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An approach to quantify climate–productivity relationships: an example from a widespread *Nothofagus* forest

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Abstract. Unique combinations of geographic and environmental conditions make quantifying the importance of factors that influence forest productivity difficult. I aimed to model the height growth of dominant *Nothofagus alpina* trees in temperate forests of Chile, as a proxy for forest productivity, by building a dynamic model that accounts for topography, habitat type, and climate conditions. Using stem analysis data of 169 dominant trees sampled throughout south-central Chile (35°50′ and 41°30′ S), I estimated growth model parameters using a nonlinear mixed-effects framework that takes into account the hierarchical structure of the data. Based on the proposed model, I used a system-dynamics approach to analyze growth rates as a function of topographic, habitat type, and climatic variability. I found that the interaction between aspect, slope, and elevation, as well as the effect of habitat type, play an essential role in determining tree height growth rates of *N. alpina*. Furthermore, the precipitation in the warmest quarter, precipitation seasonality, and annual mean temperature are critical climatic drivers of forest productivity. Given a forecasted climate condition for the region by 2100, where precipitation seasonality and mean annual temperature increase by 10% and 1°C, respectively, and precipitation in the warmest quarter decreases by 10 mm, I predict a reduction of 1.4 m in height growth of 100-yr-old dominant trees. This study shows that the sensitivity of *N. alpina*-dominated forests to precipitation and temperature patterns could lead to a reduction of tree height growth rates as a result of climate change, suggesting a decrease in carbon sequestration too. By implementing a system dynamics approach, I provide a new perspective on climate-productivity relationships, bettering the quantitative understanding of forest ecosystem dynamics under climate change. The results highlight that while temperature rising might favor forest growth, the decreasing in both amount and distribution within a year of precipitation can be even more critical to reduce forest productivity.

Key words: Chile; climate change; differential equation; mixed-effects models; tree growth.

INTRODUCTION

Site productivity is crucial for scientific understanding of forest dynamics, as well as for forest management. Productivity is the production of biomass per unit time, in a population, trophic level or an ecosystem (Kimmins 2004). Meanwhile, forest site productivity is a quantitative estimate of the potential of a unit of area to produce plant biomass (Skovsgaard and Vanclay 2008), implying that a given forest could realize a part of this potential. No valid silvicultural decision should be made without reference to site productivity and other site conditions (Daniel et al. 1979, Oliver and Larson 1996), thus, it is relevant for sustainable forest management. As tree growth depends on site productivity, the structure and composition of forests are influenced by it, as well as the change of forests through time; therefore productivity also influences forest dynamics.

The most-used index of productivity in forests assessment is the dominant height of a stand at a reference or base age because of its independence to stand density (Tesch 1980, García 1983), which is widely known as "site index". Although site index does not reflect the driving factors of site productivity (Sammi 1965), it is a robust variable to gauge site productivity, being widely used in the world. Hence, site index had been shown to be a relevant artifact for estimating forest site productivity at a lower cost and faster than by actually measuring biomass productivity. Furthermore, dominant trees capture important ecological features for providing ecosystem services, such as carbon sequestration (Luyssaert et al. 2008, Stephenson et al. 2014) and wildlife habitat (Franklin et al. 1987, Gustafsson et al. 2012), hence being

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relevant to be used as reference trees for forest productivity assessment.

In forest science, the concept of site productivity was long treated as a static part of forest ecosystems, since although it was recognized that productivity depended on topography, vegetation, and climate, this last factor was mostly considered as fixed in the literature (Assmann 1970, Daniel et al. 1979, Oliver and Larson 1996). Nowadays, however, because of climate change, I have realized that productivity would not remain constant, even at a fixed location. This turn from considering climate as constant when studying site productivity to a variable climate is likely one of the most relevant paradigm shifts in forest sciences. That is to say, site productivity is a dynamic component of forest ecosystems.

Quantifying the relationship between climate and productivity is a long endeavor in ecological studies. Estimating the effects of climate change on productivity is still an open question for natural ecosystems such as the marine (Free et al. 2019) and the forest (Morin et al. 2018) ecosystems. Several challenges are faced when studying forest productivity (Kimmins 1985), but here I only stress some of them. Not only has the space-for-time assumption been questioned in ecology (Johnson and Miyanishi 2008), but forest dynamics trajectories are also quite uncertain even in close locations (Norden et al. 2015). I think that this uncertainty in predicting forest ecosystem dynamics could be largely due to climate change patterns. Manifold attempts have been pursued in studying the relationship of forest productivity and potential drivers representing vegetation (Daubenmire 1952, 1961, Monserud 1984), topographic variables (Myers and van Deusen 1962, Monserud et al. 1990), and climate (Kimmins et al. 1990, Wang et al. 2004) features. Some other studies have focused on physiological approaches (Mäkelä 1986, Valentine 1997, Guerrieri et al. 2019) not pursued here because they rely heavily on experimental (i.e., controlled) data, and are hard to generalize because of these restriction, especially in regions and ecosystems where this type of data is not available.

Identifying the drivers of forest productivity is an intricate task. Determining the main factors (i.e., drivers) affecting forest productivity depends on the device used for assessing their importance (Healy et al. 2008, Liang et al. 2015, Gustafson et al. 2017, Hennigar et al. 2017, Chen et al. 2018, Jactel et al. 2018, Morin et al. 2018, Sheng and Xu 2019). Consequently, the statistical models to be used are core for hypothesis testing; however, not much attention is tailored toward that end. In this regard, several research claims are based on simply comparing means and fitting linear models, although nonlinearity is an intrinsic feature of forests (Stone and Ezrati 1996, Cushing et al. 2003, Messier et al. 2016), among other details that are important to be considered (Ellison and Dennis 1996). As a better way to represent the interaction between topographic variables, Beers et al. (1966) and Roise and Betters (1981) used trigonometric functions, and Stage and Salas (2007) went further and proposed related alternatives for hypotheses testing. In addition, forests are structured systems, where many factors are interacting at different levels, so it is important to takes into account the hierarchical structure of the data being used to build models when studying drivers that affect forest productivity. Overall, unravelling the effects of drivers on the climate-productivity relationship requires both data covering a wide range of environmental conditions and suitable statistical models to assess the uncertainty associated with hypotheses testing.

Although there are studies on some aspects of *Nothofagus*-dominated forests in Chile, rather few provide quantitative models to support scientific understanding and management decisions. The *Nothofagus* genus, the Southern Hemisphere beech, is often used as a key Gondwanan link in biogeographical studies and is core for the native forests of Argentina, Australia, Chile, and New Zealand (Veblen et al. 1996). Several studies have been carried out in forests dominated by *Nothofagus alpina*, *N. dombeyi*, and *N. obliqua* on forest (Veblen et al. 1981, Donoso 1995, Lusk and Ortega 2003, Pollmann and Veblen 2004, Salas et al. 2006), species autoecology (Donoso 2006), genetics (Donoso et al. 2004), regeneration (González et al. 2002), and silviculture (Grosse and Quiroz 1999). Nonetheless, research on *Nothofagus* forests productivity, a key component to understanding forest dynamics, has been mostly studied using simple descriptive approaches (Donoso et al. 1993, Echeverría and Lara 2004), modeling efforts either based on rather small sample sizes (Trincado et al. 2002) or focused on small geographic regions (Salas and García 2006, Esse et al. 2014). Hence, further analysis of the productivity of *Nothofagus* forests is needed. In the present study, using a system-dynamics approach based on efficient statistical estimation of model parameters, I focused on quantifying the climate–productivity relationship and testing how this relationship is affected by climate change. I used stem analysis data of dominant *Nothofagus alpina* trees in its entire distribution in south-central Chile. This species is one of the most important species of Patagonian temperate forests due to its wood quality and its relatively fast growth (Cubbage et al. 2007, Hildebrandt et al. 2010, Torales et al. 2012). To my knowledge, the study is the most comprehensive research on the climate–productivity relationship of temperate forests of Chile and offers a quantitative approach based on field data that could be useful elsewhere as well.

MATERIALS AND METHODS

Data

The population under study are the secondary forests belonging to the *N. obliqua*, *N. alpina*, and *N. dombeyi* forest type described by donosobtemp in south-central Chile between 35°50′ S and 41°30′ S latitude. This area covers the distribution of the most common forests of this forest type (Fig. 1), occupying 1,557,933 ha. These forests are even aged, and the *Nothofagus* predominantly occurs in the upper canopy. I used stem analysis data of sample *N. alpina* trees selected from 53 fixed-area sample plots previously established in randomly selected locations. Between two and five trees were felled per sample plot.

Data sources are fully described in Salas-Eljatib (2020). Dominant trees were selected for stem analysis, provided they were healthy and of normal shape, of seed origin, and belonging to the upper canopy. After measuring diameter at breast height (*d*) and total height (*h*), the selected trees were felled and cross-sectional disks were obtained at stump height (10–40 cm) and breast height (1.3 m), plus additional disks evenly spaced between breast height and total height. The average number of sections per tree was 10. Rings were counted in the laboratory. I reviewed the original stem analysis trees data set in order to detect missing rings counts, same ring counts in successive sections, and non-decreasing ring counts between successive height cross-sections.

Stem analysis allows us to reconstruct the past height growth. Heights and ring counts from cross-section disks are used to calculate height age pairs, and by this, I am able to reconstruct tree height growth. I used breast height age (bha), the number of complete rings at breast

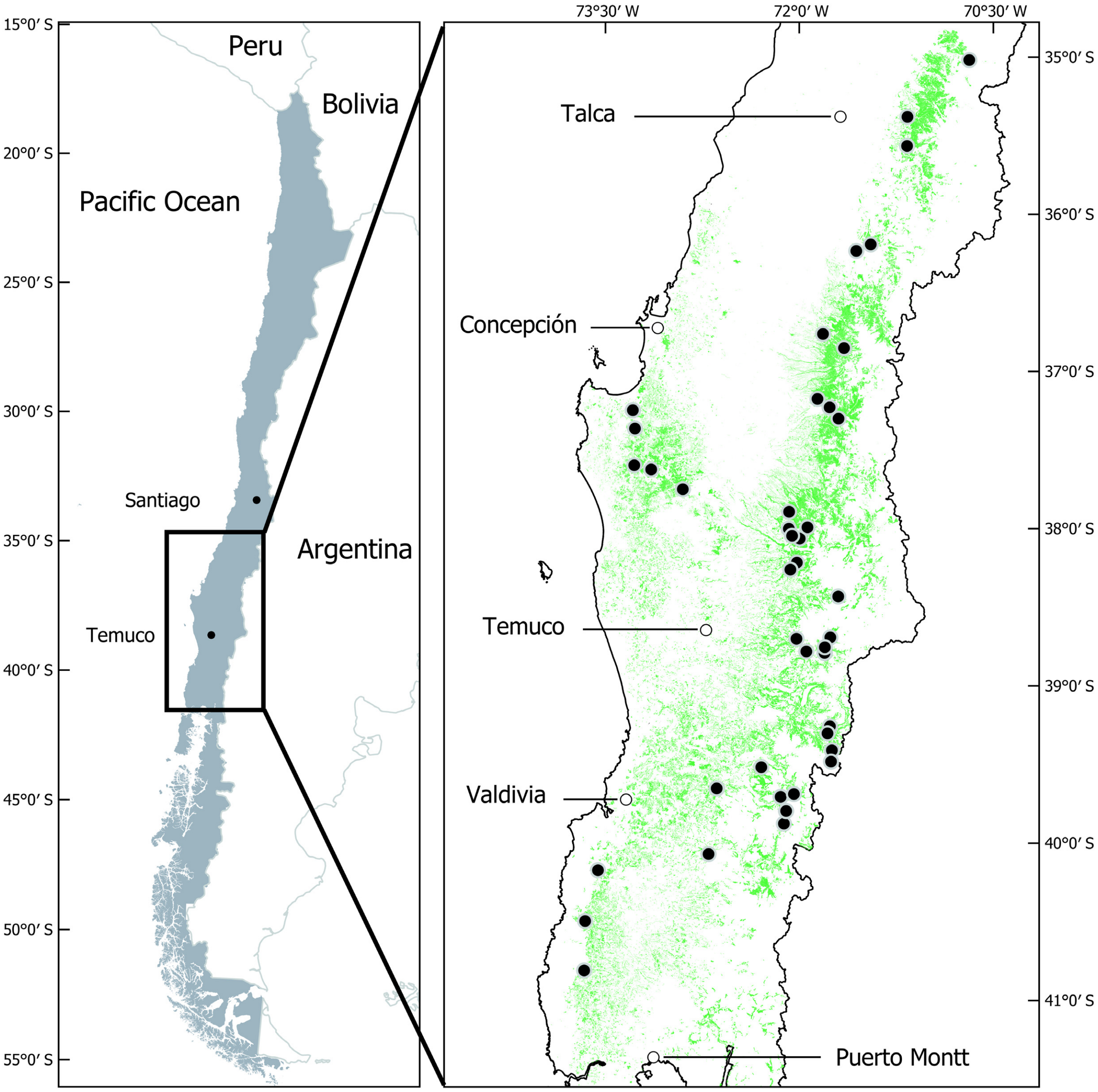

FIG. 1. Map of south-central Chile from 35°50′ S to 41°30′ S. The temperate forests of *Nothofagus alpina*–*N. dombeyi*–*N. obliqua* (green) are the population under study and they cover 1,557,933 ha. The stem analysis sample plots (black circles) and the major cities are also shown.

height, instead of total age as the time variable for the modeling efforts, based on the results of Salas and García (2006). I used the algorithm proposed by Salas-Eljatib (2021*a*) for obtaining the height–bha data pairs for each tree. Notice that, with this algorithm, I do not interpolate the heights for a given year, but the age for a given cross-section height only. Aiming to detect past suppression of trees, I carried out a screening process of plotting height growth series by tree and plot. I dropped the trees showing clear past suppression in height growth. The data spans trees of juvenile ages up to 80 yr old with total heights between 7 and 31 m (Table 1). Height growth series of dominant trees show a large variation (Appendix S1: Fig. S1) depicting the natural differences in site conditions.

Stem analysis trees were collected from sample plots, which is a key feature for growth modeling because I am able to relate tree growth with biogeoclimatic variables measured at each sample plot. Unfortunately, the field data lack complete coverage of biogeoclimatic variables. As a way of overcoming this issue, I imputed the following three types of site variables using remote sensing tools as follows:

(1). *Vegetation classification*. Although there are several vegetation classifications of Chile, I use the vegetation belts classes of Luebert and Pliscoff (2006), which are ecological units that can be cartographically represented according to bioclimatic variables and vegetative attributes of the territory. Both vegetation classifications are available in GIS format.

(2). *Topographic variables.* I acquired continuous surface elevation data at a 30 m spatial resolution, derived from the ASTER global digital elevation model, for imputing elevation, aspect, and slope for sample plots lacking these variables. From here, I obtained the variables slope, aspect, and elevation. Notice that I only impute these variables for those sample plots with missing information (i.e., 20%). Similar approaches, and resolution, have been also used in other studies to obtain the topographic variables hanberry14.

(3). *Climatic variables.* Raster images of climate variables were obtained from the climate layers (climate grids) provided by WorldClim (Hijmans et al. 2005). Although the WorldClim-based data set does not cover Chile intensively, Luebert and Pliscoff (2006) found this climate model is reliable when compared to some weather stations data in Chile. Ergo, WorldClim imputed variables are commensurate for the present study and have also successfully used worldwide (Bowman et al. 2014, Madrigal-González et al. 2016, Chen et al. 2018) and in Chile (Luebert and Pliscoff 2006, González et al. 2013). Nineteen bioclimatic variables are available from WorldClim. These represent annual trends (e.g., mean annual temperature, annual precipitation), seasonality (e.g., annual range in temperature and precipitation), and extreme or limiting environmental factors (e.g., the temperature of the coldest and warmest month, and precipitation of the wet and dry quarters). A quarter is three months (1/4 of the year). By using the imputed mean climate variables to each sample plot, I allow spatial climate variations between sites. For this study, where the climatic layers had different spatial resolutions; the values were resampled using a spline interpolation method to a pixel size of 30 m.

Modeling strategy

I used a growth rate model for height that is a linear differential equation with a power transformation, as follows:

$$\frac{dh^{\gamma}}{dt} = \beta(\alpha^{\gamma} - h^{\gamma}) \tag{1}$$

where h is tree height, t represents time, and α, β, and γ are parameters having the following interpretations: α is the upper asymptote or maximum value for the state variable h (i.e., maximum height), β is a parameter that governs the rate of change (García 1983) or scale parameter, and γ is a shape parameter. The asymptote of the model α is the maximum height, not only a parameter having a physical interpretation, but also a functional trait (Kempes et al. 2011) that captures important variation in plant strategy and function (Richardson et al. 2013). As shown by Salas-Eljatib (2020), a solution of Eq. 1 is

Table 1. Tree and cross-section-level variables summary.

	Tree (n = 169)				Cross-section (n = 1,628)		
Statistic	d (cm)	h (m)	age (yr)	bha (yr)	h_0 (m)	dt (yr)	pai (m/yr)
Minimum	5.3	7.1	19	17	0.3	0.6	0.086
Maximum	49.9	31.2	81	76	26.3	11	1.961
Mean	24.9	20.3	45.9	42.2	8.424	2.015	0.561
Median	25	21	46	42	8.3	2	0.485
CV (%)	16.2	15.1	17	18.4	22.945	9.857	15.407

Note: d is diameter at breast height, h is total height, age is total age, bha is breast height age, h_0 is height at initial time of a period, dt length of a period, and pai is periodic annual height increment.

$$h = \alpha\{1 - [1 - (h_0/\alpha)^{\gamma}[\exp] - \beta(t - t_0)]\}^{1/\gamma} \qquad (2)$$

where h is height at time t or height at the end of a period and h_0 is height at time t_0 or height at the beginning of a period. The period length is obtained by $t - t_0$. As pointed out by Salas et al. (2008), the height increment model of Eq. 2 does not depend on age, uses data having different period lengths, and can predict height increment for different period lengths. This is a nonlinear model used successfully for modeling tree growth in terms of several variables (García 1983, Valentine 1997).

The data are temporally correlated and are hierarchically nested. Each sample tree has several observations of height over time (i.e., temporally correlation), and is part of a sample of trees collected from the same sample plot (i.e., trees nested within plots). The grouped nature of these data, with repeated measures on each subject at different times, violates the basic assumption of independence that underlies a simple regression model (Pinheiro and Bates 2000). In order to account for the temporal correlation of the data and their hierarchical structure, I fit the height growth model (Eq. 2) using a nonlinear mixed-effects model. I consider the trees nested within plots as a random factor. Now, I rewrite Eq. 2 by adding the corresponding index-notation as follows:

$$h_{ijk} = \alpha\{1 - [1 - \left(h_{ij(k-1)}/\alpha\right)^{\gamma}[\exp] - \beta\left(t_{ijk} - t_{ij(k-1)}\right)]\}^{1/\gamma} + \varepsilon_{ijk}, \qquad (3)$$

where h_{ijk} is the height in the ith plot for the jth tree at the kth time and $h_{ij(k-1)}$ is the height of the same tree at time $k - 1$, that is to say, for a given period of growth for a tree, h_{ijk} and $h_{ij(k-1)}$ are the height at the end and at the beginning of the period, respectively, or h and h_0 when not considering subscripting the data structure. The period length is given by $t_{ijk} - t_{ij(k-1)}$, where t_{ijk} and $t_{ij(k-1)}$ are the time at the end and at the beginning of the period, respectively, or t and t_0 when not considering subscripting. The stochastic element ϵ_{ijk} is included in Eq. 3 in an additive fashion, intending to recognize that the model is not deterministic, except on average, i.e., the expected value.

Where to allocate the random effects in a model is not straightforward. I tested all possible combinations in Eq. 3. For instance, the full-model variant is where all the fixed-effects parameters of Eq. 3 have random effects as shown in Eq. 4

$$\begin{gathered}
h_{ijk} = \left(\alpha + a_i + a_{j,i}\right)\left\{1 - \left[1 - \left(\tfrac{h_{ij(k-1)}}{\alpha + a_i + a_{j,i}}\right)^{\gamma + c_i + c_{j,i}}[\exp] - \left(\beta + b_i + b_{j,i}\right)\left(t_{ijk} - t_{ij(k-1)}\right)\right]\right\}^{1/\left(\gamma + c_i + c_{j,i}\right)} + \varepsilon_{ijk} \\
a_i \sim \mathcal{N}\left(0, \sigma_a^2\right);\ b_i \sim \mathcal{N}\left(0, \sigma_b^2\right); c_i \sim \mathcal{N}\left(0, \sigma_c^2\right); \\
a_{j,i} \sim \mathcal{N}\left(0, \sigma_1^2\right);\ b_{j,i} \sim \mathcal{N}\left(0, \sigma_2^2\right); c_{j,i} \sim \mathcal{N}\left(0, \sigma_3^2\right); \\
\varepsilon_{ijk} \sim \mathcal{N}\left(0, \mathrm{Var}\left[\varepsilon_{ijk}\right]\right);\ \mathrm{Var}\left[\varepsilon_{ijk}\right] = \sigma^2 \delta^2_{G_{ijk}}.
\end{gathered} \qquad (4)$$

where $\mathcal{N}$ represents a Gaussian probability density function. I used variance functions to model the variance structure of the within-group errors (Pinheiro and Bates 2000). All the models were fitted allowing a different variance for the error term per stratum G (i.e., each data set source). To achieve identifiability of the different variance errors by stratum, I follow Pinheiro and Bates (2000), imposing the restriction that $\delta_1 = 1$, i.e., for stratum 1, so that δ_l, $l = 2, \ldots, S$ represent the ratio between the standard deviation of the l stratum and the first stratum. I fit the mixed-effects models by maximum likelihood, followed by the best linear unbiased predictors (BLUP; Robinson 1991) of the random effects. All models were fitted using the nlme package (Pinheiro and Bates 2000) implemented in R (R Core Team 2020). The fit of model variants was assessed by comparing the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC).

Predicting the random effects: biogeoclimatic factors submodels

After selecting the more suitable model variant of height growth, I explored predicting the random effects by relating them to biogeoclimatic variables (i.e., at the plot level). First, I explored the relationship of these random effects and the potential predictors, and later, built relationships of the following type:

$$\mathrm{RE}_i = f(\mathrm{Hab}_i, \mathrm{Topo.var}_i, \mathrm{Clim.var}_i) \qquad (5)$$

where: RE_i is the random-effect for the ith plot; $f(\cdot)$ is a functional form; and Hab_i, $\mathrm{Topo.var}_i$, and $\mathrm{Clim.var}_i$ represent variables related to habitat type, topography, and climate, respectively. Note that depending on the height growth model chosen we can have random-effects added to more than one parameter; therefore, more than one relationships among random-effects and biogeoclimatic variables were needed. I termed Eq. 5 as a biogeoclimatic factors submodel that predicts the random effects or deviations of the estimated parameters of the height growth model as a way of representing the effects of topographic and climatic factors on tree height growth. The topography-related variables are mainly used as surrogates for radiation and moisture (Pokharel and Froese 2009). Notice that I did not use edaphic variables as in Thiers (2004). However, I expect that the vegetation classes would represent most of the edaphic effects at macro-region levels, because of their relation with both longitudinal and latitudinal changes of soils in Chile. Indeed detailed edaphic variables could be used for representing microsite variation, but that goes beyond the scope of the present research. For $f(\cdot)$ in Eq. 5, I used statistical linear models considering several combination of biogeoclimatic variables as predictors, ranging from the simple addition of them to a linear equation to the model proposed by Stage and Salas (2007), which takes into account the interaction of slope, aspect, and elevation by having trigonometric transformation of variables. This equation has been used with success in other studies as well (Salas et al. 2008, Battles et al. 2009, Liang and Zhou 2010, Liang 2012, Hanberry et al. 2014, Mittanck et al. 2014, Shi et al. 2014, Oke and Thompson 2015, Young et al. 2017, Lochhead et al. 2018, Wetherbee et al. 2020). The mathematical form of this model is given in Appendix S1: Eq. S.1.

Behavior analysis

I examined the behavior of the model in a dynamic system framework. This is a continuous-time dynamical system model, where the differential equation of height (Eq. 1) is the core of it. The system is represented as follows:

$$\frac{dh}{dt}=f\left(\hat{\boldsymbol{\theta}},h,\widetilde{\mathrm{RE}}_{\hat{\boldsymbol{\theta}}}\right) \tag{6}$$

where $\hat{\boldsymbol{\theta}}$ is a vector containing the estimated model coefficients (i.e., $\hat{\alpha}$, $\hat{\beta}$, $\hat{\gamma}$), h is the height of a given dominant tree, and $\widetilde{\mathrm{RE}}_{\hat{\boldsymbol{\theta}}}$ are the predicted random-effects of the fixed-effects estimated parameters using Eq. 5. Thus, the height growth rate (i.e., dh/dt) for dominant trees is a function of biogeoclimatic factors.

For instance, let's assume that the random effects are allocated to both the α and β parameters of Eq. 3. I would need to have a model that predicts the random effects of each parameter, i.e., $\tilde{\hat{a}}$ and $\tilde{\hat{b}}$, respectively. From here, I redefine these two parameters as

$$\alpha'=\hat{\alpha}+\tilde{\hat{a}}_i \tag{7}$$

$$\beta'=\hat{\beta}+\tilde{\hat{b}}_i \tag{8}$$

where: $\hat{\alpha}$ and $\hat{\beta}$ are the estimated fixed-effects parameters; and $\tilde{\hat{a}}_i$ and $\tilde{\hat{b}}_i$ are the predicted random-effects obtained from the corresponding biogeoclimatic factors submodel (Eq. 5). The above ideas are represented in a dynamic system diagram to identify the inputs, outputs, and relationship of the elements of the system under study (Fig. 2a). Later, I solved the differential equation model of the dynamic system by setting initial conditions (h_0 = 1.3 m and t_0 = 0.5 yr) and values for the biogeoclimatic factors. Finally, I represent the resulting growth

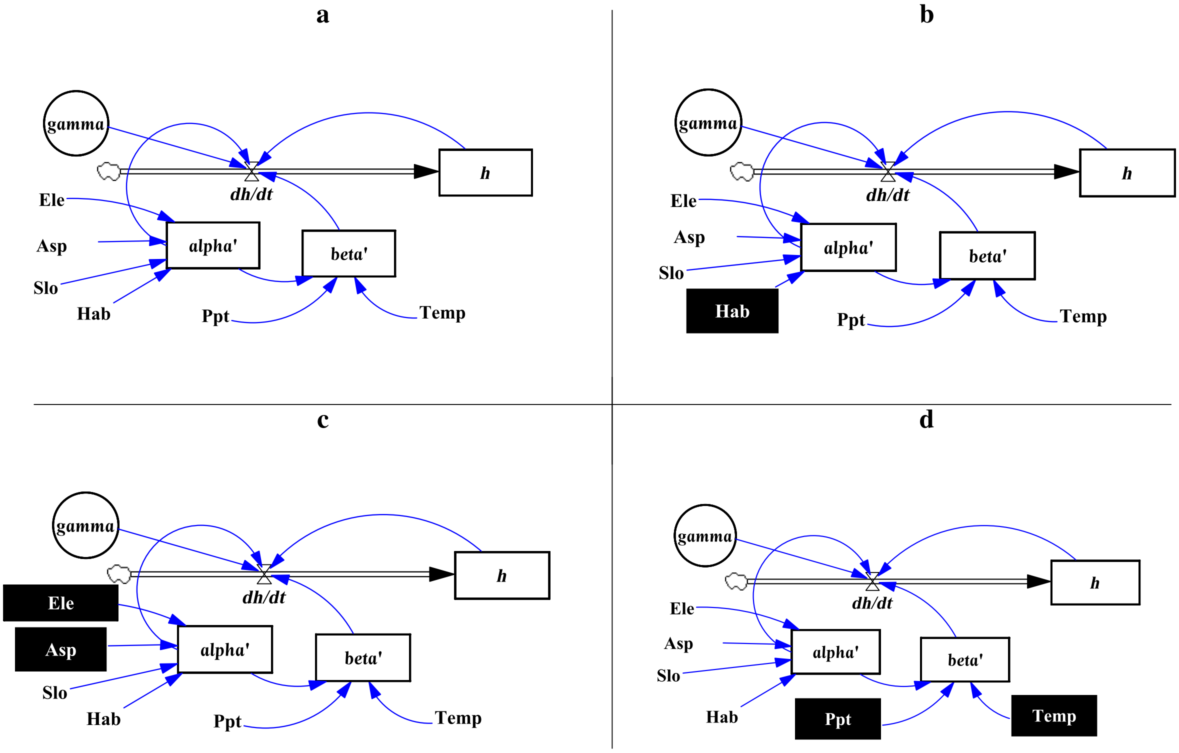

FIG. 2. Dynamic system diagrams. State variables are epitomized by boxes, derivatives by tick arrows with control valves, and the dependence of rate on state variables by curved arrows, meanwhile the remaining elements are constants. Notice that alpha′ and beta′ represents α' (Eq. 7) and β' (Eq. 8), respectively. (a) A height growth rate model represents the dynamic system as a differential equation and constant levels for input variables. The growing condition scenarios are defined by varying conditions in some input factors, such as (b) habitat types, (c) elevation and aspect, and (d) precipitation in the warmest quarter, precipitation seasonality, and mean annual temperature. A variable in a black box means that different values of it were used. Variables are Ele, elevation; Asp, aspect; Slo, slope; Hab, habitat; Ppt, precipitation; Temp, temperature; *h*, height; *dh*/*dt*, height growth rate.

trends exploiting the mathematical features of differential equations in forest ecology (Pommerening and Muszta 2015, Salas-Eljatib 2020), by plotting the growth trajectory and the growth rates against time and size.

Based on the dynamic system, I created three growing-conditions scenarios to assess the changes in forest productivity. These scenarios are a result of varying conditions of some biogeoclimatic factors. In the first scenario, I only change the habitat type, by assessing the system under the following habitat types: *N. dombeyi–Eucryphia cordifolia* , *N. alpina–N. dombeyi*, *N. alpina–N. obliqua*, and *N. alpina–Dasyphyllum diacanthoides* (Fig. 2b). In the second scenario, I varied both aspect (i.e., north and south) and elevation (300 and 800 m above sea level), generating four combinations of these two factors (Fig. 2c). In the last scenario, as a way to represent climate change effects on forest productivity, I varied the climate variables, depicting the following three climate scenarios: no change at all; a decrease of 10 mm of the precipitation in the warmest quarter and increase of a 10% in precipitation seasonality; and a decrease of 10 mm of the precipitation in the warmest quarter, an increase of a 10% in precipitation seasonality, and an increase of 1°C in mean annual temperature (Fig. 2d). These changes in climatic variables were derived from the IPCC work for South America (Christensen et al. 2007), and the values are within the range forecasted for this area for 2100.

RESULTS

Height growth model

Maximum –likelihood–based statistics comparison among all the possible height-growth-model variants show that the full model had the best fit (Appendix S1: Table S1). However, the random effects for γ are highly correlated with those for α or β (Appendix S1: Fig. S2), a condition that must be avoided (Pinheiro and Bates 2000). Thus, I selected the model having random effects in α and β (variant α, β in Appendix S1: Table S1). The estimated parameters for the growth model are consistent with the ecological features of the species (Table 2). Besides, a 95% confidence interval for the fixed-effects parameters (not shown here) do not include zero, showing that are statistically different from zero.

I suspect that h changes in time or depending on h_0. That is to say that values of h that are close to h_0 (as proxy for time) within a tree are probably correlated. I examined the autocorrelation of the residuals within trees (Appendix S1: Fig. S3) and, based on this, I argue that I have removed the correlation by accounting for the hierarchical structure of the data using a random-effects modeling framework.

Biogeoclimatic factors submodels

I evaluated several alternatives for modeling the random effects of the height-growth model, given the relationship between the random effects and predictor variables such as the geoclimatic variables (Fig. 3) and the vegetation classification proposed by Lubert and Pliscoff (2006). I selected the following submodels for each random effect:

TABLE 2. Fixed-effects estimated parameters and variance components for the proposed nonlinear mixed-effects height growth model (Eq. 4) of *Nothofagus alpina* dominant trees.

Parameter	Value
Coefficient	
$\hat{\alpha}$	33.829
$\hat{\beta}$	0.026
$\hat{\gamma}$	0.635
Variance	
$\hat{\sigma}_a$	4.789
$\hat{\sigma}_b$	0.0047977
$\hat{\sigma}$	0.93713
$\hat{\sigma}_1$	1.6050

Note: Notice that, in the proposed model, there are no random effects added to the parameter γ, consequently, I do not report the variances σ_c^2 and σ_3^2.

$$\hat{b}_i = \tau_0 + \tau_1 \mathrm{Ppseas}_i + \tau_2 \mathrm{Pptwq}_i + \tau_3 \sqrt{\mathrm{Pptwq}_i} + \tau_4 \mathrm{Temp}_i + \tau_5 \mathrm{Temp}_i^2 + \varepsilon_i \tag{9}$$

$$\hat{a}_i = f\left(\tilde{\hat{b}}_i, \mathrm{Hab}_i, \mathrm{Ele}_i, \mathrm{Asp}_i, \mathrm{Slo}_i\right) + \varepsilon_i \tag{10}$$

where $\hat{b}_i$ and $\hat{a}_i$, are the *i*th predicted (BLUP) random effects for the estimated parameters $\hat{\beta}$ and $\hat{\alpha}$, respectively. Meanwhile Ppseas is the precipitation seasonality (coefficient of variation within a year); Pptwq is the precipitation of the warmest quarter; Temp is the mean annual temperature; Hab is the vegetation belt, or habitat type; Ele is elevation (or altitude); Asp is aspect, and Slo is the slope. The functional form for Eq. 10 is represented in Appendix S1: Eq. S1. Additionally, I use the predicted effect (i.e., $\tilde{\hat{b}}_i$) from Eq. 9 in Eq. 10, which implies that the maximum height (a functional trait) is affected by the parameter governing the rate of change of the curve, which, in turn, is affected by climatic variables. These submodels are obtained from the random-effects relationship with biogeoclimatic variables, as well as from the physiological results of Thomas and Bazzaz (1999). The parameter estimates for submodels 9 and 10 are shown in Appendix S1: Table S2.

Behavior analyses

Not only do the scenarios evaluated affect the height growth of dominant trees, but also the growth rates over time and as a function of tree size. Different height-growth patterns can be expected depending on the type of habitat where *N. alpina* grows (first row of Fig. 4). These range from slower growth rates when *N. alpina* growth in habitat types mixed with *N. obliqua* to high growth rates when associated with *N. dombeyi–E. cordifolia* (species indicating favorable moisture conditions). The proposed model is capable of capturing the ecological behavior of tree growth and of helping to identify suitable growing conditions. For instance, *N. alpina* grows better at higher elevations and southern aspects (second row of Fig. 4). Besides, the difference among aspects is more pronounced at higher elevations. Finally, both mean annual temperature and two precipitation-related variables (precipitation in the warmest quarter Pptwq and precipitation seasonality Ppseas) affects forest productivity. The combined effect of decreasing Pptwq and increasing Ppseas, tend to a significant

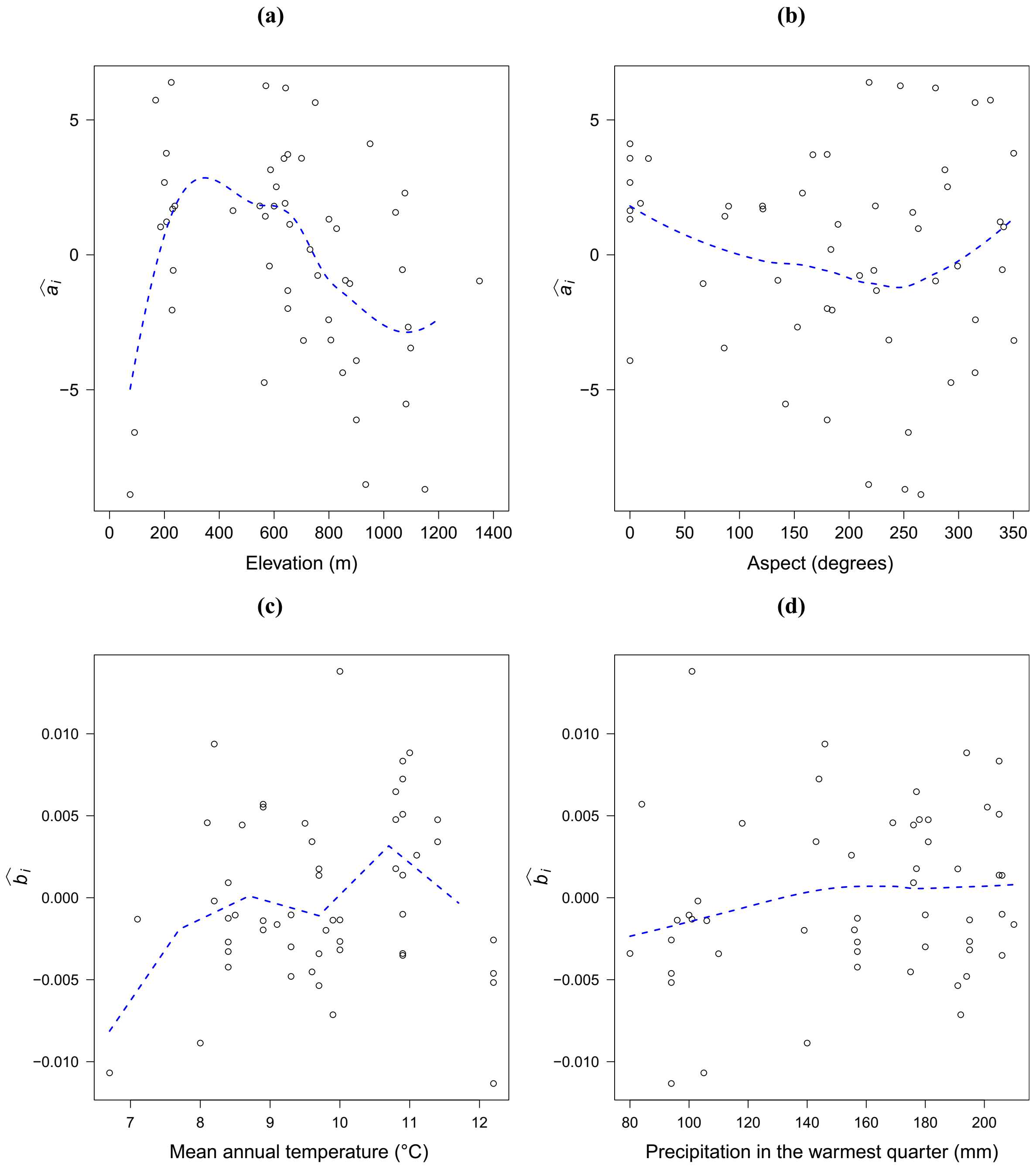

Fig. 3. Scatterplots between the random effects for the proposed height growth model and some geoclimatic variables. Panels show $\hat{a}_i$ vs. (a) elevation and (b) aspect; and $\hat{b}_i$ vs. (c) mean annual temperature and (d) precipitation in the warmest quarter of a year. The dashed curve is a smooth line.

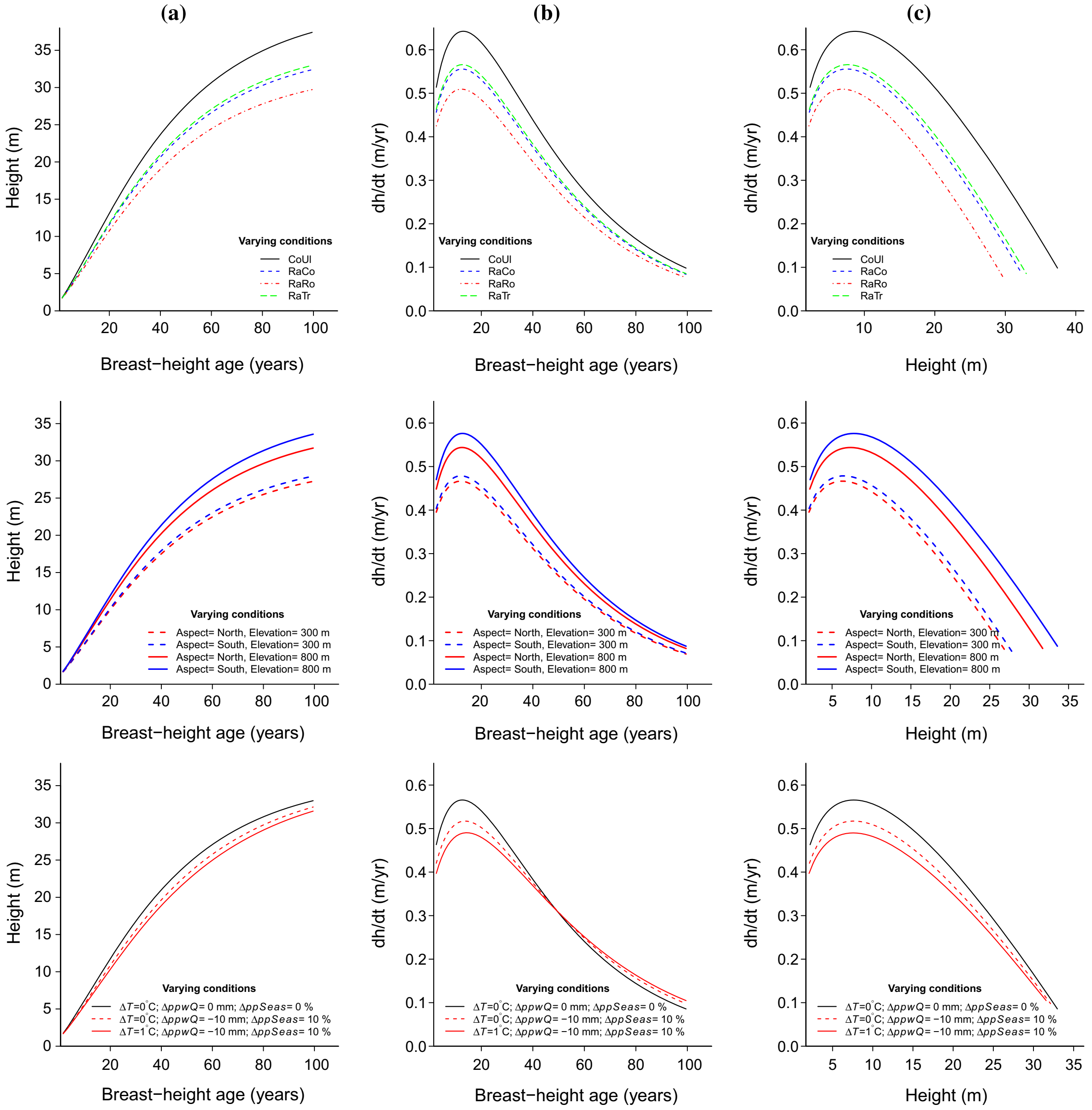

FIG. 4. Expected height growth trends for *Nothofagus alpina* dominant trees, as a proxy of forest productivity, in south-central Chile (36° – 41° S) depending on varying conditions. These trends depict (a) growth vs. age, (b) growth rate vs. age, and (c) growth rate vs. height. Different drivers of productivity were varied, as follows: habitat types (top row), aspect and elevation (middle row), and climate variables (bottom row). Unless specified, the other biogeoclimatic factors were retained at their median values. In the first-row CoUl, RaCo, RaRo, and RaTr stands for *N. dombeyi–Eucryphia cordifolia*, *N. alpina–N. dombeyi*, *N. alpina–N. obliqua*, and *N. alpina–Dasyphyllum diacanthoides*, respectively.

reduction of height growth of dominant trees (third row of Fig. 4), pointing out the relevance of climate change on any assessment of forest productivity.

DISCUSSION

The proposed height-growth model for dominant trees overcomes previous problems in site productivity modeling of *Nothofagus* forests. This model is based on the largest available stem analysis data for *N. alpina* that was distributed through the entire range of the forest type where the species largely grows (Fig. 1). I deliberately avoided inflating the sample size by interpolating heights of stem analysis data for every year, as previously done in other similar studies (e.g., Trincado et al. 2002). Moreover, I reviewed the height growth series of each tree within a plot to detect past suppression of sample trees, as a way to assure that the trees were likely to be dominant throughout their entire lives. Both the temporal correlation and hierarchical structure of the data (tree-level random effects nested with plot-level random effects) have been taken into account when fitting the growth model, making statistical inference appropriate.

Based on a new productivity model for temperate forests dominated by *N. alpina*, I show the sensitivity of dominant height growth to several to biogeoclimatic variables. These were segregated into three categories: vegetation classification, topographic features, and climatic variables. First, the use of vegetation classification for estimating forest ecosystem productivity was proposed early (Holman 1929, Daubenmire 1961, Monserud 1984) and similar approaches, either by using natural regions (Wang and Huang 2000) or forest ecosystem classification (Salas et al. 2008, Pokharel and Froese 2009), have started to be used more often again. Accordingly, I used the vegetation belts classification of Luebert and Pliscoff (2006). The proposed model can represent an important ecological feature of tree species: how a species grow in mixed forests conditions. *N. alpina* increases its productivity when growing in mixed-species habitat types. Still, especially with *N. dombeyi* and *E. cordifolia*, this is more likely due to that both species mostly growth in favorable humid settings. Furthermore, as *N. alpina* is more shade-tolerant than *N. dombeyi*, the latter species would offer suitable shelter for enhancing growth rates of the former. This last finding is also in agreement with the additive basal area phenomenon (Lusk 2002, Lusk and Ortega 2003, Aiba et al. 2007, Donoso and Lusk 2007, Donoso and Soto 2016, Parada et al. 2018), where mixed forests can develop more biomass or basal area than pure stands. As far as I am aware, this is the first study in including habitat types for modeling productivity in temperate forests; thus, moving forward toward a better ecological understanding of habitats in forest productivity. Moreover, I have shown that the habitat type alters forest productivity. This pattern is also in agreement with recent global studies on productivity–biodiversity relationships (Liang et al. 2016, Morin et al. 2018).

Second, because topography features directly affect radiation and moisture, it has been recognized as influencing tree growing conditions (Turner 1936, Myers and van Deusen 1962, Hunter and Gibson 1984, Fontes et al. 2003). Likewise, how to include topographic variables in forest productivity models has been studied (Beers et al. 1966, Stage 1976, Stage and Salas 2007). However, soil variables have been problematic to incorporate directly into forest productivity studies (Verbyla and Fisher 1989, Monserud et al. 1990, Carmean 1996). For *N. obliqua* in Chile, Thiers (2004) found, after assessing several soil characteristics on productivity, that these are most important only to represent microsite conditions. Although I did not use soil variables directly, I approximated their effects by incorporating habitat type and elevation. The biogeoclimatic factors submodel $\hat{a}_i$ not only allows differences between different aspects but also having differential effects on productivity depending on elevation. This distinguishing feature is not achieved easily with traditional linear models. Based on the proposed model, I predict more substantial differences in height growth of *N. alpina* dominant trees, i.e., forest productivity, between alternating aspects (northern vs. southern) at higher altitudes than at lower ones (second row of Fig. 4). The importance of aspect and slope on forest structure and composition had been reported in the Mediterranean region of Chile (Armesto and Martínez 1978); so the described patterns of productivity are in agreement with these authors. The $\hat{a}_i$ submodel must be considered in its entirety, regardless of whether, in a statistical sense, specific parameters may not appear nonsignificant when using traditional hypothesis testing (Stage and Salas 2007, Battles et al. 2009).

Elevation affects forest productivity in different ways. Among the topographic factors influencing tree growth and forest productivity, altitude had been central in forest ecology (Coomes and Allen 2007). Regarding an altitudinal gradient, atmospheric pressure, air and soil temperature, humidity, exposure to wind, supply of nutrients, and radiation change (Coomes and Allen 2007, Körner 2007). However, disentangling the neat effects of elevation is a complicated matter because of the multiplicity of factors being simultaneously affected. Körner (2007) offered several examples where the interpretation of results obtained for altitudinal gradients in ecology becomes difficult. For the same reason, I proposed to model the impact of altitude on forest productivity in combination with other elements. Overall, based on the differentiation of the submodel $\hat{a}_i$ with respect to elevation and assuming a flat terrain (i.e., slope = 0), I estimate that the optimum elevation for *N. alpina* is 700 m above sea level. Finally, the proposed modeling framework offers the alternative of representing global and local topographic features into forest productivity. Given such a high variation of landscape configurations in south-central Chile (i.e., the Andes, the Coastal Range, and the central valley), the model can accommodate both: the large-scale variation, represented by habitat types, elevation, and climate-related variables; and the small-scale variation, represented by the slope, aspect, and elevation interaction.

Thirdly, climatic variables were usually thought of as constant for a given forest site when estimating forest productivity. However, I now consider that climate is no longer constant on time. Among the first studies on incorporating climate effects into their growth models is the one by Jordan and Lockaby (1990). Later on, and thanks to the available climate layers, recent studies have been incorporating climate variables in their growth models (Wang et al. 2004, Madrigal-González et al. 2016). Climate is recognized as an important feature to be taken into account, and that forced to search for alternatives to addressing climate effects into well-established forest growth simulators (Crookston et al. 2010). The proposed model is sensitive to variations in precipitations, represented by both the amount of rain during the warmest quarter (Pptwq) and the seasonality (Ppseas) or distribution within a year. Meanwhile, Pptwq has a positive effect on forest productivity; Ppseas evidences a detrimental impact. The region under study is characterized by a strong latitudinal gradient in precipitation, being more humid to the south. The precipitation-related variables used here represent indicators of the water balance. For instance, Pptwq is approximately the spring/summer precipitation, which is usually related to plant growth.

Regarding the mean annual temperature, it exhibits an optimal pattern after differentiating the submodel $\hat{b}_i$ with respect to temperature. I estimate the optimum mean annual temperature for *N. alpina* in 9.98°C. Also, an increase in temperature could be favorable for forests, but only up to a limiting value. Beyond that threshold, the effects of temperature on forest productivity are adverse. Assuming a course of future climate conditions, where Ppseas and Temp increases by 10% and 1°C, respectively, and Pptwq decreases by 10 mm, I predict a reduction of 1.4 m in height growth of 100-yr-old dominant trees. This reduction is 4% of height growth under no climate change conditions. Although it might look small, this reduction suggests an important decrease in forest carbon sequestration because of the high proportion of biomass being stored by dominant trees (Luyssaert et al. 2008, Stephenson et al. 2014).

The proposed approach to quantify climate–productivity relationships has the potential to be used elsewhere. This approach combines dendrochronological data of dominant trees and freely available global climate data sets. These sort of required information would be handy to obtain for researchers working in regions with low availability of high-resolution soil-bioclimatic data. Indeed, further research is needed to provide better empirical climate data and physiological experiments to accurately envision the impact of climate change in forest productivity successfully.

Concluding Remarks

In this analysis, I offer a new simple approach for quantifying the productivity–climate relationship in temperate forests. Because of the highly variable landscape forms of the region under study, forest productivity varies widely between neighboring locations along with the distribution of the *Nothofagus alpina* forests. The proposed productivity model can represent large- and small-scale geographic variation, by taking into account habitat types, elevation, and climate-related variables; and the interaction among slope, aspect, and elevation. Ecologists need to include the effects of topography, habitat type, and climate features simultaneously into models of forest ecosystem dynamics, as these factors shift the potential paths to be followed by a forest stand.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2285/full

DATA AVAILABILITY

Time series height-data for *Nothofagus alpina* trees are available in the Figshare repository (Salas-Eljatib 2021*b*): https://doi.org/10.6084/m9.figshare.13521602.