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Climate change impacts on long-term forest productivity might be driven by species turnover rather than by changes in tree growth

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Title: Climate change impacts on long- term forest productivity might be driven by species turnover rather than by changes in tree growth.

Running Title: climate change impacts on forest functioning

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Abstract:

Aim: Forest functioning and services are impacted by climate change through two inter-related effects. First, climate change affects tree physiology, which impacts ecosystem functioning through, for example, biomass production. Second, the impact on trees' physiology might reshuffle community composition, which in turn affects ecosystem functioning. The relative importance of these two effects has rarely been studied. Here, we developed a novel modelling approach to investigate the relative importance of these two effects on forest tree biomass productivity.

Location: 11 forest sites in central Europe.

Time period: Forests long-term (2000 years) responses to historical (years 1901-1990) and end-of-the-century (2070-2100) climatic conditions.

Major taxa studied: 25 main tree species in European temperate forests.

Methods: We coupled species distribution models and a forest succession model working at complementary spatial, and temporal, scales to simulate the climatic filtering shaping potential pools of tree species, the biotic filtering shaping realized communities, and the functioning of these realized communities in the long term.

Results: With an average temperature increase (relative to 1901-1990) of 1.7°C, or less, changes in simulated forest productivity were mostly caused by changes in the growth of persisting tree species. With a temperature increase of 3.6 °C or more, at the currently climatically mild sites changes in simulated productivity were again predominantly caused by changes in tree species growth, but at the warmest and coldest sites productivity changes were mostly related to

39 changes in species composition. In general, at the coldest sites forest productivity is likely to be
40 enhanced by climate change, and at the warmest sites productivity might increase or decrease
41 depending on the future regime of precipitation.

42 Main conclusions: The complementarity of two different modelling approaches to address
43 questions at the interface between biogeography, community ecology, and ecosystem
44 functioning, allows us to discover that climate change-driven species' reshuffling importance
45 for ecosystem functioning could be stronger than expected.

46

47 **Keywords:**

48 Climate change, forest succession modelling, forest gap modelling, species distribution
49 modelling, species range shifts, temperate forests, tree growth, tree species richness.

50 Introduction

51 Forests cover about a third of the world land surface, harbour most of the terrestrial
52 biodiversity, and represent an important carbon sink. They also play a pivotal role in climate
53 regulation (Chapin, Randerson, McGuire, Foley, & Field, 2008) and provide other important
54 ecosystem services (Kumar, 2012). However, climate change is affecting many of these forest
55 ecosystem services, such as biomass production and carbon sequestration (Kirilenko & Sedjo,
56 2007), and this impact is likely to strengthen in the future (Pachauri *et al.*, 2014). The influence
57 of climate change on forests can be divided into two inter-related effects (Adler, Leiker, &
58 Levine, 2009, Morin *et al.*, 2018). Climate change affects forests by altering tree physiological
59 rates (Sack & Grubb, 2001), e.g. growth (Silva & Anand, 2013), phenology (Cleland, Chuine,
60 Menzel, Mooney, & Schwartz, 2007), or survival (Allen, Breshears, & McDowell, 2015), which
61 has direct consequences for ecosystem functioning (e.g. biomass productivity). Climate change
62 also affects forest functioning when the pressure of climate change on trees' physiology is
63 strong enough to drive species' local extinction and colonization (Bertrand *et al.*, 2011), as seen
64 in natural, experimental and simulated forests (Jucker, Bouriaud, Avacaritei, & Coomes, 2014;
65 Liang *et al.*, 2016; Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011). Understanding the
66 relative importance of these two effects, and the conditions under which each will occur, would
67 greatly help to improve the projections the potential impact of climate change on forest
68 functioning, and important forests ecosystem services such as carbon uptake and biomass
69 provision. However, the two effects have been mostly studied separately, and their relative
70 importance for forest productivity under different circumstances is almost unknown (but see
71 Coomes *et al.*, 2014; Zhang, Niinemets, Sheffield, & Lichstein, 2018).

72 The effects of climate change on species composition might amplify (Zhang *et al.*,
73 2018) or counteract (Fauset *et al.*, 2012) the effects of climate change on tree physiology.
74 Furthermore, recent studies found that effects on species composition might be greater than
75 previously expected. García-Valdés, Bugmann, and Morin (2018) found that the impact of
76 climate change-driven extinctions on temperate forests' functioning was stronger than random
77 extinctions. This implies that most Biodiversity-Ecosystem Functioning (BEF) studies (e.g.
78 Liang *et al.*, 2016), underestimate the strength of biodiversity loss caused by climate change.
79 Similarly, Morin *et al.* (2018) found that warmer and drier conditions might strongly affect
80 BEF-relationships in forests experiencing the harshest climatic conditions, illustrating the
81 importance of understanding changes in species composition for forest functioning. These
82 findings suggest that local conditions, and the magnitude of the change in climate, might
83 interact to determine the relative importance of tree physiological changes, and species
84 reshuffling, for forest functioning.

85 Nonetheless, disentangling these two effects of climate change on ecosystem
86 functioning is difficult. While estimating the effects of climate change on tree physiology could
87 be relatively straightforward through experiments or long-term observations (Hasenauer,
88 Nemani, Schadauer, & Running, 1999), estimating the effects on species composition is much
89 more complicated (Barry *et al.*, 2018). Several mechanisms underlie effects of climate change
90 on species composition. First, climatic filtering determines whether the local environmental
91 conditions are suitable for a species. Second, biotic filtering occurs when interspecific
92 interactions among potentially co-occurring species lead to the exclusion or acceptance of some
93 species. While climatic filtering is commonly studied at large spatial scales, such as regions or
94 continents (Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005), species interactions are mostly
95 studied at the local scale (Mayfield & Levine, 2010). We, therefore, studied both processes,
96 each at the relevant spatial scale, to quantify the effects of both climatic and biotic filtering on
97 future forest species composition.

98 Species distribution models (hereafter “SDMs”) typically work by correlating the
99 recorded presences of individual species with environmental variables (Gotelli *et al.*, 2009), and
100 can be used to simulate climatic filtering. Although this approach carries some caveats (see
101 Dormann *et al.*, 2012 and Discussion section), SDMs are particularly robust for measuring the
102 environmental tolerances of species that are broadly distributed (Early & Sax, 2014; Estrada,
103 Delgado, Arroyo, Traba, & Morales, 2016), as the ones considered here. Forest succession
104 models (FSMs) – also called gap model (Bugmann, 2001) – can be used to simulate forest
105 community dynamics at local scales (e.g. up to landscape level), given a specific starting species
106 pool (Chauvet, Kunstler, Roy, & Morin, 2017). FSMs are based on a minimum number of
107 ecological assumptions (Botkin, Janak, & Wallis, 1972), and rely on the ecophysiological
108 responses of trees to abiotic factors (including climate), and biotic factors (i.e. inter and intra-
109 specific interactions), to simulate individual tree growth and succession dynamics (colonizations
110 and extinctions) over time (Bugmann, 2001). FSMs can hence simulate both the biotic filtering
111 of species by forecasting the realized tree community (i.e. at long-term equilibrium), and the
112 effects of climate change on tree growth.

113 In this study, we coupled SDMs and FSMs to assess the relative importance of climate
114 change effects on tree physiology and species composition for the productivity of central
115 European forests. Previous studies have coupled SDM-like modules with a process-based
116 component simulating key processes, such as dispersal and demography (e.g. range dynamic
117 models; Sarmiento Cabral *et al.*, 2013), and/or competition, e.g. the hybrid FATE-H model that
118 considers only plant functional types (Boulangeat, Georges, & Thuiller, 2014). At a larger
119 spatial scale, Meier, Lischke, Schmatz, and Zimmermann (2012) coupled a SDM with a FSM to

120 predict the migration rates of several tree species under climate change, while accounting for
121 interspecific competition. However, to our knowledge, no previous work has compared how
122 climate change will affect forest productivity through both altered species physiology and
123 composition by coupling SDMs' with FSMs' predictions. Our study is thus among the first ones
124 to take advantage of the complementarity of the two kinds of models to address questions at the
125 interface between biogeography, community ecology, and ecosystem functioning. Specifically,
126 we used 11 forest sites as an example and aimed at answering the following questions:

127 (1) How will climate change affect long-term forest aboveground biomass productivity
128 in European temperate forests?

129 (2) What will be the relative contribution of tree growth and species composition to
130 climate-driven changes in productivity?

131 (3) How will current local climatic conditions and the magnitude of climate change
132 influence the patterns found in (1) and (2)?

133 **Material and methods**

134 In summary, we simulated the productivity of 11 forest sites across central Europe
135 under historical (1901-1990) climatic conditions, and future (2071-2100) conditions, given four
136 climate change projections. To do so, we first used SDMs (Fig. 1) to forecast the future
137 suitability of 25 common tree species (i.e. climatic filtering). We then combined the suitabilities
138 for all species in each location to generate *potential* species pools (e.g. Thuiller et al., 2005).
139 Second, starting from these potential species pools and bare-ground conditions (no trees in the
140 site), we used the local-scale FSM FORCLIM (Bugmann, 1996) to simulate 2000 years of
141 succession (i.e. biotic filtering), leading to *realized* forest communities. Finally, once each
142 community had reached equilibrium (after 1000 years) we aggregated the simulated annual
143 productivity across all trees in the site. We explain all these steps in detail below.

144

145 Study sites

146 The geographic background from which species distributions and climatic data were
147 drawn for SDMs comprises Europe from $-10^{\circ}9'23''$ to $30^{\circ}43'0''$ E and $34^{\circ}59'30''$ to $70^{\circ}58'33''$
148 N. We simulated forest growth in 11 temperate forest sites across central Europe (nine in
149 Switzerland and two in Germany; Table S1). These sites cover a broad range of temperature and
150 precipitation conditions (Table S1), and represent the diversity of environments and forest types
151 in central Europe, as illustrated in previous studies (Bugmann, 1994; Morin et al., 2011).

152

153 Climate data for Species Distribution Models

154 We used historic climate data (1961-1990 period) from the Climatic Research Unit CL
155 v. 2.0 dataset (New, Lister, Hulme, & Makin, 2002) and projected future climate data from the
156 EURO-CORDEX project (Jacob et al., 2014), both at 10' resolution. Projected future climate
157 data were downscaled via the Rossby Centre regional climate model (RCA4). We used two
158 Representative Concentration Pathways (RCPs): 4.5 and 8.5, and two Global Climate Models
159 (GCMs): CERFACS-CNRM-CM5 (CNRM-CM5) and ICHEC-EC-EARTH (EC-EARTH). We
160 used four climatic variables: mean annual growing degree-days ($> 5^{\circ}\text{C}$), mean temperature of
161 the coldest month, annual precipitation, and a summer moisture index (potential
162 evapotranspiration divided by precipitation). These variables have been previously used to
163 model plant and vertebrates in Europe and they reflect two primary properties of climate
164 (energy and water) that have been shown to affect species distributions (Araújo, Alagador,
165 Cabeza, Nogués-Bravo, & Thuiller, 2011; Morrison, Estrada, & Early, 2018). We used averaged
166 annual values of these climatic variables for the 1961-1990 period as historical climatic

167 conditions. For future climatic conditions, we used averaged simulated data of the variables for
168 the 2071-2100 period under four climate change projections

169

170 *Climate data for the Forest Succession Model*

171 We simulated 2000 years of forest dynamics with FORCLIM, given a “historical-like”
172 climate (baseline) projection and four “future-like” climate change projections (RCPs 4.5 and
173 8.5, and GCMs CNRM-CM5 and EC-EARTH). To do so we needed a generic 2,000 year-long
174 time-series of monthly temperature (T) and precipitation (P) that incorporated inter-annual
175 variability. For this purpose, we used the climate simulator embedded in FORCLIM, which uses
176 the monthly mean and standard deviation of T and P, and the correlation between them
177 (Bugmann, 1994). For the historical-like climate, we generated 2000 years of data directly using
178 the mean, standard deviation and correlation of monthly T and P (from Bugmann, 1994), which
179 was calculated from historic (1901–1990) data from the Swiss Meteorological Agency (Bantle,
180 1989). Such data had previously been used to calibrate and validate FORCLIM productivity
181 projections in our study sites. Such generic data were hence analogue but not the same as the
182 one from the 1901-1990 period.

183 To simulate future climate conditions, we could not directly use data from GCM climate
184 projections because these models use a different “historical” data for bias correction to the data
185 we used (1901-1990 data from Bugmann, 1994). To circumvent this problem, we calculated a
186 climatic anomaly for each climate projection (see Morin & Chuine, 2005). For each climate
187 projection we calculated the differences in monthly T and P between the future climate (years
188 2071-2100) and the current climate (years 2006-2016). These anomalies quantify how much T
189 and P would vary from baseline values under every climate projection. We added these
190 anomalies to the means of the historical climate data from Bugmann (1994), and for each
191 climate projection we generated 2000 years of climate data for each of the four future climate
192 projections. All climate time-series thus contained no trend. In the projected future climate time-
193 series, the estimated changes in temperature depended mostly on the RCPs, while the estimated
194 changes in precipitation depended mostly on the GCMs. The differences between the four
195 climate projections compared to historical climate (1901-1990 period from Bugmann, 1994)
196 were, ordered in increasing stress for trees: (1) RCP 4.5-CNRM-CM5, moderately warmer with
197 more precipitation; (2) RCP 4.5-EC-EARTH, moderately warmer with similar precipitation; (3)
198 RCP 8.5-CNRM-CM5, extremely warmer with more precipitation; and (4) RCP 8.5-EC-
199 EARTH, extremely warmer with similar precipitation. See Table S1 and S2 for specifics.

200

201 *Species data and the Species Distribution Models*

202 We considered 25 of the most common tree species in this region (Table S3). We used
203 presence data from the Atlas Florae Europaeae (AFE; Jalas & Suominen, 1972–1994; Jalas,
204 Suominen, & Lampinen, 1996). When a species was not recorded in the Atlas, we used
205 distribution data from EUFORGEN (<http://www.euforgen.org/>; see Table S4). Presence data
206 were on 50 km × 50 km Universal Transverse Mercator (UTM) grid cells in AFE, and range
207 maps in EUFORGEN. We transformed EUFORGEN range maps into ~50km UTM cells to run
208 the models. We calculated the average historical climatic conditions in each 50-km grid cell
209 from the 10' climate grid resolution. The relationships between historical climatic variables and
210 species' distributions were modelled using seven SDM techniques: generalized linear models
211 (GLM), generalized additive models (GAM), generalized boosting models (GBM),
212 classification tree analysis (CTA), artificial neural networks (ANN), flexible discriminant
213 analysis (FDA), and surface range envelope (SRE). Models were calibrated for the historical
214 period (1961–1990) using 80% random sample of the initial data and cross-validated against the
215 remaining 20% data, using the area under the curve (AUC) of the receiver operator
216 characteristic (ROC) and the true skill statistic (TSS). SDMs were calculated 10 times, each
217 time selecting a different 80% and 20% of the data for calibration and evaluation. Results from
218 each SDM technique was then included in an ensemble model if the AUC from cross-validation
219 was higher than 0.8 and TSS was higher than 0.6 (similar to Araújo *et al.*, 2011). However, the
220 final ensemble model for each species was calibrated using 100% of the species distribution
221 data to maximise the amount of data available for projections. For each species, the ensemble
222 was calculated using the mean probability of occurrence, weighted proportional to the AUC and
223 TSS obtained on the evaluation data. Ensemble models calibrated at 50-km resolution were
224 downscaled to obtain suitability in each 10' grid cell. We projected ensemble models to future
225 climatic conditions at 10' resolution for the four future climate projections (the combination of
226 GCMs and RCPs). This approach follows methods employed by Araújo *et al.* (2011), though
227 using more recently constructed climate data. All models were run in R (R Core Team, 2014)
228 using default options of the *biomod2* package (Thuiller, Georges, & Engler, 2013).

229

230 *Forecasting of potential tree species pool in each site*

231 For each site and climate projection, we used the SDM-predicted suitability for each
232 species to build a local species pools. To apply directly the suitability of the species based on
233 the SDM projections, instead of using an arbitrary threshold to distinguish suitable or
234 unsuitable, we built 100 potential species pools for each site and climate projection and included
235 each species proportionally to its climate suitability. For example, if the suitability of a given

236 species in a given site and for a given climate projection was 0.6, this species would be included
237 in 60 of the 100 species pools for that site and climate projection. The combination of all the
238 species, each one following the rule described above, was then done randomly.

239

240 Forest Succession Model

241 FORCLIM projections have been shown to be robust under various climatic conditions
242 across a large number of studies (Bircher, Cailleret, & Bugmann, 2015; Gutiérrez, Snell, &
243 Bugmann, 2016; Rasche, Fahse, & Bugmann, 2013; e.g. Rasche, Fahse, Zingg, & Bugmann,
244 2011). Its projections of forest biomass productivity have been validated for the same sites than
245 those used in this study and using climate values generated with the same historical means,
246 standard deviations and cross-correlations as the ones used here (Rasche et al., 2013). It has also
247 been specifically used to study climate change effects on forest functioning on these sites
248 (Didion, Kupferschmid, Wolf, & Bugmann, 2011; Mina et al., 2017; Morin et al., 2018; Rasche
249 et al., 2013).

250 In FORCLIM, the establishment, growth and mortality of trees are simulated using the
251 abiotic and biotic conditions in small independent patches (800 m² in this study). Tree location
252 in the patch is not estimated, and all trees compete for light. The properties of several patches
253 are aggregated to calculate forest properties across larger extents (Bugmann, 2001; Shugart,
254 1984). Tree establishment is modelled as a stochastic process, depending on species-specific
255 responses to light availability at the forest floor, growing degree-days, drought occurrence, and
256 minimum and maximum winter temperature. Tree growth is measured as stem diameter
257 increment, which depends on each species' optimum growth rate, abiotic conditions
258 (temperature, drought, and soil nitrogen), and biotic conditions (light availability). Therefore,
259 while competition for water and nitrogen between individuals are not taken into account
260 explicitly in the model, soil water and nitrogen contents constrain tree establishment and growth
261 differentially between species, which affects competition between trees. Competition for light is
262 modelled by calculating the amount of available light for each individual tree depending on tree
263 height and the crown sizes of competing trees. FORCLIM also incorporates a shade tolerance
264 parameter (Ellenberg, 1991), defining the classic trade-off between growth in full light and
265 survival in shade. Tree mortality has two components: (1) a 'background' mortality, which is
266 constant across time and depends on the species' maximum longevity, and (2) growth-related
267 mortality reflecting the effect of stressful conditions on tree survival (i.e., trees with decreased
268 vigour are more likely to die). The species parameters for FORCLIM can be found in Table S3,
269 and more details about the model can be found in Appendix S1, and in Didion, Kupferschmid,
270 Zingg, Fahse, and Bugmann (2009), and Bugmann (1996).

271

272 *Simulations of forest succession dynamics*

273 For each climate conditions (historical and future), we thus simulated 2000 years of
274 forest dynamics with FORCLIM. This allowed to fairly compare the historical and future periods
275 in terms of the assessment of the relative contribution of tree growth and species composition to
276 climate-driven changes in productivity. However, this implies that the simulations should not be
277 taken as predictions of forest composition and productivity for the end of the 21st century,
278 notably because the effect of species colonization may be inflated because of this design.

279 After having checked that FORCLIM simulations run in the same conditions (site,
280 climate, species pool) yielded very similar results after 2000 years, we performed one FORCLIM
281 simulation for each site ($n = 11$), each climate projection (historical and future, $n = 5$) and each
282 species pool ($n = 100$). Each simulation included 100 patches of 800 m² each, thus
283 corresponding to an 8 ha forest. FORCLIM simulations started from bare-ground conditions to
284 avoid the influence of starting conditions. For each FORCLIM simulation, only the species in the
285 site's species pool - determined by the SDMs - were allowed to colonize the patches. The
286 simulations were run for 2,000 years to allow forests to reach equilibrium in total biomass and
287 composition, thus avoiding transient states. We extracted the productivity and composition from
288 simulations after 1000 years, to allow the system to reach equilibrium. To avoid temporal
289 autocorrelation we extracted values from the first year of each century after the year 1,000 (i.e.,
290 the years 1100, 1200, ... 2000; cf. Morin *et al.*, 2011) and averaged the results from these
291 sampled years and across patches. For the calculation of the realized composition we considered
292 that a species was present in a community only if its simulated biomass reached 1 t·ha⁻¹.

293

294 *Quantifying growth and composition effects of climate change*

295 We compared the results from each site under historical and future climatic conditions.
296 To quantify the effects of climate change mediated by tree physiology, we calculated the
297 proportion of productivity change in each site that was produced by species found under both
298 present and future climatic conditions. To quantify the effects of climate change mediated by
299 species composition, we calculated the productivity loss caused by species extinction, and the
300 productivity gained by species colonization.

301

302 *Statistical analyses*

303 To test whether the future projected change in forest productivity varied across an
304 environmental gradient, we fitted linear regressions between forest productivity in each site and
305 its mean annual temperature (MAT), total annual precipitation (TAP), and precipitation relative
306 to potential evapotranspiration (P/PET). We also fitted linear regressions between the relative
307 importance of colonization and extinction, and climatic variables. The relative importance of
308 colonization and extinction was calculated by dividing the productivity change caused by either
309 colonization or extinction and the summed changes in productivity (changes were converted to
310 absolute values). Finally, we fitted a linear regression between the future change in productivity
311 in each site and its future change in realized species richness.

312 **Results**

313

314 *Climate change effects on potential species pools and richness*

315 In most of the climate change projections, species suitability increased in most of the
 316 sites (Fig. 2 A-C). However, with extreme warming (RCP 8.5) and with the driest conditions
 317 (EC-EARTH model; Fig. 2D), potential species richness increased in the coldest sites
 318 (Adelboden, Bever, Davos and Grande Dixence), but remained the same or decreased in the
 319 warmest sites (Basel, Bern, Cottbus, Huttwil, Schaffhausen, and Sion).

320

321 *Effect of climate change on realized species richness*

322 Under historical climatic conditions, realized simulated species richness varied from
 323 three in Grande Dixence and Davos to 11 in Huttwil and Bern (Fig. S1B). Under most of
 324 climate change projections, the number of realized species increased in most of the sites (Fig. 2,
 325 lower panels). Although under the extreme RCP8.5-EC-EARTH projection, the realized species
 326 richness decreased in the warmest sites (Fig. 2H).

327

328 *Climate change effects on forest productivity*

329 The impact of climate change on forest productivity varied greatly along the climatic
 330 gradient, and with different intensity depending on the climate projection (Fig. 3 A-D). The
 331 greatest impact occurred in Sion, the warmest and second driest site, where productivity
 332 decreased by between -67.6% and -100%. However, with a projected increase in precipitation
 333 greater than 10.0% (CNRM-CM5 model in Table S1), forest productivity increased in all sites
 334 (Fig. 3 A and C), except Grande Dixence, Basel and Sion. With a very weak precipitation
 335 change (EC-EARTH model in Table S1), forest productivity increased in the coldest sites and
 336 decreased in most of the warmest sites (Fig. 3 B and D).

337 Historical precipitation was positively correlated with the change in productivity under
 338 two climate change projections ($p = 0.043$ with RCP 4.5-EC-EARTH and $p = 0.034$ with RCP
 339 8.5-EC-EARTH; Fig. S2A). Temperature was negatively correlated with productivity change
 340 under one projection ($p = 0.009$ with RCP 8.5-EC-EARTH; Fig. S2B). P/PET was positively
 341 correlated with the change in productivity under three projections ($p = 0.028$ with RCP 4.5-EC-
 342 EARTH, $p = 0.027$ with RCP 8.5-CNRM-CM5, and $p = 0.002$ with RCP 8.5-EC-EARTH; Fig.
 343 S2C).

344

345 *The relative importance of the physiology and composition effects of climate change on*
346 *productivity*

347 With a moderate increase in local temperature relative to the historical period (i.e., 1.49
348 °C – 1.72 °C on average across sites; Fig. 3 E-F), the simulated changes in productivity were
349 driven almost exclusively by the effects of climate change on tree growth of persistent (i.e.
350 surviving) species. Some species increased in growth, while others grew less (Fig. S3). There
351 was a positive correlation between the increase in productivity and the increase in species
352 richness under the two GCMs ($p = 0.003$; Fig. 4), but the change in richness did not strongly
353 contributed to changes in productivity when the local temperature increase was weak (Fig. 3 E-
354 F). When the increase in local temperature was stronger (3.63 °C – 4.00 °C average rise across
355 sites), there was also a positive relationship between the increase in realized species richness
356 and the increase in productivity ($p = 0.054$ and $R^2 = 0.35$ with the CNRM-CM5, $p = 0.006$ and
357 $R^2 = 0.58$ with the EC-EARTH GCM; Fig. 4). Under this more extreme temperature rise,
358 changes in species richness (Fig. 4) and community composition (Fig. 3 G-H) strongly
359 contributed to changes in productivity.

360 The importance of community effects varied across the study sites (Fig. 3 E-H). Their
361 importance seemed related to the current local temperature, which was negatively correlated
362 with the importance of colonization under three climate projections ($p \leq 0.05$; Fig. S4C). The
363 importance of the community effects was also correlated with current P/PET under one
364 projection ($p = 0.021$; Fig. S4E) and did not correlate with current precipitation (Fig. S4 A and
365 B).

366 **Discussion**

367

368 *Contrasting responses of forest productivity across a climatic gradient*

369 Our simulations of forests located across a large climate gradient in central Europe
370 showed that future changes in forest productivity might strongly depend on local temperature,
371 P/PET, and precipitation (Fig. S2; Allen et al., 2015). However, our results showed that the
372 response in simulated productivity varied between currently cold and warm sites. Simulated
373 forest productivity increased at high elevations where cold temperature currently limits tree
374 establishment, growth and survival (Nemani et al., 2003). Climate change also created warmer
375 winters in these sites, which allowed for new species to establish by decreasing the constraints
376 on establishment for some species (Conedera, Wohlgemuth, Tanadini, & Pezzatti, 2018), and it
377 also produced longer growing periods that increased the productivity of the species currently
378 present (McMahon, Parker, & Miller, 2010). Contrarily, in the lowlands simulated productivity
379 decreased when climate change led to an increase in drought stress (by increasing temperature
380 and not changing the precipitation regime), which became a major constraint for tree growth
381 and survival (see Carnicer et al., 2011; Reyer, 2015). However, in a scenario of climate change
382 with increased precipitation and only moderate temperature increase, productivity increased in
383 the lowlands (Fig. 3A) because drought stress did not increase while winter temperature was
384 lower and the growing season was longer.

385

386 *Tree species richness and composition drive productivity in the harshest climates*

387 We found that under moderate warming, changes in projected forest productivity were
388 caused almost exclusively by the effects of climate change on tree growth (Fig 3 E-F; see
389 Coomes et al., 2014). Contrarily, under extreme warming, and in locations at both ends of the
390 temperature gradient, changes in productivity were driven mostly by changes in species
391 composition (Fig 3 G-H). The increasing correlation between the relative importance of
392 simulated colonization (i.e. the importance of composition effect) and both local temperature
393 and P/PET under the harshest climate projection (+3.6 °C and -1.1% TAP; Fig. S4 C and E)
394 further shows the strong role of species composition under harsh climatic conditions. Such
395 finding matches with empirical evidence of the role of tree richness on forest productivity along
396 the latitudinal gradient in Europe (Jucker et al. (2016)). We also observed a positive correlation
397 between the change in species richness and in productivity ($p < 0.054$ across all climate
398 projections; Fig. 4). Former theoretical studies also showed that forest productivity is especially

399 sensitive to species loss in the harshest climates (see García-Valdés *et al.*, 2018; Morin *et al.*,
400 2018).

401 The link between species richness and ecosystem productivity has been observed in
402 forests (e.g. Liang *et al.*, 2016; Paquette & Messier, 2011), and is usually explained by a greater
403 niche partitioning in more diverse communities (Loreau *et al.*, 2001; Morin *et al.*, 2011). In
404 simulated forests in the coldest sites, the effects of species richness and composition were
405 strengthened because climate change allowed new species to colonize and be productive (Fig. 3
406 and S3; Coomes *et al.*, 2014). In the warmest-driest sites, climate change caused the extinction
407 of key species (Reyer, 2015), which reduced species richness and productivity.

408 The observed importance of community composition change in cold and warm-dry sites
409 in our study (see Anderegg & HilleRisLambers, 2019; Morin *et al.*, 2018) is consistent with an
410 extension of the stress gradient hypothesis (SGH; Bertness & Callaway, 1994; Crain &
411 Bertness, 2006). This hypothesis states that the frequency of interspecific competitive
412 interactions decreases in intensity with increasing abiotic stress. In our study sites, the species
413 that went extinct with climate change were likely near the boundaries of their acceptable
414 climatic conditions without climate change. At sites with intermediate temperature, such species
415 were probably suppressed by competition when we simulated under the historical climate
416 scenario and did not contribute significantly to the total productivity of the community. Hence,
417 their extinction in the simulations using the climate change scenarios did not change importantly
418 the total productivity of the site. Contrarily, at both ends of the temperature gradient, harsh
419 climatic conditions reduced competitive interactions. This means, that in the absence of climate
420 change, species that were close to their climatic limits could still contribute substantially to the
421 total productivity of the site because they faced little competition. Hence, their extinction under
422 climate change did importantly affect the total productivity of the community. With
423 colonizations, we could expect a similar effect. The species that colonized a site because of
424 climate change were probably close to their climatic limits. In a climatically benign site, this
425 means that such species are unlikely to become dominant when arriving, and would not
426 contribute substantially to the total productivity of the community. This occurs because they
427 still have to deal with the biotic interaction milieu (McGill, Enquist, Weiher, & Westoby, 2006),
428 and were probably not a strong competitor under such conditions. In climatically harsh sites, a
429 colonizing species could immediately become important because it is less likely that it
430 encounters strong competitors.

431

432 *Increased sensitivity of warmest-driest forests to climate change*

433 Our simulations suggested that rapid and steep changes might arise in forest functioning
434 due to climate change. In the warmest site, complete elimination of the forest cover was
435 projected in the event of the most severe climate change scenario (Fig. 3H). In this scenario
436 increase in drought stress may drive the forest system to change community type (e.g. from
437 forest to scrublands or meadows). García-Valdés *et al.* (2018) hypothesized such drastic changes
438 in forest functioning when simulating a large number of species extinctions. Here, using a
439 realistic scenario of composition change, we confirmed that such a drastic change could indeed
440 occur in one of the study sites.

441

442 Limitations of the approach

443 To our knowledge this is the first study that coupled models relevant at complementary
444 spatial scales (SDMs and FSMs), to quantify the relative importance of the physiology and
445 composition effects of climate change on forest productivity. Although these simulations
446 compared climates that are only 80 years apart (from now to the end of the century), they mimic
447 long-term dynamics in order to compare mature forests. This means that simulations do not
448 consider transient processes (e.g. disturbance, management, or brief extreme climatic events).
449 Results should thus not be considered as short-term predictions, but instead estimates of the
450 importance of climate change composition effects on mature forests, in comparison with growth
451 effects. Our approach also carries some limitations: (1) we used correlative SDMs that entail
452 caveats (García- Valdés, Zavala, Araújo, & Purves, 2013; Pearson & Dawson, 2003). However,
453 correlative SDMs work well for widespread species such as those used here (Early & Sax,
454 2014) and process-based SDMs (e.g. Chuine & Beaubien, 2001) could not be used for so many
455 species. (2) Our simulations design, relying on 2000-years simulation in both historical and
456 anticipated conditions, allows assessing of the relative contribution of changes in tree growth
457 and species composition, and notably highlights the possible strength of compositional effects
458 on changing productivity. However, they cannot be directly used to infer the forest composition
459 and productivity for the end of the 21st century. In fact, local species extinction by 2100 may be
460 well reproduced by our design, because the exposition to the novel climate conditions may
461 directly affect the adult trees of the sensitive species, while preventing the establishment of
462 seedlings of these species. Yet, site colonization by new species under the new conditions
463 occurs through much slower dynamics. At least one may expect that the outcome of these new
464 colonizations on forest functioning depends whether it is simulated over 100 or 2000 years,
465 which means that the impact of these new colonizations may be overestimated in our
466 simulations (ie. mostly under strong climate change according to our results). (3) We could not
467 have measured the interaction between the physiology and composition effects unless we had

468 imposed a strong artificial control of the simulation, which would prohibit the measurement of
469 complex community responses. (4) We did not consider species currently absent from central
470 Europe. (5) We ignored the possibility of plastic, or micro-evolutionary, responses of species
471 (e.g. Jump & Peñuelas, 2005; Lavergne, Mouquet, Thuiller, & Ronce, 2010). (6) The
472 importance of the composition effects might be further strengthened by taking into account
473 interactions besides competition for light (e.g. Jactel & Brockerhoff, 2007). (7) The generated
474 climate data had a temporal resolution of one month, so extreme events occurring at shorter
475 scale were not considered. (8) We used the climatic anomaly between 2006-2016 and 2070-
476 2100 as a measurement of climate change, which probably made projections of forest responses
477 conservative. (9) Finally, we used SDMs to simulate climatic filtering, instead of using the FSM
478 for both climatic and the biotic filtering, which would have been possible as climatic
479 constrained for tree establishment are embedded in ForClim. We did so because the FSM
480 considered only two species-specific climate-derived variables to define their climatic
481 boundaries. Our climate filtering is thus much more sophisticated, relying on more variables and
482 on more complex responses, and on an ensemble of seven SDMs, although it still relies on a
483 correlative approach.

484

485 *Importance of climate change-composition effect on forests*

486 Our results highlight that composition effects on productivity could become very
487 important under extreme changes in climate. Such climate change is likely to occur given that
488 forecasts of the magnitude of climate change keep increasing (Field, 2014). Our results also
489 show that such composition effects might become especially important in some sites: negatively
490 in terms of productivity in forests in warm and dry conditions, but positively in cold conditions.
491 Hence, we believe that our projections demonstrate that the role of species range-shifts when
492 simulating impacts of climate change on forests could be more important than previously
493 anticipated, notably under harsh environmental conditions. Such role of species' range shifts
494 and community composition's changes is very often neglected in studies of climate change
495 impacts on ecosystem functioning. We thus call for more works to improve our understanding
496 of these effects, especially considering the likeliness of extreme changes in climate in the future.

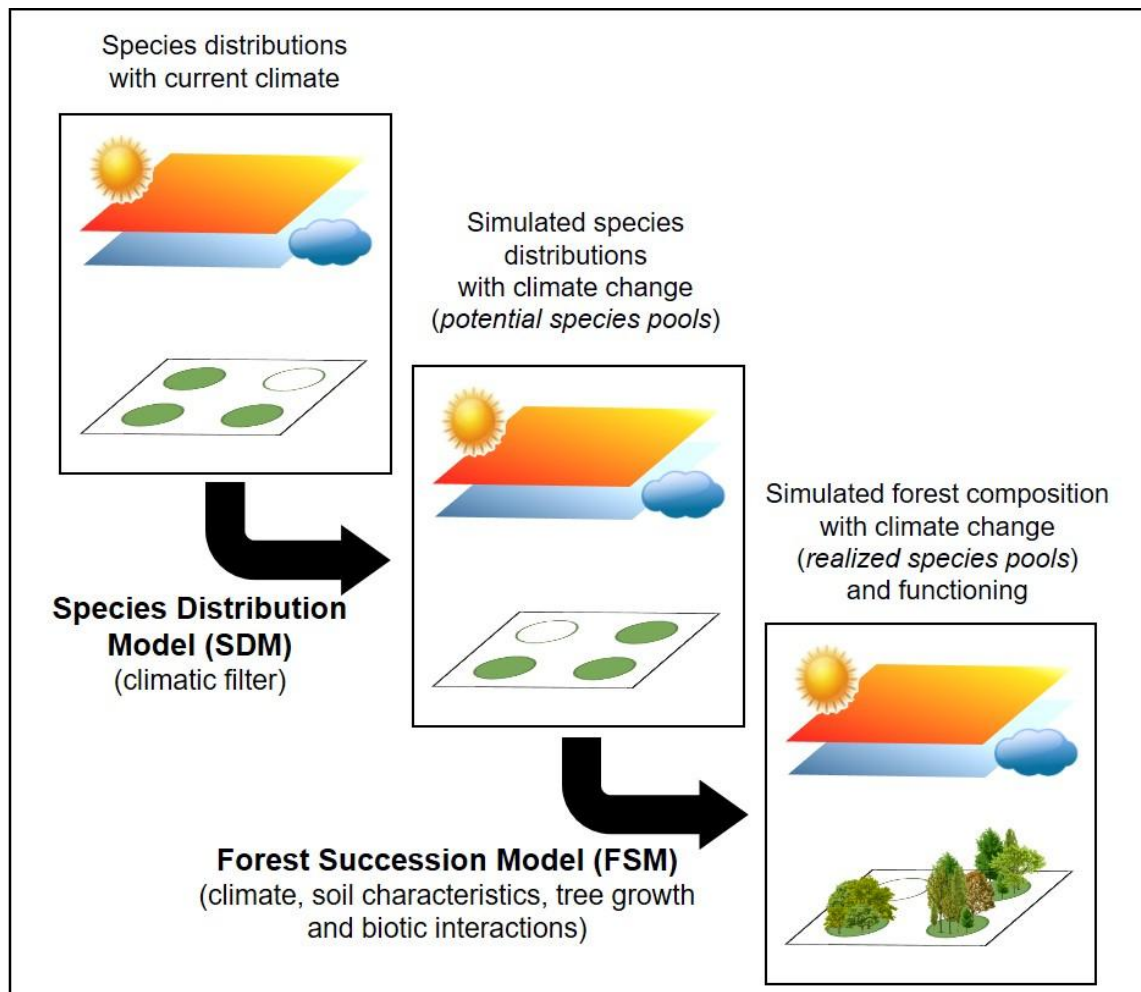
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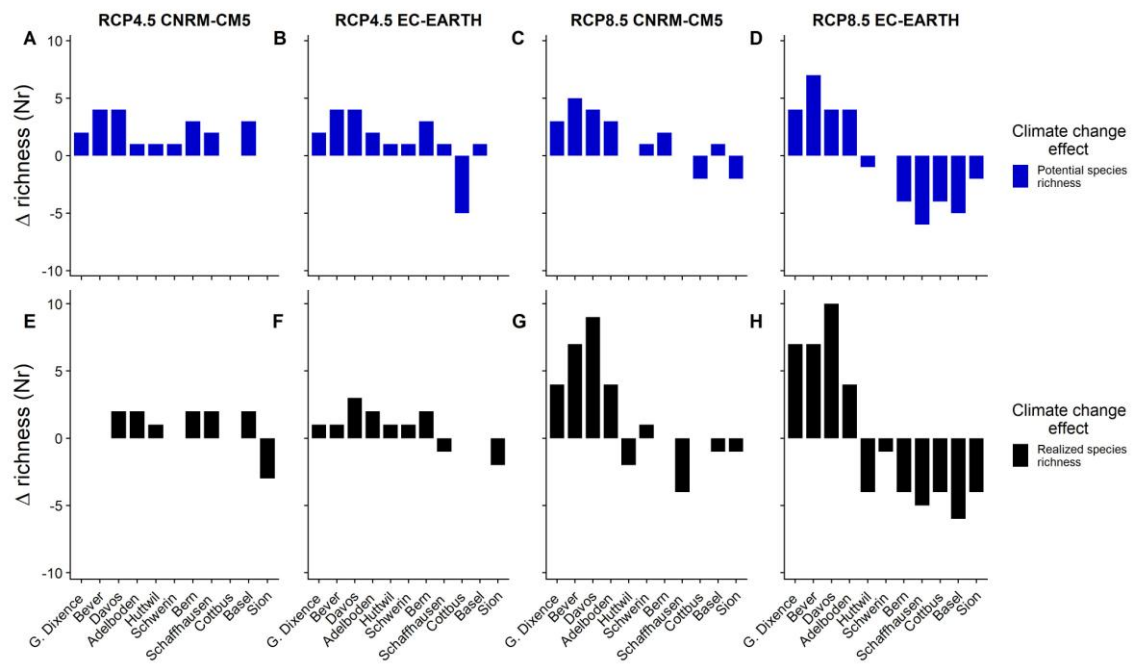
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708 **Figures**

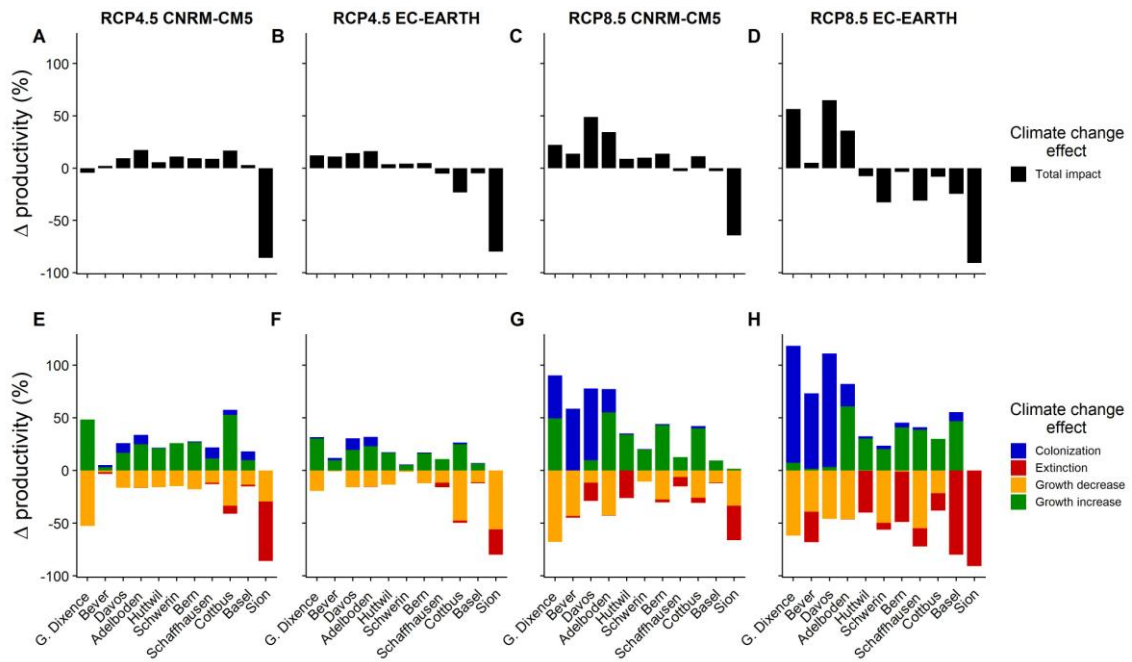
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710 Fig. 1: Models coupling used in this study. First, climatic suitabilities for 25 species were
 711 projected for each site and climate projection using SDMs (empty or filled circles). These 25
 712 suitabilities were then aggregated to build potential species pools. To include the variability
 713 inherent to the suitabilities and to avoid choosing arbitrary thresholds, we built 100 species
 714 pools for each site and climate projection (i.e. if a species had a suitability of 0.6 it was included
 715 in 60 of the 100 species pools). Finally, succession dynamics (including tree growth) on the
 716 long-term, were simulated using a FSM. Empty green circles represent climatically unsuitable
 717 (according to SDMs) sites, and filled green circles represent climatically suitable sites. Figure
 718 modified from García-Valdés and Morales-Castilla (2016).

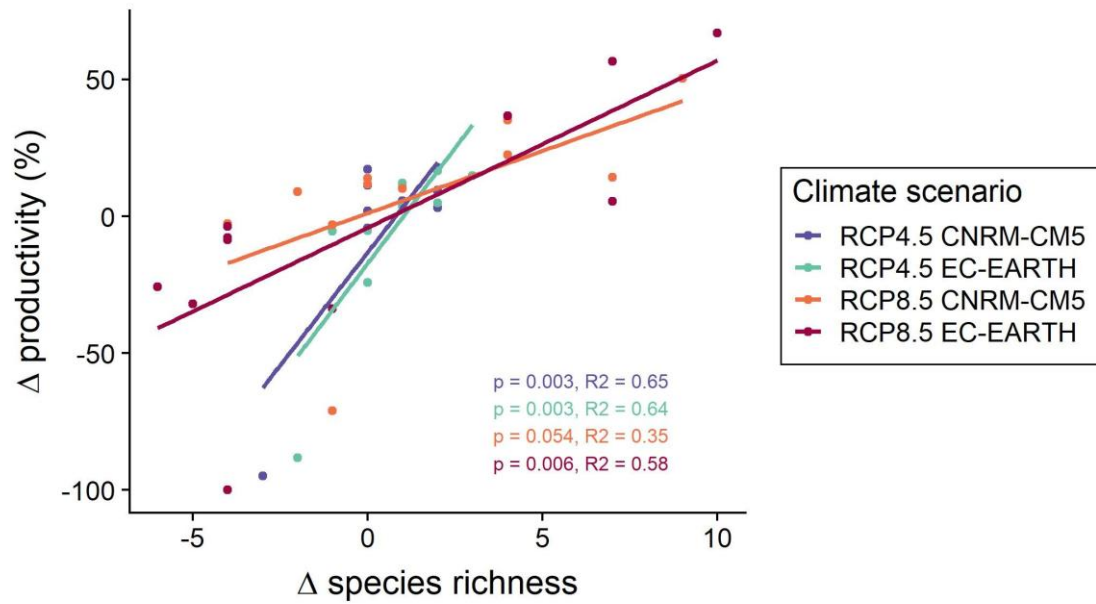


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Fig. 2: Effect of climate change on the number of potentially occurring species, projected with the SDMs assuming a threshold in suitability of 50% (upper panels), and on the number of realized species, simulated with the FSM, assuming that only species with more than 1 t.ha⁻¹ are present in each site (lower panels). No bar means that there is no change in the number of species. Sites are ranked according to their historical temperature, which correlated strongly with the importance of the community composition effects on productivity. Sites on the left have the lowest historical temperature and sites on the right have the highest temperature.



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 728 Fig. 3: Effect of climate change on each forest annual aboveground biomass productivity ($\text{t}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), relative to a baseline (i.e., current climate) projection. Study sites are ranked from the
 729 coldest (left) to the warmest (right). Upper panels show total effect, and lower panels show the
 730 effect on forest productivity of colonizations, extinctions, and growth decrease or increase of
 731 species present under both sets of conditions. To assess community composition, we considered
 732 that a species was present in a site whether its biomass reached at least $1 \text{ t}\cdot\text{ha}^{-1}$.
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735 Fig. 4: Future change in realized species richness vs. future change in forest productivity (%)
 736 under different climate change projections, relative to baseline projections using current climate.
 737 $R^2 = 0.65$ for RCP 4.5CNRM-CM5, $R^2 = 0.64$ for RCP 4.5- EC-EARTH, $R^2 = 0.35$ for RCP
 738 8.5-CNRM-CM5, and $R^2 = 0.58$ for RCP 8.5-EC-EARTH.