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

3

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32   *Data availability statement:* the original data used in this study are either available within the

33   article (table S1), are part of on the models used (FORCLIM; Bugmann, 1996), or are available in

34   the public domain: Atlas Florae Europaeae (AFE; Jalas & Suominen, 1972–1994; Jalas,

35   Suominen, & Lampinen, 1996), EUFORGEN (http://www.euforgen.org/), Climatic Research

36   Unit CL v. 2.0 (New, Lister, Hulme, & Makin, 2002) and EURO-CORDEX project (Jacob et

37   al., 2014). The climate data was accessed and processed using the DataGURU server

38   (dataguru.lu.se).

39

40   **Biosketch**

41   Raúl García Valdés (orcid.org/0000-0001-6399-4709) is a postdoct at CREAF – Univ.

42   Autònoma de Barcelona. He studies the effects of climate change on tree species distributions,

43   forest functioning, and ecosystem services. His research focus on the lack of equilibrium

44   between species distribution and climate, and on forest composition - functioning relationships.

45   He addresses these issues by combining and analysing large tree and trait databases, and by

46   developing and coupling species distribution, patch, and forest growth (or gap) models. He is

47   currently interested on how climate and tree species, or traits, composition interact and affect

48   forest properties and functioning. For a complete list of publications please visit

49   https://www.researchgate.net/profile/Raul_Garcia-Valdes

50

51 **Abstract**

52 Aim: Climate change impacts forest functioning and services through two inter-related effects.

53 First, it impacts tree growth, with effects, for example, on biomass production. Second, climate

54 change might also reshuffle community composition, with further effects on forest functioning.

55 However, the relative importance of these two effects has rarely been studied. Here, we

56 developed a novel modelling approach to investigate such importance for forest productivity.

57 Location: 11 forest sites in central Europe.

58 Time period: Historical (years 1901-1990) and end-of the-century (2070-2100) climatic

59 conditions. We simulated 2000 years of forest dynamics for each condition.

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

61 Methods: We coupled species distribution models and a forest succession model, working at

62 complementary spatial and temporal scales, to simulate the climatic filtering shaping potential

63 tree species pools, the biotic filtering shaping realized communities, and the functioning of these

64 realized communities in the long term.

65 Results: Under an average temperature increase (relative to 1901-1990) of between 1.5 ºC and

66 1.7 ºC, changes in simulated forest productivity were mostly caused by changes in the growth of

67 persisting tree species. With an average temperature increase of 3.6 ºC – 4.0 ºC, changes in

68 simulated productivity at currently climatically mild sites were again predominantly caused by

69 changes in tree species growth. However, at the currently warmest and coldest sites,

70 productivity changes were mostly related to shifts in species composition. In general, at the

71 coldest sites, forest productivity is likely to be enhanced by climate change, and at the warmest

72 sites productivity might increase or decrease depending on the future regime of precipitation.

73 Main conclusions: Combining two complementary modelling approaches that address questions

74 at the interface between biogeography, community ecology, and ecosystem functioning, reveals

75 that climate change-driven community reshuffling in the long term might be critically important

76 for ecosystem functioning.

77

81 **Introduction**

82   Forests cover about a third of the world land surface, harbour most of the terrestrial

83 biodiversity, and represent an important carbon sink. They also play a pivotal role in climate

84 regulation (Chapin, Randerson, McGuire, Foley, & Field, 2008) and provide other important

85 ecosystem services (Kumar, 2012). However, climate change is affecting many of these forest

86 ecosystem services, such as biomass production and carbon sequestration (Kirilenko & Sedjo,

87 2007), with this impact likely to be strengthen in the future (Pachauri et al., 2014). The

88 influence of climate change on forests can be divided into two inter-related effects (Adler,

89 Leiker, & Levine, 2009, Morin et al., 2018). Climate change affects forests by altering tree

90 physiological rates (Sack & Grubb, 2001), e.g. growth (Silva & Anand, 2013), phenology

91 (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007), or survival (Allen, Breshears, &

92 McDowell, 2015), which has direct consequences for ecosystem functioning (e.g. biomass

93 productivity). Climate change also affects forest functioning when the pressure of climate

94 change on trees' growth is strong enough to drive species' local extinction and colonization, as

95 seen in natural, experimental and simulated forests (Liang et al., 2016; Morin, Fahse, Scherer-

96 Lorenzen, & Bugmann, 2011; Paquette & Messier, 2011). Understanding the relative

97 importance of these two effects would greatly help to improve the projections of the impact of

98 climate change on forest functioning, and on key ecosystem services such as carbon uptake and

99 biomass provision. However, the two effects have been mostly studied separately, and very little

100 is known about their relative importance for forest productivity under different circumstances

101 (but see Coomes et al., 2014; Zhang, Niinemets, Sheffield, & Lichstein, 2018).

102   The effects of climate change on species composition might amplify (Zhang et al.,

103 2018) or counteract (Fauset et al., 2012) the effects of climate change on tree growth.

104 Furthermore, recent studies found that effects on species composition might be greater than

105 previously expected. García-Valdés, Bugmann, and Morin (2018) found that when tree species

106 go extinct in the order we would expect given climate change, reductions in the projected

107 productivity of some forests were greater than we would expect by the single effect of random

108 species loss. Thus, most of Biodiversity-Ecosystem functioning studies (e.g. Liang et al., 2016),

109 might underestimate the strength of biodiversity loss when caused by climate change. Similarly,

110 Morin et al. (2018) found that warmer and drier conditions might strongly affect Biodiversity-

111 Ecosystem functioning in forests experiencing the harshest climatic conditions, illustrating the

112 importance of understanding changes in species composition for forest functioning. These

113 findings suggest that local conditions, and the magnitude of the change in climate, might

114 interact to determine the relative importance of tree physiological changes, and species

115 reshuffling, for forest functioning.

116   Nonetheless, disentangling these two effects of climate change on ecosystem

117   functioning is difficult. While estimating the effects of climate change on tree growth could be

118   relatively straightforward through experiments or long-term observations (Hasenauer, Nemani,

119   Schadauer, & Running, 1999), estimating the effects on species composition is much more

120   complicated (Barry et al., 2018). Several mechanisms underlie the effects of climate change on

121   species composition. First, climatic filtering determines whether the local environmental

122   conditions are suitable for a species. Second, biotic filtering occurs when interactions among

123   potentially co-occurring species lead to the exclusion or acceptance of some species. While

124   climatic filtering is commonly studied at large spatial scales, such as regions or continents

125   (Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005), species interactions are mostly studied at

126   the local scale (Mayfield & Levine, 2010). We therefore studied both processes, each at the

127   relevant spatial scale, to quantify their effects on future composition of forest communities .

128   Species distribution models (hereafter "SDMs") typically work by correlating the

129   recorded presences of individual species with environmental variables (Gotelli et al., 2009), and

130   can be used to simulate climatic filtering. Although this approach carries some caveats (see

131   Dormann et al., 2012 and Discussion section), SDMs are particularly robust for measuring the

132   environmental tolerances of species that are broadly distributed (Early & Sax, 2014; Estrada,

133   Delgado, Arroyo, Traba, & Morales, 2016), as are the species considered here. Forest

134   succession models (FSMs) – also called gap models (Bugmann, 2001) – can be used to simulate

135   forest community dynamics from a few hundred square-meters up to landscape scale), given a

136   specific starting species pool (Chauvet, Kunstler, Roy, & Morin, 2017). FSMs are based on a

137   minimum number of ecological assumptions (Botkin, Janak, & Wallis, 1972), and rely on the

138   ecophysiological responses of trees to abiotic factors (including climate), and biotic factors (i.e.

139   inter and intra-specific interactions), to simulate individual tree growth and succession

140   dynamics (colonizations and extinctions) over time (Bugmann, 2001). FSMs can hence simulate

141   both the biotic filtering of species by forecasting the realized tree community (i.e. at long-term

142   equilibrium), and the effects of climate change on tree growth.

143   In this study, we coupled SDMs and FSMs to assess the relative importance of climate

144   change effects on tree growth and species composition for the productivity of central European

145   forests. Previous studies have coupled SDM-like modules with a process-based component

146   simulating key processes, such as dispersal and demography (e.g. range dynamic models;

147   Sarmento Cabral et al., 2013), and/or competition, e.g. the hybrid FATE-H model that considers

148   only plant functional types (Boulangeat, Georges, & Thuiller, 2014). At a larger spatial scale,

149   Meier, Lischke, Schmatz, and Zimmermann (2012) coupled a SDM with a FSM to predict the

150   range-shift rates of several tree species under climate change, while accounting for interspecific

151   competition. However, to our knowledge, no previous work has compared how climate change

152 will affect forest productivity through both altered species growth and composition by coupling

153 SDMs' with FSMs' projections. Our study is thus among the first to take advantage of the

154 complementarity of the two kinds of models to address questions at the interface between

155 biogeography, community ecology, and ecosystem functioning. Specifically, we used 11 forest

156 sites as an example and aimed at answering the following questions:

157   (1) How will climate change affect long-term forest aboveground biomass productivity

158 in European temperate forests?

159   (2) What will be the relative contribution of the changes in tree growth and of the shifts

160 in species composition to such changes in forest productivity?

161   (3) How will current local climatic conditions and the magnitude of climate change

162 influence the patterns found in (1) and (2)?

Material and methods

Overview

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

Study sites

The geographic background from which species distributions and climatic data were drawn for SDMs comprises Europe from −10°9′23″ E to 30°43′0″ E and 34°59′30″ N to 70°58′33″ N. We simulated forest growth in 11 temperate forest sites across central Europe (nine in Switzerland and two in Germany; Table S1). These sites cover a broad range of temperature and precipitation conditions (Table S1), and represent the diversity of environments and forest types in central Europe, as illustrated by previous studies (Bugmann, 1994; Morin et al., 2011).

Climate data for Species Distribution Models

We used historic climate data (climatology over the 1961-1990 period) from the Climatic Research Unit CL v. 2.0 dataset (New, Lister, Hulme, & Makin, 2002) and projected future climate data from the EURO-CORDEX project (Jacob et al., 2014), both at 10' resolution. Two Representative Concentration Pathways (RCPs): 4.5 and 8.5, and two General Circulation Models (GCMs): CERFACS-CNRM-CM5 (CNRM-CM5) and ICHEC-EC-EARTH (EC-EARTH) were used in this study. Projected future climate data were downscaled via the Rossby Centre regional climate model (RCA4) within the CORDEX project. We used four climatic variables: mean annual growing degree-days (> 5ºC), mean temperature of the coldest month, annual precipitation, and a summer moisture index (potential evapotranspiration divided

197   by precipitation). These variables have been previously used to model plant and vertebrates in

198   Europe and they reflect two primary properties of climate (energy and water) that have been

199   shown to affect species distributions (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller,

200   2011; Morrison, Estrada, & Early, 2018). We used averaged annual values of these climatic

201   variables for the 1961-1990 period as historical climatic conditions. For future climatic

202   conditions, we used averaged simulated data of the variables for the 2071-2100 period under

203   four climate change projections

204

205   *Climate data for the Forest Succession Model*

206   We simulated 2000 years of forest dynamics with FORCLIM, given a "historical-like"

207   climate (baseline) projection and four "future-like" climate change projections (RCPs 4.5 and

208   8.5, and GCMs CNRM-CM5 and EC-EARTH, downscaled using RCA4). To do so we needed a

209   generic 2,000 year-long time-series of monthly temperature (T) and precipitation (P) that

210   incorporated inter-annual variability. For this purpose, we used the climate simulator embedded

211   in FORCLIM, which uses the monthly mean and standard deviation of T and P, and the

212   correlation between them (Bugmann, 1994). For the historical-like climate, we generated 2000

213   years of data directly using the mean, standard deviation and correlation of monthly T and P

214   (from Bugmann, 1994), which was calculated from historic (1901–1990) data from the Swiss

215   Meteorological Agency (Bantle, 1989). Such data have previously been used to calibrate and

216   validate forest productivity simulated by FORCLIM in our study sites. These data were

217   analogous to, but not the same as the climatic time series from the 1901-1990 period (which we

218   could not use as the time series was not long enough).

219   To simulate future climate conditions, we could not directly use data from GCM climate

220   projections because these models use a different "historical" data for bias correction to the data

221   we used (1901-1990 data from Bugmann, 1994). To circumvent this problem, we calculated a

222   climatic anomaly for each climate projection (see Morin & Chuine, 2005). For each climate

223   projection we calculated the differences in monthly T and P between the future climate (years

224   2071-2100) and the current climate (years 2006-2016). These anomalies quantify how much T

225   and P would vary from baseline values under every climate projection. We added these

226   anomalies to the means of the historical climate data from Bugmann (1994), and for each

227   climate projection we generated 2000 years of climate data for each of the four future climate

228   projections. All climate time-series thus contained no trend. In the projected future climate time-

229   series, the estimated changes in temperature depended mostly on the RCPs, while the estimated

230   changes in precipitation depended mostly on the GCMs. The differences between the four

231   climate projections and historical climate (1901-1990 period from Bugmann, 1994) were: (1)

232   RCP 4.5-CNRM-CM5, moderately warmer with more precipitation; (2) RCP 4.5-EC-EARTH,

233   moderately warmer with similar precipitation; (3) RCP 8.5-CNRM-CM5, much warmer with

234   more precipitation; and (4) RCP 8.5-EC-EARTH, much warmer with similar precipitation. The

235   stress experienced by trees increases sequentially under projections 1-4. See Table S1 and S2

236   for specifics.

237

238   *Species data and the Species Distribution Models*

239   We considered 25 of the most common tree species in this region (Table S3). We used

240   presence data from the Atlas Florae Europaeae (AFE; Jalas & Suominen, 1972–1994; Jalas,

241   Suominen, & Lampinen, 1996). When a species was not recorded in the Atlas, we used

242   distribution data from EUFORGEN (http://www.euforgen.org/; see Table S4). AFE presence

243   data were from 50 km × 50 km Universal Transverse Mercator (UTM) grid cells, and

244   EUFORGEN presence data were range maps. We transformed EUFORGEN range maps into

245   ~50km UTM cells to run the models. We calculated the average historical climatic conditions in

246   each 50-km grid cell from the 10' climate grid resolution. The relationships between historical

247   climatic variables and species' distributions were modelled using seven SDM techniques:

248   generalized linear models (GLM), generalized additive models (GAM), generalized boosting

249   models (GBM), classification tree analysis (CTA), artificial neural networks (ANN), flexible

250   discriminant analysis (FDA), and surface range envelope (SRE). Models were calibrated for the

251   historical period (1961–1990) using an 80% random sample of the initial data, and cross-

252   validated against the remaining 20% of the data, using the area under the receiver operator

253   characteristic curve (AUC) and the true skill statistic (TSS). SDMs were calculated 10 times,

254   each time selecting a different 80% and 20% of the data for calibration and evaluation. Results

255   from each SDM technique were then included in an ensemble model if the AUC from cross-

256   validation was higher than 0.8 and TSS was higher than 0.6 (similar to Araújo et al., 2011).

257   However, the final ensemble model for each species was calibrated using 100% of the species

258   distribution data to maximise the amount of data available for projections. For each species, the

259   ensemble was calculated using the mean probability of occurrence, weighted proportional to the

260   AUC and TSS obtained on the evaluation data. Ensemble models calibrated at 50-km resolution

261   were downscaled to obtain suitability in each 10′ grid cell. We projected ensemble models to

262   future climatic conditions at 10′ resolution for the four future climate projections (the

263   combination of GCMs and RCPs). This approach follows methods employed by Araújo et al.

264   (2011), though using more recently constructed climate data. All models were run in R (R Core

265   Team, 2014) using default options of the *biomod2* package (Thuiller, Georges, & Engler, 2013).

266

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

268   For each site and climate projection, we used the SDM-predicted suitability for each

269   species to build a local species pools. To use the continuous suitability projections (rather than

270   use an arbitrary threshold to distinguish suitable or unsuitable), we built 100 potential species

271   pools for each site and climate projection and included each species proportionally to its climate

272   suitability. For example, if the suitability of a given species in a given site and for a given

273   climate projection was 0.6, this species would be included in 60 (randomly chosen) of the 100

274   species pools for that site and climate projection.

275

276   *Forest Succession Model*

277   FORCLIM projections have been shown to be robust under various climatic conditions

278   across a large number of studies (Bircher, Cailleret, & Bugmann, 2015; Gutiérrez, Snell, &

279   Bugmann, 2016; Rasche, Fahse, & Bugmann, 2013; e.g. Rasche, Fahse, Zingg, & Bugmann,

280   2011). Its projections of forest biomass productivity have been validated for the sites used in

281   this study and using climate values generated with the same historical means, standard

282   deviations and cross-correlations as the ones used here (Rasche et al., 2013). It has also been

283   specifically used to study climate change effects on forest functioning on these sites (Didion,

284   Kupferschmid, Wolf, & Bugmann, 2011; Mina et al., 2017; Morin et al., 2018; Rasche et al.,

285   2013).

286   In FORCLIM, the establishment, growth and mortality of trees are simulated using the

287   abiotic and biotic conditions in small independent patches (800 m^2 in this study). Tree location

288   in the patch is not estimated, and all trees compete for light. The properties of several patches

289   are aggregated to calculate forest properties across larger extents (Bugmann, 2001; Shugart,

290   1984). Tree establishment is modelled as a stochastic process, depending on species-specific

291   responses to light availability at the forest floor, growing degree-days, drought occurrence, and

292   minimum and maximum winter temperature. Tree growth is measured as stem diameter

293   increment, which depends on each species' optimum growth rate, abiotic conditions

294   (temperature, drought, and soil nitrogen), and biotic conditions (light availability, possibly

295   reduced due to shading by competitor trees). Therefore, while competition for water and

296   nitrogen between individuals are not taken into account explicitly in the model, soil water and

297   nitrogen content constrain tree establishment and growth differentially between species in a

298   given site, which in turn affects competition between trees (Appendix S1). Competition for light

299   is modelled by calculating the amount of available light for each individual tree depending on

300   tree height and the crown sizes of competing trees. FORCLIM also incorporates a shade tolerance

301   parameter (Ellenberg, 1991), defining the classic trade-off between growth in full light and

302 survival in shade. Tree mortality has two components: (1) a 'background' mortality, which is

303 constant across time and depends on the species' maximum longevity, and (2) growth-related

304 mortality reflecting the effect of stressful conditions on tree survival (i.e., trees with decreased

305 vigour are more likely to die). The species parameters for FORCLIM can be found in Table S3,

306 and more details about the model can be found in Appendix S1, and in Didion, Kupferschmid,

307 Zingg, Fahse, and Bugmann (2009), and Bugmann (1996).

308

309 *Simulations of forest succession dynamics*

310 For each set of climate conditions (historical and future), we simulated 2000 years of

311 forest dynamics with FORCLIM. This allowed us to assess the relative contribution of tree

312 growth and species composition to climate-driven changes in productivity between the historical

313 and future periods. However, this approach means that the simulations should not be taken as

314 predictions of forest composition and productivity for the end of the 21st century, because the

315 effect of, e.g. species colonization, is not realistic for short-term projections.

316 After having checked that FORCLIM simulations conducted in the same conditions (site,

317 climate, species pool) yielded very similar results after 2000 years, we performed one FORCLIM

318 simulation for each site (n = 11), each set of climate conditions (historical and future, n = 5) and

319 each species pool (n = 100). Each simulation included 100 patches of 800 m^2 each,

320 corresponding to an 8 ha forest. FORCLIM simulations started from bare-ground to avoid the

321 influence of starting conditions. For each FORCLIM simulation, only the species in the site's

322 species pool - determined by the SDMs - were allowed to colonize the patches. The simulations

323 were run for 2,000 years to allow forests to reach equilibrium in total biomass and composition,

324 thus avoiding transient states. We extracted the productivity and composition from simulations

325 after 1000 years, to allow the system to reach equilibrium. To avoid temporal autocorrelation we

326 extracted values from the first year of each century after the year 1,000 (i.e., the years 1100,

327 1200, … 2000; cf. Morin et al., 2011) and averaged the results from these sampled years across

328 patches. For the calculation of the realized community composition we considered that a species

329 was present in a community only if its simulated biomass reached 1 Mg · ha^{-1}.

330

331 *Quantifying growth and composition effects of climate change*

332 To quantify the effects of climate change mediated by tree growth change, we

333 calculated the proportion of productivity change in each site that was produced by species found

334 under both present and future climatic conditions. To quantify the effects of climate change

335 mediated by species composition shift, we calculated the productivity loss caused by species

336   extinction, and the productivity gained by species colonization. The relative importance of

337   colonization and extinction was calculated by dividing the productivity change caused by either

338   colonization or extinction by the summed changes in productivity (previously transformed to

339   absolute values).

340

341   *Statistical analyses*

342   To test whether the future projected change in forest productivity varied across an

343   environmental gradient, we fitted linear regressions between forest productivity in each site and

344   its mean annual temperature (MAT), total annual precipitation (TAP), and precipitation relative

345   to potential evapotranspiration (P/PET). Climate data were obtained from Bugmann (1994) and

346   were calculated from historic (1901–1990) data from the Swiss Meteorological Agency (Bantle,

347   1989). We also fitted linear regressions between the relative importance of colonization and

348   extinction for productivity, and the above climatic variables. Finally, we fitted a linear

349   regression between the future change in productivity and future change in realized species

350   richness at each site.

351   **Results**

352

353   *Climate change effects on potential species pools and richness (SDMs output)*

354   In most climate change projections and sites, climatic suitability for study species

355   increased (Fig. 2 A-C). However, under extreme warming (RCP 8.5) and the driest conditions

356   (EC-EARTH model; Fig. 2D), potential species richness increased in the coldest sites

357   (Adelboden, Bever, Davos and Grande Dixence), but remained the same or decreased in the

358   warmest sites (Basel, Bern, Cottbus, Huttwil, Schaffhausen, and Sion).

359

360   *Effect of climate change on realized species richness*

361   Under historical climatic conditions, simulated realized species richness varied from

362   three (out of 25) in Grande Dixence and Davos to 11 in Huttwil and Bern (Fig. S1B). Under

363   most climate change projections, the number of realized species increased in most of the sites

364   (Fig. 2, lower panels). Although under the extreme RCP8.5-EC-EARTH projection, the realized

365   species richness decreased in the warmest sites (Fig. 2H).

366

367   *Climate change effects on forest productivity*

368   The impact of climate change on forest productivity varied greatly along the climatic

369   gradient, and with different intensity depending on the climate projection (Fig. 3 A-D). The

370   greatest impact occurred in Sion, the warmest and second driest site, where productivity

371   decreased by between -67.6% and -100%. However, with a projected increase in precipitation

372   greater than 10.0% (CNRM-CM5 model in Table S1), forest productivity increased in all sites

373   (Fig. 3 A and C), except Grande Dixence, Basel and Sion. With a very weak precipitation

374   change (EC-EARTH model in Table S1), forest productivity increased in the coldest sites and

375   decreased in most of the warmest sites (Fig. 3 B and D).

376   Historical precipitation was positively correlated with the change in productivity under

377   two climate change projections (p = 0.043 with RCP 4.5-EC-EARTH and p = 0.034 with RCP

378   8.5-EC-EARTH; Fig. S2A). Temperature was negatively correlated with productivity change

379   under one projection (p = 0.009 with RCP 8.5-EC-EARTH; Fig. S2B). P/PET was positively

380   correlated with the change in productivity under three projections (p = 0.028 with RCP 4.5-EC-

381   EARTH, p = 0.027 with RCP 8.5-CNRM-CM5, and p = 0.002 with RCP 8.5-EC-EARTH; Fig.

382   S2C).

383

384 *The relative importance of the growth and composition effects on forest productivity*

385   With the climate scenario RCP 4.5, which projected a moderate increase in local

386 temperature relative to the historical period, simulated changes in productivity were driven

387 almost exclusively by the effects of climate change on tree growth of surviving species (Figs. 3

388 E-F and 4). The rise in MAT was on average between +1.5 [+1.1, +2.0] ºC and +1.7 [+1.5,

389 +2.2] ºC (Table S1), and the average rise in winter temperature was between +2.0 [+1.5, +2.6]

390 ºC and +2.7 [+2.1, +3.1] ºC (Table S2). With such temperature increase there was a positive

391 correlation between the increase in productivity and the increase in species richness under the

392 two GCMs (p = 0.003; Fig. 5), but change in species richness did not strongly contribute to

393 changes in productivity (Fig. 3 E-F). With the climate scenario RCP 8.5 that projected a

394 stronger increase in local temperature (Fig. 3 G-H), there was also a positive relationship

395 between the increase in realized species richness and the increase in productivity (p = 0.054 and

396 R^2 = 0.35 with the CNRM-CM5, p = 0.006 and R^2 = 0.58 with the EC-EARTH GCM; Fig. 5).

397 Under this more extreme temperature increase, changes in species richness (Fig. 5) and

398 community composition did strongly contribute to the changes in productivity (Figs. 3 G-H and

399 4). The increase in MAT ranged from +3.6 [+2.8 , +4.5] ºC to +4.0 [+2.9, +4.9] ºC (Table S1),

400 and the increase in winter temperature from +3.8 [+2.9, 5.5] ºC to +4.5 [+4.1, +5.6] ºC (Table

401 S2).

402   The importance of community composition effects varied across the study sites (Fig. 3

403 E-H). Their importance related to the current local temperature, which was negatively correlated

404 with the importance of colonization under three climate projections (p <= 0.05; Fig. S3C). The

405 importance of the composition effects was also correlated with current P/PET under one

406 projection (p = 0.021; Fig. S3E) and did not correlate with current precipitation (Fig. S3 A-B).

407   **Discussion**

408

409   Our simulations of forests located across a large climate gradient in central Europe

410   showed that future changes in forest productivity might strongly depend on local temperature,

411   P/PET, and precipitation (Fig. S2; Allen et al., 2015). Simulated forest productivity increased at

412   high elevations, a result which we expect to be similar for sites at high latitudes (Füssel,

413   Kristensen, Jol, Marx, & Hildén, 2017), where cold temperature currently limits tree

414   establishment, growth and survival (Nemani et al., 2003). Climate change also created warmer

415   winters in these sites (Table S2), which allowed new species to establish by decreasing the

416   constraints on establishment (as shown in empirical studies, e.g. Conedera, Wohlgemuth,

417   Tanadini, & Pezzatti, 2018). Climate change also produced longer growing periods that

418   increased the productivity of the species currently present (consistently with recently observed

419   trends, e.g. Boisvenue & Running, 2006). Contrarily, in the lowlands, simulated productivity

420   decreased when climate change led to an increase in drought stress (mostly by increasing

421   temperature and not changing the precipitation regime), which became a major constraint for

422   tree growth and survival (as observed in Carnicer et al., 2011; Reyer, 2015). However, in a

423   scenario of climate change with increased precipitation and only moderate temperature increase,

424   productivity increased in the lowlands (Fig. 3A) because drought stress did not increase while

425   winter temperature was lower and the growing season was longer (Table S2). While the former

426   (increase of temperature with a decrease in precipitation), is predicted to occur in the southern

427   half of Europe, the latter is typically predicted for higher latitudes, starting in central

428   Scandinavia (Füssel et al., 2017).

429

430   *Shifts in tree species richness and composition drive productivity in the harshest climates*

431   We found that under moderate warming, changes in projected forest productivity were

432   caused almost exclusively by the effects of climate change on tree growth (Fig 3 E-F; see

433   Coomes et al., 2014). Contrarily, under extreme warming, and in locations at both ends of the

434   temperature gradient, changes in productivity were driven mostly by changes in species

435   composition (Fig 3 G-H). The increasing correlation between the relative importance of

436   simulated colonization (i.e. a measure of the composition effect) and both local temperature and

437   P/PET under the harshest climate projection (+3.6 ºC and -1.1% TAP; Fig. S3 C and E) further

438   shows the strong role of species composition under harsh climatic conditions. This finding

439   matches with empirical evidence of the role of tree richness on forest productivity along the

440   latitudinal gradient in Europe (Jucker et al., 2016). We also observed a positive correlation

441   between the change in species richness and in productivity ($p < 0.054$ across all climate

442 projections; Fig. 5). This supports theoretical studies which find forest productivity is especially
443 sensitive to species loss in the harshest climates (see García-Valdés et al., 2018; Morin et al.,
444 2018).

445 The link between forest species richness and ecosystem productivity (e.g. Liang et al.,
446 2016; Paquette & Messier, 2011) is usually explained by a greater niche partitioning in more
447 diverse communities (Loreau et al., 2001; Morin et al., 2011). In simulated forests in the coldest
448 sites, the effects of species richness and composition were strengthened because climate change
449 allowed new species to colonize and be productive (Fig. 3 and S3; Coomes et al., 2014).
450 Contrarily, in the warmest-driest sites, climate change caused the extinction of key species
451 (Reyer, 2015), which reduced species richness and productivity.

452 The observed importance of community composition change in cold and warm-dry sites
453 in our study (see Anderegg & HilleRisLambers, 2019; Morin et al., 2018) is consistent with an
454 extension of the stress gradient hypothesis (SGH; Bertness & Callaway, 1994; Crain &
455 Bertness, 2006). This hypothesis states that the frequency of interspecific competitive
456 interactions decreases in intensity with increasing abiotic stress. In our study sites, it is likely
457 that species extinctions occurred when the species were at the boundaries of their suitability
458 before climate change. At sites with intermediate temperature, such species were probably
459 suppressed by competition before climate change and did not contribute significantly to the total
460 productivity of the community. Hence, their extinction under climate change did not change
461 greatly the total productivity of the site. Contrarily, at both ends of the temperature gradient,
462 harsh climatic conditions reduced competitive interactions. This means, that in the absence of
463 climate change, species that were close to their climatic limits could still contribute substantially
464 to the total productivity of the site because they faced weak competition. Hence, their extinction
465 with climate change substantially affected the total productivity of the community. With
466 colonizations, we could expect a similar effect. In sites with mild climate conditions, colonizing
467 species probably remained close to the species' climatic limits (as climate change had
468 transformed the site from unsuitable to suitable), and were unlikely to become dominant, thus
469 probably not contributing substantially to the total productivity. This occurs because they still
470 had to deal with biotic interactions (McGill, Enquist, Weiher, & Westoby, 2006), and were not a
471 strong competitor under such conditions (low suitability and strong competition). In climatically
472 harsh sites, colonizing species could immediately become dominant because it was less likely
473 that they encountered strong competitors, as such site have a lower species richness on average.

474

475 *Increased sensitivity of warmest forests to climate change*

476   Our simulations suggested that rapid and steep changes might arise in forest functioning

477   (i.e. productivity) due to climate change. In the warmest site, a complete elimination of the

478   forest cover was projected in the event of the most severe climate change scenario (Fig. 3H). In

479   this scenario increase in drought stress drove the forest system to a change in community type

480   (e.g. from forest to scrublands or meadows). García-Valdés et al. (2018) hypothesized such

481   drastic changes in forest functioning when simulating a large number of species extinctions.

482   Here, using a realistic scenario of composition change, we confirmed that such a drastic change

483   could indeed occur in one of the study sites.

484

485   *Limitations of the approach*

486   To our knowledge this is the first study to couple models at complementary spatial, and

487   temporal, scales (SDMs and FSMs), to quantify the relative importance of changes in growth

488   and composition in mediating the effects of climate change on forest productivity. Although

489   these simulations compared climates that are only 80 years apart (from now to the end of the

490   century), they mimic long-term dynamics in order to compare mature forests. This means that

491   simulations do not consider transient processes (e.g. disturbance, management, or brief extreme

492   climatic events). Results should thus not be considered as short-term predictions, but instead

493   estimates of the importance of climate change composition effects on mature forests, in

494   comparison with growth effects. Our approach carries other limitations: (1) we used correlative

495   SDMs that entail caveats (García- Valdés, Zavala, Araújo, & Purves, 2013; Pearson & Dawson,

496   2003). However, correlative SDMs work well for widespread species such as those used here

497   (Early & Sax, 2014) and process-based SDMs (e.g. Chuine & Beaubien, 2001) could not be

498   used for so many species. (2) Our simulation design, relying on 2000-years simulation in both

499   historical and future conditions, allows assessing the relative contribution of changes in tree

500   growth and species composition to be assessed, and notably highlights the possible strength of

501   compositional effects on changing productivity. However, these simulations cannot be directly

502   used to infer forest composition and productivity at the end of the 21st century. Local species

503   extinction by 2100 might be well reproduced by our design, because the exposition to the novel

504   climate conditions may directly affect the adult trees of the sensitive species, while preventing

505   the establishment of their seedlings. But site colonization by new species under the new

506   conditions occurs through much slower dynamics, which means that the impact of these new

507   colonizations would not be realistic for short-term projections. (3) We could not have measured

508   the interaction between the growth and composition effects unless we had imposed a strong

509   artificial control of the simulation, which would prohibit the measurement of complex

510   community responses. (4) We did not consider species currently absent from central Europe. (5)

511 We ignored the possibility of plastic, or micro-evolutionary, responses of species (e.g. Jump &

512 Peñuelas, 2005; Lavergne, Mouquet, Thuiller, & Ronce, 2010). (6) The importance of the

513 composition effects might be further strengthened by taking into account interactions besides

514 competition for light (e.g. Jactel & Brockerhoff, 2007). (7) The generated climate data had a

515 temporal resolution of one month, so extreme events occurring at shorter scale were not

516 considered. (8) Finally, we used the climatic anomaly between 2006-2016 and 2070-2100 as a

517 measurement of climate change, which probably made the projections of forest responses

518 conservative.

519

520 *Importance of climate change-composition effects on forests*

521 Our results highlight that composition effects on productivity could become very

522 important under extreme changes in climate, which is likely to occur regarding the forecasts

523 about the magnitude of climate change (Field, 2014). Our results also show that such

524 composition effects might become especially important in some sites: negatively in terms of

525 productivity in forests with warm and dry conditions, but positively in sites with cold

526 conditions. Hence, we believe that our projections demonstrate that the role of species range-

527 shifts (i.e., composition effects) when simulating impacts of climate change on forests could be

528 more important than previously anticipated, notably under harsh environmental conditions. The

529 role of species' range shifts and community composition's changes is very often neglected in

530 studies of climate change impacts on ecosystem functioning. We thus call for more research to

531 improve our understanding of these effects considering the likelihood of an extreme change in

532 climate.

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715　　　　composition amplify the response of forest biomass to climate. *Nature, 556*, 99-102.

716

717 *Data availability statement:* the original data used in this study are either available within the

718 article (table S1), are part of on the models used (FORCLIM; Bugmann, 1996), or are available in

719 the public domain: Atlas Florae Europaeae (AFE; Jalas & Suominen, 1972–1994; Jalas,

720 Suominen, & Lampinen, 1996), EUFORGEN (http://www.euforgen.org/), Climatic Research

721 Unit CL v. 2.0 (New, Lister, Hulme, & Makin, 2002) and EURO-CORDEX project (Jacob et

722 al., 2014). The climate data was accessed and processed using the DataGURU server

723 (dataguru.lu.se).

724 **Figures**
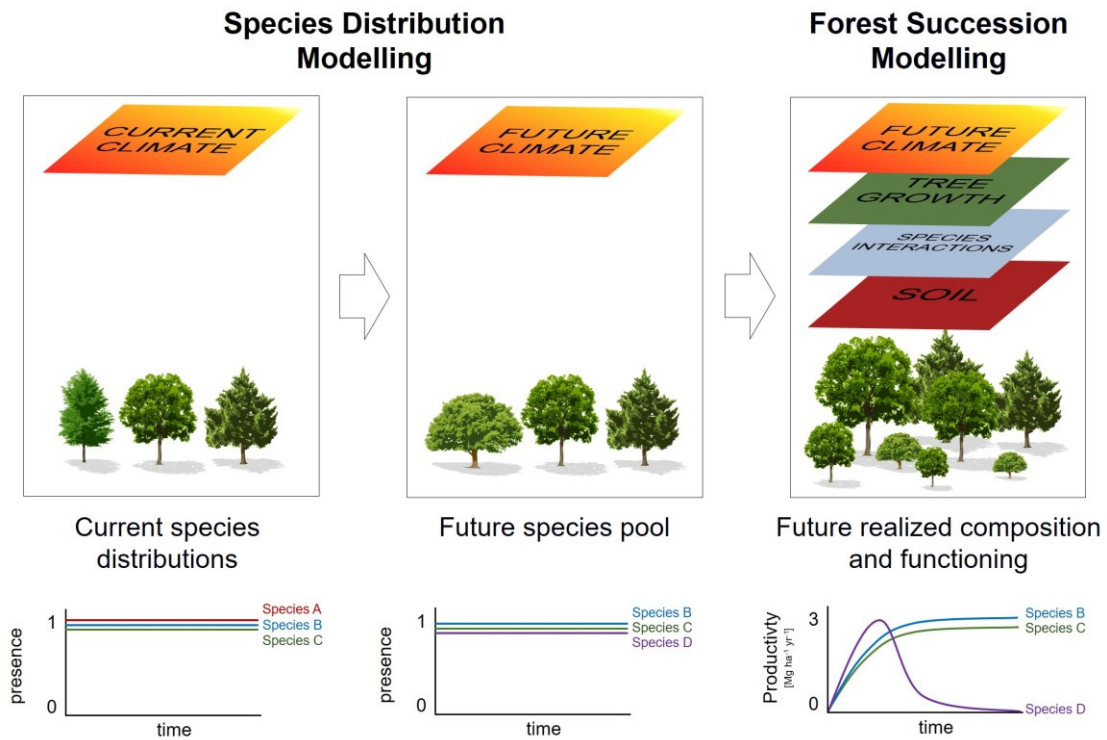
726 Fig. 1: Models coupling used in this study. First, climatic suitabilities for 25 species were

727 projected for each site and climate projection using SDMs. These 25 suitabilities were then

728 aggregated to build potential species pools. To include the variability inherent to the suitabilities

729 and to avoid choosing arbitrary thresholds, we built 100 species pools for each site and climate

730 projection (i.e. if a species had a suitability of 0.6 it was included in 60 of the 100 species

731 pools). Finally, succession dynamics (including tree growth) on the long-term, were simulated

732 using a FSM. Figure modified from García-Valdés and Morales-Castilla (2016).
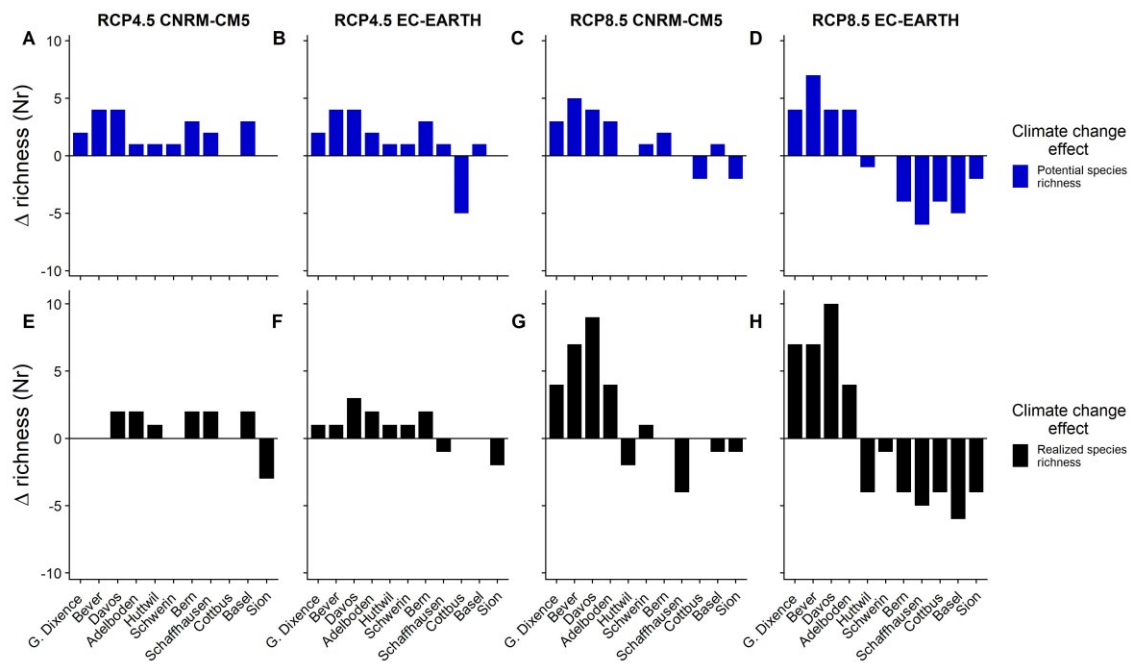
Fig. 2: Effect of climate change on the number of potentially occurring species, projected with the SDMs assuming a threshold in suitability of 50% (upper panels), and on the number of realized species, simulated with the FSM, assuming that only species with more than 1 Mg · ha^{-1} are present in each 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.
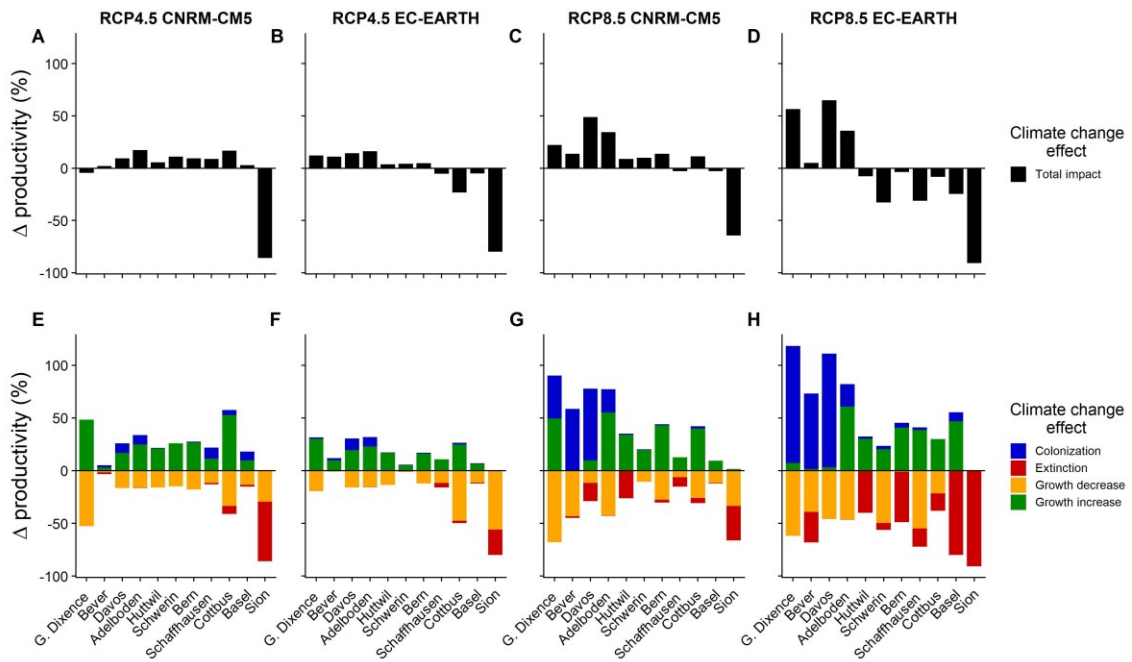
741

742 Fig. 3: Effect of climate change on each forest annual aboveground biomass productivity (Mg ·

743 ha^{-1}.yr^{-1}), relative to a baseline (i.e., current climate) projection. Study sites are ranked from the

744 coldest (left) to the warmest (right). Upper panels show total effect, and lower panels show the

745 effect on forest productivity of colonizations, extinctions, and growth decrease or increase of

746 species. To assess community composition, we considered that a species was present in a site

747 whether its biomass reached at least 1 Mg · ha^{-1}.

748

749
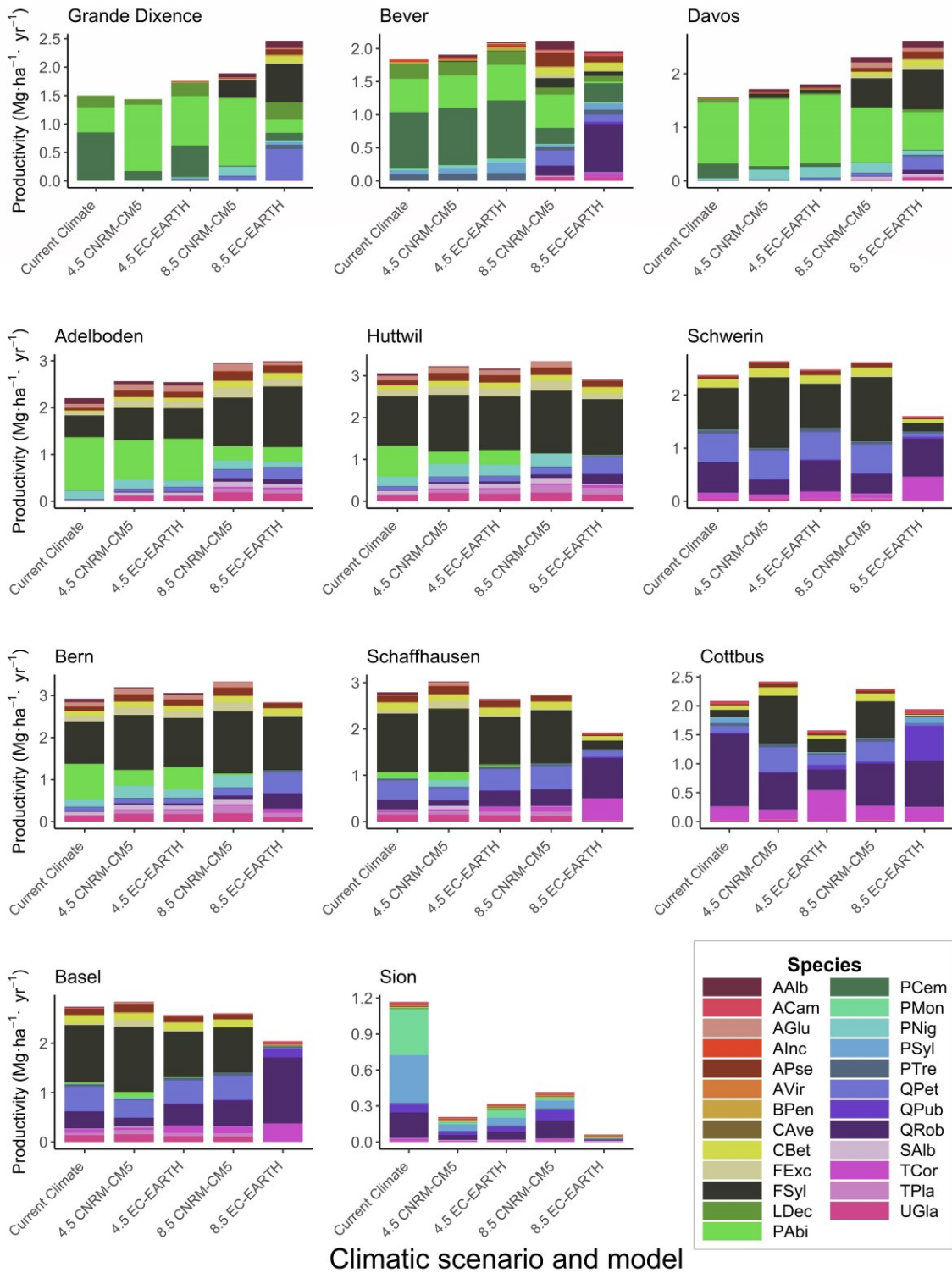
Fig. 4: Species productivity (Mg·ha^{-1}·yr^{-1}) at each site given a stable climate and four climate

change scenarios. The species codes are the following: AAlb: *Abies alba*; ACam: *Acer*

campestre; AGlu: *Alnus glutinosa*; AInc: *Alnus incana*; APse: *Acer pseudoplatanus*; AVir:

Alnus viridis; BPen: *Betula pendula*; CAve: *Corylus avellana*; CBet: *Carpinus betulus*; FExc:

Fraxinus excelsior; FSyl: *Fagus sylvatica*; LDec: *Larix decidua*; PAbi: *Picea abies*; PCem:

Pinus cembra; PMon: *Pinus montana*; PNig: *Populus nigra*; PSyl: *Pinus sylvestris*; PTre:

757   *Populus tremula*; QPet: *Quercus petraea*; QPub: *Quercus pubescens*; QRob: *Quercus robur*;

758   SAlb: *Salix alba*; TCor: *Tilia cordata*; TPla: *Tilia platyphyllos* and UGla: *Ulmus glabra*.

759
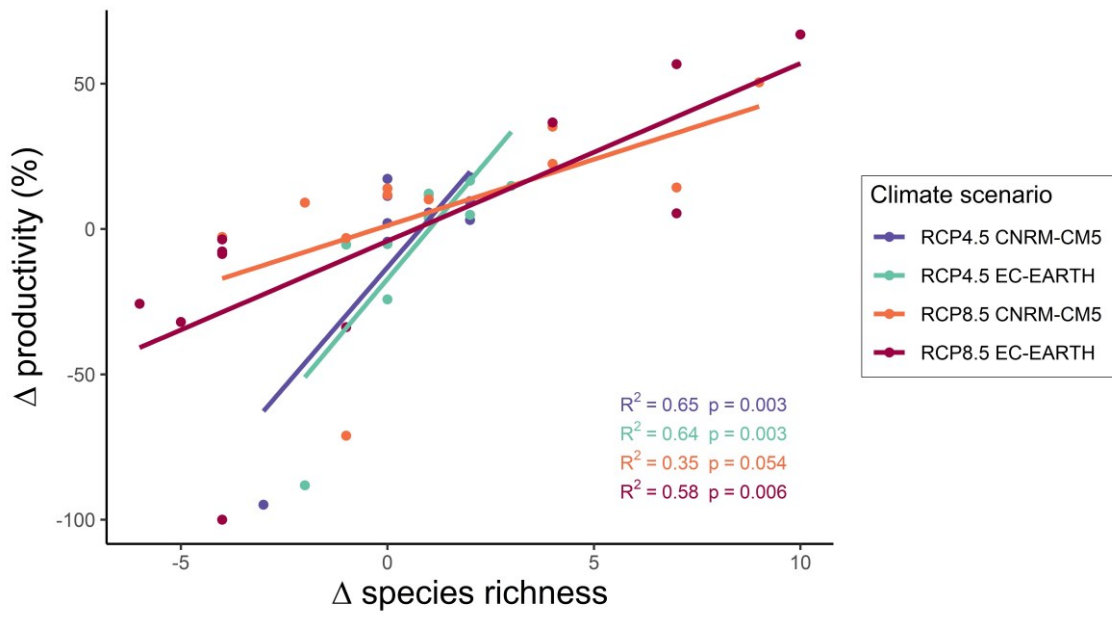
760

761   Fig. 5: Future change in realized species richness *vs*. future change in forest productivity (%)

762   under different climate change projections, relative to baseline projections using current climate.

Supporting Information

763

764   Appendix S1: FORCLIM description

765   Table S1: Study sites description of current and future conditions.

766   Table S2: Study sites description of changes in climate seasonality.

767   Table S3: Tree species parameters in FORCLIM.

768   Table S4: Information source of the species data used for the SDMs.

769   Fig. S1: Sites potential, and realized, species richness, and productivity with historical climatic
770   conditions.

771   Fig. S2: Correlation between the future change in productivity and local climate.

772   Fig. S3: Correlations between the relative contribution of colonizations and extinctions and
773   local climate.

Supporting Information

Site name	Latitude (°N)	Longitude (°E)	Elevation (m.a.s.l.)	MAT (°C)					TAP (mm)				
				Current climate	RCP 4.5		RCP 8.5		Current climate	RCP 4.5		RCP 8.5	
					CNRM-CM5	EC-EARTH	CNRM-CM5	EC-EARTH		CNRM-CM5	EC-EARTH	CNRM-CM5	EC-EARTH
Adelboden	46.5	7.6	1325	5.66	7.56	7.63	10.13	10.59	1355	1665	1415	1516	1306
Basel	47.5	7.6	317	9.34	10.54	10.8	12.5	12.84	799	887	821	845	738
Bern	46.9	7.4	570	8.02	9.44	9.62	11.41	11.68	1017	1095	1018	1100	909
Bever	46.6	9.9	1712	1.47	3.03	3.38	5.45	6.1	853	913	830	914	835
Cottbus	51.8	14.3	76	9.13	10.29	10.63	12.14	12.22	574	633	616	677	598
Davos	46.8	9.8	1590	2.5	4.01	4.26	6.53	7.18	1077	1201	1104	1239	1068
Grande Dixence	46.1	7.4	2166	1.15	2.8	3.04	5.14	5.75	1041	1050	1033	1106	982
Huttwil	47.1	7.9	638	8.08	9.54	9.7	11.49	11.75	1311	1421	1351	1423	1232
Schaffhausen	47.7	8.6	400	8.58	9.96	10.06	11.88	12.18	887	1039	900	954	925
Schwerin	53.6	11.4	45	8.43	9.57	10.01	11.26	11.29	625	709	655	727	617
Sion	46.2	8.6	542	8.94	10.91	11.13	13.35	13.73	578	592	598	673	677
Averaged differences with historical climate					+1.49 °C [+1.1 °C, +2.0 °C]	+1.72 °C [+1.5 °C, +2.2 °C]	+3.63 °C [+2.8 °C, +4.5 °C]	+4.00 °C [+2.9 °C, +4.9 °C]		+10.24 % [+0.9 %, +22.9 %]	+2.40 % [-2.7 %, +7.3 %]	+11.00 % [+5.8 %, +17.9 %]	-1.11 % [-10.6 %, +17.1 %]

Table S1: Description of the study sites: latitude, longitude, elevation, and current and future mean annual temperature (MAT) and total annual precipitation (TAP).

Table S2: Projected future change in seasonality of mean annual temperature (MAT) and total annual precipitation (TAP). Differences in temperature are expressed in ºC, and in precipitation in percentage.

Site name	Season	MAT (°C)				TAP (%)			
		RCP 4.5		RCP 8.5		RCP 4.5		RCP 8.5	
		CNRM-CM5	EC-EARTH	CNRM-CM5	EC-EARTH	CNRM-CM5	EC-EARTH	CNRM-CM5	EC-EARTH
Adelboden	Spring	0.97	1.18	3.13	3.28	-9.99	6.90	-13.98	-0.24
	Summer	2.04	2.05	5.93	6.94	53.68	-1.10	20.12	-8.40
	Autumn	1.78	2.45	4.30	5.22	12.72	11.66	34.77	-2.31
	Winter	2.81	2.22	4.54	4.28	18.95	3.64	3.56	-0.63
Basel	Spring	1.23	1.02	2.98	2.75	-8.57	6.46	-5.34	-0.91
	Summer	0.26	1.61	2.51	4.62	27.87	-10.04	1.99	-28.08
	Autumn	0.86	1.58	3.04	3.67	0.05	6.23	15.21	6.49
	Winter	2.45	1.62	4.11	2.97	21.99	17.09	14.58	1.98
Bern	Spring	1.44	1.36	3.57	3.21	-5.87	0.34	-2.30	1.40
	Summer	0.43	1.63	2.65	4.56	17.10	-8.54	6.02	-25.81
	Autumn	1.00	1.58	3.07	3.66	3.11	8.34	22.19	-7.61
	Winter	2.81	1.84	4.29	3.23	14.87	4.95	6.67	-1.95
Bever	Spring	1.04	1.20	3.14	3.23	-19.74	1.56	-8.59	-4.04
	Summer	0.92	1.69	3.52	5.18	25.83	-0.16	15.43	-4.50
	Autumn	1.55	2.77	4.87	5.98	2.08	-11.49	7.92	1.09
	Winter	2.71	1.96	4.37	4.12	9.37	1.00	8.21	0.01
Cottbus	Spring	1.17	1.43	2.58	2.62	-2.85	12.83	18.47	30.99
	Summer	0.34	1.25	2.12	3.24	13.24	-4.77	10.54	-20.09
	Autumn	0.69	1.43	2.94	3.33	4.76	8.02	30.43	-0.67
	Winter	2.43	1.89	4.40	3.17	26.20	21.01	16.21	22.04
Davos	Spring	0.98	1.20	3.02	3.07	-15.99	14.24	-11.48	5.57
	Summer	0.99	1.30	4.10	5.66	23.08	0.35	26.11	1.75
	Autumn	1.40	2.60	4.60	5.88	17.54	-6.33	21.31	-6.51
	Winter	2.69	1.94	4.42	4.11	8.37	5.28	11.84	-6.24
Grande Dixence	Spring	0.93	1.17	3.37	3.50	-20.42	-3.00	-13.57	-15.03
	Summer	1.04	1.53	3.34	4.71	19.43	-6.09	14.42	-6.90
	Autumn	1.66	2.45	4.50	5.59	-5.64	7.28	25.97	8.35
	Winter	2.96	2.40	4.73	4.61	7.05	-0.23	-3.02	-8.28
	Spring	1.48	1.30	3.49	3.18	-4.02	-2.57	-3.17	-0.75

Site	Season								
Huttwil	Summer	0.43	1.64	2.63	4.44	16.98	-5.00	3.94	-21.10
	Autumn	0.97	1.59	3.13	3.65	-1.99	8.64	18.18	-1.31
	Winter	2.98	1.94	4.42	3.43	22.25	14.24	17.44	3.41
Schaffhausen	Spring	1.32	1.12	3.03	2.79	-3.67	3.75	-3.04	6.20
	Summer	0.26	1.67	2.84	4.61	31.88	-7.15	3.46	-17.57
	Autumn	0.84	1.59	3.17	3.64	8.47	7.53	18.94	19.15
	Winter	3.07	1.52	4.15	3.32	26.01	5.60	12.69	19.39
Schwerin	Spring	1.10	1.65	2.39	2.54	-7.43	-1.28	-1.11	9.37
	Summer	0.55	1.23	1.80	3.02	15.10	3.78	10.66	-14.46
	Autumn	0.79	1.44	3.00	2.95	8.56	1.57	36.17	-2.13
	Winter	2.13	2.01	4.14	2.93	36.36	15.72	20.07	8.21
Sion	Spring	2.16	2.17	4.63	4.73	-10.48	-0.22	17.86	-7.97
	Summer	1.49	2.38	3.94	5.38	9.57	10.44	29.96	-20.77
	Autumn	1.34	1.58	3.44	3.50	-1.82	21.26	23.14	62.25
	Winter	2.93	2.65	5.65	5.55	8.63	-18.78	-5.46	30.69
Mean and range across sites	Spring	1.26	1.35	3.21	3.17	-9.91	3.54	-2.39	2.24
		[0.93, 2.16]	[1.02, 2.17]	[2.39, 4.63]	[2.54, 4.73]	[-20.42, -2.85]	[-3.00, 14.24]	[-13.98, 18.47]	[-15.03, 30.99]
	Summer	0.79	1.63	3.22	4.76	23.07	-2.57	12.97	-15.08
		[0.26, 2.04]	[1.23, 2.38]	[1.80, 5.93]	[3.02, 6.94]	[9.57, 53.68]	[-10.04, 10.44]	[1.99, 29.96]	[-28.08, 1.75]
	Autumn	1.17	1.92	3.64	4.28	4.35	5.70	23.11	-1.77
		[0.69, 1.78]	[1.43, 2.77]	[2.94, 4.87]	[2.95, 5.98]	[-5.64, 17.54]	[-11.49, 21.26]	[7.92, 36.17]	[-8.24, 1.30]
	Winter	2.72	2.00	4.47	3.79	18.19	6.32	9.35	6.24
		[2.13, 3.07]	[1.52, 2.65]	[4.11, 5.65]	[2.93, 5.55]	[7.05, 36.36]	[-18.78, 21.01]	[-5.46, 20.07]	[-8.28, 30.69]

Table S3: Tree species considered and their parameters in FORCLIM.

kName: species name.

kType: species type grouping parameter (foliage type).

kS: allometric parameter for relating diameter and height growth.

kHMax: maximum tree height (m).

kAMax: maximum tree age (years).

kG: growth rate parameter (cm.years^{-1}).

kDDMin: minimal annual degree-day sum (°C.day^{-1}).

kWiTN: mimimum winter temperature threshold (°C). If the species is assumed to have no limitation regarding minimum winter temperature, no value has been specified.

kWiTX: maximum winter temperature tolerated for regeneration (°C).

kDrTol: drought tolerance parameter (0: intolerant / 1: tolerant).

kNTol: nitrogen tolerance parameter (1: needs less N for growth / 5: needs more N for growth).

kBrow: browsing susceptibility (1=less susceptible, ..., 5=more susceptible).

kLy: light requirement of tree saplings (0=low requirement / 1=large requirement).

kLa : shade tolerance of adult trees (1=tolerant, ..., 9=intolerant).

kLQ: leaf litter quality (1=fast, 3=slow decaying).

For more details about FORCLIM, see the following references:

Bugmann H (1994) On the Ecology of mountainous forests in a changing climate: A simulation study. PhD Thesis. Eidgenössische Technische Hochschule, Zürich.

Bugmann H (1996) A simplified forest model to study species composition along climate gradients. *Ecology*, 77, 2055-2074.

Bugmann H (2001) A review of forest gap models. *Climatic Change*, 51, 259-305.

Didion M, Kupferschmid AD, Zingg A, Fahse L, Bugmann H (2009) Gaining local accuracy while not losing generality — extending the range of gap model applications. *Canadian Journal of Forest Research*, 39, 1092-1107.

kName	kType	kS	kHMax	kAMax	kG	kDDMin	kWiTN	kWiTX	kDrTol	kNTol	kBrow	kLy	kLa	kLQ
Abies alba	E5	73	60	700	117	641	--	-3	0.23	3	5	0.05	1	2
Acer campestre	D2	100	23	170	156	1062	-100	8	0.33	3	4	0.1	5	2
Acer pseudoplatanus	D3	100	37	550	125	898	-100	8	0.25	4	4	0.025	4	2
Alnus glutinosa	D2	111	31	240	250	898	-16	11	0.08	3	1	0.1	5	1
Alnus incana	D2	80	22	150	266	610	-100	7	0.08	3	1	0.2	7	1
Alnus viridis	D2	100	4	100	531	272	-100	-6	0.16	3	1	0.3	7	1
Betula pendula	D1	108	29	220	278	610	-100	9	0.16	1	1	0.3	9	2
Carpinus betulus	D3	70	27	220	177	898	-9	9	0.25	4	2	0.075	3	1
Corylus avellana	D3	142	10	70	95	898	-16	9	0.33	2	2	0.2	6	1
Fagus sylvatica	D3	64	45	430	191	723	-4	9	0.25	2	3	0.05	1	2
Fraxinus excelsior	D2	86	42	350	177	980	-17	8	0.16	5	3	0.075	6	1
Larix decidua	D2	72	52	850	170	323	-11	-1	0.25	1	3	0.4	9	3
Picea abies	E5	96	58	930	171	385	-100	-1	0.15	2	2	0.1	5	3
Pinus cembra	E5	40	26	1050	115	323	-11	-6	0.3	1	4	0.2	5	3
Pinus montana	E5	46	23	300	138	436	-100	-3	0.37	1	3	0.4	9	3
Pinus sylvestris	E4	111	45	760	119	610	-100	1	0.37	1	3	0.3	9	3
Populus nigra	D2	120	36	280	285	662	-100	12	0.08	4	2	0.1	5	2
Populus tremula	D2	126	30	140	310	610	-100	9	0.25	2	2	0.2	7	2

Quercus petraea	D3	66	45	860	195	785	-5	9	0.25	2	4	0.2	7	2
Quercus pubescens	D3	50	25	500	148	1011	-100	9	0.33	2	4	0.3	7	2
Quercus robur	D3	66	52	1060	195	1042	-17	9	0.33	2	4	0.3	9	2
Salix alba	D1	80	27	170	278	1062	-100	12	0.08	3	2	0.1	5	2
Tilia cordata	D3	106	30	940	114	1339	-19	8	0.33	4	2	0.1	5	2
Tilia platyphyllos	D3	127	39	960	110	1339	-100	8	0.25	5	2	0.075	3	2
Ulmus glabra	D3	127	43	480	153	1062	-16	11	0.25	5	3	0.075	3	1

Table S4: Information source of the species data used for the SDMs.

| Species	Source
Abies alba	AFE
Acer campestre	EUFORGEN
Acer pseudoplatanus	EUFORGEN
Alnus glutinosa	AFE
Alnus incana	AFE
Alnus viridis	AFE
Betula pendula	AFE
Carpinus betulus	AFE
Corylus avellana	AFE
Fagus sylvatica	AFE
Fraxinus excelsior	EUFORGEN
Larix decidua	AFE
Picea abies	AFE
Pinus cembra	AFE
Pinus montana	AFE
Pinus sylvestris	AFE
Populus nigra	AFE
Populus tremula	AFE
Quercus petraea	AFE
Quercus pubescens	AFE
Quercus robur	AFE
Salix alba	AFE
Tilia cordata	EUFORGEN
Tilia platyphyllos	EUFORGEN
Ulmus glabra	AFE
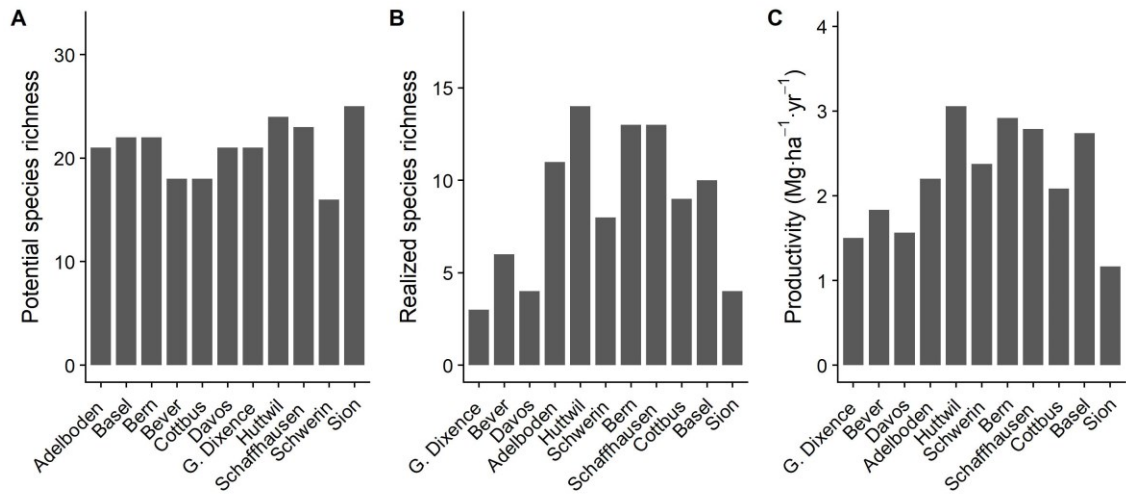
1

2 Fig. S1: Each forest's potential species richness (projected by SDMs), realized species richness
3 (projected by SDMs + ForClim), and annual aboveground wood productivity (Mg·ha^{-1}·yr^{-1}),
4 under baseline (i.e., current climate) conditions. Sites on the left have the lowest temperature
5 and sites on the right have the highest temperature.
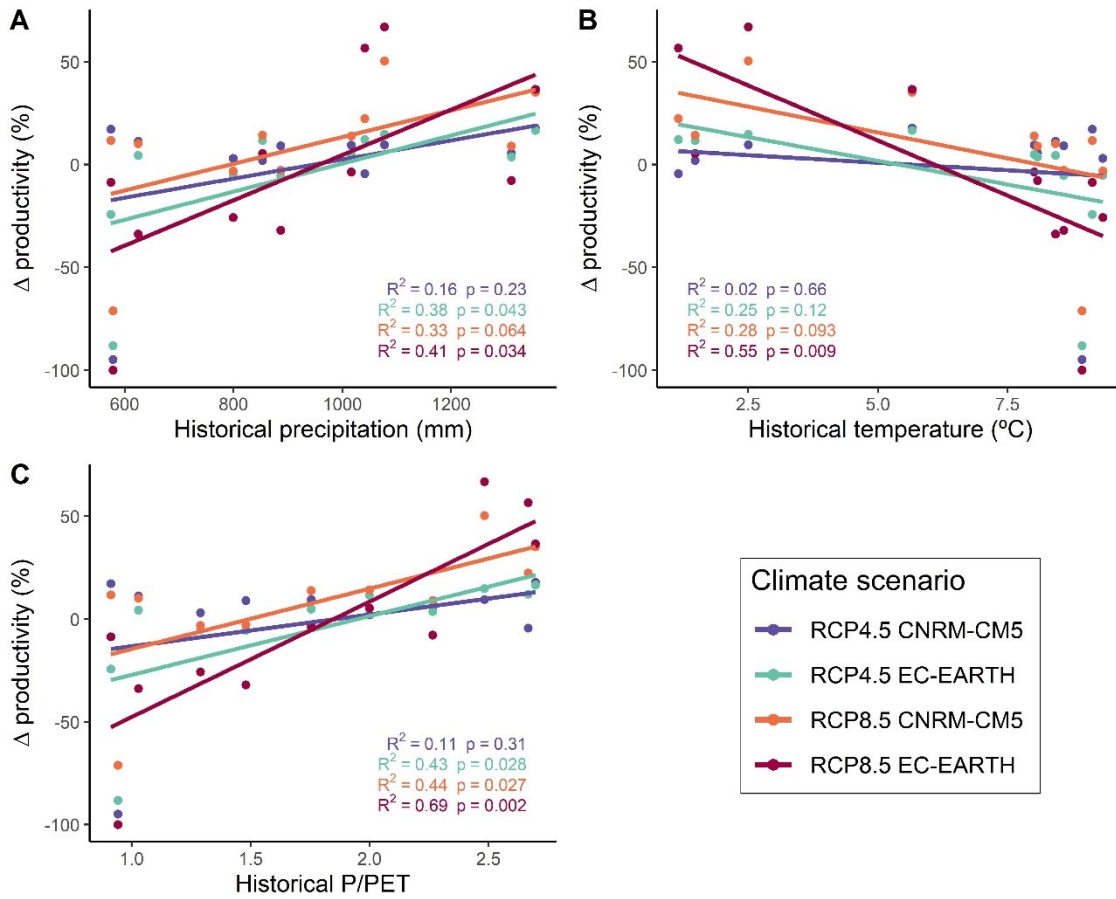
Fig. S2: Correlation between the future change in productivity, relative to baseline projections, and local temperature, precipitation and P/PET.
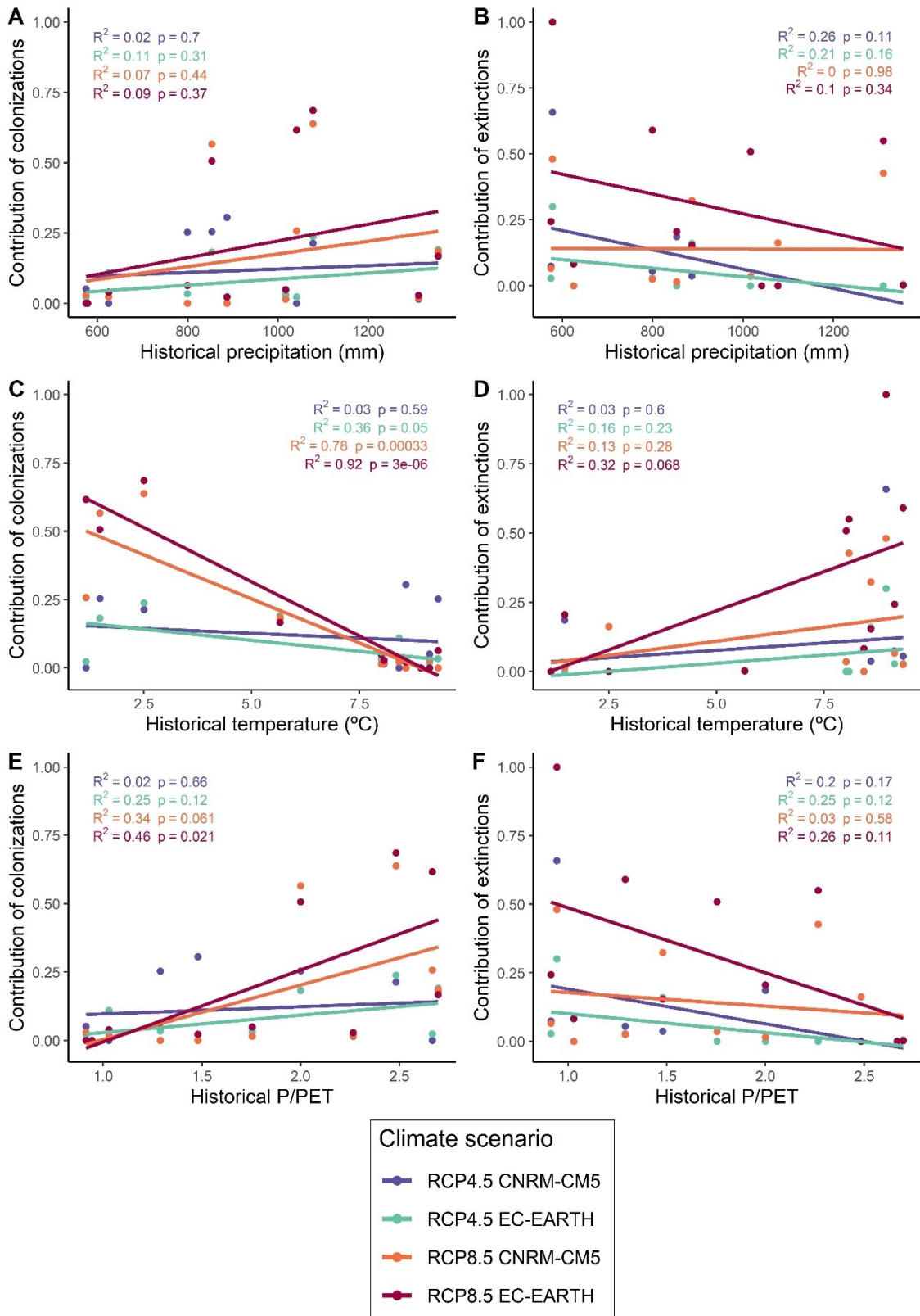
Fig. S3: Correlations between the relative contribution of colonizations and extinctions to the total future change in productivity, and local precipitation, temperature, and P/PET.

Appendix S1: FORCLIM description

14

15

16 FORCLIM v2.9.6 (Didion *et al.* 2009), is built under the classic scheme of forest gap models, and

17 is thus based on a small number of basic ecological assumptions (Shugart, 1984), i.e. (i) the

18 forest stand is abstracted as a composite of many small patches of land (800 m^2), each patch

19 having its own dynamics; (ii) patches are horizontally homogeneous, i.e. tree position within a

20 patch is not considered; (iii) the leaves of each tree are located in an indefinitely thin layer at the

21 top of the stem; and (iv) successional processes can be described on each of those patches

22 separately, i.e. there are no connections between patches. From these assumptions, the model

23 follows the standard approach of gap models: the establishment, growth, and mortality of trees

24 on the multiple forest patches are simulated, deriving stand properties at a larger spatial extent

25 by averaging the properties simulated at the patch scale, and considering abiotic and biotic

26 limitations to establishment and growth (specifically, growing degree-days, soil moisture and

27 nitrogen status as well as light availability at the height of the tree crown, i.e. the outcome of

28 inter- and intraspecific competition).

29   Trees are established with a diameter at breast height of 1.27 cm as a function of

30 species-specific responses to winter temperature, light availability at the forest floor, growing

31 degree-days and browsing pressure; principally, all species (from the species pool chosen) are

32 available for establishment, *i.e.* there is no dispersal limitation in the model. Growth (i.e., stem

33 diameter increment at breast height) is modeled using an empirical equation derived for

34 optimally growing trees (Moore, 1989). Actual tree growth is calculated by modifying the

35 optimum rate to the extent that abiotic or biotic conditions are limiting. Specifically, these are

36 growing degree-days, soil moisture and nitrogen status, crown length, as well as light

37 availability at the height of the tree crown, i.e. inter- and intraspecific competition and thus

38 changes in species composition. In the current version, the model concentrates on competition

39 for light. Other resources, such as nitrogen and soil water, are affecting species performance but

40 they are constant at the site level, ie. not impacted by trees. To calculate weather-dependent

41 factors, mean monthly temperatures and monthly precipitation sums are used. The model is

42 further constrained by soil water holding capacity. From diameter at breast height, the sizes of

43 other tree compartments (e.g., foliage, roots) and total aboveground biomass are estimated using

44 allometric equations, which partly respond to changing competition and thus to diversity

45 changes (Bugmann, 1994; Didion, Kupferschmid, Zingg, Fahse, & Bugmann, 2009). Species

46 coexistence in forest gap models is brought about by two main mechanisms: first, trade-offs

47 evident from the life-history strategies, such as high rates of colonization often being tied to low

48 shade tolerance, or a typically short lifespan of early successional, fast-growing trees; and

second, the fact that cyclical succession is occurring on each individual patch, such that species with different properties are able to dominate during different parts of the cycle. Tree mortality is stochastic and has a background and a growth-related component. The former depends on species maximum longevity, whereas the latter is an integral proxy for stress conditions, i.e. tree vigor; since competition affects individual tree growth, it also has an indirect effect on the simulated mortality rates via growth-related mortality. Species parameters are provided in Table S2.

FORCLIM has evolved from a simulator of forests in the Swiss Alps to a general model that is applicable to temperate forests of central Europe, eastern North America, the Pacific Northwest of the US, northeastern China and the Colorado Front Range of the Rocky Mountains (Bugmann, 2001; Bugmann & Cramer, 1998; Bugmann & Fischlin, 1996; Bugmann & Solomon, 2000; Shao, Bugmann, & Yan, 2001). To our knowledge FORCLIM is the only forest succession model that has been demonstrated to be applicable "out of the box", *i.e.* without any re-parameterization, across widely different climates while still keeping a species resolution, which supports its generality.

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