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ORIGINAL ARTICLE

Managing mixed stands can mitigate severe climate change impacts on French alpine forests

Marion Jourdan[1,2,3] · Thomas Cordonnier[4] · Philippe Dreyfus[5,6] · Catherine Riond[7] · François de Coligny[8] · Xavier Morin[1]

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Abstract
Climate change affects forest ecosystem processes and related services due to climate variability. These might affect ecosystem functioning, especially productivity. Regarding management issues, mixed stands are considered a relevant option to maintain forest cover and ecosystem services under climate change. However, the possibility to maintain these mixed stands with management actions with positive effects on forest functioning under climate change remains uncertain and deserves further investigations. Relying on a simulation-based study with a forest gap model (ForCEEPS), we thus addressed the following questions: (1) Are monospecific stands vulnerable to climate change? (2) Would mixed stands significantly mitigate climate change effects on forest productivity and wood production under climate change? (3) Would conversion to mixed stand management affect significantly forest productivity and wood production under climate change compare to monospecific management? In this study, we quantified potential climate change effect (using RCP 8.5 and present climate) and management's effect in the French Alps, focusing on five species (*Fagus sylvatica*, *Abies alba*, *Picea abies*, *Pinus sylvestris*, and *Quercus pubescens*). We tested different scenarios, with various composition, structure, or environmental conditions, under climate change. These simulations showed that monospecific stands currently growing in stressful conditions would be vulnerable to climate change. Managing mixed stands or conversion from pure to mixed stands would make it possible to maintain higher productivity in the long term than monospecific stands, depending on the species and the sites considered. Our results will feed into discussion on forest management in the context of climate change.

Keywords Species diversity · monospecific forests · Mixed forests · Gap model · Forest management · Climate change

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✉ Marion Jourdan
marion.jourdan@universite-paris-saclay.fr

Thomas Cordonnier
thomas.cordonnier@inrae.fr

Philippe Dreyfus
philippe.dreyfus@onf.fr

Catherine Riond
catherine.riond@onf.fr

François de Coligny
francois.decoligny@inrae.fr

Xavier Morin
xavier.morin@cefe.cnrs.fr

1 CEFE UMR 5175, CNRS-Université de Montpellier - EPHE - IRD, 1919 Route de Mende, F-34293 Montpellier Cedex 5, France

2 Agence de l'environnement et de la maitrise de l'énergie, ADEME, Angers, France

3 ESE, CNRS, AgroParisTech, Univ. Paris-Saclay, F-91400 Orsay, France

4 Université Grenoble Alpes, INRAE, UR LESSEM, 38000 Grenoble, France

5 INRAE, UR 0629 URFM Ecologie des Forêts Méditerranéennes, Centre de Recherche PACA, Avignon, France

6 Département RDI, ONF, Office National des Forêts, Avignon, France

7 Département RDI, ONF, Office National des Forêts, Chambéry, France

8 INRAE, UMR931 AMAP, Botany and Computational Plant Architecture, TA A-51/PS2, Boulevard de la Lironde, 34398 Montpellier Cedex 5, France

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Introduction

In the Northern Hemisphere, climate change will lead to increased temperature and changes in precipitation regime (not spatially homogeneous) as well as more frequent and more intense extreme climatic events during the next decades (Pachauri et al. 2014), particularly with strong drought. Warmer and drier conditions can lead to medium or long-term damage in forest ecosystems (Bréda et al. 2006a; Linares et al. 2010), including massive mortality events (Margalef-Marrase et al. 2020; Senf et al. 2020). Furthermore, beyond these direct impacts, climate change effect can be also indirect by altering community composition and species richness (Bertrand et al. 2011; Lenoir et al. 2008), which in turn will impact ecosystem functioning (Loreau 1998). Stressful climatic events also increase the vulnerability of forest stands to pathogen attacks (Desprez-Loustau et al. 2006) or fire risks (Dale et al. 2001).

Numerous studies have shown that species richness may strongly modify ecosystem functioning, and especially increase productivity (Cardinale et al. 2007; Hooper et al. 2005) or multifunctionality (Gamfeldt et al. 2013). Focusing on forests, a few experimental (Jones et al. 2005; Pretzsch 2005), observation-based (Forrester et al. 2016; Toïgo et al. 2015), and modeling studies (Morin et al. 2020; Morin et al. 2011, 2018) have also found that diversity may lead to an overyielding effect in comparison with monospecific stands. Several studies focusing on specific richness-productivity relationship have also aimed at exploring the impact of climate on these patterns (Blois et al. 2013; Paquette and Messier 2011). Due to these positive effects, favoring species richness or mixed stands has been considered a good option to mitigate climate change negative impacts on forest ecosystem functioning (e.g., Hisano et al. 2018).

Recent studies have shown that even only two species stands can mitigate climate change impacts, through increasing and/or stabilizing stand productivity (Del Río et al. 2017). Thus, mixed stands management could be an efficient solution to sustain forest functioning and better preserve their services (e.g., Schwaiger et al. 2018). However, results are actually more contrasted when considering mixed stands with other composition, with either positive or negative effects of species mixing on ecosystem functioning (Grossiord et al. 2014; Merlin et al. 2015), depending on environmental conditions and species composition (Grossiord et al. 2014a; Jucker et al. 2014). For instance, mixed stands can have a negative effect on stand response to drought stress (Grossiord et al. 2014b). Better understanding of how mixed stands may behave differently from monospecific stands in various ecological conditions is thus required, for instance, by using pseudo-experimental approaches on specific mixed stands (del Río et al. 2014; Jourdan et al. 2019; Pretzsch et al. 2013) or experimental approaches (e.g., BIOTREE, Schererlorenzen et al. 2007, or ORPHEE, Castagneyrol et al. 2014). In the first case, climate change effect is taken into account indirectly according to the space-for-time substitution, using environmental gradients (Jourdan et al. 2019; Jucker et al. 2014), for instance, latitudinal (e.g., in the Alps, Pretzsch et al. 2010) or altitudinal gradients or via rainfall exclusion in experimental studies (Estiarte et al. 2016). However, such field-based approaches relying on gradients allow a limited climatically analogy (Vallet and Perot 2018). In the second case, the number of tested forest types is limited, because such experimental protocols are difficult to carry out and expensive to monitor in the long term. Moreover, testing forest management scenarios in situ is a difficult task, only possible with long-term studies (Gavinet et al. 2019). Modeling approaches make it possible to simulate the dynamics of forest stands, while considering climate change and management. More generally, to deal with the high uncertainty characterizing future climate, forest models appear as a key tool to test various scenarios (Cordonnier et al. 2018; Morin et al. 2020), complementing empirical and experimental approaches.

In Europe, the majority of temperate forests are managed (Morneau et al. 2008; Naudts et al. 2016; Sabatini et al. 2018) and the main stand structural characteristics (total basal area, tree density, species composition) of these forests have been controlled since up to several centuries (Naudts et al. 2016; Whitlock et al. 2018). In a context of energy transition and carbon sequestration, in which wood resources are more and more targeted by public policies (Valade et al. 2018), developing sustainable forest management under climate change that fulfills both ecological and economic challenges appears an essential task to maintain every forest ecosystem services. Stand management can be an efficient tool to mitigate the negative impacts of intensive droughts and promoting forest adaptation (Millar et al. 2007), through controlling density (Trouvé et al. 2017) or structural heterogeneity (Cordonnier et al. 2018) including species mixing (Engel et al. 2021). It is however difficult to anticipate the combined effect of climate change and management on the long-term maintenance of species mixing in forest stands as well as the resulting effect on forest functioning (Cordonnier et al. 2018).

Yet, quantifying and predicting ecosystem change in composition and functioning under climate change and with forest management remains a difficult task (Morin et al. 2018), because of the great uncertainty in climate changes prediction (Pachauri et al. 2014) and the difficulties to forecast synergy between climate change and its direct and indirect impacts. In context embedding so many uncertainties, modeling approaches may be pivotal to test climate change impacts and management effects on forest ecosystems (Ameztegui et al. 2017; Reyer et al. 2015). In fact, models allow working on long-term time scales (up to a century) and simulating future climate change impact (i.e., not like dendrochronology studies impacted by past climate). These tools are especially relevant to explore different stand management effects, whereas it is more difficult with other approaches in forests. More and more forest models integrate climate, making it possible to consider the effect of climate variation in their predictions of future forest structure and provision of ecosystem services at the local scale. Some are process-based models, such as 3-PG (Landsberg and Waring 1997) or CASTANEA (Dufrêne et al. 2005), some are gap models, e.g., ForClim (Bugmann 1996), and some are landscape models, such as iLand (Seidl et al. 2012). Several models are calibrated and validated on forest types occurring in the Alps: for example, LandClim (Schumacher et al. 2006), iLand, TreeMig (Lischke et al. 2006), LANDIS (Petter et al. 2020), or 3-PG (Forrester et al. 2021).

In this study, we used the individual gap model ForCEEPS (Morin et al. 2021), derived from ForClim (Bugmann 1996), to carry out forest simulations in the French Alps, integrating climate change and forest management and the five most common species in these forests. We simulated monospecific and mixed forests (some combinations of the five species) over the next century in four sites in the French Alps. The simulations were run using a severe climate change scenario and applying six different management scenarios (some of them being oriented towards the promotion of mixed stands). More specifically, we aimed at answering the following questions (Fig. S1):

(1) Are monospecific stands vulnerable to climate change?
(2) Would mixed stands significantly mitigate climate change effects on forest productivity and wood production under climate change?
(3) Would conversion to mixed stand management affect significantly forest productivity and wood production under climate change compare to monospecific management?

Material and methods

Description of the forest dynamics model

General description

ForCEEPS v1.1 is a forest dynamics model simulating population dynamic of one or several tree species in small parcels of land (“patches”) (Morin et al. 2021). The model is individual-based and predicts forest composition, biomass, and productivity, by considering abiotic (climate and soil properties) and biotic constraints (competition for light) to tree establishment, growth, and survival (see Fig. S2). The patches are independent, and dynamics at the forest level are obtained by aggregating patches together (Bugmann 2001).

The main processes (seedlings recruitment, growth, and death) included in the version of ForCEEPS used in the present study are derived from FORCLIM 2.9.6. (Bugmann 1996) and described in Morin et al. (2021) (available on CAPSIS, Dufour-Kowalski et al. 2012). The dynamics are simulated at the individual level (and not at the cohort level, i.e., every tree of one species with the same age), without explicit spatialization, allowing to integrate individual variability within a species. ForCEEPS has been calibrated for the main forest types in French territory and validated by showing both its ability to both reproduce observed species composition and its strong accuracy in predicting forest productivity at the stand scale for the main forest types in France, covering a large range of climatic and environmental conditions, including French Alps (Morin et al. 2021), showing a strong ability to reproduce potential species composition, and stand productivity under the current climate.

Tree establishment is determined by species-specific responses to five factors: minimum winter temperature, degree-days sum during the growing season, soil water content, light availability, and browsing pressure (Bugmann 1996). The model does not consider seed and seedling stages; thus, saplings are established with a diameter at breast height of 1.27 cm. Dispersal limitation is not taken into account in this model and patches receive an annual seed rain of all species included in the simulation, assuming the presence of seed-bearing trees around the simulated forest (Bugmann 2001). We detailed seedlings composition and seedling intensity effects on monospecific stand vulnerability (Box S1).

Tree growth (height and diameter) depends on a species-specific optimal growth rate that is modified by abiotic (temperature, soil water content (SWC), and nitrogen content in the soil) and biotic factors (size-dependent competition between trees). The main mechanism driving interactions among trees in ForCEEPS is competition for light. Forest successional dynamics is triggered by canopy gaps and thus relies on differential species growth responses to light conditions. Species with different shade tolerances have different light response curves. In full light, light-demanding species (i.e., mainly early-succession species) grow faster than shade-tolerant species (i.e., usually late-successional species) that have, on average, a weaker maximum growth rate. The realized growth rate of shade-tolerant species becomes relatively stronger than shade-intolerant ones because of decreasing light availability. Furthermore, although each species has species-specific tolerances to environmental drivers, there is no competition for SWC and soil nitrogen taken into account in the model. However, SWC varies across years depending on the temperature and precipitations of the site.

Tree mortality is driven by both stochastic and deterministic processes and depends on two components: (i) a “background” mortality and (ii) a stress-dependent mortality. Background mortality is a stochastic process occurring at low frequency, increasing with trees age and depending on species' maximum longevity. Stress-dependent mortality relies on the growth pattern of each tree: if a tree grows very slowly during several successive years, it is more prone to die than a tree with a better growth.

The model works with climate time-series and can thus consider either data reflecting current climate or future climate scenarios. ForCEEPS now includes a new silvicultural module able to simulate successive thinning operations, as described in Supplementary Material (Box S2). We defined and used silvicultural scenarios that differed according to the targeted basal area (proxy of stand biomass) after each thinning, rotation (time between each thinning), and targeted proportion of each species. At each thinning, trees are logged until objective basal area is reached, from above or from below thinning.

ForCEEPS is developed on the CAPSIS modeling platform that host several forest models. This platform has an ethical and scientific charter. Any researcher adhering to this charter has access to the source code of ForCEEPS and can use it (as well as all the other models included in CAPSIS). (For more details, see http://capsis.cirad.fr/capsis/presentation.)

Species parameters

In ForCEEPS, each species is defined by 13 parameters (Table S1) that have been estimated from a large body of literature data and experimental or observational data (very close to FORCLIM parameter and available in Morin et al. 2021). Hereafter, we consider these parameters as species "traits" as they determine physiological species responses to environmental conditions. The variability among species traits reflects several trade-offs of tree life-history strategies. It is worth noticing that observed functional patterns at community scale are emergent properties from species responses to processes embedded in the model.

Sites and species

Studied sites Simulations ran on four sites in the French Alps, covering a large latitudinal gradient related to important variations of temperature and precipitation: Bauges, Vercors Méaudre, Vercors Lente, and Mont Ventoux (Box S3). Each site was characterized by latitude, soil field capacity, and slope. Monthly mean temperatures and monthly sums of precipitation, with inter-annual variations, characterized the climate of each site. Two different elevations were tested for each site, one at 1000 m (low elevation) and 1300 m (high elevation).

Studied species We considered five species in this study: common beech (*Fagus sylvatica*), spruce (*Picea abies*), silver fir (*Abies alba*), Scots pine (*Pinus sylvestris*), and pubescent oak (*Quercus pubescens*). The first four species are widespread in the French Alps and represent economic issues and/or patrimonial interest in mountain forests. Although it is mainly present in the Southern Alps, we also considered pubescent oak because this species could increase its presence in the whole Alps in response to climate change and become an opportunity for forest manager in the next decades.

These five species allowed studying various types of mixtures, because of the physiological and ecological differences between species. Beech and oak are broadleaved species while spruce, fir, and Scots pine are coniferous species. Beech and fir are late-successional and shade-tolerant species, while spruce is a mid-seral species. Spruce is very sensitive to high temperatures in summer and is the most drought-sensitive species (Caudullo et al. 2016). Beech is also sensitive to water stress, but recovers easily after an intense drought event (Lebourgeois et al. 2005). Silver fir is less sensitive to drought, but grows better in humid conditions (Lebourgeois et al. 2010; Mauri et al. 2016) while Scots pine and pubescent oak are more early-succession and light-demanding species, tolerating drier conditions (Pasta et al. 2016).

According to various models (Cheaib et al. 2012; Falk and Hempelmann 2013; Ruosch et al. 2016), most of the target species (spruce, fir, beech, and Scots pine) will regress on French territory and in the Alps in particular. Predictions about pubescent oak forecast an expansion in Northern France, but there are too few studies focusing on this species to ensure such a trend (Bertrand et al. 2012).

Even if we considered just five species at the beginning of the simulations, we allowed other species to colonize the patches during the simulations due to their observed abundance in the sites (sycamore maple, *Acer pseudoplatanus*; or mountain ash tree, *Sorbus aucuparia*).

Climatic data

In this study, we looked for comparing simulation results between current climate and changing climate. Climate variables were delivered by Météo-France (available in «Drias», Météo-France and project GICC Drias - CERFACS, IPSL). For the simulations under the current climate, we used monthly temperatures and precipitation for the last 50 years. Then, we created climate series, selecting randomly yearly climate conditions (monthly temperature and precipitation), to obtain climate 150 years' time-series of "stable" conditions between 2000 and 2150, i.e., with inter-annual variability but without any long-term trend in variable means. For the simulations under climate change, we used data generated according to the RCP 8.5 scenario (IPCC—Pachauri et al. 2014), i.e., the most extreme available scenario (in temperature and precipitation), as our aim was to address the potential mitigating effect of managed mixed stands under sever climate change (with CNRM as GCM and RC4A as RCM, corrected with

Adamont method, Verfaillie et al. 2017). Climate data for the future are available between 2000 and 2100, but we wanted to study a longer period (150 years). Thus, we generated climate data between 2100 and 2150 by selecting randomly yearly climate conditions (monthly temperature and precipitation) between 2075 and 2100, i.e., stabilized conditions after 2100.

Simulation design

In this study, we used six silvicultural scenarios. They differed according to the basal area (BA) remaining in the stand after thinning (20m^2/ha, 30m^2/ha, or 80% of BA before thinning) and objective composition ("stable management" and "conversion management"). "Stable management" aims to reproduce field management scenario maintaining initial structure of forest (including forest composition). It was applied to monospecific and mixed stands, according to which thinning operations aimed at conserving initial species composition. "Conversion management" aims to reproduce field management scenario changing initial structure of forest (including forest composition). It consisted in thinning operations that preserved not—aimed species—up to a stated abundance—in a monospecific stand. Regarding mixed stands, the targeted distribution values of relative abundances in the "stable" option are 50–50 or 80–20 for two species stands and 40–40–20 for three species stands. In our study, used "conversion" option, the initial composition was monospecific and the targeted composition was 50–50 for two species mixed stands, and 30–30–40 for three species mixed stands (with 40% of the initial species of monospecific stand). In each case, rotation time was 12 years, as recommended by silvicultural guides of the French Northern Alps (Gauquelin 2006). Each configuration of forest composition is shown in Fig. S3. We used three different simulation designs to answer to our three questions.

First, to study monospecific stands vulnerability to climate change (question 1), we worked on the four sites, considering both altitudes and with both climate scenarios (current climate and climate RCP 8.5, see Fig. S3). In this study, we concentrated on long-term changes and not in particular on extreme events as windstorm, wildfire, or insect outbreaks (Lecina-Diaz et al. 2020). Even if we considered they are crucial points, our model does not allow studying vulnerability to these particular events yet. The simulations started from mature forest inventory, representative of the Alps forest studied here (from Jourdan et al. 2020, summarized in Table S2). Each tree is characterized by species, DBH, age, total height, without spatial coordinates. In this part, we did not consider any management actions, because we aimed at assessing the intrinsic monospecific stand vulnerability to climate change.

Studying mixed management effect on stand productivity and maintenance (questions 2 and 3), we also worked on the four sites and considering both altitudes, but for climatic conditions, we focused on RCP 8.5 climate. We considered monospecific and 2- and 3-species mixed stands. We worked with "stable management" option (question 2) and "conversion management" option (question 3) on monospecific stand for each of the three defined thinning objectives (see above). Note that the other species were allowed to colonize the site over the simulation.

Preliminary analyses showed that simulations with the same characteristics (site, initial inventory, and climate) and only varying for their stochastic parameters used in some processes (mortality, recruitment) led to similar results (see Fig. S4). We thus decided to perform only one simulation (with 50 independent patches of 1000 m^2) per case, i.e., one initial inventory for one altitude/site/climate/management, for the sake of simulation time. The simulations were initialized with data from mature forest inventory plots surveyed in the context of a previous study (Jourdan et al. 2019; see the detailed description of field sites, design, and data collection). To study a complete stand rotation, simulations were run over 150 years.

Analyses

Vulnerability of monospecific stands

In this study, we considered three types of stands: (i) monospecific stands composed of species at their range limit, (ii) monospecific stands composed of weakly competitive species in middle of their range, and (iii) monospecific stands composed of strongly competitive species in the middle of their range. In our study, the first situation (i) corresponds to fir and beech stands in Ventoux and spruce stands in Vercors. The second situation (ii) corresponds to oak in all sites and Scots pine in Ventoux. The third situation (iii) corresponds to spruce in Bauges, and fir and beech in Bauges and Vercors. As Spruce was not adapted in Ventoux in current climate, we did not discuss this case further.

We studied monospecific stand vulnerability through three indices (question 1): (1) final stand composition (calculated with basal area proportion of each species at the end of the simulation) as the stand may experience the colonization by the other species during the simulation, (2) final productivity (which we considered a proxy of wood flux), (3) final basal area (which we considered a forest cover), and (4) basal area of dead trees.

We considered monospecific stands to be stands with more than 80% (on basal area) of the targeted species. To determine the vulnerability of each monospecific stand, we compared the proportion of the target species, between current and future climate conditions simulations. Monospecific stands vulnerability to climate change is then quantified by the objective species ratio of species proportion between climate change and current climate.

Vulnerability was also assessed by comparing monospecific stand productivity (in BAI, i.e., m^2/ha/year) under current and future climate conditions.

We assessed monospecific stand vulnerability by comparing basal area across simulation, i.e., proxy of stand dynamics, under current and future climate conditions.

Finally, monospecific stand survival to climate change was assessed by comparing annual proportion of dead trees of objective species (using basal area, m^2/ha), under current and future climate conditions.

Mixed vs. monospecific stand management

Then, we compared mixed (2- or 3-species) and monospecific stand management, studying wood harvested, via basal area harvested (m^2/ha). We first carried out this analysis for "stable management" scenarios, comparing monospecific 2-species and 3-species stands managed to maintain initial specific proportions (question 2). Then, we carried out this analysis for "conversion management" scenarios, comparing monospecific stands managed to obtain monospecific, 2-species or 3-species stands (question 3). The effect of management on harvested wood was tested with the Tuckey test and Kruskal test.

Results

Are monospecific stands vulnerable to climate change?

Monospecific stand vulnerability related to species identity

Under current climate After 150 years of simulation under current climate, the relative abundance of the main species in monospecific stands may decrease significantly, depending on the species and the site considered (Fig. 1 and Table S3). Monospecific Scots pine stands did not persist on any site under current climate: less than 25% for Scots pine in Vercors and Bauges after 150 years, substituted by spruce, fir, and beech. Monospecific spruce stands were predicted to not persist in Ventoux under the current climate (less than 25%, mostly substituted by beech and fir), but showed a better ability to remain monospecific stands in Bauges and Vercors (close to 70%, Fig. 1) after 150 years of simulation. Monospecific fir and beech stands showed also a strong ability to remain monospecific stands over time, with a decrease in relative abundance between 30 and 40%. Monospecific oak stands persisted in current climate in Bauges and Ventoux after 150 years, with a decrease in relative abundance around 40%, and in Vercors.

Under climate change After 150 years of simulation, we found that climate change greatly affected monospecific stands in each site, with an intensity depending on species and site considered. For monospecific spruce stands, the results showed a higher loss in spruce proportion for all sites, until total spruce disappearance (Ventoux and Vercors Lente). Monospecific spruce stands were very vulnerable in Vercors sites, with a predicted final proportion between 0 and 35% (Fig. 1). This vulnerability was lower in Bauges (Fig. 1, spruce stands' final proportion remains higher than 40%). For monospecific Scots pine stands, the proportion remained comparable under climate change (around 20%), except in Ventoux (Fig. 1), where monospecific stands were much better maintained (more than 50% instead of 20%). For monospecific fir and beech stands, climate change effect depended on the site: proportion at the end of the simulation decreased in Ventoux (from 75 to 0%) substituted by Scots pines and other species, and slightly decreased in Vercors and Bauges (Fig. 1). Monospecific beech and fir stands were highly vulnerable in Ventoux and benefited from the strong vulnerability of spruce in Vercors sites. Oaks' proportion in initially monospecific oak stands remained similar in climate change (compared to current climate) in Bauges and became higher in average in Vercors (from less than 50 to 70%) and in Ventoux (from 70 to more than 90%). Other species represented less than 10% of final BA, regardless of site and species, except in Ventoux.

We studied objective species proportion trend during the time (Fig. 1). Decrease of this proportion is gradual for all stands, except in spruce, fir, and beech stand in Ventoux

Stand vulnerability through average productivity

In Bauges and Vercors (Fig. 2), monospecific stands' productivity was not affected by climate change, except around 75 years (annual precipitation rates are lower than average in RCP 8.5, see Box S3). In Ventoux (Fig. 2), monospecific stands were vulnerable for all species at middle term (51–100 years), but not at long term (101–150 years). Between 51 and 100 years, species productivity decreased drastically. Then, between 101 and 150 years, productivity recovered at equivalent or greater level than monospecific stands in current climate, except for oak stand (with productivity almost divided by two). Because of change in species composition, climate change effect did not affect mean productivity of monospecific stands in the long term.

Stand vulnerability through stand basal area

In Bauges, monospecific stands did not appear vulnerable; i.e., we found no difference between final basal area under current climate and under climate change (Fig. 3). In Vercors, monospecific stand of fir and spruce are vulnerable at middle term (51–100 years), but not at long term (101–150 years). Monospecific stand of others species are not vulnerable. In Ventoux, all monospecific stands were sharply

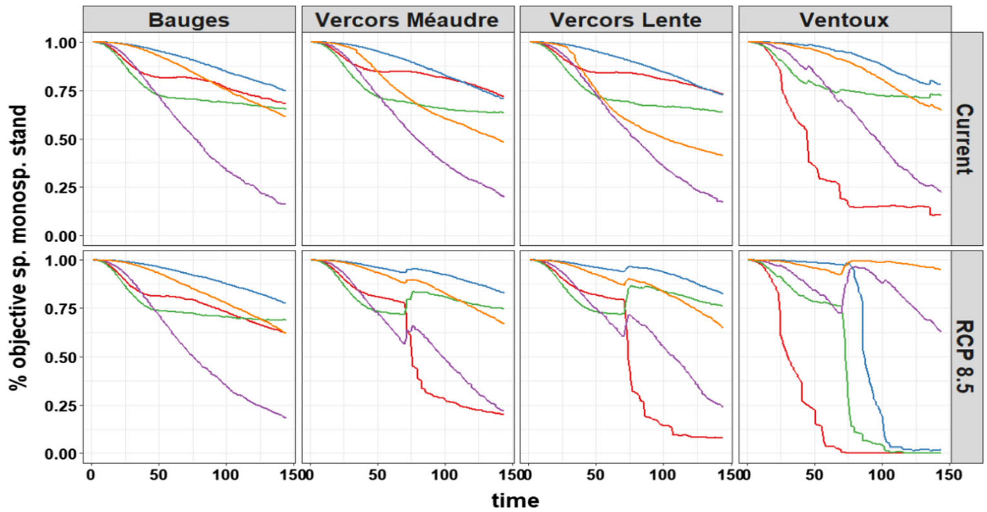

Fig. 1 Proportion of target species across the simulation. Proportion of the target species (computed with basal area, average of both altitudes) in monospecific stands without management for each set of climate conditions across the 2000–2150 period. Each species is represented separately: beech (blue), Scots pine (purple), fir (green), spruce (red), and pubescent oak (orange). Each vertical panel refers to one site: Bauges, Vercors Méaudre, Vercors Lente, and Ventoux. Each row represents each climate: current climate or climate change (RCP 8.5)

vulnerable (Fig. 3), with a decrease between 48% (for fir stands) and 18% (for oak and spruce stands).

Dead of monospecific stands

In Bauges (Fig. 4), the mortality monospecific stand was not affected by climate change. For Vercors, mortality of pubescent oak monospecific stand decreased between current climate and climate change, and mortality of spruce monospecific stand was affected by climate change. For Ventoux, mortality of beech and fir monospecific stand increased with climate change.

Would mixed stands or conversion stands mitigate climate change effects on forest?

“Stable management” scenario

For all sites, initial stand species richness affected wood harvest. Wood harvest was not significantly different between monospecific and 2-species and 3-species mixed stands in the first 50 years (Fig. 5a). In the last 50 years simulated, wood harvest was significantly different between monospecific and 3-species mixed stands. Wood harvest was also significantly different between 2- and 3-species mixed stands, with wood harvest increasing with stand initial species richness, except in Ventoux and Vercors Lente (no significant difference between monospecific and 2-species mixed stands).

“Conversion management” scenario

Wood harvest was significantly correlated (p-value < 0.05 with Pearson test) with stand conversion for the period 2100–2150 (conversion level represented by stand targeted specific richness): 0.17 for Ventoux, 0.28 for Bauges and Vercors Lente, and 0.29 for Vercors Méaudre. For all sites, wood harvest in the long term, i.e., between 100 and 150 years, depended strongly on stand targeted species richness. In the last 50 years, wood harvest of monospecific stands managed in conversion to 3-species mixed stands was

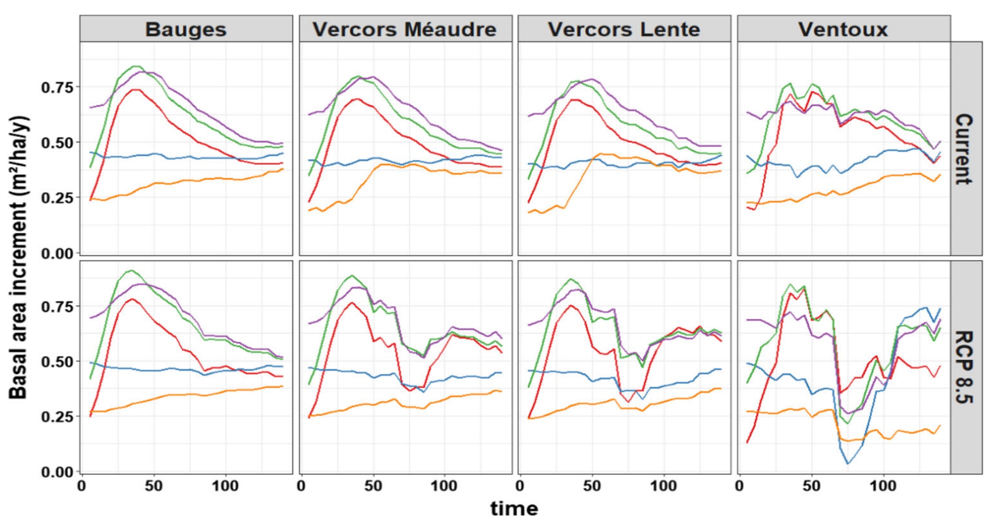

Fig. 2 Mean productivity in basal area of target species. Mean productivity in basal area of the target species in monospecific stands without management for each set of climate conditions, average of both altitudes. Each species is represented separately: beech (blue), Scots pine (purple), fir (green), spruce (red), and pubescent oak (orange). Each column represents each site, from left to right: Bauges, Ventoux, Vercors Lente, and Vercors Méaudre. Each row represents each climate: current climate or climate change (RCP 8.5)

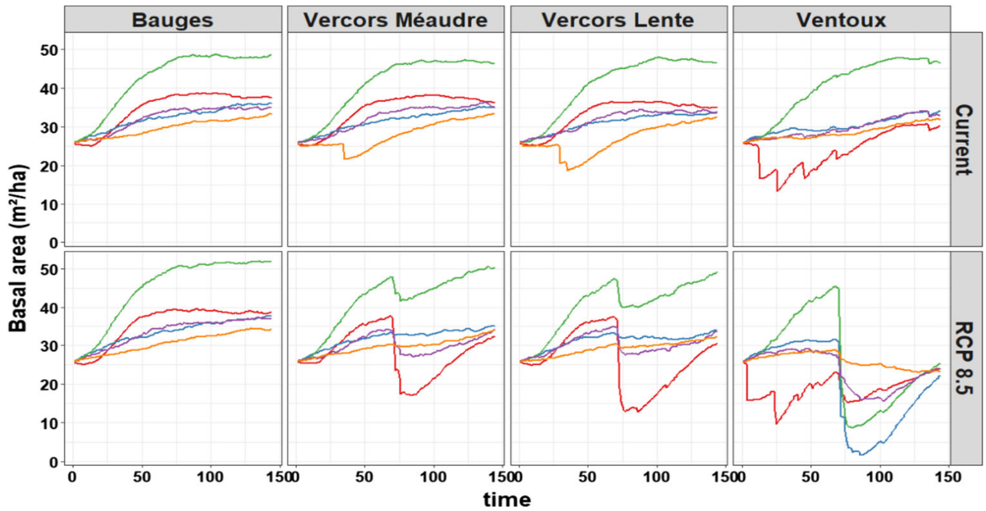

Fig. 3 Total basal area across the simulation. Total stand basal area of the target species in monospecific stands without management for each set of climate conditions across simulation, average of both altitudes. Each species is represented separately: beech (blue), Scots pine (purple), fir (green), spruce (red), and pubescent oak (orange). Each panel corresponds to one site: Bauges, Ventoux, Vercors Lente, and Vercors Méaudre. Each row represents each climate: current climate or climate change (RCP 8.5)

significantly higher than for monospecific stands with "stable" management (Fig. 5b), except in Ventoux. Thus, increasing species richness up to three species increased the possible wood harvest, except in the Ventoux site (Fig. 5b).

We also observed that stands experiencing the conversion management allowed reaching similar levels of harvested wood after 150 years than stands managed as mixed stands since the beginning of the simulation. Moreover, increasing diversity effect had the same pattern for both management scenarios. Moreover, conversion and stable mixed stand managements were equivalent in wood harvested, but depending on species, site, and period considered (Table S4). Conversion management of monospecific stands induced different responses depending of species: higher wood harvested than corresponding mixed stands (for fir), lower wood harvested (for pubescent oak and Scots pine, except in Ventoux), while for spruce and beech the pattern depended on site and period.

With a linear model (Box S4), we concluded mixture management has a significant and positive effect on mean wood harvest. Moreover, increasing drought induced decreasing wood harvest. However, this trend became weaker with increasing species richness (for sylvicultural scenario with objective basal of 30m^2/ha). This result showed a buffer effect of mixture management on drought in our specific case.

Discussion

Monospecific stand vulnerability under climate change

Our simulations suggested that climate change might strongly alter monospecific stands productivity in our study area (French Alps), depending on site and species considered. This pattern echoes other projections for the French Alps (Mina et al. 2017) indicating that climate change induces large alterations in the sustainability of many forest ecosystem

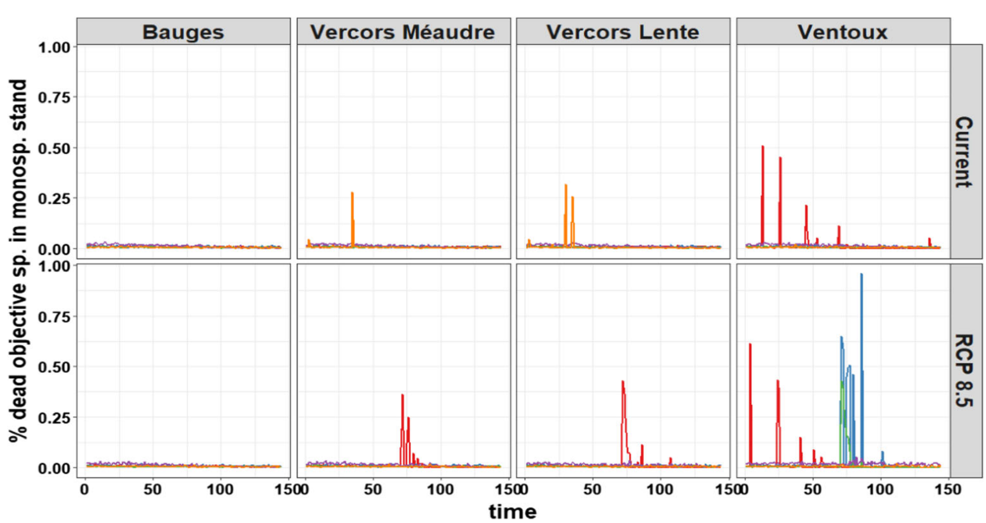

Fig. 4 Dead trees proportion of target species across the simulation. Mean annual mortality in basal area of the target species in monospecific stands without management for each set of climate conditions across simulation, average of both altitudes. Each species is represented separately: beech (blue), Scots pine (purple), fir (green), spruce (red), and pubescent oak (orange). Each column represents each site, from left to right: Bauges, Ventoux, Vercors Lente, and Vercors Méaudre. Each row represents each climate: current climate or climate change (RCP 8.5)

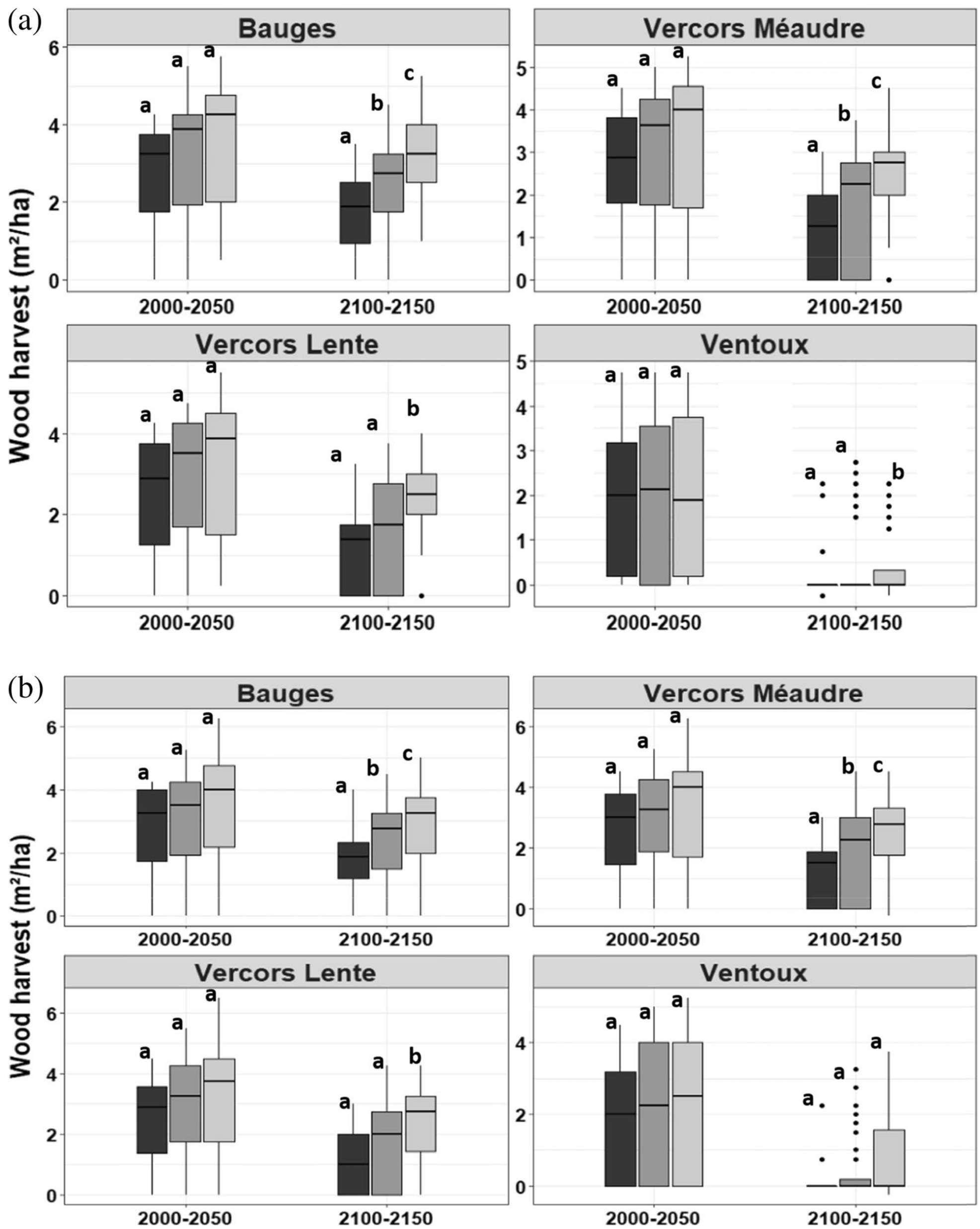

Fig. 5 Wood harvested with different **a** diversity levels and **b** conversion managements. **a** Wood harvest for initial (the first 50 years of the simulation) and final (the last 50 years of the simulation) time periods, with "stable management" scenarios (i.e., the management selected aims to stabilize initial stand composition). Objective species richness is represented by gray panel (1, 2, and 3 species, respectively, in black, dark gray, and light gray). Each part corresponds to one site: Bauges, Ventoux, Vercors Lente, and Vercors Méaudre. By site and period, we have 24 plots for monospecific stand, 72 plots for 2-species mixed stand, and 108 for 3-species mixed stand. Letters correspond to significant differences in wood harvest across diversity levels ($p < 0.05$), with a Tukey test for Bauges, Vercors Méaudre, and Vercors Lente and a Kruskal test for Ventoux. **b** Wood harvest for initial (the first 50 years of the simulation) and final (the last 50 years of the simulation) time periods, with "stable" and "conversion" management scenarios. The management selected aims to target a final stand composition, which can be different from the initial stand composition: 1 species (no differences, stable management), 2 species, or 3 species (conversion management), respectively, in black, dark gray, and light gray. Objective species richness is represented by gray panel. Each part corresponds to one site: Bauges, Ventoux, Vercors Lente, and Vercors Méaudre. By site and period, we have 24 plots for stable management, 96 plots for 2-species mixed stand conversion, and 144 for 3-species mixed stand conversion. Letters correspond to significant differences in wood harvest across diversity levels ($p < 0.05$), with a Tukey test for Bauges, Vercors Méaudre, and Vercors Lente and a Kruskal test for Ventoux

services (timber production, carbon storage, protection against rockfall and avalanches) and biodiversity conservation.

Monospecific fir and beech stands in Ventoux are highly vulnerable to dry conditions and soil water deficit, as summarized in Bréda et al. (2006b) review (for fir, see also Lebourgeois et al. 2013; Sánchez-Salguero et al. 2017). The trend depicted by our results is consistent with this review (according to our metrics): basal area of target species decreased very quickly (barely 50 years after the beginning of the simulation) and dropped to 10% of total proportion after 150 years under climate change because of increasing basal area of dead trees, induced by increasing dry conditions. The gaps in canopy induced by mortality events allowed pioneer or post-pioneer species (e.g., Scots pine or oak) to colonize the patch (after 100 years, Fig. S5). Thus, the mean productivity of monospecific stands did not seem vulnerable after 150 years in Ventoux because Scots pine and pubescent oak have replaced the less tolerant to drought species (either spruce, fir, or beech). However, some studies found higher vulnerability of Scots pine at its southern range limits in Switzerland (Bigler et al. 2006; Dobbertin et al. 2005), which may reduce competitive advantage of Scots pine in case of severe climate change. Moreover, pubescent oak and Scots pine stands seem to be sensitive to soil and atmospheric water deficits (Poyatos et al. 2008), which could also impact average productivity under repeated drought events.

For spruce stands in Vercors (Lente and Méaudre sites), the same trend was found. Spruce proportion decreased because of drier and warmer conditions. In fact, drought (through drought index) significantly affects spruce proportion (see Box S5). High vulnerability of monospecific spruce stands productivity was already identified in the Alps in both observed data under past and current climate (Hartl-Meier et al. 2014), because of high sensitivity to drought (see Lu et al. 1996 in Vosges mountain). Pubescent oak could benefit from the disappearance of spruce. However, decreasing proportion of most drought-sensitive species induced increasing proportion of most drought-tolerant species (Niinemets and Valladares 2006) that were subjected to strong competitive interactions in current climate.

Effect of mixed management on stands productivity

In our study, mixed stand management seemed to increase wood harvest after 100 years of simulation, maintaining forest cover. Our conclusions highlight that managing for increasing or maintaining species richness has generally positive impacts on productivity. Mixed stands without management could also be less vulnerable than monospecific stands, but it was not our point here. According to previous studies, mixed stand management was put forward as a good option to maintain forest functioning and services (e.g., spruce-birch stand, Felton et al. 2010) by accelerating conversion from monospecific to mixed stands or by maintaining mixed stands. Mixed stands have actually been reported to reduce species sensitivity to drought (fir in fir-beech or fir-spruce stands, Lebourgeois et al. 2013, but see also Grossiord et al. 2014b), and to increase (beech in beech-oak stands, Pretzsch et al. 2013; beech-spruce stand, Pretzsch et al. 2014; or Scots pine-oak stand, Steckel et al. 2019) or stabilize (beech-Scots pine stand, Del Río et al. 2017; beech-fir stands, Jourdan et al. 2019) species productivity when compared to monospecific stands.

In our simulations, monospecific stands of species at their range limit cannot be maintained in the coming decades (spruce, fir and beech in Ventoux, and spruce in Vercors), because these species are too vulnerable to climate change. This is in agreement with Mina et al.'s simulation study (2017) that found a sharp decrease of spruce proportion in mixed Vercors' stands under severe climate change scenarios and under different management scenarios. Moreover, Hlásny et al. (2017) showed that managing forests with higher diversity induces higher wood production of spruce in Eastern Alps with climate change (i.e., with higher temperature increase) compared to monospecific stand management.

In the Ventoux site, there is a complete substitution of initial species composition of late- or middle-succession species, i.e., spruce, fir, and beech, by early-succession species, i.e., Scots pine and oak. Such substitution pattern has been predicted with correlative species distribution models in North American forest ecosystems (Iverson and Prasad 2001) and in Mediterranean-alpine ecosystems (Benito et al. 2011). This trend is perhaps poorly estimated in our study because we considered a limited number of competitive species under stressful conditions (Scots pine and pubescent oak). However, one should notice that the interaction with other early-succession species (other pine species, for example) may change Scots pine or pubescent oak average productivity (Riofrío et al. 2017).

Our simulations showed that mixed stands with three species mixtures may allow a significant increase in harvested wood in comparison with monospecific stands, without altering their vulnerability to climate change. Consistently, our results also strongly suggest that converting monospecific stands may significantly improve stand performance both in terms of harvested wood and decrease in vulnerability to climate change (see Box S4). That being said, managed monospecific stand would be more productive than a mixed stand if the species is more drought-tolerant (for example, pubescent oak in Ventoux), in comparison with mixed stand management. Nevertheless, the knowledge on which composition, including monospecific stands, performs best under new climatic conditions would provide key information to managers about possible management options to ensure both the production and preservation of forests under climate change.

One interesting conclusion of our study is that the targeted composition was not necessarily the final composition, indicating that some mixed stands are more difficult to manage than others (Bauhus et al. 2017; Cordonnier et al. 2018). For example, in "stable management," a significant part of simulations did not reach the targeted species composition after 150 years (Fig. S6). This shows that instead of defining an a priori given composition, managers could instead adopt a management approach accompanying the natural dynamics of mixtures provided that the new species are adapted to the anticipated future climate. This approach would better fit with the concept of adaptive management that takes advantage of unpredicted events (Rist et al. 2013).

Methodological limitations or aspects

Although this study is among the first ones to test the effect of management scenarios for several forest types under climate change, it must be reminded that our simulations relied on simplified mechanisms compared to real processes and stochastic events involved in forest dynamics and ecosystem functioning. For example, competitive dynamics in ForCEEPS are focused on light acquisition and do not explicitly consider tree roots. Thus, competition for water and nutrients acquisition is only indirectly considered. Moreover, results' uncertainties are due not only to lack of knowledge on forest dynamics under climate change, but also to difficulties to reproduce some critical mechanisms (like photosynthesis or respiration outside the current temperature range). Other modeling approaches could have been used, like process-based ecophysiological models in which productivity is simulated through the outcome of photosynthesis, respiration, and allocation processes of the different compartments of the forest ecosystem (Dufrêne et al. 2005; Jonard et al. 2020; Landsberg et al. 2003). However, ForCEEPS presents a balance between complexity and generality and is notably more easily calibrated for new species, as it requires only a limited number of parameters (Morin et al. 2020). Furthermore, a perspective to obtain more robust predictions could be to couple ForCEEPS with an ecophysiological process-based model.

In addition, this study does not consider the possible role of extreme climatic events—extreme droughts, windstorms, or insect outbreak—on forest dynamics (Albrich et al. 2020; Lecina-Diaz et al. 2020; Senf et al. 2020), while such factors may greatly impact forest composition and functioning. Future works extending this study should include such climate-related drivers.

Furthermore, in this study, we considered that the establishment probability of species does not depend on the proportion of mature trees in the simulation, but only on the list initially decided and on climatic conditions. This simplification, classically done in gap models (Bugmann 2001), was also justified by the assumption that the studied forests are quite spatially heterogeneous, meaning that monospecific stands are surrounded by mixed forests (Jourdan et al. 2020).

Nevertheless, beyond these limits, we believe that ForCEEPS has a great potential to be a relevant tool in both functional ecology and forest management, especially because it is relatively easy to calibrate for many species. Regarding functional ecology, using such a model would for instance allow testing hypotheses related to changing inter-specific dominance in forests under climate change (García-Valdés et al. 2020). Regarding forest management, such a model could allow to test forestry itineraries under various climate scenarios, which very few models can achieve so far.

Forest management in context of climate change

In this study, we explored how management may help in maintaining forest cover and productivity to preserve—and maybe even improve in some cases—some ecosystem services provided by forests in the French Alps. However, because this study relied on simulations, our discussion on management should not be taken as a proper recommendation, but as an open debate. Furthermore, we focused here on wood harvest and forest cover, but obviously, management decisions must also consider other ecosystem services as forests are strongly multifunctional ecosystems (van der Plas et al. 2016), especially in mountains.

In our study, despite temperature and precipitation changes, pubescent oak seemed to remain less competitive than fir and beech in Vercors. This would suggest that favoring a shift in composition towards less drought-sensitive species in these sites—for instance with assisted migration (McLachlan et al. 2007; Vitt et al. 2010)—does not always appear relevant, while other management actions, like specific "favorable" forestry, could be sufficient. By "favorable" forestry for one species, we mean the promotion of the development of this species through stand management. Contrariwise, if forest cover decreases drastically, assisted migration of Mediterranean species (*Quercus pubescens*, *Quercus ilex*, *Pinus halepensis*, *or Pinus pinea*) could become an interesting option to maintain forest cover and limit soil erosion, depending on the specific soil requirement of each species. In our case, our results may inform about one type of migration: translocation just beyond the range limit (assisted range expansion; Leech et al. 2011), as we tested with monospecific stand of pubescent oak in Vercors and Bauges or Scots Pine in Bauges. Indeed, limited dispersal abilities and/or highly fragmented habitat (Vitt et al. 2010) can induce difficulties for some species to colonize available nearby habitat. In the case of Scots pine, which is already widely present in the South of Alps, this strategy of management seems appropriate.

Conclusion and perspectives

In this study, the simulations showed that monospecific stands currently growing in the southern part of their range would be vulnerable to climate change, i.e., spruce, fir, and beech stands in Ventoux or spruce stand in Vercors. Simulations showed also that other monospecific stands can persist under climate change in the Northern Alps, i.e., beech and fir stands in Bauges and Vercors. Then, we observed that managing mixed stands or conversion from pure to mixed stands would make it possible to maintain higher productivity in the long-term than monospecific stands, depending on species and sites considered. Our results may bring new elements to the discussion on forest management in the context of climate change, although we tested a limited number of combinations of "species composition-climate scenario-management scenario." Therefore, these simulations should rather be considered to be trends depicted at the forest level and not as precise recommendations at the stand level. Finally, considering operational cost of management actions and impact of change on wood quality should also be included in future studies. New simulations should be carried out to follow up the present work and determine more precisely which management would allow optimal wood harvest, for each site. For instance, it might be interesting to test mixtures with more than three species. Our modeling approach could easily study the same species over latitudinal gradients by controlling species proportion with four or five species. For instance, we could add other species, especially for Ventoux, such as other pine species (*Pinus pinaster*, *Pinus nigra*, *or Pinus halepensis*, for wood industry, and *Pinus pinea*, for non-wood forest products), other oaks species (*Quercus ilex*, *Quercus pyrenaica* or *Quercus suber*, for example), or maybe a non-native species (*Robinia pseudoacacia*).

Regarding the model outputs, it would be highly relevant to extend the range of ecosystem services studied. We briefly mentioned the protective forest role in mountain areas and conservation-related services, but many other services may be considered, if the model allows it: maintenance of micro-habitat (Courbaud et al. 2016), maintenance of carbon and nutrients cycles functioning (Corbeels et al. 2005), carbon storage (Delpierre et al. 2012), or spiritual or recreational dimension (McFarlane and Boxal 2000). More generally, it would be crucial to consider other ecosystems services to be important to maintain as wood production, to test various scenarios related to different forest policies (Morán-Ordóñez et al. 2020).

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Author contribution XM, CR, PD, TC, and MJ designed the research and methodology. XM and FdC developed the model and parameterized the species, including the management module, with the help of PD. MJ and BC carried out the simulations; MJ analyzed the data; MJ and XM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Simulations results will be deposited in the Dryad Digital Repository or Figure share and ForCEEPS is available on the CAPSIS platform, as ForCEEPS v1.1.

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