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

Running Title: climate change impacts on forest functioning

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Abstract:

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

Location: 11 forest sites in central Europe.

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

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

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

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

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

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

Keywords:

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

Introduction

Forests cover about a third of the world land surface, 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, 2012). However, climate change is affecting many of these forest ecosystem services, such as biomass production and carbon sequestration (Kirilenko & Sedjo, 2007), and this impact is likely to strengthen in the future (Pachauri *et al.*, 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), e.g. 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 trees' physiology is strong enough to drive species' local extinction and colonization (Bertrand *et al.*, 2011), as seen in natural, experimental and simulated forests (Jucker, Bouriaud, Avacaritei, & Coomes, 2014; Liang *et al.*, 2016; Morin, Fahse, Scherer-Lorenzen, & Bugmann, 2011). Understanding the relative importance of these two effects, and the conditions under which each will occur, would greatly help to improve the projections the potential impact of climate change on forest functioning, and important forests ecosystem services such as carbon uptake and biomass provision. However, the two effects have been mostly studied separately, and their relative importance for forest productivity under different circumstances is almost unknown (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 physiology. Furthermore, recent studies found that effects on species composition might be greater than previously expected. García-Valdés, Bugmann, and Morin (2018) found that the impact of climate change-driven extinctions on temperate forests' functioning was stronger than random extinctions. This implies that most Biodiversity-Ecosystem Functioning (BEF) studies (e.g. Liang *et al.*, 2016), underestimate the strength of biodiversity loss caused by climate change. Similarly, Morin *et al.* (2018) found that warmer and drier conditions might strongly affect BEF-relationships in forests experiencing the harshest climatic conditions, illustrating the importance of understanding changes in species composition for forest functioning. These findings suggest that 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. While estimating the effects of climate change on tree physiology could be relatively straightforward through experiments or long-term observations (Hasenauer, Nemani, Schadauer, & Running, 1999), estimating the effects on species composition is much more complicated (Barry *et al.*, 2018). Several mechanisms underlie effects of climate change on species composition. First, climatic filtering determines whether the local environmental conditions are suitable for a species. Second, biotic filtering occurs when interspecific interactions among potentially co-occurring species lead to the exclusion or acceptance of some species. While climatic filtering is commonly studied at large spatial scales, such as regions or continents (Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005), 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 the effects of both climatic and biotic filtering on future forest species composition.

Species distribution models (hereafter “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 the ones considered here. Forest succession models (FSMs) – also called gap model (Bugmann, 2001) – can be used to simulate forest community dynamics at local scales (e.g. up to landscape level), 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 intra-specific interactions), to simulate individual tree growth and succession dynamics (colonizations and extinctions) over time (Bugmann, 2001). FSMs can hence 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 climate change effects on tree physiology 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; Sarmiento 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 a SDM with a FSM to

predict the migration 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 physiology and composition by coupling SDMs' with FSMs' predictions. Our study is thus among the first ones to take advantage of the complementarity of the two kinds 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:

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

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

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

Material and methods

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 succession (i.e. biotic filtering), leading to *realized* forest communities. Finally, once each community had reached equilibrium (after 1000 years) we aggregated the simulated annual productivity across all trees in the site. 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 $-10^{\circ}9'23''$ to $30^{\circ}43'0''$ E and $34^{\circ}59'30''$ to $70^{\circ}58'33''$ 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 in previous studies (Bugmann, 1994; Morin et al., 2011).

Climate data for Species Distribution Models

We used historic climate data (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. Projected future climate data were downscaled via the Rossby Centre regional climate model (RCA4). We used two Representative Concentration Pathways (RCPs): 4.5 and 8.5, and two Global Climate Models (GCMs): CERFACS-CNRM-CM5 (CNRM-CM5) and ICHEC-EC-EARTH (EC-EARTH). We used four climatic variables: mean annual growing degree-days ($> 5^{\circ}\text{C}$), mean temperature of the coldest month, annual precipitation, and a summer moisture index (potential evapotranspiration divided by precipitation). These variables have been previously used to model plant 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 1961-1990 period as historical climatic

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

Climate data for the Forest Succession Model

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

To simulate future climate conditions, we could not directly use data from GCM climate projections because these models use a different “historical” data for bias correction to 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 monthly T and P between the future climate (years 2071-2100) and the current climate (years 2006-2016). These anomalies quantify how much T and P would vary from baseline values under every climate projection. We added these anomalies to the means of the historical climate data from Bugmann (1994), and for each climate projection we generated 2000 years of climate data for each of the four future climate projections. 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, while the estimated changes in precipitation depended mostly on the GCMs. The differences between the four climate projections compared to historical climate (1901-1990 period from Bugmann, 1994) were, ordered in increasing stress for trees: (1) RCP 4.5-CNRM-CM5, moderately warmer with more precipitation; (2) RCP 4.5-EC-EARTH, moderately warmer with similar precipitation; (3) RCP 8.5-CNRM-CM5, extremely warmer with more precipitation; and (4) RCP 8.5-EC-EARTH, extremely warmer with similar precipitation. See Table S1 and S2 for specifics.

Species data and the Species Distribution Models

We considered 25 of the most common tree species in this region (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/>; see Table S4). Presence data were on 50 km × 50 km Universal Transverse Mercator (UTM) grid cells in AFE, and range maps in EUFORGEN. We transformed EUFORGEN range maps into ~50km UTM cells to run the models. We calculated the average historical climatic conditions in each 50-km grid cell from the 10' climate grid resolution. The relationships between historical 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), artificial neural networks (ANN), flexible discriminant analysis (FDA), and surface range envelope (SRE). Models were calibrated for the historical period (1961–1990) using 80% random sample of the initial data and cross-validated against the remaining 20% data, using the area under the curve (AUC) of the receiver operator characteristic (ROC) and the true skill statistic (TSS). 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 was then included in an ensemble model if the AUC from cross-validation was higher than 0.8 and TSS was higher than 0.6 (similar to Araújo *et al.*, 2011). However, the final ensemble model for each species was calibrated using 100% of the species distribution data to maximise 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 on 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 employed by Araújo *et al.* (2011), though 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).

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

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

Forest Succession Model

FORCLIM projections have been shown to be robust under various climatic conditions across a large number of studies (Bircher, Cailleret, & Bugmann, 2015; Gutiérrez, Snell, & Bugmann, 2016; Rasche, Fahse, & Bugmann, 2013; e.g. Rasche, Fahse, Zingg, & Bugmann, 2011). Its projections of forest biomass productivity have been validated for the same sites than those used in this study and using climate values generated with the same historical means, standard deviations and cross-correlations as the ones used here (Rasche et al., 2013). It has also been specifically used to study climate change effects on forest functioning on 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 m² 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 minimum and maximum winter temperature. Tree growth is measured as stem diameter increment, which depends on each species' optimum growth rate, abiotic conditions (temperature, drought, and soil nitrogen), and biotic conditions (light availability). Therefore, while competition for water and nitrogen between individuals are not taken into account explicitly in the model, soil water and nitrogen contents constrain tree establishment and growth differentially between species, which affects competition between trees. 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: (1) a 'background' mortality, which is constant across time and depends on the species' maximum longevity, and (2) 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 Table S3, and more details about the model can be found in Appendix S1, and in Didion, Kupferschmid, Zingg, Fahse, and Bugmann (2009), and Bugmann (1996).

Simulations of forest succession dynamics

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

After having checked that FORCLIM simulations run in the same conditions (site, climate, species pool) yielded very similar results after 2000 years, we performed one FORCLIM simulation for each site ($n = 11$), each climate projection (historical and future, $n = 5$) and each species pool ($n = 100$). Each simulation included 100 patches of 800 m² each, thus corresponding to an 8 ha forest. FORCLIM simulations started from bare-ground conditions to avoid the influence of starting conditions. For each FORCLIM simulation, only the species in the site's species pool - 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 1000 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 1100, 1200, ... 2000; cf. Morin et al., 2011) and averaged the results from these sampled years and across patches. For the calculation of the realized composition we considered that a species was present in a community only if its simulated biomass reached 1 t·ha⁻¹.

Quantifying growth and composition effects of climate change

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

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). We also fitted linear regressions between the relative importance of colonization and extinction, and climatic variables. The relative importance of colonization and extinction was calculated by dividing the productivity change caused by either colonization or extinction and the summed changes in productivity (changes were converted to absolute values). Finally, we fitted a linear regression between the future change in productivity in each site and its future change in realized species richness.

Results

Climate change effects on potential species pools and richness

In most of the climate change projections, species suitability increased in most of the sites (Fig. 2 A-C). However, with extreme warming (RCP 8.5) and with the driest conditions (EC-EARTH model; Fig. 2D), 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).

Effect of climate change on realized species richness

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

Climate change effects 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 (Fig. 3 A-D). The greatest impact occurred in Sion, the warmest and second driest site, where productivity decreased by between -67.6% and -100%. However, with a projected increase in precipitation greater than 10.0% (CNRM-CM5 model in Table S1), forest productivity increased in all sites (Fig. 3 A and C), except Grande Dixence, Basel and Sion. With a very weak precipitation change (EC-EARTH model in Table S1), forest productivity increased in the coldest sites and decreased in most of the warmest sites (Fig. 3 B and D).

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

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

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

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

Discussion

Contrasting responses of forest productivity across a climatic gradient

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

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 (Fig 3 E-F; see Coomes et al., 2014). Contrarily, under extreme warming, and in locations at both ends of the temperature gradient, changes in productivity were driven mostly by changes in species composition (Fig 3 G-H). The increasing correlation between the relative importance of simulated colonization (i.e. the importance of composition effect) and both local temperature and P/PET under the harshest climate projection (+3.6 °C and -1.1% TAP; Fig. S4 C and E) further shows the strong role of species composition under harsh climatic conditions. Such finding matches with empirical evidence of the role of tree richness on 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 ($p < 0.054$ across all climate projections; Fig. 4). Former theoretical studies also showed 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 species richness and ecosystem productivity has been observed in forests (e.g. Liang et al., 2016; Paquette & Messier, 2011), and is usually explained by a greater niche partitioning in more diverse communities (Loreau et al., 2001; Morin et al., 2011). In simulated forests in the coldest sites, the effects of species richness and composition were strengthened because climate change allowed new species to colonize and be productive (Fig. 3 and S3; Coomes et al., 2014). In the warmest-driest sites, climate change caused the extinction of key species (Reyer, 2015), which reduced species richness and productivity.

The observed importance of community composition change in cold and warm-dry sites in our study (see 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, the species that went extinct with climate change were likely near the boundaries of their acceptable climatic conditions without climate change. At sites with intermediate temperature, such species were probably suppressed by competition when we simulated under the historical climate scenario and did not contribute significantly to the total productivity of the community. Hence, their extinction in the simulations using the climate change scenarios did not change importantly the total productivity of the site. Contrarily, 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 because they faced little competition. Hence, their extinction under climate change did importantly affect the total productivity of the community. With colonizations, we could expect a similar effect. The species that colonized a site because of climate change were probably close to their climatic limits. In a climatically benign site, this means that such species are unlikely to become dominant when arriving, and would not contribute substantially to the total productivity of the community. This occurs because they still have to deal with the biotic interaction milieu (McGill, Enquist, Weiher, & Westoby, 2006), and were probably not a strong competitor under such conditions. In climatically harsh sites, a colonizing species could immediately become important because it is less likely that it encounters strong competitors.

Increased sensitivity of warmest-driest forests to climate change

Our simulations suggested that rapid and steep changes might arise in forest functioning due to climate change. In the warmest site, complete elimination of the forest cover was projected in the event of the most severe climate change scenario (Fig. 3H). In this scenario increase in drought stress may drive the forest system to change 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 scenario of composition change, we confirmed that such a drastic change could indeed occur in one of the study sites.

Limitations of the approach

To our knowledge this is the first study that coupled models relevant at complementary spatial scales (SDMs and FSMs), to quantify the relative importance of the physiology and composition 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 estimates of the importance of climate change composition effects on mature forests, in comparison with growth effects. Our approach also carries some limitations: (1) 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 used here (Early & Sax, 2014) and process-based SDMs (e.g. Chuine & Beaubien, 2001) could not be used for so many species. (2) Our simulations design, relying on 2000-years simulation in both historical and anticipated conditions, allows assessing of the relative contribution of changes in tree growth and species composition, and notably highlights the possible strength of compositional effects on changing productivity. However, they cannot be directly used to infer the forest composition and productivity for the end of the 21st century. In fact, local species extinction by 2100 may be well reproduced by our design, because the exposition to the novel climate conditions may directly affect the adult trees of the sensitive species, while preventing the establishment of seedlings of these species. Yet, site colonization by new species under the new conditions occurs through much slower dynamics. At least one may expect that the outcome of these new colonizations on forest functioning depends whether it is simulated over 100 or 2000 years, which means that the impact of these new colonizations may be overestimated in our simulations (ie. mostly under strong climate change according to our results). (3) We could not have measured the interaction between the physiology and composition effects unless we had

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

Importance of climate change-composition effect on forests

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

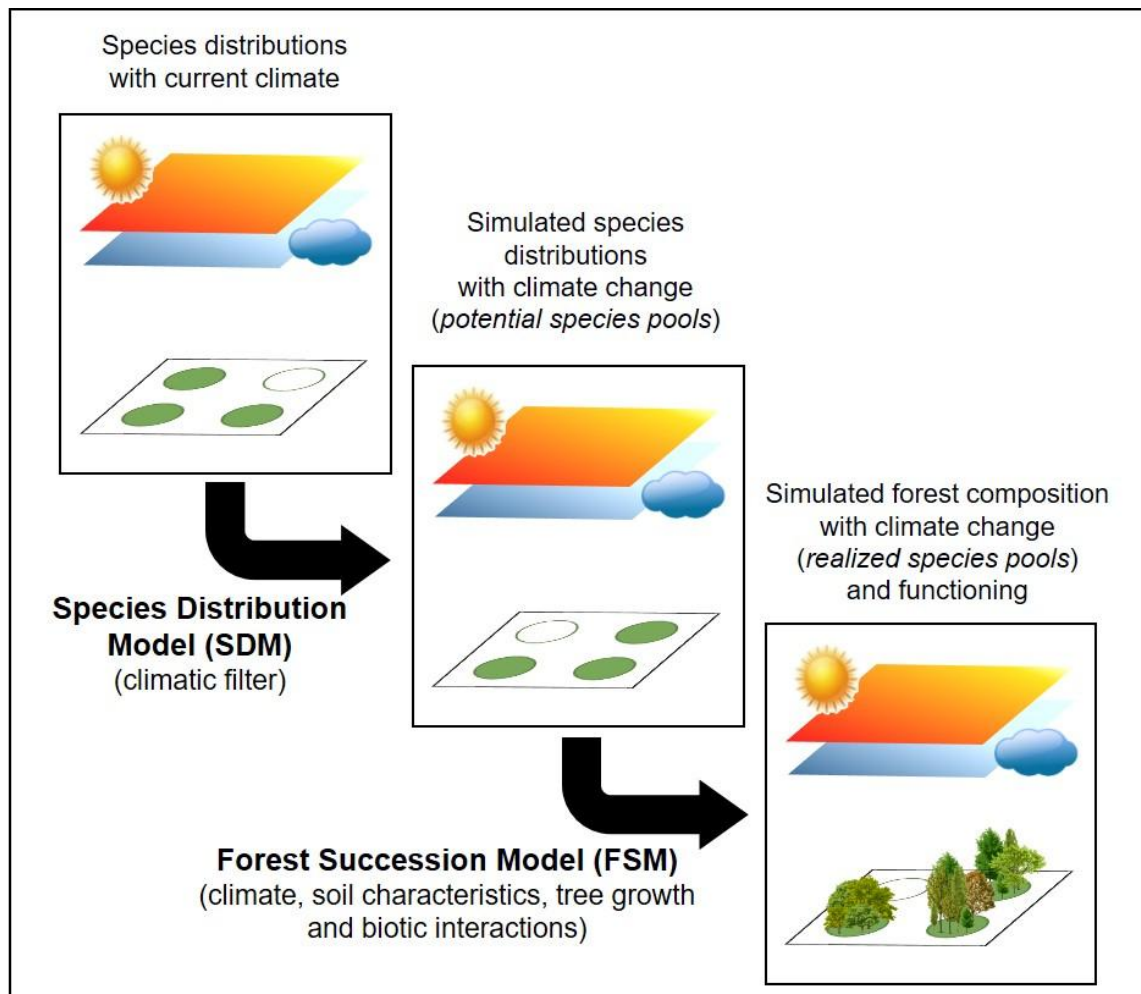
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708 **Figures**

709

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

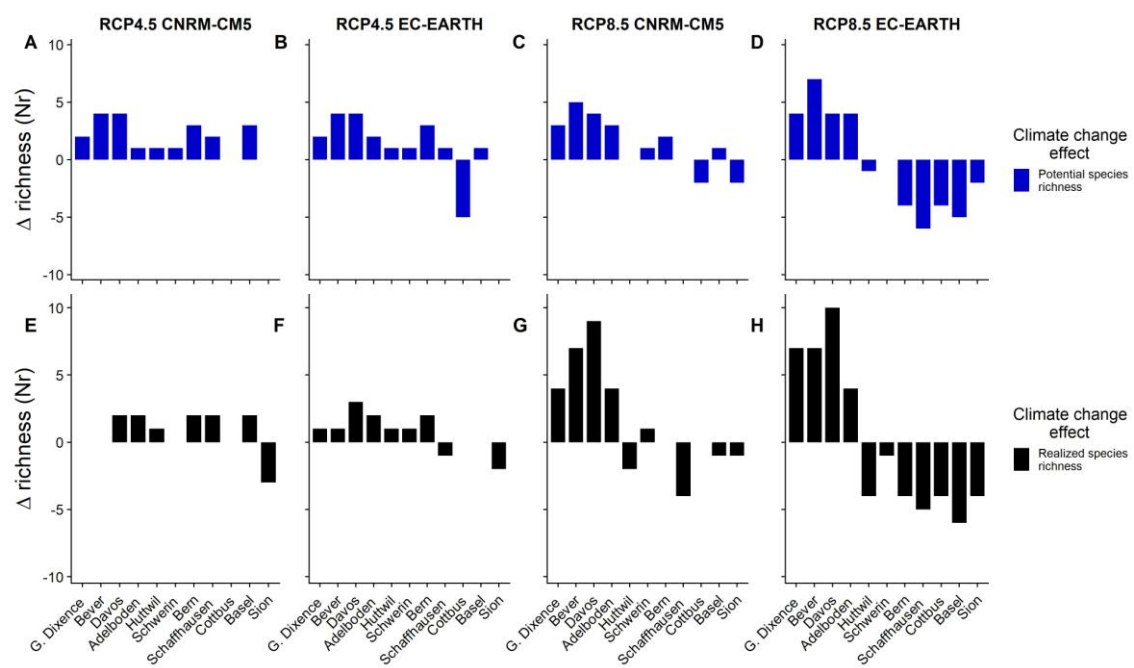


Fig. 2: Effect of climate change on the number of potentially occurring species, projected with the SDMs assuming a threshold in suitability of 50% (upper panels), and on the number of realized species, simulated with the FSM, assuming that only species with more than 1 t.ha⁻¹ are present in each site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

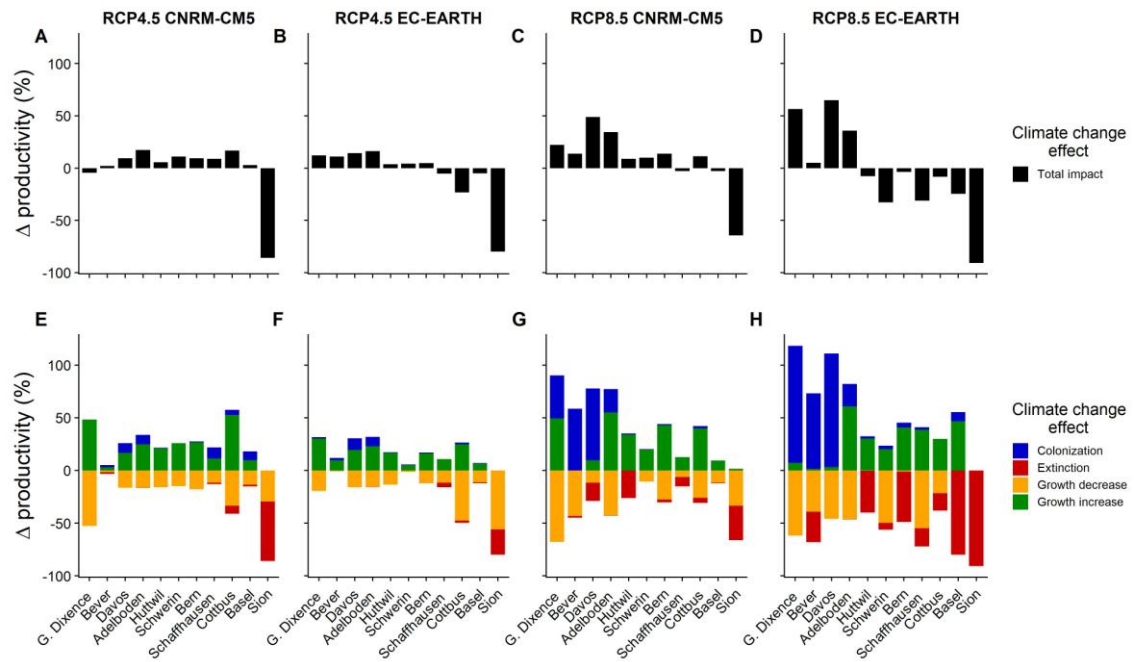


Fig. 3: Effect of climate change on each forest annual aboveground biomass productivity ($\text{t} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$), relative to a baseline (i.e., current climate) projection. Study sites are ranked from the coldest (left) to the warmest (right). Upper panels show total effect, and lower panels show the effect on forest productivity of colonizations, extinctions, and growth decrease or increase of species present under both sets of conditions. To assess community composition, we considered that a species was present in a site whether its biomass reached at least $1 \text{ t} \cdot \text{ha}^{-1}$.

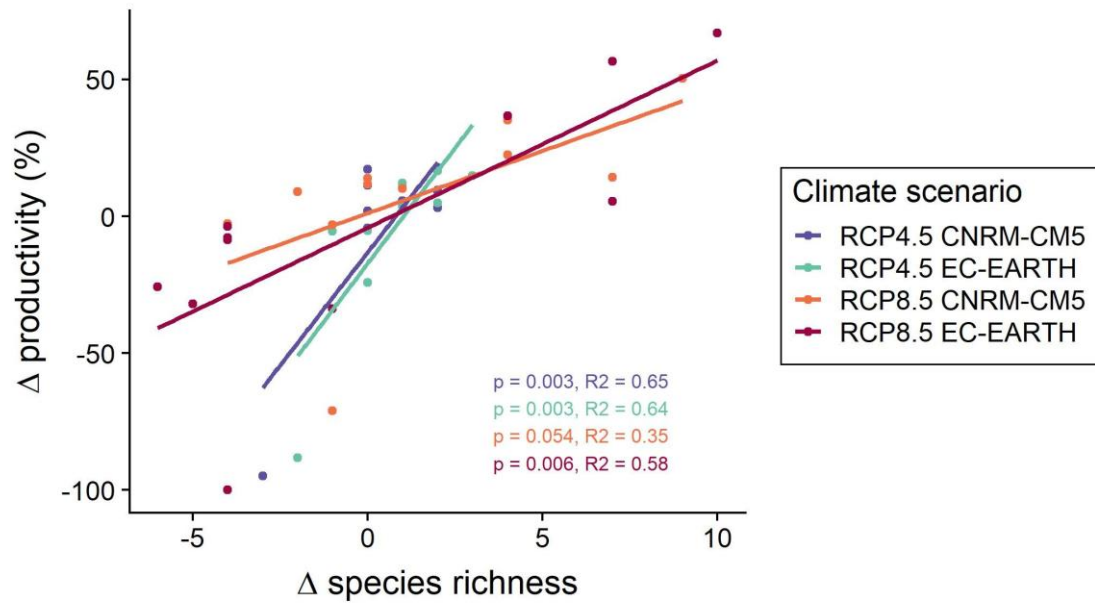


Fig. 4: Future change in realized species richness vs. future change in forest productivity (%) under different climate change projections, relative to baseline projections using current climate. $R^2 = 0.65$ for RCP 4.5CNRM-CM5, $R^2 = 0.64$ for RCP 4.5- EC-EARTH, $R^2 = 0.35$ for RCP 8.5-CNRM-CM5, and $R^2 = 0.58$ for RCP 8.5-EC-EARTH.