		<u>5</u> :	<u>8:2 ± 3</u>	<u>5:3</u>	<u>98:2±36:0</u>	

	Deleted: six	
-7	Deleted: For Analyses I and III and the	observ [144]
//	Deleted: IC-Default, IC-FC, ICensus	and TL([145])
$\parallel$	Deleted: -Default, NBG-FC, NBG-TLS	, and the [146]
[]	Deleted: instead	
I/	Merged Cells	([147])
/ /	Moved (insertion) [8]	
$\ $	Deleted: Analysis I	
	Deleted: Analysis II	
11	Deleted: Analysis II	
$\ $	Deleted, Allarysis III	
$\  $	Deleted: NBG-Default	
[]])	Deleted: IC-ILS	
$\left\  \right\ $	Deleted Cells	( [154])
11//	Deleted Cells	( [155])
//	Moved (insertion) [6]	
//	Deleted: NBG-TLS	
/	Moved (insertion) [7]	
 S	Deleted: SA	)
$\sum_{i=1}^{n}$	(Formatted	( [149])
1	Formatted	( [151])
	Deleted: IC-Default	)
	Moved up [8]: Units	
	Deleted: IC-FC	
	Formatted	[148]
	Merged Cells	( [152])
	Formatted	( [153])
	Formatted	( [150])
	Deleted: NBG-FC	
	<b>Deleted:</b> 2.9 ± 0.	
	<b>Deleted:</b> 1.879 ± 0.1	[158]
	<b>Deleted:</b> 4.6 + 0.2	([138])
	Deleted Cells	[150]
	Deleted: 4.4 + 0.1	([139])
	Deloted: 2.	([160])
	Deletede *	
	Deleteu:	
	Deleted: 2 ± 0.2	
	<b>Deleted:</b> 3 ± 0.2	
	Deleted: 3.21	( [157])
	Deleted: 1 <sup>2</sup>	
	Formatted	( [156])
	Inserted Cells	[161]
	<b>Deleted:</b> 12.6 ± 0.2	)
	Deleted Cells	[162]
	<b>Deleted:</b> 19.6 ± 0.2	)
	Deleted Cells	[163]
	Deleted: 136.4 - 24.	( [164])
	Deleted: 14.2 ± 0.2	)
	Deleted Cells	( [165])
	Deleted: ·	
	Deleted: 147.1 ± 0.2	[166]
	Deleted: 23.9 ± 0.	
	Deleted: ± 0.2	
	<b>Deleted:</b> 14.8 ± 0.7	
	Deleted: 10.0 + 0.1	
	Deleted Cells	[171]
	Deleted: 11.0 + 0.5	<u> </u>
	Delated: 12 + 0.5	
	Deleted: 10. 1 20. 2 : 0.1	( [168])
	Deleted: 101.80 ± 2 ± 0.1	( [170])
	Deleted: *	
	Deleted: ·m <sup>-2</sup> ·	( [167])
	Deleted 83 - 07	



Figure 1: Initial conditions in terms of tree size distribution and <u>species</u> composition (A), horizontal position, basal area (<u>the size of the circles in panel B is proportional to the individual basal area</u>), and <u>species</u> composition (B). The species colour legend applies to both panels and is kept the same for Figure <u>2 and Table 1</u>. In the simulations, all trees were classified into <u>either</u> a single <u>or multiple</u> plant functional types according to the species-PFT of Table 1.

Deleted: not

Deleted: scale

Deleted: 3 below.

Deleted: type (Mid-successional temperate deciduous)....









l





I



for the respective allometries, see Table 2) to the predicted uncertainty in ED2.2 of multiple state variables (PAR = photosynthetically active radiation reaching the ground, LAI = leaf-on ecosystem leaf area index, AGB = final ecosystem aboveground biomass, GPP = leaf-on ecosystem gross primary production) for multiple model configuration (columns) and with or without TRY constraints on SLA and V<sub>c.max</sub> (rows). Only those parameters that contributed at least once to 5% or more of the total variance were included in the panels. Parameter description and distributions are given in Table 4. The settings of the model configurations are detailed in Table 5.



Figure 6: Tree size distribution for multiple model configurations starting from near bare-ground conditions after 100 years of simulations (coloured bars), and how they compare to the field inventory (grey), The histograms and the vertical error bars represent the means  $\pm$  one standard deviation of the ensemble member runs. Only runs that generated vegetation were kept for plotting this figure.





Figure 7: Ecosystem average of the leaf area density vertical distribution for the month of June for different model configurations (colourd lines and envelopes) without (left) and with (right) TRY constraints on SLA and V<sub>C.max</sub>. The envelopes encompass the mean ± one standard deviation of the 500 ensemble member runs\_Only runs that generated vegetation were kept for plotting the NBG envelopes. The settings of the model configurations are detailed in Table 5.

Deleted: Posterior distributions of SLA (A) and  $V_{cmax}$  (B) when using the default allometries and inventory initial conditions (black), the inventory initial conditions (black), the inventory (blue) or the TLS-derived allometries and initial conditions (grey) to fit model parameters (Analysis III). Those distributions can be compared to the measured traits (coloured dots) and the community-weighted means (black dots). The radius of the dots is proportional to the basal area for the respective species (or the total basal area for the CWM) in the inventory (see also Table 1). The vertical dashed lines (red) indicate ED2.2 default values for both parameters.



#### References

- Åkerblom, Markku, Pasi Raumonen, Eric Casella, Mathias I. Disney, F. Mark Danson, Rachel Gaulton, Lucy A. Schofield, and Mikko Kaasalainen. 2018. "Non-Intersecting Leaf Insertion Algorithm for Tree Structure Models." Interface Focus 8 (2): 20170045. https://doi.org/10.1098/rsfs.2017.0045.
- Albani, Marco, David Medvigy, George C. Hurtt, and Paul R. Moorcroft. 2006. "The Contributions of Land-Use Change, CO2 Fertilization, and Climate Variability to the Eastern US Carbon Sink." Global Change Biology 12 (12): 2370–90. https://doi.org/10.1111/j.1365-2486.2006.01254.x. Antonarakis, A. S., J. W. Munger, and P. R. Moorcroft. 2014. "Imaging Spectroscopy- and Lidar-
- Derived Estimates of Canopy Composition and Structure to Improve Predictions of Forest Carbon Fluxes and Ecosystem Dynamics." Geophysical Research Letters 41 (7): 2535–42. https://doi.org/10.1002/2013GL058373.
- Antonarakis, A., S. Saatchi, R. Chazdon, and P. Moorcroft. 2011. "Using Lidar and Radar Measurements to Constrain Predictions of Forest Ecosystem Structure and Function." Ecological Applications : A Publication of the Ecological Society of America. https://doi.org/10.1890/10-0274.1.
- Asner, Gregory P., Roberta E. Martin, Christopher B. Anderson, Katherine Kryston, Nicholas Vaughn, David E. Knapp, Lisa Patrick Bentley, et al. 2017. "Scale Dependence of Canopy Trait Distributions along a Tropical Forest Elevation Gradient." New Phytologist 214 (3): 973-88. https://doi.org/10.1111/nph.14068.
- Atkin, Owen K., Keith J. Bloomfield, Peter B. Reich, Mark G. Tjoelker, Gregory P. Asner, Damien Bonal, Gerhard Bönisch, et al. 2015. "Global Variability in Leaf Respiration in Relation to Climate, Plant Functional Types and Leaf Traits." New Phytologist 206 (2): 614-36. https://doi.org/10.1111/nph.13253.
- Babst, Flurin, Andrew D. Friend, Maria Karamihalaki, Jingshu Wei, Georg von Arx, Dario Papale, and Richard L. Peters. 2020. "Modeling Ambitions Outpace Observations of Forest Carbon Allocation." Trends in Plant Science 0 (0). https://doi.org/10.1016/j.tplants.2020.10.002.
- Bonan, Gordon. 2019. Climate Change and Terrestrial Ecosystem Modeling. 1st ed. Cambridge University Press. https://doi.org/10.1017/9781107339217. Bonan, Gordon B. 2008. "Forests and Climate Change: Forcings, Feedbacks, and the Climate
- Benefits of Forests." Science 320 (5882): 1444-49.
- Breugel, Michiel van, Johannes Ransijn, Dylan Craven, Frans Bongers, and Jefferson S. Hall. 2011. "Estimating Carbon Stock in Secondary Forests: Decisions and Uncertainties Associated with Allometric Biomass Models." Forest Ecology and Management 262 (8): 1648–57. https://doi.org/10.1016/j.foreco.2011.07.018.
- Bürkner, Paul-Christian. 2017. "Brms: An R Package for Bayesian Multilevel Models Using Stan." Journal of Statistical Software 80 (1). https://doi.org/10.18637/jss.v080.i01
- Burrascano, S., R. Copiz, E. Del Vico, S. Fagiani, E. Giarrizzo, M. Mei, A. Mortelliti, F. M. Sabatini, and C. Blasi. 2015. "Wild Boar Rooting Intensity Determines Shifts in Understorey Composition and Functional Traits." Community Ecology 16 (2): 244-53. https://doi.org/10.1556/168.2015.16.2.12.
- Burt, Andrew, Mathias Disney, and Kim Calders. 2019. "Extracting Individual Trees from Lidar Point Clouds Using Treeseg." *Methods in Ecology and Evolution* 10 (3): 438–45. https://doi.org/10.1111/2041-210X.13121.
- Butt, Nathalie, Gordon Campbell, Yadvinder Malhi, Mike Morecroft, Katie Fenn, and Matt Thomas. 2009. "Initial Results from Establishment of a Long-Term Broadleaf Monitoring Plot at
- Wytham Woods, Oxford, UK," January. Calders, Kim, Jennifer Adams, John Armston, Harm Bartholomeus, Sebastien Bauwens, Lisa Patrick Bentley, Jerome Chave, et al. 2020. "Terrestrial Laser Scanning in Forest Ecology: Expanding the Horizon." Remote Sensing of Environment 251 (December): 112102. https://doi.org/10.1016/j.rse.2020.112102.
- Calders, Kim, John Armston, Glenn Newnham, Martin Herold, and Nicholas Goodwin. 2014. "Implications of Sensor Configuration and Topography on Vertical Plant Profiles Derived from Terrestrial LiDAR." Agricultural and Forest Meteorology 194 (August): 104–17. https://doi.org/10.1016/j.agrformet.2014.03.022.
- Calders, Kim, Glenn Newnham, Andrew Burt, Simon Murphy, Pasi Raumonen, Martin Herold, Darius Culvenor, et al. 2015. "Nondestructive Estimates of Above-Ground Biomass Using Terrestrial Laser Scanning." *Methods in Ecology and Evolution* 6 (2): 198–208. https://doi.org/10.1111/2041-210X.12301.

Deleted: Baldocchi, Dennis, Eva Falge, Lianhong Gu, Richard Olson, David Hollinger, Steve Running, Peter Anthoni, et al. 2001. "FLUXNET: A New Tool to Study the Temporal and Spatial Variability of Ecosystem-Scale Carbon Dioxide, Water Vapor, and Energy Flux Densities." *Bulletin of the American Meteorological* Society 82 (11): 2415-34 https://doi.org/10.1175/1520-0477(2001)082<2415:FANTTS>2.3.CO;2.¶

- Calders, Kim, Niall Origo, Andrew Burt, Mathias Disney, Joanne Nightingale, Pasi Raumonen, Markku Åkerblom, Yadvinder Malhi, and Philip Lewis. 2018. "Realistic Forest Stand Reconstruction from Terrestrial LiDAR for Radiative Transfer Modelling." *Remote Sensing* 10 (6): 933. https://doi.org/10.3390/rs10060933.
- Calders, Kim, Niall Origo, Mathias Disney, Joanne Nightingale, William Woodgate, John Armston, and Philip Lewis. 2018. "Variability and Bias in Active and Passive Ground-Based Measurements of Effective Plant, Wood and Leaf Area Index." *Agricultural and Forest Meteorology* 252 (April): 231–40. https://doi.org/10.1016/j.agrformet.2018.01.029.
- Cano, Isabel Martínez, Elena Shevliakova, Sergey Malyshev, S. Joseph Wright, Matteo Detto, Stephen W. Pacala, and Helene C. Muller-Landau. 2020. "Allometric Constraints and Competition Enable the Simulation of Size Structure and Carbon Fluxes in a Dynamic Vegetation Model of Tropical Forests (LM3PPA-TV)." *Global Change Biology* 26 (8): 4478– 94. https://doi.org/10.1111/gcb.15188.
- Chave, <u>Jérome</u>, Maxime <u>Réjou-Méchain</u>, Alberto B??rquez, Emmanuel Chidumayo, Matthew S. Colgan, Welington B C Delitti, Alvaro Duque, et al. 2014. "Improved Allometric Models to Estimate the Aboveground Biomass of Tropical Trees." *Global Change Biology* 20 (10): 3177–90. https://doi.org/10.1111/gcb.12629.
- Collalti, A., S. Marconi, A. Ibrom, C. Trotta, A. Anav, E. D'Andrea, G. Matteucci, et al. 2016. "Validation of 3D-CMCC Forest Ecosystem Model (v.5.1) against Eddy Covariance Data for 10 European Forest Sites." *Geoscientific Model Development* 9 (2): 479–504. https://doi.org/10.5194/gmd-9-479-2016.
- Collalti, Alessio, Peter E. Thornton, Alessandro Cescatti, Angelo Rita, Marco Borghetti, Angelo Nolè, Carlo Trotta, Philippe Ciais, and Giorgio Matteucci. 2019. "The Sensitivity of the Forest Carbon Budget Shifts across Processes along with Stand Development and Climate Change." *Ecological Applications* 29 (2): e01837. https://doi.org/10.1002/eap.1837.
- Coomes, David A, Steven Heathcote, Elinor R Godfrey, James J Shepherd, and Lawren Sack. 2008. "Scaling of Xylem Vessels and Veins within the Leaves of Oak Species." *Biology Letters* 4 (3): 302–6. https://doi.org/10.1098/rsbl.2008.0094.
- Cornelissen, J. H. C. 1996. "An Experimental Comparison of Leaf Decomposition Rates in a Wide Range of Temperate Plant Species and Types." *Journal of Ecology* 84 (4): 573–82. https://doi.org/10.2307/2261479.
- Cornelissen, J. H. C., B. Cerabolini, P. Castro-Díez, P. Villar-Salvador, G. Montserrat-Martí, J. P. Puyravaud, M. Maestro, M. J. A. Werger, and R. Aerts. 2003. "Functional Traits of Woody Plants: Correspondence of Species Rankings between Field Adults and Laboratory-Grown Seedlings?" *Journal of Vegetation Science* 14 (3): 311–22. https://doi.org/10.1111/j.1654-1103.2003.tb02157.x.
- Cornelissen, Jhc, Pc Diez, and R Hunt. 1996. "Seedling Growth, Allocation and Leaf Attributes in a Wide Range of Woody Plant Species and Types." *Journal of Ecology* 84 (5): 755–65. https://doi.org/10.2307/2261337.
- Cornwell, William K., Johannes H. C. Cornelissen, Kathryn Amatangelo, Ellen Dorrepaal, Valerie T. Eviner, Oscar Godoy, Sarah E. Hobbie, et al. 2008. "Plant Species Traits Are the Predominant Control on Litter Decomposition Rates within Biomes Worldwide." *Ecology Letters* 11 (10): 1065–71. https://doi.org/10.1111/j.1461-0248.2008.01219.x.
- Diaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. Ć. Cornelissen, A. Jalili, G. Montserrat-Martí, et al. 2004. "The Plant Traits That Drive Ecosystems: Evidence from Three Continents." *Journal of Vegetation Science* 15 (3): 295–304. https://doi.org/10.1111/j.1654-1103.2004.tb02266.x.
- Dietze, Michael C., and Paul R. Moorcroft. 2011. "Tree Mortality in the Eastern and Central United States: Patterns and Drivers." *Global Change Biology* 17 (11): 3312–26. https://doi.org/10.1111/j.1365-2486.2011.02477.x. Dietze, Michael C., Shawn P. Serbin, Carl Davidson, Ankur R. Desai, Xiaohui Feng, Ryan Kelly, Rob
- Dietze, Michael C., Shawn P. Serbin, Carl Davidson, Ankur R. Desai, Xiaohui Feng, Ryan Kelly, Rob Kooper, et al. 2014. "A Quantitative Assessment of a Terrestrial Biosphere Model's Data Needs across North American Biomes." *Journal of Geophysical Research: Biogeosciences* 119 (3): 286–300. https://doi.org/10.1002/2013JG002392.
- Dietze, Michael C., Michael S. Wolosin, and James S. Clark. 2008. "Capturing Diversity and Interspecific Variability in Allometries: A Hierarchical Approach." Forest Ecology and Management 256 (11): 1939–48. https://doi.org/10.1016/j.foreco.2008.07.034.
- Dokoohaki, Hamze, Marissa S Kivi, Rafael Martinez-Feria, Fernando E Miguez, and Gerrit Hoogenboom. 2021. "A Comprehensive Uncertainty Quantification of Large-Scale Process-Based Crop Modeling Frameworks." Environmental Research Letters 16 (8): 084010.

Deleted: Camino, Carlos, Victoria Gonzalez-Dugo, Pilar Hernandez, and Pablo J. Zarco-Tejada. 2019. "Radiative Transfer Vcmax Estimation from Hyperspectral Imagery and SIF Retrievals to Assess Photosynthetic Performance in Rainfed and Irrigated Plant Phenotyping Trials." *Remote Sensing of Environment* 231 (September): 111186. https://doi.org/10.1016/j.rse.2019.05.005.¶

Deleted: J??r??me

Deleted: R??jou-M??chain

#### https://doi.org/10.1088/1748-9326/ac0f26.

- Ehbrecht, Martin, Peter Schall, Christian Ammer, and Dominik Seidel. 2017. "Quantifying Stand Structural Complexity and Its Relationship with Forest Management, Tree Species Diversity and Microclimate." Agricultural and Forest Meteorology 242 (August): 1–9. https://doi.org/10.1016/j.agrformet.2017.04.012.
- Esprey, L. J, P. J Sands, and C. W Smith. 2004. "Understanding 3-PG Using a Sensitivity Analysis." Forest Ecology and Management, Synthesis of the physiological, environmental, genetic and silvicultural determinants of the growth and productivity of eucalypts in plantations., 193 (1): 235–50. https://doi.org/10.1016/j.foreco.2004.01.032.
- Falster, Daniel S., Remko A. Duursma, Masae I. Ishihara, Diego R. Barneche, Richard G. FitzJohn, Angelica Vårhammar, Masahiro Aiba, et al. 2015. "BAAD: A Biomass And Allometry Database for Woody Plants." *Ecology* 96 (5): 1445–1445. https://doi.org/10.1890/14-1889.1.
   Fan, Guangpeng, Liangliang Nan, Yanqi Dong, Xiaohui Su, and Feixiang Chen. 2020. "AdQSM: A
- Fan, Guangpeng, Liangliang Nan, Yanqi Dong, Xiaohui Su, and Feixiang Chen. 2020. "AdQSM: A New Method for Estimating Above-Ground Biomass from TLS Point Clouds." *Remote Sensing* 12 (18): 3089. https://doi.org/10.3390/rs12183089.
- Fenn, K., Y. Malhi, M. Morecroft, C. Lloyd, and M. Thomas. 2015. "The Carbon Cycle of a Maritime Ancient Temperate Broadleaved Woodland at Seasonal and Annual Scales." *Ecosystems* 18 (1): 1–15. https://doi.org/10.1007/s10021-014-9793-1.
- Fer, Istem, Ryan Kelly, Paul R. Moorcroft, Andrew D. Richardson, Elizabeth M. Cowdery, and Michael C. Dietze. 2018. "Linking Big Models to Big Data: Efficient Ecosystem Model Calibration through Bayesian Model Emulation." *Biogeosciences* 15 (19): 5801–30. https://doi.org/10.5194/bg-15-5801-2018.
- Fischer, Fabian Jörg, Isabelle Maréchaux, and Jérôme Chave. 2019. "Improving Plant Allometry by Fusing Forest Models and Remote Sensing." *New Phytologist* 223 (3): 1159–65. https://doi.org/10.1111/nph.15810.
- Fisher, R. A., S. Muszala, M. Verteinstein, P. Lawrence, C. Xu, N. G. McDowell, R. G. Knox, et al. 2015. "Taking off the Training Wheels: The Properties of a Dynamic Vegetation Model without Climate Envelopes, CLM4.5(ED)." Geoscientific Model Development 8 (11): 3593–3619. https://doi.org/10.5194/gmd-8-3593-2015.
- Fisher, Rosie A., Charles D. Koven, William R. L. Anderegg, Bradley O. Christoffersen, Michael C. Dietze, Caroline E. Farrior, Jennifer A. Holm, et al. 2018. "Vegetation Demographics in Earth System Models: A Review of Progress and Priorities." *Global Change Biology* 24 (1): 35–54. https://doi.org/10.1111/gcb.13910.
- <u>Fisher, Rosie, Nate McDowell, Drew Purves, Paul Moorcroft, Stephen Sitch, Peter Cox, Chris</u> <u>Huntingford, Patrick Meir, and F. Ian Woodward. 2010. "Assessing Uncertainties in a Second-Generation Dynamic Vegetation Model Caused by Ecological Scale Limitations." *New* <u>Phytologist 187 (3): 666–81. https://doi.org/10.1111/j.1469-8137.2010.03340.x.</u></u>
- Friedlingstein, P., P. Cox, R. Betts, L. Bopp, W. von Bloh, V. Brovkin, P. Cadule, et al. 2006. "Climate–Carbon Cycle Feedback Analysis: Results from the C4MIP Model Intercomparison." *Journal of Climate* 19 (14): 3337–53. https://doi.org/10.1175/JCLI3800.1.
- Friedlingstein, Pierre, Malte Meinshausen, Vivek K. Arora, Chris D. Jones, Alessandro Anav, Spencer K. Liddicoat, and Reto Knutti. 2014. "Uncertainties in CMIP5 Climate Projections Due to Carbon Cycle Feedbacks." *Journal of Climate* 27 (2): 511–26. https://doi.org/10.1175/JCLI-D-12-00579.1.
- Garnier, Eric, Sandra Lavorel, Pauline Ansquer, Helena Castro, Pablo Cruz, Jiri Dolezal, Ove Eriksson, et al. 2007. "Assessing the Effects of Land-Use Change on Plant Traits, Communities and Ecosystem Functioning in Grasslands: A Standardized Methodology and Lessons from an Application to 11 European Sites." *Annals of Botany* 99 (5): 967–85. https://doi.org/10.1093/aob/mcl215.
- Giarrizzo, Eleonora, Sabina Burrascano, Tommaso Chiti, Francesco de Bello, Jan Lepš, Laura Zavattero, and Carlo Blasi. 2017. "Re-visiting Historical Semi-natural Grasslands in the Apennines to Assess Patterns of Changes in Species Composition and Functional Traits." https://pubag.nal.usda.gov/catalog/5879480.
- Hackenberg, Jan, Heinrich Spiecker, Kim Calders, Mathias Disney, and Pasi Raumonen. 2015. "SimpleTree —An Efficient Open Source Tool to Build Tree Models from TLS Clouds." *Forests* 6 (11): 4245–94. https://doi.org/10.3390/f6114245.
- Hall, Jeanette, Keith Kirby, and A Whitbread. 2001. National Vegetation Classification: Field Guide to Woodland.
- Hopkinson, Chris, Laura Chasmer, Colin Young-Pow, and Paul Treitz. 2011. "Assessing Forest Metrics with a Ground-Based Scanning Lidar." *Canadian Journal of Forest Research*,

Deleted: Elzhov, Timur V., Katharine M. Mullen, Andrej-Nikolai Spiess, and Ben Bolker. 2016. Minpack.Lm: R Interface to the Levenberg-Marquardt Nonlinear Least-Squares Algorithm Found in MINPACK, Plus Support for Bounds (version 1.2-1). https://CRAN.R-project.org/package=minpack.Im.¶

February. https://doi.org/10.1139/x03-225.

- Hurtt, G. C., J. Fisk, R. Q. Thomas, R. Dubayah, P. R. Moorcroft, and H. H. Shugart. 2010. "Linking Models and Data on Vegetation Structure." *Journal of Geophysical Research: Biogeosciences* 115 (G2). https://doi.org/10.1029/2009JG000937.
- Hurtt, G., M. Zhao, R. Sahaipal, A. Armstrong, R. Birdsey, E. Campbell, K. Dolan, et al. 2019. "Beyond MRV: High-Resolution Forest Carbon Modeling for Climate Mitigation Planning over Maryland, USA." Environmental Research Letters 14 (4): 045013. https://doi.org/10.1088/1748-9326/ab0bbe.
- Jones, Hamlyn G., and Robin A. Vaughan. 2010. *Remote Sensing of Vegetation: Principles, Techniques, and Applications*. OUP Oxford.
- Jupp, David L. B., D. S. Culvenor, J. L. Lovell, G. J. Newnham, A. H. Strahler, and C. E. Woodcock. 2009. "Estimating Forest LAI Profiles and Structural Parameters Using a Ground-Based Laser Called 'Echidna®." *Tree Physiology* 29 (2): 171–81. https://doi.org/10.1093/treephys/tpn022.
- Kattge, Jens, Gerhard Bönisch, Sandra Díaz, Sandra Lavorel, Iain Colin Prentice, Paul Leadley, Susanne Tautenhahn, et al. 2020. "TRY Plant Trait Database – Enhanced Coverage and Open Access." *Global Change Biology* 26 (1): 119–88. https://doi.org/10.1111/gcb.14904.
- Kattge, Jens, Wolfgang Knorr, Thomas Raddatz, and Christian Wirth. 2009. "Quantifying Photosynthetic Capacity and Its Relationship to Leaf Nitrogen Content for Global-Scale Terrestrial Biosphere Models." *Global Change Biology* 15 (4): 976–91. https://doi.org/10.1111/j.1365-2486.2008.01744.x.
- Keeling, Helen C., and Oliver L. Phillips. 2007. "The Global Relationship between Forest Productivity and Biomass." *Global Ecology and Biogeography* 16 (5): 618–31. https://doi.org/10.1111/j.1466-8238.2007.00314.x.

Keenan, Trevor F., and Ülo Niinemets. 2016. "Global Leaf Trait Estimates Biased Due to Plasticity in the Shade." Nature Plants 3 (1): 1–6. https://doi.org/10.1038/nplants.2016.201.

- Kleyer, M., R. M. Bekker, I. C. Knevel, J. P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, et al. 2008. "The LEDA Traitbase: A Database of Life-History Traits of the Northwest European Flora." *Journal of Ecology* 96 (6): 1266–74. https://doi.org/10.1111/j.1365-2745.2008.01430.x.
- LeBauer, David S., Dan Wang, Katherine T. Richter, Carl C. Davidson, and Michael C. Dietze. 2013. "Facilitating Feedbacks between Field Measurements and Ecosystem Models." *Ecological Monographs* 83 (2): 133–54.
- Liebergesell, Mario, Björn Reu, Ulrike Stahl, Martin Freiberg, Erik Welk, Jens Kattge, J. Hans C. Cornelissen, Josep Peñuelas, and Christian Wirth. 2016. "Functional Resilience against Climate-Driven Extinctions – Comparing the Functional Diversity of European and North American Tree Floras." PLOS ONE 11 (2): e0148607. https://doi.org/10.1371/journal.pone.0148607.
- https://doi.org/10.1371/journal.pone.0148607.
  Lin, J. C., M. R. Pejam, E. Chan, S. C. Wofsy, E. W. Gottlieb, H. A. Margolis, and J. H. McCaughey. 2011. "Attributing Uncertainties in Simulated Biospheric Carbon Fluxes to Different Error Sources." *Global Biogeochemical Cycles* 25 (2). https://doi.org/10.1029/2010GB003884.
- Lloyd, J., S. Patiño, R. Q. Paiva, G. B. Nardoto, C. A. Quesada, A. J. B. Santos, T. R. Baker, et al. 2010. "Optimisation of Photosynthetic Carbon Gain and Within-Canopy Gradients of Associated Foliar Traits for Amazon Forest Trees." *Biogeosciences* 7 (6): 1833–59. https://doi.org/10.5194/bq-7-1833-2010.
- Longo, Marcos, Ryan G. Knox, David M. Medvigy, Naomi M. Levine, Michael C. Dietze, Yeonjoo Kim, Abigail L. S. Swann, et al. 2019. "The Biophysics, Ecology, and Biogeochemistry of Functionally Diverse, Vertically and Horizontally Heterogeneous Ecosystems: The Ecosystem Demography Model, Version 2.2 – Part 1: Model Description." *Geoscientific Model Development* 12 (10): 4309–46. https://doi.org/10.5194/gmd-12-4309-2019.
- Longo, Marcos, Sassan Saatchi, Michael Keller, Kevin Bowman, António Ferraz, Paul R. Moorcroft, Douglas C. Morton, et al. 2020. "Impacts of Degradation on Water, Energy, and Carbon Cycling of the Amazon Tropical Forests." *Journal of Geophysical Research: Biogeosciences* 125 (8): e2020JG005677. https://doi.org/10.1029/2020JG005677.
- Lovell, J. L., D. L. B. Jupp, D. S. Culvenor, and N. C. Coops. 2003. "Using Airborne and Ground-Based Ranging Lidar to Measure Canopy Structure in Australian Forests." *Canadian Journal* of Remote Sensing 29 (5): 607–22. https://doi.org/10.5589/m03-026.
- Lovenduski, Nicole S., and Gordon B. Bonan. 2017. "Reducing Uncertainty in Projections of Terrestrial Carbon Uptake." *Environmental Research Letters* 12 (4): 044020. https://doi.org/10.1088/1748-9326/aa66b8.
- Luo, Yiqi, Ensheng Weng, Xiaowen Wu, Chao Gao, Xuhui Zhou, and Li Zhang. 2009. "Parameter Identifiability, Constraint, and Equifinality in Data Assimilation with Ecosystem Models."

- *Ecological Applications* 19 (3): 571–74. https://doi.org/10.1890/08-0561.1. Maas, H.-G., A. Bienert, S. Scheller, and E. Keane. 2008. "Automatic Forest Inventory Parameter Determination from Terrestrial Laser Scanner Data." International Journal of Remote Sensing 29 (5): 1579-93. https://doi.org/10.1080/01431160701736406.
- Maire, Vincent, Ian J. Wright, I. Colin Prentice, Niels H. Batjes, Radika Bhaskar, Peter M. van Bodegom, Will K. Cornwell, et al. 2015. "Global Effects of Soil and Climate on Leaf Photosynthetic Traits and Rates." Global Ecology and Biogeography 24 (6): 706–17. https://doi.org/10.1111/geb.12296.
- Massoud, Elias C., Chonggang Xu, Rosie A. Fisher, Ryan G. Knox, Anthony P. Walker, Shawn P. Serbin, Bradley O. Christoffersen, et al. 2019. "Identification of Key Parameters Controlling Demographically Structured Vegetation Dynamics in a Land Surface Model: CLM4.5(FATES)." Geoscientific Model Development 12 (9): 4133-64. https://doi.org/10.5194/gmd-12-4133-2019.
- McGuire, A. D., S. Sitch, J. S. Clein, R. Dargaville, G. Esser, J. Foley, M. Heimann, et al. 2001. Carbon Balance of the Terrestrial Biosphere in the Twentieth Century: Analyses of CO2, Climate and Land Use Effects with Four Process-Based Ecosystem Models." Global Biogeochemical Cycles 15 (1): 183–206. https://doi.org/10.1029/2000GB001298.
- Medlyn, B. E., F.-W. Badeck, D. G. G. De Pury, C. V. M. Barton, M. Broadmeadow, R. Ceulemans, P. De Angelis, et al. 1999. "Effects of Elevated [CO2] on Photosynthesis in European Forest Species: A Meta-Analysis of Model Parameters." Plant, Cell & Environment 22 (12): 1475–95. https://doi.org/10.1046/j.1365-3040.1999.00523.x.
- Medvigy, D., S. C. Wofsy, J. W. Munger, D. Y. Hollinger, and P. R. Moorcroft. 2009. "Mechanistic Scaling of Ecosystem Function and Dynamics in Space and Time: Ecosystem Demography Model Version 2." Journal of Geophysical Research: Biogeosciences 114 (G1). https://doi.org/10.1029/2008JG000812.
- Medvigy, David, and Paul R. Moorcroft. 2012. "Predicting Ecosystem Dynamics at Regional Scales: An Evaluation of a Terrestrial Biosphere Model for the Forests of Northeastern North America." Philosophical Transactions of the Royal Society of London B: Biological Sciences 367 (1586): 222-35. https://doi.org/10.1098/rstb.2011.0253.
- Meunier, Félicien, Hans Verbeeck, Betsy Cowdery, Stefan A. Schnitzer, Chris M. Smith-Martin, Jennifer S. Powers, Xiangtao Xu, et al. 2021. "Unraveling the Relative Role of Light and Water Competition between Lianas and Trees in Tropical Forests: A Vegetation Model Analysis." Journal of Ecology 109 (1): 519-40. https://doi.org/10.1111/1365-2745.13540
- Milla, Rubén, and Peter B. Reich. 2011. "Multi-Trait Interactions, Not Phylogeny, Fine-Tune Leaf Size Reduction with Increasing Altitude." *Annals of Botany* 107 (3): 455–65. https://doi.org/10.1093/aob/mcq261.
- Moorcroft, Paul R., G. C. Hurtt, and Stephen W. Pacala. 2001. "A Method for Scaling Vegetation Dynamics: The Ecosystem Demography Model (ED)." *Ecological Monographs* 71 (4): 557–86.
   Niinemets, Ülo. 2001. "Global-Scale Climatic Controls of Leaf Dry Mass Per Area, Density, and
- Thickness in Trees and Shrubs." *Ecology* 82 (2): 453–69. https://doi.org/10.1890/0012-9658(2001)082[0453:GSCCOL]2.0.CO;2. Ogaya, R., and J. Peñuelas. 2003. "Comparative Field Study of Quercus Ilex and Phillyrea Latifolia:
- Photosynthetic Response to Experimental Drought Conditions.' https://doi.org/10.1016/S0098-8472(03)00019-4.
- Oleson, Keith, M. Lawrence, B. Bonan, Beth Drewniak, Maoyi Huang, D. Koven, Samuel Levis, et al. 2013. "Technical Description of Version 4.5 of the Community Land Model (CLM)."
- https://doi.org/10.5065/D6RR1W7M. Ordoñez, Jenny C., Peter M. van Bodegom, Jan-Philip M. Witte, Ruud P. Bartholomeus, Jurgen R. van Hal, and Rien Aerts. 2010. "Plant Strategies in Relation to Resource Supply in Mesic to Wet Environments: Does Theory Mirror Nature?" The American Naturalist 175 (2): 225-39. https://doi.org/10.1086/649582.
- Paine, C. E. Timothy, Lucy Amissah, Harald Auge, Christopher Baraloto, Martin Baruffol, Nils Bourland, Helge Bruelheide, et al. 2015. "Globally, Functional Traits Are Weak Predictors of Juvenile Tree Growth, and We Do Not Know Why." *Journal of Ecology* 103 (4): 978–89. https://doi.org/10.1111/1365-2745.12401.
- Peaucelle, Marc, Cédric Bacour, Philippe Ciais, Nicolas Vuichard, Sylvain Kuppel, Josep Peñuelas, Luca Belelli Marchesini, et al. 2019. "Covariations between Plant Functional Traits Emerge from Constraining Parameterization of a Terrestrial Biosphere Model." Global Ecology and Biogeography 28 (9): 1351-65. https://doi.org/10.1111/geb.12937.

Peylin, Philippe, Cédric Bacour, Natasha MacBean, ébastien Leonard, Peter Rayner, Sylvain

Kuppel, Ernest Koffi, et al. 2016. "A New Stepwise Carbon Cycle Data Assimilation System Using Multiple Data Streams to Constrain the Simulated Land Surface Carbon Cycle." Geoscientific Model Development 9 (9): 3321–46. https://doi.org/10.5194/gmd-9-3321-2016.

- Poulter, Benjamin, Fred Hattermann, Ed Hawkins, Sönke Zaehle, Stephen Sitch, Natalia Restrepo-Coupe, Ursula Heyder, and Wolfgang Cramer. 2010. "Robust Dynamics of Amazon Dieback to Climate Change with Perturbed Ecosystem Model Parameters." *Global Change Biology* 16 (9): 2476–95. https://doi.org/10.1111/j.1365-2486.2009.02157.x.
- Raczka, Brett, Michael C. Dietze, Shawn P. Serbin, and Kenneth J. Davis. 2018. "What Limits Predictive Certainty of Long-Term Carbon Uptake?" *Journal of Geophysical Research: Biogeosciences* 123 (12): 3570–88. https://doi.org/10.1029/2018JG004504.
   Raumonen, Pasi, Mikko Kaasalainen, Markku Åkerblom, Sanna Kaasalainen, Harri Kaartinen, Mikko
- Raumonen, Pasi, Mikko Kaasalainen, Markku Åkerblom, Sanna Kaasalainen, Harri Kaartinen, Mikko Vastaranta, Markus Holopainen, Mathias Disney, and Philip Lewis. 2013. "Fast Automatic Precision Tree Models from Terrestrial Laser Scanner Data." *Remote Sensing* 5 (2): 491–520. https://doi.org/10.3390/rs5020491.
- Reich, Peter B., Jacek Oleksyn, and Ian J. Wright. 2009. "Leaf Phosphorus Influences the Photosynthesis–Nitrogen Relation: A Cross-Biome Analysis of 314 Species." *Oecologia* 160 (2): 207–12. https://doi.org/10.1007/s00442-009-1291-3.
- Rezende, L. F. C., B. C. Arenque-Musa, M. S. B. Moura, S. T. Aidar, C. Von Randow, R. S. C. Menezes, J. P. B. H. Ometto, et al. 2016. "Calibration of the Maximum Carboxylation Velocity (Vcmax) Using Data Mining Techniques and Ecophysiological Data from the Brazilian Semiarid Region, for Use in Dynamic Global Vegetation Models." *Brazilian Journal of Biology* 76 (2): 341–51. https://doi.org/10.1590/1519-6984.14414.
- Richardson, Andrew D., Mathew Williams, David Y. Hollinger, David J. P. Moore, D. Bryan Dail, Eric A. Davidson, Neal A. Scott, et al. 2010. "Estimating Parameters of a Forest Ecosystem C Model with Measurements of Stocks and Fluxes as Joint Constraints." *Oecologia* 164 (1): 25– 40.
- Roberts, J., R. Hopkins, and M. Morecroft. 1999. "Towards a Predictive Description of Forest Canopies from Litter Properties." *Functional Ecology* 13 (2): 265–72. https://doi.org/10.1046/j.1365-2435.1999.00312.x.
- Rogers, Alistair, Belinda E. Medlyn, Jeffrey S. Dukes, Gordon Bonan, Susanne von Caemmerer, Michael C. Dietze, Jens Kattge, et al. 2017. "A Roadmap for Improving the Representation of Photosynthesis in Earth System Models." *New Phytologist* 213 (1): 22–42. https://doi.org/10.1111/nph.14283.
- Saarinen, Ninni, Kim Calders, Ville Kankare, Tuomas Yrttimaa, Samuli Junttila, Ville Luoma, Saija Huuskonen, Jari Hynynen, and Hans Verbeeck. n.d. "Understanding 3D Structural Complexity of Individual Scots Pine Trees with Different Management History." *Ecology and Evolution* n/a (n/a). Accessed February 19, 2021. https://doi.org/10.1002/ece3.7216.
- Savill, Peter, Christopher Perrins, Keith Kirby, and Nigel Fisher. 2010. Wytham Woods: Oxford's Ecological Laboratory. OUP Oxford.
- Scherer-Lorenzen, Michael, Ernst-Detlef Schulze, Axel Don, Jens Schumacher, and Eberhard Weller. 2007. "Exploring the Functional Significance of Forest Diversity: A New Long-Term Experiment with Temperate Tree Species (BIOTREE)." *Perspectives in Plant Ecology*, *Evolution and Systematics* 9 (2): 53–70. https://doi.org/10.1016/j.ppees.2007.08.002.
  Sellers, P. J. 1985. "Canopy Reflectance, Photosynthesis and Transpiration." *International Journal of*
- Remote Sensing 6 (8): 1335–72. https://doi.org/10.1080/01431168508948283. Shiklomanov, Alexey N., Ben Bond-Lamberty, Jeff W. Atkins, and Christopher M. Gough. 2020.
- <u>"Structure and Parameter Uncertainty in Centennial Projections of Forest Community</u> Structure and Carbon Cycling." *Global Change Biology* 26 (11): 6080–96. https://doi.org/10.1111/gcb.15164.
- Shiklomanov, Alexey N., Ben Bond-Lamberty, Jeff W. Atkins, and Christopher M. Gough. 2020. "Structure and Parameter Uncertainty in Centennial Projections of Forest Community Structure and Carbon Cycling." *Global Change Biology*, August, gcb.15164. https://doi.org/10.1111/gcb.15164.
- Shipley, B. 2002. "Trade-Offs between Net Assimilation Rate and Specific Leaf Area in Determining Relative Growth Rate: Relationship with Daily Irradiance." *Functional Ecology* 16 (5): 682–89. https://doi.org/10.1046/j.1365-2435.2002.00672.x.
- Stiers, Melissa, Katharina Willim, Dominik Seidel, Martin Ehbrecht, Myroslav Kabal, Christian Ammer, and Peter Annighöfer. 2018. "A Quantitative Comparison of the Structural Complexity of Managed, Lately Unmanaged and Primary European Beech (Fagus Sylvatica L.) Forests." *Forest Ecology and Management* 430 (December): 357–65.

Deleted: Rezende, L. C., B. Arenque, C. von Randow, M. S. Moura, S. D. Aidar, M. S. Buckeridge, R. Menezes, L. S. Souza, and J. P. Ometto. 2013. "Calibration of the Maximum Carboxylation Velocity (Vcmax) for the Caatinga for Use in Dynamic Global Vegetation Models (DGVMs)." *AGU Fall Meeting Abstracts* 11 (December): B11A-0366.¶

Deleted: Sakschewski, Boris, Werner von Bloh, Alice Boit, Anja Rammig, Jens Kattge, Lourens Poorter, Josep Peñuelas, and Kirsten Thonicke. 2015. "Leaf and Stem Economics Spectra Drive Diversity of Functional Plant Traits in a Dynamic Global Vegetation Model." *Global Change Biology* 21 (7): 2711–25. https://doi.org/10.1111/gcb.12870.¶

https://doi.org/10.1016/j.foreco.2018.08.039.

- Takoudjou, Stéphane Momo, Pierre Ploton, Bonaventure Sonké, Jan Hackenberg, Sébastien Griffon, Francois de Coligny, Narcisse Guy Kamdem, et al. 2018. "Using Terrestrial Laser Scanning Data to Estimate Large Tropical Trees Biomass and Calibrate Allometric Models: A Comparison with Traditional Destructive Approach." Methods in Ecology and Evolution 9 (4): 905–16. https://doi.org/10.1111/2041-210X.12933.
- Tanago, Jose Gonzalez de, Alvaro Lau, Harm Bartholomeus, Martin Herold, Valerio Avitabile, Pasi Raumonen, Christopher Martius, et al. 2018. "Estimation of Above-Ground Biomass of Large Tropical Trees with Terrestrial LiDAR." *Methods in Ecology and Evolution* 9 (2): 223–34. https://doi.org/10.1111/2041-210X.12904.
- Thomas, M. V., Y. Malhi, K. M. Fenn, J. B. Fisher, M. D. Morecroft, C. R. Lloyd, M. E. Taylor, and D. D. McNeil. 2011. "Carbon Dioxide Fluxes over an Ancient Broadleaved Deciduous Woodland in Southern England." *Biogeosciences* 8 (6): 1595–1613. https://doi.org/10.5194/bg-8-1595-2011.
- Thomas, R. Quinn, George C Hurtt, Ralph Dubayah, and Mariya H Schilz. 2008. "Using Lidar Data and a Height-Structured Ecosystem Model to Estimate Forest Carbon Stocks and Fluxes over Mountainous Terrain." Canadian Journal of Remote Sensing 34 (sup2): S351–63. https://doi.org/10.5589/m08-036.
- Viovy, Nicolas. 2018. "CRUNCEP Version 7 Atmospheric Forcing Data for the Community Land Model." UCAR/NCAR - Research Data Archive. https://doi.org/10.5065/PZ8F-F017.
- Viskari, Toni, Alexey Shiklomanov, Michael C. Dietze, and Shawn P. Serbin. 2019. "The Influence of Canopy Radiation Parameter Uncertainty on Model Projections of Terrestrial Carbon and Energy Cycling." *PLOS ONE* 14 (7): e0216512. https://doi.org/10.1371/journal.pone.0216512.
- Wang, Y., J. Hyyppä, X. Liang, H. Kaartinen, X. Yu, E. Lindberg, J. Holmgren, et al. 2016. "International Benchmarking of the Individual Tree Detection Methods for Modeling 3-D Canopy Structure for Silviculture and Forest Ecology Using Airborne Laser Scanning." *IEEE Transactions on Geoscience and Remote Sensing* 54 (9): 5011–27. https://doi.org/10.1109/TGRS.2016.2543225.
- Wang, Ying Ping. 2003. "A Comparison of Three Different Canopy Radiation Models Commonly Used in Plant Modelling." *Functional Plant Biology: FPB* 30 (2): 143–52. https://doi.org/10.1071/FP02117.
- Wei, Helin, Youlong Xia, Kenneth E. Mitchell, and Michael B. Ek. 2013. "Improvement of the Noah Land Surface Model for Warm Season Processes: Evaluation of Water and Energy Flux Simulation." *Hydrological Processes* 27 (2): 297–303. https://doi.org/10.1002/hyp.9214.
- Williams, Ian N., and Margaret S. Torn. 2015. "Vegetation Controls on Surface Heat Flux Partitioning, and Land-Atmosphere Coupling." *Geophysical Research Letters* 42 (21): 9416–24. https://doi.org/10.1002/2015GL066305.
- Wirth, Christian, and Jeremy W. Lichstein. 2009. "The Imprint of Species Turnover on Old-Growth Forest Carbon Balances - Insights From a Trait-Based Model of Forest Dynamics." In Old-Growth Forests: Function, Fate and Value, edited by Christian Wirth, Gerd Gleixner, and Martin Heimann, 81–113. Ecological Studies. Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-540-92706-8\_5.
- Wramneby, Anna, Benjamin Smith, Sönke Zaehle, and Martin T. Sykes. 2008. "Parameter Uncertainties in the Modelling of Vegetation Dynamics—Effects on Tree Community Structure and Ecosystem Functioning in European Forest Biomes." *Ecological Modelling* 216 (3): 277– 90. https://doi.org/10.1016/j.ecolmodel.2008.04.013.
- 90. https://doi.org/10.1016/j.ecolmodel.2008.04.013.
  Wright, Ian J., Peter B. Reich, Mark Westoby, David D. Ackerly, Zdravko Baruch, Frans Bongers, Jeannine Cavender-Bares, et al. 2004. "The Worldwide Leaf Economics Spectrum." *Nature* 428 (6985): 821–27. https://doi.org/10.1038/nature02403.
- Zaehle, S., S. Sitch, B. Smith, and F. Hatterman. 2005. "Effects of Parameter Uncertainties on the Modeling of Terrestrial Biosphere Dynamics." *Global Biogeochemical Cycles* 19 (3). https://doi.org/10.1029/2004GB002395.
- Zhao, Wenguang, and Russell J. Qualls. 2005. "A Multiple-Layer Canopy Scattering Model to Simulate Shortwave Radiation Distribution within a Homogeneous Plant Canopy." Water Resources Research 41 (8). https://doi.org/10.1029/2005WR004016.

Deleted: Tan, Kun, Philippe Ciais, Shilong Piao, Xiaopu Wu, Yanhong Tang, Nicolas Vuichard, Shuang Liang, and Jingyun Fang. 2010. "Application of the ORCHIDEE Global Vegetation Model to Evaluate Biomass and Soil Carbon Stocks of Qinghai-Tibetan Grasslands." *Global Biogeochemical Cycles* 24 (1). https://doi.org/10.1029/2009GB003530.¶

#### Supplementary material

### Supplementary section 1: list of references extracted from TRY used in this study

Diaz et al. 2004; Cornelissen 1996; Kleyer et al. 2008; Cornelissen, Diez, and Hunt 1996; Ogaya and Peñuelas 2003; Reich, Oleksyn, and Wright 2009; Cornwell et al. 2008; Wright et al. 2004; Cornelissen et al. 2003; Burrascano et al. 2015; Wirth and Lichstein 2009; Maire et al. 2015; Paine et al. 2015; Liebergesell et al. 2016; Shipley 2002; Ordoñez et al. 2010; Scherer-Lorenzen et al. 2007; Falster et al. 2015; Niinemets 2001; Garnier et al. 2007; Giarrizzo et al. 2017; Coomes et al. 2008; Kattge et al. 2009; Atkin et al. 2015; Medlyn et al. 1999; Milla and Reich 2011).





Figure S1: Initial conditions in terms of tree size distribution and PFT composition (A), horizontal position, basal area, and PFT composition (B), and a three-dimensional visualisation of the ecosystem PFT composition in ED2.2 (C). The PFT colour legend applies to all three panels.

l



Figure S2: TLS-derived model allometries for the aboveground woody biomass (A), tree height (B), crown area (C), and leaf biomass (D) for either a single PFT (grey lines) or multiple PFTs (coloured lines). The data to which the TLS allometries were fitted (coloured points corresponding to the species-PFT classification of Table 1) were obtained using TLS. The root-mean-square deviation relative to the observed mean of each variable is also indicated for each model (grey:  $N_{PFT} = 1$ , black:  $N_{PFT} = 2$ ) or PFT (shades of green). Coefficients used to plot the allometries can be found in Table 3.



Figure S3: Residual plots of the woody biomass (A), tree height (B), crown area (C), and leaf biomass (D) allometric models using either a single PFT (grey dots and lines) or multiple PFTs (coloured dots and lines).



Ì



I



Figure S7: Decomposition of the simulated LAI variance into process (orange), parameter (green), and residual (mauve) uncertainty for multiple model configurations (columns) and with or without TRY constraints on SLA and  $V_{c.max}$  (rows). The parameter uncertainty was further decomposed into the contribution of the allometric, TRY-constrainable (SLA and  $V_{c.max}$ ), and other parameters (shades of green). The radii of the pie charts are proportional to the total variance of the ecosystem LAI in each configuration for the leaf-on season (May-October). The settings of the model configurations are detailed in Table 5.

I



Figure S8: Decomposition of the simulated AGB variance into process (orange), parameter (green), and residual (mauve) uncertainty for multiple model configurations (columns) and with or without TRY constraints on SLA and  $V_{c,max}$  (rows). The parameter uncertainty was further decomposed into the contributions of the allometric, TRY-constrainable (SLA and  $V_{c,max}$ ), and other parameters (shades of green). The radii of the pie charts are proportional to the total variance of the final AGB in each configuration. The settings of the model configurations are detailed in Table 5.

I



I

Page 12: [1] Deleted	Author	3/16/22 11:40:00 PM
Page 12: [2] Deleted	Author	3/16/22 11:40:00 PM
V.		
		2/1//22 11 40 00 DM
Page 13: [3] Deleted	Author	3/16/22 11:40:00 PM
<b>V</b>		
Page 13: [4] Deleted	Author	3/16/22 11:40:00 PM
▼		
Page 13: [5] Deleted	Author	3/16/22 11:40:00 PM
• ••g• ••• [•] = •••••		
T		
Page 15: [6] Deleted	Author	3/16/22 11:40:00 PM
▼		
Page 1: [7] Formatted	Author	3/16/22 11:40:00 PM
Footer		
Page 22. [8] Formatted	Author	3/16/22 11·40·00 PM
Font: Arial, 9 pt	Tutiloi	
· • · · · · · · · · · · · · · · · · · ·		
Page 22: [9] Formatted Tal	ble	Author 3/16/22 11:40:00 PM
Formatted Table		
Page 22: [10] Formatted	Author	3/16/22 11:40:00 PM
Font: 9 pt		
Page 22. [11] Formattad	Author	3/16/22 11·40·00 PM
Font: 9 pt	Autiof	5/10/22 11.70.00 1 11
Page 22: [12] Deleted Cells	Author	3/16/22 11:40:00 PM
Deleted Cells		
Page 22: [13] Deleted Cells	Author	3/16/22 11:40:00 PM
Deleted Cells		
		2/1//22 11 40 00 DM
Page 22: [14] Deleted Cells	Author	3/16/22 11:40:00 PM

**Deleted Cells** 

I

Page 22: [15] Deleted	Author	3/16/22 11:40:00 PM
-----------------------	--------	---------------------

Page 22: [16] Moved to page 23 (Move #4) Author 3/16/22 11:40:00 PM

Page 22: [16] Moved to page 23 (Move #4) Author 3/16/22 11:40:00 PM

Page 22: [17] Split CellsAuthor3/16/22 11:40:00 PMSplit Cells

Page 22: [18] Formatted Author 3/16/22 11:40:00 PM

Font: 9 pt, Bold

 Page 22: [19] Formatted Table
 Author 3/16/22 11:40:00 PM

 Formatted Table

 Page 22: [20] Formatted
 Author
 3/16/22 11:40:00 PM

 Font: 9 pt, Bold
 Font: 9 pt, Bold
 Font: 9 pt, Bold
 Font: 9 pt, Bold

Page 22: [21] Split CellsAuthor3/16/22 11:40:00 PMSplit Cells

 Page 22: [22] Formatted
 Author
 3/16/22 11:40:00 PM

 Font: 9 pt
 Font: 9 pt
 Font: 9 pt
 Font: 9 pt

Page 22: [23] Deleted Cells Author 3/16/22 11:40:00 PM Deleted Cells

Page 22: [24] Deleted Cells Author 3/16/22 11:40:00 PM Deleted Cells

Page 22: [25] Deleted Cells Author 3/16/22 11:40:00 PM Deleted Cells

 Page 22: [26] Formatted
 Author
 3/16/22 11:40:00 PM

 Indent: Left:
 0.75 cm, Space After:
 0 pt

 Page 22: [27] Formatted
 Author
 3/16/22 11:40:00 PM

 Font: 9 pt
 Font: 9 pt
 Font: 9 pt
 Font: 9 pt

Page 22: [28] Formatted	Author	3/16/22 11:40:00 PM
Space After: 0 pt		
Page 22: [29] Formatted	Author	3/16/22 11:40:00 PM
Font: 9 pt		
Page 22. [30] Formatted	Author	3/16/22 11·40·00 PM
Font: 9 nt	Autio	5/10/22 11.40.00 I MI
i ont. 5 pt		
Page 22: [31] Formatted	Author	3/16/22 11:40:00 PM
Indent: Left: 0.75 cm		
Page 22: [32] Formatted	Author	3/16/22 11:40:00 PM
Font: 9 pt		
Page 22: [33] Formatted	Author	3/16/22 11:40:00 PM
Font: 9 pt		
Page 22: [34] Deleted Cells	Author	3/16/22 11:40:00 PM
Deleted Cells		
Deleted Cells		
Deleted Cells	shla	Author 2/16/22 11:40:00 DM
Deleted Cells Page 22: [35] Formatted Table	able	Author 3/16/22 11:40:00 PM
Deleted Cells           Page 22: [35] Formatted Table	able	Author 3/16/22 11:40:00 PM
Deleted Cells           Page 22: [35] Formatted Table	able	Author 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Page 22: [36] Deleted Cells	Able	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells	able Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells	able Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells	able Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells	Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells	able Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells	able Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells         Deleted Cells	Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells         Page 22: [38] Formatted         Font: 9 nt Bold	Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Page 22: [37] Deleted Cells         Page 22: [38] Formatted         Font: 9 pt, Bold	Author Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells         Page 22: [38] Formatted         Font: 9 pt, Bold	Author Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells         Page 22: [38] Formatted         Font: 9 pt, Bold         Page 22: [39] Formatted	Author Author Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells         Page 22: [38] Formatted         Font: 9 pt, Bold         Page 22: [39] Formatted         Indent: Left: 0.75 cm	Author Author Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells         Page 22: [38] Formatted         Font: 9 pt, Bold         Page 22: [39] Formatted         Indent: Left: 0.75 cm	Author Author Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells         Page 22: [38] Formatted         Font: 9 pt, Bold         Page 22: [39] Formatted         Indent: Left: 0.75 cm	Author Author Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM
Deleted Cells          Page 22: [35] Formatted Table         Formatted Table         Page 22: [36] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Deleted Cells         Page 22: [37] Deleted Cells         Page 22: [38] Formatted         Font: 9 pt, Bold         Page 22: [39] Formatted         Indent: Left: 0.75 cm         Page 22: [40] Formatted	Author Author Author Author Author Author	Author 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM 3/16/22 11:40:00 PM

Page 22: [41] Formatted Author 3/16/22 11:40:00 PM

Font: 9 pt

Page 22: [42] FormattedAuthor3/16/22 11:40:00 PMHeading 4, Justified, Indent: Left:0 cm, First line:0 cm

Page 1: [43] Formatted Author 3/16/22 11:40:00 PM

Footer

Page 23: [44] Deleted Author 3/16/22 11:40:00 PM

Page 23: [44] Deleted Author 3/16/22 11:40:00 PM

Page 23: [44] Deleted Author 3/16/22 11:40:00 PM

 Page 23: [45] Inserted Cells
 Author
 3/16/22 11:40:00 PM

 Inserted Cells
 Inserted Cells
 Inserted Cells

Page 23: [46] Inserted Cells	Author	3/16/22 11:40:00 PM
Inserted Cells		

 Page 23: [47] Formatted
 Author
 3/16/22 11:40:00 PM

 Font: Arial, 8 pt
 Image: 200 pt
 Image:

Page 23: [48] Deleted Cells Author 3/16/22 11:40:00 PM Deleted Cells

 Page 23: [50] Formatted
 Author
 3/16/22 11:40:00 PM

 Centered
 Image: Centered
 Image: Centered

 Page 23: [51] Formatted
 Author
 3/16/22 11:40:00 PM

 Font: Arial, 8 pt
 6

 Page 23: [52] Merged Cells Author
 3/16/22 11:40:00 PM

 Merged Cells
 Page 23: [52] Merged Cells

Page 23: [53] Formatted	Author	3/16/22 11:40:00 PM	
Font: Arial, 8 pt			
Page 23: [54] Formatted	Author	3/16/22 11:40:00 PM	
Font: Arial, 8 pt			
Page 23: [55] Formatted A	Author	3/16/22 11:40:00 PM	
Centered			
Page 23: [56] Formatted	Author	3/16/22 11:40:00 PM	
Font: Arial, 8 pt			
Page 23: [57] DeletedA	Author	3/16/22 11:40:00 PM	
▼			
Page 23: [58] Formatted	Author	3/16/22 11:40:00 PM	
Font: 8 pt			
Page 23: [59] Formatted	Author	3/16/22 11:40:00 PM	
Font: 8 pt			
Page 23: [59] Formatted A	Author	3/16/22 11:40:00 PM	
Font: 8 pt			
Page 23: [60] Merged Cells A	Author	3/16/22 11:40:00 PM	
Merged Cells			
5			
Page 23: [61] Formatted A	Author	3/16/22 11:40:00 PM	
Font: Arial, 8 pt			
· · F ·			
Page 23: [62] Formatted	Author	3/16/22 11:40:00 PM	
Font: Arial, 8 pt, Subscrip	ot		
Page 23: [63] Formatted A	Author	3/16/22 11:40:00 PM	
Font: Arial, 8 pt			
Page 23: [64] Inserted Cells		Author 3/16/22 11:40:00	) PM
Incorted Calls			

I

Font: Arial 8 pt					
Page 23: [66] Formatted	Author	3/16/22 1	1:40:00 PM		
Font: Arial, 8 pt					
		4 (1	2/16/22 11 4	0.00 DM	
Page 23: [67] Inserted Cell	S	Author	3/16/22 11:4	0:00 PM	
Inserted Cells					
Page 23: [68] Deleted	Author	3/16/22 1	1:40:00 PM		
v					
Page 23: [69] Formatted	Author	3/16/22 1	1:40:00 PM		
Font: 8 pt					
Page 23: [70] Formatted	Author	3/16/22 1	1:40:00 PM		
Font: Arial, 8 pt					
Page 23: [71] Inserted Cell	s	Author	3/16/22 11:4	0:00 PM	
Inserted Cells					
Page 23: [72] Formatted	Author	3/16/22 1	1:40:00 PM		
Font: Arial, 8 pt					

Page 23: [65] Formatted Author 3/16/22 11:40:00 PM

Page 23: [73] Formatted	Author 3/16/22 11:40:00 PM
Font: Arial, 8 pt	

Page 23: [74] Formatted	Author	3/16/22 11:40:00 PM	
Font: Arial, 8 pt			

 Page 23: [75] Formatted
 Author
 3/16/22 11:40:00 PM

 Font: Arial, 8 pt
 5

Page 23: [76] Inserted Cells	Author	3/16/22 11:40:00 PM
Inserted Cells		

Page 23: [77] Formatted	Author	3/16/22 11:40:00 PM	
Font: Arial, 8 pt			

Page 23: [78] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 8 pt

I.

Page 23: [79] Deleted	Author	3/16/22 11:40:00 PM
Page 1: [80] Formatted	Author	3/16/22 11:40:00 PM
Footer		
Page 24: [81] Formatted	Author	3/16/22 11:40:00 PM
Left, Border: Top: (No	border),	Bottom: (No border), Left: (No border), Right: (No border), Between : (No
border)		
Page 24: [82] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt		
Page 24: [83] Merged Cells	a Author	3/16/22 11:40:00 PM
Merged Cells		
Page 24: [84] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt		
Page 24: [85] Inserted Cell	S	Author 3/16/22 11:40:00 PM
Inserted Cells		
Page 24: [86] Inserted Cell	S	Author 3/16/22 11:40:00 PM
Inserted Cells		
Page 24: [87] Inserted Cell	S	Author 3/16/22 11:40:00 PM
Inserted Cells		
Page 24: [88] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, Not Bold		
Page 24: [89] Merged Cells	s Author	3/16/22 11:40:00 PM
Merged Cells		
Page 24: [90] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, Not Bold		
Page 24: [91] Formatted	Author	3/16/22 11:40:00 PM

Font: Arial, 9 pt, Not Bold, Superscript

Page 24: [92] Inserted Cells	Author 3/16/22 11:40:00 PM
Inserted Cells	
Page 24: [93] Inserted Cells	Author 3/16/22 11:40:00 PM
Inserted Cells	
Page 24: [94] Split Cells Author	3/16/22 11·40·00 PM
Split Cells	5/10/22 11:40:00 1 1/1
Page 24: [95] Formatted Author	3/16/22 11:40:00 PM
Left, Space After: 0 pt, Border:	Top: (No border), Bottom: (No border), Left: (No border), Right: (No border),
Between : (No border)	
, ,	
Page 24: [96] Formatted Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt, Not Bold	
Page 24: [97] Formatted Author	3/16/22 11·40·00 PM
Font: Arial 9 pt Not Bold	5/10/22 11:40:00 1 11
Page 24: [98] Formatted Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt, Not Bold, Supe	erscript
Page 24: [00] Formatted Author	3/16/22 11:40:00 PM
Fage 24: [99] Formatted Author Font: Arial 9 pt Not Bold	5/10/22 11:40.00 F M
Tont. Anal, 5 pt, Not Dold	
Page 24: [100] Formatted Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt, Not Bold	
D 24. [101] E	2/17/20 11 40.00 DM
Fage 24: [101] Formatted Author	3/16/22 11:40:00 PM
Font. Anal, 9 pt, Not Bold	
Page 24: [102] Formatted Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt, Not Bold	
Page 24: [103] Deleted Cells	Author 3/16/22 11:40:00 PM
Deleted Cells	
Page 24: [104] Formatted Author	3/16/22 11:40:00 PM
and the second s	

Page 24: [104] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt		
Page 24: [105] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt, Not Bo	ld	
Page 24: [106] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt		
Page 24: [107] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt		
Page 24: [108] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial. 9 pt		
<i>/</i> 1		
Page 24: [109] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt		
Page 24: [110] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt		
· •		
Page 24: [111] Deleted Cell	S	Author 3/16/22 11:40:00 PM
Deleted Cells		
Page 24: [112] Formatted	Author	3/16/22 11:40:00 PM
Left, Border: Top: (No b	border),	Bottom: (No border), Left: (No border), Right: (No border), Between : (No
horder)		
501001/		
Page 24: [113] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt, Not Bo	old, Not S	Superscript/ Subscript
Page 24: [114] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt, Not Bo	old	
· · ·		
Page 24: [115] Formatted	Author	3/16/22 11:40:00 PM
Font: Arial, 9 pt		

# Page 24: [116] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt

# Page 24: [117] Formatted Author 3/16/22 11:40:00 PM

Font: 9 pt, Bold

Page 24: [118] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt

 Page 24: [119] Formatted
 Author
 3/16/22 11:40:00 PM

 Font: 9 pt, Bold
 Font: 9 pt, Bold
 Font: 9 pt, Bold
 Font: 9 pt, Bold

Page 24: [121] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt

# Page 24: [122] Formatted Author 3/16/22 11:40:00 PM

Left, Border: Top: (No border), Bottom: (No border), Left: (No border), Right: (No border), Between : (No border)

Page 24: [123] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt, Not Bold

Page 24: [124] FormattedAuthor3/16/22 11:40:00 PMFont: Arial, 9 pt, Not Bold

Page 24: [125] FormattedAuthor3/16/22 11:40:00 PMFont: Arial, 9 pt, Superscript

# Page 24: [126] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt

# Page 24: [127] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt

Page 24: [128] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt

# Page 24: [129] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt

# Page 24: [130] Split Cells Author 3/16/22 11:40:00 PM

Split Cells

# Page 24: [131] Formatted Author 3/16/22 11:40:00 PM

Left, Border: Top: (No border), Bottom: (No border), Left: (No border), Right: (No border), Between : (No border)

# Page 24: [132] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt, Not Bold, Not Superscript/ Subscript

Page 24: [133] FormattedAuthor3/16/22 11:40:00 PMFont: Arial, 9 pt, Not Bold

Page 24: [134] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt

Page 24: [135] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt

Page 24: [136] Deleted CellsAuthor3/16/22 11:40:00 PMDeleted Cells

 Page 24: [137] Formatted
 Author
 3/16/22 11:40:00 PM

 Font: Arial, 9 pt
 Image: Second Seco

# Page 24: [138] Formatted Author 3/16/22 11:40:00 PM

Left, Border: Top: (No border), Bottom: (No border), Left: (No border), Right: (No border), Between : (No border)

Page 24: [139] Formatted Author 3/16/22 11:40:00 PM

Font: Arial, 9 pt

Page 24: [141] Deleted Cells Author 3/16/22 11:40:00 PM

**Deleted Cells** 

I

I

I

I

Page 24: [142] Formatted	Author	3/16/22 11:40:00 PM
Normal		
Page 1: [143] Formatted	Author	3/16/22 11:40:00 PM
Footer		
Page 26: [144] Deleted	Author	3/16/22 11:40:00 PM
۷		
Page 26: [144] Deleted	Author	3/16/22 11:40:00 PM
۲		
Page 26: [145] Deleted	Author	3/16/22 11:40:00 PM
Dama 2(. [145] Dalatad	A 4 h	2/16/00 11.40.00 DM
Page 26: [145] Deleted	Autnor	3/16/22 11:40:00 PM
Page 26: [146] Deleted	Author	3/16/22 11:40:00 PM
۷		
Page 26: [146] Deleted	Author	3/16/22 11:40:00 PM
<b>X</b>		
Page 26: [146] Deleted	Author	3/16/22 11:40:00 PM
Page 26: [147] Merged Cel Merged Cells	ls	Author 3/16/22 11:40:00 PM
inelged colle		
Page 26: [148] Formatted	Author	3/16/22 11:40:00 PM
Font: Not Bold		
Page 26: [149] Formatted	Author	3/16/22 11:40:00 PM
Font: 9 pt, Bold		
Page 26: [150] Formatted	Author	3/16/22 11:40:00 PM
Font: Calibri, 9 pt, Bold		
Page 26: [151] Formatted	Author	3/16/22 11:40:00 PM
<b>J I I</b>		

Font: 9 pt, Bold

Page 26: [152] Merged Cells		Author	· 3/16/22 11:40:00 PM
Merged Cells			
-			
Page 26: [153] Formatted	Author	3/16/22 1	11:40:00 PM
Font: Not Bold			
Page 26: [154] Deleted Cells		Author	· 3/16/22 11:40:00 PM
Deleted Cells			
Page 26: [155] Deleted Cells		Author	· 3/16/22 11:40:00 PM
Deleted Cells			
Page 26: [156] Formatted A	Author	3/16/22 1	11:40:00 PM
Superscript			
Page 26: [157] Deleted         A	Author	3/16/22 1	11:40:00 PM
			۲
Page 26: [157] Deleted	Author	3/16/22 1	11·40·00 PM
1 age 20. [157] Detettu F	Author	5/10/22 1	11.70.00 1 11
			۲
Page 26: [158] Deleted         A	Author	3/16/22 1	11:40:00 PM
			۲
Page 26: [158] Deleted	Author	3/16/22 1	11:40:00 PM
Page 26: [159] Deleted Cells		Author	· 3/16/22 11:40:00 PM
Deleted Cells			
Page 26: [160] Deleted Cells		Author	· 3/16/22 11:40:00 PM
Deleted Cells			
Page 26: [161] Inserted Cells		Author	· 3/16/22 11:40:00 PM
Inserted Cells			
		A /-	
Page 26: [162] Deleted Cells		Author	· 3/16/22 11:40:00 PM
Deleted Cells			
Page 26: [163] Deleted Cells		Author	· 3/16/22 11:40:00 PM
Deleted Cells			
Page 26: [164] Deleted	Author	3/16/22 1	11:40:00 PM

I

I

1

1

Page 26: [164] Deleted	Author	3/16/22 11:40:00 PM
------------------------	--------	---------------------

1

I

I

 Page 26: [165] Deleted Cells
 Author 3/16/22 11:40:00 PM

 Deleted Cells
 Cells

Page 26: [166] Deleted	Author	3/16/22 11:40:00 PM	
			۲
Page 26: [166] Deleted	Author	3/16/22 11:40:00 PM	
			<b>V</b>
Page 26: [167] Deleted	Author	3/16/22 11:40:00 PM	
			<b>v</b>
Page 26: [167] Deleted	Author	3/16/22 11:40:00 PM	<b>x</b>
Tuge 201 [107] Deleted	ruthor		_
Dage 26. [169] Deleted	Author	2/16/22 11.40.00 DM	
Page 20: [108] Deleted	Author	3/10/22 11:40:00 PM	
			۲
Page 26: [168] Deleted	Author	3/16/22 11:40:00 PM	
			τ
Page 26: [169] Deleted	Author	3/16/22 11:40:00 PM	
			Χ
Page 26: [169] Deleted	Author	3/16/22 11:40:00 PM	
			۲
Page 26: [170] Deleted	Author	3/16/22 11:40:00 PM	
			۷
Page 26: [170] Deleted	Author	3/16/22 11:40:00 PM	
			τ
Page 26: [171] Deleted Cell	ls	Author 3/16/22 11:4	0:00 PM
Deleted Cells			

Page 26: [172] Deleted	Author	3/16/22	11:40:00 PM	
				τ
Page 26: [172] Deleted	Author	3/16/22	11:40:00 PM	
				τ
Page 26: [173] Inserted C	ells	Author	3/16/22 11:4	0:00 PM
Inserted Cells				

Page 26: [174] Deleted	Author	3/16/22 11:40:00 PM	
			τ
Page 26: [174] Deleted	Author	3/16/22 11:40:00 PM	
			Υ
Page 26: [175] Deleted	Author	3/16/22 11:40:00 PM	
			•

Page 26: [175] Deleted	Author	3/16/22 11:40:00 PM	
			Y
Page 26: [176] Deleted Cells		Author 3/16/22 11:4	0:00 PM
Deleted Cells			
Page 26: [177] Deleted Cells		Author 3/16/22 11:4	0:00 PM
Deleted Cells			
Page 26: [178] Deleted Cells		Author 3/16/22 11:4	0:00 PM
Deleted Cells			
Page 26: [179] Deleted	Author	3/16/22 11:40:00 PM	
			τ
Page 26: [179] Deleted	Author	3/16/22 11:40:00 PM	
			τ
Page 26: [180] Deleted	Author	3/16/22 11:40:00 PM	
			τ
Page 26: [180] Deleted	Author	3/16/22 11:40:00 PM	
			۲
Page 26: [181] Deleted	Author	3/16/22 11:40:00 PM	
			۲
Page 26: [181] Deleted	Author	3/16/22 11:40:00 PM	
			۲
Page 26: [182] Inserted Cells	5	Author 3/16/22 11:4	0:00 PM
Inserted Cells			
Page 26: [183] Deleted	Author	3/16/22 11:40:00 PM	
			۲
Page 26: [183] Deleted	Author	3/16/22 11:40:00 PM	
			۲
Page 26: [184] Deleted	Author	3/16/22 11:40:00 PM	
			۲
Page 26: [184] Deleted	Author	3/16/22 11:40:00 PM	
			۲
Page 26: [185] Deleted Cells		Author 3/16/22 11:4	0:00 PM
Deleted Cells			

1

I

I

1

I

 Page 26: [186] Deleted Cells
 Author 3/16/22 11:40:00 PM

 Deleted Cells
 Author 3/16/22 11:40:00 PM

Page 26: [187] Deleted Cells	Author 3/16/22 11:40:00 PM
Deleted Cells	
Page 26: [188] Inserted Cells	Author 3/16/22 11:40:00 PM
Inserted Cells	
Page 26: [189] Formatted Author	3/16/22 11:40:00 PM
Font: 9 pt	
Page 26. [190] Formatted Author	3/16/22 11·40·00 PM
Font: 9 nt	5/10/22 11.70.00 1 19
i ont. o pr	
Page 26: [190] Formatted Author	3/16/22 11:40:00 PM
Font: 9 pt	
·	
Page 26: [190] Formatted Author	3/16/22 11:40:00 PM
Font: 9 pt	
D 26. [100] E	2/17/22 11, 40,00 DM
Fage 26: [190] Formatted Author	5/16/22 11:40:00 PM
Font. 9 pt	
Page 26: [190] Formatted Author	3/16/22 11:40:00 PM
Font: 9 pt	
·	
Page 26: [190] Formatted Author	3/16/22 11:40:00 PM
Font: 9 pt	
D 26. [100] E	2/17/22 11, 40,00 DM
Page 26: [190] Formatted Author	3/16/22 11:40:00 PM
Font. 9 pt	
Page 26: [190] Formatted Author	3/16/22 11:40:00 PM
Font: 9 pt	
Page 26: [191] Formatted Author	3/16/22 11:40:00 PM
Font: 9 pt	
Page 26: [191] Formatted Author	3/16/22 11:40:00 PN

Font: 9 pt

Т

 Page 26: [192] Formatted
 Author
 3/16/22 11:40:00 PM

 Font: 9 pt
 Formatted
 Formatted<

Page 28: [193] Deleted	Author	3/16/22 11:40:00 PM		l
			τ	
Page 32: [194] Deleted	Author	3/16/22 11:40:00 PM		L
Page 41: [195] Deleted	Author	3/16/22 11:40:00 PM		