RESEARCH PAPER

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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Abstract

Aim: Climate change impacts forest functioning and services through two inter-related effects. First, it impacts tree growth, with effects, for example, on biomass production. Second, climate change also reshuffles community composition, with further effects on forest functioning. However, the relative importance of these two effects has rarely been studied. Here, we developed a new modelling approach to investigate these relative importances for forest productivity.

Location: Eleven forest sites in central Europe.

Time period: Historical (1990) and end-of-21st-century climate-like conditions. We simulated 2,000 years of forest dynamics for each set of conditions.

Major taxa studied: Twenty-five common 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 that shapes potential tree species pools, the biotic filtering that shapes realized communities and the functioning of these realized communities in the long-term.

Results: Under an average temperature increase (relative to 1901–1990) of between 1.5 and 1.7 °C, changes in simulated forest productivity were caused mostly by changes in the growth of persisting tree species. With an average temperature increase of 3.6–4.0 °C, changes in simulated productivity at sites that currently have a mild climate were again caused predominantly by changes in tree species growth. However, at the warmest and coldest sites, changes in productivity were related mostly to shifts in species composition. In general, at the coldest sites, forest productivity is likely to be enhanced by climate change, whereas at the warmest sites the productivity might increase or decrease depending on the future precipitation regime.

Main conclusions: A combination of two complementary modelling approaches that address questions at the interface between biogeography, community ecology and ecosystem functioning, reveals that climate change-driven community reshuffling in the long term might be crucially important for ecosystem functioning.

1 | INTRODUCTION

Forests cover about a third of the land surface of the world, harbour most of the terrestrial biodiversity and represent an important carbon sink. They also play a pivotal role in climate regulation (Chapin, Randerson, McGuire, Foley, & Field, 2008) and provide other important ecosystem services (Kumar, 2010). However, climate change is affecting many of these forest ecosystem services, such as biomass production and carbon sequestration (Kirilenko & Sedjo, 2007), with this impact likely to be stronger in the future (Pachauri & Meyer, 2014). The influence of climate change on forests can be divided into two inter-related effects (Adler, Leiker, & Levine, 2009; Morin et al., 2018). Climate change affects forests by altering tree physiological rates (Sack & Grubb, 2001), such as growth (Silva & Anand, 2013), phenology (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007) or survival (Allen, Breshears, & McDowell, 2015), which has direct consequences for ecosystem functioning (e.g., biomass productivity). Climate change also affects forest functioning when the pressure of climate change on the growth of trees is strong enough to drive local extinction and colonization of species, as seen in natural, experimental and simulated forests (Liang et al., 2016; Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011; Paquette & Messier, 2011). Understanding the relative importance of these two effects would greatly help to improve projections of the impact of climate change on forest functioning, and on key ecosystem services, such as carbon uptake and biomass provision. However, the two effects have usually been studied separately, and very little is known about their relative importance for forest productivity under different climatic conditions (but see Coomes et al., 2014; Zhang, Niinemets, Sheffield, & Lichstein, 2018).

The effects of climate change on species composition might amplify (Zhang et al., 2018) or counteract (Fauset et al., 2012) the effects of climate change on tree growth. Furthermore, recent studies found that climate change effects on species composition might be greater than previously expected. García-Valdés, Bugmann, and Morin (2018) found that when tree species go extinct in an order imposed by climate change, reductions in the projected productivity of some forests were greater than we would expect from the single effect of random species loss. Thus, most of the biodiversity–ecosystem functioning studies (e.g., Liang et al., 2016) might underestimate the extent of biodiversity loss caused by climate change. Likewise, Morin et al. (2018) found that warmer and drier conditions might strongly affect biodiversity–ecosystem functioning relationships in forests experiencing the harshest climatic conditions, illustrating the importance of understanding changes in species composition for forest functioning.

These findings suggest that the local conditions and the magnitude of the change in climate might interact to determine the relative importance of tree physiological changes and species reshuffling for forest functioning.

Nonetheless, disentangling these two effects of climate change on ecosystem functioning is difficult. Although estimating the effects of climate change on tree growth could be relatively straightforward, through experiments or long-term observations (Hasenauer, Nemani, Schadauer, & Running,1999), estimating the effects on species composition is more complicated (Barry etal., 2019). Climate change effects species composition are due to several mechanisms. First, climatic filtering determines whether the local environmental conditions are suitable for a species. Second, biotic filtering occurs when interactions among potentially co-occurring species lead to the exclusion of some species. Climatic filtering is commonly studied at large spatial scales, such as regions or continents (Thuiller, Lavorel, Araújo, Sykes, & Prentice,2005), whereas species interactions are mostly studied at the local scale (Mayfield & Levine,2010). We therefore studied both processes, each at the relevant spatial scale, to quantify their effects on the future composition of forest communities.

Species distribution models (SDMs) typically work by correlating the recorded presences of individual species with environmental variables (Gotelli et al., 2009) and can be used to simulate climatic filtering. Although this approach carries some caveats (see Dormann et al., 2012 and Discussion section), SDMs are particularly robust for measuring the environmental tolerances of species that are broadly distributed (Early & Sax, 2014; Estrada, Delgado, Arroyo, Traba, & Morales, 2016), as are the species considered here. Forest succession models (FSMs), also called gap models (Bugmann, 2001), can be used to simulate forest community dynamics from a few hundred square metres up to the landscape scale), given a specific starting species pool (Chauvet, Kunstler, Roy, & Morin, 2017). FSMs are based on a minimum number of ecological assumptions (Botkin, Janak, & Wallis, 1972) and rely on the ecophysiological responses of trees to abiotic factors (including climate) and biotic factors (i.e., inter and intraspecific interactions) to simulate individual tree growth and succession dynamics over time (Bugmann, 2001). Forest succession models can simulate both the biotic filtering of species, by forecasting the realized tree community (i.e., at long-term equilibrium), and the effects of climate change on tree growth.

In this study, we coupled SDMs and FSMs to assess the relative importance of the effects of climate change on tree growth and species composition for the productivity of central European forests. Previous studies have coupled SDM-like modules with a process-based component simulating key processes, such as dispersal

and demography (e.g., range dynamic models; Sarmento Cabral et al., 2013), and/or competition (e.g., the hybrid FATE-H model that considers only plant functional types; Boulangeat, Georges, & Thuiller, 2014). At a larger spatial scale, Meier, Lischke, Schmatz, and Zimmermann (2012) coupled an SDM with a FSM to predict the range-shift rates of several tree species under climate change, while accounting for interspecific competition. However, to our knowledge, no previous work has compared how climate change will affect forest productivity through both altered species growth and composition, by coupling the projections of SDMs with those of FSMs. Our study is thus among the first to take advantage of the complementarity of the two types of models to address questions at the interface between biogeography, community ecology and ecosystem functioning. Specifically, we used 11 forest sites as an example and aimed at answering the following questions. First, how will climate change affect long-term forest aboveground biomass productivity in European temperate forests? Second, what will be the relative contribution of the changes in tree growth and of the shifts in species composition to such changes in forest productivity? Third, how will local climatic conditions and the magnitude of climate change influence the patterns found in answer to the first two questions?

2 | MATERIAL AND METHODS

2.1 | Overview

In summary, we simulated the productivity of 11 forest sites across central Europe under historical-like climate conditions (years 1901–1990, i.e., baseline projection), and future-like (years 2071–2100, i.e., future projections) climate conditions, given four climate change projections. To do so, we first used SDMs (Figure 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 2,000 years of forest succession (i.e., biotic filtering), leading to realized forest communities. Once each community had reached equilibrium (after 1,000 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 to the differences in productivity between the baseline and the future projections. We explain all these steps in detail below.
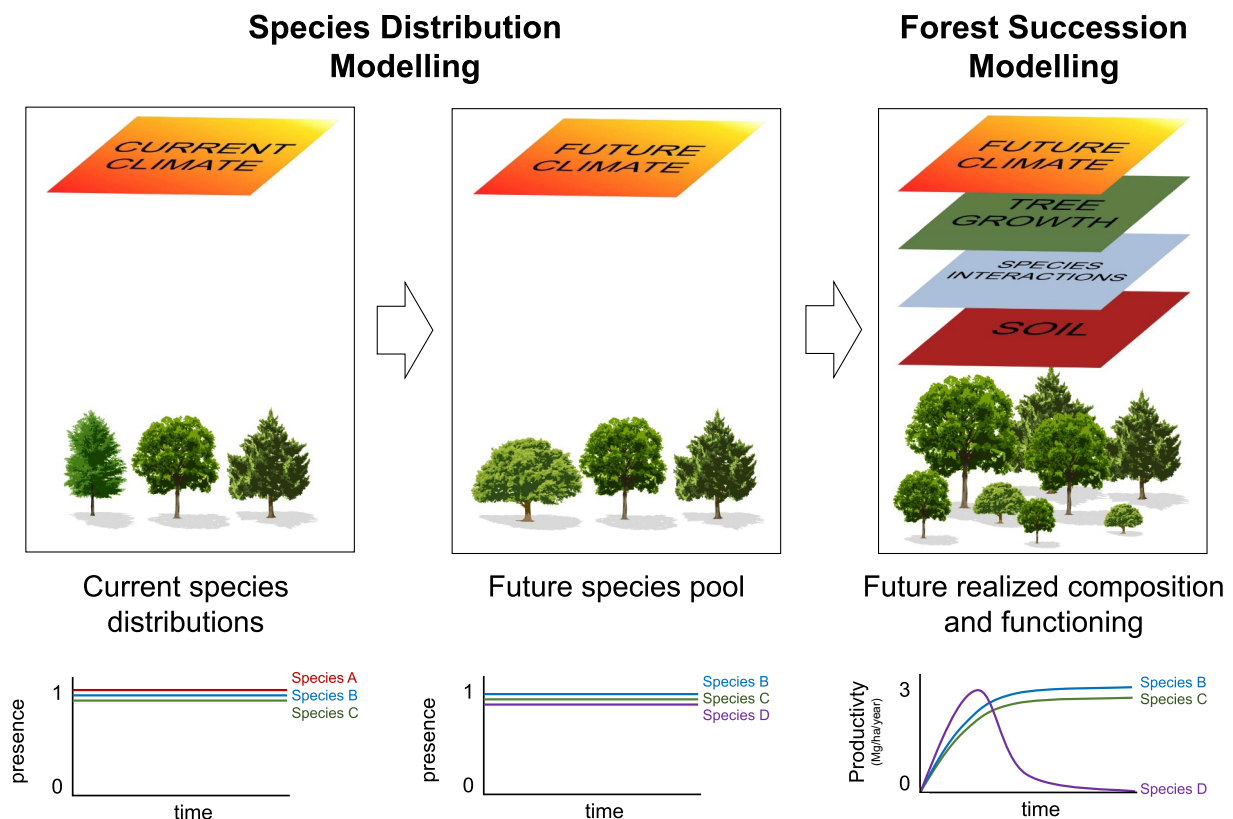
FIGURE 1 Coupling of models used in this study. First, climatic suitabilities for 25 species were projected for each site and climate projection using species distribution models. These 25 suitabilities were then aggregated to build potential species pools. To include the variability inherent to the suitabilities and to avoid choosing arbitrary thresholds, we built 100 species pools for each site and climate projection (i.e., if a species had a suitability of .6 it was included in 60 of the 100 species pools). Finally, succession dynamics (including tree growth) in the long term were simulated using a forest succession model. Figure modified from García-Valdés and Morales-Castilla (2016)

2.2 | Study sites

The geographical background from which species distributions and climatic data were drawn for SDMs comprises Europe from 10°9′23″ W 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; Supporting Information Table S1). These sites cover a broad range of temperature and precipitation conditions (Supporting Information 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).

2.3 | Climate data for species distribution models

We used climate data over the period 1961–1990 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 (> 5 °C), mean temperature of the coldest month, annual precipitation and a summer moisture index (potential evapotranspiration divided by precipitation). These variables have been used previously to model plants and vertebrates in Europe and they reflect two primary properties of climate (energy and water) that have been shown to affect species distributions (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011; Morrison, Estrada, & Early, 2018). We used averaged annual values of these climatic variables for the period 1961–1990 for calibration and for the baseline projection. For future climatic conditions, we used averaged simulated data of the variables for the period 2071–2100 given four climate change projections.

2.4 | Climate data for the forest succession model

We simulated 2,000 years of forest dynamics with FORCLIM, given a historical-like climate (baseline projection) and four future-like climate change projections (RCP4.5 and RCP8.5 and GCMs CNRM-CM5 and EC-EARTH, downscaled using RCA4). To do so, we needed a generic 2,000-year-long time series of monthly temperature (Tmonthly) and precipitation (Pmonthly) that incorporated inter-annual variability. For this purpose, we used the climate simulator embedded in FORCLIM, which uses the monthly mean and standard deviation of Tmonthly and Pmonthly, and the correlation between them (Bugmann, 1994). For the historical-like climate, we generated 2,000 years of data directly using

the mean, standard deviation and correlation of Tmonthly and Pmonthly (from Bugmann, 1994), which was calculated from data from the 1901–1990 period from the Swiss Meteorological Agency (Bantle, 1989). Such data have been used previously to calibrate and validate forest productivity simulated by FORCLIM in our study sites. These data were analogous to, but not the same as the climatic time series from the period 1901–1990 (which we could not use because the time series was not long enough).

To simulate future climate conditions, we could not use data from GCM climate projections directly, because these models use different historical data for bias correction from the data we used (1901–1990 data from Bugmann, 1994). To circumvent this problem, we calculated a climatic anomaly for each climate projection (see Morin & Chuine, 2005). For each climate projection, we calculated the differences in Tmonthly and Pmonthly between the future climate (years 2071–2100), and the current climate (years 2006–2016). These anomalies quantify how much Tmonthly and Pmonthly would vary from baseline values under each climate projection. We added these anomalies to the means of the historical climate data from Bugmann (1994) and, for each climate projection, we generated 2,000 years of climate data. All climate time series thus contained no trend. In the projected future climate time series, the estimated changes in temperature depended mostly on the RCPs, whereas the estimated changes in precipitation depended mostly on the GCMs. The differences between the four climate projections and historical climate (from Bugmann, 1994) were: (a) RCP4.5-CNRM-CM5, moderately warmer with more precipitation; (b) RCP4.5-EC-EARTH, moderately warmer with similar precipitation; (c) RCP8.5-CNRM-CM5, much warmer with more precipitation; and (d) RCP8.5-EC-EARTH, much warmer with similar precipitation. The stress experienced by trees increases sequentially under projections a–d (for specifics, see Supporting Information Tables S1 and S2).

2.5 | Species data and the species distribution models

We considered 25 of the most common tree species in this region (Supporting Information Table S3). We used presence data from the Atlas Florae Europaeae (AFE; Jalas & Suominen, 1972–1994; Jalas, Suominen, & Lampinen, 1996). When a species was not recorded in the Atlas, we used distribution data from EUFORGEN (http://www. euforgen.org/species/; see Supporting Information Table S4). The AFE presence data were from 50 km × 50 km universal transverse mercator (UTM) grid cells, and EUFORGEN presence data were range maps. We transformed EUFORGEN range maps into c. 50 km UTM cells to run the models. We calculated the average climatic conditions in each 50 km grid cell from the climate grid at 10' resolution.

The relationships between climatic variables and species distributions were modelled using seven SDM techniques: generalized linear models (GLM), generalized additive models (GAM), generalized boosting models (GBM), classification tree analysis (CTA),

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artificial neural networks (ANN), flexible discriminant analysis (FDA) and surface range envelope (SRE). Models were calibrated for the period 1961–1990 using an 80% random sample of the initial data and cross-validated against the remaining 20% of the data, using the area under the receiver operator characteristic curve (AUC) and the true skill statistic (TSS). The SDMs were calculated 10 times, each time selecting a different 80 and 20% of the data for calibration and evaluation. Results from each SDM technique were included in an ensemble model if the AUC from cross-validation was > .8 and TSS was > .6 (similar to Araújo et al., 2011). However, the final ensemble model for each species was calibrated using 100% of the species distribution data to maximize the amount of data available for projections. For each species, the ensemble was calculated using the mean probability of occurrence, weighted proportional to the AUC and TSS obtained with the evaluation data. Ensemble models calibrated at 50 km resolution were downscaled to obtain suitability in each 10′ grid cell. We projected ensemble models to future climatic conditions at 10′ resolution for the four future climate projections (the combination of GCMs and RCPs). This approach follows methods used by Araújo et al. (2011), albeit using more recently constructed climate data. All models were run in R (R Core Team, 2014) using default options of the *biomod2* package (Thuiller, Georges, & Engler, 2013).

2.6 | Forecasting of potential tree species pool in each site

For each site and climate projection, we used the SDM-predicted suitability for each species to build a local species pool. To use the continuous suitability projections (rather than using an arbitrary threshold to distinguish suitable or unsuitable habitat), we built 100 potential species pools for each site and climate projection and included each species in proportion to its climate suitability. For example, if the suitability of a given species in a given site and for a given climate projection was .6, this species would be included in 60 (randomly chosen) of the 100 species pools for that site and climate projection.

2.7 | Forest succession model

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

In FORCLIM, the establishment, growth and mortality of trees are simulated using the abiotic and biotic conditions in small independent patches (800 m^2 in this study). Tree location in the patch is not estimated, and all trees compete for light. The properties of several patches are aggregated to calculate forest properties across larger extents (Bugmann, 2001; Shugart, 1984). Tree establishment is modelled as a stochastic process, depending on species-specific responses to light availability at the forest floor, growing degree-days, drought occurrence and the minimum and maximum winter temperature. Tree growth is measured as the stem diameter increment, which depends on the optimum growth rate of each species, abiotic conditions (temperature, drought and soil nitrogen) and biotic conditions (light availability, i.e., the level of shading by competitor trees). Therefore, although competition for water and nitrogen between individuals is not taken into account explicitly in the model, soil water and nitrogen content constrain tree establishment and growth differently between species in a given site, which, in turn, affects competition between trees (Supporting Information Appendix S1). Competition for light is modelled by calculating the amount of available light for each individual tree depending on tree height and the crown sizes of competing trees. FORCLIM also incorporates a shade tolerance parameter (Ellenberg, 1991), defining the classic trade-off between growth in full light and survival in shade. Tree mortality has two components: (a) a "background" mortality, which is constant across time and depends on the maximum longevity of the species; and (b) growth-related mortality, reflecting the effect of stressful conditions on tree survival (i.e., trees with decreased vigour are more likely to die). The species parameters for FORCLIM can be found in the Supporting Information (Table S3), and more details about the model can be found in the Supporting Information (Appendix S1) and in the papers by Bugmann (1996) and Didion, Kupferschmid, Zingg, Fahse, and Bugmann (2009).

2.8 | Simulations of forest succession dynamics

For each set of climate conditions (historical and future), we simulated 2,000 years of forest dynamics with FORCLIM. This allowed us to assess the relative contribution of tree growth and species composition to climate-driven changes in productivity between the historical and future periods. However, this approach means that the simulations should not be taken as predictions of forest composition and productivity for the end of the 21st century, because the effect of species colonization, for instance, is not realistic for short-term projections.

After having checked that FORCLIM simulations conducted in the same conditions (site, climate and species pool) yielded very similar results after 2,000 years, we performed one FORCLIM simulation for each site (n = 11), each set of climate conditions (historical and future, n = 5) and each species pool (n = 100). Each simulation included 100 patches of 800 m^2 each, corresponding to an 8 ha forest. FORCLIM simulations started from bare ground to avoid the influence of starting conditions. For each FORCLIM simulation,

only the species in the species pool at the site (determined by the SDMs) were allowed to colonize the patches. The simulations were run for 2,000 years to allow forests to reach equilibrium in total biomass and composition, thus avoiding transient states. We extracted the productivity and composition from simulations after 1,000 years, to allow the system to reach equilibrium. To avoid temporal autocorrelation, we extracted values from the first year of each century after the year 1,000 (i.e., the years 1,100, 1,200, ... 2000; cf. Morin et al., 2011) and averaged the results from these sampled years across patches. For the calculation of the realized community composition, we considered that a species was present in a community only if its simulated biomass reached 1 Mg/ha.

2.9 | Quantification of effects of climate change on growth and composition

To quantify the effects of climate change on forest productivity mediated by changes in tree growth, we calculated the proportion of change in productivity in each site that was produced by species found in both present and future climatic conditions. To quantify the effects of climate change on forest productivity mediated by a shift in species composition, we calculated the productivity loss caused by species extinction and the productivity gained by species colonization. The relative importance of colonization and extinction was calculated by dividing the change in productivity caused by either colonization or extinction by the sum of changes (in absolute values) in productivity.

2.10 | Statistical analyses

To test whether the future projected change in forest productivity varied across an environmental gradient, we fitted linear regressions between forest productivity in each site and its mean annual temperature (MAT), total annual precipitation (TAP) and precipitation relative to potential evapotranspiration (P/PET). Climate data were obtained from Bugmann (1994) and were calculated from data of the 1901–1990 period from the Swiss Meteorological Agency (Bantle, 1989). We also fitted linear regressions between the relative importance of colonization and extinction for productivity and the above climatic variables. Finally, we fitted a linear regression between the future change in productivity and future change in realized species richness at each site.

3 | RESULTS

3.1 | Effects of climate change on potential species pools and richness (output from SDMs)

With most climate change projections and in most sites, the climatic suitability for the studied species increased (Figure 2a–c). However,

under extreme warming (RCP8.5) and in the driest conditions (EC-EARTH model; Figure 2d), the potential species richness increased in the coldest sites (Adelboden, Bever, Davos and Grande Dixence), but remained the same or decreased in the warmest sites (Basel, Bern, Cottbus, Huttwil, Schaffhausen and Sion).

3.2 | Effects of climate change on realized species richness

Under historical climatic conditions, simulated realized species richness varied from three (out of 25) in Grande Dixence and Davos to 11 in Huttwil and Bern (Supporting Information Figure S1b). Under most climate change projections, the number of realized species increased in most of the sites (Figure 2, lower panels). However, under the extreme RCP8.5-EC-EARTH projection, the realized species richness decreased in the warmest sites (Figure 2h).

3.3 | Effects of climate change on forest productivity

The impact of climate change on forest productivity varied greatly along the climatic gradient and with different intensity depending on the climate projection (Figure 3a–d). The greatest impact occurred in Sion, the warmest and second driest site, where productivity decreased by between −67.6% and −90.7%. However, with a projected increase in precipitation > 10.0% (CNRM-CM5 model, see Supporting Information Table S1), forest productivity increased in all sites (Figure 3a,c), except Grande Dixence, Basel and Sion. With a very weak precipitation change (EC-EARTH model, see Supporting Information Table S1), forest productivity increased in the coldest sites and decreased in most of the warmest sites (Figure 3b,d).

TAP was positively correlated with the change in productivity under two climate change projections (p = .043 with RCP4.5-EC-EARTH and p = .034 with RCP8.5-EC-EARTH; Supporting Information Figure S2a). Temperature was negatively correlated with productivity change under one projection (p = .009 with RCP8.5-EC-EARTH; Supporting Information Figure S2b). The P/PET ratio was positively correlated with the change in productivity under three projections (p = .028 with RCP4.5-EC-EARTH, p = .027 with RCP8.5-CNRM-CM5 and p = .002 with RCP8.5-EC-EARTH; Supporting Information Figure S2c).

3.4 | The relative importance of the effects of growth and composition on forest productivity

With the climate scenario RCP4.5, which projected a moderate increase in local temperature relative to the historical period, simulated changes in productivity were driven almost exclusively by the effects
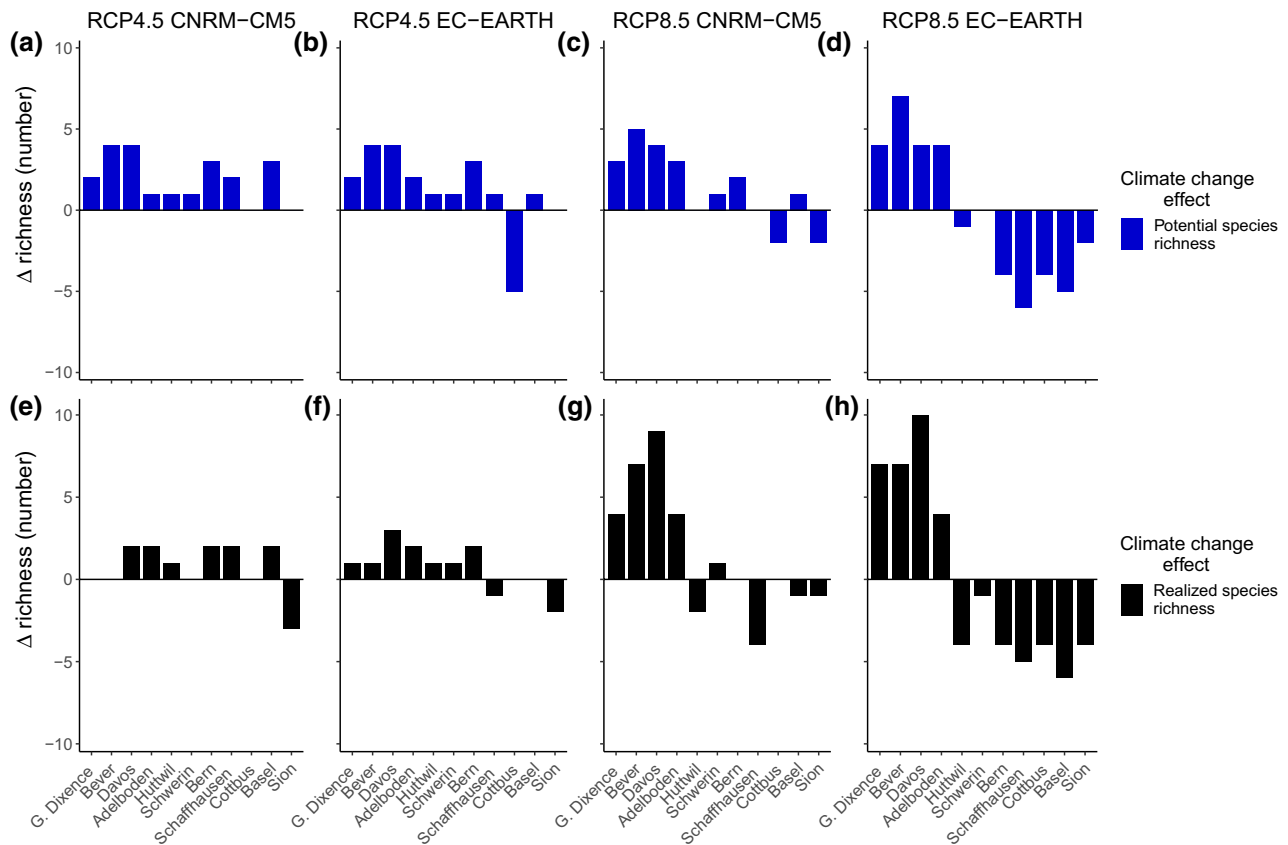
FIGURE 2 Effect of climate change on the number of potentially occurring species, projected with the species distribution models, assuming a threshold in suitability of 50% (upper panels), and on the number of realized species, simulated with the forest succession model, assuming that only species with ≥ 1 Mg/ha 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 mean annual temperature. Sites on the left have the lowest MAT and sites on the right the highest MAT.

of climate change on the tree growth of surviving species (Figures 3e,f and 4). The rise in MAT was, on average, between +1.5 [ranging from +1.1 to +2.0] °C and +1.7 [+1.5, +2.2] °C (Supporting Information Table S1), and the average rise in winter temperature was between +2.0 [+1.5, +2.6] °C and +2.7 [+2.1, +3.1] °C (Supporting Information Table S2). With this temperature increase, there was a positive correlation between the increase in productivity and the increase in species richness under the two GCMs (p = .003; Figure 5), but the change in species richness did not contribute greatly to changes in productivity (Figure 3e,f). With the climate scenario RCP8.5, which projected a greater increase in local temperature (Figure 3g,h), there was also a positive relationship between the increase in realized species richness and the increase in productivity (p =.054 and R^2 = .35 withthe CNRM-CM5, and p = .006 and R^2 = .58 with the EC-EARTH GCM; Figure 5). Under this more extreme temperature increase, changes in species richness (Figure 5) and community composition did contribute greatly to the changes in productivity (Figures 3g,h and 4). The increase in MAT ranged from +3.6 [+2.8, +4.5] °C to +4.0 [+2.9, +4.9] °C (Supporting Information Table S1), and the increase in winter temperature ranged from +3.8 [+2.9, +5.5] °C to +4.5 [+4.1, +5.6] °C (Supporting Information Table S2).

The importance of community composition effects varied across the study sites (Figure 3e–h). Their importance was related to the

local temperature, which was negatively correlated with the importance of colonization under three climate projections (p ≤ .05; Supporting Information Figure S3c). The importance of the composition effects was also correlated with P/PET under one projection (p = .021; Supporting Information Figure S3e) and was not correlated with precipitation (Supporting Information Figure S3a,b).

4 | DISCUSSION

Our simulations of forests located across a large climate gradient in central Europe showed that future changes in forest productivity might depend strongly on local temperature, P/PET and precipitation (Supporting Information Figure S2; Allen et al., 2015). Simulated forest productivity increased at high elevations, which is a result that we expect to be similar to other sites at high latitudes (Füssel, Kristensen, Jol, Marx, & Hildén, 2017), where cold temperature currently limits tree establishment, growth and survival (Nemani et al., 2003). Climate change created warmer winters in these sites (Supporting Information Table S2), which allowed new species to establish by decreasing the constraints on establishment (as shown in empirical studies, e.g., Conedera, Wohlgemuth, Tanadini, & Pezzatti, 2018). Climate change also produced longer growing periods that increased the productivity
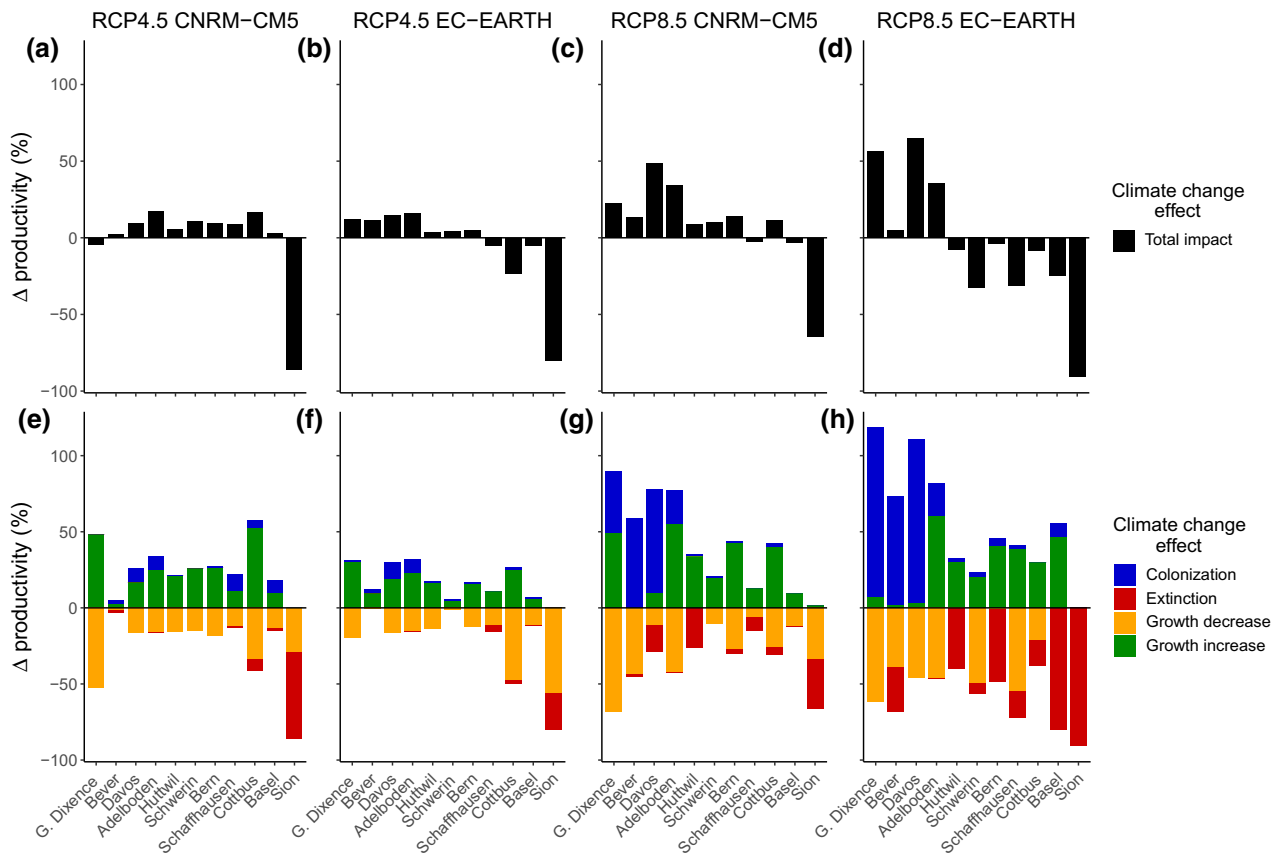
FIGURE 3 Effect of climate change on each forest annual aboveground biomass productivity (in megagrams per hectare per year), relative to a baseline (i.e., historical climate) projection. Study sites are ranked from the coldest (left) to the warmest (right). Upper panels show the total effect, and lower panels show the effect of colonizations, extinctions and growth decrease or increase on forest productivity. To assess community composition, we considered that a species was present in a site when its biomass was ≥ 1 Mg/ha

of the species currently present (consistent with recently observed trends, e.g., Boisvenue & Running, 2006). On the contrary, in the lowlands, simulated productivity decreased when climate change led to an increase in drought stress (mostly by increasing the temperature and not changing the precipitation regime), which became a major constraint for tree growth and survival (as observed also by Carnicer et al., 2011 and Reyer, 2015). However, in a projection of climate change with increased precipitation and only a moderate increase in temperature, productivity increased in the lowlands (Figure 3a) because drought stress did not increase, while winter temperature was lower and the growing season was longer (Supporting Information Table S2). The increase of temperature with a decrease in precipitation is projected to occur in the southern half of Europe, whereas the milder temperature due to climate change is typically predicted for higher latitudes (Füssel et al., 2017).

4.1 | Shifts in tree species richness and composition drive productivity in the harshest climates

We found that under moderate warming, changes in projected forest productivity were caused almost exclusively by the effects of

climate change on tree growth (Figure 3e,f; see Coomes et al., 2014). On the contrary, under extreme warming and in locations at both ends of the temperature gradient, changes in productivity were driven mostly by changes in species composition (Figure 3g,h). The increasing correlation under the harshest climate projections (RCP8.5-CNRM-CM5 and RCP8.5-EC-EARTH) between the relative importance of simulated colonization (i.e., a measure of the composition effect) and both local temperature and P/PET (Supporting Information Figure S3c,e) also shows the strong role of species composition in harsh climatic conditions. This finding matches with empirical evidence of the role of tree richness in forest productivity along the latitudinal gradient in Europe (Jucker et al., 2016). We also observed a positive correlation between the change in species richness and in productivity ($p \leq .05$ across all climate projections; Figure 5). This supports previous studies, which found that forest productivity is especially sensitive to species loss in the harshest climates (see García-Valdés et al., 2018; Morin et al., 2018).

The link between forest species richness and ecosystem productivity (e.g., Liang et al., 2016; Paquette & Messier, 2011) is usually attributed to a greater niche partitioning in more diverse communities (Loreau et al., 2001; Morin et al., 2011). In our simulated forests in the coldest sites, the effects of species richness
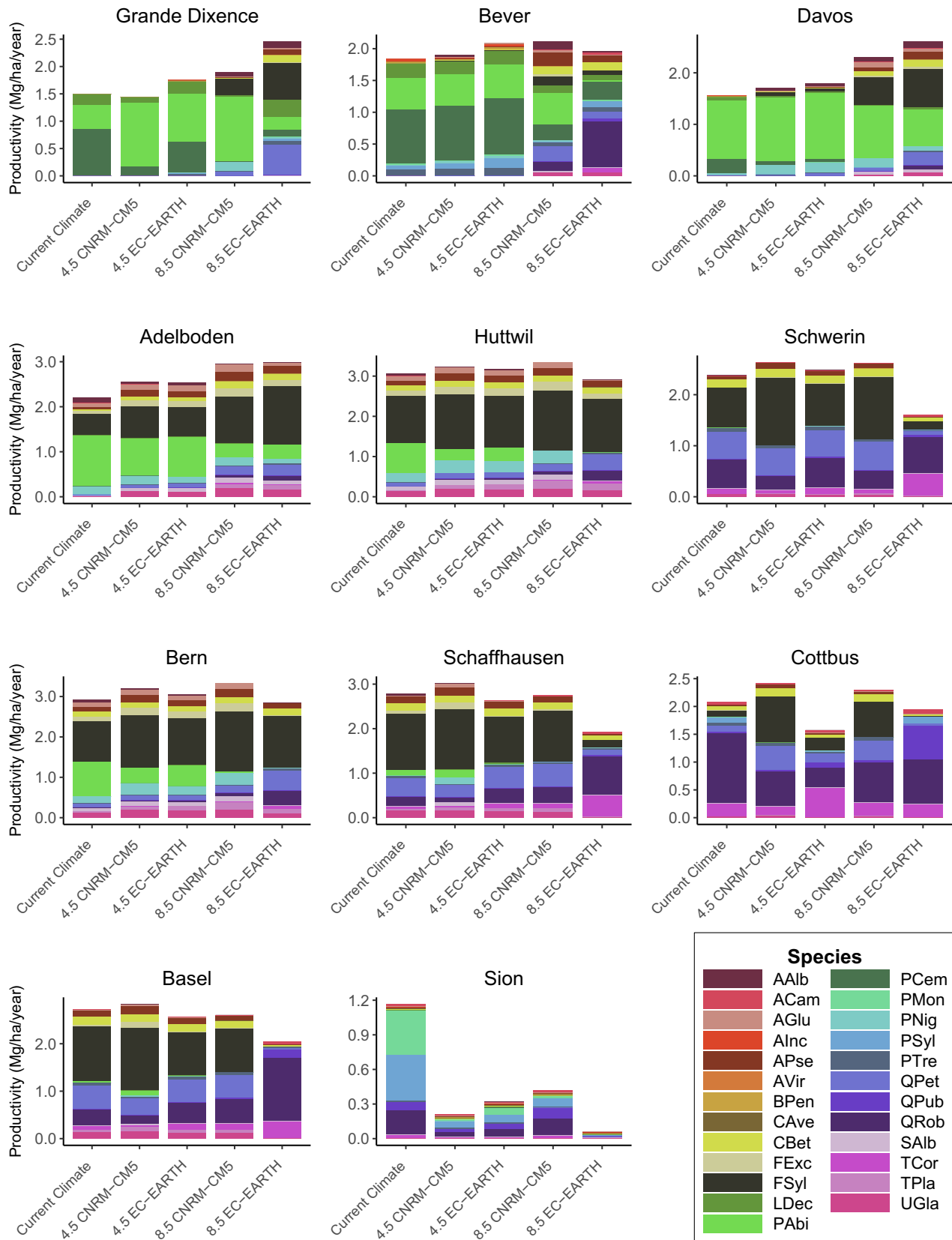
FIGURE 4 Species productivity (in megagrams per hectare per year) at each site, given a stable climate and four climate change projections. The species codes are as follows: AAlb = *Abies alba*; ACam = *Acer campestre*; AGlu = *Alnus glutinosa*; AInc = *Alnus incana*; APse = *Acer pseudoplatanus*; AVir = *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 = *Populus tremula*; QPet = *Quercus petraea*; QPub = *Quercus pubescens*; QRob = *Quercus robur*; SAlb = *Salix alba*; TCor = *Tilia cordata*; TPla = *Tilia platyphyllos*; UGla = *Ulmus glabra*
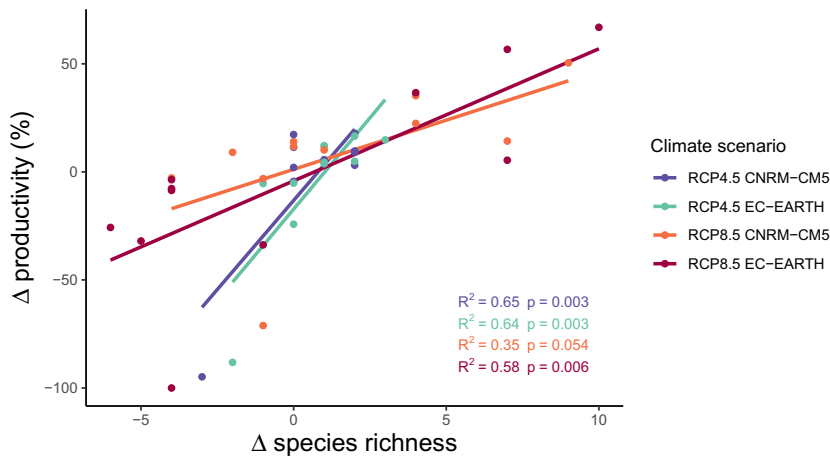
FIGURE 5 Future change in realized species richness versus future change in forest productivity (expressed as a percentage) under different climate change projections, relative to baseline projections using historical climate

and composition were strengthened because climate change allowed new species to colonize and be productive (Figure3; Supporting Information FigureS3; Coomes etal., 2014). On the contrary, at the warmest and driest sites, climate change caused the extinction of key species (Reyer,2015), which reduced species richness and productivity.

The observed importance of changes in community composition in cold sites and in warm-dry sites in our study (see also Anderegg & HilleRisLambers, 2019; Morin et al., 2018) is consistent with an extension of the stress gradient hypothesis (SGH; Bertness & Callaway, 1994; Crain & Bertness, 2006). This hypothesis states that the frequency of interspecific competitive interactions decreases in intensity with increasing abiotic stress. In our study sites, it is likely that species extinctions occurred when the species were at the boundaries of their suitability before climate change. At sites with intermediate temperature (mild conditions), such species were probably suppressed by competition before climate change and did not contribute significantly to the total productivity of the community. Hence, their extinction under climate change did not greatly change the total productivity of the site. In contrast, at both ends of the temperature gradient, harsh climatic conditions reduced competitive interactions. This means that in the absence of climate change, species that were close to their climatic limits could still contribute substantially to the total productivity of the site, since they faced weak competition. Hence, their extinction due to climate change substantially affected the total productivity of the community. With colonizations, we observed a similar effect. In the sites with mild climate conditions, colonizing species probably remained close to their climatic limits (because climate change had transformed the sites from unsuitable to suitable) and they were unlikely to become dominant, thus probably did not contribute substantially to the total productivity. This occurred because colonizing species still had to deal with biotic interactions (McGill, Enquist, Weiher, & Westoby, 2006) and were not strong competitors in these conditions (low suitability and strong competition). In climatically harsh sites, colonizing species could become dominant immediately, because they were less likely to encounter strong competitors.

4.2 | Increased sensitivity of warmest forests to climate change

Our simulations suggested that rapid and steep changes might arise in forest functioning (i.e., productivity) because of climate change. In the warmest site, an almost complete elimination of the forest cover was projected in the event of the most severe climate change projection (Figure 3h). In this projection, an increase in drought stress could drive the forest system to a change in community type (e.g., from forest to scrublands or meadows). García-Valdés et al. (2018) hypothesized such drastic changes in forest functioning when simulating a large number of species extinctions. Here, using a realistic projection of the change in composition, we confirmed that such a drastic change could indeed occur in one of the study sites.

4.3 | Limitations of the approach

To our knowledge, this is the first study to couple models at complementary spatial and temporal scales (SDMs and FSMs) to quantify the relative importance of changes in growth and composition in mediating the effects of climate change on forest productivity. Although these simulations compared climates that are only 80 years apart (from now to the end of the century), they mimic long-term dynamics in order to compare mature forests. This means that simulations do not consider transient processes (e.g., disturbance, management or brief extreme climatic events). Results should thus not be considered as short-term predictions, but instead as estimates of the importance of different effects of climate change on forest functioning.

Our approach carries other limitations. First, we used correlative SDMs that entail caveats (García-Valdés, Zavala, Araújo, & Purves, 2013; Pearson & Dawson, 2003). However, correlative SDMs work well for widespread species, such as those studied here (Early & Sax, 2014), and process-based SDMs (e.g., Chuine & Beaubien, 2001) could not be used for so many species. Second, our simulation design, relying on 2,000 years of simulation using both historical and future conditions, allows the relative contributions of changes in tree growth and species composition to be assessed and, notably,

highlights the possible strength of compositional effects on changing productivity. However, these simulations cannot be used directly to infer forest composition and productivity at the end of the 21st century. Local species extinction by 2100 might be well reproduced by our design, because exposure to the new climatic conditions might directly affect the adult trees of the sensitive species, while preventing the establishment of their seedlings. But colonization of sites by new species in the new conditions will occur through much slower dynamics, which means that the impact of these new colonizations would not be realistic for short-term projections. Third, we could not have measured the interaction between the effects of growth and composition unless we had imposed a strong artificial control of the simulation, which would prohibit the measurement of complex community responses. Fourth, we did not consider species currently absent from central Europe. Fifth, we ignored the possibility of plastic, or micro-evolutionary, responses of species (e.g., Jump & Peñuelas, 2005; Lavergne, Mouquet, Thuiller, & Ronce, 2010). Sixth, the importance of the effects of composition might be strengthened further by taking into account interactions besides competition for light (e.g., Jactel & Brockerhoff, 2007). Seventh, the climate data generated had a temporal resolution of 1 month, meaning that extreme events occurring at a shorter scale were not considered. Finally, we used the climatic anomaly between only 2006–2016 and 2070–2100, as a measurement of climate change, which probably made the projections of forest responses conservative.

4.4 | Importance of effects of climate change on the composition of forests

Our results highlight that effects of composition on productivity could become very important under an extreme change in climate, which is likely to occur given the forecasts of the magnitude of climate change (Field, 2014). Our results also show that such effects of composition might become especially important in some sites: negatively in terms of productivity in forests with warm and dry conditions, but positively in sites with cold conditions. Hence, we believe that our projections demonstrate that the role of species range shifts (i.e., composition effects) when simulating impacts of climate change on forests could be more important than previously anticipated, notably in harsh environmental conditions. The role of species range shifts and changes in community composition is very often neglected in studies of the impacts of climate change on ecosystem functioning. We thus call for more research to improve our understanding of these effects, considering the likelihood of an extreme change in climate.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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