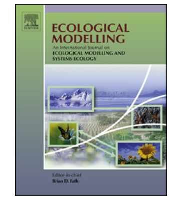
Ecological Modelling 313 (2015) 84–93

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



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

Aitor Ameztegui [a,b,*], Lluís Coll [a,c], Christian Messier [b,d]

[a] Forest Sciences Centre of Catalonia (CEMFOR-CTFC), Ctra. Sant Llorenç de Morunys km. 2, E-25280 Solsona, Catalonia, Spain
[b] Centre for Forest Research (CEF), Département des Sciences Biologiques, Université du Québec à Montréal, Montréal, Québec H3C 3P8, Canada
[c] CREAF, Centre for Ecological Research and Forestry Applications, Autonomous University of Barcelona, Cerdanyola del Vallès, E-08193 Catalonia, Spain
[d] Institut des Sciences de la Forêt Tempérée, Département des Sciences Naturels, Université du Québec en Outaouais, Ripon, Québec J0V 1V0, Canada

ARTICLE INFO

Article history:
Received 5 March 2015
Received in revised form 16 June 2015
Accepted 17 June 2015
Available online 5 July 2015

Keywords:
Modelling
Forest dynamics
Climate change
Ecotones
SORTIE-ND
Pyrenees

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;

* Corresponding author at: Centre for Forest Research (CEF), Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, Québec H3C 3P8, Canada. Tel.: +1 514 987 3000x4866.
E-mail address: ameztegui@gmail.com (A. Ameztegui).

http://dx.doi.org/10.1016/j.ecolmodel.2015.06.029
0304-3800/

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 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