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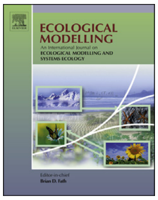

# Modelling the effect of climate-induced changes in recruitment and juvenile growth on mixed-forest dynamics: The case of montane–subalpine Pyrenean ecotones

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ABSTRACT

Most predictive models forecast significant upward displacement of forest species due to increases in temperatures, but not all the species respond in the same way to changes in climate. In temperate or mountain systems, biotic competitive interactions drive species distributions, and responses to climate change will ultimately depend upon productive and demographic processes such as growth, recruitment and mortality. We parameterized and used an individual-based, spatially explicit model of forest dynamics (SORTIE-ND) to investigate the role of species-specific differences in juvenile performance induced by climate change (juvenile growth and recruitment ability) in the dynamics of mixed forests located in the montane–subalpine ecotone of the Pyrenees. We assessed this role for two types of forests composed of three species with differing light requirements and sensitivity to climate change: (1) a mixed forest with two shade-intolerant pines (*Pinus uncinata* and *Pinus sylvestris*) and (2) a mixed forest composed by a shade-intolerant pine and a shade-tolerant fir (*Abies alba*). Our results show that for species with similar light requirements (i.e., both pines), small differences in sapling growth response to climate change can lead to significant differences in future species composition (an increase in *P. sylvestris* growth of 10% leads to an increase in its abundance from 42% to 50.3%). Conversely, in pine-fir forests, shade-tolerance results more decisive than climate-induced changes in growth in driving the future forest composition.

## 1. Introduction

Changes in climate are expected to alter the distribution of plants in mountainous areas, and most predictive models forecast an upward displacement of species, tracking increases in temperatures (Malcolm et al., 2002; Theurillat and Guisan, 2001). However, not all the species respond in the same way to changes in climate. For instance, upward expansion of species ranges in mid-mountain areas has been observed mainly when the spread of montane species was accompanied by an upward retreat of the lower limit of subalpine species due to climatically-induced dieback or decline (Jump et al., 2009; Lenoir et al., 2008; Peñuelas and Boada, 2003). When this is not the case, an absence of displacement, and even downslope movements of subalpine forests into the montane belt, have also occurred (Bodin et al., 2013; Hättenschwiler and Körner, 1995; Lenoir et al., 2010), revealing a more complex scenario in which forest responses to climate change ultimately depend upon species-specific demographic processes such as recruitment, growth and mortality (Coll et al., 2013). In this context, dynamic vegetation models offer an useful tool for predicting changes in the occurrence, abundance, and productivity of plant species in a long-term perspective (Bugmann et al., 2005; Graf et al., 2007; Snell et al., 2014). These models explicitly consider the effects of environmental conditions and biotic interactions on individual plant performance, making them especially suitable for assessing the evolution of systems where the species-specific responses are expected to lead to changes in the interactions among species.

Different factors commonly drive the leading and trailing edges of a given species' distribution (Coll et al., 2013; Purves, 2009; Thuiller et al., 2008). Generally, it is accepted that low temperatures determine the upper limit, whereas limited water availability and high temperatures often set the lower extreme (Loehle, 2000, 1998;

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Rickebusch et al., 2007). Yet, when no moisture limitation exists – such as in some temperate and mountain systems – biotic competitive interactions drive the lower boundary of ranges, and species find their low distributional limit when they confront other species with higher competitive ability (Loehle, 2003, 2000; MacArthur, 1984). This is the case for the mid-mountain forests of the Eastern Pyrenees (NE Spain), which are defined by the conjunction of *Pinus uncinata* Ram. ex DC with *Pinus sylvestris* L. and *Abies alba* Mill. In these forests, located in the ecotone between the montane and subalpine belt, *P. sylvestris* and *A. alba* find their upper elevational boundary, whereas *P. uncinata* thrives at its lower limit. Climate change predictions in the region include increases in temperatures but also slight reductions in precipitation with more intense and longer drought periods (Barrera-Escoda and Cunillera, 2011), but there are important uncertainties on the consequences that climate change can have on species-specific performance and forest dynamics. The uncertainties are particularly large for the juvenile stage, even though juveniles are known to be more sensitive to climate and to respond faster to variations in the environment than adults (Barbeito et al., 2012).

We used a spatially-explicit, individual-based model of forest dynamics (SORTIE-ND, Pacala et al., 1996, 1993), to investigate the possible long-term impact of climate-induced changes in juvenile performance (recruitment and growth) on the dynamics of mixed forests composed by (i) two species with similar ecological requirements, and (ii) two contrasting tree species, growing in the Pyrenean montane–subalpine forests. This model has been successfully used to test the effects of growth rate differential, disturbance rate and shade tolerance on competitive displacement, using theoretical pairs of species in which the growth of one of them was suppressed (Loehle, 2003). Here, we use SORTIE-ND to test the competitive dynamics of real, co-existing pairs of species under different climatic scenarios, taking into account their different ecological characteristics and requirements.

We aimed to determine if species-specific differences in juvenile performance associated with climate change are sufficient to predict changes in species composition in mixed forests located at the ecotone between montane and subalpine belts, even in the absence of disturbance or decline processes of the subalpine species (*P. uncinata*). We hypothesize that even small species-specific differences in the growth response of juveniles to climate change can be important for the future dynamics of the forest when it is composed of species with similar successional status (i.e., pines), no matter their relative recruitment success. In contrast, differences in initial composition would overcome potential climatic-induced variations in growth when the forest is composed of species differing in successional status (i.e., *P. uncinata* and *A. alba*).

## 2. Materials and methods

### 2.1. Study area and species

We studied the three most common tree species in the Eastern Pyrenees: (i) *P. uncinata* Ram. ex DC, a shade-intolerant to mid-tolerant conifer that in the Pyrenees is restricted to the subalpine belt (above 1600 m a.s.l.); (ii) *P. sylvestris* L., a shade-intolerant, widespread species that is semi-tolerant to drought and dominates the montane belt of the Pyrenees, and (iii) *A. alba* Mill., which is also distributed along the montane belt, but restricted to humid sites on shady, north-facing slopes. These species differ in their successional status and ecological requirements, but they can co-exist in a strip that is located between 1600 and 2000 m a.s.l., where they constitute the montane–subalpine ecotone. In these ecotones, *P. sylvestris* and *A. alba* find their upper elevational boundary, whereas *P. uncinata* thrives at its lower limit. The presence of the three species in the same stand is relatively uncommon in our study area, so we chose the two most common associations of these species: (i) a mixed pine forest (*P. uncinata*–*P. sylvestris*) and (ii) a pine-fir forest (*P. uncinata*–*A. alba*).

Climate change predictions in the region include increases in temperatures but also slight reductions in precipitation with more intense and longer drought periods (Barrera-Escoda and Cunillera, 2011). Such changes could affect the performance of montane species (*P. sylvestris* and *A. alba*), but are expected to affect in a lower extent the subalpine species (*P. uncinata*), which responds less to climate in terms of demography (Ameztegui and Coll, 2013; Coll et al., 2013; Gómez-Aparicio et al., 2011; Ruiz-Benito et al., 2013). Consequently, in these transition areas, climate change is not likely to lead to rapid upward retractions of *P. uncinata* – at least in the short-term – but might still induce species-specific differences in performance (i.e., recruitment, growth and mortality), leading to a breakup of current interspecific relationships.

### 2.2. Model description and parameterization

Simulations were performed using SORTIE-ND version 7.01 (http://www.sortie-nd.org) (Canham et al., 2005), which is a spatially explicit, individual-based model of forest dynamics based on the model SORTIE, first developed by Pacala et al. (1996). In SORTIE-ND, trees are categorized as seedlings, saplings, adults or snags, and the specific location of each tree is considered. SORTIE-ND simulates the recruitment, growth, and mortality of every individual within a plot using a combination of species-specific empirical and mechanistic processes. Population-level forest dynamics occur as the result of the life histories of every single individual in a plot and its interaction with other individuals and the environment, making it a good tool for modelling the dynamics of complex, mixed forests (Bose et al., 2015; Canham et al., 2004). We parameterized SORTIE for the transition forests between montane and subalpine elevational belts in the Pyrenees. The parameterization has been done over the last years through several field studies. The values of all the parameters used in this study are provided in Appendix A.

#### 2.2.1. Adult growth and mortality

In SORTIE-ND, adult radial growth depends on tree size, competition and climate, as shown in Canham et al. (2006) and Gómez-Aparicio et al. (2011). Diameter growth of trees is thus estimated as:

$$\text{Diam. Growth} = \text{PDG} \cdot \text{Size effect} \cdot \text{Temp. effect} \cdot \text{Prec. effect} \cdot \text{Crowding effect} \quad (1)$$

where PDG is the maximum potential diameter growth (in $\text{mm yr}^{-1}$), whereas size effect, crowding effect, temperature effect and precipitation effect are all factors that act to reduce the estimated maximum growth rate and which vary depending upon the conditions affecting a tree. Each of these effects is a scalar that ranges between 0 and 1. For *P. sylvestris* and *P. uncinata*, we obtained PDG, size effect, temperature effect and precipitation effect directly from the equations developed by Gómez-Aparicio et al. (2011) using data from Spanish Forest Inventory (IFN, Direccion General para la Biodiversidad, 2007). The crowding effect for these two species, and all the parameters in the case of *A. alba*, were estimated using likelihood methods (i.e., we estimated those parameters that maximized the likelihood of observing the growth responses measured in the field), using data from the IFN in the Catalan Pyrenees. More details on the sample sizes, parameter estimation and model selection can be found in Appendix B. We tried to obtain senescence patterns of adult mortality from the IFN using repeated-measures, but the young age of most Pyrenean forests did not allow us obtaining good estimators of senescence (as acknowledged by Ruiz-Benito et al., 2013). We thus assigned

**Table 1**
Summary of model runs for the mixed pine forest and pine-fir forest, including scenarios for the effects of climate on recruitment ability (5 scenarios for each case study) and juvenile growth (4 and 7 cases, respectively). Each of the 55 scenarios was run 10 times to account for stochasticity of some processes in the SORTIE-ND model. PIUN, *Pinus uncinata*; PISY, *Pinus sylvestris*; ABAL, *Abies alba*.

| Variables | Pine mixed forest (*P. uncinata*–*P. sylvestris*) | | Pine-fir forest (*P. uncinata*–*A. alba*) | |
|---|---|---|---|---|
| | Scenarios | Number | Scenarios | Number |
| Recruitment (as initial stand composition) | 90% PIUN–10% PISY<br>70% PIUN–30% PISY<br>50% PIUN–50% PISY<br>30% PIUN–70% PISY<br>10% PIUN–90% PISY | 5 | 90% PIUN–10% ABAL<br>70% PIUN–30% ABAL<br>50% PIUN–50% ABAL<br>30% PIUN–70% ABAL<br>10% PIUN–90% ABAL | 5 |
| Juvenile growth (as % of current, observed growth of each species) | PISY: 100% – 110% – 125% –150%<br>PIUN: 100% | 4 | ABAL: 50% – 75% – 90% – 100% –110% – 125% – 150%<br>PIUN: 100% | 7 |
| Total | | 20 | | 35 |

a maximum value of tree size for each species by combining data from the IFN and expert knowledge.

To reflect the effect of climate change on adult growth, we allowed climate to vary annually according to regionalized predictions made for the Catalan Pyrenees from the main emissions scenarios described in the IPCC Fourth Assessment report (Barrera-Escoda and Cunillera, 2011; IPCC, 2007). Future projections of mean monthly temperature and precipitation obtained for each scenario are summarized in Appendix C. Preliminary analyses showed that the simulation results were virtually identical regardless of the climate scenario chosen (data not shown), so we present here the results obtained for the severe emissions scenario (A2).

### 2.2.2. *Juvenile growth and mortality*

In SORTIE-ND, seedling and sapling radial growth are a function of understory light availability, and we used equations developed for the three study species in the area (Ameztegui and Coll, 2011). Light availability in the understory depends on the sum of the light intercepted by all the trees in a forest. In turn, light interception by a given tree depends on its size, shape and crown openness, which were parameterized in a previous study (Ameztegui et al., 2012). Juvenile mortality was determined as a function of recent radial growth history, assuming that growth is an integrated measure of whole-plant carbon assimilation and using field-data from 150 living and dead saplings of each species (Ameztegui and Coll, 2011).

## 2.3. *Effect of climate on juvenile performance: simulated scenarios and model runs*

The effects of some of the components of climate change on juvenile performance of the study species have been studied elsewhere (see for example Jach and Ceulemans (1999) or Domisch et al. (2001), but the results of these previous studies cannot be directly translated into the model – as we did for adult growth – because most of them have been conducted in other growing conditions or because they use different response variables. Consequently, we decided to assess the effect of climate change on recruitment and juvenile growth using a more theoretical approach.

To incorporate in our simulations the potential effects of climate change on the recruitment ability of species, we defined five theoretical initial conditions in terms of species composition: (i) 90% of regeneration of *P. uncinata* and 10% of the montane species (*P. sylvestris* or *A. alba*, depending upon the case study); (ii) 70% *P. uncinata* and 30% of the other species; (iii) 50% of each species (i.e., baseline); (iv) 30–70%; and (v) 10–90% (Table 1). All of these initial scenarios can be currently found in the study area, depending upon the abundance of each species and the environmental conditions.

To include the effects of climate change on juvenile performance, we modified the juvenile growth equations that were developed for these species in a previous work (Ameztegui and Coll, 2011) by a number of scalars. The values of the scalars were different for each species, matching the best current knowledge about the range of expected species-specific responses to changes in climate in the study area (Ameztegui and Coll, 2013). For *P. sylvestris*, we hypothesized that this species may benefit from a future increase in temperatures, since its current upper elevational limit is commonly considered to be climatically driven (Domisch et al., 2001; Hättenschwiler and Körner, 1995; Ninot et al., 2007). Therefore, we tested scenarios in which the juvenile growth rate of *P. sylvestris* increased by 0% (i.e., current measured growth rate), 10%, 25% and 50% of current measured values. More uncertainties exist regarding the possible response of *A. alba* juveniles to predicted changes in climate. Its growth could be favoured by warmer temperatures (Lenoir et al., 2009; Rabasa et al., 2013). Yet, as a drought-sensitive species, it may also suffer drought-induced decline, as has been already observed at its southernmost distribution limit in the peripheral ranges of the Pyrenees (Ameztegui and Coll, 2013; Macias et al., 2006). Therefore, in addition to the current growth scenario, we tested three scenarios in which growth was enhanced by 10%, 25% and 50%, versus three other scenarios in which growth was reduced in the same proportions. Finally, we assumed no effect of climate change on *P. uncinata* juvenile growth, since this species has shown very little response in performance to variations in both temperature and precipitation, including recruitment (Coll et al., 2013), and both juvenile and adult growth and mortality (Ameztegui and Coll, 2013; Gómez-Aparicio et al., 2011; Ruiz-Benito et al., 2013).

The combination of the 5 different initial proportions in recruitment and the different scenarios of juvenile growth rate (4 for the mixed pine forest; 7 for the pine-fir forest), produced a total of 55 different initial conditions to simulate (Table 1). Each simulated plot had 9 ha of surface and included 1000 juveniles $\text{ha}^{-1}$ of each species, randomly located across the plot. All seedlings corresponded to a size class bounded between 1 and 2.5 cm DBH, with the size of each individual being randomly chosen from a uniform distribution within that size class. Each simulation was run for 200 years, and each scenario was simulated ten times to account for stochasticity in some of the SORTIE-ND sub-models, such as tree

**Table 2**
Comparison of the predicted output (stem density, basal area, mean tree size and species composition) for baseline simulations at $t = 100$ years with values obtained from the Spanish Forest Inventory (IFN). Values are mean ± standard error and n indicates the number of IFN plots used to obtain the estimations. Details on the criteria to select the evaluation plots are included in Appendix D.

| | Pine mixed forest (*P. uncinata*–*P. sylvestris*) | | Pine-fir forest (*P. uncinata*–*A. alba*) | |
|---|---|---|---|---|
| | Predicted (baseline simulation) | Observed (IFN, $n = 24$) | Predicted (baseline simulation) | Observed (IFN, $n = 12$) |
| Stem density (stems $ha^{-1}$) | 676.4 ± 2.3 | 628.2 ± 58.7 | 808.9 ± 9.1 | 957.9 ± 156.0 |
| Basal area ($m^2\ ha^{-1}$) | 39.8 ± 0.1 | 36.5 ± 3.1 | 32.9 ± 0.5 | 41.9 ± 5.7 |
| Mean tree size (cm) | 24.5 ± 0.3 | 25.4 ± 0.7 | 19.0 ± 0.5 | 17.5 ± 5.1 |
| Proportion of *P. uncinata* (% of stem density) | 43.0 ± 0.4 | 55.0 ± 4.3 | 40.5 ± 1.2 | 43.6 ± 4.8 |
| Proportion of *P. uncinata* (% of basal area) | 41.5 ± 0.6 | 41.3 ± 4.8 | 82.1 ± 0.9 | 70.4 ± 15.5 |

spatial distribution (Deutschman et al., 1997; Vanhellemont et al., 2011).

### 2.4. Model evaluation and statistical analyses

To evaluate the model output against real data, we compared the stem density, basal area, mean tree size, diameter distribution and species composition obtained in baseline simulations (no effect of climate change, i.e. balanced composition of regeneration and current growth rate) against values obtained from the IFN for the Catalan Pyrenees (NE Spain). We performed several pre-defined filters to ensure that only mixed, mature forests composed by the study species were selected. Details on the criteria to select the evaluation plots are included in Appendix D.

To test the effects of the explanatory variables on forest dynamics, we defined two response variables: maximum total basal area of the plot during the simulation period ($m^2\ ha^{-1}$); and the proportion of the montane species (either *P. sylvestris* or *A. alba*, depending upon the case study) after100 years. We used linear models to test the effects of the explanatory variables (recruitment ability and juvenile growth) on the total basal area, while their effects on the proportion of basal area of a given species were modelled using beta regression, an approach that allows modelling of data that are measured on a continuous scale and restricted to the interval 0-1 (Cribari-Neto and Zeileis, 2010; Ferrari and Cribari-Neto, 2004). The effect of each explanatory variable on the dependent variable was assessed via Akaike Information Criterion (AIC), by comparing a model containing the variable with a 'null model', which assumes no effect of the explanatory variable (Burnham and Anderson, 2002). This approach is preferred to classical frequentist statistical hypothesis tests (e.g., ANOVA) when applied to simulation model outputs, since the number of replications, which ultimately drives *P*-values, is a trivial notion given current computing power (White et al., 2014). All analyses were performed in R 3.0.2 (R Development Core Team, 2014).

## 3. Results

### 3.1. Model evaluation

Stem density, basal area, mean tree size and species composition estimated for the baseline simulations were consistent with values currently observed for mixed-conifer forests in the Catalan Pyrenees (Table 2), as were diameter distributions (Fig. 1). The baseline simulation (i.e., with no effect of climate change) for the forest composed by *P. uncinata* and *P. sylvestris* predicted asymptotic growth of the stand, which reached a maximum basal area of 40 $m^2\ ha^{-1}$ around year 100–120 (Fig. 2a). Plot total basal area remained then relatively stable for some years, until it started to decrease from year 150 onwards, due to senescence of the largest trees. Stem density continuously decreased throughout the simulated period, from 1400 stems $ha^{-1}$ at year 20 to less than 500 stems $ha^{-1}$ at the end of the simulation (Fig. 2b), and values after 100 years matched those obtained for IFN mature plots (Table 2). The higher growth rate of *P. sylvestris* led to a higher initial basal area for this species during the first 100 years, but its dominance began to decrease from year 110 onwards. At current growth rates and given balanced regeneration composition (50% of each species), the model predicted a balanced between-species partitioning of basal area by year 200, as also observed in the IFN plots (Table 2), although it slightly underestimated the presence of *P. sylvestris* in the lowest diameter classes ($DBH < 10$, Fig. 1).

In the case of pine-fir forest, the baseline simulations correctly estimated the composition and structure of these forests according to IFN, although they slightly underestimated the total basal area and stem density of the plot (Table 2). During the first few decades, there was clear dominance by pine, which reached a maximum basal area of 32.6 $m^2\ ha^{-1}$ at year 120 (Fig. 2c). There were more stems per hectare for fir than for pine from year 30 onwards (Fig. 2d), but the low growth rate of fir maintained its basal area at values less than 10 $m^2\ ha^{-1}$ throughout the simulation period. As the dominance of pines progressively decreased, the slow growth of *A. alba* prevented a species substitution, resulting in a global decrease in total basal area of the plot from year 150 onwards.

### 3.2. Effects of recruitment and juvenile growth scenarios on mixed-forest dynamics

For the association of both shade-intolerant species (*P. uncinata*–*P. sylvestris*), initial species composition affected the maximum total basal area of the plot throughout the simulation period (Table 3). Higher initial proportions of *P. sylvestris* in the stand led to higher maximum values of basal area, but the differences were somewhat small and probably not biologically relevant (*sensu* Martínez-Abraín, 2008). For instance, when this species accounted for 90% of the initial stand, the maximum basal area was only 4 $m^2\ ha^{-1}$ greater than when the stand was dominated by *P. uncinata*. There was no evidence that juvenile growth rate affected the predicted values of maximum basal area (Table 3). In all of the tested scenarios, the final abundance of *P. sylvestris* in the stand was higher than its initial abundance (Fig. 3a). Although initial species composition of the stand was the main factor affecting its final composition, inter-specific differences in juvenile growth rate also resulted in major differences in final stand composition, with a strong interaction between both factors (Table 3). Enhanced juvenile growth of *P. sylvestris* induced stronger changes in final stand composition in the cases when initial composition was balanced or when *P. sylvestris* was slightly underrepresented, even resulting in rank-reversal in species dominance (Fig. 4). For example, the final proportion of *P. sylvestris* in the stand varied little with enhanced growth when the initial proportion of this species was 90%, but it rose from 14.3% to 31.4% of plot total basal area for the scenario in which the initial proportion of *P. sylvestris* was 10%.

For the ecologically contrasted *P. uncinata*–*A. alba* association, both maximum stand basal area and the proportion of fir were only

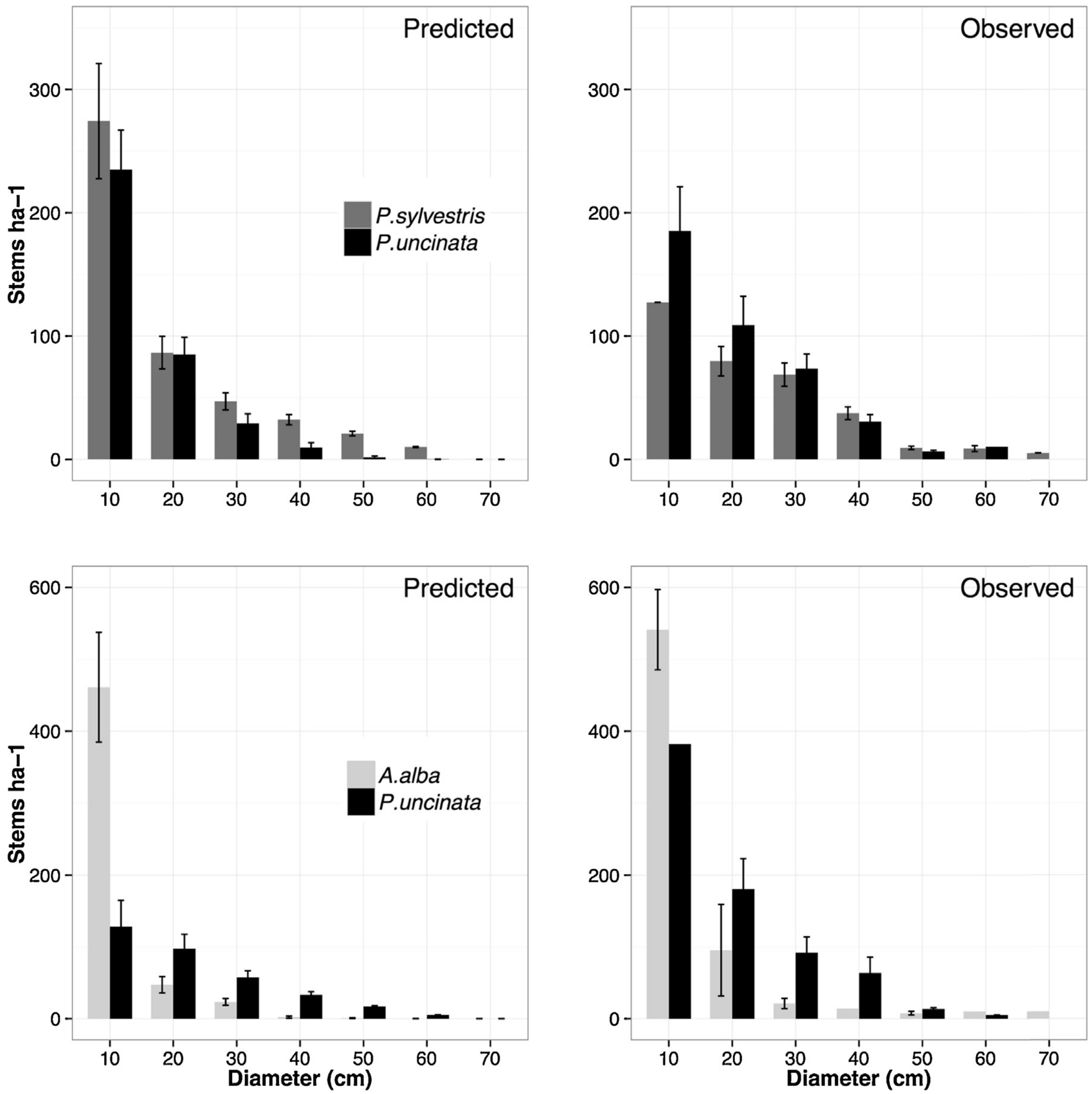

**Fig. 1.** Comparison of the predicted diameter distribution for baseline simulations at $t = 100$ years with observed values obtained from the Spanish Forest Inventory (IFN). Values are mean ± standard error. Details on the criteria used to select the evaluation plots are included in Appendix D. The baseline simulations represent the dynamics of a forest with a balanced initial composition of regeneration and no climatic constraints on juvenile or adult growth.

affected by initial composition and not by juvenile growth (Table 3). The initial proportion of fir in the stand caused significant changes in total basal area: the more fir, the lower the total basal area, but in all cases fir lost presence in the stand when compared to the initial composition (Fig. 4b). Even when the initial fir proportion was 70%, the final stand was dominated by pine, which had greater basal area during the simulation period (Fig. 5). Only when the initial presence of fir was 90% did this species escape from competitive effects that

**Table 3**
Comparison of alternate models (using $AIC_c$) relating maximum basal area and species composition after 100 years of simulation to recruitment and juvenile growth of mixed pine (*P. uncinata* and *P. sylvestris*) and pine-fir forests (*P. uncinata* and *A. alba*).

| $AIC_c$ values | Mixed pine forest (*P. uncinata*–*P. sylvestris*) | | Pine-fir forest (*P. uncinata*–*A. alba*) | |
|---|---|---|---|---|
| Variable | Maximum basal area | Proportion of *P. sylvestris* | Maximum basal area | Proportion of *A. alba* |
| Null | 0 | 0 | 0 | 0 |
| Recruitment | **−608.3** | **−847.7** | **−1587.4** | **−1714.8** |
| Juvenile growth | −5.6 | **−13.8** | 9.7 | 8.9 |
| Recr. + Juv. growth | – | **−415.3** | – | – |
| Recr. * Juv. growth | – | **−418.2** | – | – |

The null model is given a ΔAIC of zero. For univariate models, the difference in AIC between this model and all others is reported, and $\Delta AIC < 0$ for a model indicates better empirical support for that model than for the null model. Values in bold indicate strong empirical support for that model (i.e., $\Delta AIC < -10$). When there is support for more than one independent variable, ΔAIC of the bivariate model indicates differences in AIC compared to the best univariate model (i.e., support for the interaction).

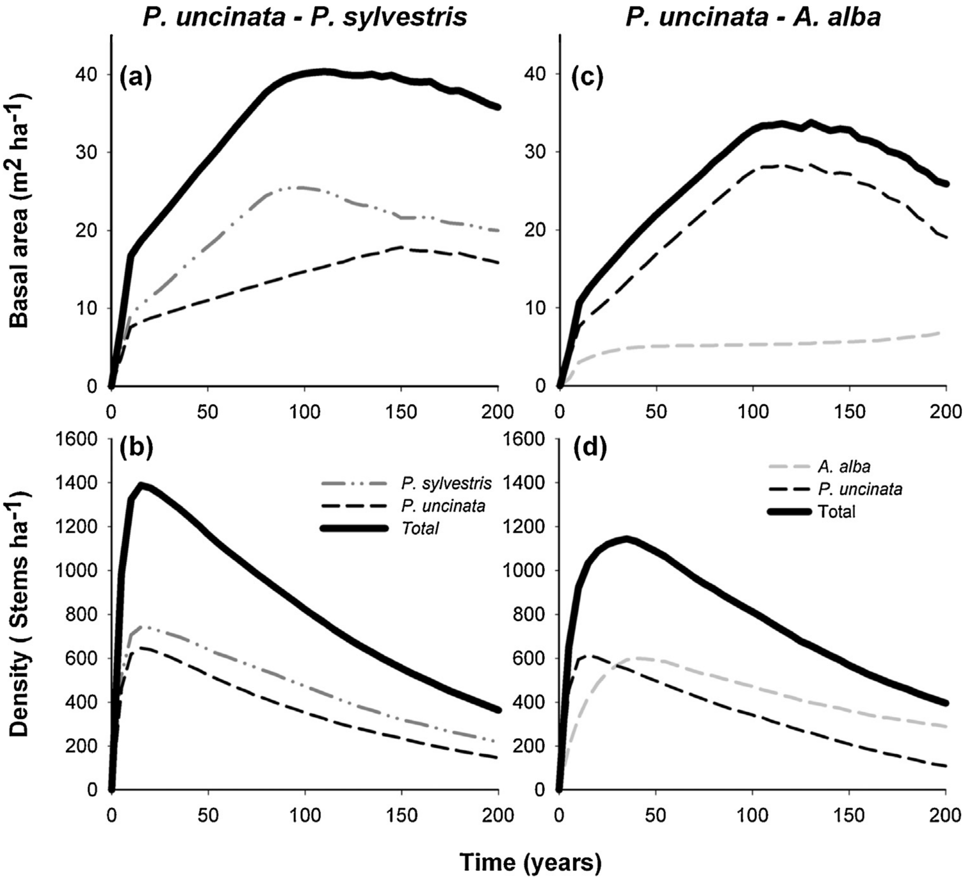

**Fig. 2.** Output of the SORTIE-ND baseline simulations for a mixed pine forest (left panel) and a mixed pine-fir forest (right panel) over a 200-year simulation period showing (a and c) basal area (m$^2$ ha$^{-1}$) and (b and d) density (stems ha$^{-1}$) of adult trees (DBH > 7.5 cm) for *Pinus uncinata*, *Pinus sylvestris* and *Abies alba*. The baseline simulations represent the dynamics of a forest with a balanced initial composition of regeneration and no climatic constraints on juvenile or adult growth. The values that are shown for each figure are the mean output for the ten repetitions run for each scenario.

were exerted by pine and was the most abundant species in the final stand in terms of basal area.

## 4. Discussion

### 4.1. Climate-induced changes in forest dynamics in mixed-pine forests

Our results show that when the montane–subalpine ecotone is composed of species with similar ecological characteristics (i.e., *Pinus* species), climatically induced differences in performance – either in recruitment or growth – can promote significant increases in the relative abundance of the montane species. In effect, for montane species such as *P. sylvestris*, for which regeneration is currently limited by cold temperatures, higher reproductive success and increases in juvenile growth rate can be expected with the new climatic conditions, and it is likely that these species will increase their presence and dominance in the mixed-forests located close to their upper elevational limit. If the increase in the length of the growing season follows the same rate that has been observed to date, increases in growth rates up to 20–25% can be expected in the short- to medium-term (Peñuelas et al., 2002). Under this scenario, our results show that these changes are sufficient to induce substantial changes in the composition of these forests. The effect of juvenile growth on future species composition was particularly important when *P. sylvestris* was slightly underrepresented (30% of the initial composition). Therefore, even in a scenario in which its recruitment ability may not be particularly favoured by climatic conditions or the disturbances regime, a potential compensatory effect that offsets this constraint could exist through enhanced growth of already established juveniles, so that an increase presence of Scots pine in the montane–subalpine ecotone can yet be expected.

### 4.2. Climate-induced changes in forest dynamics in mixed pine-fir forests

In mixed-forests constituted of species with different ecological characteristics, such as the pine-fir association, interspecific biotic competition can overcome climate-induced variations in performance, at least when both species are present at comparable developmental stages. Potentially enhanced growth rates of a shade-tolerant species such as silver fir would not lead to significant changes in forest dynamics, mainly due to the faster height growth accrued by intolerant pines under non-limiting light conditions and the subsequent competitive effects that are exerted on the seedlings of the shade-tolerant fir (Aunós et al., 2007). More interestingly, our results suggest that reduction in fir juvenile growth, which would derive from its greater drought-sensitivity (Pagès and Michalet, 2003; Peguero-Pina et al., 2007; Robakowski et al., 2005, 2003), would not affect its persistence in the stand either. As a shade-tolerant species, silver fir has developed a conservative resource-use strategy that allows it to remain suppressed in the understory for years, due to its intrinsic ability to maintain low radial growth when growing under shade conditions (Ameztegui and Coll, 2011). This behaviour is observed in the model simulations, where the low abundance of fir in the final stand is not a

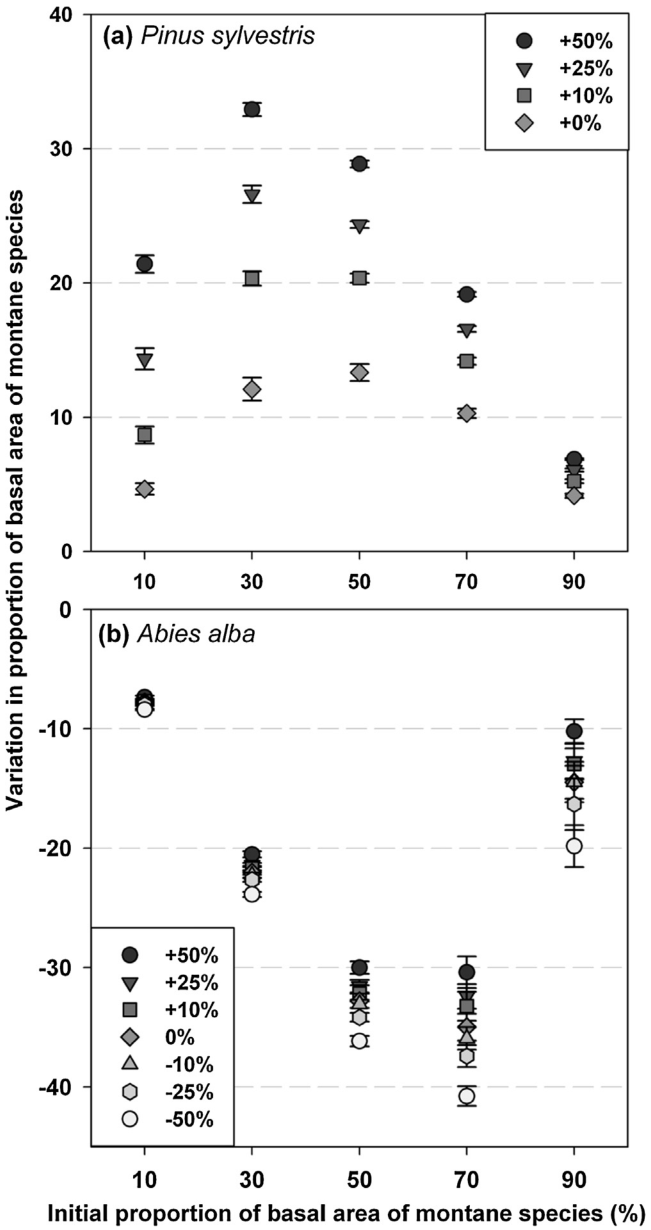

**Fig. 3.** Variation in the proportion of montane species in the stand at year 100 expressed as a percentage of total basal area of the stand (BA, $m^2\ ha^{-1}$) and as compared to the initial proportion. A value of 0 would indicate no change in the proportion of montane species after 100 years, whereas positive values indicate an increase in the dominance of those species, and negative values a decrease. Results are shown for several scenarios, which combine different initial stand composition and juvenile growth rates for (a) *Pinus sylvestris* and (b) *Abies alba.* Symbols represent mean output for ten simulations run for each scenario; error bars are the standard errors of these repetitions (see text for details). Legend indicates the simulated growth rate for juveniles of montane species relative to current growth. Note that the scale is different for each panel.

consequence of its high mortality rate; rather, it is caused by its low growth rate when the stand is dominated by pines.

### 4.3. *The effect of shade tolerance on climate-induced dynamics*

Previous simulations using pairs of theoretical species showed that shade tolerance has a profound effect on the rate of competitive displacement (Loehle, 2003), and faster migration rates have been reported for early successional species (Meier et al., 2012). Our results confirm these observations, but also highlight that the low spread of shade-tolerant species may not only be a consequence of dispersal limitations, but also of the competitive effects exerted by more shade-intolerant species residing in the subalpine belt. Simulations with a pure stand of *A. alba* during preliminary analyses showed that the model correctly predicted the structure and productivity of this species when it was growing alone (stem density: 534.4 stems $ha^{-1}$; basal area: 30.4 $m^2\ ha^{-1}$; mean tree size: 19.9 cm at year 100), thereby indicating that the low degree of development of fir in the simulated stands was not a result of a poor prediction of fir's growth by the model per se, but a consequence of the dominance effect of pine and its higher growth rate.

Hence, the chances that a tolerant species such as silver fir reaches the canopy and constitutes a mature forest will depend largely upon its ability to establish before the regeneration of more shade-intolerant species and to initially dominate the understory (Aunós et al., 2007; Fisichelli et al., 2014). As a shade-tolerant species, *A. alba* usually anticipates regeneration and thus dominates the understory, leading to a greater stem density in mature stands (Aunós et al., 2007). This behaviour is observed in our simulations, in which fir had to constitute at least 90% of initial stand composition in order to dominate the stand at maturity.

This ability to dominate the understory could be affected by climatic conditions, but will mainly be determined by the structure of the adult forest, which ultimately depends on the regime of natural and anthropogenic disturbances (Loehle, 2003). Major disturbances would favour shade intolerant pioneers relative to shade-tolerant species, slowing down the invasion rate, whereas partial canopy removal may favour the recruitment of shade-tolerant seedlings that would eventually dominate the forest at maturity. Indeed, the current presence of fir in the montane–subalpine ecotone often indicates the progressive densification and closure of the stands as an advanced step in the recolonization of open areas or as a reduction in cutting pressure (Ameztegui et al., 2010; Poyatos et al., 2003).

### 4.4. *Shortcomings of the model and future research directions*

Although the results presented here are based on theoretical scenarios of change in recruitment and juvenile growth, they provide valuable information about the different paths that the dynamics of a mixed forest can take depending on how climate affects each of the species that compose it. As in any modelling approach involving future predictions and climate change, we could not validate the obtained results with real data, making it difficult to elucidate if the results obtained were a behaviour of the studied natural system or a merely propriety of the model. Therefore, all conclusions from our results depend upon the extent to which the model is able to mimic the dynamics of the studied ecosystems. SORTIE-ND proved to correctly predict stem density, basal area, species composition and diameter distribution observed for mixed-conifer forests in the Catalan Pyrenees, making us confident of its ability to mimic the dynamics of these systems.

Nevertheless, a number of processes were not explicitly incorporated in the model that could have had an effect in our predictions. Tree mortality, for example, is one of the most important processes driving the dynamics of forest populations at the trailing edge (Hampe and Petit, 2005; Loehle, 2003). In this study we assumed that sapling mortality was a function of recent radial growth. The role of growth as an integrated measure of whole-plant carbon assimilation and a proxy for mortality is well established (Kobe et al., 1995), and recent studies have highlighted competition and forest structure as the most important determinants of tree mortality in Spanish forests (Benito-Garzón et al., 2013; Ruiz-Benito et al., 2013). However, if resident subalpine species such as *P. uncinata* die back under future climatic change prior to the immigration of montane species, the competitive restrictions that are exerted on shade-tolerant species may be less

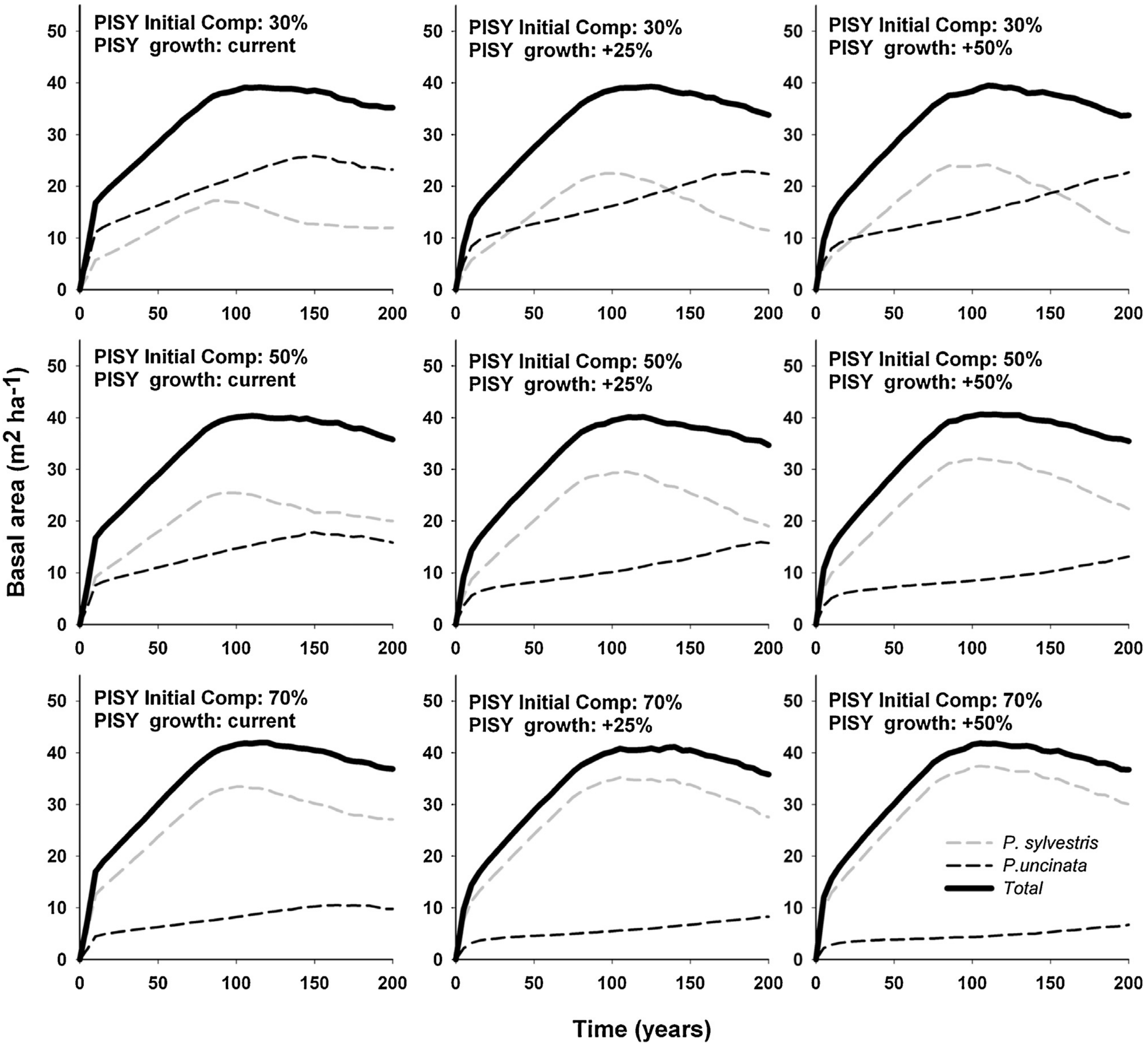

**Fig. 4.** Basal area ($m^2$ $ha^{-1}$) of adult trees of *Pinus uncinata* and *Pinus sylvestris* that was predicted by SORTIE-ND for a mixed pine forest over a 200-year simulation period under different combined scenarios of recruitment ability (rows) and juvenile growth rate (columns). The values that are shown are the mean output for the ten repetitions run for each scenario. PISY: *Pinus sylvestris*.

important than in the scenarios that were tested. Nevertheless, as stated in the introduction, the current knowledge about this species does not suggest this scenario for the next few decades (Ameztegui and Coll, 2013; Ruiz-Benito et al., 2013).

The model SORTIE-ND assumes that light is the main factor driving the dynamics of the forests. Although this has been shown to be true in our study area (see Ameztegui and Coll (2011), other factors such as the availability of water and nutrients (or other microsite conditions) could also affect the dynamic of the simulated systems, particularly in the case of mixed pine-fir stands (Peguero-Pina et al., 2007; Toromani et al., 2011). Unfortunately, SORTIE-ND does not currently allow the inclusion of more than two limiting resources in the growth functions, and therefore we could not explicitly test the potential effect of other factors in our predictions. However, these limiting factors are likely to act in the same direction as light limitations, i.e. they would probably limit fir growth more than pine growth and thus they may not significantly alter the observed trends. In any case, the explicit assessment of the role of these other factors is one of the next steps worth considering. At a larger scale, natural and anthropogenic disturbances can sharply modify the environment and create conditions that are more favourable to some species than to others, depending on their periodicity, size and severity (Schumacher et al., 2004; Seidl et al., 2011). Adequately addressing the potential role of disturbances on forest dynamics would hence require an additional calibration effort that is beyond the scope of this paper. Previous simulations have suggested that large scale disturbances would favour shade intolerant species, whereas smaller scale disturbances such as the partial removal of the canopy would favour the more shade tolerant species (Loehle, 2003).

Last, extreme climatic events and inter-annual variability in climate have the potential to affect forests much more than gradual changes in temperature (Lindner et al., 2014), and periods of severe drought or extreme cold temperatures can induce large mortalities for the study species when they grow beyond the limits of their current range (Ameztegui and Coll, 2013). Yet, we still lack information on how climate change will affect these processes to incorporate them into predictive models in a meaningful way, and

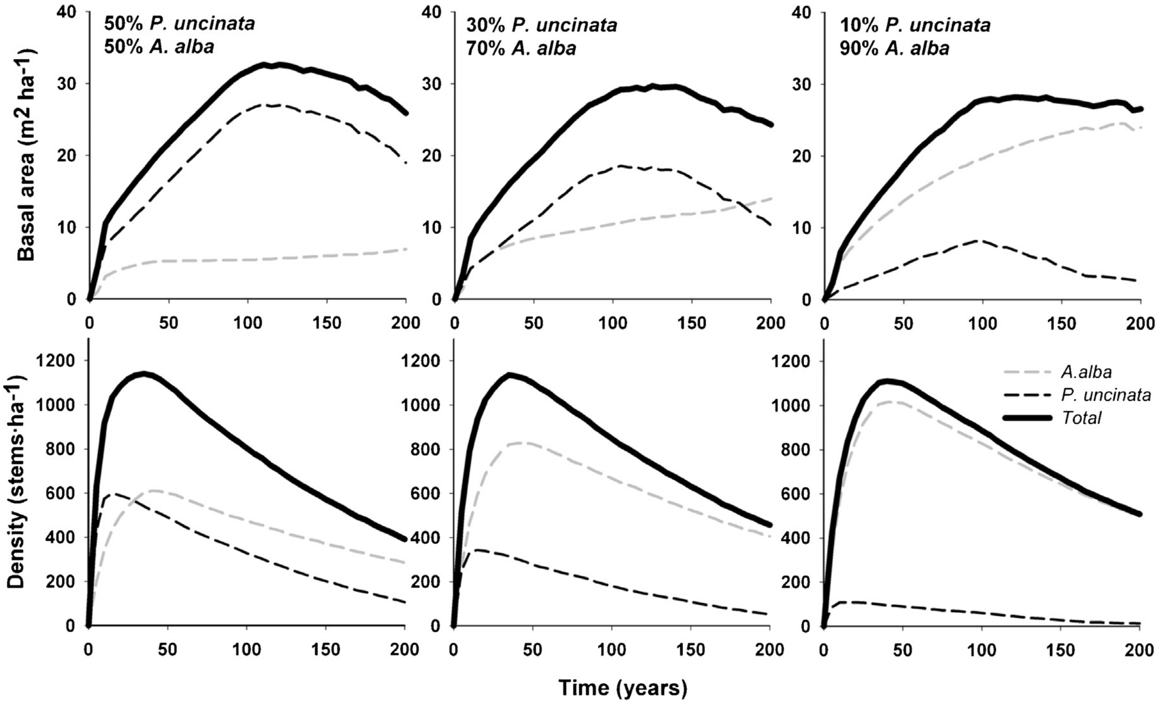

**Fig. 5.** Basal area (m$^2$ ha$^{-1}$) and stem density (stems ha$^{-1}$) of adult trees of *Pinus uncinata* and *Abies alba* predicted by SORTIE-ND for a mixed pine-fir forest over a 200-year simulation period under different scenarios of recruitment ability, expressed as different initial species composition. The values that are shown for each figure are the mean output for the ten repetitions run for each scenario.

it must also be considered that increasing the complexity of a model often leads to higher uncertainty and is not always a guarantee of better predictions (Kimmins et al., 2008).

## 5. Conclusion

We found that species-specific, climate-induced changes in juvenile performance (either recruitment or juvenile growth) can lead to changes in long-term forest dynamics, but that that this effect is affected by the shade tolerance of the montane species. In the case of the ecologically contrasted *P. uncinata -A. alba* pairing, high dominance of the former and the ability of the latter to remain suppressed in the understory appeared to buffer potential effects of changes in fir juvenile growth rate due to climate change. Moreover, climatically induced changes in juvenile performance (recruitment and growth) emerged as being more important than adult growth in terms of driving the dynamics of these mixed forests. The model of forest dynamics that we used (SORTIE-ND) proved to be adequate for simulating the productivity, species composition, and dynamics of Pyrenean mixed forests. The model explicitly deals with interspecific competition, and we believe that it constitutes a valuable tool for analyzing the main processes that can foster or constrain the dynamics of mixed forests located in the ecotone between montane and subalpine belts. Given the large uncertainties that still exist regarding initial life stages of the species, we stress the need for further research that would help us not only to construct more realistic projections of forest dynamics, but also to better understand, predict and anticipate the effects of climate change on our forests.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.06.029

## References

Ameztegui, A., Brotons, L., Coll, L., 2010. Land-use changes as major drivers of mountain pine (*Pinus uncinata* Ram.) expansion in the Pyrenees. Glob. Ecol. Biogeogr. 19, 632–641.

Ameztegui, A., Coll, L., 2011. Tree dynamics and co-existence in the montane–sub-alpine ecotone: the role of different light-induced strategies. J. Veg. Sci. 22, 1049–1061.

Ameztegui, A., Coll, L., 2013. Unraveling the role of light and biotic interactions on seedling performance of four Pyrenean species under environmental gradients. For. Ecol. Manage. 303, 25–34.

Ameztegui, A., Coll, L., Benavides, R., Valladares, F., Paquette, A., 2012. Understory light predictions in mixed conifer mountain forests: role of aspect-induced variation in crown geometry and openness. For. Ecol. Manage. 276, 52–61.

Aunós, Á., Martínez, E., Blanco, R., 2007. Tipología selvícola para los abetales españoles de *Abies alba* Mill. Investig. Agrar. Sist. y Recur. For. 16, 52–64.

Barbeito, I., Dawes, M.A., Rixen, C., Senn, J., Bebi, P., 2012. Factors driving mortality and growth at treeline: a 30-year experiment of 92 000 conifers. Ecology 93, 389–401.

Barrera-Escoda, A., Cunillera, J., 2011. Primer informe sobre la generació d'escenaris climàtics regionalitzats per a Catalunya durant el segle XXI. Informe tècnic. Servei Meteorològic de Catalunya, Departament de Territori i Sostenibilitat, Generalitat de Catalunya, Barcelona, Spain.

Benito-Garzón, M., Ruiz-Benito, P., Zavala, M.A., 2013. Interspecific differences in tree growth and mortality responses to environmental drivers determine potential species distributional limits in Iberian forests. Glob. Ecol. Biogeogr. 22, 1141–1151.

Bodin, J., Badeau, V., Bruno, E., Cluzeau, C., Moisselin, J.-M., Walther, G.-R., Dupouey, J.-L., 2013. Shifts of forest species along an elevational gradient in Southeast France: climate change or stand maturation? J. Veg. Sci. 24, 269–283.

Bose, A.K., Harvey, B.D., Coates, K.D., Brais, S., Bergeron, Y., 2015. Modelling stand development after partial harvesting in boreal mixedwoods of eastern Canada. Ecol. Model. 300, 123–136.

Bugmann, H., Zierl, B., Schumacher, S., 2005. Projecting the impacts of climate change on mountain forests and landscapes. Adv. Glob. Chang. Res. 23, 477–487.

Burnham, K.P., Anderson, D., 2002. Model Selection and Multi-Model Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York, USA.

Canham, C.D., LePage, P.T., Coates, K.D., 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Can. J. For. Res. 34, 778–787.

Canham, C.D., Murphy, L.E., Papaik, M.J., 2005. SORTIE-ND: Software for Spatialy-explicit Simulation of Forest Dynamics.

Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., Twery, M.J., 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecol. Appl. 16, 540–554.

Coll, M., Peñuelas, J., Ninyerola, M., Pons, X., Carnicer, J., 2013. Multivariate effect gradients driving forest demographic responses in the Iberian Peninsula. For. Ecol. Manage. 303, 195–209.

Cribari-Neto, F., Zeileis, A., 2010. Beta regression in R. J. Stat. Softw. 34, 1–24.

Deutschman, D.H., Levin, S.A., Devine, C., Buttel, L.A., 1997. Scaling trees to forests: analysis of a complex simulation model. Science 277, 1684.

Direccion General para la Biodiversidad, 2007. Tercer Inventario Forestal Nacional (1997–2007). Ministerio de Medio Ambiente, Madrid.

Domisch, T., Finér, L., Lehto, T., 2001. Effects of soil temperature on biomass and carbohydrate allocation in Scots pine (*Pinus sylvestris*) seedlings at the beginning of the growing season. Tree Physiol. 21, 465–472.

Ferrari, S., Cribari-Neto, F., 2004. Beta regression for modelling rates and proportions. J. Appl. Stat. 31, 799–815.

Fisichelli, N.A., Frelich, L.E., Reich, P.B., 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography (Cop.) 37, 152–161.

Gómez-Aparicio, L., García-Valdés, R., Ruiz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. Glob. Chang. Biol. 17, 2400–2414.

Graf, R.F., Bollmann, K., Bugmann, H., Suter, W., 2007. Forest and landscape structure as predictors of capercaillie occurrence. J. Wildl. Manage. 71, 356–365.

Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. Ecol. Lett. 8, 461–467.

Hättenschwiler, S., Körner, C., 1995. Responses to recent climate warming of *Pinus sylvestris* and *Pinus cembra* within their montane transition zone in the Swiss Alps. J. Veg. Sci. 6, 357–368.

IPCC, 2007. Climate change 2007: the physical science basis. In: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, UK and New York, NY, USA.

Jach, M.E., Ceulemans, R., 1999. Effects of elevated atmospheric $CO_2$ on phenology, growth and crown structure of Scots pine (*Pinus sylvestris*) seedlings after two years of exposure in the field. Tree Physiol. 19, 289–300.

Jump, A.S., Mátyás, C., Peñuelas, J., 2009. The altitude-for-latitude disparity in the range retractions of woody species. Trends Ecol. Evol. 24, 694–701.

Kimmins, J.P. (Hamish), Blanco, J.A., Seely, B., Welham, C., Scoullar, K., 2008. Complexity in modelling forest ecosystems: how much is enough? For. Ecol. Manage. 256, 1646–1658.

Kobe, R.K., Pacala, S.W., Silander, J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. 5, 517–532.

Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E., Dullinger, S., Pauli, H., Willner, W., Svenning, J.-C., 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography (Cop.) 33, 295–303.

Lenoir, J., Gégout, J.-C., Marquet, P.A., de Ruffray, P., Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. Science 320, 1768–1771.

Lenoir, J., Gégout, J.-C., Pierrat, J.-C., Bontemps, J.-D., Dhôte, J.-F., 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). Ecography (Cop.) 32, 765–777.

Lindner, M., Fitzgerald, J.B., Zimmermann, N.E., Reyer, C., Delzon, S., van der Maaten, E., Schelhaas, M.-J., Lasch, P., Eggers, J., van der Maaten-Theunissen, M., Suckow, F., Psomas, A., Poulter, B., Hanewinkel, M., 2014. Climate change and European forests: what do we know, what are the uncertainties, and what are the implications for forest management? J. Environ. Manage. 146, 69–83.

Loehle, C., 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. J. Biogeogr. 25, 735–742.

Loehle, C., 2000. Forest ecotone response to climate change: sensitivity to temperature response functional forms. Can. J. For. Res. 30, 1632–1645.

Loehle, C., 2003. Competitive displacement of trees in response to environmental change or introduction of exotics. Environ. Manage. 32, 106–115.

MacArthur, R.H., 1984. Geographical Ecology: Patterns in the Distribution of Species. Princeton University Press, Princeton, NJ, USA.

Macias, M., Andreu, L., Bosch, O., Camarero, J.J., Gutiérrez, E., 2006. Increasing aridity is enhancing silver fir (*Abies alba* Mill.) water stress in its south-western distribution limit. Clim. Change 79, 289–313.

Malcolm, J.R., Markham, A., Neilson, R.P., Garaci, M., 2002. Estimated migration rates under scenarios of global climate change. J. Biogeogr. 29, 835–849.

Martínez-Abraín, A., 2008. Statistical significance and biological relevance: a call for a more cautious interpretation of results in ecology. Acta Oecol. 34, 9–11.

Meier, E.S., Lischke, H., Schmatz, D.R., 2012. Climate, competition and connectivity affect future migration and ranges of European trees. Glob. Ecol. Biogeogr. 21, 164–178.

Ninot, J.M., Carrillo, E., Font, X., Carreras, J., Ferre, A., Masalles, R.M., Soriano, I., Vigo, J., 2007. Altitude zonation in the Pyrenees. A geobotanic interpretation. Phytocoenologia 37, 371–398.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements. II. Estimation, error analysis and dynamics. Ecol. Monogr. 66, 1–43.

Pacala, S.W., Canham, C.D., Silander, J.A., 1993. Forest models defined by field-measurements. I. The design of a northeastern forest simulator. Can. J. For. Res. 23, 1980–1988.

Pagès, J.-P., Michalet, R., 2003. A test of the indirect facilitation model in a temperate hardwood forest of the northern French Alps. J. Ecol. 91, 932–940.

Peguero-Pina, J.J., Camarero, J.J., Abadia, A., Martin, E., Gonzalez-Cascon, R., Morales, F., Gil-Pelegrín, E., 2007. Physiological performance of silver-fir (*Abies alba* Mill.) populations under contrasting climates near the south-western distribution limit of the species. Flora 202, 226–236.

Peñuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). Glob. Chang. Biol. 9, 131–140.

Peñuelas, J., Filella, I., Comas, P., 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. Glob. Chang. Biol. 8, 531–544.

Poyatos, R., Latron, J., Lloret, F., 2003. Land use and land cover change after agricultural abandonment – the case of a Mediterranean Mountain Area (Catalan Pre-Pyrenees). Mt. Res. Dev. 23, 362–368.

Purves, D.W., 2009. The demography of range boundaries versus range cores in eastern US tree species. Proc. R. Soc. Biol. Sci. 276, 1477–1484.

R Development Core Team, 2014. R: A Language and Environment for Statistical Computing.

Rabasa, S.G., Granda, E., Benavides, R., Kunstler, G., Espelta, J.M., Ogaya, R., Peñuelas, J., Scherer-Lorenzen, M., Gil, W., Grodzki, W., Ambrozy, S., Bergh, J., Hódar, J.A., Zamora, R., Valladares, F., 2013. Disparity in elevational shifts of European trees in response to recent climate warming. Glob. Chang. Biol. 19, 2490–2499.

Rickebusch, S., Lischke, H., Bugmann, H., Guisan, A., Zimmermann, N.E., 2007. Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data. For. Ecol. Manage. 246, 251–263.

Robakowski, P., Montpied, P., Dreyer, E., 2003. Plasticity of morphological and physiological traits in response to different levels of irradiance in seedlings of silver fir (*Abies alba* Mill). Trees 17, 431–441.

Robakowski, P., Montpied, P., Dreyer, E., 2005. Responses to temperature and shade in *Abies alba* seedlings from diverse provenances. Scand. J. For. Res. 20, 459–470.

Ruiz-Benito, P., Lines, E.R., Gómez-Aparicio, L., Zavala, M.A., Coomes, D.A., 2013. Patterns and drivers of tree mortality in Iberian forests: climatic effects are modified by competition. PLOS ONE 8, e56843.

Schumacher, S., Bugmann, H., Mladenoff, D.J., 2004. Improving the formulation of tree growth and succession in a spatially explicit landscape model. Ecol. Model. 180, 175–194.

Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganičová, K., Netherer, S., Arpaci, A., Bontemps, J.-D., Bugmann, H., González-Olabarria, J.R., Lasch, P., Meredieu, C., Moreira, F., Schelhaas, M.-J., Mohren, F., 2011. Modelling natural disturbances in forest ecosystems: a review. Ecol. Model. 222, 903–924.

Snell, R.S., Huth, A., Nabel, J.E.M.S., Bocedi, G., Travis, J.M.J., Gravel, D., Bugmann, H., Gutiérrez, A.G., Hickler, T., Higgins, S.I., Scherstjanoi, M., Reineking, B., Zurbriggen, N., Lischke, H., 2014. Using dynamic vegetation models to simulate plant range shifts. Ecography (Cop.) 37, 1184–1197.

Theurillat, J.P., Guisan, A., 2001. Potential impact of climate change on vegetation in the European Alps: a review. Clim. Change 50, 77–109.

Thuiller, W., Albert, C.H., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., Sykes, M.T., Zimmermann, N.E., 2008. Predicting global change impacts on plant species' distributions: future challenges. Perspect. Plant Ecol. Evol. Syst. 9, 137–152.

Toromani, E., Sanxhaku, M., Pasho, E., 2011. Growth responses to climate and drought in silver fir (*Abies alba*) along an altitudinal gradient in southern Kosovo. Can. J. For. Res. 41, 1795–1807.

Vanhellemont, M., Baeten, L., Verbeeck, H., Hermy, M., Verheyen, K., 2011. Long-term scenarios of the invasive black cherry in pine-oak forest: impact of regeneration success. Acta Oecol. 37, 203–211.

White, J.W., Rassweiler, A., Samhouri, J.F., Stier, A.C., White, C., 2014. Ecologists should not use statistical significance tests to interpret simulation model results. Oikos 123, 385–388.