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RESEARCH ARTICLE

Light competition affects how tree growth and survival respond to climate

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Abstract

1. Competition between individuals is a key process that drives tree growth and survival in forests. Ecological theories predict that the effect of competition should be weaker in stressful environments. However, quantitative studies have failed to reach a consensus on the direction of the interaction between climate and competition. In this study, we demonstrate that this interaction appears clearly when we explicitly focus on light competition.
2. We analysed the effect of light competition on tree growth and survival along both temperature and aridity gradients for the 33 major European tree species. We collected forest inventories from nine European countries, encompassing over 1 million trees from Spain to Scandinavia. We used species-specific crown allometric equations to connect this extensive database to the SamsaraLight ray tracing model and to calculate a tree-based light competition index from the light intercepted by the tree crown.
3. Within a given species' climatic niche, the effect of light competition on tree growth and survival decreased towards both the dry and cold margins, supporting the stress gradient hypothesis. Climate mainly affected tree growth in light, with slower growth in drier or colder conditions. In contrast, for survival, climate mainly affected trees in shade, with better survival in the dry or cold stress margins.
4. Among species, the mean sensitivity of tree growth and survival to light competition decreased with increasing mean aridity niche and shade tolerance of the species.

5. *Synthesis*. Our study emphasises the importance of considering species-specific interactions between light competition and climate on tree growth and survival. The impact of climate change on an individual tree is likely to depend on its light competition status within the forest stand, as well as its species-specific climatic niche and shade tolerance.

KEYWORDS
climatic gradients, continental range, individual-based model, light competition, plant–climate interactions, plant–plant interactions, shade tolerance, tree growth and survival

1 | INTRODUCTION

Climate change may cause a decline in tree growth and survival due to changes in temperature and in water regimes (Lindner et al., 2010; McDowell et al., 2020). In forests, individual trees are directly affected by the local climate, which depends on weather conditions, but they are also indirectly affected through competition from neighbouring trees (Jump et al., 2017; Ruiz-Benito et al., 2013). Climate is likely to influence species competitiveness as well as the individual tree's response to competition, leading to changes in tree dynamics (Clark et al., 2011, 2014). Therefore, studying the effect of competition along climatic gradients is key to understanding how individual trees respond to climate and hence, to better grasp how forest species assemblages and structures will vary with climate change (Magalhães et al., 2021).

Several authors have suggested that the effect of competition varies along abiotic stress gradients and is weaker in stressful environments (Bertness & Callaway, 1994; Craine, 2005; Grime, 1979; Maestre et al., 2009; Tilman, 1980). Grime (1979) argued for a weaker competitive effect in less productive and more stressful environments since, for the tree, conserving energy may be a better strategy than competing for the limited resources available when stress is high. However, soon thereafter, Tilman (1980) emphasised the need to clarify which resources are involved. This is especially important in productive environments, where the abundance of below-ground resources leads to intense asymmetric competition for access to light; on the contrary, in stressful environments, the limited availability of water or nutrients in the soil leads to intense competition for access to the below-ground resources. Later on, the stress gradient hypothesis considered not only competition but also facilitation processes (Bertness & Callaway, 1994; Maestre et al., 2009). These authors put forward the idea that the net competition effect should decrease with increasing abiotic stress due to an increase in the frequency of facilitative interactions. One example of direct facilitation is canopy photoprotection in arid areas: direct exposure to strong sunlight could lead to greater heat and desiccation, and excessive irradiance or UV radiation stress (Demmig-Adams & Adams III, 2006; Valladares & Niinemets, 2008). Another example is the beneficial effect of a dense canopy in cold areas, where the canopy layer protects tree organs from fatally low temperatures by limiting the upward dissipation of heat and by reducing the cooling effect of the wind (Charrier et al., 2015).

So far, studies that have attempted to assess how the effect of competition on tree growth and survival varies along climatic gradients have all concluded that there is a significant and important interaction between climate and competition (Coomes & Allen, 2007; Fernández-de-Uña et al., 2015; Ford et al., 2017; Gómez-Aparicio et al., 2011; Kunstler et al., 2011; Rollinson et al., 2016; Ruiz-Benito et al., 2013; Taccoen et al., 2021). However, they have reported conflicting directions for this interaction, highlighting the need to be more specific about exactly which climatic gradient is being analysed and which resources underpin the competitive interactions. For example, studies in the Mediterranean area have found a greater competition effect in water-limited environments (Gómez-Aparicio et al., 2011; Ruiz-Benito et al., 2013), while studies in temperate regions have observed a greater competition effect in more productive sites where access to light is limited (Ford et al., 2017; Kunstler et al., 2011).

The first step towards disentangling the interactions between climate and competition is to analyse competition for a specific resource, rather than use a generic competition index. Previous studies have used crowding indices as proxies for the competition experienced by an individual tree. These models assume that the more neighbours an individual is surrounded by, and the larger these neighbours are, the more competition it faces. The main drawback of crowding indices is that they aggregate many processes and may be misleading when we are trying to understand the effect of competition for a specific resource along large abiotic stress gradients, where stress factors are likely to vary between bioclimatic zones (Magalhães et al., 2021). Some studies have attempted to distinguish the effects of light competition from those of competition for below-ground resources by using an asymmetric crowding index to represent access to light and a symmetric index to represent access to water and nutrients (Ford et al., 2017). However, asymmetric versus symmetric crowding indices are not process-based and remain poor proxies for competition for a specific resource. We propose to focus on the role of the interaction between climate and light competition. Light competition is known to be a key process in forests and is an important determinant of both forest structure and tree dynamics (Pacala et al., 1996), with tree species strongly varying in their level of shade tolerance

(Valladares & Niinemets, 2008) and their sensitivity to light competition (Kunstler et al., 2011). In addition, models for estimating tree light competition are more advanced than models representing competition for other resources, such as water or nutrients, making it possible to study variations in light competition effect at larger scales (Craine & Dybzinski, 2013).

This brings us to the second line of inquiry: using large-scale studies covering broad environmental gradients to further understand forest responses to climate (Ruiz-Benito et al., 2020). Large-scale studies are crucial if we wish to include species' climatic margins, where demographic performance is likely to vary for a given species (Kunstler et al., 2021). Another major advantage of large-scale studies is that they make it possible to compare numerous species, which helps to answer the question of whether the sensitivity to competition varies among species depending on their climatic niche or ecological strategies. The direction and intensity of the climate–competition interaction effect is likely to vary with a species' tolerance to resource limitation (Maestre et al., 2009). For instance, Kunstler et al. (2011) found that the importance of competition for tree growth decreases with increasing productivity along the bioclimatic gradients of temperature and aridity, and that the mean importance of competition is higher for shade-intolerant species than for shade-tolerant species. These results emphasise the importance of not only examining competition-climate interactions for multiple species on a large geographical scale but also comparing the sensitivity of different species to light competition based on their ecological strategies.

Herein, we present a large-scale study of the effect of light competition on individual tree growth and survival across Europe, made possible by the availability of a database of over 1 million trees, including nine European countries from Spain to Scandinavia. Firstly, to analyse the effect of light competition, we derived a tree-level light competition index from the SamsaraLight ray tracing model (Courbaud et al., 2003, 2015), a spatially explicit and tree-based model that estimates the amount of light intercepted by a given tree based on light beam interception and attenuation by the 3D crowns of each tree in the stand. We used species-specific crown allometries to represent the tree crown structure in space. Then, we considered two climatic gradients: temperature and aridity. We used a water balance model based on soil structure, monthly water fluxes and snow melt to derive a plot-level aridity index. Finally, we fitted species-specific tree-based growth and mortality models as a function of climate and light competition. We then used the models to predict annual tree growth and survival under different climates and levels of light competition to test whether the effect of light competition varied along the two climatic gradients, with high aridity in drier climates and low temperatures in colder climates constraining tree dynamics. The main hypothesis is that the net light competitive effect will be dependent on the balance between the negative effect of shading (reduced carbon assimilation) and its positive effects (reduced evaporative demand, reduced frost stress, …). This balance is likely to change along climatic gradients, depending on the relative importance of these climatic stresses. In addition, the benefit of being in full light will not be the same depending on the occurrence of other climatic constraints. The performance improvement should be smaller when water supply is low or when low temperature stress is high. We addressed this question at two different scales: (i) within species—between the climatic margins of a given species, and (ii) among species—by comparing responses for different species with different levels of shade tolerance and different mean climatic niches. We hypothesised that (i) within a given species' climatic niche, the effect of light competition on growth and survival would be weaker at the cold or dry species stress margins, and (ii) among species and across Europe, the species mean sensitivity to light competition on growth and survival would be weaker for shade-tolerant species, and for species whose mean climatic niche is located either in the hot, dry Mediterranean region or in cold boreal regions.

2 | MATERIALS AND METHODS

Figure 1 summarises the methodology and the main hypotheses of the study.

2.1 | Ontogenic, light competition index and climatic variables

2.1.1 | Forest inventories

We harmonised forest inventory databases from nine European countries from Spain to Scandinavia covering most of the European climatic gradient (see the country-specific databases, references and harmonisation protocols in Appendix 1). The growth dataset was composed of 1,081,974 trees across 106,340 plots with 33 different species, and the mortality dataset was composed of 1,052,965 living trees and 30,050 dead trees across 104,658 plots with 29 different species (see Figure 1 in the Appendix 1 for the species distribution). Most of the databases are National Forest Inventories that consist of visit-revisit surveys where trees are sampled within circular plots whose radii depend on tree size (circular areas ranging from 0.008 ha for smaller trees to 0.196 ha for larger trees). The years between the two surveys vary among and within countries (ranging from 5 to 20 years). All the databases contain either the exact or the blurred location of the plot. All the databases provide the species, the diameter at breast height (dbh) and the tree status (i.e. living, dead or harvested) recorded for each sampled tree during both the first and second surveys. The position of the tree and its precise crown dimensions were not available in most databases, so we excluded them from our calculations. We removed all trees below 10 cm in dbh to harmonise the data. We also removed any plots with records of harvested trees or signs of disturbance between the two surveys, as this might influence our estimations of light competition. We analysed only the species with at least 1000 living individuals, 100 dead individuals (for the study of tree survival only) and present on at least 500 different plots. We computed tree annual diameter growth

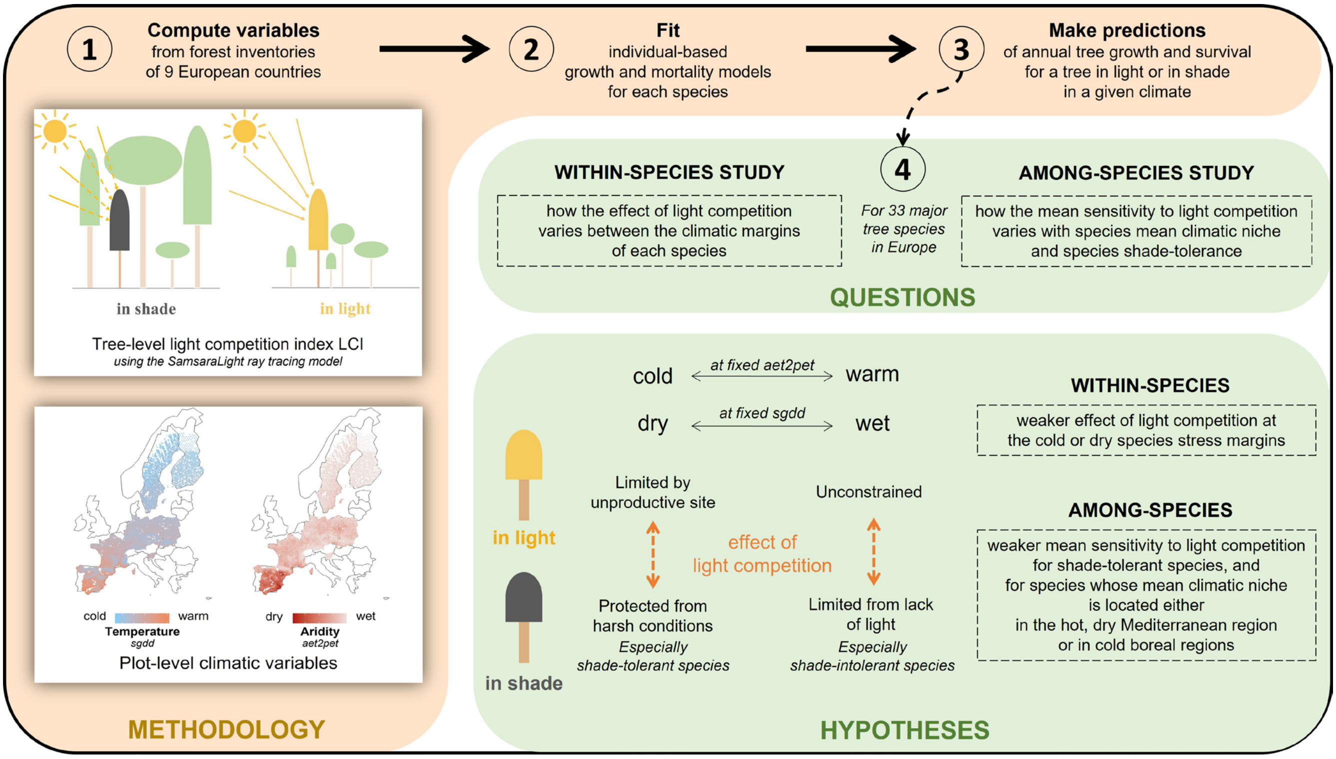


FIGURE 1 Methodology, questions and hypotheses of the study. (1) Ontogenic, light competition index and climatic variables used for each tree. (2) Fit of tree-based growth and mortality models for each species. (3) Predictions from the fitted species-specific models for annual tree growth and survival probability for a tree in light or in shade in different climates. (4) Testing these predictions for two ecological questions on how the effect of light competition varies along two bioclimatic gradients, both within and among species.

as the difference in tree dbh between the two surveys divided by the time between the two surveys.

2.1.2 | Light competition index

We used the SamsaraLight ray tracing model (a spatially explicit and tree-based model, Courbaud et al., 2003, 2015) on virtual stands representing the statistical sampling of the trees from forest inventory plots, to estimate the amount of light energy intercepted by each tree within each plot throughout the year (see the methodology in Figure 2). We represented light competition for a given tree i within a plot by defining a light competition index LCI, which we calculated as $\mathrm{LCI}_i = 1 - \frac{E_i}{\mathrm{Epot}_i}$, where E_i is the total light intercepted by the tree i and Epot_i is the potential light the tree i would intercept if it had no neighbours, both E_i and Epot_i in MJ.year^{-1}. LCI = 0 represents a tree in full light (i.e. no light competition), whereas LCI = 1 represents a tree in full shade (i.e. strong light competition). Therefore, our tree-based light competition index reflects the three-dimensional occupation of space by individuals of different heights, crown structures and leaf densities, and takes into account the geometry and intensity of the light beams specific to the stand location.

To assess whether our light competition index was a better predictor than more classical competition indices, we also computed two non-spatially explicit crowding indices typically used to represent stand competition: BAtotal (which is not light specific and is expressed as the total basal area of the plot) and BAlarger (which is generally considered to capture light competition but excludes crown characteristics and light processes and is expressed as the total basal area of the trees in the plot larger than the focal tree), both in m^{-2}.ha^{-1}. In order to standardise the two indices per hectare, we added the basal area of the sampled trees multiplied by their sampling weight.

SamsaraLight

We divided the virtual stand into square cells of 5mx5m, with trees explicitly located in the stand with a simplified representation of their crowns. Firstly, we estimated both the diffuse and direct rays of sunlight that would arrive each month and quantified their energy, direction and angle, depending on stand location (see more details in Appendix 2.1). Secondly, we projected each single ray towards the centre of each cell in the stand. Thirdly, when a ray was intercepted by the crown of a tree, we computed the associated intercepted light energy. We considered the crown as a turbid medium and applied the Beer–Lambert law (see equation in Figure 2b), which includes the incident energy of the ray E_{incident}, the length of the path throughout the crown L and the leaf area density (LAD) of the tree LAD. We assumed that the leaves were opaque, arranged homogeneously and not aggregated within the crown, thus setting k and σ to constants ($k = 0.5$ and $\sigma = 1$; Ligot, Balandier, Courbaud, & Claessens, 2014). Thus, we were able to estimate the attenuation of the energy of each light ray after successive interceptions by

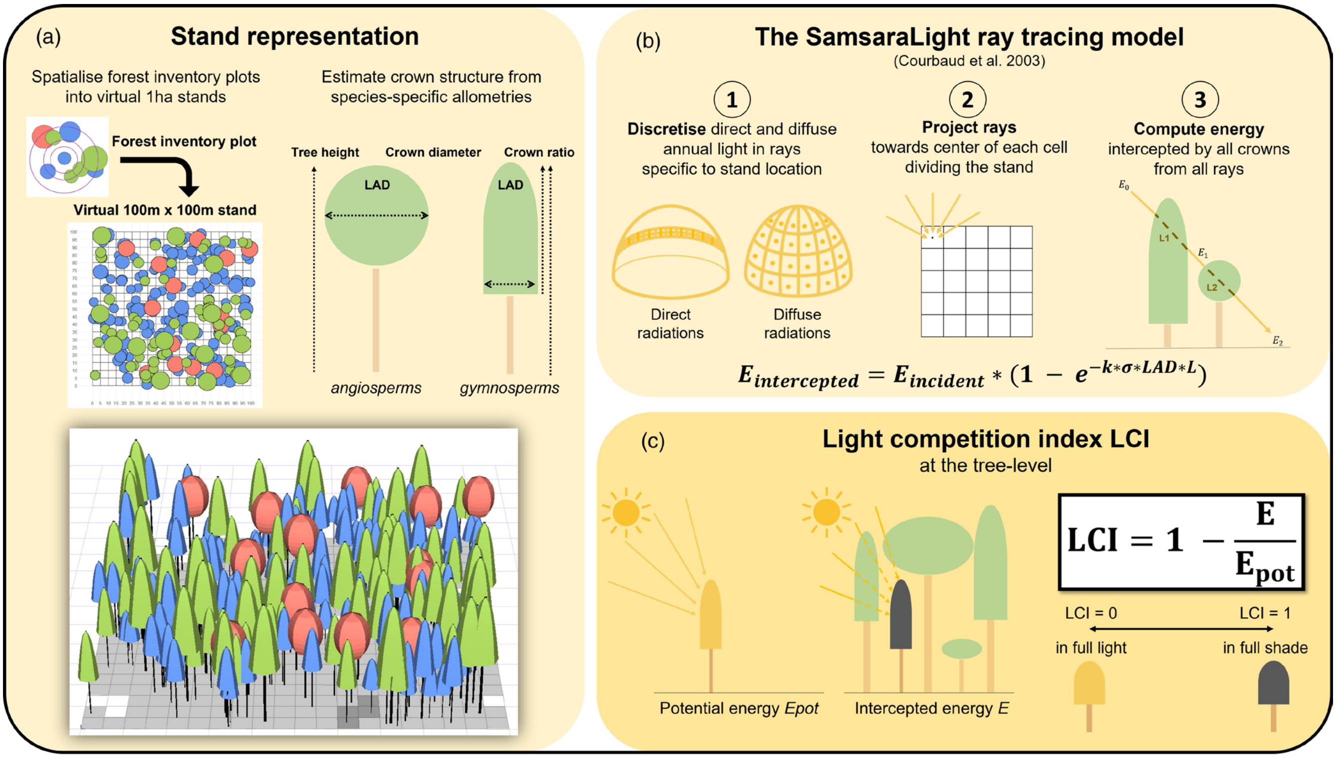


FIGURE 2 Methodology to compute the tree-based light competition index LCI. (Panel a) We generated virtual 100 m × 100 m stands from observed European forest inventory plots by replicating each sampled tree according to its weight per hectare and assigning each tree a random location within the stand. Then, we represented the 3D crown structure of each tree from species-specific allometries, and we assigned a leaf area density (LAD) value depending on the species shade tolerance and its taxonomic group (angiosperm or gymnosperm). (Panel b) Brief explanation of the SamsaraLight ray tracing model. (Panel c) We linked the SamsaraLight ray tracing model to the virtual stands, and by averaging estimated values of the replicated trees, we estimated the tree-level value of both the potential intercepted energy without neighbours and the intercepted energy considering the attenuation of rays by competing crowns. Finally, we computed a tree-based light competition index LCI to estimate the light competition from a given tree's neighbours while accounting for plot location.

the tree crowns and calculate the sum of the energy intercepted from each ray, for all the trees in the stand. To account for the fact that we did not have any data on the environment surrounding the stand, we represented plot boundaries using a torus system (Courbaud et al., 2003).

We did not consider the topography of the plot to compute light interception, as we did not have both the exact coordinates nor information about the slope and orientation for all plots. Radiation data from the PVGIS database (Huld et al., 2012) were based on the incident energy on a horizontal plane and virtual plots were considered to be flat with a null slope.

Virtual stands

To link the SamsaraLight model to the forest inventory plots and calculate the light intercepted by each tree, we needed to create an explicit representation of the plots. However, the trees in the forest inventories are statistically sampled within a plot and do not provide a complete representation of the stand. In general, trees are sampled within circles of different sizes, depending on their diameter and the protocol of each country, and are therefore assigned a statistical weight corresponding to the number of equivalent trees in a one-hectare stand. Thus, for each plot, we generated a representative virtual one-hectare stand (100 × 100 m in size) consisting of the sampled trees replicated as many times as their associated weight per hectare and randomly positioned in the stand. The replicated trees in the virtual stand allowed us to derive the mean intercepted energy of each sampled tree and to determine the uncertainty due to not knowing the exact location of the sampled trees. The uncertainty around the mean estimated light competition index was slight enough that we were able to discriminate between trees in shade and trees in light, even with random tree positions (see Appendix 2.5).

Tree crowns

To calculate the light intercepted by a tree, we needed to explicitly represent its crown. We used the species-specific allometric relationships in Touzot et al. (under revision), which predict tree height, crown diameter and crown ratio (ratio of crown depth to tree height) from the species, dbh and local crowding index of the tree (see equations in Appendix 2.2). We defined tree crown shape as ellipsoidal for broadleaved species and semi-ellipsoidal for conifers. We approximated LAD for each species based on species succession status, building on the idea that late successional species can sustain a higher leaf density in their crowns (Leuschner &

Meier, 2018; see methodology in Appendix 2.3). These allometric equations do not account for within-species climatic effects on crown dimensions. However, according to Lines et al. (2012), within-species effects are of a much smaller magnitude than interspecific differences.

2.1.3 | Climatic variables

To model tree growth and survival response to climate, we selected two climatic variables known to be key factors in forest productivity (Boisvenue & Running, 2006): the sum of growing degree days (*sgdd*) and the ratio of actual to potential evapotranspiration (*aet2pet*). *sgdd* is related to the annual temperatures at the plot and the length of the growing season, and *aet2pet* is a proxy for the aridity of the plot. For each plot, we computed *sgdd* and *aet2pet* for each year between the two surveys; we added 2 years before the first survey to take into account the lag effect of climate on tree dynamics (Kunstler et al., 2021) and then averaged the results over the time period.

The sum of growing degree days

sgdd was computed as the sum of the daily mean temperatures above 5.5°C during the year (Zimmermann & Kienast, 1999). As we had monthly data, we considered that the mean temperature of any given day was equal to the mean temperature of the month. We extracted monthly mean temperatures from the Chelsa database (Karger et al., 2021) for each plot at a resolution of one arcsec (around 1 km × 1 km). Since altitude can vary greatly in a 1 km × 1 km cell, especially in mountainous regions, and since Chelsa climatic variables are estimated at the mean altitude of the cell, we corrected the monthly temperatures with altitude. To do so, we used a moving window regression (MWR) approach to estimate the local temperature lapse rate (see methodology in Appendix 3.1).

Ratio of actual to potential evapotranspiration

aet2pet was computed from an annual water balance by estimating the soil water holding capacity from soil variables (SoilGrids database, Poggio et al., 2021; and European Commission JRC, Panagos et al., 2012) and the monthly flux of soil water content from precipitation, snow melt and potential evapotranspiration pet from climatic variables (Chelsa database, Karger et al., 2021; see methodology in Appendix 3.2, inspired by Piedallu et al., 2013 and McCabe & Markstrom, 2007). For each month, we computed actual evapotranspiration *aet* with the monthly water entry, taking into account that as the soil water content decreases it becomes increasingly difficult for the tree to absorb water from the soil to meet the *pet* requirement. Finally, we computed monthly *aet2pet* as the ratio between actual evapotranspiration *aet* and potential evapotranspiration *pet*, and we averaged monthly values for a given year. *aet2pet* ranges from 0 (dry) to 1 (no water stress).

2.2 | Species-specific tree-based growth and mortality models

2.2.1 | Model definitions

We followed the growth and survival model designed in Kunstler et al. (2021).

Growth model

For each species, we fitted a linear mixed model (LMM) to predict the logarithm of the annual increment in dbh G (in mm.year^{-1}). We performed a log-transformation to avoid heteroscedasticity (we removed null and negative growth; 4.39% of the growing trees). For *sgdd*, we fitted two different forms, including a unimodal relationship, to represent two alternative hypotheses: an asymptotic inverse function to represent a biological optimum at high *sgdd* (Equation 1), and a quadratic polynomial function to represent different optima along the *sgdd* range (Equation 2). In contrast, for *aet2pet* we only used an asymptotic function to represent a biological optimum for growth at an *aet2pet* of 1 (indicating no water stress). The choice of these response curves is based on a preliminary exploration of the data with smoothing functions. We used maximum likelihood to compare the models and restricted maximum likelihood to estimate model parameters. We used the lme function from the nlme package (Pinheiro et al., 2022) in R version 4.2.2 (R Core Team, 2022) to fit the models.

$$\begin{aligned}\log\left(G_{i,p}\right) = a_{0,c} + a_{0,p} + a_1.\,\mathrm{dbh}_i + a_2.\log\left(\mathrm{dbh}_i\right) + \\ a_3.\,\mathrm{LCI}_i + a_4.\,\frac{1}{sgdd_p} + a_5.\,\frac{1}{aet2pet_p} + \\ a_6.\,\mathrm{LCI}_i.\,\frac{1}{sgdd_p} + a_7.\,\mathrm{LCI}_i.\,\frac{1}{aet2pet_p} + \epsilon_i\end{aligned} \tag{1}$$

$$\begin{aligned}\log\left(G_{i,p}\right) = a_{0,c} + a_{0,p} + a_1.\,\mathrm{dbh}_i + a_2.\log\left(\mathrm{dbh}_i\right) + \\ a_3.\,\mathrm{LCI}_i + a_4.\,sgdd_p + a_5.\,sgdd_p^2 + a_6.\,\frac{1}{aet2pet_p} + \\ a_7.\,\mathrm{LCI}_i.\,sgdd_p + a_8.\,\mathrm{LCI}_i.\,\frac{1}{aet2pet_p} + \epsilon_i\end{aligned} \tag{2}$$

where $G_{i,p}$ is the annual increment in dbh of tree i in plot p; dbh_i is the dbh of tree i at first survey; LCI_i is the light competition index of tree i; $sgdd_p$ is the sum of growing degree days for plot p; and $aet2pet_p$ is the aridity index for plot p. Parameters a_1 to a_8 are the estimated regression coefficients. $a_{0,p}$ is a normal random plot effect to account for the non-independence of the trees in the same plot. $a_{0,c}$ is the country-specific intercept to account for country-specific protocols. ϵ_i is the normal error term.

Mortality model

For each species, we estimated the annual probability of mortality of an individual tree by fitting a generalised linear model (GLM). We used a complementary log–log link function (*cloglog*) and added the logarithm of the time between surveys as an offset coefficient to account for different times between surveys. We used the same predictor variables as for the growth models (see equations in Appendix 5.1). However, we did not include a plot random effect because it caused fitting difficulties, as too many plots had no dead trees. We fitted the model with the glm function in R (R Core Team, 2022).

2.2.2 | Data resampling, cross-validation and model selection

Since our dataset contained relatively few individuals in extreme climates or in large diameter classes, we performed a weighted resampling to reduce the number of individuals in over-represented classes. We then performed a k-fold cross-validation on this new dataset: we randomly split the data into five folds, then fitted the models on the first four folds and estimated a prediction error on the fifth independent fold. We repeated this process for each fold. To account for uncertainty in the selection of model variables, we fitted all the possible sub-models of both equation 1 (asymptotic function of *sgdd*) and Equation 2 (quadratic function of *sgdd*) by removing one by one the climatic variables (*sgdd* and *aet2pet*) and the interaction with light competition LCI. We selected the best models based on the Akaike information criteria (ΔAIC < 2 compared with the lowest AIC) and used the AIC weight to average the predictions from the selected models (Wagenmakers & Farrell, 2004; see detailed methodology in Appendix 5.2). We applied this method 20 times to account for stochasticity in the weighted resampling.

2.2.3 | Comparison between competition indices

To assess the reliability of our light competition index *LCI*, we compared tree growth and mortality models that included either LCI or the classical crowding indices (i.e. BAtotal or BAlarger). When considering competition with BAtotal, we also tested for the interaction with dbh (BAtotalXdbh) to reveal any possible size effect on the symmetric competition. We also fitted a control model where no competition indices were included (control). We compared the models using $\Delta\mathrm{AIC}_{\mathrm{control}}$ (difference in AIC with the control model). We quantified the prediction error with the mean absolute error (MAE) for annual growth predictions and with the AUC ROC indicator (area under ROC curve) as an indicator of model sensitivity and specificity of the mortality models (Bradley, 1997). Model performance and the response curves for the growth and survival models with LCI are presented in Appendices 5.4 and 5.5 for each species.

2.3 | Predictions of annual tree growth and survival probability

For each species, we used the fitted growth and mortality models to predict the annual diameter increment and survival probability of a tree of that species growing either in shade (LCI = 0.9) or in light (LCI = 0.1) in a given climate. We fixed the individual tree size at its species-specific observed mean value. We averaged the coefficients of the country variable weighted by the number of observations of the species in that country. The methodology used in Section 2.2.2 allowed us to predict 100 values of annual diameter increment and survival probability (20 weighted resamplings × 5 folds), from which we were able to derive a 95% error interval between the 2.5% and the 97.5% quantiles of the predictions (Geyer, 2013).

2.4 | Effect of light competition along temperature and aridity gradients

We derived metrics to study how the effect of light competition varies both within a given species' climatic range and among species (all equations in Appendix 6.1).

2.4.1 | Within-species study

Species climatic margins

We predicted the annual growth and survival probability of a tree in either light or shade within the two margins of both temperature (*sgdd*) and aridity (*aet2pet*) gradients. We defined the two margins of a climatic gradient as the 2.5% and 97.5% quantiles of the species-specific observed values of the given climatic variable while fixing the other climatic variable to its species-specific observed mean value.

Difference in the effect of light competition between species' climatic margins

For each species, we computed the effect of light competition on tree growth η^{growth} (and survival) as the difference in annual growth (and in annual survival probability) between light and shade conditions within each of the four climatic species margins (aridity: $\eta^{\mathrm{growth}}_{\mathrm{wet}}$ and $\eta^{\mathrm{growth}}_{\mathrm{dry}}$, temperature: $\eta^{\mathrm{growth}}_{\mathrm{warm}}$ and $\eta^{\mathrm{growth}}_{\mathrm{cold}}$). Then, we computed the difference in the effect of light competition on tree growth (and survival) between the margins of the aridity gradient $\Delta\eta^{\mathrm{growth}}_{aet2pet} = \eta^{\mathrm{growth}}_{\mathrm{wet}} - \eta^{\mathrm{growth}}_{\mathrm{dry}}$ and between the margins of the temperature gradient $\Delta\eta^{\mathrm{growth}}_{sgdd} = \eta^{\mathrm{growth}}_{\mathrm{warm}} - \eta^{\mathrm{growth}}_{\mathrm{cold}}$. $\Delta\eta > 0$ means that the effect of light competition was greater in the species' wet margin on the aridity gradient, or in the species' warm margin on the temperature gradient. To estimate the average species response, we fitted a mixed model with species as a random effect, for both growth and survival and for each climatic gradient. We used the lme function from the nlme package (Pinheiro et al., 2022) to obtain the predicted mean of the margin effect and the associated standard error and *p*-value.

Difference in the effect of climate on a tree in light and a tree in shade

For each species, we computed tree annual growth (and annual survival probability) in each of the four margins, for a tree in light and a tree in shade. Then, for each climatic gradient and for both a tree in light and a tree in shade, we fitted a mixed model to predict the growth (and survival) in a given margin, with species as a random effect. We also obtained the predicted mean of the margin effect and the associated standard error and p-value.

2.4.2 | Among-species study

Mean sensitivity to light competition

We defined the mean sensitivity of a given species to light competition in terms of growth Ω^{growth} and survival $\Omega^{survival}$ as the relative effect of light competition in the species' mean climatic niche. Mean sensitivity to light competition is calculated as the log ratio of growth (and survival) between a tree in light and a tree in shade, all calculated at the species-specific observed mean value of *sgdd* and *aet2pet* in the dataset.

Relationships between species mean sensitivity to light competition and species' ecological strategies

To describe the species' ecological strategies, we considered each species' mean climatic niche and its shade tolerance shadetol. Species mean *sgdd* and *aet2pet* ($sgdd_{mean}$ and $aet2pet_{mean}$) were strongly correlated, with hot, dry climates at low latitudes and cold, wet climates at high latitudes (see Appendix 4.1.1 and Figure 17 in Appendix). It was therefore difficult to separate the relative contribution of *sgdd* and *aet2pet* when comparing species with different mean climatic niches. We finally chose $aet2pet_{mean}$ as a proxy of species location within the European climatic gradient, as it performed better than $sgdd_{mean}$ or the first axis of a PCA with $sgdd_{mean}$ and $aet2pet_{mean}$ (see comparison of results in Appendix 6.2.2). We used the species-specific shade tolerance values from Niinemets and Valladares (2006). We complemented the database for Mediterranean species with values from Poorter et al. (2012). If the species was not specified in either database, we set the species' shade tolerance as the average of all species in the same genus. Shade tolerance, defined as the minimum light at which a given species, is able to grow, was a continuous value ranging from 0 (shade-intolerant species) to 5 (highly shade-tolerant species). For the sake of graphical representation only, we have assigned a shade tolerance group to each species: shade-intolerant (species in [0,2.25[), mid shade-tolerant (species in [2.25,3.75[) and highly shade-tolerant (species in [3.75,5]).

We fitted a LMM to predict species mean sensitivity to light competition (in terms of growth Ω^{growth} or survival $\Omega^{survival}$) as a function of species shade tolerance shadetol and species mean aridity niche $aet2pet_{mean}$, plus their interactions. We fitted the model with the mean of the 100 predicted values of species mean sensitivity to light competition (see Section 2.3) and we included species as a random effect.

3 | RESULTS

3.1 | Our light competition index was a better predictor of growth and survival than were generic crowding indices

Globally, over all the species studied, the model including the light competition index LCI explained both tree growth and survival better than did the classical crowding indices (lower $\Delta AIC_{control}$, see Table 1). Over the 100 fits of a given species, the LCI model was the best fitting competition index for 19 out of 33 species for growth, and for 26 out of 29 species for survival. The LCI model was also better at predicting individual growth (the MAE of predictions on independent data for all species was 1.407 mm.year^{-1} compared with 1.483 mm.year^{-1} for the control model), and the individual survival probability (the mean area under the ROC curve of predictions on new data for all species was 0.700 compared with 0.659 for the control model).

The benefit of using LCI rather than crowding indices was greater for the survival models than for the growth models. For growth, although the three comparison indicators for the LCI model were much better than for the asymmetric index BAlarger, they were only slightly better than for the non-resource-specific symmetric index

TABLE 1 Comparison of the four competition indices and the control model (i.e. no competition index).

	Growth			Survival		
	$\Delta AIC_{control}$	$n_{species}$	MAE (in mm.year^{-1})	$\Delta AIC_{control}$	$n_{species}$	AUC ROC
Control	0%	0	1.483	0%	0	0.659
BAlarger	−0.89%	0	1.444	−1.38%	1	0.679
BAtotal	−1.60%	1	1.424	−1.52%	1	0.682
BAtotalXdbh	−2.35%	13	1.410	−1.78%	1	0.686
LCI	**−2.64%**	**19**	**1.407**	**−2.68%**	**26**	**0.700**

Note: $\Delta AIC_{control}$ is the mean relative difference in Akaike information criteria (AIC) with the control model for all the species and their 100 associated fits, weighted by the number of individuals in each species. $n_{species}$ is the number of species for which the competition index was the best (lowest mean AIC over the 100 fits). MAE is the mean absolute error, and AUC ROC is the area under the ROC curve, averaged for all the species and their 100 associated fits. In bold is the best-performing competition index.

BAtotalXdbh (see $\Delta\mathrm{AIC}_{\mathrm{control}}$, n_{species} and MAE for growth in Table 1). In contrast, for survival, the model with LCI outperformed all the non-resource-specific indices (BAlarger, BAtotal and BAtotalXdbh) whether they were symmetric or asymmetric (see $\Delta\mathrm{AIC}_{\mathrm{control}}$, n_{species} and AUC ROC for survival in Table 1).

3.2 | The effect of light competition decreased towards both the colder and drier species climatic margins

Along the temperature gradient, the effect of light competition was significantly greater in the warm species margin than in the cold margin for 13 out of 33 species for growth (Figure 3, Panel 1a), and for 12 out of 29 species for survival (Figure 3, Panel 1b). The difference in the average effect of light competition across all species between the warm and cold margins was significant on annual tree diameter growth with a mean difference of 0.922 $\mathrm{mm.year}^{-1}$ (95% confidence interval [0.306, 1.538], p value < 0.01) and was also significant on annual tree survival probability with a mean difference of 0.010 ([0.002, 0.018], p value < 0.05). Along the aridity gradient, the effect of light competition was significantly greater in the wet than in the dry species margin for 9 out of 33 species for growth (Figure 3, Panel 2a), and for 13 out of 29 species for survival (Figure 3, Panel 2b). The difference in the average effect of light competition across all species between the wet and dry margins was significant on annual tree diameter growth with a mean difference of 0.527 $\mathrm{mm.year}^{-1}$ ([0.166, 0.887], p value < 0.01) and was also significant on annual tree survival probability with a mean difference of 0.004 ([0.002, 0.007], p value < 0.01).

We did not find clear relationships between species ecological strategies (shade tolerance or environmental distribution range) and the intensity of $\Delta\eta$ (difference in light competition effect between species' margins) (analyses not shown).

3.3 | The effect of climate differed for trees in light and trees in shade

On average across species, our results show that a tree in light grows significantly faster in its warm margin than in its cold margin (1.074 $\mathrm{mm.year}^{-1}$ [0.426, 1.722], p value < 0.01) and also significantly faster in its wet margin than in its dry margin (0.666 $\mathrm{mm.year}^{-1}$ [0.194, 1.139], p value < 0.01; Figure 4, Panel 1a, yellow shapes). However, there was no significant effect of climate on the annual diameter growth of a tree in shade (Figure 4, Panel 1a, grey shapes). In contrast, for survival, a tree in shade survives significantly better in its cold margin than in its warm margin (−0.011 [−0.02, −0.002], p value < 0.05) and also significantly better in its dry margin than in its wet margin (−0.004 [−0.007, −0.002], p value < 0.01; Figure 4, Panel 1b, grey shapes). However, there was no significant effect of climate on the annual survival probability of a tree in light (Figure 4, Panel 1b, yellow shapes).

The European beech (*Fagus sylvatica L.*) is a major tree species in Europe and is therefore an interesting illustrative species for the results we show above (Figure 4, Panels 2a–d). Beech trees in light grow faster in their warm or wet climatic margins while beech trees in shade survive better in their cold or dry climatic margins, resulting in a stronger effect of light competition in the warm and in the wet margins for both growth and survival.

3.4 | Species mean sensitivity to light competition varied with species mean aridity niche and shade tolerance

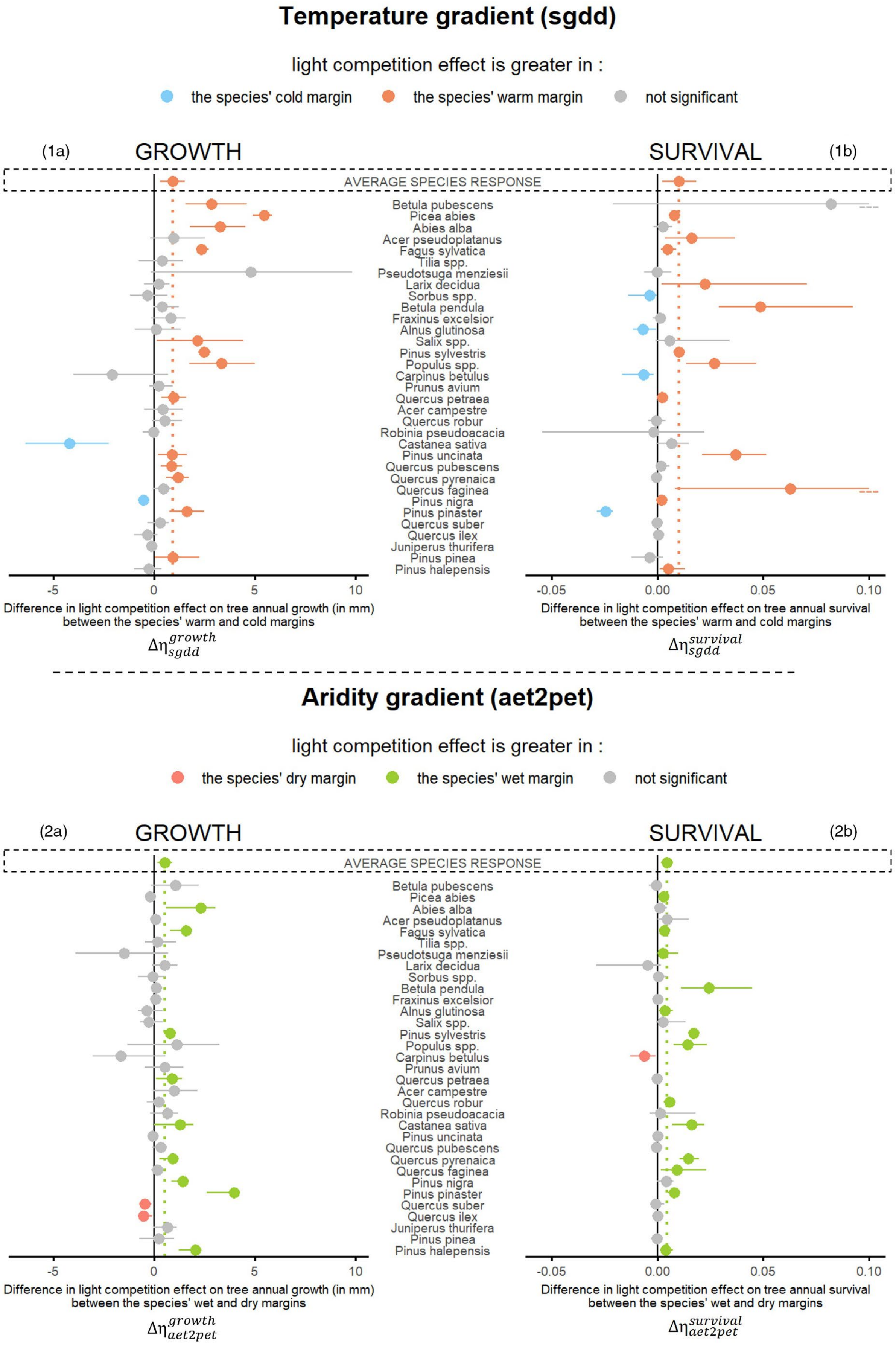
For growth, there was a significant interaction effect between species mean aridity niche and species shade tolerance (p value < 0.001). The species mean sensitivity to light competition decreased with species mean aridity niche, especially for more shade-tolerant species (Figure 5a). For survival, there was a significant positive effect of species mean aridity niche (p value < 0.01) and a significant negative effect of shade tolerance (p value < 0.01) on species mean sensitivity to light competition (Figure 5b). It is interesting to note that two shade-intolerant species with a wet mean climatic niche showed a low sensitivity to light competition for survival: *Betula pubescens* (shadetol = 1.46 and $aet2pet_{\mathrm{mean}} = 0.90$ with $\Omega_{\mathrm{survival}} = 0.011$, species number 6 in Appendix 6.2.2) and *Larix decidua* (shadetol = 1.85 and $aet2pet_{\mathrm{mean}} = 0.95$ with $\Omega_{\mathrm{survival}} = 0.007$, species number 12 in Appendix 6.2.2). These species are also associated with cold climates (*Betula pubescens* $sgdd_{\mathrm{mean}} = 1297^{\circ}\mathrm{C}$ and *Larix decidua* $sgdd_{\mathrm{mean}} = 1664^{\circ}\mathrm{C}$). The regressions are plotted in insets of Figure 5 (Panel A for growth and Panel B for survival) and coefficients are presented in Appendix 6.2.2. See also species' mean climatic niche and the equivalent of Figure 5 including species names in Appendix 6.2.2.

4 | DISCUSSION

4.1 | Our light competition index was a better predictor of growth and survival than were generic crowding indices

Our light competition index appeared to be a better predictor than classical competition indices based on symmetric or asymmetric crowding intensities (BAlarger, BAtotal and BAtotalXdbh in Table 1).

FIGURE 3 Differences in the effect of light competition on tree growth (Panel a) and survival (Panel b) between species' warm vs cold margins (Panel 1) and wet vs dry margins (Panel 2). For each species, the point represents the predicted mean and the error bar represents the 95% percentile interval, based on the 100 species predictions. The '- - -' symbol below the error bar indicates that the error bar extends beyond the figure and has been truncated to simplify the figure (see Appendix 6.2.1 for full length error bar figures). Species with error bars that do not cross 0 are considered significant. The average species response is based on a LMM (see Section 2.4.1) with the error bar representing the 95% confidence interval around the mean prediction. Species are ordered from top to bottom by $aet2pet_{\mathrm{mean}}$ (i.e. species living in wetter to drier climates).


Temperature gradient (sgdd)
light competition effect is greater in :
● the species' cold margin
● the species' warm margin
● not significant
(1a)
GROWTH
SURVIVAL
(1b)
AVERAGE SPECIES RESPONSE
Betula pubescens
Picea abies
Abies alba
Acer pseudoplatanus
Fagus sylvatica
Tilia spp.
Pseudotsuga menziesii
Larix decidua
Sorbus spp.
Betula pendula
Fraxinus excelsior
Alnus glutinosa
Salix spp.
Pinus sylvestris
Populus spp.
Carpinus betulus
Prunus avium
Quercus petraea
Acer campestre
Quercus robur
Robinia pseudoacacia
Castanea sativa
Pinus uncinata
Quercus pubescens
Quercus pyrenaica
Quercus faginea
Pinus nigra
Pinus pinaster
Quercus suber
Quercus ilex
Juniperus thurifera
Pinus pinea
Pinus halepensis
-5
0
5
10
-0.05
0.00
0.05
0.10
Difference in light competition effect on tree annual growth (in mm) between the species' warm and cold margins
$\Delta\eta_{sgdd}^{growth}$
Difference in light competition effect on tree annual survival between the species' warm and cold margins
$\Delta\eta_{sgdd}^{survival}$
Aridity gradient (aet2pet)
light competition effect is greater in :
● the species' dry margin
● the species' wet margin
● not significant
(2a)
GROWTH
SURVIVAL
(2b)
AVERAGE SPECIES RESPONSE
Betula pubescens
Picea abies
Abies alba
Acer pseudoplatanus
Fagus sylvatica
Tilia spp.
Pseudotsuga menziesii
Larix decidua
Sorbus spp.
Betula pendula
Fraxinus excelsior
Alnus glutinosa
Salix spp.
Pinus sylvestris
Populus spp.
Carpinus betulus
Prunus avium
Quercus petraea
Acer campestre
Quercus robur
Robinia pseudoacacia
Castanea sativa
Pinus uncinata
Quercus pubescens
Quercus pyrenaica
Quercus faginea
Pinus nigra
Pinus pinaster
Quercus suber
Quercus ilex
Juniperus thurifera
Pinus pinea
Pinus halepensis
-5
0
5
10
-0.05
0.00
0.05
0.10
Difference in light competition effect on tree annual growth (in mm) between the species' wet and dry margins
$\Delta\eta_{aet2pet}^{growth}$
Difference in light competition effect on tree annual survival between the species' wet and dry margins
$\Delta\eta_{aet2pet}^{survival}$

Our 3D light interception model takes into account individual tree height, species-specific crown geometries and the relative energy carried by light rays coming from different directions in the sky (varying with plot latitude and cloud cover; Huld et al., 2012); it has been shown to robustly simulate light measured with hemispherical photographs (André et al., 2021; Courbaud et al., 2003; Ligot, Balandier, Courbaud, Jonard, et al., 2014). Competition among trees in a forest is primarily influenced by canopy cover, and implies light competition (Pacala et al., 1996), which may explain why our light competition index produced better predictions. The difference among indices was even more significant when predicting survival, which indicates that light competition may be an important factor in the tree survival process.

4.2 | The effect of light competition decreased towards both the colder and drier species climatic margins

Our results in Figure 3 highlight the importance of considering the species-specific interactive effect between light competition and climate, and support ecological theories that predict a decreasing effect of competition with increasing abiotic stress (Bertness & Callaway, 1994; Grime, 1979; Maestre et al., 2009; Tilman, 1980). Coomes and Allen (2007) found similar results for mountain beech growth along an altitudinal gradient in New Zealand: the intensity of asymmetric competition decreased with altitude (i.e. as the environment became colder and more stressful). In contrast, for survival, Ruiz-Benito et al. (2013) found a stronger effect of asymmetric competition on tree mortality under stressful hotter and drier conditions along a Mediterranean climatic gradient, and Taccoen et al. (2021) found excess mortality of suppressed trees with increasingly stressful hot temperatures. The latter studies were based on crowding indices that were not specific to light competition. This opens the door to confusion between light competition and competition for soil resources, by capturing more intense competition through a greater competition for water in drier, more stressful environments. This highlights the importance of using an explicit resource-specific competition index.

Few species in Figure 3 stood out and showed a reverse directional effect (i.e. greater light competition effect in cold and dry margins). A possible explanation could be that these species are typical of forests with intensive management strategies (e.g. high thinning intensity, coppice, plantation outside the native ecological niche). More specifically, the vast majority of these species are mainly managed in coppice, such as *Carpinus betulus* (European hornbeam), *Castanea sativa* (sweet chestnut), *Quercus suber* (cork oak, plus specific management by bark removal) and *Quercus ilex* (evergreen oak). This could lead to inappropriate estimates of crown dimensions, light interception and tree dynamics due to complex crown shapes. Another hypothesis is the unusual ecological niche of some species, leading to possible difficulties in estimating the environmental drivers. For example, *Alnus glutinosa* (black alder), which grows very close to rivers, or *Pinus pinaster* (maritime pine), which has been widely planted outside its native range.

In our study, we simplified the climatic effect to two dimensions, a negative effect of low temperature and a negative effect of high aridity. This allowed us to hypothesise that abiotic stress would increase along the temperature gradient towards the species' cold margin and along the aridity gradient towards the species' dry margin. We are aware that climatic effects can be much more complex: isolated excessive temperatures can be stressful enough to perturb photosynthesis (as photosynthesis has a thermal optimum at around 45°C, Bennett et al., 2021); or complex interactions exist between temperature and aridity (Ruehr et al., 2016). However, we believe that in arid areas, our two climatic variables capture the main climatic constraint on tree dynamics, given the spatial (all of Europe) and temporal scale (time between surveys ranging from 5 to 20 years) of our data.

4.3 | The effect of climate differed for trees in light and trees in shade

Our results in Figure 4 showed that trees in shade and trees in light responded differently to the stand climatic conditions, resulting in an effect of light competition that varied along climatic gradients. However, the processes underlying these interactions between climate and light competition were different for growth and survival.

For growth (Figure 4, Panel 1a), we showed that trees in light grow faster in both their wet and their warm species margins, whereas there was no difference in growth for trees in shade. This could indicate control by the most limiting factor (van der Ploeg et al., 1999); a tree in shade will not be able to benefit from the favourable conditions of non-limited climatic conditions (with adequate warmth and sufficient water) because it does not have access to its primary resource for photosynthesis: light. Similarly, Ford et al. (2017) observed an effect of climate on the growth of four tree species only when crowding competition was low, since high competition constrained growth even when climatic conditions were favourable.

For survival (Figure 4, Panel 1b), we found that trees in shade had a better chance of surviving in both their cold and their dry species margins, whereas there was no significant difference in survival for trees in light. These results support the stress gradient hypothesis (Bertness & Callaway, 1994; Maestre et al., 2009), which suggests that the importance of facilitative interactions increases in stressful environments. Shade stress intensity depends on climatic conditions (Holmgren et al., 1997), becoming less stressful in colder and drier species margins. Shade can help trees in arid areas by protecting them from photo-inhibition, defined as prolonged exposure to light that causes stress (e.g. through increased heat, drought conditions, excessive irradiance or UV radiation). Photo-inhibition therefore reduces carbon assimilation (Demmig-Adams & Adams III, 2006). Similarly, in colder environments, shade provided by the canopy above protects the tree from harsh conditions, such as frost or wind (Charrier et al., 2015).

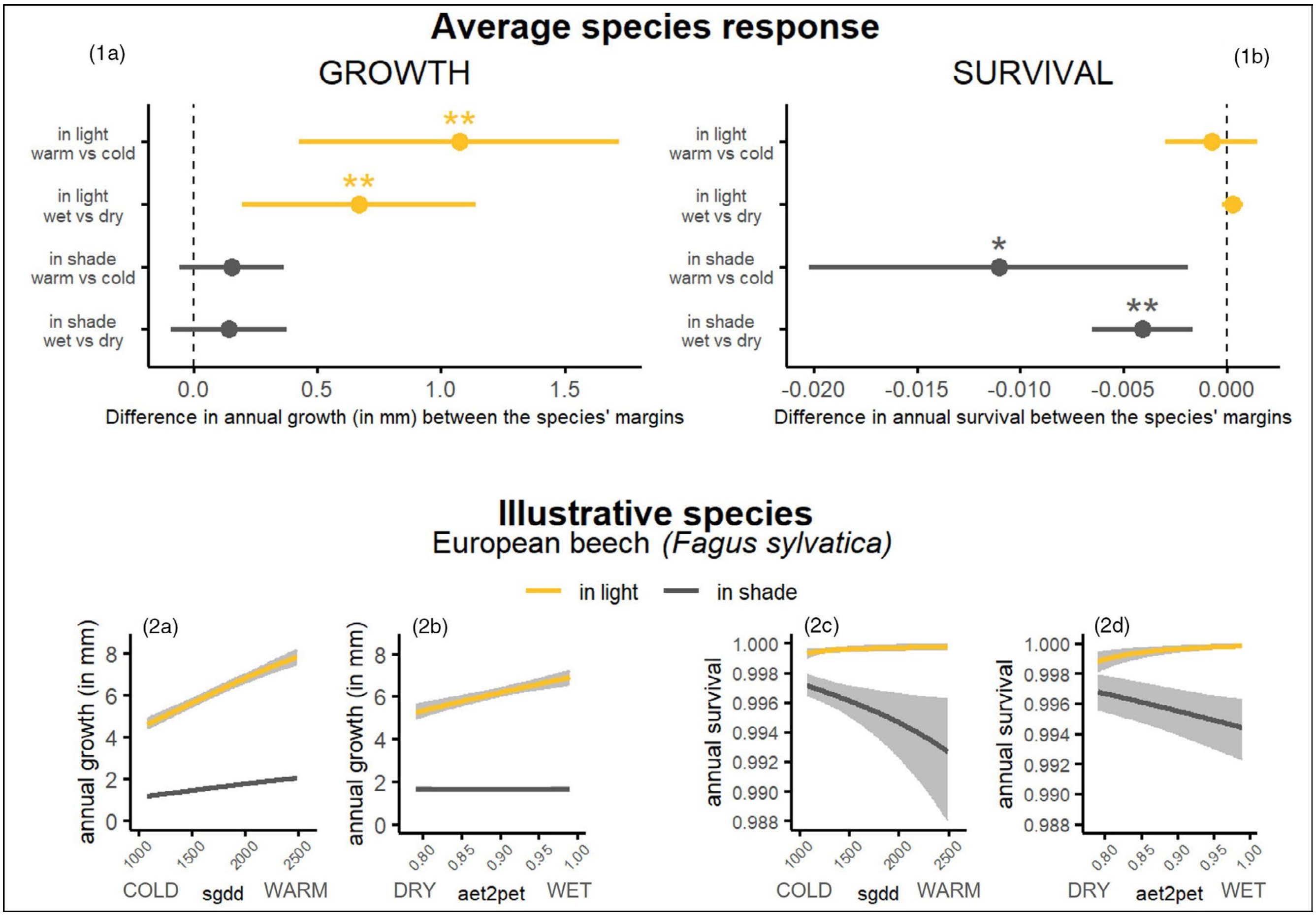


FIGURE 4 Panels (1a and b) show the average response across all species of the difference between margins (warm vs. cold and wet vs. dry) in growth (1a) and survival (1b) for a tree in light and a tree in shade. The error bars show the 95% confidence interval around the mean prediction. Significance of the species margin effect is shown by ****p* value < 0.001; ***p* value < 0.01 and **p* value < 0.05 (see Section 2.4.1). Panels (2a–d) show the prediction of annual growth and survival probability for a major species in Europe, the European beech (*Fagus sylvatica* L.), along its species-specific temperature and aridity gradients. The grey areas represent the confidence interval around the values predicted from the 100 species sets of parameters.

However, the higher survival of trees in shade in stressful conditions cannot be explained by facilitation processes alone. We do not have a clear physiological explanation for this pattern, but two mechanisms could be involved. First, stressful abiotic conditions could lead to plastic variation in traits that allow greater allocation of resources to reserve and structure organs. This process, which is characteristic of a conservative strategy (see Zhou et al., 2024 for cold environments and Rodriguez-Zaccaro & Groover, 2019 for dry environments), could also favour greater tolerance to shade, as observed in cases of polytolerance (Valladares et al., 2016). On the contrary, low-stress abiotic conditions could lead to a plastic allocation of resources for a faster foliage and height growth, characteristic of a shade-avoidance strategy (Henry & Aarssen, 2001), which could be inefficient in the long term for suppressed trees and costly for their survival. At present, there is a lack of studies that have investigated these physiological mechanisms on an intraspecific scale and under different environmental conditions.

4.4 | Species mean sensitivity to light competition varied with species mean aridity niche and shade tolerance

The results in Figure 5 highlight that species mean sensitivity to light competition varies with species mean aridity niche. The effect of light competition on both tree growth and survival was weaker for species whose mean climatic niche is located in more arid climates (i.e. hot, dry Mediterranean climates). Also, on an interspecific scale, our results support the ecological theories that predict a decreasing effect of competition with increasing abiotic stress (Bertness & Callaway, 1994; Grime, 1979; Maestre et al., 2009; Tilman, 1980).

Our results in Figure 5 show that species mean sensitivity to light competition in terms of growth and survival also varied with species shade tolerance. For survival (Figure 5b), our study highlights a direct effect of species shade tolerance, with the species mean sensitivity to light competition decreasing as species shade tolerance increases. These results are relevant because the shade tolerance

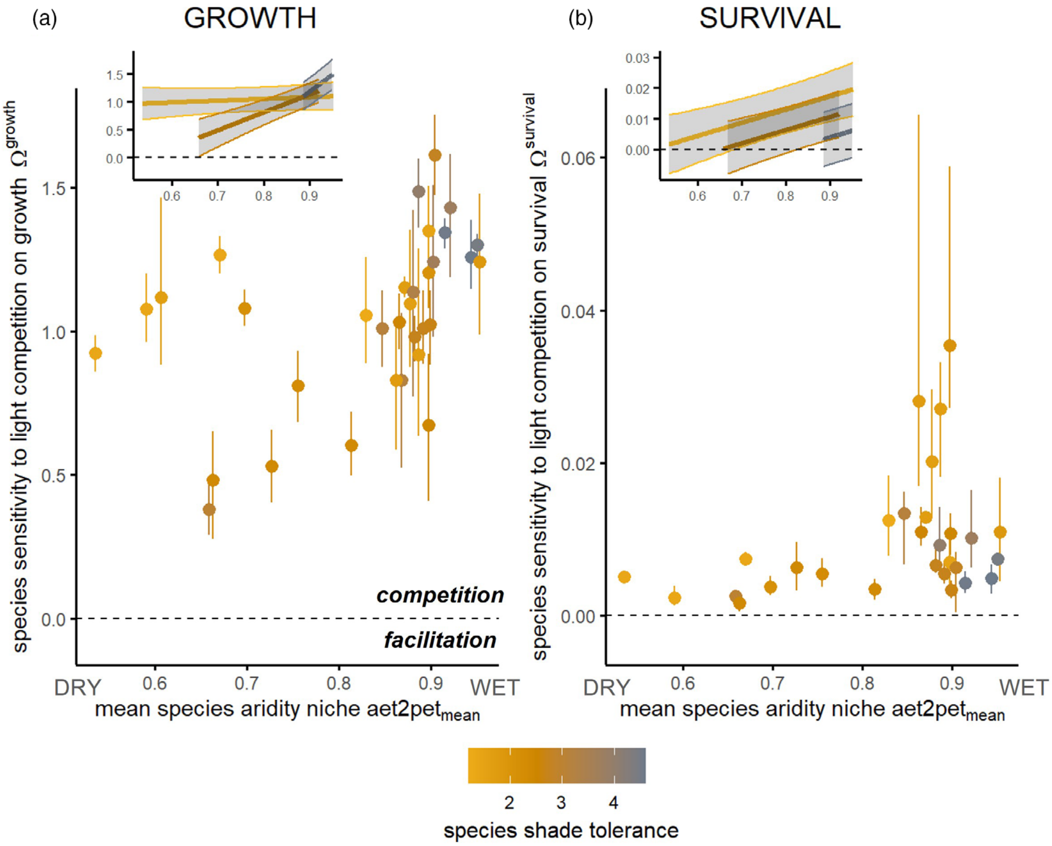


FIGURE 5 Relationships between species mean sensitivity to light competition and species mean aridity niche and shade tolerance for tree growth (Panel a) and survival (Panel b). Points represent the species mean sensitivity averaged over the 100 predictions and error bars represent the 95% quantile interval for the 100 predictions. Insets show the regressions for three values of shade tolerance, respectively 1.5 (shade-intolerant, yellow line), 3 (mid shade-tolerant, brown line) and 4.5 (highly shade-tolerant, black line). The range of the regression on the *x*-axis ($aet2pet_{mean}$) was calculated for each of the three shade tolerance groups from the minimum to the maximum mean aridity niche of the species in that group.

index in Niinemets and Valladares (2006), which we used in our study, is based on the ability of a species to survive in a given level of shade. Similarly, Kulha et al. (2023) found that the effect of asymmetric competition on tree mortality was weaker for shade-tolerant species. For growth (Figure 5a), however, we found an interactive effect between species shade tolerance and species mean climatic niche. The decrease in the species mean sensitivity to light competition towards drier sites was more pronounced for shade-tolerant species. As a result, species living in wetter climates were equally and strongly sensitive to light competition on their growth, regardless of their shade tolerance: trees in light grew rapidly, while trees in shade did not. On the contrary, when comparing species associated with Mediterranean climates, there was an effect of species shade tolerance, with shade-intolerant species being more sensitive to light competition than mid shade-tolerant species. It is important to note that in the Mediterranean climates in our study, all the shade-intolerant species were of the genus *Pinus*, and all the mid shade-tolerant species were of the genus *Quercus*; we did not observe any shade-tolerant species in the Mediterranean area. It is therefore difficult to disentangle the genus effect from the shade tolerance effect. As Niinemets and Valladares (2006) showed an inverse relationship between species shade- and drought tolerance, it is likely that the shade-intolerant genus *Pinus* would be more drought-tolerant, and therefore, Pinus trees in high light could still grow rapidly even with high aridity.

We found a strong negative correlation between species $sgdd_{mean}$ and $aet2pet_{mean}$ along the European latitudinal gradient, with species either living in hot, dry Mediterranean climates at low latitudes or in colder, wetter climates at higher latitudes. This could explain why we found that species mean sensitivity to light competition was not weaker for species associated with cold, stressful climates. In fact, the species in colder climates were also associated with wetter ones, for which we found a greater species mean sensitivity to light competition. We also found that there was a high variability in species mean sensitivity to light competition that was not explained by shade tolerance or $aet2pet_{mean}$, which could indicate effects of other climatic dimensions or ecological strategies. For instance, *Betula pubescens Ehrh.* (downy birch) and *Larix decidua Mill.* (European Larch), despite being shade-intolerant species, had low sensitivity to light competition for survival. In fact, these two species stand out because their mean climatic niche is exceptionally cold compared with the rest of the European climatic gradient.

4.5 | On the complexity of representing tree competition for resources

Our light competition index resulted in an improvement in growth and survival predictions compared with non-resource-specific competition indices (Table 1). This is all the more remarkable as we were unable to take full advantage of the spatially explicit light interception model due to limitations in the forest inventories we used. Firstly, we did not know the exact location of each tree and therefore used random locations. This could lead to an underestimation of the light intercepted by a tree in a gap, or an overestimation for a tree in a dense patch. Second, we used simplified crown shapes based on species-specific crown allometries that ignore the possible adaptability of trees to the surrounding environment. LiDAR would be a promising technology to more precisely represent crown structure and plasticity in forest plots (Terryn et al., 2023), which are likely to improve the estimation of light interception by individual trees. Unfortunately, such data are not currently available for use in European national forest inventories.

We recognise that our light competition index could be correlated to competition for below-ground resources (Craine & Dybzinski, 2013). However, by using a 3D light interception model that takes into account specific characteristics of light (influence of crown shape, geometry and intensity of the light rays, effect of latitude, etc.), we have constructed a competition index that is as specific to light as possible. It was difficult to accurately account for competition for below-ground resources, as explicit physical models of competition for water and nutrients are less common in the literature (Craine & Dybzinski, 2013). These models require detailed information on tree root geometry and soil structure (e.g. HETEROFOR 1.0 model, Wergifosse et al., 2020) and are not yet well suited for large-scale studies. It would have been interesting to observe variations in the effect of competition for below-ground resources along climatic gradients in parallel with light competition. Following the theory of Tilman (1980), we could expect inverse relationships between below-ground and light competition, with the effect of water or nutrient competition increasing on constrained sites.

4.6 | Implications for forest community dynamics

Our study highlights the need to consider interactions between light competition and climatic conditions to correctly predict forest responses to global change. The intensity of the effect on annual tree growth and survival may seem low, but will be amplified over consecutive years through an increasing access to light for the dominant trees and a decreasing access for the suppressed ones. This corresponds to the process of size differentiation among individuals (Oliver & Larson, 1996). Because light competition is more important in climates with higher productivity, differentiation may play a greater role there than in forests where resources are scarce and stress is high. We expect the environment to become more stressful with climate change, which may lead to less differentiation between trees in light and in shade, with potential implications on forest dynamics, structure, biodiversity and ecosystem services (Lindner et al., 2010; McDowell et al., 2020).

AUTHOR CONTRIBUTIONS

Nathéo Beauchamp conceived the ideas and designed the methodology with the help of Georges Kunstler and Benoit Courbaud. Nathéo Beauchamp, Georges Kunstler, Paloma Ruiz-Benito, Miguel A. Zavala, Jarosław Socha, Paweł Hawryło, Matija Klopčič, Emil Cienciala, Vladimír Šebeň, Jonas Dahlgren and Aleksi Lehtonen helped format the forest inventory data. Laura Touzot and Georges Kunstler calibrated the crown allometries. Benoit Courbaud designed and made available the SamsaraLight model. Nathéo Beauchamp formatted the climatic, soil and radiation data with the help of Georges Kunstler and Benoit Courbaud. Nathéo Beauchamp analysed the data with the help of Georges Kunstler and Benoit Courbaud. Nathéo Beauchamp led the writing of the manuscript with important contributions from Georges Kunstler, Benoit Courbaud, Laura Touzot and Paloma Ruiz-Benito. All authors reviewed the drafts and gave final approval for publication. Our study presents a study based on forest inventories from different countries across Europe. Our collective efforts in this study involve researchers and technicians from France, Spain, Germany, Poland, the Czech Republic, Slovenia, Slovakia, Sweden and Finland. The collaboration was open to all interested parties, fostering a dynamic exchange of ideas and expertise across international borders. In promoting inclusivity, we recognise the importance of embracing diverse voices within the scientific community.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14489.

DATA AVAILABILITY STATEMENT

The growth and mortality model outputs needed to reproduce the analysis of this study are stored in the Zenodo repository https://doi.org/10.5281/zenodo.14557538 (Beauchamp, 2024). The parameters of the crown allometries used for each species are available in the same Zenodo. The pipelines for creating the calibration database, calibrating the growth and mortality models, and analysing the output parameters of the models are available in the GitHub repository https://github.com/NatheoB/lightcompet_climate.

Most of the raw national forest inventories are publicly available: Spain (https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-forestal-nacional.html), France (https://inventaire-forestier.ign.fr/dataifn/), Germany (https://bwi.info/Download/de/BWI-Basisdaten/ACCESS2003/), Sweden/Finland in Ratcliffe et al. (2020). For some countries, the raw data cannot be made open because of national regulations, but they can be requested directly from the institutions. They are available on request from the relevant national institute of the country concerned: Slovenia (http://www.zgs.si/eng/homepage/index.html), Poland (https://buligl.pl/web/buligl-en/w/national-forest-inventory), Czech Republic (https://www.czechterra.cz/), Slovakia (https://web.nlcsk.org/en/home-en/).

All soil, radiation, and climate data we used are publicly available: Chelsa climatic data (https://envicloud.wsl.ch/#/?bucket=https%3A%2F%2Fos.zhdk.cloud.switch.ch%2Fchelsav2%2F&prefix=%2F), WorldClim elevation rasters (https://www.worldclim.org/data/worldclim21.html), SRTM30 elevation rasters (https://dwtkns.com/srtm30m/), SoilGrids soil data (https://files.isric.org/soilgrids/latest/data/), European JRC soil rooting depth data (https://esdac.jrc.ec.europa.eu/content/european-soil-database-derived-data) and PVGIS radiation data (https://joint-research-centre.ec.europa.eu/photovoltaic-geographical-information-system-pvgis/getting-started-pvgis/api-non-interactive-service_en).

The SamsaraLight ray tracing model (more details at https://capsis.cirad.fr/capsis/help_en/samsaralight) is publicly available for non-commercial use in the Capsis platform, a simulation platform for forest dynamics models (more details at https://capsis.cirad.fr/capsis/home).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supplementary Materials.

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