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Climate change altered the dynamics of stand dominant height in forests during the past century – Analysis of 20 European tree species

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1 **Climate change altered the dynamics of stand dominant height**
2 **in forests during the past century - analysis of 20 European**
3 **tree species**

4 **Running head:** Climate change altered forest height dynamics

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29

30 **Abstract**

31 Analyzing how climate change has affected forest growth is crucial for predicting future

32 dynamics and adapting forest management to future climate change. In this paper, we

33 investigate how climate change has modified stand dominant height dynamics and site

34 index of 20 European tree species. We used an innovative method based on an annual

35 height increment equation to model stand dominant height as a function of climate back to

36 1872 and of other stand environmental conditions. We used these models to simulate stand

37 dominant height dynamics and site index under two different climates (prior to climate

38 change and actual recent climate) to analyze the impact of climate change over the past

39 century. To build our models, we combined the recently published FYRE long-term climate
40 database, which provides daily data since 1871, with data from more than 17,000 forest
41 stands of the French National Forest Inventory network. Higher temperature, precipitation
42 and climatic water balance generally favor stand dominant height dynamics when the
43 variables are considered separately. However, the positive effects often saturate at the
44 higher end of the variable distribution. Over the past century, the effect of climate change
45 on the site index has varied widely among species, ranging from a decrease of less than 3%
46 to an increase of more than 5%. The effect of climate change has also varied within species,
47 with more positive effects on initially temperature-limited stands for some species. For the
48 species and environmental conditions considered, our results highlight a positive response
49 of site index to past climate change for most species, albeit with between- and within-
50 species differences. Our results also suggest that this positive response could become
51 negative under continued climate change. These conclusions, as well as the quantitative
52 relationships we provide between climate and stand dominant height dynamics or site
53 index, will help design management strategies to adapt forests to climate change.

54 **1. Introduction**

55 In the context of rapid climate change, indicators used in forest management should take
56 into account the impact of climate change on forest dynamics. This is a prerequisite for
57 implementing management strategies that promote adaptation to climate change.

58 Stand productivity, defined as “the potential of a particular forest stand to produce
59 aboveground wood volume” (Skovsgaard and Vanclay, 2008) is a key indicator for forest

60 management (Socha et al., 2020). Since it largely depends on climatic and soil factors, it is
61 important to develop models assessing the impact of climate change on site productivity. In
62 pure even-aged stands, the average height of the tallest trees, defined as “dominant height”,
63 is an interesting indicator to analyze stand productivity. In such stands, the increase in
64 stand dominant height indeed correlates with stand volume growth and is largely
65 independent of stand density, provided that thinning is not done from above (Skovsgaard
66 and Vanclay, 2008). A common indicator of stand productivity in pure even-aged forest is
67 therefore site index, defined as stand dominant height at a given reference age, *e.g.* at 100
68 years (Skovsgaard and Vanclay, 2008).

69 Stand dominant height dynamics and site index depend on environmental conditions
70 (Vallet and Perot, 2016; Sharma et al., 2015; Scolforo et al., 2020). It is therefore important
71 to better understand how climate change affect both. Existing studies across a variety of
72 species and contexts have generally found a positive effect of higher temperature and water
73 availability on site index (*e.g.* Messaoud and Chen, 2011; Brandl et al. 2018; González-
74 Rodríguez and Diéguez-Aranda, 2021) and stand dominant height dynamics (*e.g.* Vallet and
75 Perot, 2016). However, the sign and magnitude of climate effect vary among species and
76 environmental conditions (Albert and Schmidt, 2010; Pau et al., 2022) and the positive
77 effects of temperature or precipitation may saturate when they reach a certain level (*e.g.*
78 Brandl et al., 2018). Such climate–growth relationships have been well studied for some
79 iconic European tree species such as *Picea abies* (L.) H.Karst or *Fagus sylvatica* L.. However,
80 climate–growth relationships are scarcer for other species such as *Quercus pubescens* Willd.,
81 *Fraxinus excelsior* L. or *Larix decidua* Mill., and it would be useful for forest managers to
82 have information for a larger number of species.

83 The site index for a given site depends on the year of establishment of the stand, in relation
84 to changes in climate, atmospheric CO₂ concentration, or N deposition (Sharma et al. 2012;
85 Socha et al., 2021; Messaoud et al., 2022). Bontemps et al. (2012) even found that
86 environmental changes during stand lifetime influence the stand dominant height
87 dynamics, suggesting that the site index evolves during stand lifetime. However, to our
88 knowledge, empirical quantitative relationships on the scale of stand lifetime between on
89 the one hand stand dominant height dynamics or site index and on the other hand climate
90 change are still lacking for many species. Such relationships would be very useful for forest
91 management to anticipate short-term effects of climate change on stand productivity.

92 One challenge in establishing these relationships is relating stand dominant height
93 observations to climate data at the scale of the year (or a few years). One solution would be
94 to relate annual (or multi-year) climate data to height data at the same temporal resolution.
95 Such high-frequency height data come mainly from stem analysis (Bontemps and Bouriaud
96 2014). However, stem analysis often focuses on a low number of species and comes at the
97 cost of a small number of observations (Bontemps and Bouriaud 2014). This may limit the
98 ability to identify a relationship between climate and stand dominant height, and this may
99 limit the range of climate conditions to which the relationship applies. In contrast, national
100 forest inventories (NFIs) provide large-scale, spatially intensive, randomly sampled data
101 from forest stands and include a large number of species (Bontemps and Bouriaud, 2014;
102 Aguirre et al., 2022). They therefore allow the detection of climate impacts under different
103 resource limitations (Charru et al., 2017). National forest inventories have been used to
104 infer relationships between climate and site index (Brandl et al., 2018) and between climate
105 and stand dominant height dynamics (Vallet and Perot, 2016; Stimm et al., 2021). However,

106 these inventories generally do not include annual series of age and height measurements
107 from the year of establishment. This makes it difficult to study the effects of climate change
108 over the lifetime of stands, and generally leads to building stand dominant height models
109 based only on an aggregate equation linking mean climate to observed stand dominant
110 height (Vallet and Perot, 2016).

111 Spatial heterogeneity in climate influences the effects of climate change on stand dominant
112 height dynamics and site index for a given species or between species. For example, Albert
113 and Schmidt (2010) showed that *Picea abies* site index responded more negatively to
114 climate change in water-limited environments and *Fagus sylvatica* site index responded
115 more positively to climate change in temperature-limited environments. Generalizing such
116 results to a larger number of species could help to design forest adaptation strategies to
117 climate change.

118 This paper has three main objectives: first, to develop species-specific models linking
119 climate to stand dominant height dynamics for a large number of European tree species,
120 capable of capturing the impact of climate variation during stand life and accounting for
121 non-linear climate effects; second, to analyze the effect of each climatic variable on site
122 index; third, to assess the impact of climate change over the past century on stand dominant
123 height dynamics and site index.

124 To this end, we developed an original modeling strategy that takes into account the
125 influence of annual climate on stand dominant height dynamics even without repeated
126 measurements of stand dominant height. This strategy allowed us use the data from the
127 French National Forest Inventory (IGN, 2022) and thus to calibrate our models on more

128 than 17,000 stands covering a wide range of species and climate conditions. This modeling
129 strategy relies on the reconstruction of an unobserved stand dominant height trajectory
130 from stand origin based on initial stand dominant height, stand age, and a theory-based
131 stand dominant height increment equation (Tomé et al., 2006; Bontemps et al., 2009)
132 incorporating annual climate. This approach relies critically on the long-term FYRE climate
133 database, which dates back to 1871(Devers et al., 2021). We then used these models to
134 assess the impact of climate change during the past century by comparing simulated stand
135 dominant height dynamics (and site index) under two scenarios: with a climate prior to
136 climate change and with actual climate.

137 Based on these stand dominant height models taking into account annual climate and the
138 associated simulations, we examined the following question:

139 • Question 1: How do individual climatic variables influence stand dominant height
140 and site index? We tested the following hypotheses:

141 – Hypothesis 1: Higher temperature, precipitation and climatic water balance
142 during spring and summer favor site index, but these positive effects may
143 saturate beyond a certain value, and in the case of temperature may even be
144 reversed.

145 • Question 2: What was the effect of climate change on stand dominant height and site
146 index during the last century? We tested the following hypotheses:

147 – Hypothesis 2a: Climate change has had a different effect (sign and magnitude)
148 depending on the species during the period considered;

149 – Hypothesis 2b: For a given species, the effect of climate change during the
150 period considered varied depending on the climate context of the stand.

151 **2. Materials and methods**

152 **2.1. General approach**

153 For each of 20 European tree species, we built a species-specific model to relate observed
154 stand dominant height (SDH) to (i) SDH at the stand establishment date, (ii) climate data
155 series from the stand establishment date, and (iii) other site variables. We then used these
156 models to simulate the SDH dynamics of each stand for a period of 70 years under a
157 reference climate representing the climate before climate change (1891-1920 mean
158 climate) and under the actual climate of the recent period (1950-2020 climate series). This
159 allowed us to evaluate the impact of climate change on SDH dynamics during the last
160 century. We then computed simulated site index as simulated SDH at the age of 70 years.
161 Therefore, simulated site index depends on stand climate history, which enabled us to study
162 the impact of climate change on site index.

163 **2.2. Data used for modeling and simulation**

164 **2.2.1. National Forest Inventory data and variables**

165 We used data from the French National Forest Inventory (IGN, 2022) from 2006 to 2020.
166 Each year, 5000 to 6000 temporary forest plots are measured throughout the French
167 metropolitan territory, through a progressive survey of a grid with a resolution of 1 km.
168 This ensures uniform coverage of the territory for each measurement year. For each stand,

169 the NFI data provides canopy cover per tree species and forest vertical structure (even-
170 aged or uneven-aged forest), determined within a 25m-radius circle. Dominant trees are
171 defined as the six largest-diameter trees in a 15m-radius circle. Age and height are
172 generally measured for two of these dominant trees, referred to as “measured dominant
173 trees” in the rest of this section. In some specific configurations (a single living tree, or high-
174 value trees that could not be cored), a single dominant tree is measured. Supplementary
175 Material A give some details on these data, which are described in detail in IGN (2022) and
176 in Vallet and Perot (2016).

177 **2.2.2. Stands and species selection**

178 We considered even-aged pure stands. We defined a stand as even-aged if (i) the NFI
179 labeled it as such, and (ii) in case two dominant trees were measured, the difference in age
180 between the oldest measured dominant tree and the youngest measured dominant tree is
181 below 25% of the age of the youngest measured dominant tree. The latter condition
182 ensured that all dominant trees in the stand share roughly the same history. We considered
183 a stand to be pure if all of the following conditions were met: (i) a single species represents
184 more than 75% of the canopy cover, (ii) both measured dominant trees belong to the same
185 species, and (iii) the species with the highest canopy cover had the highest basal area. We
186 excluded stands with incomplete data (*cf.* section 2.2.4 and 2.2.5 for the list of explanatory
187 variables) and stands whose establishment date was older than the depth of the climate
188 data, namely 1871 (*cf.* section 2.2.3. for the calculation of stand establishment date). Finally,
189 we considered the 20 species with the highest number of observations in the NFI database.
190 We ended with 17,462 stands. For 15,802 of them, age and height were measured for two

191 trees, and for the others, age and height were measured for a single tree. Table 1 shows the
192 list of species studied together with the corresponding number of stands. We show the
193 geographic repartition of the stands per species in supplementary materials (Fig. A.1).

194 **2.2.3. Calculation of stand age, stand dominant height at observation date and stand** 195 **establishment date**

196 Following Assmann and Davis (1970), we defined SDH as the average height of the 100
197 biggest trees within a hectare. To get SDH over an area of n hundred-square-meters ($n <$
198 100), SDH has to be computed as the mean height of the $n-1$ biggest trees to correct for
199 sample bias (Vallet and Perot, 2016). According to the French NFI protocol, the two
200 measured dominant trees are selected within the six biggest trees over a 7 hundred-square-
201 meters surface, so the mean height of these two trees provides an unbiased estimate of SDH
202 at the observation year (Vallet and Perot, 2016). Therefore, we calculated SDH at the
203 observation year as the mean height of the two measured dominant trees. We defined
204 stand age as the average age of the two measured dominant trees. We defined stand
205 establishment date as the NFI observation year minus stand age. The NFI protocol defined
206 tree age as the number of years between the date when the tree height was 1.3 m and the
207 observation date. Therefore, at the stand establishment date, SDH was always 1.3 m. When
208 age and height were measured for a single tree, we considered stand age and SDH to be
209 equal to respectively the age and height of that tree. This still provided us with an unbiased
210 estimation of stand dominant height. Damaged trees were excluded from our calculation. If
211 NFI stand surveys were conducted between January and April of year t , the stand had not
212 yet benefited from the spring and summer growing season of that year, so we considered

213 the observation year to be $t - 1$. Table 1 shows the SDH distribution, stand age distribution
214 and stand establishment date range per species.

Species	Number of stands	SDH (m)		Age (year)				Stand establishment date	
		Mean	s.d	Mean	s.d.	Min	Max	Min	Max
<i>Abies alba</i> Mill., 1768	817	25.5	6.2	72.7	33.6	9	147	1871	2002
<i>Betula pendula</i> Roth, 1788	106	16.0	4.5	31.2	16.5	4	83	1932	2009
<i>Carpinus betulus</i> L., 1753	97	19.5	4.9	63.4	25.5	11	125	1885	2003
<i>Castanea sativa</i> Mill., 1768	440	17.7	4.8	43.9	26.1	5	141	1871	2013
<i>Fagus sylvatica</i> L., 1753	1,470	23.4	7.2	83.1	35.0	8	147	1871	2006
<i>Fraxinus excelsior</i> L., 1753	334	21.6	6.9	50.9	28.2	6	131	1875	2011
<i>Larix decidua</i> Mill., 1768	151	19.0	6.1	67.5	36.0	7	137	1873	2009
<i>Picea abies</i> (L.) H.Karst., 1881	1,338	22.9	6.6	42.7	22.5	7	145	1871	2011
<i>Picea sitchensis</i> (Bong.) Carrière, 1855	143	22.3	6.9	31.0	10.3	5	63	1944	2013
<i>Pinus halepensis</i> Mill., 1768	344	12.5	3.9	50.1	23.6	6	137	1875	2010
<i>Pinus nigra</i> subsp. <i>nigra</i> J.F.Arnold, 1785	413	15.0	5.3	53.2	29.3	6	135	1881	2012
<i>Pinus nigra</i> var. <i>corsicana</i> (Loudon) Hyl., 1913	526	16.0	5.9	30.6	20.3	4	146	1871	2015
<i>Pinus pinaster</i> Aiton, 1789	2,424	16.8	6.5	30.3	20.8	2	132	1876	2018
<i>Pinus sylvestris</i> L., 1753	1,551	15.8	5.9	59.3	27.6	5	144	1873	2011
<i>Pseudotsuga menziesii</i> (Mirb.) Franco, 1950	1,449	24.1	8.6	30.6	13.0	4	110	1910	2015
<i>Quercus petraea</i> (Matt.) Liebl., 1784	2,472	22.2	6.1	80.6	33.4	7	149	1871	2010
<i>Quercus pubescens</i> Willd., 1805	1,019	13.9	4.3	67.6	25.0	7	145	1871	2006
<i>Quercus robur</i> L., 1753	2,105	20.7	5.4	70.3	30.9	8	149	1871	2006
<i>Quercus rubra</i> L., 1753	114	18.5	6.2	26.4	16.3	4	81	1930	2006
<i>Robinia pseudoacacia</i> L., 1753	149	18.0	5.1	32.3	18.0	5	94	1916	2014

215 Table 1: Calibration data. Only stands with complete data and with establishment date from 1871 are considered.

216 NFI data contain a single SDH measure for each stand. s.d. : standard deviation

217 2.2.4. Climate data and climate variables

218 We used temperature and precipitation data from the FYRE database (Devers et al., 2020a;

219 2020b; 2021) for the period 1871-2012 and the Météo France SAFRAN database (Vidal et

220 al., 2010) for 2013-2020. This temporal depth was necessary to cover the full stand life
221 span observed in our data. The Safran data consist in an interpolation merging observations
222 and background data over 608 climatologically homogeneous zones covering metropolitan
223 France, then disaggregated onto a 8 km grid taking into account altitude (Devers et al.,
224 2020). FYRE data consist in a reanalysis over the same 8 km grid, assimilating observation
225 into the SCOPE background (Devers et al., 2020). The FYRE data include 25 climate series,
226 which represent equally plausible meteorological series (Caillouet et al., 2019). We used the
227 average of these 25 climate series. For both the FYRE and SAFRAN data, we converted daily
228 data to monthly data by averaging daily temperature and summing daily precipitation. For
229 each grid cell, we computed the mean difference between FYRE data and SAFRAN data over
230 the period 1990-2012, and we added this difference to SAFRAN data over 2013-2020 to
231 correct for the bias between the two data sources. We used the 1990-2012 period to
232 compute the bias because it represents a compromise between having enough data and
233 covering a period close enough to the period over which we want to implement the
234 correction (namely 2013-2020). We then created a single gridded climate database by
235 concatenating FYRE data over 1871-2012 and SAFRAN unbiased data over 2013-2020.

236 To derive the temperature series at each NFI site, we corrected the grid-based climate data
237 for an elevation gradient following Devers et al. (2020). For each of the 608 homogeneous
238 climate areas, we defined an altitude gradient by fitting a linear model between the mean
239 temperature and the mean altitude of each grid cell. In case there was less than three grid
240 cells in a homogeneous climatic area, we grouped these cells with the cells of the closest
241 homogeneous climatic area. We used this gradient to correct the climate series for each NFI
242 site, based on the difference between the NFI site elevation and the corresponding grid cell

243 elevation. We applied a similar procedure to determine precipitation at each NFI site.
244 Because elevation correction for precipitation is not relevant in lowland areas, we applied
245 the correction only when the difference between the NFI site elevation and the
246 corresponding grid cell elevation was greater than 300m (Devers et al., 2020)

247 To combine the influence of temperature and precipitation, we calculated a monthly
248 climatic water balance, defined as the difference between precipitation and potential
249 evapotranspiration (Lebourgeois and Piedallu, 2005). Potential evapotranspiration was
250 derived from monthly temperature and radiation using the Turc formula (Lebourgeois and
251 Piedallu, 2005). Monthly radiation without nebulosity was obtained following Piedallu and
252 Gégout (2007). Since this radiation varies little between years, we assumed that the
253 monthly radiation was equal to the monthly values for the year 2000. To account for light
254 interception by clouds, we corrected the radiation value with the average monthly
255 nebulosity between 1960 and 2019, following Piedallu and Gégout (2007). The nebulosity
256 data were taken from Harris et al. (2020).

257 We defined climate year t as the period from September of year $t - 1$ to August of year t .
258 We did this because growth during the growing season of year t can be influenced by
259 precipitation during the previous fall and winter (Bravo-Oviedo et al., 2008). This definition
260 led us to limit our analysis to the climate years 1872-2020, since the FYRE database starts
261 in January 1871.

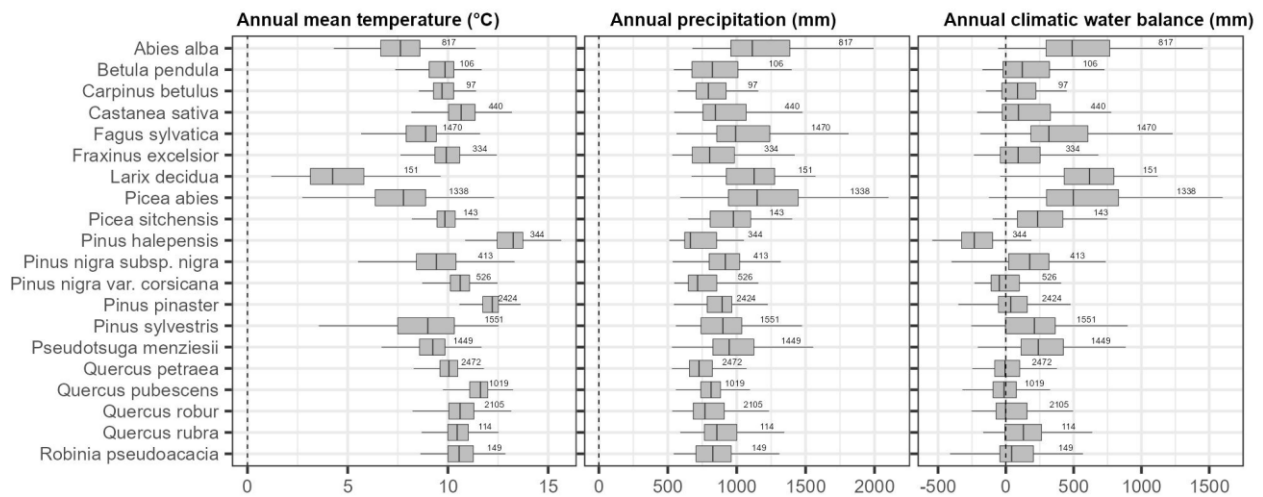
262 For each stand and each climate year t , we calculated mean temperature, total precipitation,
263 and total climatic water balance for fall (September to November of year $t - 1$), winter
264 (December of year $t - 1$ to February of year t), spring (March to May of year t) and summer

265 (June to August of year t) as well as for two semesters (September of year $t - 1$ to February
266 of year t and March of year t to August of year t) and for the entire climate year. We
267 calculated the annual sum of growing degree days (SGDD), defined as the sum of
268 temperature above 5.5°C over all days from January to December (Kunstler et al., 2021). In
269 this calculation, we approximated daily temperature based on the mean temperature of the
270 corresponding month. In total, we retained 22 climatic variables.

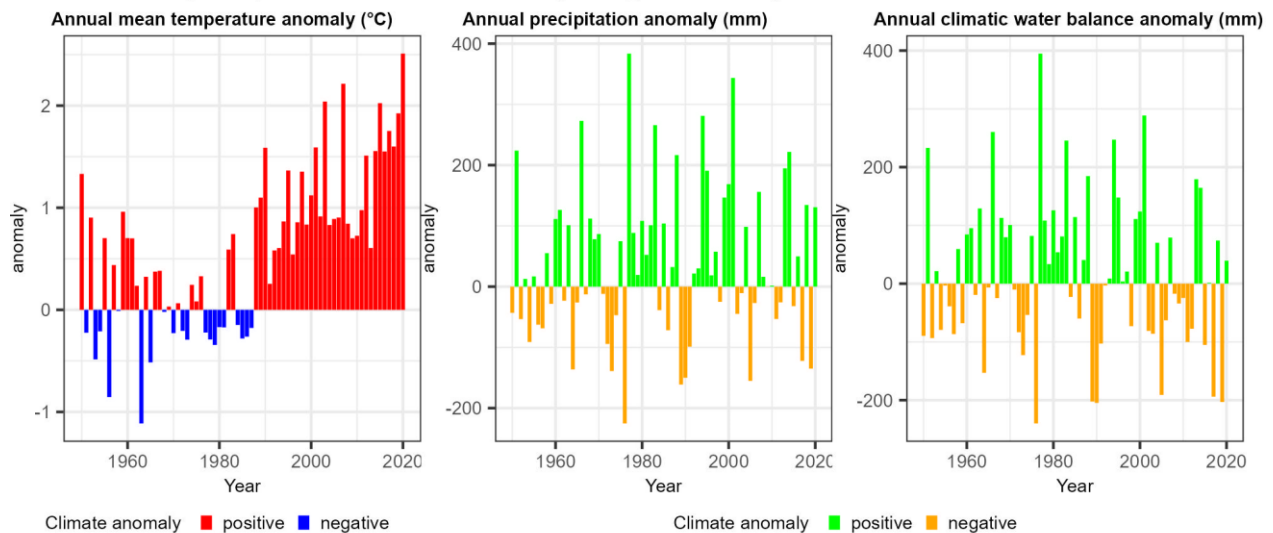
271 We defined a reference climate to represent the climate prior to climate change. For each
272 climatic variable, we defined the reference climate as the mean of the variable over the
273 period 1891-1920. Figure 1 shows the distribution of annual climatic variables per species
274 for the reference climate and climate anomalies over the recent period (1950-2020)
275 compared to the reference climate.

276 To calibrate our models, we standardized each of the 22 climatic variables per species by
277 subtracting the mean and dividing by the standard deviation. For each species, we
278 calculated the mean and standard deviation based on the distribution of each variable
279 across all stands of that species for the period 1872-2020.

Reference climate (average 1891- 1920)



Climate anomaly compared to reference climate (average 1891-1920)



280

281 *Figure 1: Reference climate per species (first row) and climate anomalies in the recent period*
 282 *(1950-2020) compared to the average of the reference period (1891-1920) (second row), for*
 283 *mean temperature (left), total precipitation (middle) and total climatic water balance (right).*
 284 *A higher climatic water balance corresponds to a wetter climate. In the second row, the result*
 285 *for a given year is obtained by averaging all stands, regardless of species.*

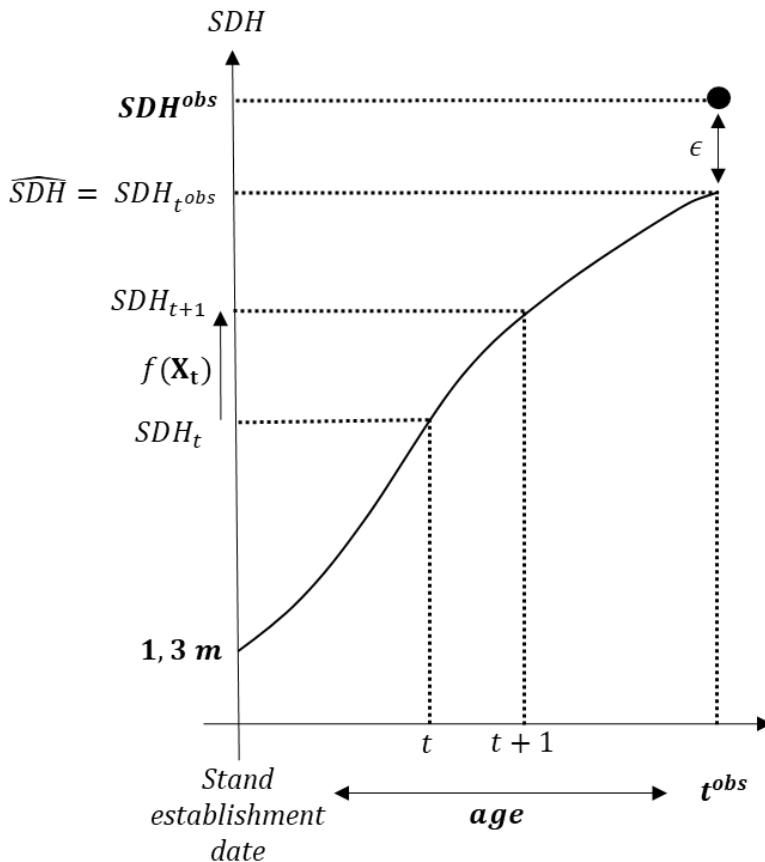
286

2.2.5. Non-climate environmental data s

287 The French NFI provides field data for soil texture, soil depth, rock presence, rock
288 emergence, slope and herbaceous species presence. We used NFI data on herbaceous
289 species presence to calculate bioindicated values for C:N ratio, P₂O₅ and soil pH (Gégout et
290 al., 2005). We calculated a soil water holding capacity following Piedallu et al. (2018) based
291 on NFI data on soil texture, soil depth, and rock presence and emergence. This calculation
292 was not possible for soils labeled as “organic soil” in NFI data, so we excluded such stands
293 from the analysis (21 stands). Finally, NFI data do not provide field measurement of slope
294 for stands located on complex topography. Therefore, we excluded such stands from the
295 analysis (288 stands). Supplementary Material C provides details and summary statistics
296 for the 14 non-climatic variables (Tab. C.1 to C.4). To calibrate our models, we standardized
297 each of the non-climate environmental variables per species by subtracting the mean and
298 dividing by the standard deviation. For each species, we calculated the mean and standard
299 deviation based on the distribution of each variable across all stands of that species.

300 **2.3. Modeling stand dominant height and site index as a function of**
 301 **annual climatic variables**

302 **2.3.1. Model equations**



303
 304 *Figure 2: Modeling strategy to model stand dominant height (SDH) dynamics of a given stand.*
 305 *Variables available in the NFI database or climate database are shown in bold: observed SDH*
 306 *(SDH^{obs}), stand observation year (t^{obs}), stand age (age) and annual environmental*
 307 *conditions (X_t). \widehat{SDH} is the modeled SDH at the time of observation and ϵ is the modeling*
 308 *error. From the stand establishment date ($t^{obs} - age$), we reconstructed the unobserved*
 309 *annual trajectory of SDH (SDH_t) year by year using a theory-based function (f) that relates*

310 *the unobserved SDH increment between year t and $t+1$ to observed contemporary*
311 *environmental conditions.*

312 The French NFI data do not include observations for annual SDH or SDH annual increment,
313 so it was not possible to model directly SDH increments as a function of annual climate. We
314 therefore used an indirect strategy (cf. Figure 2): for each species, we modeled SDH
315 observations (one per stand) as a function of the series of annual climatic stand conditions
316 from stand establishment date and of non-climatic stand conditions. Our model relies on
317 the fact that (i) SDH at a given age is the sum of annual SDH increments over the period
318 between stand establishment date and the age considered and (ii) annual SDH increments
319 can be described by a theoretical function of non-climatic conditions, climatic conditions
320 and SDH at the beginning of the period (Bontemps et al., 2009; Zeide, 1993).

321 Equation 1 describes for a given stand the relationship between observed stand dominant
322 SDH^{obs} and the series of SDH increment (ΔSDH_t). In this equation, 1.3 meters is the stand
323 dominant height at the stand establishment date (cf. section 2.2.3), t^{obs} is the observation
324 year, age is the age, and ϵ is a heteroscedastic Gaussian residual error. To take into
325 account increasing error with SDH, we assumed $\epsilon \sim N(0, \sigma^2 \widehat{SDH}^{2\delta})$ where \widehat{SDH} is the
326 fitted value of SDH at the observation year for the stand under consideration, σ is a positive
327 parameter independent of the stand and δ is a scalar parameter independent of the stand.

328
$$SDH^{obs} = 1.3 + \sum_{t=t^{obs}-age}^{t^{obs}-1} \Delta SDH_t + \epsilon \quad (\text{Equation 1})$$

329 Equation 2 describes for a given stand how we replaced unobserved annual SDH increment
330 (ΔSDH_t) by a theoretical function of environmental variables and SDH at the beginning of

331 the period. Zeide (1993) suggests writing SDH increment as the sum of an expansion term
332 f_{exp} and a decline term f_{decl} , to reflect catabolic and anabolic processes, respectively.
333 Among the equations presented by Zeide (1993), we chose the Chapman-Richards equation
334 because it reflects physiological processes, assuming that catabolic processes depend on
335 size, modified by a species-specific shape term β_0 , and that anabolic processes are size-
336 dependent (Tomé et al., 2006). To ensure the biological soundness of our models, we
337 imposed $\Delta SDH_t > 0$ to ensure that SDH does not decrease over time, for a given stand. In
338 Equation 2, X_t^{exp} and X_t^{decl} are the sets of explanatory variables at year t used to predict the
339 expansion and the decline terms, respectively.

$$340 \quad \Delta SDH_t = \max[0, f_{exp}(X_t^{exp}).SDH_t^{\beta_0} - f_{decl}(X_t^{decl}).SDH_t] \quad (\text{Equation 2})$$

341 We assumed that the expansion term was a species-specific function of the climate of the
342 year in which the increment occurred and of other environmental variables. We assumed
343 that the decline term was a species-specific function that depended only on temperature
344 variables. We made this choice because the decline term reflects respiration, and
345 respiration is primarily temperature dependent (Valentine, 1997). Finally, we assumed the
346 shape term β_0 to be a species-specific constant. We made f_{exp} and f_{decl} non-divergent
347 following Antón-Fernández et al. (2016): we expressed both f_{exp} and f_{decl} as a species-
348 specific intercept (A_0 and C_0 , respectively), multiplied by a logistic function of the
349 explanatory variables (*cf.* Equation 3 and Equation 4). α and γ are species-specific
350 parameter vectors associated with the explanatory variables. We expect A_0 and C_0 to be
351 positive, but we did not constraint the model to ease convergence. *A posteriori*, we checked
352 that the parameter value was positive or that the parameter value was not significantly

353 different from 0, using a p-value of 0.05 to define significance. In case there are no
 354 explanatory variable for the expansion term (resp. the decline term), the logistic function in
 355 equations 3 and 4 is replaced by a factor 0.5. This allows interpreting $\frac{A_0}{2}$ (resp. $\frac{C_0}{2}$) as the
 356 value of the expansion term (resp. decline term) for a stand at the species mean
 357 environmental conditions.

$$358 \quad f_{exp}(X_t^{exp}) = A_0 \cdot \frac{\exp(\alpha \cdot X_t^{exp})}{1 + \exp(\alpha \cdot X_t^{exp})} \quad (\text{Equation 3})$$

$$359 \quad f_{decline}(X_t^{decl}) = C_0 \cdot \frac{\exp(\gamma \cdot X_t^{decl})}{1 + \exp(\gamma \cdot X_t^{decl})} \quad (\text{Equation 4})$$

360 Equation 5 gives the final model for a given species and a given stand.

$$361 \quad SDH^{obs} = 1.3 + \sum_{t=t^{obs}-age}^{t^{obs}-1} \max \left[0, A_0 \cdot \frac{\exp(\alpha \cdot X_t^{exp})}{1 + \exp(\alpha \cdot X_t^{exp})} SDH_t^{\beta_0} - C_0 \cdot \frac{\exp(\gamma \cdot X_t^{decl})}{1 + \exp(\gamma \cdot X_t^{decl})} SDH_t \right] + \epsilon \quad (\text{Equation 5})$$

362 **2.3.2. Parameter inference and model selection**

363 For each species, we calibrated the model presented in Equation 5 using the data presented
 364 in section 2.2. For a given set of explanatory variables, we used the *nlminb* function in the
 365 “stats” R-package version 4.2.0 (R Core Team, 2022) and the TMB R-package version 1.9.0
 366 (Kristensen et al. 2016) to minimize the model negative log-likelihood (*nll*, given by
 367 Equation 6) with respect to the species-specific parameters $A_0, C_0, \alpha, \gamma, \beta_0$. In Equation 6, n
 368 is the number of stands for the species considered, i is a stand index and \widehat{SDH}_i is the
 369 prediction for stand i of the model given in Equation 5. The *nlminb* function allows
 370 optimizing expressions without simple analytical form, and the TMB package makes the
 371 computation faster.

372
$$nll = \frac{n}{2} \cdot \ln(2\pi) + \sum_{i=1}^n \ln(\sigma \widehat{SDH}_i^\delta) + \frac{1}{2} \sum_{i=1}^n \left(\frac{SDH_i^{obs} - \widehat{SDH}_i}{\sigma \widehat{SDH}_i^\delta} \right)^2 \text{ (Equation 6)}$$

373 For each species, we followed a stepwise variable selection process (Vallet and Perot, 2016;
374 Mina et al., 2018). In this process, we considered the standardized 22 climatic variables and
375 14 non-climatic variables. We also considered the square of each climatic variable and the
376 square of pH, C:N ratio and P₂O₅ indicator to identify potential saturation or non-monotonic
377 effects. At each step, (i) for each variable non-included in the model yet, we tested the
378 inclusion of the variable in the expansion term, (ii) for temperature variables, we also
379 tested the inclusion in the decline term and (iii) we selected the model that most decreased
380 the Bayesian information criterion (BIC). The BIC penalizes the inclusion of an additional
381 variable in the model more than AIC, which limits the risk of overfitting. We repeated this
382 process until the BIC reached its minimum. To avoid collinearity, we used a variance
383 inflation factor (VIF) (O'Brien, 2007). We excluded all models with variables with a VIF
384 greater than 2 from the model selection process. To avoid issues in parameter identification
385 due to the appearance of the same variable in both the expansion and decline terms, we
386 allowed a given temperature variable to appear either in the expansion or decline terms,
387 but not both. For *Castanea sativa*, *Picea sitchensis*, *Quercus rubra* and *Betula pendula*, we
388 excluded the qualitative variable reflecting the calcareous nature of the bedrock, because
389 more than 90% of the stands were on the same type of bedrock.

390 **2.3.3. Assessment of model quality**

391 To assess the risk of overfitting for each species-specific model, we calculated the difference
392 between model prediction error using data not used for calibration and model prediction
393 error using calibration data. We refer to this difference in prediction error as “model

394 optimism”. To do this, we implemented a fivefold cross-validation. First, we randomly
395 divided our sample into five equally sized subsamples. Then we repeated the following
396 procedure for each subsample: (i) we considered this subsample as a validation subsample
397 and the remaining four subsamples as a single calibration subsample, (ii) we calibrated the
398 model presented in equation 5 on this calibration subsample and (iii) we calculated the root
399 mean square error (RMSE) over this calibration subsample and the RMSE over the
400 validation subsample and (iv) we defined an intermediate optimism indicator as the
401 relative difference between the RMSE calculated on the validation subsample and the RMSE
402 calculated on the calibration subsample. If the difference was negative, we considered it to
403 zero. We defined the final optimism indicator as the average of the five intermediate
404 optimism indicators. The higher the optimism indicator, the higher the prediction error
405 when the model was applied to new data compared to the error when it was applied to
406 calibration data. Details can be found in Supplementary Material D. We also calculated the
407 RMSE, root mean square percentage error (RMSPE) and bias of each species-specific model
408 when calibration was done on the whole sample (*cf.* Supplementary Material D for
409 calculation details).

410 **2.4. Simulations to analyze the partial effect of climatic variables and** 411 **the effect of climate change on stand dominant height and site index**

412 To analyze the impact of each climatic variable and climate change on SDH and site index,
413 we ran simulations based on the models we calibrated. To allow for interspecific
414 comparisons, we stopped the simulation at age 70 years, which corresponds to the lowest

415 observed maximum age amongst our species (see Tab. 1). We therefore defined the site
416 index as SDH at age 70 years.

417 For each species, we analyzed the partial effect of each variable, defined as the effect of a
418 variation in that variable on site index, holding all other variables constant. To do this, we
419 simulated the site index using the model developed in 2.3, while varying the variable from
420 the 0.05 to the 0.95 percentile of its species-specific range. We defined this species-specific
421 range as the distribution of annual values of the variable from 1872 to 2020 over all stands
422 of the species. For these simulations, we set all other variables to their mean values.

423 We then analyzed the impact of climate change over the last century, taking into account
424 the simultaneous evolution of the different climatic variables. For each species, we
425 simulated the SDH dynamics of each observed stand under the pre-climate change
426 reference climate (1891-1920 mean) and under the actual climate of the recent period
427 (1950 to 2020 climate series). We analyzed the impact of climate change on both (i) the
428 shape of the SDH trajectory and (ii) the percentage variation of the site index between the
429 recent and the reference climates.

430 **3. Results**

431 **3.1. Importance of climatic variables**

432 Some climatic variables were selected in our models for all species except *Pinus nigra subsp.*
433 *nigra* and *Picea sitchensis*. Species differed in the type of variable selected (temperature,
434 precipitation, climatic water balance, SGDD) and the season of the year for which the
435 variable was selected. Non-climate environmental characteristics such as C:N ratio, soil pH,

436 slope were often selected in the models. Detailed parameters are given in Supplementary
437 Material G (Table G. 1).

438 **3.2. Performance of the models**

439 Depending on the species, the RMSE varied between 2.4 m and 3.8 m and the RMSPE varied
440 between 14.3% and 29.9% over the stands used for calibration, while bias was null for all
441 species (*cf.* Supplementary Material, table D.1). Model optimism decreased with increasing
442 number of calibration points and was below 10% for all species with more than 200
443 calibration stands (*cf.* Supplementary Material Fig. D.1).

444 **3.3. Partial effect of climatic variables on site index**

445 Higher temperature, precipitation, and climatic water balance during spring and summer
446 generally favored the site index, defined as SDH at 70 years (Figure 3). For a large number
447 of species and variables, site index reached a maximum value and then saturated at the
448 upper end of the variable range. The decrease in site index at the upper end of the variable
449 distribution for some species and variables is quite weak. We also found a positive
450 saturation effect of fall and winter temperature for three species. We found more
451 contrasting results for fall and winter precipitation and climatic water balance, with a
452 positive saturating effect for some species, optimal values for other species, and a negative
453 effect for other species. The magnitude of the partial effect depended on the species and the
454 variable. Spring and summer temperature and precipitation generally had the most positive
455 effects. Our results show an outlier behavior for *Castanea sativa*: for this species, summer
456 temperature had a negative effect on the site index.



457

458

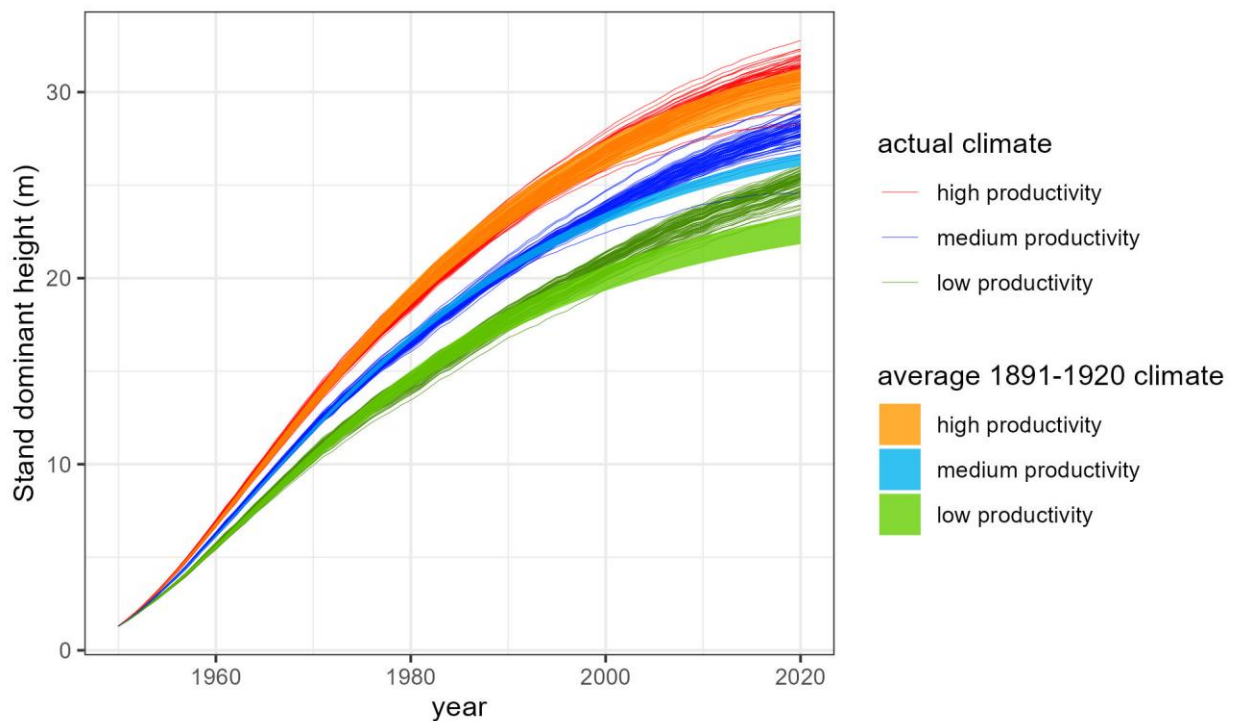
459 *Figure 3: Partial effect of climatic variables on site index. Each graph represents site index (y-axis) as a function of climate (x-axis).*
460 *Each color represents a species. Each column corresponds to a specific season, each line corresponds to variable. First line:*
461 *temperature (mean temperature of the period for the six first columns, and annual sum of growing degree days for the seventh*

462 column), second line: precipitations, third line: climatic water balance. In each graph, only the species for which a climate effect
463 was found are represented. See the Material and Methods section for an explanation of how partial effect was calculated.

464 **3.4. Effect of climate change on stand dominant height over the past**
465 **century**

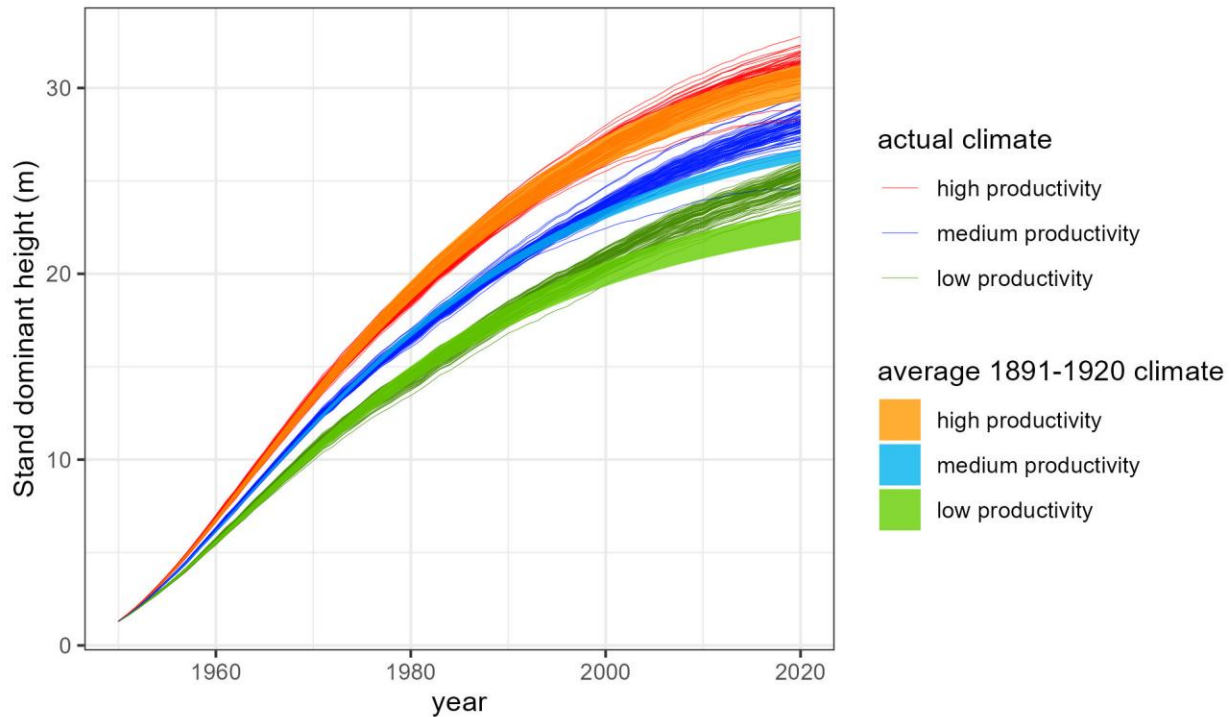
466 **3.4.1. Effect of climate change on stand dominant height dynamics**

467 We simulated SDH dynamics for each species under both the actual 1950-2020 climate and
468 the reference 1891-1920 average climate. To illustrate,



469 Figure 4 compares the SDH dynamics for *Abies alba*. After 40 years of almost no effect, the
470 effect of climate change became positive. This positive effect was more pronounced at the
471 lowest levels of productivity, where productivity is defined as the site index under the
472 reference climate. We found a similar pattern for *Fagus sylvatica* and *Picea abies*
473 (Supplementary Material Fig. E.1), but other species showed contrasting responses.
474

475

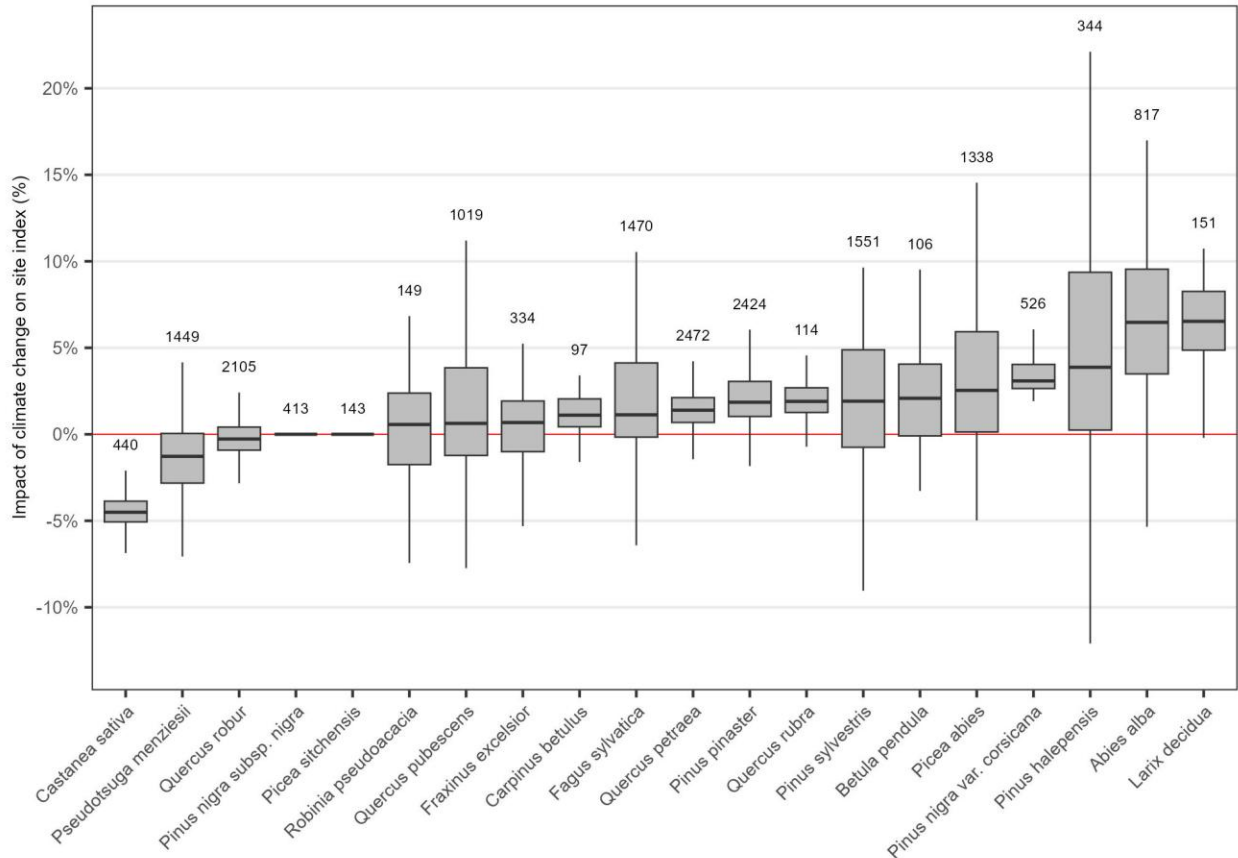


476

477 *Figure 4: Simulated SDH dynamics for actual recent climate (solid line, climate series 1950 to*
 478 *2020) and reference climate (ribbon, average climate 1891-1920) for *Abies alba* stands.*
 479 *Stands were grouped into three categories according to their productivity, defined as site*
 480 *index under the reference climate: productivity quantiles 0.05 to 0.15 (green), 0.45 to 0.55*
 481 *(blue) and 0.85 to 0.95 (red).*

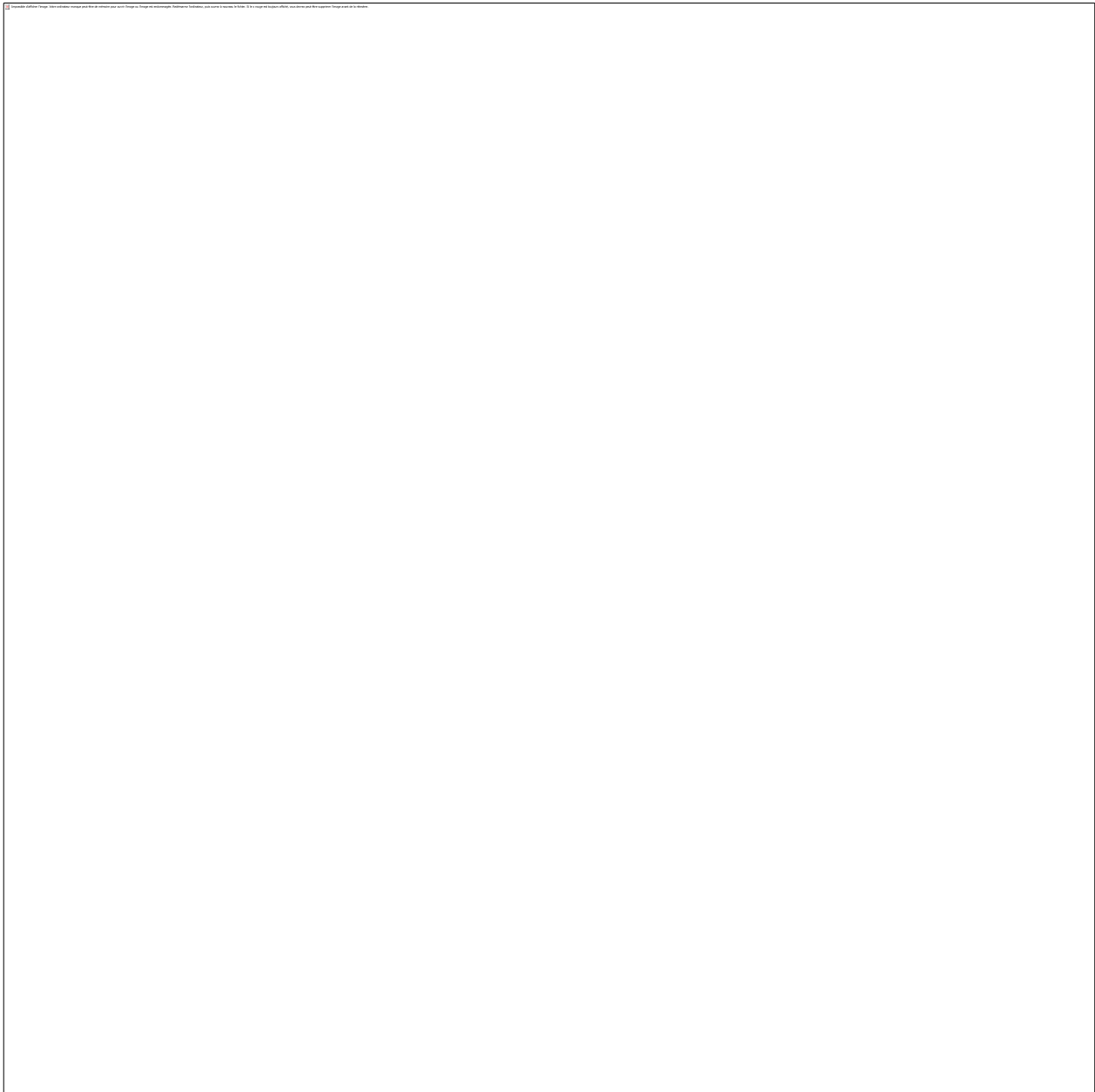
482 **3.4.2. Interspecific responses to climate change**

483 The median impact of climate change on the site index was positive for 15 species, negative
 484 for three species, and null for two species (Figure 5). The positive impacts were generally
 485 stronger than the negative impacts: the median impact was above 3% for four species,
 486 while only *Castanea sativa* had a negative impact below 3%. We did not find a general
 487 interspecific pattern linking the mean climate impact to the species' climate niche prior to
 488 climate change (*cf.* Supplementary Material F, Fig. F.1 and Fig F.2).



489
 490 Figure 5: Climate change effect on site index. Boxplots show the distribution of climate
 491 change effect over NFI stands for each species. Climate change effect was calculated as the
 492 relative difference between the simulated site index under the actual recent climate (1950-
 493 2020 climate series) and the reference climate (1891-1920 average). For each species, the
 494 number of calibration stands is given above the box. Outliers are not shown. Intraspecific
 495 response to climate change

496 We found intraspecific variation in the effects of climate change on the site index (Figure 5).
 497 For six species, the median impact was positive, but the first quartile impact was negative.
 498 For nine species, the effect of climate change on the site index was positive at the cold edge
 499 of the species' temperature range and negative or close to zero at the warm edge (Figure 6).



502
503 *Figure 6: Climate change effect on site index as a function of mean annual temperature over*
504 *the reference period (1891-1920). Boxplots show the distribution of climate change effect on*
505 *site index across the NFI stands for each species. The effect of climate change was calculated*
506 *as the relative difference between the simulated site index under the actual climate (1950-*
507 *2020 climate series) and the reference climate (1891-1920 average). The x-axis represents the*
508 *average climate of the stand over the reference period (1891-1920). For *Betula pendula*,*
509 **Fagus sylvatica* and *Pinus halepensis*, some whiskers extend beyond the box; their values are*

510 *given at the extremities of the corresponding boxplots. Outliers are not shown. Boxplots in*
511 *white are based on fewer than 10 stands.*

512 **4. Discussion**

513 In this paper, we analyzed the impact of past climate change on SDH dynamics and site
514 index for 20 common European tree species and we analyzed interspecific and intraspecific
515 differences in SDH and site index response to climate change. In the discussion, we first
516 point out the interest of our modeling approach; we will emphasize some limitations of this
517 approach; then we comment on the partial effect of climatic variable on site index; then we
518 discuss the impact of climate change during the last century on SDH dynamics and site
519 index, and finally we elaborate on implications for management.

520 **4.1. Interest of the approach**

521 To our knowledge, this is the first time annual SDH trajectories have been empirically
522 modeled for 20 species, taking into account annual climate over the past century. We
523 achieved this by combining French NFI data and FYRE long-term climate data, and by using
524 a theory-based annual SDH increment equation. The FYRE data allowed us to model SDH
525 dynamics for stands as old as 150 years while accounting for annual climate. The French
526 NFI data include a large number of stands per species and cover a large climatic gradient,
527 which allowed us to identify climate effects. Different stand age classes at the time of stand
528 observation allowed us to partially decorrelate age with date. The French NFI data provided
529 us with field measurements of non-climatic variables to use as covariates, limiting potential
530 bias due to overrepresentation of older stands on infertile sites (Socha et al., 2021). The

531 theory-based SDH increment equation we used ensured that our approach was biologically
532 consistent (Tomé et al., 2006).

533 Our approach has operational advantages over stem analysis. Stem analysis requires
534 intensive field sampling for each stand, and is generally conducted in the context of a
535 specific study. The number of stands used in stem analysis studies can therefore be quite
536 limited (Bontemps and Bouriaud, 2014) although some studies are based on a large number
537 of stands (Socha et al., 2021; Pau et al., 2022). In contrast, the French NFI data are
538 representative of the species' distribution in the study area. They cover a large climatic
539 gradient and include numerous stands of common species. Our approach allowed us to
540 derive SDH-dynamics models for rarely studied species such as *Larix decidua*, *Quercus*
541 *pubescens* and *Fraxinus excelsior*. The main advantage of stem analysis over our approach is
542 that it provides a temporal series of SDH measurements, whereas our approach relies on a
543 single SDH measurement. Stem analysis also provides more accurate height measurements
544 compared to NFI data. In the future, it would be interesting to compare our simulated SDH
545 dynamics with observed SDH dynamics and with SDH dynamics simulated by a model
546 based on stem analysis.

547 The RMSE we found are in the same order of magnitude as in other studies based on NFI
548 data (Seynave et al., 2008; Sharma et al., 2012) but higher than in studies based on stem
549 analysis (Socha et al., 2021). The optimism of our models is generally low, indicating good
550 robustness, especially for species with a large number of calibration stands. Parameter
551 values for species with high model optimism should be used with caution.

552 **4.2. Limits of the approach**

553 The NFI data do not provide information on stand history. This forced us to make several
554 assumptions. First, we assumed that the dominant trees at observation time had been
555 dominant throughout stand development. This is a common assumption in SDH studies.
556 Second, we assumed that SDH dynamics were independent of competition history. This is
557 justified for a wide range of densities (Skovsgaard and Vanclay, 2008). The inclusion of a
558 competition variable could still be interesting (Vallet and Perot, 2016). Third, we did not
559 include interactions in our models because this could have led to overparameterized
560 models. Fourth, we did not include nitrogen deposition in our model because due to a lack
561 of historical data. This variable has been identified as an important driver of SDH in the late
562 20th century (Bontemps et al., 2011). As a proxy, we included the C:N ratio at the
563 observation date in our models. This allowed us to account for spatial heterogeneity, but
564 not temporal changes. Atmospheric CO₂ concentrations are sometimes considered to be an
565 important driver of the increase in tree growth during the last century, but this role is still
566 under debate, especially since the positive effect may be restricted to young stages (Asshoff,
567 Zotz, and Körner, 2006; Boisvenue and Running, 2006; McDowell et al., 2020). We did not
568 include this variable in our models because it would have created a temporal trend that
569 could have prevented us from identifying the effect of climatic variables. Because we did not
570 properly disentangle the effects of climate, atmospheric nitrogen deposition, and
571 atmospheric CO₂ concentration in our models, some of the effect we attributed to climate
572 could be related to the other two factors. Complementing this study with process-based
573 models may be useful to disentangle these effects.

574 4.3. Partial effect of climatic variables on site index

575 Our results regarding the partial effect of climatic variables confirm our hypothesis 1 that
576 an increase in temperature, precipitation and climatic water balance during spring and
577 summer favors the site index, but that these positive effects may saturate when the climatic
578 variable reaches a certain level. However, contrary to our hypothesis, our results do not
579 clearly show a negative effect of temperature above a certain threshold. Indeed, the
580 decrease of site index at the upper range of the variable distribution for some species and
581 variables is not very pronounced and may simply reflect the fact that we integrated
582 saturation and non-monotonic effects in the model using a quadratic form.

583 For commonly studied species, our results are largely consistent with the literature,
584 especially (i) the generally positive effect of temperature and SGDD (Albert and Schmidt,
585 2010; Álvarez-Álvarez et al., 2011; González-Rodríguez and Diéguez-Aranda, 2020), (ii) the
586 generally positive effect of precipitation and climatic water balance (Vallet and Perot, 2016;
587 Stimm et al., 2021), (iii) the saturation effect beyond a certain level of temperature
588 (Seynave et al. 2008; Caicoya and Pretzsch, 2021; Pau et al., 2022) or precipitation (Brandl
589 et al., 2018) and (iv) the existence of interspecific differences in the climatic variables and
590 seasons affecting SDH (Vallet and Perot, 2016). Table 2 compares the species-specific
591 effects we found with those reported in the literature for the five most common European
592 tree species, as listed by (Mahnken et al., 2022). The present work allows to extend such
593 results to species for which, to our knowledge, the climate – SDH relationship has hardly
594 been studied yet, such as *Larix decidua*, *Fraxinus excelsior* or *Quercus pubescens*.

595 These effects on site index are consistent with the expected response based on tree
596 physiology. The positive effects of higher spring and summer temperature probably relate

597 to an increase photosynthetic efficiency or a lengthening of the growing season (Brandl et
598 al., 2018). Saturation may occur because temperature is no longer the limiting factor, or
599 because high temperature increase evapotranspiration and hydric stress, and reduce
600 photosynthesis (Lindner et al., 2010; Anderson-Teixeira et al., 2022). The lack of a clear
601 signal of negative effects of temperature above a certain level may relate to the fact that
602 such extreme temperature have only occurred in recent years, and therefore their effects
603 are not well captured in our multi-decadal modeling strategy. The negative effect of high
604 winter temperature for some species may relate to disturbance of bud break or high winter
605 respiration (Seynave et al., 2008). The generally positive impact of spring and summer
606 precipitation and climatic water balance, and the saturation of this positive effect at the
607 wetter edge of the range, may be related to a positive effect of relaxing the water constraint
608 only in water-limited environments. With respect to fall and winter precipitation and
609 climatic water balance, the interspecific diversity of responses suggests that species have
610 different levels of tolerance to water excess or develop under specific stand conditions.
611 Negative responses can be explained by nutrient depletion in the case of too much water
612 (Álvarez-Álvarez et al., 2011) or by snow damage (Seynave et al., 2008). The outlier
613 behavior of *Castanea sativa* (negative effect of summer temperature) could be due to the
614 impact of the chestnut ink disease, which can hinder tree growth, especially under drought
615 conditions (Maurel et al., 2001). In our dataset, this may have translated into a correlation
616 between the warmer and drier recent climate and less dynamic growth in young stands.

617

Species	Effects found in this study	Convergence with the literature for some effects	Other effects found in the literature
<i>Picea abies</i>	summer temperature (+, sat.) summer water availability (+, sat.)	Seynave et al. (2005), Albert and Schmidt (2010), Sharma et al. (2012), Vallet and Perot (2016), Antón-Fernández et al. (2016), Brandl et al. (2018), Caicoya and Pretzsch (2021)	Seynave et al. (2005): spring temperature (+), summer temperature (-) Antón-Fernández et al. (2016): summer water availability (opt.) Brandl et al. (2018): winter temperature (-) Caicoya and Pretzsch (2021): GS temperature (-)
<i>Fagus sylvatica</i>	GS temperature (+, sat.) winter water availability (-) summer water availability (+)	Seynave et al. (2008), Albert and Schmidt (2010), Vallet and Perot (2016), Brandl et al. (2018)	Seynave et al. (2008): summer temperature (-), winter temperature (opt.)
<i>Pinus sylvestris</i>	spring temperature (+) winter water availability (opt.)	Fries et al. (1998), Sharma et al. (2012), Antón-Fernández et al. (2016), González-Rodríguez and Diéguez-Aranda (2021)	Vallet and Perot (2016): July water balance (+) Antón-Fernández et al. (2016): summer water availability (opt.)
<i>Quercus robur</i>	GS water availability (+, sat.)	Pilcher and Gray (1982)*, Stimm et al. (2021)*	Pilcher and Gray (1982)*: winter temperature (-), GS temperature (+) Stimm et al. (2021)*: summer temperature (+, sat.)
<i>Quercus petraea</i>	spring temperature (+, sat.) winter water availability (+)	Pilcher and Gray (1982)*, Vallet and Perot (2016)	Pilcher and Gray (1982)*: GS water availability (+), winter temperature (-) Stimm et al. (2021)*: summer temperature (+, sat.), GS water availability (+)

Table 2: Comparison between the partial effects of climatic variables in our study and in the literature for the five most common tree species in Europe. '+': positive impact; '-': negative impact; 'sat.' means that the effect saturates at the higher range of the variable's distribution; 'GS': growing season (spring and summer); *: studies that did not distinguish between *Quercus petraea* and *Quercus robur*, 'opt.': optimal value. 'Water availability' refers both to precipitation and climatic water balance.

618 4.4. Analysis of climate change during the last century on stand 619 dominant height

620 Our models allow us to compare SDH dynamics under the actual recent climate (1950 to
621 2020) with the climate before climate change. For some species, the effects of climate
622 change were small in the first decades of the simulations and positive thereafter. This
623 relates to a period of relative cooling in France between 1950 and 1990, followed by a
624 period of strong temperature increase (*cf.* Figure 1). Such temporal variations in the effects
625 of climate change support the relevance of modeling SDH dynamics while taking into
626 account climate variations during stand life. At the final simulation age of 70 years, the
627 effect of climate change on SDH varied between species and between stands for a given
628 species. In the following sections, we analyze first the interspecific and then the
629 intraspecific variation of the site index in response to climate change, where site index I_s
630 defined as SDH at the age of 70 years.

631 4.4.1. Interspecific analysis

632 Our results confirm our hypothesis 2a that climate change during the last century has had
633 different effects on different species, both in terms of sign and magnitude. The increase in
634 the site index over the period considered for the majority of species studied is consistent
635 with an increase in forest productivity over the last decades (Boisvenue and Running, 2006;
636 Bontemps et al. 2009; Messaoud et al., 2022). Together with nitrogen deposition and CO₂
637 increase, climate change is a key driver of recent changes in forest growth in Europe
638 (Boisvenue and Running, 2006; Bontemps et al. 2009; Charru et al. 2017).

639 Interspecific differences in the effect of climate change on SDH may be related to differences
640 in species ecology, but also to interspecific differences in the pre-climate change climate
641 niche and the actual climate change experienced by the species (*cf.* Figure 1 and
642 Supplementary Material Fig. B.1 and Fig. B.2). We did not find a clear pattern linking the
643 species-specific mean effect of climate change on site index to species-specific mean initial
644 climate niche (*cf.* Supplementary Material Fig. F.1 and Fig. F.2). This suggests that species
645 ecology and experienced climate change are also key drivers of this effect. Studying another
646 growth variable and fewer species, Charru et al. (2017) found that species-specific mean
647 changes in basal area increment between 1982 and 2005 could be related to species-
648 specific mean initial climate niche, with a more positive effect for species that initially
649 experienced the coldest temperature and highest precipitation. When focusing on the same
650 species as Charru et al. (2017), our results suggest such a pattern.

651 Our results shed light on past limitations to species growth and provide insight into future
652 impacts of ongoing climate change. Over the period we considered, climate change affected
653 all species in two ways: increasing annual and summer mean temperature as well as
654 decreasing summer precipitation and / or climatic water balance (*cf.* Supplementary
655 Material Fig. B.1 and Fig. B.2). Increasing temperature favor simulated height growth, while
656 decreasing summer precipitation or climatic water balance negatively affects growth (*cf.*
657 section 4.3.). The generally positive effect of climate change on the site index we found for
658 the period 1950-2020 compared to the climate of 1891-1920 probably reflects that most of
659 the species studied were temperature-limited in France during the period 1891-1920. Our
660 finding of a strong positive effect of climate change on mountain species (*Larix decidua*,
661 *Abies alba*, and to a lesser extent *Picea abies*) is consistent with the fact that mountain
662 species are particularly temperature-limited (Charru et al., 2017). Nevertheless, the

663 positive effect of climate change on SDH could turn negative if temperature continue to
664 increase and precipitation continue to decrease, due to saturation of the positive partial
665 effect of temperature increase and the negative partial effect of precipitation (or climatic
666 water balance) decrease (*cf.* section 4.3.). Studies have already found observations of
667 negative impacts of climate change on growth under water limitation (Lindner et al., 2014)
668 or projected negative impacts on site index of future climate change Albert and Schmidt
669 (2010). We also found such negative effects of climate change for *Pseudotsuga menziesii* and
670 *Quercus robur*. The negative effect on *Castanea sativa* should be interpreted with caution
671 (see 4.3).

672 **4.4.2. Intraspecific analysis**

673 Our results confirm our hypothesis H2b that, for a given species, the impact of climate
674 change over the last century varied among stands depending on their climate context.
675 Intraspecific variation in the impact of climate change on site index can be related to
676 differences in environmental conditions, management history, or plant genetics (Kremer et
677 al., 2012). Here, we focused on the first dimension, as the French NFI does not provide data
678 on management history or genetics. The intraspecific relationship we found between
679 climate change effects and initial stand temperature for a large number of species reflects
680 that, for a given species, different climatic contexts produce different growth limitations
681 (Lindner et al., 2014; Kunstler et al., 2021; Guyennon et al., 2023). For nine species, our
682 results suggest that climate change alleviated a temperature limitation at the cold edge of
683 the species' distribution in France, while it had only a small positive or even negative effect
684 on stands at the warm edge of the distribution. Such a pattern is consistent with the results
685 of Albert and Schmidt (2010), Messaoud and Chen (2011) and Ols et al. (2020). The

686 mountain species we analyzed (*Abies alba*, *Picea abies*, *Larix decidua*) follow this pattern,
687 which is consistent with the temperature limitation they experience at high altitudes
688 (Charru et al., 2017). Finally, *Pinus halepensis* follows the same pattern, probably because it
689 is adapted to warmer climates than that of France. For the other species, the identification
690 of intraspecific patterns relating climate change effects to the reference climate is more
691 complex.

692 **4.5. Implication for management**

693 Our results raise awareness of the risk of switching from positive climate change effect on
694 SDH to negative effects due to ongoing climate change. The magnitude and timing of this
695 switch for a given stand will depend on the species, the current climatic context and the
696 climate change that the stand will experience. Our results may help forest managers to
697 identify which species to favor when managing a pure even-aged stand. Furthermore, our
698 models could be used to project SDH dynamics under future climate scenarios, although
699 caution should be taken when running simulations outside the calibration range of
700 empirical models. Thus, it may be useful to integrate our work into models used to inform
701 management strategy.

702 Our results also suggest that climate change may alter the relative competitiveness of
703 species for light in mixed stands, due to interspecific differences in the effect of climate
704 change on SDH dynamics. This may lead to changes in forest composition if climate change
705 penalizes the height growth of some shade-intolerant species more than the height growth
706 of shade-tolerant species (Bontemps et al., 2012; Messaoud et al., 2022). Taking this effect
707 into account is important for the management of mixed stands. This is even more true in a

708 context where forest managers are encouraged to diversify species to adapt forests to
709 climate change.

710 **5. Conclusion**

711 For 20 European species, we developed stand dominant height dynamics models taking
712 into account annual climate, based on data from more than 17,000 forest stands surveyed
713 by the French National Forest Inventory and a 150-years climate database.

714 We found that climate change over the past century had contrasting effects between and
715 within species. For the majority of species studied, most stands have benefited from climate
716 change, as shown by comparing the average climate of 1891-1920 with the actual recent
717 climate of 1950-2020. For some species, however, we found that a significant percentage of
718 stands were already experiencing negative impacts. The relationship between temperature
719 and within-species differences in climate change effects suggests that climatic context may
720 drive differences in response to climate change for a given species.

721 These results suggest that future forest response to continued climate change will vary by
722 species, initial stand climate context, and stand climate trends. They also suggest that
723 continued increases in temperature and decreases in summer precipitation may lead to
724 more negative trends than observed in the past. Consideration of these different aspects is
725 critical to inform management to adapt forests to future climate change.

726

727 Additional files

- 728 • Supplementary Material (provided in a separate file) contains additional information
729 regarding some points mentioned in the main text
- 730 • R code to prepare data, calibrate models and analyze results as well as model
731 parameters are available at
732 https://github.com/matthieucombaud/paper_dominant-height-20-species

733 Data Availability Statement

- 734 • French NFI data that support the findings of this study are openly available at IGN –
735 Inventaire forestier national français, Données brutes, Campagnes annuelles 2005 et
736 suivantes, <https://inventaire-forestier.ign.fr/data/FN/>. NFI's stands exact altitudes
737 were obtained from IGN – Inventaire forestier national (contact: <https://www.ign.fr>)
- 738 • FYRE climate data that support the findings of this study are openly available on
739 Zenodo, for precipitation (Devers, Alexandre, Vidal, Jean-Philippe, Lauvernet, Claire,
740 & Vannier, Olivier. (2020a). *FYRE Climate: Precipitation* [Data set]. Zenodo.
741 <https://doi.org/10.5281/ZENODO.4005573>) and for temperature (Devers,
742 Alexandre, Vidal, Jean-Philippe, Lauvernet, Claire, & Vannier, Olivier. (2020b). *FYRE*
743 *Climate: Temperature* [Data set]. <https://doi.org/10.5281/zenodo.4006472>)
- 744 • Safran climate data were obtained from Meteo France through the SICLIMA platform
745 (<https://agroclim.inrae.fr/siclima/>). Meteo France can be contacted through the
746 webpage <https://donneespubliques.meteofrance.fr/>

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760

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