Modeling productivity of silver birch (*Betula pendula* Roth.) combining phytocentric and geocentric approaches in northwestern Europe

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Abstract

The current climate emergency and its associated impacts on forest ecosystems are leading forest owners and managers to consider a broader diversity of species to enhance forest resilience. In this context, there is a growing interest in lesser-used timber species, such as silver birch, a promising candidate for forest diversification in Western Europe. Estimates of site productivity are essential to guide forest management decisions, but have not yet been accurately determined for silver birch in northwestern Europe. This study pursuits two main goals: (a) providing dominant height growth curves for birch in southern Belgium; (b) identifying the key biophysical factors affecting the productivity of silver birch within the study area.

In this study, we tested and compared 16 growth models on a stem analysis dataset gathering the past height growth of 68 birch trees from 40 stands. The Duplat and Tran-Ha I model best predicted the dominant height growth. Using this model, the site index (SI) was estimated for 103 stands distributed throughout the study area and its variation was modeled in response to biophysical variables (climatic, edaphic and topographic). The best selected model (R^2 adj=0.50) revealed a positive effect of mean annual temperature on the SI, although limited when maximal soil water content was low. This model was ultimately used to map the spatial variation in birch yield potential in the study area, highlighting the ecological conditions under which birch silviculture could be promoted.

Keywords

Betula pendula – Silver birch – Site index – Height growth – Soil water content – Mean annual temperature

1 Introduction

Forests provide a wide range of essential services contributing to human well-being worldwide (Brockerhoff et *al*., 2017). However, the significant increase in natural disturbances poses a serious threat to the provisioning of forest ecosystem services (Patacca et *al*., 2023; Wolf and Paul-Limoges, 2023). Over the last decades, European forests have experienced an increase in extreme events related to climate change (Büntgen et *al*., 2021). As a result, increased mortality has been observed for all major tree species (George et *al*., 2022). Norway spruce (*Picea abies*), one of the most important economic species in Europe, has greatly suffered from the extreme drought of 2018, whose conditions favored a bark beetle outbreak, leading to several million hectares of damaged forests (Arthur et *al*., 2024; Hlásny et *al*., 2021). European beech (*Fagus sylvatica*), another major timber tree species, has also demonstrated high climate sensitivity, with significant growth declines ranging from -20% to -90% depending on the region considered, to be expected by 2090 (Martinez del Castillo et *al*., 2022). Mortality episodes have also been observed in species previously noted as drought-tolerant, including pedunculate and sessile oaks (*Quercus robur, Quercus petraea*), as well as Scots pine (*Pinus sylvestris*; Schuldt et *al*., 2020). This alarming context forces us to deeply reconsider the way forests are managed (Bolte et *al*., 2009; Millar et *al*., 2007).

One solution consists of enhancing forest resilience by promoting forest diversification through the integration of species presumed to be more tolerant to future climatic conditions (Bolte et *al*., 2009; Messier et *al*., 2022). Forest diversification can be ensured by selecting non-native species or provenances better adapted to the future climatic conditions (Williams and Dumroese, 2013). However, the introduction of non-native species, although drought-tolerant, entails major risks for native biodiversity as this might lead to habitat losses and introduction of invasive species (Aurore et *al*., 2024; Dimitrova et *al*., 2022; Felton et *al*., 2016; Mueller and Hellmann, 2008). Alternatively, the possibility of enriching forest stands with abundant but

lesser used timber species, e.g., Norway mapple (*Acer platanoides*), European hornbeam (*Carpinus betulus*), little leaved lime (*Tilia cordata*), silver birch (*Betula pendula*), is increasingly being considered (Koch et *al*., 2022; Walentowski et *al*., 2017) even though their vulnerability to climate change remains to be clarified (Fuchs et *al*., 2021; Hemery et *al*., 2010; Kunz et *al*., 2018; Latte et *al*., 2020; Leuschner et *al*., 2024; Matisons et *al*., 2022). Among those indigenous species, silver birch (*Betula pendula* Roth.) seems to be a promising candidate (Biber et *al*., 2020; Dubois et *al*., 2020).

Silver birch is a light-demanding pioneer species distributed throughout Eurasia, which represents the widest distribution range of all European broadleaved tree species (Ellenberg, 1996). This exceptionally large ecological range is explained by the broad climatic tolerance and sustained growth on various soil conditions, even on constraining sites (Atkinson, 1992). Birch colonizes disturbed environments and can contribute to the rapid restoration of wood production, highlighting the importance of early successional stages in maintaining forest ecosystem resilience (Bormann et *al*., 2015; Swanson et *al*., 2010). As a nurse species, birch creates favorable conditions for the establishment of other species (Stark et *al*., 2015). It provides light in the understory and improves soil fertility, porosity and water infiltration, promoting the development of mixed forests (Jonczak et *al*., 2020; Perala and Alm, 1990). Apart from the Baltics and Finland, silver birch has received little attention for commercial purposes (Dubois et *al*., 2020; Hynynen et *al*., 2010; Lee et *al*., 2024). However, the physical and mechanical properties of birch timber make it as valuable as beech, a species of significant economic importance (Luostarinen and Verkasalo, 2000). Birch species are gaining in popularity in Western Europe where the possibility of producing large-sized logs with adapted and dynamic silvicultural practices has recently been assessed (Dubois et *al*., 2021). The short rotation associated with birch silviculture (50 years; Dubois et *al*., 2021) is a significant advantage in the context of climate change, as trees are exposed to extreme climatic events for

a shorter period of time (Lindner et *al*., 2000; Spittlehouse and Stewart, 2003). As birch has only recently gained the interest of foresters, key information for its management, especially regarding its productivity potential, is still lacking.

Site productivity refers to the quantitative estimation of a site-specific capacity to produce plant biomass (Skovsgaard and Vanclay, 2008). This estimation remains crucial for guiding forest management decisions, helping forest owners and managers in species selection (i.e., species-site suitability), designing optimal silvicultural strategies, predicting timber yield, and assessing carbon sequestration potential. Site productivity can be estimated through two approaches (Skovsgaard and Vanclay, 2008): phytocentric and geocentric. For even-aged stands, the phytocentric approach is usually applied to estimate the site index (SI), i.e., the dominant height reached by a forest stand at a reference age (Skovsgaard and Vanclay, 2008). As the height growth of dominant tree is known to be less affected by stand density than its diameter growth, SI mainly depends on site conditions (Spurr and Barnes, 1973). Dominant height growth curves, linking height and age of dominant trees, have usually been modeled using nonlinear relationships. The resulting models have notably been used to predict the dominant height at a given age and, therefore, to estimate phytocentric SI.

However, in some situations (e.g. unknown forest stand age, non-forested area, juvenile stand), SI cannot be assessed using phytocentric methods and can be estimated from other site characteristics using a geocentric approach (Skovsgaard and Vanclay, 2008). This approach is based on the empirical relationship between site productivity and biophysical factors (climate, soil and topography). This method can take into account the non-stationarity of forest productivity over time, which is crucial in the context of climate change (Bontemps et *al*., 2009). The geocentric approach have been used to predict future trends in height growth (Albert and Schmidt, 2010; Brandl et *al*., 2018; Pau et *al*., 2022) and to better understand the ecological niche constraints of species (Seynave et *al*., 2008). As spatial biophysical data are often easily

available, the geocentric approach is a cost-effective way to predict site index over large areas (e.g. Aertsen et *al*., 2012; Parresol et *al*., 2017).

Although birch productivity is well documented in the northern regions (Eriksson et *al*., 1997; Karlsson et *al*., 1997; Lee et *al*., 2024; Liziniewicz et *al*., 2022), this important information remains poorly explored in other parts of its distribution range (Diéguez-Aranda et *al*., 2006; Hein et *al*., 2009), particularly in northwestern Europe where birch silviculture is gaining popularity. Our study has two main objectives: (i) develop a model for predicting *B.pendula* site index based on dominant height and age using a phytocentric approach; (ii) develop a second model identifying the key biophysical factors affecting *B.pendula* site index through a geocentric approach. This model was ultimately used to map the spatial variation in birch yield potential in the study area.

2 Material and Methods

2.1 Study area

The study area was located in southern Belgium of northwestern Europe (Fig. 1). The sites covered a wide range of ecological conditions and were distributed across two ecoregions, known as the lowlands and the uplands (Campioli et *al*., 2012). The lowlands ecoregion was characterized by low elevations (173±88 m), the lowest amount of rainfall (863±84 mm) and the highest temperature (9.2±0.5 °C) while the uplands ecoregion was characterized by high elevations (428±90 m), low temperatures (7.7±0.5 °C) and high amounts of rainfall (1105±110 mm). The study focused on silver birch (*Betula pendula* Roth.), but due to similar morphological characteristics, some individuals may belong to downy birch (*Betula pubescens* Ehrh.), the other birch species found in Belgium.

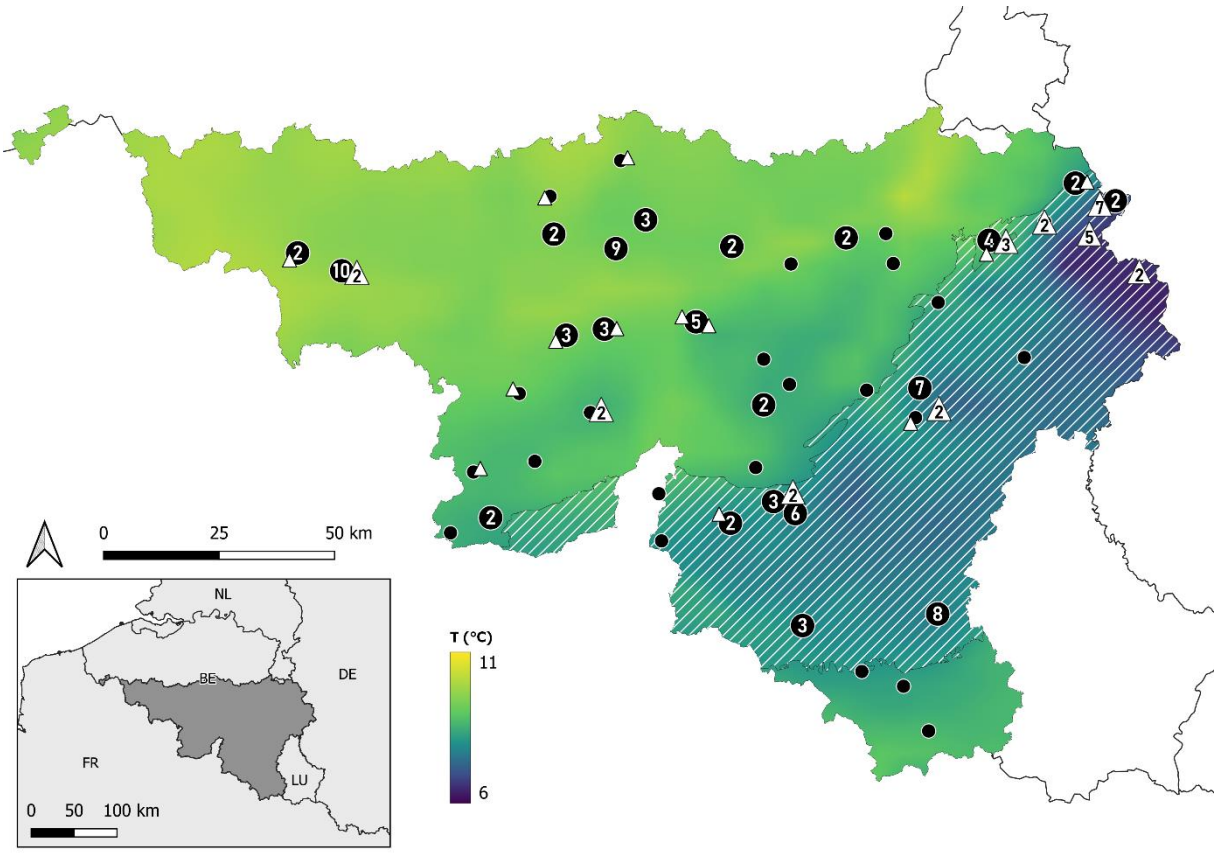

Fig. 1: Birch locations in southern Belgium for the phytocentric (triangular white dots) and geocentric approach (round black dots) with mean annual temperature over the 30-year period

1961-1990. Numbers indicate several dots close to each other. Striped area indicates the uplands ecoregion within the study area.

2.2 Phytocentric approach

The phytocentric approach consisted in collecting records of height and age of dominant trees with stem analysis (section 2.2.1) and modelling the relationship between height (H_{DOM}) and age (Age; Eq. 1; section 2.2.2) of dominant trees. Each model included the b_i parameter that was fitted individually for each stand *i* and that expressed stand productivity level (Perin et *al*., 2013).

$$H_{DOM} = f(\text{Age}, b_i, a, c, d, p, r) \quad (1)$$

with *a*, *c*, *d*, *p*, *r* the fixed parameters.

For any pair of Age and H_{DOM}, b_i could be estimated by inversion of eq. 1 (Eq. 2):

$$b_i = f(H_{DOM}, \text{Age}, a, c, d, p, r) \quad (2)$$

With H_{DOM} and Age corresponding to the dominant height and age of an even-aged stand *i*. Consequently, combining eq. 1 and eq. 2, the dominant height reached at the reference age, i.e. the site index could be estimated (Eq. 3):

$$SI_i = H_{DOM} \text{ at } Age_{ref} = f(H_{DOM}, \text{Age}, Age_{ref}, a, c, d, p, r) \quad (3)$$

With SI_i corresponding to the site index and Age_{ref} to the chosen reference age.

2.2.1 Stem analysis

Stem analyses (SA) were used to reconstruct the past height growth of birch trees (Fig. 2). The trees for SA were selected from 40 even-aged stands covering most of the birch range and geographical locations, with elevation ranging from 63.9 m to 601.6 m and from acid peaty soils to well-drained rich soils (triangular white dots in Fig. 1). 23 stands were sampled in 2004 and 17 more stands in 2019 and 2020. For each stand, sampling points were established within small homogeneous groups of birch trees covering 0.1 ha. SA were conducted within plots of 500 m² centered on these homogeneous groups to minimize edge effects from surrounding

158 stands. For logistical reasons, the number of trees sampled per plot was limited to three, with
159 an average of two trees per plot. This corresponds to the 60 largest trees per hectare, with an
160 average of 40 largest trees per hectare. Although this approach differs from the usual definition
161 of stand dominant height - the mean height of the 100 largest trees per hectare - it has already
162 been suggested as appropriate for small-sized sampling units or cases where only a few leading
163 trees can be measured (Carmean, 1996; Le Goff et *al*., 1982). For every cut tree, stem disks
164 were collected at the base (0.2 or 0.5 m) as well as at breast height (1.3 m). Subsequent disks
165 were collected with 2 m intervals up to the top of the tree. The name of the sample plot, the tree
166 number and disk height were written on the non-working surface of the disks. The disk
167 thickness was approximately 8 cm (4 cm above and 4 cm below the line). The disks were placed
168 in a cool and ventilated place for drying to prevent fungi development.
169 After being air-dried, the working surfaces of the disks were planed and progressively sanded
170 (grit 80-320). For the disks collected in 2004, the number of rings was counted on 2 to 3 paths
171 from pith to bark on each disk using a binocular microscope. The disks from later samplings
172 (2019 and 2020) were scanned at high resolution (≥ 1200 DPI) with an Epson® scanner
173 (10000XL), rings were then counted on different paths using the WinDendro® 2021 software
174 (Regents Instruments). Birch trees that had uncertain age estimates due to heart rot, or had
175 anomalies in the growth trajectories were excluded from the dataset. As cross-section lengths
176 did not coincide with periodic height growth, the height-age data from the SA were corrected
177 following the method proposed by Salas-Eljatib (2021). The resulting dataset characteristics
178 can be found in Table 1.

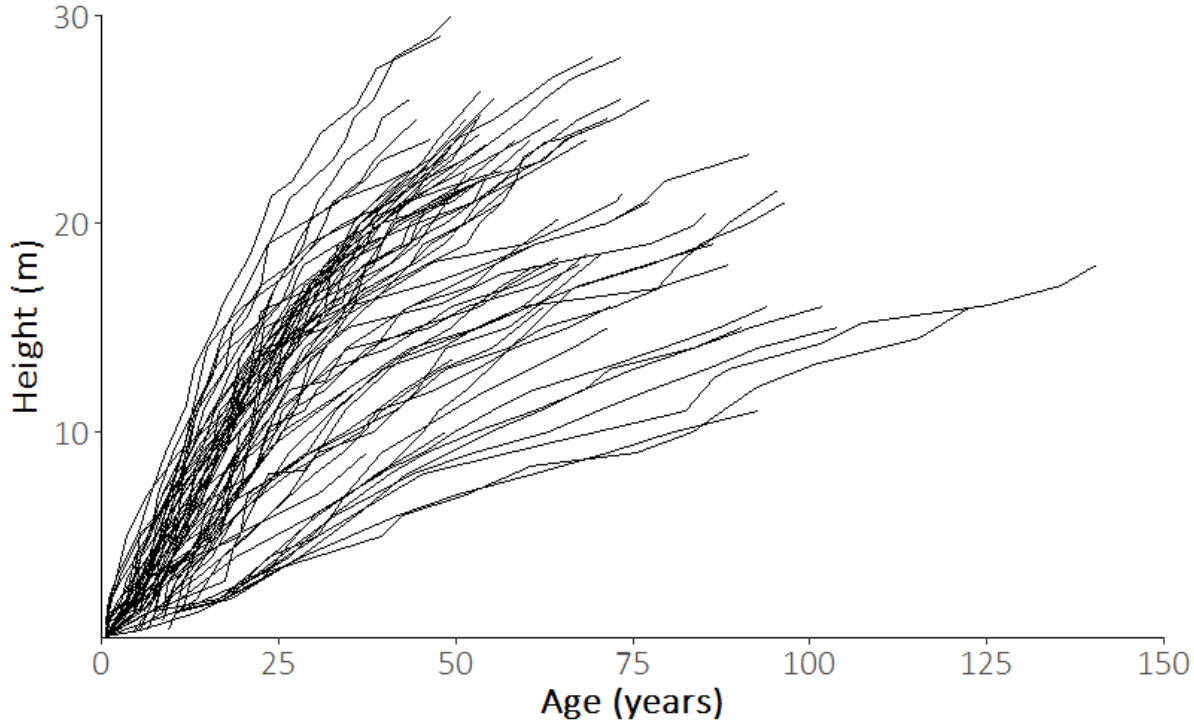

Fig. 2: Observed height-age series from the stem analysis of the 68 birch trees sampled in 40 stands in southern Belgium.

Table 1: Summary statistics of stands used in stem analyses for lowlands and uplands.

	Lowlands	**Uplands**
No. of sites	14	26
No. of trees	29	39
No. of paired age-height records	526	495
Mean age ± sd (years)	58.7 ± 10.4	69.7 ± 25
Mean height ± sd (m)	24.7 ± 2.5	19.1 ± 3.8
Mean altitude ± sd (m)	188.6 ± 82.9	459.8 ± 112.3

2.2.2 Dominant height growth curves

We tested 16 commonly used non-linear models to predict dominant height growth in response to tree age (Table 2; Perin et *al*., 2013). All functions were fitted using non-linear mixed effects models computed with the *nlme* R package (Pinheiro et *al*., 2024). We addressed the first order autocorrelation (i.e., the height reached at age *n* is correlated with the height reached at age *n*-

189 *1*) and heteroscedasticity using a continuous autoregressive correlation structure as well as a
190 variance power function of total age. A parameter *b* was estimated for each stand (i.e., *b*~stand
191 in the fixed parameters of the nlme function) and a tree-level random effect was added to this
192 parameter to account for differences between SAs performed in the same stand (i.e., *b*~1|tree in
193 the random parameters of the nlme function). The other parameters (*a*,*c*,*d*,*p*,*r*), hereafter
194 referred to as model fixed parameters, were considered as fixed effects and, for each of them, a
195 unique value was fitted over the whole dataset.
196 The statistical performance of the tested models was assessed examining the maximized log-
197 likelihood (LogLik), the Akaike Information Criterion (AIC), the root-mean-square error
198 (RMSE) and the distribution of residuals.
199 The best model was selected based on the overall consideration of the aforementioned criteria.
200 We verified that the model fixed parameters had value significantly different from zero (p-
201 value<0.05; Table A1). Furthermore, we assessed the trend in the residuals of the best selected
202 model as a function of age and ecoregion (lowlands and uplands; see Fig. 1) using an analysis
203 of covariance. This test was performed to determine whether the model fitting should also
204 depend on the ecoregion.

205 *Table 2: Names, abbreviations and mathematical formulations of all model functions tested on*
206 *the SA dataset. The productivity level parameter corresponds to b_i whereas a, c, d, p and r are*
207 *model fixed parameters.*

Name	Abbreviation	Mathematical equation
Mitscherlich	M	$b_i * \left(1 - \exp\left(\frac{(a - Age)}{c}\right)\right)$
Gompertz	G	$b_i * \exp\left(-exp\left(\frac{(a - Age)}{c}\right)\right)$
Modified Gaussian	MG	$b_i * \left(1 - \exp\left(-\left(\left(\frac{(Age - a)}{c}\right)^2\right)\right)\right)$
Log-logistic	Log	$\frac{b_i}{(1 + \left(\frac{Age}{a}\right)^{-c})}$
Arc-tangent	Arc	$\left(\frac{b_i}{\pi}\right) * \left(\frac{\pi}{2} + \text{atan}\left(\frac{(Age - a)}{c}\right)\right)$
Hyberpolic amplitude	Hyp	$\left(\frac{b_i}{\pi}\right) * \left(\frac{\pi}{2} + \text{asin}\left(\tanh\left(\frac{(Age - a)}{c}\right)\right)\right)$
Johnson Schumacher	JS	$b_i * \exp\left(\frac{-c}{(Age - a)}\right)$
Chapman-Richards anamorphic	CN	$b_i * (1 - \exp(-a * Age))^c$
Chapman-Richards polymorphic	CP	$a * (1 - \exp(-b_i * Age))^c$
Bailey and Clutter anamorphic	BN	$\exp\left(b_i + a * \left(\frac{1}{Age}\right)^c\right)$
Bailey and Clutter polymorphic	BP	$\exp\left(a + b_i * \left(\frac{1}{Age}\right)^c\right)$
Duplat and Tran-Ha I	DTI	$(a * Age + b_i) * \left(1 - \exp\left(-\left(\frac{Age}{c}\right)^d\right)\right)$
Duplat and Tran-Ha II	DTII	$(a * Age + b_i) * \left(1 - \exp\left(-\left(\frac{Age}{c}\right)^d\right)\right) + p * Age$
Duplat and Tran-Ha III	DTIII	$(a * Age + b_i) * \left(1 - \exp\left(-\left(\frac{Age}{c}\right)^d\right)\right)^r + p * Age$

Duplat and Tran-Ha IV	DTIV	$(a * \ln(Age) + b_i) * \left(1 - \exp\left(-\left(\frac{Age}{c}\right)^d\right)\right)$
Duplat and Tran-Ha V	DTV	$(a * \ln(Age) + b_i) * \left(1 - \exp\left(-\left(\frac{Age}{c}\right)^d\right)\right) + p * Age$

2.2.3 Selection of a reference age

The reference age used to compute SI is commonly set at 50 or 100 years for long-lived tree species such as spruce, oak and beech (Albert and Schmidt, 2010; Seynave et *al*., 2008). However, this age cannot be used to define the site index for birch, whose longevity rarely exceeds 100 years and for which recommended rotation are between 50 and 60 years (Dubois et *al*., 2021). We chose a reference age of 30 years following the recommendations of (Goelz and Burk, 1992) (see Appendix B). This reference age also corresponded to the end of the maximum growth phase of birch (Wilhelm and Rieger, 2023).

2.2.4 Cross-validation

The validation of the best model was performed using a repeated k-folds cross validation procedure which is assumed to be more accurate and reliable for the estimation of predictive accuracy compared to the simple k-folds cross validation (Nakatsu, 2021). The dataset was randomly divided into k=4 roughly equal-sized parts (17 trees), three folds being used for model training (training dataset) which is then applied to the remaining part (validation dataset). The best model formula (section 2.1.1) was fitted on each training dataset, resulting in four models and four set of fixed parameters (*a*,*c*,*d*,*p*,*r*). For each tree in the validation dataset, the *b* parameter was estimated based on the fixed parameters by inverting the mathematical equation (Eq. 2). The *b* parameter was estimated using the age-height couple for which the age was the closest to the best reference age found in section 2.1.3. Once *b* parameter was estimated, it was possible to predict the dominant height (Eq. 1) for all other age-height couples for each tree of

229 the validation dataset. For each validation dataset, the mean error (mean of the residuals; ME)
230 and RMSE were calculated based on the observed and predicted heights.
231 The whole procedure was repeated 10 times, resulting in 40 validation ME and RMSE which
232 were averaged and used as indicators of the model predictive performance.

233 2.3 Geocentric approach

234 Using additional plot data and the fitted dominant height growth curves (section 2.2.2), the SI
235 (Eq. 3), a proxy of birch productivity, was estimated for 103 stands and modeled in response to
236 variables describing biophysical conditions (Eq. 4).

237 $SI = f(\text{edaphic, climatic, topographic})$ (4)

238 2.3.1 Sampling design

239 This approach was applied to 103 circular plots (Table 3), in even-aged stands located across
240 southern Belgium (round dots in Fig. 1). For each stand, dominant height was calculated based
241 on the 100 largest trees per ha whereas stand age was obtained by counting rings on increment
242 cores collected from one or two dominant trees.

243 *Table 3: summary statistics of the 103 sample plots for the geocentric approach*

	Mean	**Standard deviation**	**Minimum**	**Maximum**
Age (years)	45	14	21	94
Dominant height (m)	21.2	3.9	9.3	28.9
Circumference at 1.3m (cm)	84	29	35	177
Site index (m)	16.9	2.9	7.0	24.6
Plot area (m^2)	557	354	30	2324
Number of trees per ha	737	637	96	2333

244

245 2.3.2 Variables extraction

246 Using the equation developed in section 2.2.2, the *b* parameter was estimated for each stand
247 based on its age and dominant height, and the site index (dominant height at 30 years; response
248 variable) was then calculated.

Meteorological data were extracted from databases of the Royal Meteorological Institute of Belgium. We computed several climatic variables over the 30-year period from 1961-1990, which was assumed as the period having mostly influenced trees growth until they reached the reference age of 30 years (see section 2.2.3). Based on daily observational gridded data with a spatial resolution of 5 km (Journée et *al*., 2019), the following variables were determined for each stand location: mean annual temperature (MAT; °C), mean April-September (growing season) temperature (GST; °C), annual precipitation (PREC; mm) and April-September precipitation sum (GSP; mm), summer water balance (SWB; mm) and growing season length (GSL; days). The SWB corresponded to the difference between the precipitation and the potential evapotranspiration during the period April-September. The GSL was calculated according to European Climate Assessment (Schulzweida and Quast, 2015), as the difference between the first day with a mean temperature exceeding 10°C for at least 6 consecutive days and the first day with mean temperature below 10°C for at least 6 consecutive days (within the last 6 months).

A topographic categorical variable was included in the analysis. This variable was obtained from a 10 m resolution digital map classifying the landscape into four categories: cold north-east facing slopes (NESLP), south-west facing slopes (SWSLP), neutral sites (NS) and valley bottom (VB; Wampach et *al*., 2017).

Edaphic variables potentially influencing tree growth were also included in the analysis. Forest soil nutrient availability (NUT), obtained from spatial data with a resolution of 10 m, was classified into four categories: hyper-oligotrophic soils (H-OLIGO), oligotrophic soils (OLIGO), lightly acidic soils (ACID), and mesotrophic to rich soils (MESO; Lisein et al., 2022). We also considered the soil depth (SD; cm) and the maximal soil water content (SWC; mm), which were available as spatial data with a resolution of 10 m (Legrain et *al*., 2014;

273 Ridremont et *al*., 2011). SWC depended on the soil texture, stoniness and the maximum depth
274 of the soil profile. Summary statistics of all variables are presented in Table 4.

275 *Table 4: Summary statistics of biophysical variables used in the geocentric approach*

Type	Class	Variable	Description	Mean	St.dev.	Min	Max
Continuous	Climatic	MAT	Mean annual temperature (°C)	8.64	0.70	7.07	9.66
		GST	April-September mean temperature (°C)	13.24	0.61	11.78	14.17
		PREC	Precipitation sum (mm)	950.0	140.9	774.7	1268.0
		GSP	April-September precipitation sum (mm)	453.2	50.9	387.7	597.0
		GSL	Growing season length (days)	184.5	9.3	163.6	200.7
		SWB	Summer water balance (mm)	-17.25	54.07	-92.18	143.0
	Edaphic	SD	Soil depth (cm)	87.82	35.21	20.00	125.00
		SWC	Soil water content (mm)	152	76	14	261
Type	**Class**	**Variable**	**Description**	**Levels**	**No. observation**		
Categorical	Topographic	TOPO	Topographic position	NESLP	4		
				SWSLP	9		
				NS	81		
				VB	9		
	Edaphic	NUT	Nutrient availability	H-OLIGO	12		
				OLIGO	38		
				ACID	31		
				MESO	22		

276

2.3.3 Statistical analyses

The climatic, topographic and edaphic variables were used to develop a geocentric model in order to predict SI using generalized additive models (GAM) with the *mgcv* package in R (Wood et *al*., 2016). This statistical tool provides flexibility in cases of non-linear relationships between predictors and the response variable. As a first step, different models were built with all variables, except those with Pearson's correlations values exceeding 0.7 or -0.7, in order to avoid collinearity (Figure S2). Then, a manual backward stepwise approach was used to remove variables according to the AIC value. The best model was selected based on the lowest AIC value and the smallest number of retained variables, ensuring a parsimonious and easily interpretable model. An interaction term was investigated between the remaining climatic and soil variables. We verified model assumptions examining model residuals over predicted values. Using 10 repeated 5-fold cross-validations, we calculated the RMSE and adjusted R^2 for each model to estimate its prediction error and the percentage of variance explained by the selected predictors (Table S4).

2.3.4 Mapping predictions of the site index in southern Belgium

The best geocentric model was used to produce maps of the potential SI of silver birch over the study area for the reference period 1961-1990 and by considering an increase of 1.5°C in mean annual temperature compared to this reference period. To do so, a regular grid of points spaced 100 m apart was generated across southern Belgium. For each point, the values of model variables were extracted, and SI (the dominant height at 30 years) was then predicted using our geocentric model. The SI predictions were categorized based on whether they fell within the model's calibration domain. Predictions within the calibration domain corresponded to mean annual temperature (MAT) and soil water content (SWC) values within the range of the obervations. Predictions outside the calibration domain were further subdivided: those within the observed range of SI values and those outside the observed range of SI. Predictions in this

latter category were excluded and highlighted using a unique color for clarity. All predictions were rasterized using the R package *Stars* (Pebesma and Bivand, 2023). For illustrative purposes, the same methodology was applied to produce a second predictive map assuming a 1.5°C increase in MAT, the other model variable (SWC) remaining unchanged. The two predictive maps were then used to calculate and illustrate the percentage increase in SI associated with the 1.5°C temperature rise. Additionally, for each predictive map, the associated GAM standard error map was also produced.

3 Results

3.1 Phytocentric approach

3.1.1 Dominant height growth models

The models based on the Duplat and Tran-Ha equations (DTI, DTII, DTIII, DTIV, DTV: described in Table 2) presented the best statistics, with the lowest AIC, LogLik and RMSE values (Table 5). Although the model based on the modified Gaussian equation ranked first according to the AIC criteria, the RMSE was among the worst. Models based on Arc-tangent and hyperbolic equations (Arc, Hyp) performed relatively poorly as indicated by their high AIC and RMSE values and their low LogLik values (Table 5). The other models (G, CP, CN, M, Log, JS, BN, BP) showed similar but lower performance statistics.

The models based on the DTI, DTII and DTV equations presented very similar performance. The DTV model ranked second according to the AIC and logLik criteria, followed by the DTI and DTII models. The DTI model had fewer fixed parameters (*a*, *c*, *d*) compared to the DTII and DTV models (*a*, *c*, *d*, *p*), which helps to avoid over-parameterization. After a visual inspection of the residuals, the DTI model was selected for predicting dominant height. The analysis of covariance showed no significant difference between the residuals for the stands located in the lowlands and in the uplands (Table A2). Dominant height growth curves, developed for site index values of 5, 10, 15 and 20 m at 30 years, were well representative of birch potential productivity in Belgium (Fig. 3).

The residuals of the DTI growth model showed no heteroscedasticity in the range of height prediction (Figure A1). Across all age classes, the mean value of residuals remained below 0.5 m, indicating the DTI model's strong performance across various age ranges (Figure A2). The fixed parameters (*a*, *c*, *d*) in the best model were highly significantly different from zero, leading us to retain all of them (Table A1).

The formulation of the best model (DTI) was:

$$H_{DOM} = (a * Age + b_i) * \left(1 - \exp\left(-\left(\frac{Age}{c}\right)^d\right)\right) \quad (5)$$

where H_{DOM} was the dominant height (in m); Age was the stand age; *a*, *c*, *d* were the model fixed parameters; b_i was the site-specific parameter depicting stand productivity.

The productivity level of a given stand can be calculated for any dominant height-age pair, with an inversion of Eq. 5:

$$b_i = \frac{H_{DOM}}{1-\exp\left(-\left(\frac{Age}{c}\right)^d\right)} - a * Age \quad (6)$$

The SI of a given stand was found by combining Eq. 5 and Eq. 6:

$$SI = \left(a * (Age_{ref} - \text{Age}) + \frac{H_{DOM}}{1-\exp\left(-\left(\frac{Age}{c}\right)^d\right)}\right) * \left(1 - \exp\left(-\left(\frac{Age_{ref}}{c}\right)^d\right)\right) \quad (7)$$

where Age_{ref} is the selected reference age (chosen to be 30 years).

The results of the cross-validation for the DTI model indicated a RMSE of 1.41 m and a ME of -0.024 m (Table S1).

346 *Table 5: Akaike Information Criterion (AIC), maximised log-likelihoods (LogLik) and root*

347 *mean square error (RMSE; m) for all models tested on the SA dataset.*

Model	AIC	LogLik	RMSE	ΔAIC
MG	2506.4	-1207.2	4.03	0.0
DTV	2506.9	-1205.4	1.22	0.5
DTI	2507.3	-1206.6	1.23	0.9
DTII	2508.0	-1206.0	1.22	1.6
DTIII	2513.5	-1207.8	1.33	7.1
DTIV	2533.2	-1219.6	1.26	26.8
BP	2552.8	-1230.4	1.39	46.4
CP	2557.2	-1232.6	1.38	50.7
BN	2581.7	-1244.8	1.47	75.3
JS	2588.6	-1248.3	1.47	82.2
Log	2590.2	-1249.1	1.48	83.7
M	2604.7	-1256.4	1.55	98.3
CN	2607.4	-1257.7	1.50	100.9
G	2720.2	-1314.1	1.74	213.8
Hyp	2839.7	-1373.9	2.32	333.3
Arc	2898.4	-1403.2	3.04	392.0

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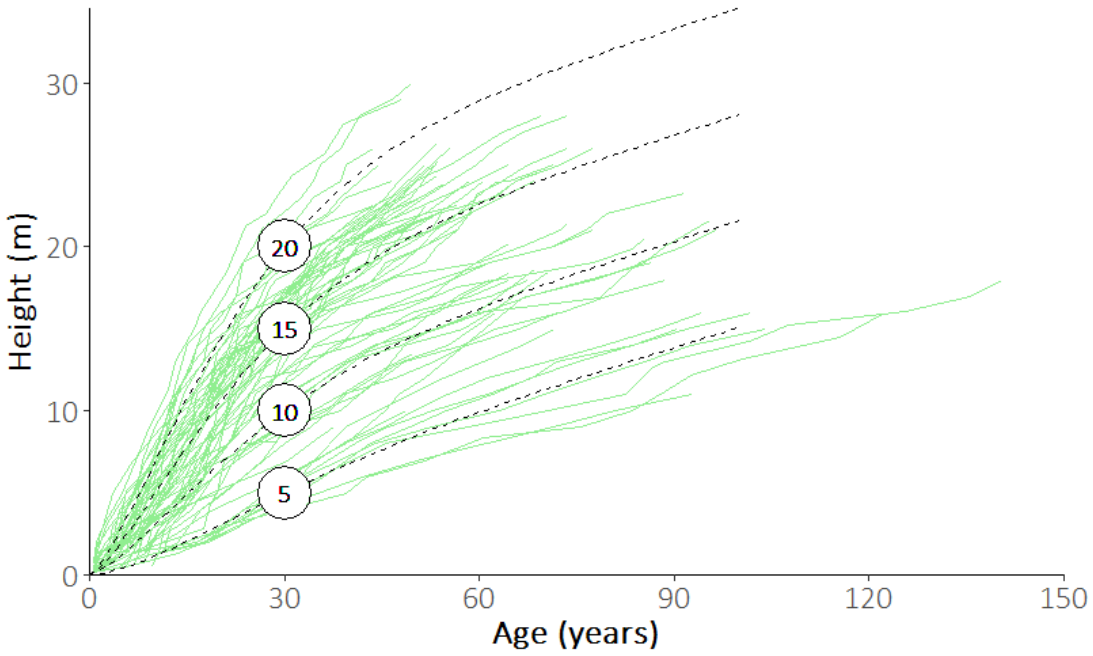


349

350 *Fig. 3: Duplat and Tran-Ha I model height trajectories corresponding to given values of site*

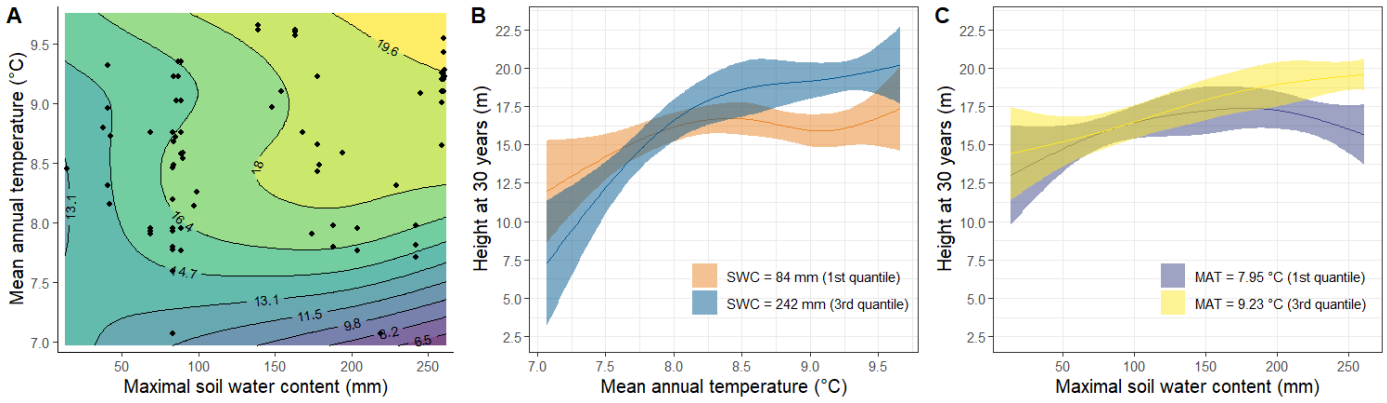
351 *index (5, 10, 15 and 20 m at a reference age of 30 years, dashed lines). These model predictions*

352 *were superposed on the observed height growth series from stem analysis (green solid lines).*

3.2 Geocentric approach

3.2.1 Effects of climate and soil factors on birch productivity

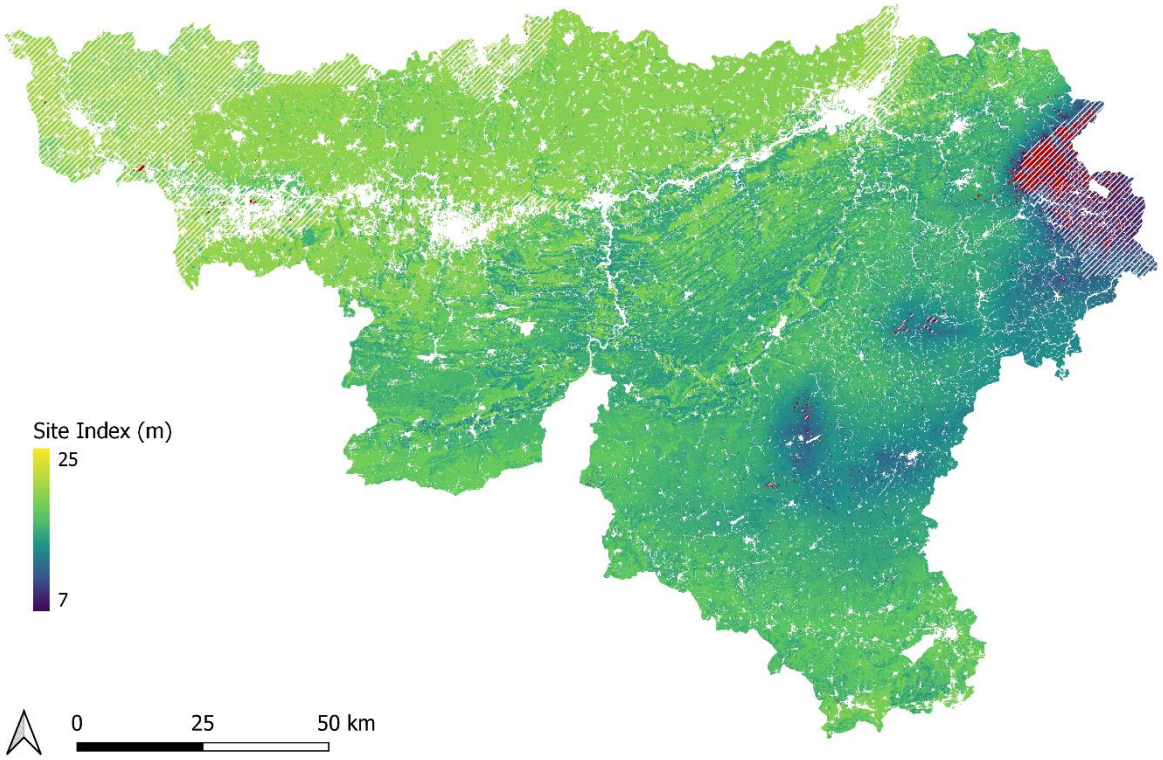
The stepwise selection procedure identified the best model as the one including a climatic variable, the mean annual temperature (MAT) interacting with an edaphic variable, the maximal soil water content (SWC) (Table S3). This model explained 55 percent of the deviance (Table C1) and the examination of residuals over predicted values did not reveal any particular trend (Figure C1). The positive effect of temperature on the SI depended on the value of the maximal soil water content considered. The positive effect of temperature on the SI was limited for SWC values below 100 mm (Fig. 4A). For a given and low value of SWC (84 mm), the increase in mean annual temperature led to a small increase in SI, while this increase was stronger for a high value of SWC (242 mm). Above 8°C in MAT, the increase in SI became less pronounced for a given and high value of SWC (242 mm), while the SI tended to decrease slightly from this threshold temperature when a low value of SWC (84 mm) was considered. Specifically, below 8°C, the increase in SI was about 10 m per degree for a SWC value of 242 mm, whereas the increase was much lower for a SWC value of 84 mm, at about 5 m per degree (Fig. 4B). The increase in SWC had a positive effect on the site index, particularly pronounced from 8°C in MAT (Fig. 4A). For a given mean annual temperature value of 7.95°C, the SI started to decrease from a SWC value of about 200 mm (Fig. 4C).



371 *Fig. 4: Biophysical factors driving birch site index (dominant height at 30 years; predicted*
372 *values in m) in southern Belgium. (A) Contour plot showing the effect of interaction between*
373 *the mean annual temperature (MAT; °C) and the maximal soil water content (SWC; mm) on*
374 *site index values; black dots correspond to the observations. (B) Effect of MAT on site index*
375 *for two levels of SWC: the first quantile (84 mm) and the third quantile (242 mm). (C) Effect of*
376 *SWC on site index for two levels of MAT: the first quantile (7.95°C) and the third quantile*
377 *(9.23°C).*

3.2.2 Mapping predictions of the site index in southern Belgium

The highest productivity (≃ 20 m at 30 years) was found in the northern and southernmost parts of the study area. Intermediate values of site index (≃ 15 m at 30 years) were encountered in the uplands (hatched area in Fig. 1) while the lowest values (≃ 10 m at 30 years) were mainly found in the eastern part (Fig. 5). The standard error was less than 1.63 m for 90 percent of the predictions within the study area for the reference period (1961-1990) and less than 7.21 m with 1.5 additional degrees in MAT (Figure S6; Figure S7). Regarding the reference period, part of the east and some areas in the west were outside the model's calibration range, representing a total of 13 % of the study area. The majority of predictions outside the range of observed SI values were in the east, accounting for about 1% of the study area (Fig. 5). These values increased to 71% and 0.2% respectively for the 1.5 additional degrees scenario. The part of the study area that remained within the model calibration range roughly corresponded to the upland ecoregion (Figure S5).



391

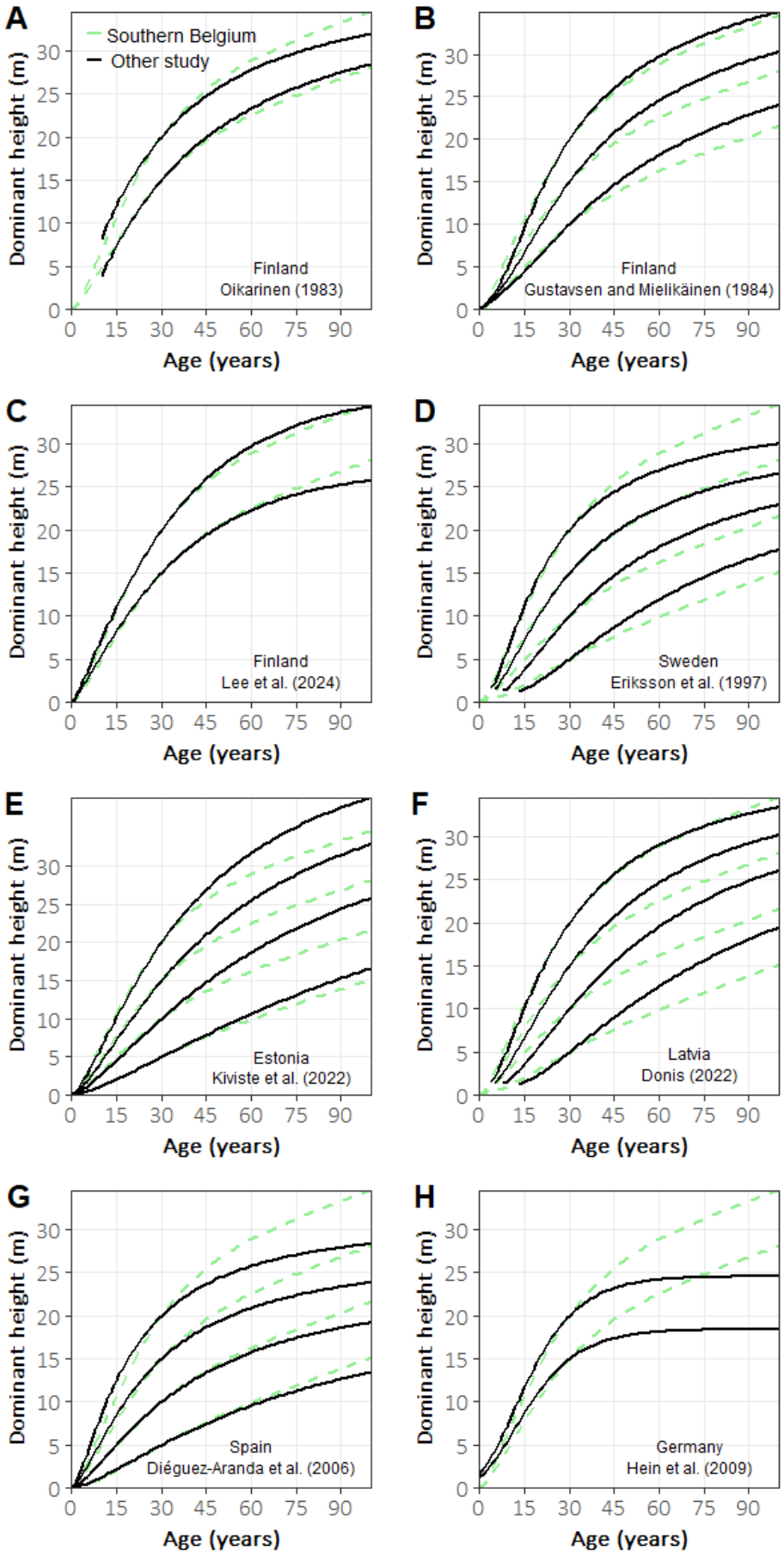
392 *Fig. 5: Predicted site index (dominant height at 30 years in m) for silver birch in southern*
393 *Belgium. White striped areas are those outside the model's calibration domain (MAT or SWC*
394 *value lower [higher] than the minimum [maximum] value used to calibrate the model).*
395 *Predictions outside the range of observed values of site index are displayed in red.*

4 Discussion

4.1 Phytocentric approach

The Duplat and Tran-Ha equations appeared best suited to model dominant height trajectories (Table 5). In accordance with previous studies examining the dominant height growth of other broadleaved species such as cherry and sycamore maple (Claessens et *al*., 1999) and softwood species such as spruce and larch (Perin et *al*., 2013; Zhang et *al*., 2022), the complexity of these models - having more parameters than the other tested models - seems required to fit the data. The estimated site index curves of our study were compared to those of other previous studies by fixing the SI at a reference age of 30 years (Fig. 6). The different site index curves show similar growth patterns with an early rapid height growth followed by a gradual decrease, which is typical for pioneer tree species. However, differences in growth patterns are observed and may be explained by local variations in the height growth dynamics, the type of data used to develop productivity curves (permanent sample plots, temporary sample plots, or stem analysis), the type of model (sigmoidal or non-sigmoidal), and the birch species studied (silver birch, downy birch, or a combination of both). Among the studies reviewed, only the productivity curves from Eriksson et *al*. (1997), Diéguez-Aranda et *al*. (2006), and Hein et *al*. (2009) were constructed using stem analysis, while the others relied on permanent or temporary sample plots. Among the studies based on stem analysis, the growth pattern described by the German model differs most significantly from ours, notably due to its horizontal asymptote, which is absent in the other productivity curves. Furthermore, similar to the situation in Wallonia, the productivity curves of Gustavsen and Mielikäinen (1984), Donis (2022), Eriksson et *al*. (1997), and Kiviste et *al*. (2022) were developed for both birch species combined, whereas those of Lee et *al*. (2024), Oikarinen (1983), and Hein et *al*. (2009) were specifically calibrated for silver birch, and Diéguez-Aranda et *al*. (2006) curves were fitted exclusively for downy birch. Additionally, the models of Oikarinen (1983) and Gustavsen and Mielikäinen (1984) are

not based on sigmoidal growth functions, unlike those used in the other studies. Finally, it is important to highlight that these differences may also be due to the sampling, notably the age range. It should be noted that, in the most fertile conditions, our model shows more sustained growth than most of the other models. Indeed, we sampled mostly relatively young trees (<50 years) for the higher productivity classes. Beyond 50 years, the height growth is extrapolated which makes the comparison with other models at these ages less accurate. This reflects a common sampling bias where higher productivity classes are generally represented by younger trees, while lower productivity classes tend to include older trees (Socha et *al*., 2016).


A
Southern Belgium
Other study
Finland
Oikarinen (1983)
B
Finland
Gustavsen and Mielikäinen (1984)
C
Finland
Lee et al. (2024)
D
Sweden
Eriksson et al. (1997)
E
Estonia
Kiviste et al. (2022)
F
Latvia
Donis (2022)
G
Spain
Diéguez-Aranda et al. (2006)
H
Germany
Hein et al. (2009)
Dominant height (m)
Age (years)

429

Fig. 6: Comparison of the dominant height growth curves of this study for site index values at a reference age of 30 years and other published dominant height growth curves from Sweden (Eriksson et al., 1997), Finland (Gustavsen and Mielikäinen, 1984; Lee et al., 2024; Oikarinen, 1983), Estonia (Kiviste et al., 2022), Latvia (Donis, 2022*), North-Western Spain (Diéguez-Aranda et al., 2006) and Germany (Hein et al., 2009).* Site index curves were developed from breast height age instead of stump age as is our case. To compare their curves with our own, we thus applied correction ages, being the time needed for a birch to grow from stump to breast height, of 12, 7, 4 and 3 years for 5, 10, 15 and 20 m site indices classes respectively.*

4.2 Geocentric approach

The geocentric approach highlighted the key biophysical factors influencing birch growth: a climatic variable, the mean annual temperature interacting with an edaphic variable, the maximal soil water content.

In northwestern Europe, birch productivity seems to be promoted by the increase in mean annual temperature (Fig. 4B). This result is in line with previous studies, which have also reported a positive effect of temperature on height growth, as a warmer climate can especially lead to a longer growing season (Albert and Schmidt, 2010; Álvarez-Álvarez et *al*., 2011; Brandl et *al*., 2018; Combaud et *al*., 2024; Pau et *al*., 2022). The stimulating effect of temperature on growth tends to saturate after 8°C (Fig. 4B) for silver birch. This saturation effect could be attributed to temperature ceasing to be a limiting factor for growth, or because rising temperatures may increase evapotranspiration, hydric stress, and reduce photosynthetic activity (Lindner et *al*., 2010). In this study, we were not able to capture a reverse effect of further warming on birch growth given that our climatic range might be insufficient, underlining

453 the importance of extending the study area, particularly in the southern part of the distribution
454 range (Fontes et *al*., 2010).
455 The positive effect of temperature on birch productivity is likely limited by soil water
456 availability. The interaction between temperature and soil water content moderated the positive
457 effect of temperature (Fig. 4A), suggesting that birch growth could be constrained by low soil
458 water availability in warmer regions of northwestern Europe, as trees tend to limit
459 evapotranspiration to avoid water loss and the risk of cavitation (Brandl et *al*., 2018). In the
460 lowland ecoregion of southern Belgium, warmer temperatures lead to a longer growing season,
461 promoting height growth. Soil is generally loamy and deep with sufficient water content,
462 protecting the trees from water shortage in drought periods. However, a warmer climate will
463 not necessarily increase productivity in this ecoregion, as temperature is not the main growth-
464 limiting factor (Fig. 7). Birch silviculture may thrive on sites where soil water content does not
465 limit growth.
466 In the northern part of its distribution range, where growth is limited by low temperatures, silver
467 birch may eventually benefit from rising temperatures, especially in stands characterized by
468 high soil water content (Fig. 4C; Fig. 7). Currently, the uplands ecoregion shows low
469 productivity values (10 m-15 m at 30 years) because of low temperature in growing season.
470 Specifically, the easternmost part of this ecoregion is characterized by peaty soils (SWC>200
471 mm), leading to root hypoxia, which tends to reduce birch growth (Glenz et *al*., 2006). These
472 conditions correspond to the ecological niche constraints of *B. pendula*, which is known to
473 thrive less in cooler climates and wetter soils, as evidenced by its distribution range extending
474 further south than north (Atkinson, 1992). However, the uplands ecoregion may become
475 suitable for birch silviculture in the coming decades (Fig. 7), as the growing season will likely
476 lengthen.

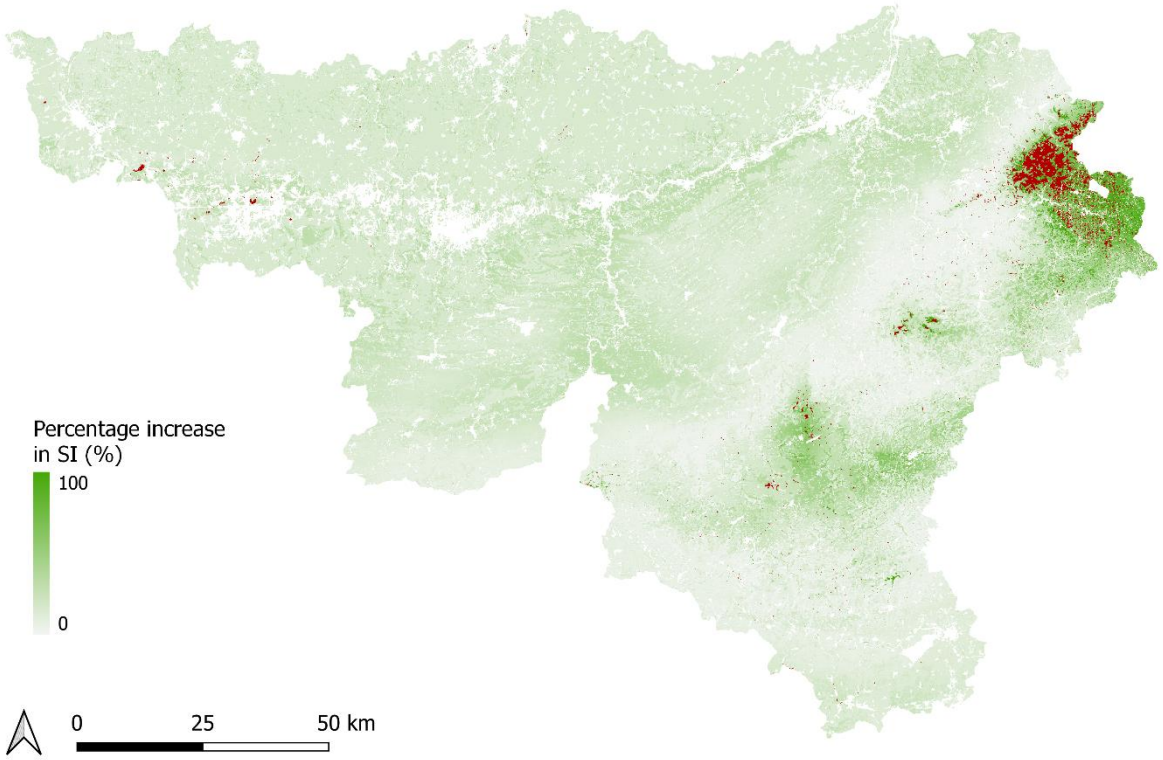


Fig. 7: Estimated increase in the site index (SI) of silver birch in southern Belgium due to an increase of 1.5°C in mean annual temperature (compared to the reference period 1961-1990). Predictions outside the range of observed values of site index are displayed in red.

4.3 Applicability of the phytocentric and geocentric models

The phytocentric model is valid for pure, even-aged birch stands originating from natural regeneration, regardless of the birch species. Given the wide range of growth conditions represented in the sampling, the model is applicable throughout southern Belgium (Figure S8.2). However, its application in other regions may result in inaccurate productivity estimates due to local variations in height growth patterns (Fig. 6). The site index can be reliably estimated for stands aged between 20 and 60 years. In the case of stands younger than 20 years, the estimation of the site index should be considered with caution due to the high level of uncertainty in the SI estimation error (Figure S8.1). Due to the limited number of observations

beyond 60 years, the interpretation of the site index for older stands should be approached with caution. The proposed model is calibrated at the tree level rather than the stand level. Unlike stand-level models, it does not account for silvicultural interventions that can lead to dominant height reaching a horizontal asymptote more quickly or even decreasing. Nonetheless, if the model is applied in contexts where the dominant tree cohort remains relatively stable, the differences between tree- and stand-level predictions should be minimal. Stability in this cohort can be maintained through target trees silviculture, which focuses management efforts on a limited number of dominant trees, as recommended for birch (Dubois et al., 2021). Peak height growth occurs around 10 years of age (Fig. 8), emphasizing the importance of early management to capitalize on birch's growth potential, as recommended for birch silviculture in Western Europe (Dubois et al., 2021).

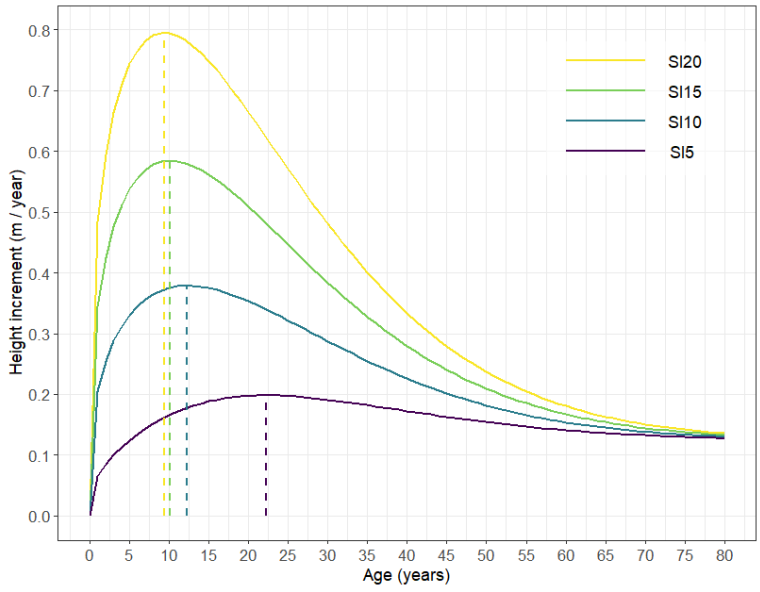


Fig. 8: Height increment curves for each class of productivity (5, 10, 15 and 20 m at 30 years). Dashed lines indicate the peak height growth.

The geocentric model is intended to guide the management of pure stands of silver birch. It is applicable in southern Belgium (Figure S8.2), except in the west of the lowlands ecoregion and the northwest of the uplands ecoregion, where the lack of data—and consequently the extrapolation beyond the model's calibration climatic range—leads to inaccurate site index estimates (error of 3.2 m; 95% intervals; Figure S6). The model's climatic applicability range is limited to regions with an average annual temperature between 7.5°C and 9.5°C, and its use is not recommended for areas with a soil water content below 50 mm (Fig. 4). However, the temperature increases induced by climate change imply that 70% of the region (Figure S5), mostly corresponding to the lowlands ecoregion, will exceed the model's calibration climatic range by 2070, resulting in SI estimation errors of up to 8.1 m (95% intervals; Figure S7). Nonetheless, predictions remain reliable in the uplands ecoregion (error of 1.2 m; 95% intervals; Figure S7), where an increase in the potential productivity of birch is to be expected, provided that soil water reserves remain sufficient (> 150 mm; Fig. 7).

4.4 Study limitations and perspectives

Stem analysis is the fastest way to obtain detailed information on tree growth without the need for long-term measurements, as it is the case with permanent sample plots (Raulier et *al*., 2003). Stem analysis provides insight into past growth dynamics across multiple variables at the tree level, making it a valuable tool for understanding historical growth trends (Salas-Eljatib, 2021). However, this method has certain limitations. A key issue is the assumption that the sampled trees were dominant throughout their lives, which is not guaranteed. Consequently, stem analysis may overestimate dominant height growth (Raulier et *al*., 2003), and dominant trees at the time of sampling may have experienced periods of lower dominance at younger ages (Magnussen and Penner, 1996). However, silver birch maintains vigorous growth and vitality only when growing as a dominant tree (Hynynen et *al*., 2010), as this shade-intolerant species is highly sensitive to competition for light, especially from close neighbours (Vanhellemont et

al., 2016). This is particularly relevant in naturally regenerated stands, being the most common type of birch stands in Belgium, where intraspecific competition is intense (Dubois et *al*., 2020). Given the ecological characteristics of birch, the dominance assumption seems reasonable, but this should be verified by comparing our results with permanent sample plots data.

The method proposed by Goelz and Burk (1992), based on the relative error of height predictions at different ages, led to the selection of a reference age of 30 years for silver birch. This choice was influenced by several considerations, including the preference for a reference age younger than the minimum rotation age set at 50 years in a target tree silvicultural approach as proposed by Dubois et al. (2021). However, the choice of reference age using the relative error method is highly dependent on the age range covered by the dataset. In this study, the number of observations decreases significantly after 30 years, making it difficult to select a reference age closer to the minimum rotation age. While a reference age that is too young may lead to errors in site index estimation, Diéguez-Aranda et al. (2005) emphasised that, from a practical perspective, a younger reference age allows earlier decisions on silvicultural treatments. In general, a reference age of 50 years is often used for birch. However, based on the relative error method, Diéguez-Aranda et al. (2006) proposed a reference age of 20 years for downy birch in northwestern Spain. In our case, height growth decreases sharply from around 30 years, making this age a suitable compromise for defining the site index of silver birch.

The two birch species were not considered separately to produce the dominant height growth model. However, the height growth curve of the two species might differ. Some authors have put forward the hypothesis of a possible hybridization between *B.pendula* and *B.pubescens* despite a different ploidy (Tsuda et *al*., 2017; Vetchinnikova and Titov, 2023), silver birch being diploid (2n=28) and downy birch being tetraploid (2n=56; Palmé et al., 2004, 2003). Comparing the growth patterns of these two species and hybrids with precise genetic identification could

554 reveal whether separate growth models are necessary to enhance site index estimates, as
555 demonstrated by Johansson (2013) for hybrid aspen.
556 Due to the absence of past silvicultural management and the lack of interest for birch, the
557 sampling was limited. In this study, the geocentric method-based model considered a limited
558 climatic range. However, to account for climate change, the sampling area should be expanded
559 to encompass a broader climatic range, which will allow for more reliable predictions (Aertsen
560 et *al*., 2012).
561 The geocentric model relies on spatial data. Although easily accessible, cartographic data limits
562 the choice of variables and may be imprecise, leading to a small percentage of the explained
563 variability (Pinno et *al*., 2009). In our study, the use of spatial data led to a relatively high
564 percentage of variability being explained (R^2 adj=0.50; Table C1) and allowed birch potential
565 productivity to be mapped at a large scale, providing forest managers with recommendations at
566 a regional scale. In southern Belgium (17,000 km^2), environmental conditions–such as climate,
567 topography, and soil–have been well-studied over time. Soil properties were mapped between
568 1950 and 1990 and subsequently digitized (Legrain et *al*., 2014). At a smaller scale, field data
569 could be obtained in order to quantify the loss of precision associated with the use of spatial
570 data and the eventual need of additional calibration procedures.
571 In the geocentric approach, we used climate data averaged over a 30-year period. This does not
572 allow to take into account the impact of short-term extreme climatic events, such as droughts,
573 which can be detrimental for growth. A dendroecological analysis is needed to assess the impact
574 of such extreme climatic events on birch growth (Fritts and Swetnam, 1989).

Conclusion

Using a phytocentric approach, we developed dominant height growth curves for birch based on stem analyses of 68 trees from 40 stands covering most of the birch range geographic locations and site conditions in southern Belgium. Among the models tested, the Duplat and Tran-Ha I model best predicted the dominant height growth. This model can now be used as a practical tool for forest owners and managers to assess the potential productivity of any even-aged birch stand.

We used a geocentric approach to investigate the relationship between the site index of silver birch and biophysical factors. The main factors influencing the site index were the mean annual temperature and the maximal soil water content. The positive effect of higher temperature was limited by soil water content. These results suggest that, in the context of a warmer climate, birch productivity could increase in the uplands where soil water availability is high but decrease in the lowlands on dry soils. The predictive maps identify optimal areas for birch silviculture and regions where its productivity may increase, providing crucial insights for guiding forest management strategies.

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