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To cite this version:

E-Ping Rau, Fabian Fischer, Émilie Joetzjer, Isabelle Maréchaux, I Fang Sun, et al.. Transferability of an individual- and trait-based forest dynamics model: A test case across the tropics. Ecological Modelling, 2022, 463, pp.109801. 10.1016/j.ecolmodel.2021.109801 . hal-03432028

HAL Id: hal-03432028
https://hal.inrae.fr/hal-03432028

Submitted on 5 Jan 2024

Version of Record: https://www.sciencedirect.com/science/article/pii/S030438002100346X
Manuscript_d9d73e87f1bb9782c2dcde9f5ac338ab

Transferability of an individual- and trait-based forest dynamics model: a test case across the tropics

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Abstract

Individual-based forest models (IBMs) are useful to investigate the effect of environment on forest structure and dynamics, but they are often restricted to site-specific applications. To build confidence for spatially distributed simulations, model transferability, i.e. the ability of the same model to provide reliable predictions at contrasting sites, has to be thoroughly tested. We tested the transferability of a spatially explicit forest IBM, TROLL, with a trait-based species parameterization and global gridded climate forcing, by applying it to two sites with sharply contrasting climate and floristic compositions across the tropics, one in South America and one in Southeast Asia. We identified which parameters are most influential for model calibration and assessed the model sensitivity to climatic conditions for a given calibration. TROLL produced realistic predictions of forest structure and dynamics at both sites and this necessitates the recalibration of only three parameters, namely photosynthesis efficiency, crown allometry and mortality rate. All three relate to key processes that constrain model transferability and warrant further model development and data acquisition, with mortality being a particular priority of improvement for the current generation of vegetation models. Varying the climatic conditions at both sites demonstrate similar, and expected, model responses: GPP increased with temperature and irradiance, while stem density and aboveground biomass declined as temperature increased. The climate dependence of productivity and biomass was mediated by plant respiration, carbon allocation and mortality, which has implications both on model development and on forecasting of future carbon dynamics. Our detailed examination of forest IBM transferability unveils key processes that need to improve in genericity before reliable large-scale implementations can be envisioned.

Keywords: TROLL, forest simulations, model calibration, climate forcing, Taiwan, Amazonia

1. Introduction

Forests harbor more than half of the total terrestrial biodiversity (Gardner et al., 2010) and contribute to climate change mitigation (Ellison et al., 2017; Mitchard, 2018). However, forest disturbances are important drivers of canopy cover change and they will likely impact tropical forest structure, diversity, and functioning in the future (Feng et al., 2018; Malhi et al., 2009; Zemp et al., 2017). These projections depend on a detailed understanding of the processes that link the abiotic environment and forest dynamics, as can be achieved through integration into simulation models (Fisher et al., 2018; Shugart et al., 2018). Confronting the robustness, reliability and realism of such models is crucial to gain confidence in their predictions (Prentice et al., 2015).

Dynamic global vegetation models (DGVMs) adopt a coarse representation of the coupling between vegetation and biogeochemical cycles. Their simplified description of vegetation dynamics assume a limited set of vegetation structure and summarize plant diversity with a few plant functional types (PFTs). Modern DGVMs simulate demographic processes and trait variability (Fisher et al., 2010; Koven et al., 2020; Sakschewski et al., 2015; Sato et al., 2007; Scheiter et al., 2013). However, difficulties remain in representing plant recruitment and mortality, translating into uncertainties in model projections of forest dynamics (Fisher et al., 2018).

Unlike DGVMs, individual-based forest models (IBMs) explicitly simulate tree establishment, growth, competition, and mortality, simulating forest structure and dynamics at the stand scale (Bugmann, 2001; DeAngelis and Grimm, 2014; Fischer et al., 2016; Shugart, 1984). Forest IBMs adopt a fine-grained representation of the diversity and structure of tree assemblages, which facilitates the exploration of mixed-species forest responses to climate variability (Maréchaux et al., 2021). One drawback is that the calibration of forest IBMs is data demanding, and requires data at a fine spatial and temporal scale. For this reason, IBMs have traditionally been restricted to stand-scale application, and even if their extension to regional or global scale is technically possible (Shugart et al., 2018, 2015), one fundamental challenge is to explore the model validity across space.

At the heart of model upscaling is the question of model transferability (Wenger and Olden, 2012; Yates et al., 2018): when a model has been calibrated at one site, how well does it simulate the vegetation dynamics at another site? Model transferability hinges upon how well the model is able to capture forest processes at any given site, and on whether the same biogeochemical and biophysical processes hold across sites (Fyllas et al., 2017; Sullivan et al., 2020). For instance, process-based models couple forest processes to environmental drivers in a generic way, through mechanistic modules, such as photosynthesis, water uptake, allocation. These processes are parameterized locally through measurable traits with consistent biological and ecological meaning (e.g. functional traits). This means that, in theory, a completely process-based model should be transferable to any site, provided that measurements of the environmental drivers (e.g., climatic variables) and relevant traits of all locally present tree species are available.

However, for some processes, current knowledge is insufficient to develop generic functions, and a simplified representation is necessary to encapsulate finer processes mediated by environmental, biogeographic or evolutionary factors. As a result, part of the site-specificity is hidden in the model equations and parameters themselves. These site-specific parameters need to be re-calibrated from one site to the other to ensure reliable simulation outputs, which increases calibration efforts and hampers transferability (Lehmann and Huth, 2015; Maréchaux et al., 2021). Even generic equations have typically been formulated using input data from specific sites and under specific conditions, which will not always be consistent with the data provided for model initialization at other sites (Huber et al., 2018). This issue is especially important for tropical forests, which have high variability in composition, structure and functioning within and between sites, making model transferability and upscaling a greater challenge (Castanho et al., 2016; Johnson et al., 2016; Townsend et al., 2008).

Model transferability in part depends on the availability of standardized and spatially distributed data on forest structure and function. For example, site-specific information can be prescribed for a model through trait-based data on floristic diversity (Fyllas et al., 2014, Maréchaux and Chave, 2017) or remote sensing data (Fischer et al., 2019; Joetzjer et al., 2017; Shugart et al., 2015). Consistent climatic boundary conditions, derived from weather models and data assimilation systems, also increase model transferability (Bugmann and Fischlin, 1996; Fauset et al., 2019). This also facilitates the evaluation of how a model responds to changes in climate forcing conditions: for example, in light-limited tropical rainforests, we expect that GPP will exhibit weakly positive or even negative relationship with increasing temperature, due to increasing competition, mortality and faster turnover (Allen et al., 2010; Clark et al., 2010; McDowell et al., 2018).

Another way to improve model transferability is to convert modules that are implicitly site-specific into more generic formulations that encode site-specific conditions only through dependence on environmental and floristic composition. This can be facilitated by performing tests to identify model processes that are currently particularly site-specific: the improvement of the representation of those processes, through theoretical and empirical work across multiple sites, should then be prioritized. For instance, we expect that outputs of forest IBMs will be highly sensitive to parameters of mortality, and a more accurate mechanistic representation of mortality should improve the reliability of model projections under conditions beyond the range of the original calibration data (Johnson et al., 2016; Bugmann et al., 2019). Although several studies have explored the issue of transferability of forest IBMs (Bugmann and Solomon, 1995; Lagarrigues et al., 2015; Ma et al., 2017; Shuman et al., 2015), they have so far been limited to temperate and boreal forests with low tree species diversity.

In this study, we explored the conditions of transferability of a forest IBM between two contrasting tropical forest sites chosen to maximize dissimilarity in geography, floristic composition and environmental conditions, evaluating separately the effect of parameter calibration and of climate forcing. We asked the following questions:

(1) How well does a locally calibrated forest IBM perform when transferred at another site? We expect a degradation of model performance with no fine-tuning at the contrasting site.

(2) What key parameters determine model performance during model transfer? We expect that, since most fundamental processes are captured by generic formulations in the model, only few parameters will be identified as in need of recalibration: these parameters point to limitations in model representation of the underlying processes.

(3) What are the expected responses to climatic conditions? In the absence of water limitation, as in light-limited rainforests, GPP should increase with temperature and irradiance, while biomass should depend less on temperature.

2. Materials and methods

2.1 Model description

The TROLL model is a spatially explicit individual-based model in which the aboveground space of a forest stand is divided into 3D cells of size 1 m^3 (hereafter called voxels; Chave, 1999; Maréchaux and Chave, 2017). Solar irradiance (photosynthetic photon flux density, PPFD) is computed inside each voxel as the irradiance fraction transmitted immediately above the focal voxel. We considered only vertical light transmittance in the canopy; for trees at the edge of the simulated plot, we simulate light interception only for the part of the crown that is inside the plot, and then scale total assimilation with crown radius. At most, one tree can establish in each 1 × 1 m pixel at any given time, and only self-standing stems ≥ 1 cm in trunk diameter at breast height (DBH) are explicitly modelled (herbaceous plants and lianas are not included). The effects of topography and water balance are not modeled. Seeds and seedlings < 1 cm DBH are indirectly modeled as part of a regeneration compartment, with inputs from an external seed rain and seed production within the simulated stand. Each modelled tree is a 3D object, characterized by DBH, height, crown radius, crown depth, total leaf surface area, and age. Trees are assigned species-specific trait values, which influence processes such as photosynthesis, growth and mortality.

At each monthly timestep, the model simulates carbon assimilation (photosynthesis), respiration, carbon allocation and growth for each tree, and also simulates seed dispersal or tree death when conditions are met. Tree growth is the result of an explicit balance between carbon assimilation (photosynthesis) and respiration. Carbon assimilation is represented with the C3 photosynthesis model (Farquhar et al., 1980), which depends on temperature, irradiance, vapor pressure deficit (VPD), and atmospheric CO_2 concentration. During a monthly timestep, photosynthesis is calculated over half-hourly periods of a representative day (monthly mean values of temperature, irradiance and VPD); atmospheric CO_2 concentration is assumed constant. Stomatal conductance is modelled following Medlyn et al. (2011). We define the parameter φ (quantum carbon yield per quantum photon) as the initial slope of the photosynthetic carbon assimilation against irradiance curve; this parameter controls carbon uptake in light-limited conditions (Farquhar et al., 1980). The value of φ depends on environment and species, and it has been shown to be an important source of uncertainty in vegetation models (Domingues et al., 2014; Mercado et al., 2009).

After the gross assimilated carbon is calculated from the photosynthesis model, net assimilated carbon is calculated as the gross assimilated carbon minus respiration. Net assimilated carbon is then allocated into biomass in different organs based on parameters of fixed fractions, resulting in tree growth and leaf flush dynamics in the same timestep. The resulting changes in tree height, crown shape and position, and leaf density will then influence the calculation of the light environment and photosynthesis of each tree in the next timestep.

The allometric relationship relating tree height and DBH is assumed to be species-specific, while allometric functions relating DBH and crown size are assumed the same for all trees. Crown radius grows as a function of DBH, following a non-linear relationship: $CR = e^{(CR_a + CR_b \times \ln DBH)}$ where CR_a and CR_b are general parameters provided in input. Hence higher CR_a indicates larger crowns for trees of all sizes, whereas higher CR_b indicates that larger trees have disproportionately larger crowns than smaller trees. Identical values of CR_a and CR_b are prescribed for all species given the paucity of available data, even if it is acknowledged that crown size allometry can vary within species, across species and across sites (Jucker et al., 2017; Loubota Panzou et al., 2021).

In TROLL, tree mortality results from several processes: (i) stochastic mortality, modelled as function of a maximal background mortality rate m and a linearly decreasing relationship with species-specific wood density (WD), so that: $m_{eff} = m - \alpha \times WD$ (α being positive, m is the maximal possible value of the mortality rate); (ii) carbon starvation if net assimilated carbon is negative over a consecutive period exceeding leaf lifespan, so that old leaves have all died while no new leaves could be produced (assuming no internal carbon storage); and (iii) stochastic treefall events, assumed to depend on a tree height threshold, where the parameter vC represents the variability of this threshold. Both m and vC hence summarize complex processes that are not modeled mechanistically.

A schematic diagram, which illustrates the structures and processes controlling the individual- and community-level dynamics of a forest in the TROLL model, can be found in Maréchaux and Chave (2017) (Appendix S5, Figure S1). Necessary inputs for a run of TROLL include (i) climate forcing data for the simulated location,

(ii) species-specific parameters of plant traits for the simulated forest, and (iii) species-independent parameters. The source code of TROLL (v2.5) is written in C++ and is available at https://github.com/troll-code/troll. On a computing cluster, each simulation of 200 × 200 m and 500 years uses around 15 min of CPU time.

2.2 Global climate forcing

The TROLL model requires the following climate forcing variables: monthly mean values of daytime and nighttime mean temperature, cumulated rainfall, mean wind speed, and daytime mean irradiance, daytime mean vapor pressure deficit (VPD), and average normalized daily variation of temperature, irradiance and VPD.

We used the CRU-NCEP reanalysis as a standardized climate forcing (version 8; version 7 archived at https://rda.ucar.edu/datasets/ds314.3/) (Viovy, 2018). The CRU-NCEP data set is a global gridded (0.5° × 0.5°) sub-daily (6-hourly) climate product spanning the 1901-2016 period. It provides seven climatic variables: temperature, precipitation, wind, downward longwave and shortwave radiations, air specific humidity, and atmospheric pressure, resulting from the combination of observation-based CRU TS 3.2 data (Harris et al., 2014) and model-based NCEP-NCAR data (Kalnay et al., 1996). We constructed reference monthly mean conditions based on the time range 1980-2016, a period for which the most observations are available, in order to ensure higher accuracy (Kistler et al., 2001), and calculated and extracted climatic variables necessary for TROLL input (Appendix A).

2.3 Study site and species parameterization

We parameterized the TROLL model for Nouragues, French Guiana, South America, and Fushan, Taiwan, Southeast Asia. Aside from the difference in climatic patterns, there is no floristic overlap between Nouragues and Fushan, and tree trait distribution at the two sites differ widely: for example, there is no overlap in the interquartile range of leaf mass per area (LMA; g.m^{-2}) values (41.62 - 73.86 at Fushan, and 82.71 - 111.45 at Nouragues) and of wood density (g.cm^{-3}) values (0.464 - 0.524 at Fushan, and 0.600 - 0.727 at Nouragues).

The Nouragues Ecological Research Station includes a 12-hectare (400 m × 300 m) plot in a moist lowland tropical forest, part of the Amazonian biome. The Nouragues site experiences two months of dry season per year, with mean annual precipitation around 3000 mm, mean annual temperature around 26°C, and a mean relative humidity around 99% (Bongers et al., 2001). Since plot establishment in 1994, censuses were completed regularly (2001, 2007, 2012, 2017). All self-standing stems DBH ≥ 10 cm were identified, measured, tagged and mapped. The plot has 622 tree species (Chave et al., 2008; Maréchaux and Chave, 2017).

The Fushan Forest Dynamics Plot (FDP) is a 25-hectare (500 m × 500 m) plot in a moist broadleaf subtropical forest in the northeast of Taiwan (Su et al., 2007), and is a part of ForestGEO (Forest Global Earth Observatory; Anderson-Teixeira et al., 2015; Condit, 1998). The Fushan site is under influence of northeasterly monsoon in winter, and frequent typhoon visits in summer and autumn, with mean annual precipitation around 4200 mm, mean annual temperature around 18°C, and a mean relative humidity around 95%. Plot elevation ranges from 600 m to 733 m (Su et al., 2007). Since plot establishment in 2004, censuses were completed every five years, where all self-standing stems with a DBH ≥ 1 cm were identified, measured, tagged and mapped, with a total of 110 recorded tree species in the plot (Su et al., 2007).

Species-specific parameters of TROLL include leaf mass per area (LMA; $g.m^{-2}$), nitrogen and phosphorus content per mass (N_{mass}, P_{mass} $g.g^{-1}$), wood density ($g.cm^{-3}$), maximum DBH (cm), DBH-height allometric parameters, and regional relative abundance. We implemented all 622 species in the model for the Nouragues site: a complete set of measured trait values were available for 163 species, and for the other species, a combination of species-specific values and genus means or abundance-weighted community means were assigned (Maréchaux and Chave, 2017). For the Fushan site, we implemented 94 species for which a complete set of measured trait values were available: this represents ca. 90% of the trees. The methodology of data collection is detailed in Appendix B.

Climatic data were extracted from the CRU-NCEP dataset at both sites. We also used local climate data, in order to force the model simulations. At Nouragues, semi-hourly meteorological data are available from 2013 to 2019, recorded 400 m away from the plot (4° 05' N, 52° 41' W). At Fushan, daily meteorological data are available from 1991 to 2012, with hourly data from 2013 to 2016, recorded at a meteorological station 3 km east of the forest plot (24° 45′ N, 121° 35′ E). A comparison of the local versus gridded climatic conditions is provided in Appendix C.

For all simulations, we simulated forest regeneration from bare soil for a reference plot area of 4 hectares (200 m × 200 m) for a duration of 500 years (6000 monthly timesteps): based on trial simulation, after 500 years, the forest has reached a steady state.

2.4 Global parameter calibration

In addition to species-specific parameters, TROLL includes a set of 41 species-independent parameters (or 'global' parameters). The majority of these parameters can be measured empirically: initialization (plot size, initial size and leaf densities of trees etc.) and trait variability (intraspecific variation and covariance). Other parameters could vary across sites and they are the primary target of this study.

We first performed a preliminary sensitivity analysis on five parameters tested in a previous study (Maréchaux and Chave, 2017), which revealed that the model had a low sensitivity to the light extinction coefficient (*k)*, and to carbon allocation fractions: f_{wood} and f_{canopy}. We also found that stem density was not adequately estimated at Fushan (Appendix D): we hypothesized that asymmetric light competition and tree mortality may be factors shaping stem density. Thus, we focused on the calibration of five parameters (φ, vC, CR_a, CR_b, m; Table 1) for which it is difficult to obtain precise field estimates. We examined model responses by varying these parameters across a range of values, while using fixed values taken from literature for all other parameters, including k, f_{wood} and f_{canopy}.

For φ, vC and m, we generated uniform prior distributions, bounded within the reported value range. CR_a and CR_b, the slope and intercept of the log-transformed crown radius to DBH relationship are strongly correlated, so we generated correlated standard normal distributions using the Cholesky decomposition assuming a Pearson's r of 0.8, then transformed them to Beta prior distributions (of Beta(2, 2)), bounded within the empirically observed value ranges.

We performed 500 calibration runs for both study sites. For each simulation, three parameters (φ, vC and m) were randomly drawn from the uniform prior distribution, and the two crown allometry parameters (CR_a and CR_b) were drawn as a pair from the correlated Beta prior distributions. Goodness of fit was assessed using four summary metrics: stem density (DBH $\geq$ 10 cm; N_{10}, trees ha^{-1}), large stem density (DBH $\geq$ 30 cm; N_{30}, trees ha^{-1}), aboveground biomass (AGB, Mg ha^{-1}), and gross primary productivity (GPP, MgC ha^{-1} yr^{-1}). These metrics summarize both forest structure and functioning and overall constrain the model well. Empirical values for these metrics were obtained from census data for N_{10}, N_{30} and AGB, and from a global gridded database for GPP (Madani and Parazoo, 2020).

For each summary metric and each simulation, we calculated the steady-state value (defined as the mean over the last 100 years of simulation), and qualitatively described trends of model outcome and model sensitivity to each parameter using scatter plots of parameters against output metrics (Appendix E). Model goodness-of-fit was derived from individual summary statistics using an Euclidean distance between the simulated metrics and empirical values (centered and scaled), and we reported median and interquartile range of parameter values of the simulations with the 10% best overall fit (i.e., 50 best simulations out of 500).

We quantified parameter "informativeness", i.e. the degree to which the dispersion of the posterior parameter distribution is reduced compared to the prior distribution, using the ratio between the interquartile range (IQR) of the best-fit simulations to that of all simulations: a smaller ratio indicates higher parameter informativeness. Finally, we reported the temporal trends of the four summary metrics, and discussed their fit with field observation values.

2.5 Forest response to climatic conditions: a virtual experiment

To study the dependence of forest structure and dynamics on temperature, irradiance and VPD, we performed the following simulated experiment. In the CRU-NCEP dataset, we selected a subset of points corresponding to lowland light-limited rain forest within the 35°N – 35°S latitude range, based on elevation (< 1000 m), climate (annual precipitation > 2000 mm yr^{-1}; Guan et al., 2015; Wagner et al., 2016), and land cover (ESA 'forest' CCI Land Cover classes: 50, 60, 70, 80, and 90). At both study sites, we then performed 500 simulations, each time using the three climatic variables at a randomly sampled point within the selected subset, and using "optimal parameter values", the general parameter values of the one simulation that provided the best overall fit during calibration with the initial climatic condition (Table 2). The aim of this experiment is to explore the response of a forest stand as its climate forcing changes, with a range and correlation structure between the climatic variables that are realistic for tropical forests, and to examine if this climate effect is consistent between sites.

To select the reference pixels, we used precipitation data from CRU-NCEP, the C3S Global Land Cover product for 2018 (accessible at https://maps.elie.ucl.ac.be/CCI/viewer/download.php; ESA, 2017), and elevation data from the SRTM product (accessible at http://www.earthenv.org/topography) (Amatulli et al., 2018). We used the *gdal_translate* utility to rescale the Land Cover data (300 m × 300 m) and elevation data (1 km × 1 km) to match the spatial scale of CRU-NCEP (0.5° × 0.5°). This resulted in a set of 3753 "reference climate" pixels, of which we randomly sampled 500, using the corresponding climatic variables to force simulations for both Fushan and Nouragues.

To evaluate model sensitivity, we used the same four summary metrics (N_{10}, N_{30}, AGB, GPP). For each metric, we calculated the steady-state value of each simulation (mean value of the last 100 simulated years), and described the trends of model outcome and model sensitivity to each variable using scatter plots of climatic variables against output metrics. In order to quantify the degree of influence of each climatic variable, we fitted linear models with climatic variables as independent terms and the summary metrics as dependent terms, and reported semi-partial coefficients as effect size. Assumptions for linear models were tested and confirmed; two sample points with temperature lower than 15°C were identified as high-leverage points, but their inclusion did not significantly deviate the statistical estimates (Appendix F).

2.6 Data analysis

Data processing, statistical analysis and visualization were performed in R 3.3.0 (R Core Team, 2019). Apart from those already mentioned elsewhere, R packages *ggplot2*, *ggpubr*, *ncdf4*, *raster*, *data.table*, *geosphere*, *sp*, *tidyr*, *extRemes*, and *BIOMASS* were used for this study (Dowle and Srinivasan, 2020; Gilleland and Katz, 2016; Hijmans, 2020, 2019; Kassambara, 2020; Pierce, 2019; Rejou-Mechain et al., 2017; Venables and Ripley, 2002; Wickham, 2020, 2016).

3. Results

Model outcomes were highly sensitive to φ, CR_a and m, and to a lesser extent to CR_b. Higher quantum yield (φ) led to higher large-stem density and AGB and a sharp increase in productivity. Higher overall crown size (larger CR_a values) led to lower stem density and AGB, and a slight increase in productivity; its relationship with large-stem density and AGB was non-linear at Fushan. Higher mortality rates (m) led to reduced large-stem density and AGB (Figure E1 & E2). The parameter values corresponding to the simulation maximizing the goodness of fit were similar between the two sites for φ and CR_b, but differed markedly for *vC*, CR_a and *m* (Table 2).

We used the IQR ratio as measure of parameter informativeness: lower IQR ratio signifies higher informativeness. The most informative parameter was found to be CR_a, informative at both sites (0.55 at Fushan and 0.38 at Nouragues). φ was informative at Nouragues (0.38) but less so at Fushan (0.78), and *m* was informative at Fushan (0.33) but less so at Nouragues (0.75). CR_b and *vC* were only moderately informative (values > 0.6 at both sites) (Figure 1).

Temporal change of all four summary statistics (N_{10}, N_{30}, AGB and GPP) were qualitatively similar at both sites, showing sigmoidal increase for stem densities (N_{10} and N_{30}). We observed , a gradual increase of AGB and rapid increase and stabilization of GPP at both sites, and an initial overshoot of N_{10} at Nouragues but not at Fushan (Table 3, Figure 2). At Nouragues, all steady-state estimated metric values showed a good fit to field values; at Fushan, N_{10} was underestimated (ca. 14%), GPP was overestimated (ca. 9%,), and N_{30} and AGB showed reasonably good fit to field values. Both climate forcings yielded similar model outputs, matching well field observations: N_{10} values were similar, N_{30} and AGB values were slightly lower when using ground-based climate forcing at Fushan, and GPP values were markedly lower when using ground-based climate forcing at both sites (Figure 2).

Median climate values across sampled pixels were: temperature = 26.25°C, irradiance = 207.6 $W.m^{-2}$, VPD = 0.644 kPa. Temperature, irradiance and VPD all had significant effects on simulated forest structure and functioning, although effect sizes varied. Temperature effect on N_{10} was strongly negative at Fushan but non-significant at Nouragues; it had strong negative effects on N_{30} and AGB but a weak positive effect on GPP at both sites. Irradiance had a positive effect on all four metrics at both sites, and are especially strong for GPP. VPD had weakly negative effects on GPP at both sites; its effects on the other three metrics were weakly positive at Fushan and non-significant at Nouragues. Overall, effect sizes were weaker at Nouragues than at Fushan (except for irradiance effects on N_{30} and AGB) (Figure 3, Table 4).

4. Discussion

In this study, we tested the transferability of a forest IBM, and demonstrated that the model predicts forest structure and functioning with reasonable accuracy at two species-rich forest sites in different bioregions. Parameters controlling photosynthetic efficiency, crown allometry and background mortality were found to be key for model calibration. We showed that calibration could help identify influential processes in trait-based forest IBMs and suggests that there is potential of IBM upscaling with improved representation of influential processes and parameter estimation.

4.1 Transferability of an individual-based model

The TROLL model was designed to incorporate a detailed representation of forest diversity while remaining relatively easy to parameterize at a forest site, by prescribing each species using a set of commonly measured traits (Maréchaux and Chave, 2017). This approach alleviates the calibration burden of model transfer (DeAngelis and Grimm, 2014) and facilitates the implementation of large-scale testing of individual-based models. However, not all parameters used in the model are directly observable or easily measurable in the field: some are integrators of multiple processes not explicitly represented within the model. So the issue of model transferability still stands, and we here ask whether a calibrated parameter set for one site performs well elsewhere.

We estimated model parameters through model inversion, comparing model outputs against field observations (Hartig et al., 2012). This approach has been used for several DGVM parameterizations, usually by calibrating against eddy-covariance data (Ichii et al., 2010; Pappas et al., 2013; Restrepo-Coupe et al., 2017). Here, goodness-of-fit depends on four summary statistics of forest structure (stem density) and functioning (biomass and productivity) that are usually available in field inventory data or global gridded data. In the future, the approach could be improved by using the whole height or diameter distribution of the simulated forest, or by adopting a likelihood-based approach (Hartig et al., 2014, 2012).

We calibrated the model at two contrasted tropical forest sites. In spite of their marked differences in climatic conditions, species composition and functional diversity, the simulated forests matched field observations by calibrating a limited subset of parameters. This supports the view that forest models with trait-based parameterization are capable of capturing site-specific characteristics that underpin community dynamics and structure at a given forest site. We speculate that the use of trait-based species parameterization contributes to the reduced need for refitting (i.e., higher model genericity) (Christoffersen et al., 2016; Fisher et al., 2018; Fyllas et al., 2014; Pappas et al., 2016). Parameters that do differ across sites point to potential improvements in the model, a discussion we now turn to.

4.2 Parameter calibration

We performed calibrations for three parameters that influence predicted forest structure and functioning: photosynthetic efficiency (φ), crown allometry (CR_a), and tree mortality (m). As φ represents the actual quantum yield of photosynthesis (the amount of fixed carbon per light flux absorbed by the chloroplasts), higher φ value results in higher carbon assimilation (when light is limiting) and higher GPP. This parameter only leads to a moderate increase in large stem density (N_{30}) and AGB, and an even smaller effect on overall stem density (N_{10}), indicating that forest demography and biomass accumulation are not solely conditioned by productivity, but also hinge on respiration, carbon allocation, and carbon residence time (Álvarez-Dávila et al., 2017; Johnson et al., 2016; Malhi et al., 2015).

Model calibration was not sensitive to TROLL's species-independent carbon allocation parameters (appendix D), but it should be pointed out that carbon allocation does vary across and even within species (Malhi et al., 2015; Negrón-Juárez et al., 2015). Therefore, including a more mechanistic or trait-mediated representation of carbon allocation may unveil more heterogeneity in forest dynamics, and is an important objective in future model development (Merganičová et al., 2019; Negrón-Juárez et al., 2015; Schippers et al., 2015; Trugman et al., 2019).

In TROLL, crown allometry directly controls light use efficiency and tree competition. Higher CR_a values mean that trees have wider crowns at a given diameter, and achieve higher carbon assimilation rates due to increased light interception, leading to the observed pattern of increase in GPP with increased CR_a. Wider crowns also create more intense shading for smaller trees in the understory and cause higher tree turnover and mortality, leading to the observed pattern of decreasing stem density and AGB. Stand structure also strongly depends on the level of prescribed inter- and intraspecific variability of crown allometry, which determine how complementarity in crown architecture could increase light use efficiency and promote coexistence (Pretzsch, 2019; Vieilledent et al., 2010).

Mortality is an important calibration parameter in TROLL. Tree mortality is a complex process, and in current IBMs, it is often modeled empirically, and thus remains one of the main sources of model uncertainty (Bugmann et al., 2019). In the

FORMIND model, the mortality rate is empirically correlated with environmental variables such as precipitation and soil property, which vary across space (Rödig et al., 2018, 2017). Such simplifications limit our ability to explore how different causes of tree mortality impact forest structure (McDowell et al., 2018).

Natural disturbance events such as fire, drought or wind are responsible for a significant proportion of tree mortality (Fischer et al., 2018; McDowell et al., 2018; Peterson et al., 2019), and they impact forest structure and functioning (Ibanez et al., 2019; Magnabosco Marra et al., 2018; Pugh et al., 2019). The two forest sites selected for this study depend on different wind disturbance regimes: notably, Fushan is influenced by frequent tropical cyclones (Dowdy et al., 2012; Lin et al., 2011), while Nouragues is not exposed to cyclones. At Nouragues, TROLL simulates an overshoot of stem density during early succession, indicating self-thinning, but not at Fushan. One hypothesis for this pattern is that cyclones shape a more open canopy at Fushan, resulting in a less intense self-thinning. This may also explain why the optimal value for the mortality rate (*m*) is lower at Fushan than at Nouragues. It would be important to devise more mechanistic representations of disturbance events in TROLL.

4.3 Upscaling of individual-based models

Various efforts have been made to upscale IBMs to the regional or global scale. Individual-based approaches have been coupled to or developed within DGVMs (Fisher et al., 2018; Sakschewski et al., 2015; Sato et al., 2007) to represent cohort processes. Ma et al. (2017) prescribed environmental data for simulations of the FORCCHIN IBM model at several flux tower sites, and validated the simulated carbon flux against flux tower data. Rödig et al. (2018, 2017a) performed regionalization for the FORMIND model by calibrating the mortality parameter at a number of sites and correlating it with environmental variables (precipitation and soil properties), and performing simulations at sites over the entire Amazon using mortality parameters predicted from the environmental variables. Simulated temporal dynamics of canopy height were then compared with remote sensing data to determine the succession status of each site, which was then used to generate Amazon-wide estimation of other forest attributes such as biomass and productivity.

Yet, these studies assigned trees to a small number of plant functional types that relied on empirical parameterization. Our study, although smaller in scope, is a proof of concept demonstrating that trait-based IBM upscaling is achievable with minimal calibration and is therefore realistic in the tropics, provided that trait measurements exist and tree floristic composition is available at the focal site. Moreover, since model output contains detailed information about forest composition, TROLL could also help answer how plant diversity responds to environmental changes.

With every forest model, assumptions are made about which parameters are species-dependent and which are not. The model described here, TROLL, is designed with the aim to contain as much species-specific information that is currently available. For an individual-based model, this choice does not necessarily incur higher computational burden than the plant functional type approach, since in both cases every individual tree is simulated. However, supplying models with species-specific information requires considerably more parameterization effort. With the ongoing collection effort of plant traits in permanent plots around the world, the assembly of global trait databases (Anderson-Teixeira et al., 2015; Chave et al., 2009; Kattge et al., 2020) and development of techniques to measure new plant traits, we expect that it will be easier to generalize this approach to many sites. Here we show that of the species-independent parameters, only a few require site-specific calibration for realistic model output to be achieved, and identifying these parameters helps identifying priorities for future theoretical and modeling development, as well as for field measurements (Medlyn et al., 2016).

4.4 Climate impact on forests using IBMs

Another important part of assessing transferability of forest IBMs consists in evaluating how the model responds to environmental forcing, an important step in understanding how forests respond to climate change (Shugart et al., 2018). We here examined the effect of climate forcing without the need of re-calibration (Fauset et al., 2019; Shugart et al., 2018). Many forest IBMs prescribe climatic conditions based on locally measured data (Ma et al., 2017; Shuman et al., 2015), yet it is important to provide a consistent climate forcing condition even at places where local measurements do not exist, and to ensure comparability among sites. The integration of the gridded CRU-NCEP climate dataset as model input fulfills this condition, and thus further simplifies large-scale implementation.

TROLL simulations at the Fushan and Nouragues sites with different climatic conditions demonstrate that the model reproduces a general pattern of climatic response that remain nearly identical upon model transfer, with only quantitative differences between sites. The simulated positive relationship of GPP with temperature and irradiance and the negative relationship with VPD are in agreement with expectations (Malhi et al., 2015; Reyer, 2015).Under the current model version, VPD constrains leaf stomatal conductance in the photosynthesis process, and we found a weak effect of VPD. As water availability is one of the key climatic factors that shape forest dynamics and functioning (Álvarez-Dávila et al., 2017; Feng et al., 2018; Galbraith et al., 2010; Poorter et al., 2017), further investigation of forest response to drought and soil water stress is necessary, and will be the focus of future model development.

At both sites, we observed a decoupling between the response of productivity and that of stem density and AGB. With increasing temperature, GPP increased while large tree density and AGB decreased. These observations are consistent with empirical studies that showed that productivity is a poor predictor of biomass in old-growth tropical forests (Johnson et al., 2016; Malhi et al., 2015). Biomass accumulation is controlled by numerous processes other than carbon assimilation, including mortality, functional composition, and size structure (Allen et al., 2010; Bugmann et al., 2019; Johnson et al., 2016).

The Fushan site responded more to variation in climatic conditions than Nouragues. One interpretation of this finding is that the native bioclimatic conditions of Nouragues were closer to the average condition of reference climatic conditions, whereas Fushan has a fringe climatic condition (subtropical). Consequently, constraining the Fushan forest to average tropical forest climatic conditions had more effect than on the Nouragues forest.

4.5 Conclusion and perspectives

We have demonstrated that a detailed exploration of the calibration and transferability of trait-based forest IBMs offers an opportunity to assess the genericity of model assumptions. Even though our results are based on model simulations, they do pave the way towards a much more systematic exploration of model behavior across a wide range of sites that are representative of a variety of forest types.

We here identify two main priorities for future individual-based model development: 1) including more detailed and mechanistic representation of important physiological processes, such as disturbance-driven tree mortality (Seidl et al., 2014, 2011; Uriarte et al., 2009), and 2) improving constraints of key parameters with detailed and spatially distributed data, such as informing crown allometry with remote sensing data (Calders et al., 2018; Fischer et al., 2020; Shugart et al., 2015). With the help of improvements in these two directions, we argue that upscaling of individual-based vegetation models with detailed, trait-based species description need not be associated with high calibration burden, and that they have great potential for large-scale implementation.

Acknowledgements

Simulations were run on the OLYMPE cluster at CALMIP, Toulouse. We thank Dr. Shiang-Yue Lu and Hui-Hsueh Huang at TFRI (Taiwan Forestry Research Institute) for providing us with the local climate data at the meteorological station were provided by via communications with, whom we thank. This work was supported by the “Investissement d’Avenir” grants managed by the Agence Nationale de la Recherche (CEBA, ref. ANR-10-LABX-25-01; TULIP, ref. ANR-10-LABX-0041; ANAEE-France: ANR-11-INBS-0001).

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Figures

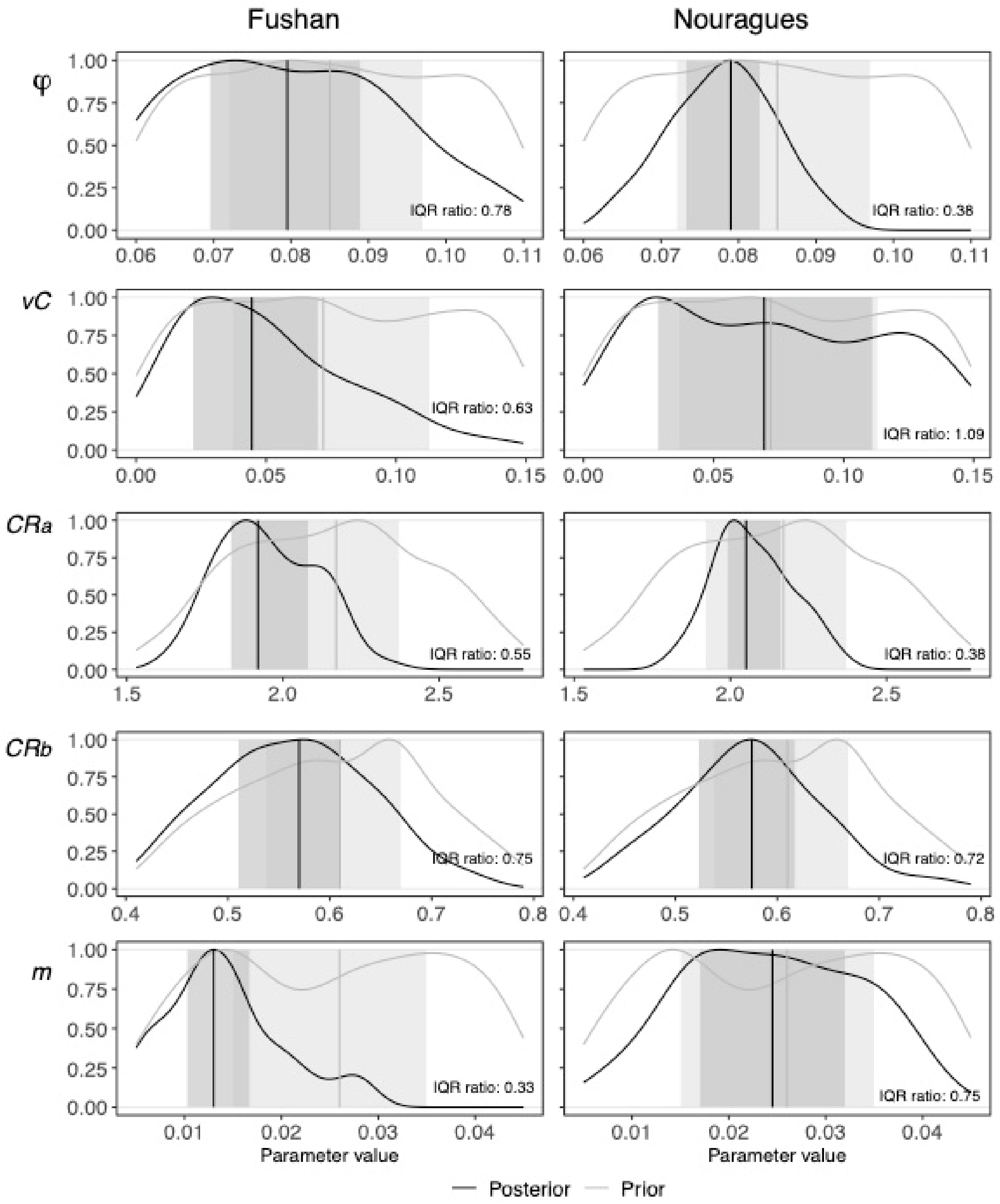


Figure 1. Prior (gray) and posterior (black) distributions for five parameters: φ (quantum yield), vC (treefall parameter), CR_a and CR_b (intercept and slope terms of the crown radius allometry), and m (background mortality). Results are reported for the Fushan site (Taiwan), and for the Nouragues site (French Guiana). Curves represent density functions, and vertical lines represent median value of the distributions. Shaded areas indicate interquartile range (IQR) of prior (light gray) and posterior (dark gray) distributions. IQR ratio is calculated as the posterior divided by prior IQR: lower IQR ratio is thus indicative of a higher parameter informativeness.

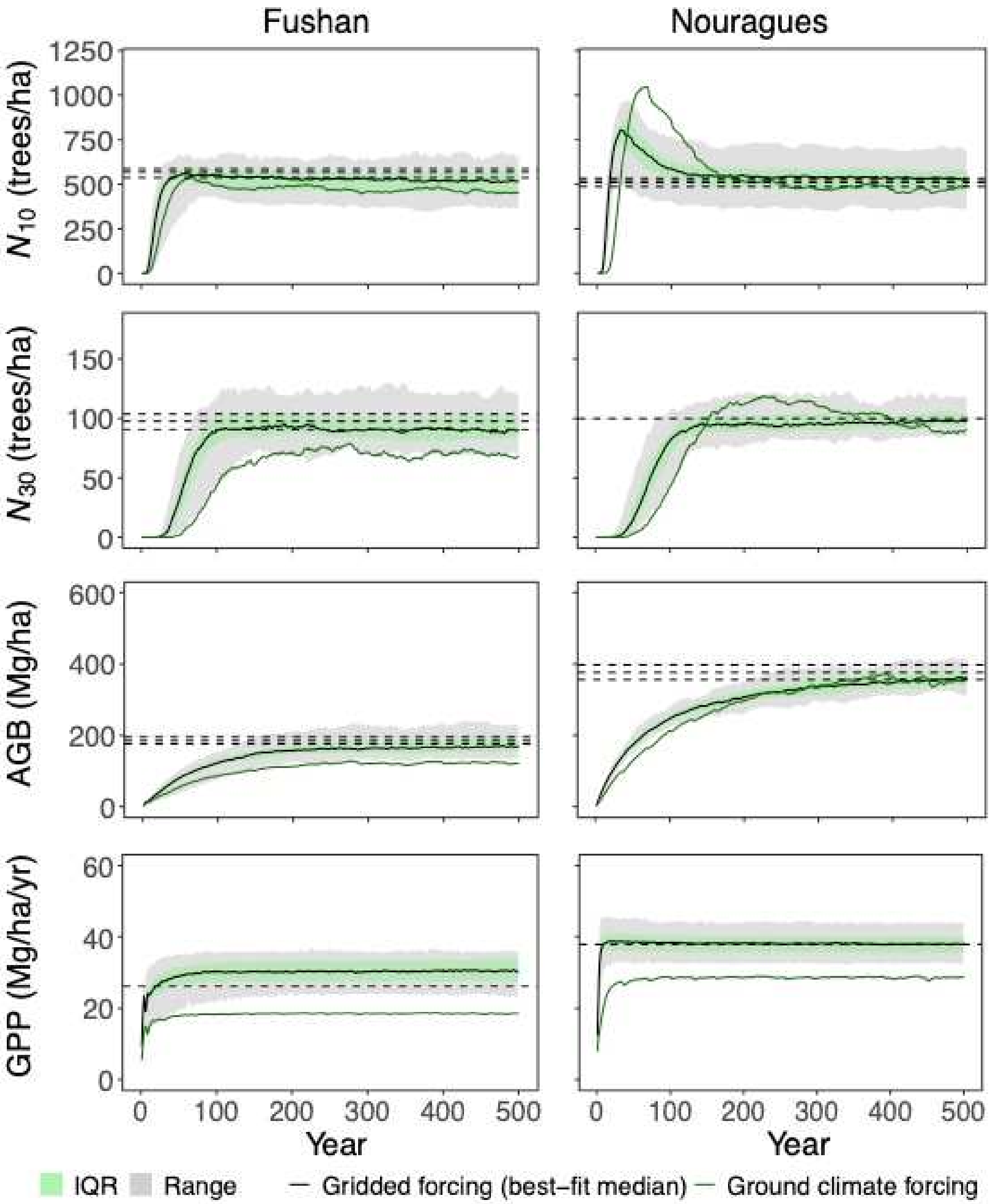


Figure 2. Successional dynamics of best-fit simulations at the Fushan and Nouragues sites, for four variables. Green shades represent the interquartile range, and gray shades represent the entire range of variation. Solid lines: median value of the best-fit simulations (black: gridded climate forcing; dark green: ground climate forcing); dashed lines: empirical values.

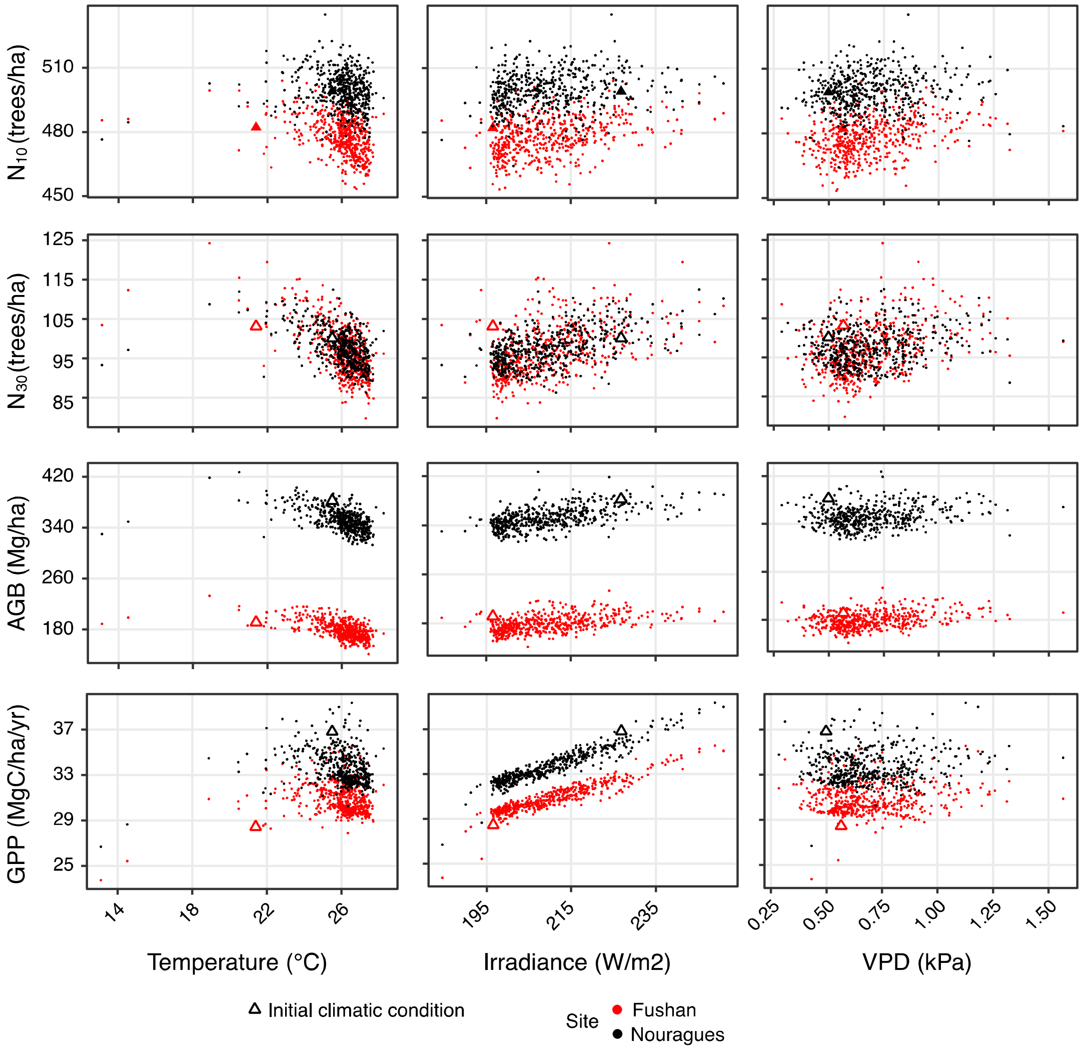


Figure 3. Effect of climatic conditions on forest structure and functioning at both sites (red: Fushan; black: Nouragues). Triangles indicate the simulations done under climatic condition of the original site.

Tables

	Description	Prior range
φ	quantum carbon yield per quantum photon	0.030-0.110 (Mercado *et al.* 2009)
vC	variability of the tree height-dependent stochastic treefall process	0.0-0.15
CR_a	intercept of the log-transformed CR-DBH allometry	1.5-2.8 (Fischer *et al.* 2020)
CR_b	slope of the log-transformed CR-DBH allometry	0.4-0.8 (Fischer *et al.* 2020)
m	maximal background mortality rate	0.005-0.045

Table 1. Parameters of the TROLL model calibrated at the two tropical forest sites.

Parameter	Fushan	Nouragues
φ	0.071 (0.070 – 0.089)	0.074 (0.073 – 0.082)
vC	0.099 (0.022 – 0.070)	0.031 (0.029 – 0.111)
CR_a	1.93 (1.833 – 2.080)	2.10 (1.990 – 2.163)
CR_b	0.51 (0.510 – 0.610)	0.57 (0.523 – 0.618)
m	0.006 (0.005 – 0.017)	0.023 (0.017 – 0.032)

Table 2. Optimal parameter values (parameter values of the simulation with best overall fit) at each site. Values in parentheses indicate the interquartile range of 50 best-fit simulations.

Metrics	Fushan	Nouragues
N_{10}	-14.4% (-18.1% – 0.8%)	-2.5% (-9.0% – 12.4%)
N_{30}	-5.9% (-14.9% – 5.3%)	0.1% (-8.4% – 4.2%)
AGB	-3.1% (-17.4% – 3.3%)	2.9% (-9.4% – 1.0%)
GPP	8.6% (5.6% – 28.5%)	-2.9% (-6.3% – 5.6%)

Table 3. Percentage difference between summary statistics of the optimal simulation (simulation with the best overall fit) and the mean empirical value. Values in parentheses indicate the interquartile range of percentage differences of the 50 best-fit simulations.

	Fushan				Nouragues			
	N_{10}	N_{30}	AGB	GPP	N_{10}	N_{30}	AGB	GPP
Temperature	**-0.341**	**-0.553**	**-0.489**	0.135	*-0.049*	**-0.385**	**-0.413**	0.032
Irradiance	0.251	0.296	**0.329**	**0.953**	0.142	**0.436**	**0.476**	**0.947**
VPD	0.228	0.230	0.183	-0.226	*0.061*	*0.039*	*0.027*	-0.202

Table 4. Effect size of each climatic variable on the output metrics at both sites, expressed in semi-partial correlation coefficients. Effect sizes with absolute values larger than 0.3 are indicated in bold. Italic indicates non-significant effects ($p > 0.05$).

Appendix A: generation of monthly mean climatic variables for TROLL input

Automated global reanalysis climate data calculation and extraction

The CRU-NCEP data are stored in NetCDF format, and the following variables are available: *Tair* for air temperature (K), *rain* for precipitation (mm), *WindN* and *WindE* for each of the two horizontal directional components of wind speed (m/s), SW*down* for incoming short-wave radiation exposure (J/m^2), *Qair* for air specific humidity, and *PSurf* for surface atmospheric pressure (Pa). We retrieved data for the period from 1980 to 2016, a period when many direct observations complemented model-based inferences in CRU-NCEP.

We processed the CRU-NCEP data across the entire land surface on Earth using the Climate Data Operators (cdo) tool (Schulzweida, 2019) and stored the results in NetCDF files, with a total of 74 files (2 files for each year). For each year, one file contains the monthly mean values of the following climatic variables: mean, maximum and minimum daily temperature (°C), mean and maximum daily irradiance (W/m^2), mean and maximum daily VPD (vapor pressure deficit, kPa), as well as monthly total precipitation (mm); another file contains the 6-hourly average wind speed (m/s), calculated as the quadratic average of the two wind speed components. Irradiance was calculated as the short-wave radiant exposure, divided by the time length of each measurement interval (6 hours, i.e. $6 \times 3600 = 21600$ seconds). VPD was calculated from temperature (T, °C), air specific humidity (R, unitless), and surface atmospheric pressure (P, kPa) with the following equations (Buck, 1981; Monteith and Unsworth, 2008):

$$VP_{sat} = 0.61121 \times e^{(18.678-\frac{T}{234.5})\times(\frac{T}{257.14+T})} \tag{A1}$$

$$VPD = VP_{sat} - \frac{R\times P}{0.622+0.378\times R} \tag{A2}$$

where VP_{sat} is the temperature-dependent saturated vapor pressure.

Subsequently, we used an R script to extract the monthly climatic variables from the files for a geographic coordinate, and generated a text file that is used as an input file for TROLL.

Appendix B: Data at Fushan FDP

At Fushan FDP, local meteorological data, daily from 1991 to 2012 and hourly from 2013 to 2016, was recorded at a meteorological station three kilometers east of Fushan FDP (24° 45′ N, 121° 35′ E). Temperature and humidity were measured by a Rotronic MP101A meteorological probe, precipitations by a tipping bucket rain gauge, irradiance by an E20 Silicon pyranometer (Homeray), and instantaneous wind speed by a Wind Monitor Model 05103 (Young).

In Fushan FDP, the sampling of functional traits was conducted in 2009, where 1 to 26 individuals per species were chosen randomly according to accessibility of tree canopy, and 1 to 3 intact and mature leaves or leaflets exposed to sunlight were collected for each individual. Collected leaves were sealed in Ziploc® bag with wet paper towels and kept in an insulated cooler box in order to prevent from water loss until transport back to the field station. There, the fresh weight of the leaves was measured to a precision of 0.1 mg, and they were scanned with a flatbed scanner within 12 hours. Leaf area (LA, cm^2) was quantified with the software ImageJ (Rasband 1997). The leaf samples were subsequently oven-dried at 80 °C for 72 - 96 hours, until constant dry weight. Leaf mass per area (LMA, g/m^2) were then calculated as dry weight divided by fresh leaf area (Pérez-Harguindeguy et al., 2013). Nitrogen and phosphorus content (N_{mass} and P_{mass}, mg/g) were determined by the microplate method (Huang et al., 2011; Iida et al., 2014).

Wood density (WD, g/cm^3) was measured following the ForestGEO wood density measurement protocol (Condit, 2008; Iida et al., 2014), by taking wood core samples of randomly chosen individuals outside the plot, measuring fresh volume by water displacement method and dry weight after oven-drying at 80 °C. Wood density was calculated as dry weight divided by fresh volume.

The allometric relationship between DBH and tree height (H) in the TROLL model was assumed to follow a Michaelis-Menten function with two parameters, asymptotic height (h_{max}) and the Michaelis constant (a_h), numerically equal to the diameter at which the tree height is half of h_{max}:

$$H = \frac{h_{max} \times DBH}{a_h + DBH} \tag{B1}$$

Although DBH values for all individuals were available, tree heights were only measured for 1 to 18 individuals for each species, depending on the accessibility of tree individuals. Due to the scarcity of available height data, a hierarchical Bayesian model was used to estimate model parameters: the model assumed that the species-specific Michaelis-Menten parameters $h_{max,\,i}$ and $a_{h,\,i}$ for species i are distributed normally around common hyperparameters h_{max} and a_h (Molto et al., 2014). Parameters are close to the hyperparameters when data points are scarce for a particular species, while the species parameters dominate when data points are numerous for the species. Calculations were carried out with the software STAN and the R package *RStan* (Stan Development Team, 2016a, 2016b).

Appendix C: comparisons of different climate forcing sources.

The comparison between three climatic variables (temperature, precipitation, irradiance) extracted from CRU-NCEP data and ground station data showed that apart from minor differences, the climatic variables were largely congruent between CRU-NCEP and ground measures for the two ground study sites, the main difference being that seasonal variability for irradiance and precipitation was noticeably larger in ground data than in CRU-NCEP data at Fushan (Figure C1-2).

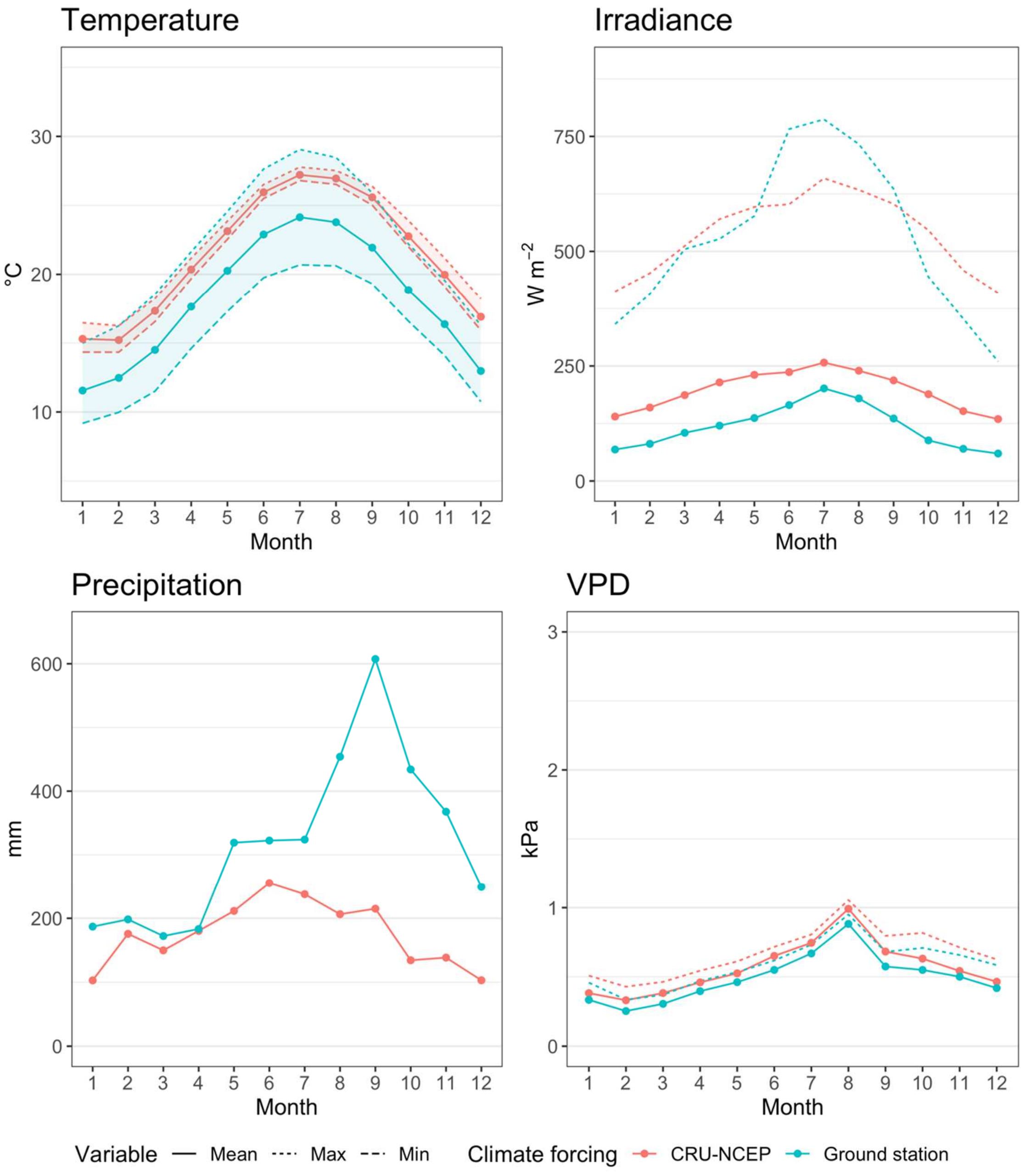


Figure C2. Comparison of climatic variables from CRU-NCEP gridded data or ground-based data at Nouragues.

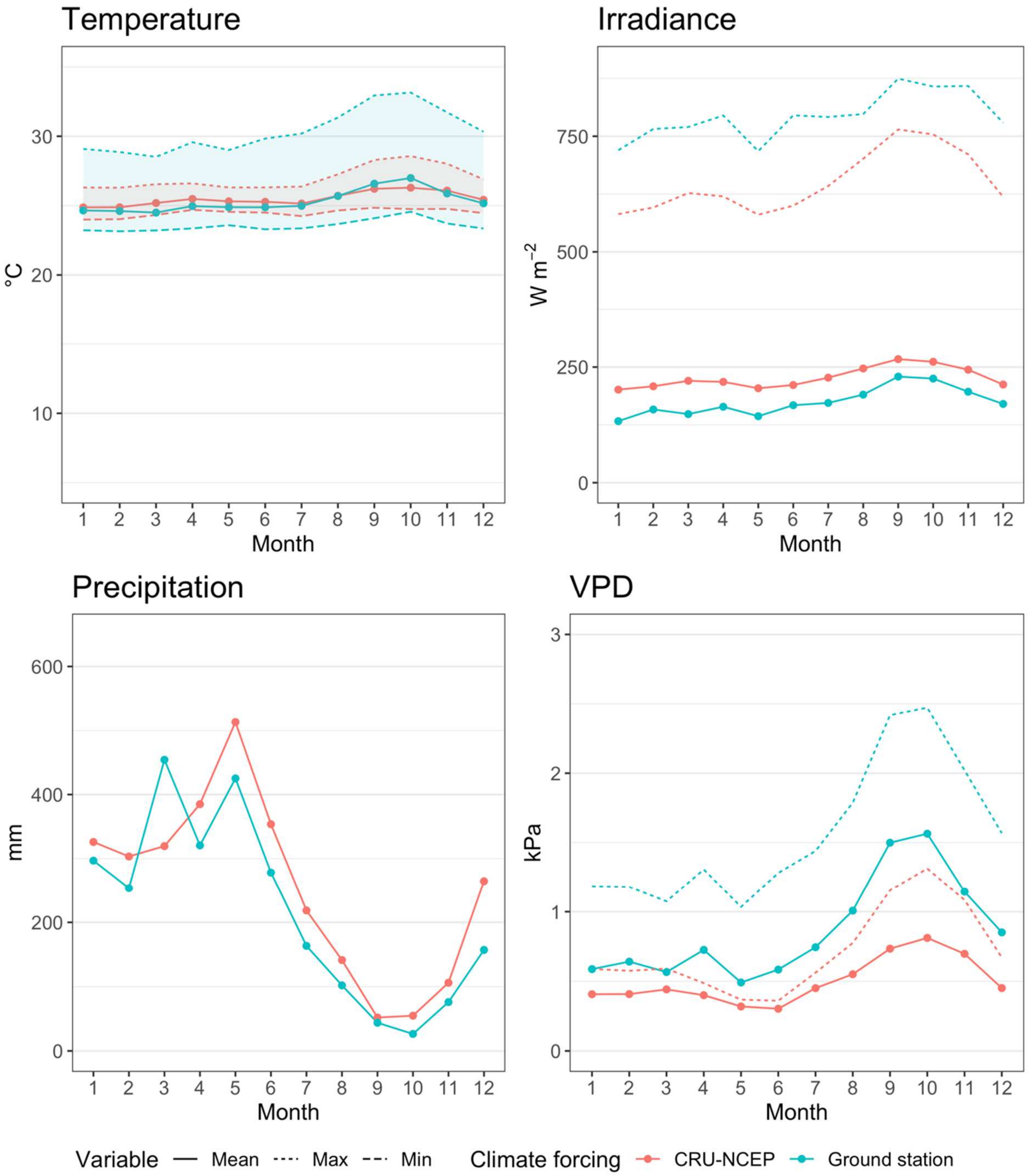


Figure C2. Comparison of climatic variables from CRU-NCEP gridded data or ground-based data at Nouragues.

Appendix D: preliminary parameter calibration

In the preliminary calibration tests, three other parameters were calibrated besides the parameters φ and *m*: *k*, the light extinction coefficient, describes the proportion of light extinction by each canopy layer; f_{wood} represents the fraction of assimilated carbon allocated to aboveground wood (branches and stem), and f_{canopy} represents the fraction allocated to canopy (twigs, leaves, and reproductive organs) (Table D1). We conducted the calibration tests following the same procedure as described in the main text, performing 500 simulations and selecting simulations with the 10% best overall fit (i.e., 50 simulations). The results indicated that model output was weakly sensitive to *k*; model sensitivity to f_{wood} and f_{canopy}, was non-negligible, but the overall model output did not deviate clearly from the observed value range no matter what their calibrated values were (Fig. D1 & D2). As a result, in all subsequent simulations we set a constant value for these three parameters. For *k*, we chose the lower bound value of 0.5 since reported values for forest ecosystems in Zhang *et al.* (2014) are primarily cluster around 0.5. For the allocation parameters, an intermediate value within the reported range was chosen ($f_{wood} = 0.35$, $f_{canopy} = 0.25$).

k	light extinction coefficient	0.50-0.95 (Cournac *et al.* 2002, Zhang *et al.* 2014)
φ	quantum carbon yield per quantum photon	0.030-0.110 (Mercado *et al.* 2009)
f_{wood}	fraction of NPP allocated to aboveground wood	0.20-0.45 (Aragão *et al.* 2009, Malhi *et al.* 2011)
f_{canopy}	fraction of NPP allocated to canopy	0.20-0.45 (Aragão *et al.* 2009, Malhi *et al.* 2011)
m	maximal background mortality rate	0.005-0.045

Table D1. Parameters of the TROLL model calibrated at the two tropical forest sites in preliminary tests.

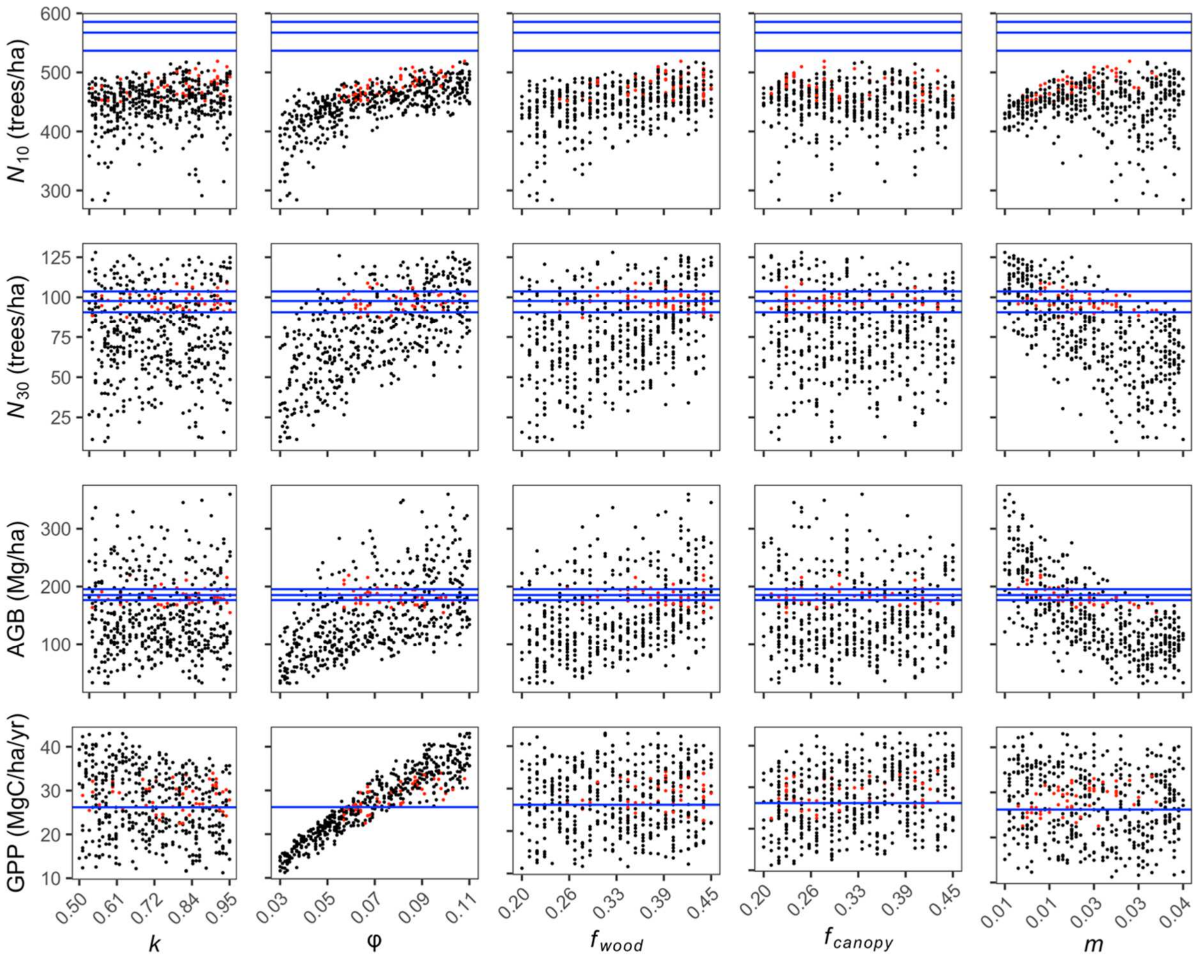


Figure D1. Calibration of TROLL general parameters for Fushan (k: light extinction coefficient; φ: quantum yield; f_{wood} and f_{canopy}: carbon allocation to different plant organs; m: background mortality). Horizontal blue lines are observed values from field censuses. Each point represents one simulation, and red points are best-fit simulations.

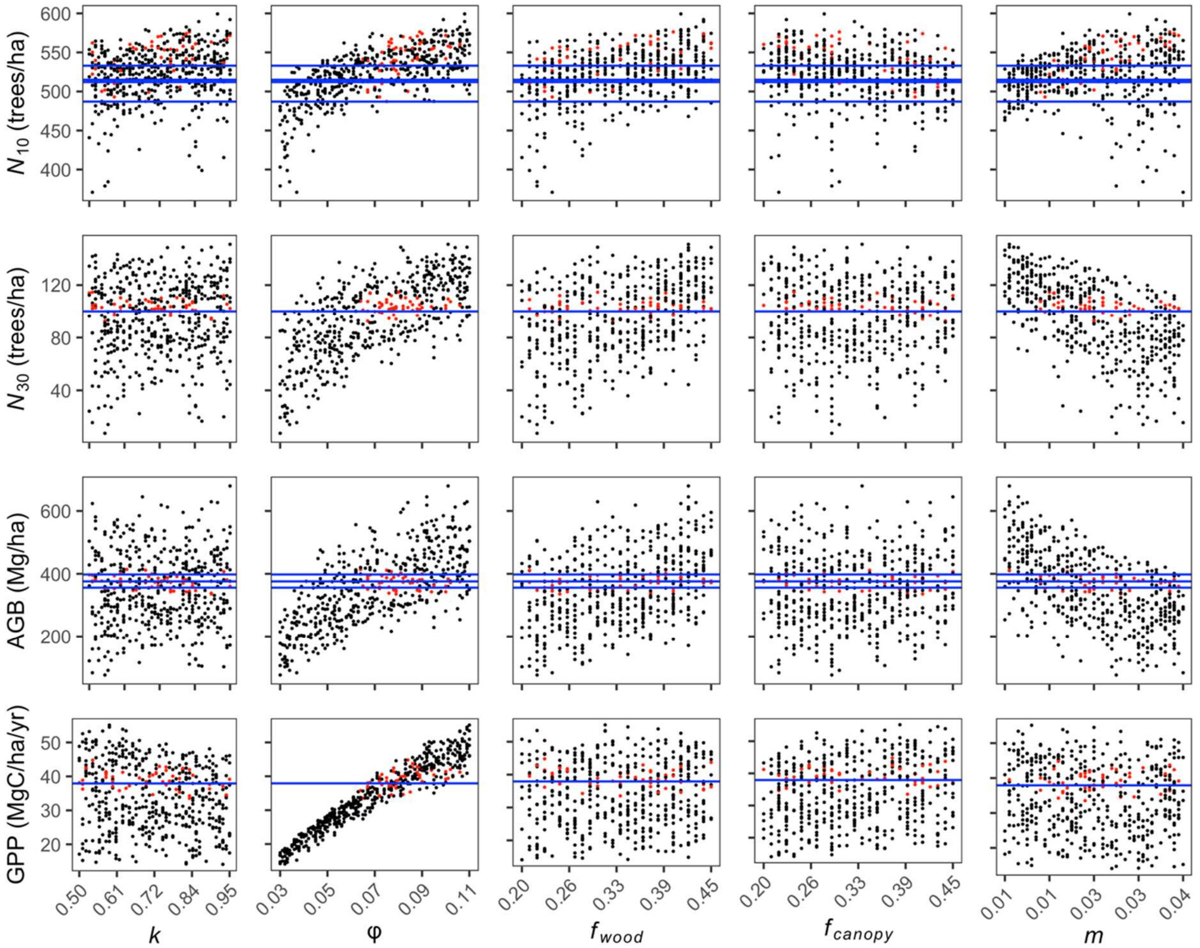


Figure D2. Calibration of TROLL general parameters for Nouragues (*k*: light extinction coefficient; φ: quantum yield; f_{wood} and f_{canopy}: carbon allocation to different plant organs; *m*: background mortality). Horizontal blue lines are observed values from field censuses. Each point represents one simulation, and red points are best-fit simulations.

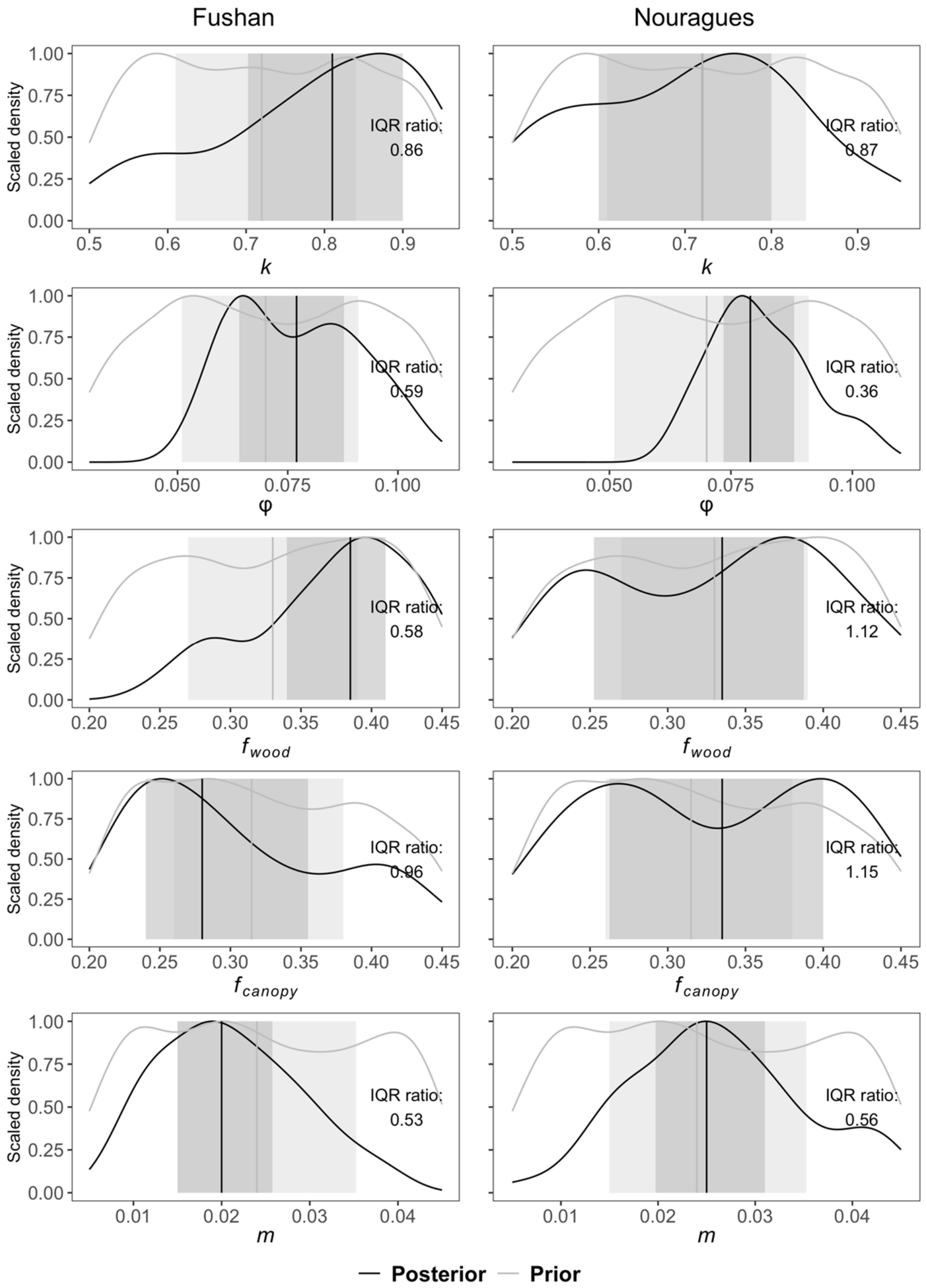


Figure D3. Prior (grey) and posterior (black) density distributions for parameter values (k: light extinction coefficient; φ: quantum yield; f_{wood} and f_{canopy}: carbon allocation to different plant organs; m: background mortality). Solid vertical lines indicate median and dashed vertical lines indicate interquartile range (IQR). Parameter informativeness is calculated as the ratio between IQR of best-fit simulations and that of all simulations.

Appendix E: parameter calibration

We conducted calibration tests on five parameters: φ (quantum carbon yield per quantum photon), *vC* (variability of the tree height-dependent stochastic treefall process) CR_a, CR_b (intercept and slope terms of the log-transformed CR-DBH allometry), and *m* (maximal background mortality rate), following the procedure as described in the main text, performing 500 simulations and selecting simulations with the 10% best overall fit (i.e., 50 simulations). The results showed that model output was strongly sensitive to φ, CR_a and *m*, and to a lesser exten to CR_b.

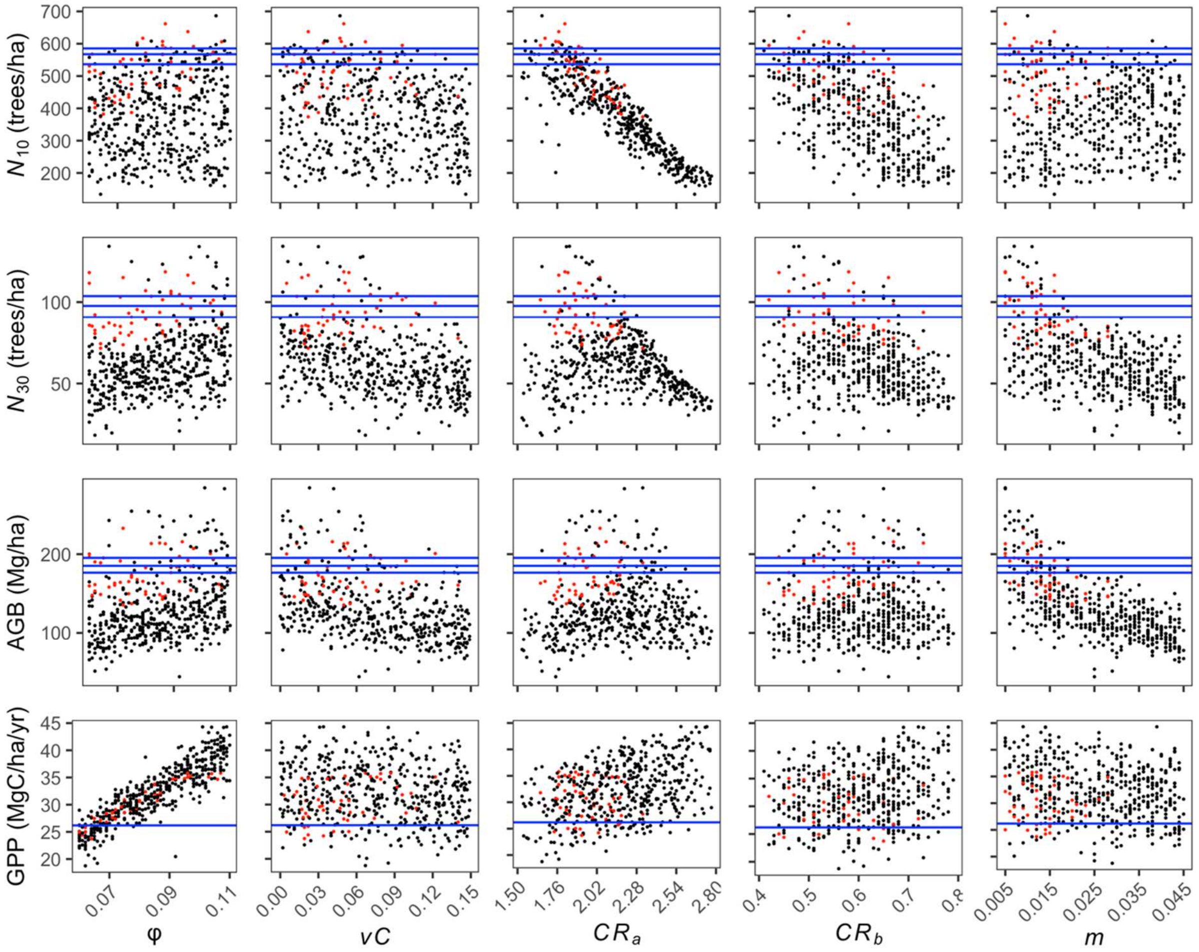


Figure E1. Calibration of TROLL general parameters (φ: quantum yield; *vC*: treefall parameter; CR_a and CR_b: intercept and slope terms of the crown radius allometry; *m*: background mortality) for Fushan. Horizontal blue lines are observed values from field censuses. Each point represents one simulation, and red points are the best-fit simulations (10% best simulations).

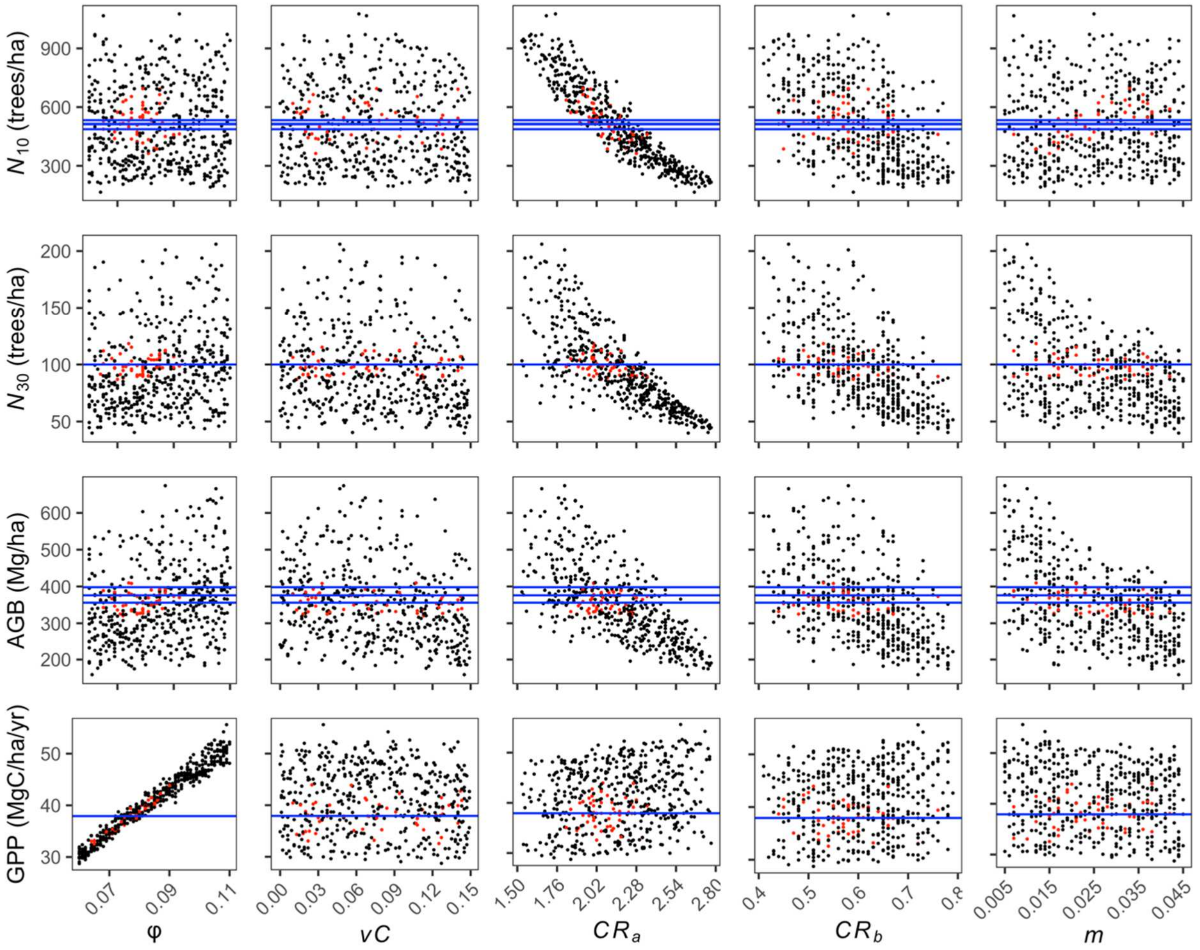
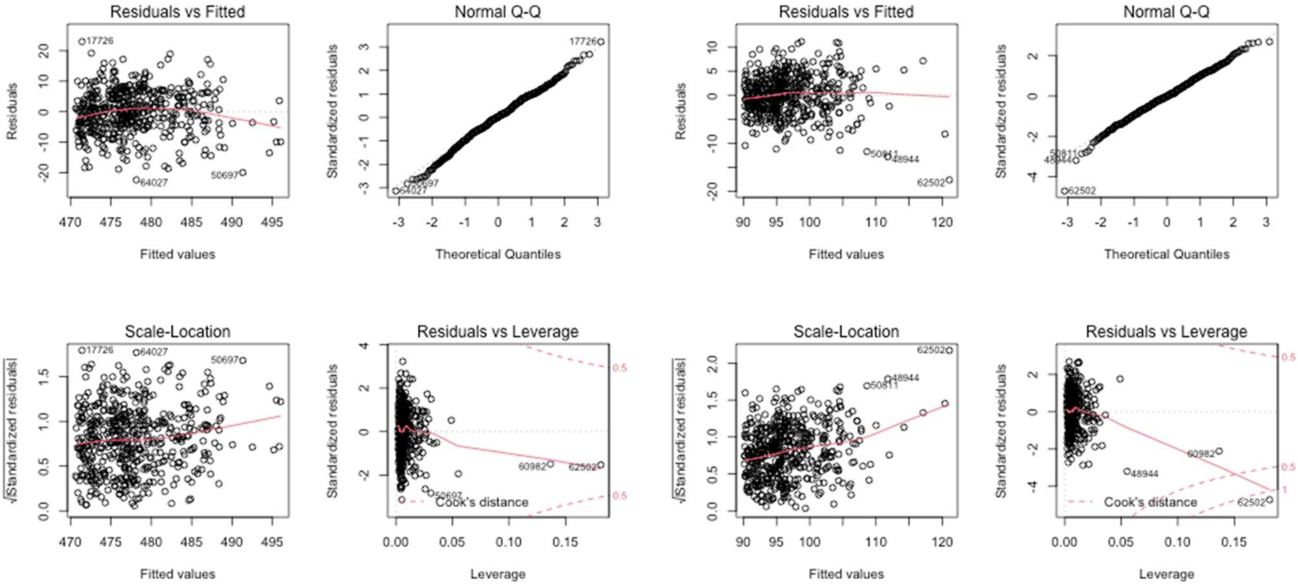
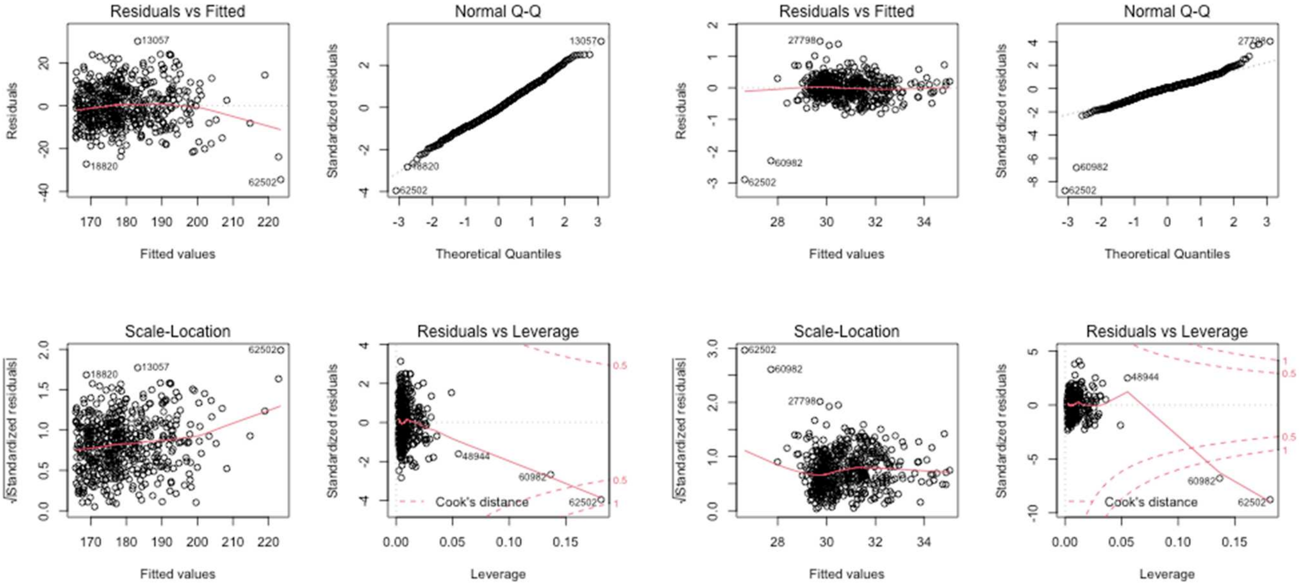


Figure E2. Calibration of TROLL general parameters (φ: quantum yield; *vC*: treefall parameter; CR_a and CR_b: intercept and slope terms of the crown radius allometry; *m*: background mortality) for Nouragues. Horizontal blue lines are observed values from field censuses. Each point represents one simulation, and red points are the best-fit simulations (10% best simulations).

Appendix F: verification of assumptions for linear model for the sampled climate experiment

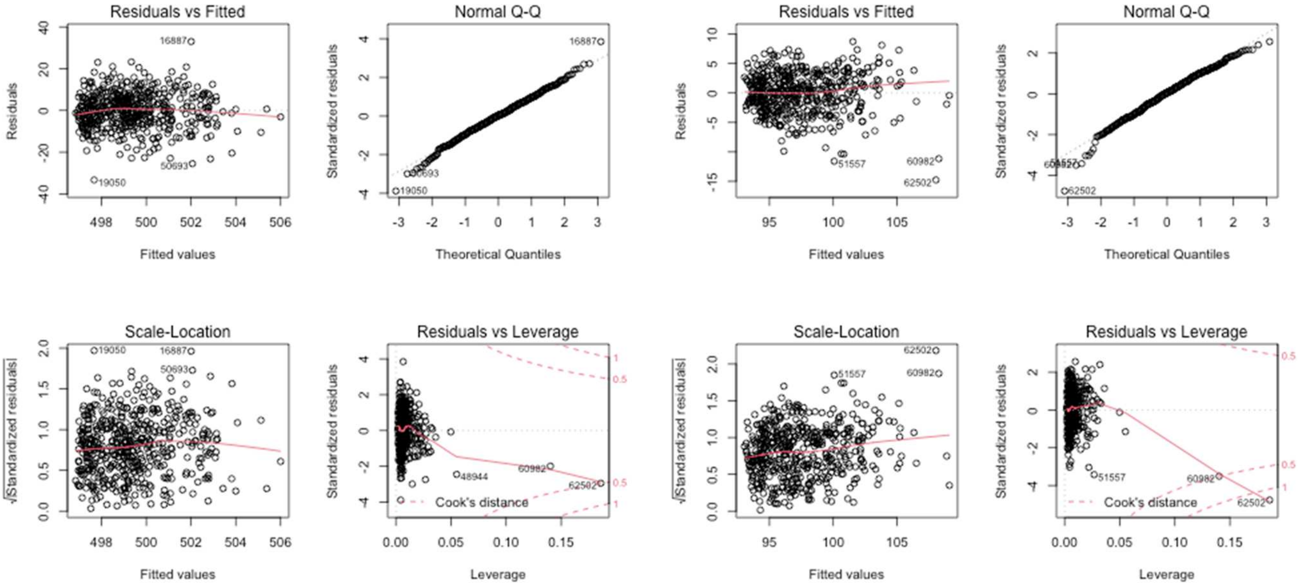


N10 N30

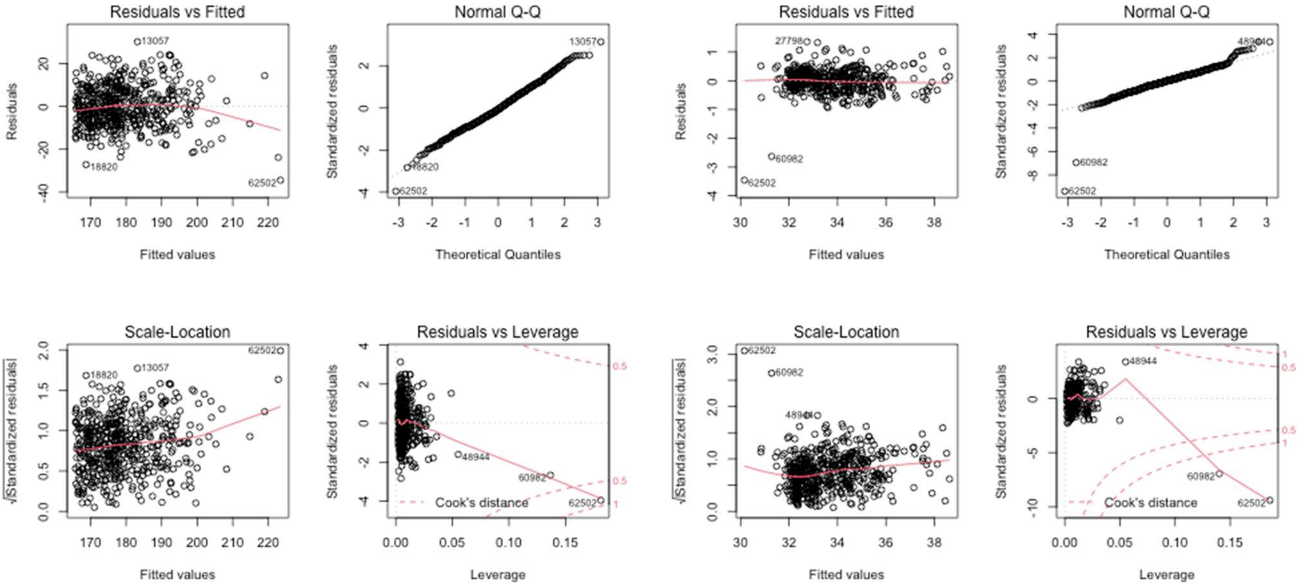


AGB GPP

Figure F1. Diagnostic plots of linear model for the sampled climate experiment at Fushan, with each summary statistics as dependent variables and the three climatic variables (temperature, irradiance and VPD) as independent variables. The four graphs represent respectively residual linearity, residual normality, residual homoscedasticity, and presence or absence of leverage points (influential points).

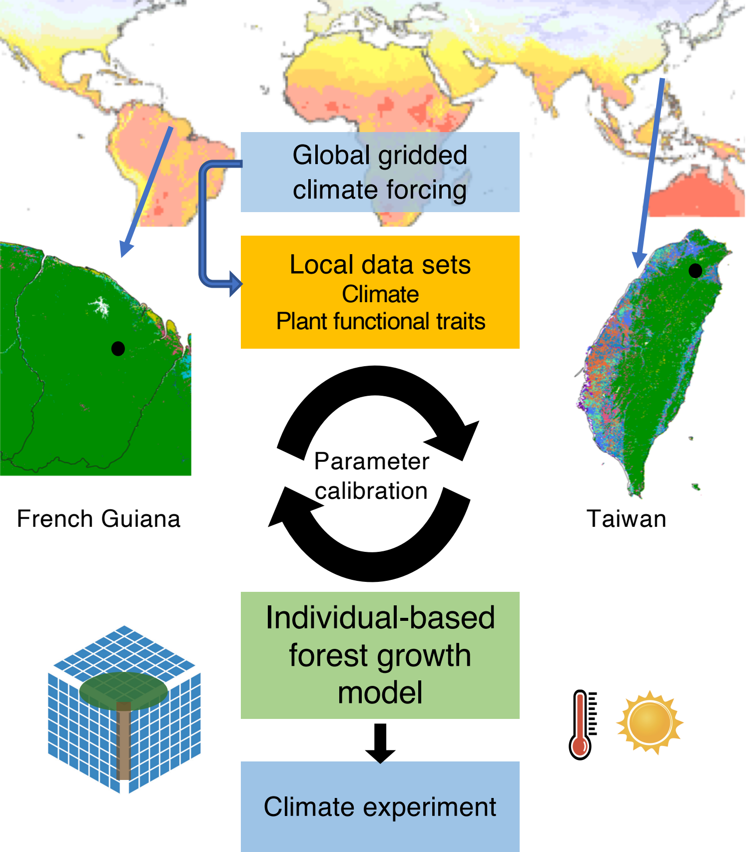


N10 N30



AGB GPP

Figure F2. Diagnostic plots of linear model for the sampled climate experiment at Nouragues, with each summary statistics as dependent variables and the three climatic variables (temperature, irradiance and VPD) as independent variables. The four graphs represent, respectively, residual linearity, residual normality, residual homoscedasticity, and presence or absence of leverage points (influential points).


Global gridded
climate forcing
Local data sets
Climate
Plant functional traits
Parameter
calibration
French Guiana
Taiwan
Individual-based
forest growth
model
Climate experiment