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# A Process-based Model Approach to test for evolutionary rescue in forest ecosystems under climate change

Louis Devresse<sup>1</sup>, François de Coligny<sup>2</sup>, Freya Way<sup>3</sup>, and Xavier Morin<sup>1</sup>

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## Abstract

In recent years, forests all around the world have experienced increased mortality induced by heat waves and extreme drought events related to climate change. Forecasting the long-term future of forest ecosystems and tree species under a changing environment necessarily raises the issue of evolutionary dynamics. Questions are being raised about the potential for long living organisms such as trees to adapt to a rapid climate change and the extent to which our management actions on forests affect the evolutionary responses of tree species. Additionally, in mixed forests, interspecific interactions can affect the probability of evolutionary rescue of species. As tackling these questions is difficult with experimental approaches, the impacts of climate change on forests are frequently investigated through modelling approaches. Yet, species evolution has often been missed from current models predicting the consequences of global warming on forests. In this study, we therefore propose an approach that integrates evolution into a multi-species, process-based forest model that has been validated on forest inventory data, to test eco-evolutionary hypotheses and explore potential impacts of forest management practices on the fate of forests. Here, we illustrate our approach with a case study in which we showed that greater trait variability and heritability reduced the loss of forest cover after drought induced mortality events, over a short timescale (century). We also showed that adding new species into the forest improved recovery after climate change but could also prevent the evolutionary rescue of local species.

**Keywords:** Ecology, Evolution, Modelling, Quantitative Genetic, Forest Ecology, Climate Change, Eco-Evolution, Process-Based modelling

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## Introduction

2

3 There is growing concern about the vulnerability of temperate forests in the coming years,  
4 given the speed that climatic conditions have/ are anticipated to change significantly (Dyderski et  
5 al., 2018; Wessely et al., 2024). At the global scale, a large number of forests have already experi-  
6 enced increased mortality induced by heat waves and extreme drought events related to climate  
7 change (Hartmann et al., 2022). Because of the difficulty to experiment on mature forests and  
8 regarding the long-term perspective of such impacts, the impacts of climate change on forests  
9 are frequently investigated through modeling approaches. Among these, process-based models  
10 have been particularly advocated, in comparison to correlative/phenomenological models, be-  
11 cause they are expected to be more robust to predict trends under new conditions. Processes  
12 based models have already been used to simulate, for instance: species range shifts (Dormann  
13 et al., 2012), change in ecosystem productivity (Guillemot et al., 2017; Morin et al., 2018) and  
14 response to drought events (Ruffault et al., 2022). However, due to their inherent requirements,  
15 the development of process-based models has been limited by computing power and code archi-  
16 tecture, but mostly by ecological knowledge. This is even truer for fine-scale models (simulating  
17 individual trees in patch-scale communities) that are often parameterized for the same dominant  
18 species and focus mainly on monospecific and even-aged forests (see discussion in Morin *et al.*  
19 2021). However, a relevant way of mitigating the impact of climate change could be through fos-  
20 tering species diversity and complexity in forests (Astigarraga et al., 2023; Hisano et al., 2018).  
21 More precisely, tree species diversity can potentially stabilize forest growth in a changing cli-  
22 mate (Morin et al., 2018; Pardos et al., 2021), buffer the impact of disturbance in communities  
23 (Silva Pedro et al., 2015), and increase the likelihood of a forest containing species pre-adapted  
24 to future environments (positive selection effect) (Loreau and Hector, 2001). In order to test such  
25 findings, it is important that we develop models capable of handling coexisting sets of species.

26 Furthermore, forecasting the future of forest ecosystems and tree species over the coming  
27 centuries with a changing environment, necessarily requires consideration of the importance of  
28 evolutionary dynamics. In fact, questions are being raised about potential for long living organ-  
29 isms such as trees to adapt to a rapid climate change (Alberto et al., 2013) and the extent to  
30 which our actions on forests affect the evolutionary responses of tree species (Lefèvre et al.,  
31 2014). More specifically, in the context of on-going climate warming, will there be a probability  
32 for evolutionary rescue of tree species to occur, in terms of the persistence of a population or  
33 even a species that would have gone extinct in the absence of genetic adaptation. Implementing  
34 evolution in forest models requires simulating new processes and thus obtaining new parame-  
35 ters, which is partly why evolutionary processes are still so rarely implemented in forest models.  
36 In other words, most predictions of the future of tree species have been made just using fixed  
37 responses, without incorporating evolutionary adaptation. However, recent works suggest that  
38 considering evolutionary process may strongly impact models' projections of climate change im-  
39 pacts on forest ecosystems and their interactions with forest management practices (Gloy et al.,  
40 2023; Godineau et al., 2023; Kramer et al., 2015; Oddou-Muratorio and Davi, 2014).

41 Previously cited studies that have integrated evolution into vegetation models concerned  
42 monospecific or even-aged forests. However, evolution and species diversity can interact in  
43 complex and unpredictable ways. Species diversity could buffer the effect of an environmental  
44 change on community processes but could also reduce the possibilities of species' evolutionary

45 rescue, particularly for rare species (De Mazancourt et al., 2008; Eldijk et al., 2020; Johansson,  
46 2008; Price and Kirkpatrick, 2009; Thompson and Fronhofer, 2019). Yet, studies on this topic  
47 are recent and mainly rely on theoretical approaches based on general models.

48 We propose a methodology to address these issues in the context of forest ecosystems, by  
49 adapting a process-based model that has been validated for most forest types in France, includ-  
50 ing both monospecific and mixed forests, ForCEEPS (Morin et al., 2021) (Fig. 1). In this model,  
51 species are defined by a set of specific parameters. Here we aim at adding a new evolutionary  
52 module allowing species-specific parameters to evolve within the course of the simulation. We  
53 focused on three main traits, of interest for competition and tolerance to drought. One of the key  
54 novel aspects of our approach is thus to use a process-based model that is able to simulate multi-  
55 species tree communities, to test for the effect of evolutionary dynamics on forest ecosystems.  
56 This module can be grafted or adapted for any individual-based model in the future.

57 To illustrate the range of issues that can be addressed with our methodology, we have chosen  
58 to explore several topics of interest to theoretical ecologists as well as forest managers, through  
59 a case study centered on a montane forest of beech and fir (*Fagus sylvatica* and *Abies alba*) in  
60 southeastern France, subjected to a RCP 4.5 global warming scenario. In such conditions, beech-  
61 fir forests face extinction in ForCEEPS simulations without evolution. We have thus explored the  
62 prospects of evolutionary rescue for the two focal species through three questions:

- 63 (1) *Evolutionary rescue in two species mixture and monoculture*. Is the possibility of evolution-  
64 ary rescue of fir and beech reduced when both species coexist in mixed stands (hereafter  
65 beech-fir “mixture treatment”) compared with monospecific stands, at comparable abun-  
66 dances (hereafter “monospecific treatment”)?
- 67 (2) *Evolutionary rescue and genetic enrichment*. Does the introduction of individuals adapted  
68 to more arid conditions enhance the probability of evolutionary rescue (hereafter “ge-  
69 netic enrichment scenario”) (Fady et al., 2016; Hlásny et al., 2014)?
- 70 (3) *Evolutionary rescue and species enrichment*. Does introducing new species that are better  
71 adapted to arid conditions lead to the extinction of beech and fir, under conditions where  
72 their evolutionary rescue is otherwise feasible (hereafter “specific enrichment scenario”).  
73 This treatment can be interpreted as migration dynamics in response to climate change  
74 at a regional scale or as assisted migration of more thermophilic species. (Hisano et al.,  
75 2018; Hlásny et al., 2014)?

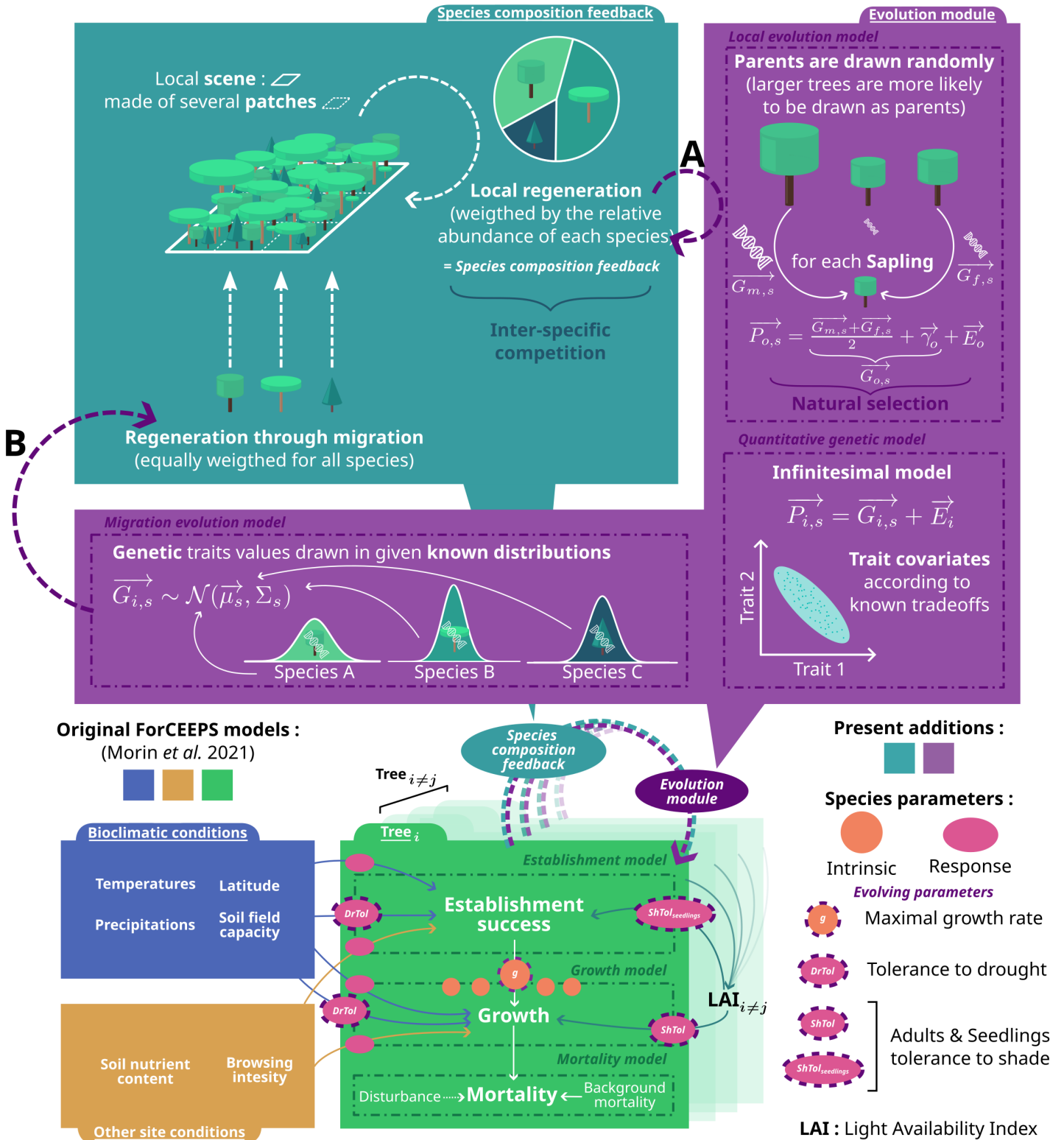


Figure 1

**Figure 1** – Overview of the ForCEEPS model and recent developments discussed in this article. **Blue, yellow, and green boxes** corresponding to components of the original ForCEEPS model's fundamental mechanisms (for further details, refer to Morin *et al.* 2021). **Teal and purple boxes** highlight the innovations introduced in this study. **Teal Box** illustrate the feedback between the forest species composition and regeneration: more abundant species contribute more to the seed rain. Furthermore, akin to most classic gap models, an option is available to activate a uniform seed rain for all species, irrespective of abundance, and is named as 'migration' here. Individuals originating from this process are attributed to an external provenance. **Purple Box:** The most noticeable change to the ForCEEPS model reported here is the introduction of an evolution module. This module allows the evolution of a set of traits (species parameters) under the assumptions of the infinitesimal quantitative genetic model. Each individual trait is comprised of a genetic and an environmental contribution, in the present case, respectively,  $G_{i,s}$  is heritable and centred around the trait's former values and  $E_i$  is a random non heritable noise. The relative importance of these contributions depends on traits heritability ( $h^2$ ). The module accommodates simultaneous evolution of covarying genetic components of traits along established trade-offs. The evolution module comprises two components: **A)** For a locally generated offspring  $o$ , its phenotype was determined by the average genotype of two randomly selected local parents ( $G_{m,s}$  and  $G_{f,s}$ ) to what we add within-family variation ( $\gamma_o$ ) and environmental noise ( $E_o$ ). Local adults can be drawn like parents if they are older than the known age of maturity for the species and if they are not declining ("slow growth" status). Larger reproducers are more likely to be parents. **B)** For migrant offspring their genetic values are drawn in predefined distributions. These distributions also can be updated throughout the simulations based on the means and variances of traits across replicated sites. Starting from an inventory, new phenotypes are given to each tree following the same process as described for the migrating individuals. In this case, tree's genetic values are drawn in the starting trait distributions (see methods).

## Methods

76

77 The ForCEEPS model (Morin *et al.*, 2021, 2020) (Fig. 1, blue, green and yellow boxes) simulates forest dynamics, through recruitment, growth, death of trees, on small patches of land  
78 (usually ca. 1000 m<sup>2</sup>). The model is individual-based and considers abiotic and biotic constraints.  
79 Its key process is competition for light, primary driver of the of temperate forests dynamics  
80 (Kohyama and Takada, 2012), which is mediated by environmental conditions, especially climate.  
81 Variables are simulated at the patch scale (e.g. species basal area, standing biomass, productivity)  
82 and can be summed across patches to derive forest properties at a larger spatial scale.  
83

### 84 Regeneration and Species Composition Feedback

85 In classic gap models, regeneration often consisted of a constant "seed rain" across time and  
86 species for all species considered as able to reproduce in the simulation (Bugmann, 1996; Didion  
87 *et al.*, 2009; Morin *et al.*, 2021), assuming that the simulated forests were included in a forest  
88 landscape in which the listed species can reproduce and disperse. Yet, this scheme rendered  
89 regeneration independent on the actual state of the simulated forest. Following former work  
90 (Vallet, 2023), we further developed regeneration in ForCEEPS by implementing a new option,  
91 allowing for "local regeneration". We added a feedback of the actual site composition (in terms  
92 of species' relative presence based on basal area) on the identity of the colonizing seedlings each  
93 year (Fig. 1 teal box, arrow A). We also kept the possibility of having a regeneration identical to  
94 the classic scheme of gap models, i.e. as a "migration" regeneration mode (Fig. 1 teal box, arrow  
95 B). If activated, this migration regeneration happens in addition to the local regeneration, and is  
96 weighted by a migration parameter  $M$  (where  $M = 1$  implies migration regeneration in addition  
97 to alocal, and  $M = 0$  implies that only local regeneration occurs).

## 98 Evolution Module

99 The core of this work was the incorporation of a module simulating evolutionary dynamics  
100 into the ForCEEPS model (Fig. 1 purple box). This module required species traits to be both vari-  
101 able and inheritable, with evolutionary forces impacting the distribution of these traits through  
102 time. Here we specifically selected three species-specific parameters as focal evolving traits,  
103 chosen for their relevance in responding to selection pressures imposed by climate change and  
104 competition:

- 105 • Drought tolerance ( $DrTol_s$ ): a continuous index ranging between 0 (intolerant) and 1 (tol-  
106 erant).
- 107 • Adults shade tolerance ( $ShTol_s$ ) and its counterpart, the seedlings' shade tolerance ( $ShTolSeedling_s$ ).  
108  $ShTol_s$  is a continuous index from 1 (shade tolerant) to 9 (shade intolerant) that impacts  
109 the growth rate of adults.  $ShTolSeedling_s$  is a similar index between 0 (tolerant) and 1  
110 (intolerant) that impacts seedling establishment.
- 111 • Maximal growth rate ( $g_s$ ), unitless.

112 Base species values, i.e. the initial trait values before modification by the simulated evolu-  
113 tionary dynamics, of  $DrTol_s$ ,  $ShTol_s$  and  $ShTolSeedling_s$  come from a compilation from (Bugmann,  
114 1996; Ellenberg and Mueller-Dombois, 1965; Niinemets and Valladares, 2006; Rameau et al.,  
115 2008). Base values for  $g_s$  are inferred from actual measurements from French national forest  
116 inventory (Morin et al., 2021).

## 117 Initialisation phase

118 The three formerly described traits are treated as quantitative and so are assumed to be in-  
119 fluenced by a large number of additive genes, each of which contributes infinitesimally to an in-  
120 dividual's phenotype (infinitesimal model *sensu* Fisher, 1914) (Barton et al., 2017). Consequently,  
121 traits initially follow a normal distribution in populations. Starting from a given inventory (from  
122 data or from former simulations) a phenotype was attributed to each individual as an array of  
123 values for each evolving trait through random draws in multi-normal distributions:

$$(1) \quad \vec{P}_{i,s} = \vec{G}_{i,s} + \vec{E}_i$$

Where  $\vec{G}_{i,s} \sim \mathcal{N}(\vec{\mu}_s, \Sigma_G)$  and,  $\vec{E}_i \sim \mathcal{N}(\vec{0}, \Sigma_E)$

124 where  $G_{i,s}$  and  $E_{i,s}$  are respectively the genetic and environmental contributions to the phe-  
125 notype array  $P_{i,s}$  of individual  $i$  of species  $s$ ;  $\mu_s$  is an array containing the former ForCEEPS  
126 species specific parameters of ( $DrTol_s$ ,  $ShTol_s$  and  $g_s$ ). Consequently,  $G_{i,s}$  and  $P_{i,s}$  are centered  
127 around the old ForCEEPS parameterization described above whereas  $E_{i,s}$  is a random non heri-  
128 table noise.  $\Sigma_G$  and  $\Sigma_E$  are the genetic and environmental variance-covariance matrices as de-  
129 scribed below:

$$\Sigma_G = h^2 \cdot \Sigma_P \quad \text{and} \quad \Sigma_E = (1 - h^2) \cdot \Sigma_P$$

130 where  $h^2$  is the heritability (assumed here to be equal for all traits ranging from 0.1 to 0.4) and  
131  $\Sigma_P$  is a variance-covariance matrix.  $\Sigma_P$  values depend on the initial intraspecific trait variability



132 is set as a fraction ( $VR$ ) of the interspecific variability in traits observed in the pool of species pa-  
 133 rameterized in ForCEEPS (Morin et al., 2021).  $VR$  is the fraction of each trait's standard variation  
 134 at the inter-specific scale for all species parameterized in ForCEEPS (Morin et al., 2021) (Table  
 135 S.1).

$$\Sigma_P = \text{diag}(\overrightarrow{sd_{intra}}) \cdot \Sigma_c \cdot \text{diag}(\overrightarrow{sd_{intra}}) \quad \text{Where} \quad \overrightarrow{sd_{intra}} = VR \cdot \overrightarrow{sd_{inter}}$$

136 where  $sd_{intra}$  is the intraspecific traits standard deviation array and  $\Sigma_c$ , the trait correlation  
 137 matrix. Trait correlations values comes from a compilation of relative growth rates (RGR) from  
 138 the TRY database (Kattge et al., 2020) and data on drought and shade tolerance from (Niinemets  
 139 and Valladares, 2006) for all native European tree species within the database in order to mea-  
 140 sure correlations on the largest set of species possible (Fig. S.1). The relative growth rate data  
 141 were filtered to include only observations under least restrictive growth conditions within data  
 142 sources. Subsequently, these values were averaged per species and data source and then aggre-  
 143 gated across all data sources for each species, with equal weighting assigned to each source.

144 An exception was made for the individual's seedling tolerance to shade:  $ShTol_{seedling_{i,s}}$  that  
 145 was linearly inferred by the individual's adult tolerance to shade ( $ShTol_{i,s}$ ) difference with the  
 146 base species shade tolerance value ( $ShTol_s$ ):

$$ShTol_{seedling_{i,s}} = ShTol_{seedling_s} + \frac{1}{8} \cdot (ShTol_{i,s} - ShTol_s)$$

## 147 Evolution phase

148 After the initialization, traits are inherited through the process described below and illus-  
 149 trated in (Fig. 1 purple box arrow A) as the simulation runs. For locally regenerated individuals,  
 150 new seedlings of species  $s$  were attributed two parents randomly chosen among a pool of repro-  
 151 ducer trees. A tree is considered as reproducer if it is older than the species-specific maturity  
 152 age and if it is not in status of "slow growth". This "slow growth" status happens when a tree has  
 153 been growing less than a specific threshold for a specified number of years (here three years),  
 154 which would occur when environmental factors such as temperature or light availability are too  
 155 stringent for the tree (Morin et al., 2021). We assume that in such conditions, trees do not invest  
 156 in reproduction. The probability of each tree from the reproducer pool to be drawn as parent  
 157 is weighted by its size (assessed as its relative basal area in the reproducer pool, assuming that  
 158 larger trees leave more offspring). Once a seedling is attributed two parents, each of its non-  
 159 evolving traits is set as equal to the species' base trait value (Morin et al., 2021) while the values  
 160 of each of the three evolving traits is defined as the mean of the genetic trait values of both  
 161 parents, to which a genetic ( $\gamma_o$ ) and an environmental noise is added ( $e_o$ ):

$$\overrightarrow{P_{o,s}} = \underbrace{\frac{\overrightarrow{G_{m,s}} + \overrightarrow{G_{f,s}}}{2}}_{\overrightarrow{G_{o,s}}} + \overrightarrow{\gamma_o} + \overrightarrow{E_o}, \text{Where}$$

$$\overrightarrow{\gamma_o} \sim \mathcal{N}(\overrightarrow{0}, \Sigma_G \cdot \frac{1}{2}) \quad \text{and} \quad \overrightarrow{E_o} \sim \mathcal{N}(\overrightarrow{0}, \Sigma_E)$$



162 With,  $P_{o,s}$  the phenotype of offspring  $o$ , for a given species  $s$  and  $G_{m,s}$  and  $G_{f,s}$  the genotype  
 163 of the mother and father', respectively. The genetic noise  $\gamma_o$  originates from the within-family  
 164 genetic variance, also called the segregation variance as it results from the process of Mendelian  
 165 segregation of alleles. Without selection, setting its variance to half the starting genetic vari-  
 166 ance keeps the overall population's genetic variance constant through generations, as computing  
 167 the mean breeding value of two parents to obtain those of the offspring will result in reducing  
 168 population's genetic variance by half each generation. Under the infinitesimal model, assuming  
 169 sufficiently large and stable ancestral populations and dismissing inbreeding, this genetic noise  
 170 variance is constant across generation and normally distributed, regardless the distributions of  
 171 the parents' genetic values (Bulmer, 1971). In contrast, for seedlings originating from migration  
 172 (Fig. 1 purple box arrow B), phenotypes are drawn in multi-normal distributions as described in  
 173 equation (1) with the difference that the means can differ from those of local seedlings. These  
 174 distributions can either be set at the beginning of the simulation, or can be updated during the on-  
 175 going simulation to represent at best the genetic composition of replicate populations evolving  
 176 simultaneously. In this case, the means and variances of species' traits are updated as the arith-  
 177 metic means of the species trait's means and variances across replicated sites sharing identical  
 178 biotic conditions. In all cases, the  $\Sigma_E$  variances are fixed at the start of the simulation depending  
 179 on  $h^2$  and  $VR$ , and remain constant throughout the simulation.

## 180 Case Study

181 To illustrate how this new evolutionary module could be used, we carried-out simulations  
 182 related to the questions outlined in the introduction through a case study with montane beech-  
 183 fir forests. Beech-fir forests are typical ecosystem of montane forests in Europe (Toïgo et al.,  
 184 2015).

### 185 *Site an climate data.*

186 Our case study was based on two sites: a focal one in Southern East France (hereafter "Drôme"), a  
 187 typical ecological site for beech-fir forests (44°55'01.2" N; 5°17'27.6" E: 1146 mm of yearly pre-  
 188 cipitations and mean temperatures of 5.9°C), and a drier but otherwise complementary site (here-  
 189 after "Montagne Noire"), at the southern limit where beech-fir forests could be found (43°27'55.4"N;  
 190 2°16'43.2"E: 983 mm of yearly precipitations and mean temperatures of 9.3°C). The model's site  
 191 parameters for the Drôme site were derived from field measurements, and those for the Mon-  
 192 tagne Noire site were arbitrarily set to be identical to ensure comparability between the two  
 193 sites (Table S.2). Climate data consisted of monthly temperature and precipitation data available  
 194 from the CHELSA (CMIP5, BCG model) (Karger et al., 2020), which were-organized into three  
 195 periods:

- 196 • A historical period based on records of climate conditions at the coordinates of both sites  
 197 from 1900 to 2000, repeated over 1000 years.
- 198 • A 100-year warming period including data from 2000 to 2100 for the RCP 4.5 scenario.
- 199 • A stabilization period consisting in a repetition of the previous climatic projections from  
 200 years 2090 to 2100, randomly repeated over 1000 years.

### 201 *Simulation plan.*

202 Each simulation starts by a baseline-simulation in which ForCEEPS is run with the evolution  
 203 module deactivated and the species composition feedback activated during the historical period  
 204 (1000 years), starting from bare ground, in order to obtain mature and age-structured forests (i.e.

205 a pseudo-equilibrium state). Then, to address our three questions, we implemented the simula-  
206 tion framework depicted in Fig. S.2, with the evolution module activated. Each question was  
207 explored through four scenarios of  $h^2$  (0.1, 0.2, 0.3, 0.4) and four scenarios of  $VR$  (0.1, 0.2, 0.3,  
208 0.4) (thus 16 evolutionary scenarios) in order to cover cases ranging from the systematic extinc-  
209 tion of both species in all replicates to the recovery of abundances above or close to the initial  
210 levels of both species after 1000 years of climate stabilization.

### 211 1. *Evolutionary rescue in two species mixture and monoculture.*

212 For this question, we explored three modes of forest composition: mixed beech-fir, monospecific  
213 beech, and monospecific fir. Scenes contained 50 patches of mixed beech-fir, 42 patches of  
214 monospecific beech and 11 patches of monospecific fir, with the number differing in order to  
215 keep a similar number of individuals of each species. We ran 50 replicates of each of the three  
216 composition modes for each evolutionary scenario (totalling to  $50 \times 3 \times 16 = 2400$  simulations) in  
217 the Drôme site, with its associated climate projections.

### 218 2. *Evolutionary rescue and genetic enrichment.*

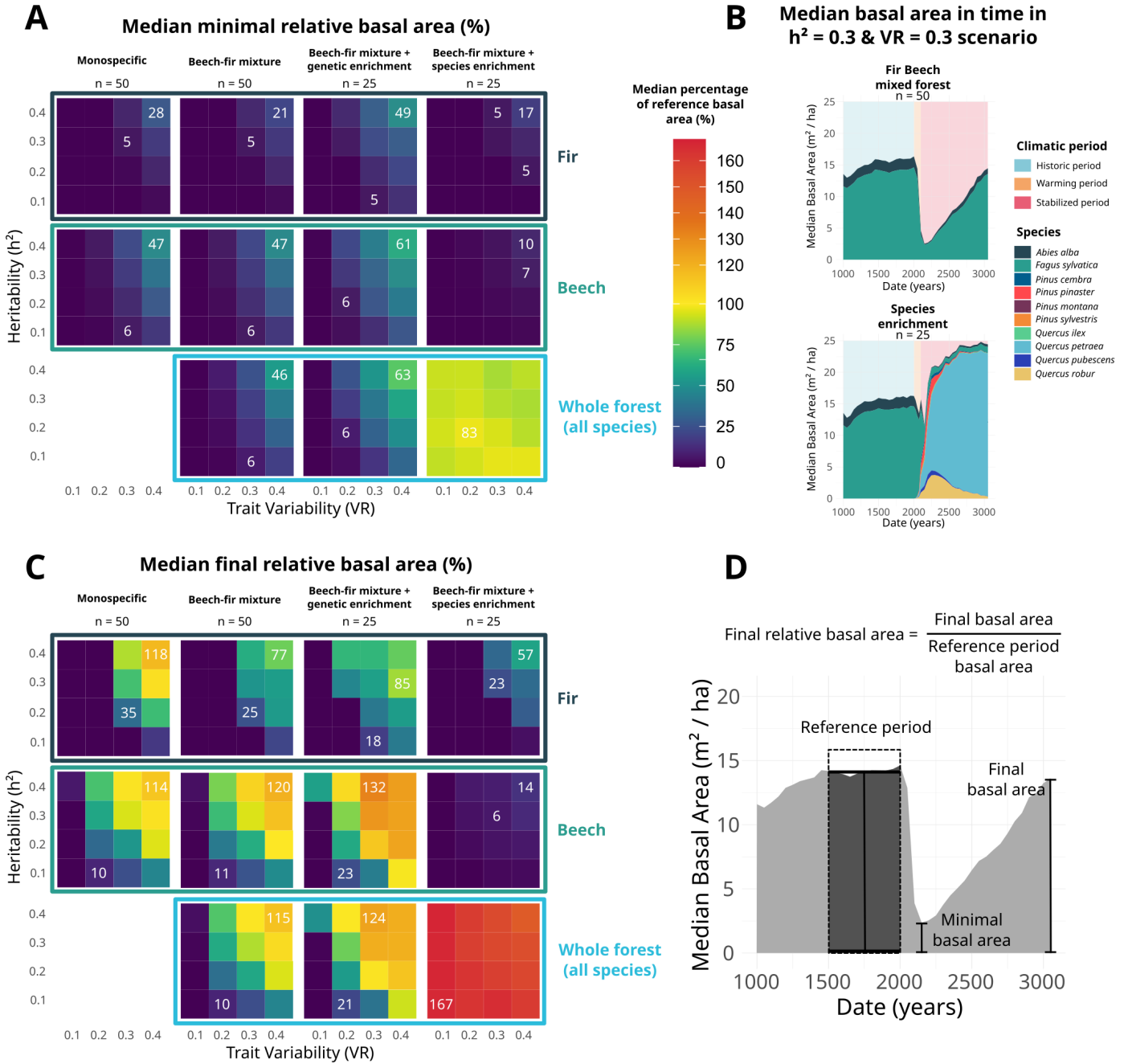
219 Here we compared the previously mentioned mixed beech-fir mode with a “genetic enrichment”  
220 treatment. This latter was identical to the mixed beech-fir of question 1, with the difference that  
221 we added immigration of pre-adapted beech and fir individuals during the 100-year warming  
222 period. The migration parameter  $M$  was arbitrarily set to 0.1 to allow new genotypes to colonize  
223 with a marginal impact on equilibrium basal area. To obtain average phenotypic values for pre-  
224 adapted migrants, we carried out 25 simulations of 1000 years of mixed beech-fir forest with  
225 the drier historical climate of the Montagne Noire. We carried out only 25 replicates of this  
226 treatment, as computation time was significantly larger ( $25 \times 16 = 400$  simulations). Monospecific  
227 and genetically enriched simulations were run but did not differ from the two species mixture.

### 228 3. *Evolutionary rescue and species enrichment.*

229 For this last question, we introduced the species enrichment treatment that was similar to Ques-  
230 tion 2, but we added individuals coming from a given set of eight other species (Table. S.3) during  
231 the warming period through migration ( $M = 0.1$ ). In this mode, migrant individuals had pheno-  
232 typic values drawn from multi-normal phenotypic distributions whose means for the evolving  
233 trait were the base values parameterized for these species (Morin et al., 2021). Again, for rea-  
234 sons of computation time, we only carried out 25 replicates of this treatment and only started  
235 simulations from mixed beech-fir forests ( $25 \times 16 = 400$  simulations).

## 236 **Data analysis and software**

237 Climate, site, and trait values were analyzed and transformed into the desired formats and  
238 figures using R software 4.3.0 (R Core Team 2023). In figures, trait values per species were aver-  
239 aged by weighting them by the basal area of each individual, in order to be representative of the  
240 population in a given year (and to not give too much weight to the large pool of unfit seedlings  
241 that cannot survive several consecutive years). Evolution rates were also measured in Haldanes  
242 ( $H_0$ ) according to Gingerich (1983) between the years 2000 and 2100. Exact  $H_0$  values are given  
243 with their 95% confidence intervals for all replicates for the  $h^2$  and  $VR = 0.3$  evolutionary sce-  
244 narios as it led to the most realistic evolutionary rates (Bone and Farres, 2001). The ForCEEPS  
245 model as well as its evolution module can be distributed via Capsis, a simulation platform for  
246 forest growth and dynamics models (Dufour-Kowalski et al., 2012).



**Figure 2 – A.** Median minimal relative forest basal area (see D) following climate change in a forest of Drôme site for the various scenarios of heritability ( $h^2$ ) and intra- to interspecific trait standard deviation ratio (VR). Number of replicates is indicated under the treatment type and exact recovery percentages are given for maximum and for minimum relative cover over 5%. **B.** Median forest basal area over the whole time series, for a  $h^2$  and VR of 0.3 in beech-fir mixture and in the species enrichment treatment. **C.** Median forest basal area recovery 1000 years after climate change (RCP 4.5) relatively to a reference period (see D). **D.** Calculation of relative basal areas (RBA).

247

## Results & Discussion

248

### 1. Does mixing fir and beech dampen evolutionary rescue?

249

The median minimal Relative Basal Area (RBA) (Fig. 2) can be interpreted as the population's

250

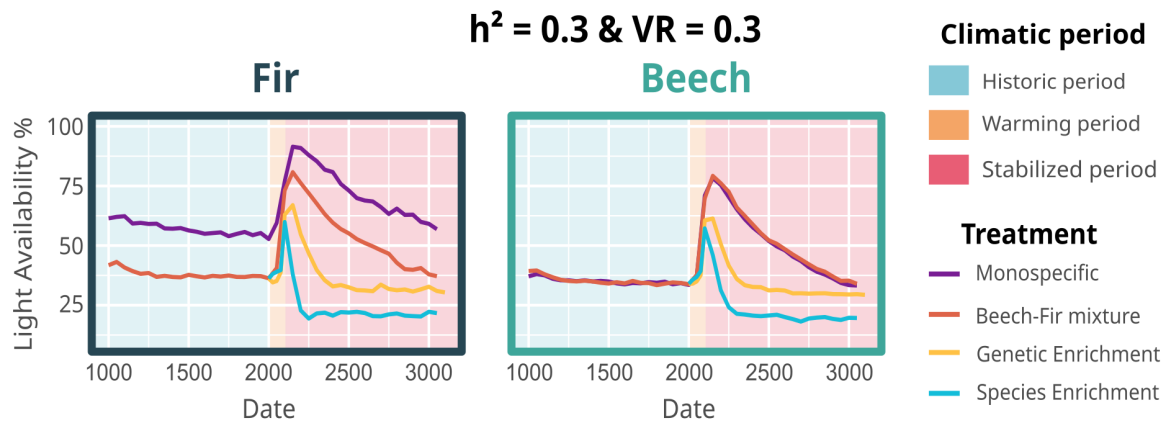
safety margin for its persistence. VR and  $h^2$  had a strong impact on minimum RBA (Fig. 2.A),

251 highlighting the relevance of evolutive process even in the short term, as minimum RBA typi-  
 252 cally occurs soon after the end of the warming phase (100-200 years post warming) (Fig. 2.B,  
 253 Fig. 3 & Fig. S.3). The 5% threshold of median minimum RBA was reached for minimum  $h^2$  and  
 254 VR of 0.3 in fir in both monospecific and mixed treatment populations. In beech populations,  
 255 the same threshold was reached for "slower" evolutionary scenarios of  $h^2$  of 0.1 and VR of 0.3  
 256 (Fig. 2.A). The most preadapted species encountered lowest risks of extinction, i.e. beech with  
 257  $DrTol = 0.25$  as opposed to fir with  $DrTol = 0.23$ . The lack of differences between the monospe-  
 258 cific and mixture treatments in terms of safety margin was due to the release from competition  
 259 for light due to high mortality in the warming period (Fig. 3 & Fig. S.3). Therefore, mixing did not  
 260 impact the chances of evolutionary rescue for both species. In the long term however, fir recov-  
 261 ery was lowered in the mixture treatment, as shown by the median final RBA of 77% in mixture  
 262 against 118% in the monospecific treatment, for the faster evolutionary scenario (Fig. 2.C).

263 In mixed species forests, evolution favoured the dominant species, which is in line with our ex-  
 264 pectations and theoretical works (De Mazancourt et al., 2008; Eldijk et al., 2020; Thompson and  
 265 Fronhofer, 2019). Two non-exclusive interpretations could explain this phenomenon: 1) beech  
 266 was favoured because its populations were initially larger, reducing drift and increasing the prob-  
 267 ability of the population hosting more drought tolerant individuals (monopolization hypothesis);  
 268 and/or 2) beech was initially more preadapted due to its higher base value for  $DrTol$  (preadap-  
 269 tation hypothesis).  $DrTol$  evolution toward higher values was a determinant of population' re-  
 270 covery, with populations that reached higher  $DrTol$  showing the highest recoveries (Fig. 4). As  
 271 expected, higher  $DrTol$  values were reached for higher  $h^2$  and VR scenarios, however, there were  
 272 no differences in fir and beech  $DrTol$  evolutionary trajectories between monospecific and two-  
 273 species mixed populations (Fig. 5.A), regardless the evolutionary scenario (Fig. S.4). What's more,  
 274 the evolution rates of  $DrTol$  for the evolutionary scenarios of  $h^2$  and VR = 0.3 between 2000  
 275 and 2100 are identical (0.23 [0.22; 0.25] and 0.23 [0.20; 0.25]  $H_0$ ) (Fig. S.5). However, over the  
 276 long term (year 3000), for an evolution reaching the same  $DrTol$  values, recoveries are better in  
 277 monospecific than in mixture treatment (Fig. 4). We interpreted this result as the return of com-  
 278 petition for light as the main process shaping the community. Mixing the two species only had  
 279 an impact on fir  $ShTol$  evolution on the long term (Fig. 5.B, Fig. S.6). Fir individuals in the two-  
 280 species mixed forests faced stronger shading regimes compared to the less dense monospecific  
 281 fir forest (Fig. 3 & Fig. S.3). Overall, the general evolutionary path of target traits was a selection  
 282 toward higher  $DrTol$  at the cost of unconstrained  $ShTol$  evolution while  $g$  was maintained at  
 283 similar levels than the base values by selection (Fig. 5.B; Fig. S.6).

## 284 2. Does genetic enrichment improve population recovery after climate change?

285 Genetic enrichment treatment is to be compared with the two-species mix treatment (as in  
 286 Question 1). As expected, this scenario led to the highest rates of evolution during the warming  
 287 period, with beech  $H_0 = 0.50$  [0.46; 0.51] and fir  $H_0 = 0.39$  [0.35; 0.43] for the  $h^2$  and VR = 0.3  
 288 scenario (Fig. S.5). These values are within the largest known  $H_0$  for plant adaptation to abrupt  
 289 changes in natural populations (Bone and Farres, 2001). In concrete terms, genetic enrichment  
 290 led to a higher safety margin (minimal RBA) and to a larger number of evolutionary scenarios in  
 291 which both beech and fir experienced evolutionary rescue (Fig. 2.A). While genetic enrichment  
 292 helped both species track climate change in the short term (minimum RBA around 2100 years),  
 293 it led to a less linear relationship between evolutionary regimes ( $h^2$  and VR) and final RBA in the

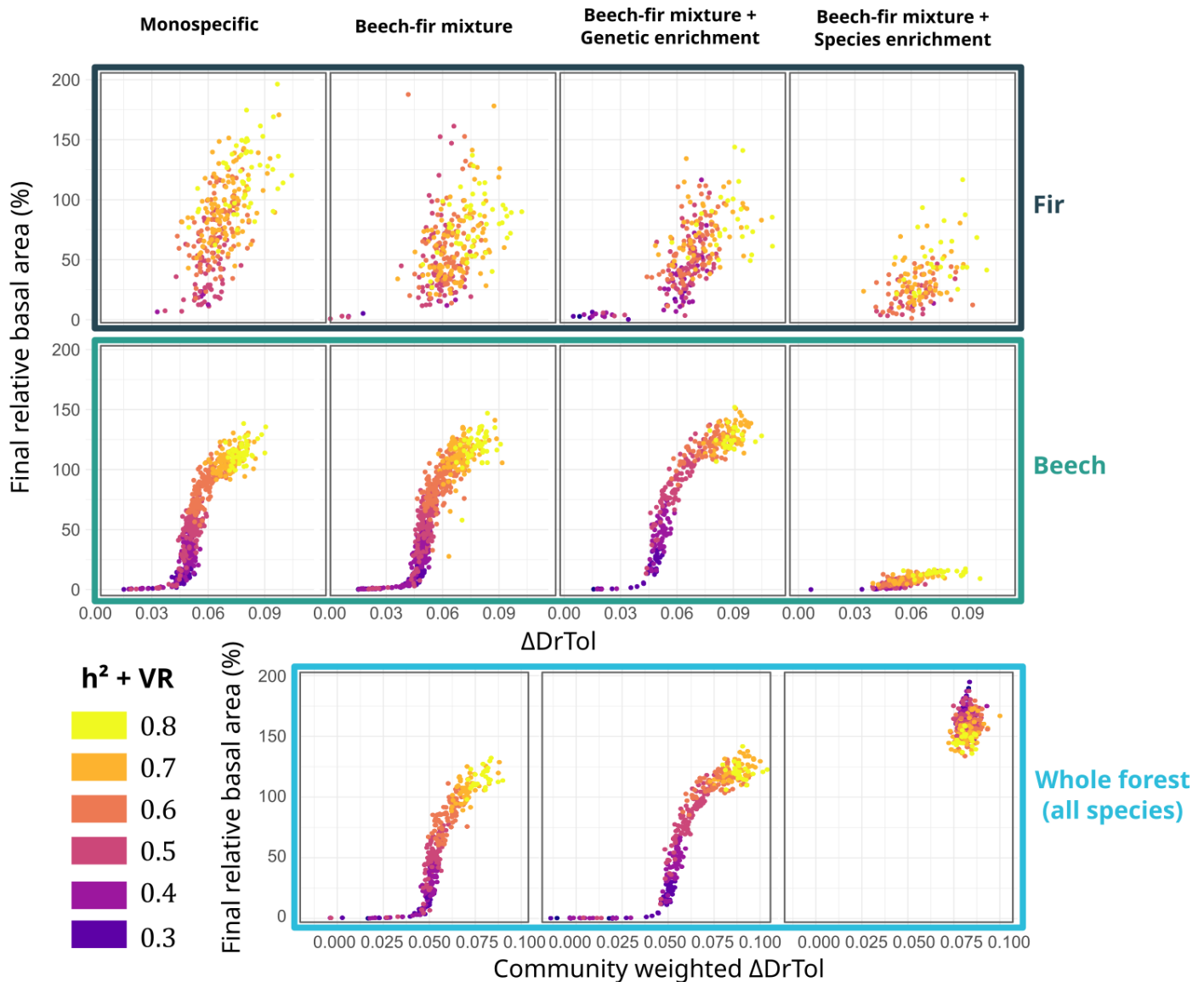


**Figure 3** – Median across replicates of the mean individual relative light availability in time for populations of beech and fir in the four treatments in the  $h^2$  &  $VR = 0.3$  evolutionary scenario. Background color indicates the climatic periods (see methods). For other evolutionary scenarios see Fig. S.3.

394 long term in comparison with the mixture treatment from question 1. In contrast with the mix-  
 395 ture treatment, highest recoveries (final RBA) no longer happened for the fastest evolutionary  
 396 scenarios ( $h^2$  and  $VR = 0.4$ ) for fir and beech populations individually and at the community scale  
 397 (Fig. 2.C). Additionally for fir, lower recoveries occurred for equivalent  $DrTol$  evolution in the ge-  
 398 netic enrichment compared to the mixture (flatter  $DrTol$  to final RBA recovery curve) (Fig. 4).  
 399 Genetic enrichment favored the previously dominant species. Notably, beech populations' high-  
 400 est recoveries were in slower evolutionary scenarios, which can be interpreted either by lower  
 401 tolerance to shade evolving in beech in the genetic enrichment (Fig. 5.B) thus causing lower  
 402 growth rates as shading increases, or by a higher competition regime as both species recover  
 403 more. Altogether, this showed that with genetic enrichment, evolution speed was no longer the  
 404 limiting factor for species and community recovery, and that the role of trade-offs among traits  
 405 and species competition became more important in the forests fate.

### 306 3. Does importing new species prevent local species' evolutionary rescue?

307 The species enrichment treatment must also be compared with the two-species mixture  
 308 treatment. In the species enrichment treatment, fir and beech became extinct in the majority  
 309 of evolutive scenarios, including scenarios where both species experienced evolutionary rescue  
 310 in the beech-fir treatment (Fig. 2.A & C). This result is consistent with our expectations and liter-  
 311 ature on the subject. The arrival of newly preadapted species can endanger local evolving ones  
 312 (De Mazancourt et al., 2008). We observed a turnover between beech and sessile oak (*Quercus*  
 313 *petraea*), a more thermophilous species (with higher  $DrTol$ ). Surprisingly, contrary to the previ-  
 314 ous treatments, in all evolutionary scenarios, fir populations decreased relatively less than beech  
 315 ones (Fig. 2.A & C). We interpret this result as meaning that in this treatment, i) beech was no  
 316 longer the dominant species due to the presence of more drought-tolerant species, and ii) beech  
 317 recovered less rapidly than fir because of its lower  $g$ . Fir and beech populations recoveries (final  
 318 RBA) were lower in the species enrichment treatment for equivalent  $DrTol$  evolution in compar-  
 319 ison with the two-species mixture treatment from question 1. The difference between the two  
 320 treatments was greater for beech populations where  $+0.07$  in  $\Delta DrTol$  was enough to reach over  
 321 100% of final RBA in the two species mixture. In the species enrichment treatment, all beech  
 322 populations had recoveries below 25% even for  $\Delta DrTol$  above  $+0.07$  (Fig. 4). Species enrichment

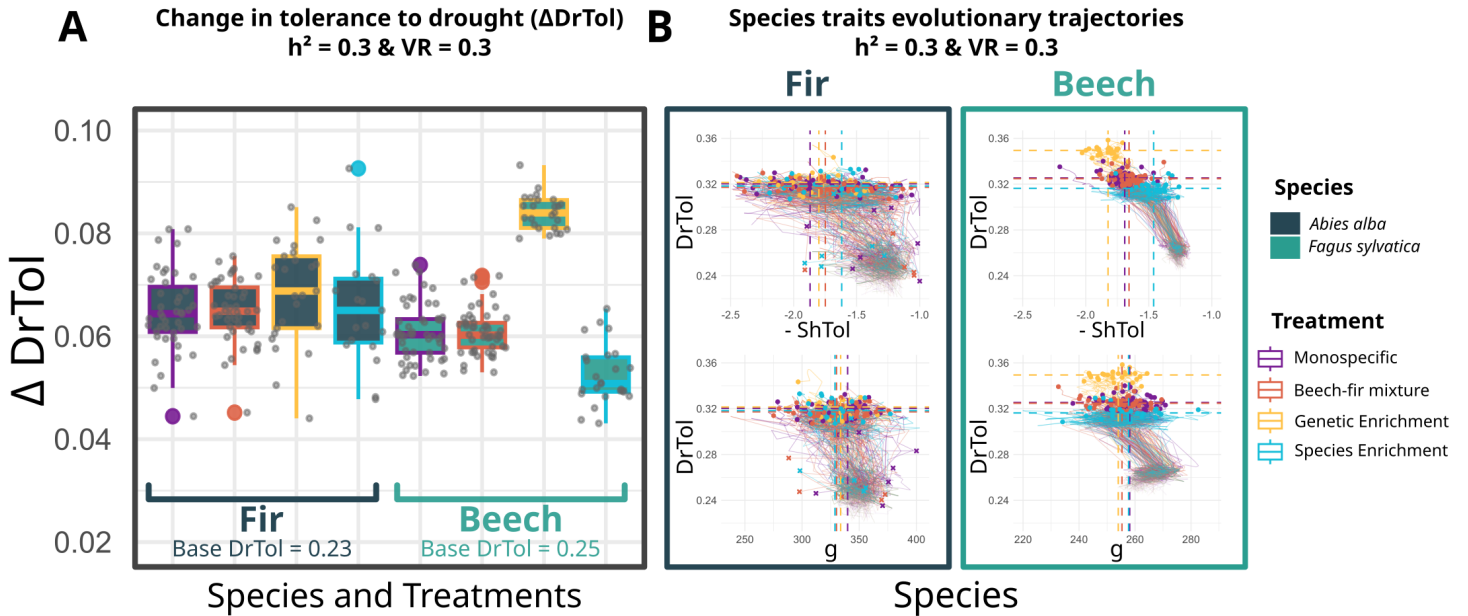


**Figure 4** – Final relative basal area (see Fig. 2.D) as a function of evolutionary change in tolerance to drought ( $\Delta DrTol$ ) for fir and beech species, and community weighted  $\Delta DrTol$  (i.e. difference between the average  $DrTol$  of species weighted by their relative abundances in the reference period and last decade of the simulations) for the whole forest for different forest type scenarios.

323 tended to slow down  $DrTol$  evolution only in beech populations but not in fir's (Fig. 5.A & Fig. S.4).  
 324 In the species enrichment treatment, slower  $DrTol$  evolution in beech in the long term was asso-  
 325 ciated with a maintenance of higher  $ShTol$  compared to the beech-fir mixture (Fig. 5 & Fig. S.4).  
 326 This result is in line with the view of a niche conservatism induced by interspecific interactions  
 327 (Peterson et al., 1999; Wiens et al., 2010). However,  $DrTol$  evolutionary rates were unaffected  
 328 by species introduction in the short term (during the warming period) with  $H_0 = 0.26$  [0.23; 0.29]  
 329 in fir and  $H_0 = 0.37$  [0.36; 0.38] in beech for the species enrichment treatment against respec-  
 330 tively 0.23 [0.20; 0.25] in fir and 0.35 [0.34; 0.36] in beech for the beech-fir mixture treatment).  
 331 It is worth noting that species-enriched forests were the forests with larger values of leaf cover



332 for beech and fir individuals across all evolutive scenarios and management treatments (Fig. 3. &  
 333 Fig. S.3). Altogether, those results indicate that species-enriched forests quickly re-faced a light  
 334 competition driven regime as new species colonize. At the whole forest scale (sum of all species  
 335 basal area), species enrichment allowed for the most major recoveries and the highest minimal  
 336 relative basal area, with all final recoveries over 130% and all minimal relative basal area above  
 337 75% (Fig. 2.A & C). Therefore, our case study tends to confirm the view that species range shifts  
 338 could mitigate the impact of climate change on forest ecosystems in some scenarios, but at the  
 339 risk of losing local species if their evolutionary capacities are too low (Hisano et al., 2018).



**Figure 5 – A.** Change in tolerance to drought between year 2100 and year 3100 ( $\Delta DrTol$ ) for the fir and beech in the different forest types for a scenario of  $h^2$  and  $VR$  of 0.3 (see Fig. S.4 for all  $h^2$  and  $VR$  scenarios). **B.** Forest evolutionary trajectories for the three evolving traits ( $DrTol$ ,  $-ShTol$  and  $g$ ) for fir and beech in the different treatments (see Fig. S.6 for other  $h^2$  and  $VR$  scenario in monospecific and fir-beech mixed forest).  $DrTol$  is plotted against the negative model parameter ( $ShTol$ ) for the sake of clarity (more shade tolerant populations toward the left and less shade tolerant populations toward the right). The large dots represent trait values in 3100 and the crosses represent trait values during population extinctions.

340

### Limits and Future Applications

341 Here we propose an evolution module for individual-based models of forest dynamics. We  
 342 illustrated the importance of considering evolutionary processes with a case study focusing on  
 343 the fate of tree species confronted to climate change. One fundamental limit of our case study  
 344 is the arbitrary choice of stabilizing the climate after 100 years of warming (at the end of the pre-  
 345 dictions available in climate projections), which thus limits conclusions on any long-term effect.  
 346 In fact, we noticed that in all treatments but the species enrichment one, populations started to  
 347 recover only once the climate has stabilized (Fig. 2.B & Fig. 3). This was expected, because as  
 348 the environment changes, trait evolution lags behind a moving optimum value (Bürger and Lynch,  
 349 1995), even for the faster evolutionary scenarios tested. This shows that to simulate long term



350 impacts of climate change on species evolution, not only the speed and the absolute values of  
351 changing climate matters, but also the duration of the simulated change.

352 Abiotic conditions (such as climate variables) are not the only dynamic environmental com-  
353 ponents impacting tree species evolution under our eco-evolutionary framework in which, pop-  
354 ulations dynamics feed back on species' evolutive trajectories through competitive interactions.  
355 Interspecific competition did not lower the chances of evolutionary rescue in the two species  
356 mixture as the two focal species were primarily impacted by climate change. Ecological inter-  
357 actions impacted evolutive trajectories only in the species enrichment treatment as new pre-  
358 adapted species colonize the forest. However, the rate of evolution could be overestimated in  
359 the smallest populations (near extinction) due to a violation of the infinitesimal model assump-  
360 tion of large populations. Consequently, intra-family variance might have been overestimated  
361 by considering it constant, whereas it should have decrease in small populations due to inbreed-  
362 ing. This decrease could be accounted for in the future by tracking the pedigree of individuals  
363 (Barton et al. 2017). Doing so could, however, lead to an overestimation of the influence of ge-  
364 netic drift by considering the forest as a closed system whereas gene flow is considered to be  
365 important and inbreeding is typically low in tree populations (Petit and Hampe, 2006) except for  
366 isolate populations (Mimura and Aitken, 2007). Furthermore, tracking pedigree would also be  
367 computationally expensive for large populations.

368 To understand the role of the interactions between trees in our framework, it is essential  
369 to highlight that we focused here on one main ecological interaction, i.e. competition for light  
370 (although mediated by other environmental conditions, and notably drought stress). Introducing  
371 pre-adapted species to future environments in this context leads to a competitive hierarchy  
372 for light, ultimately resulting in the dominance of imported species over local ones. Given that  
373 we have imposed negative trade-offs between shade tolerance and growth on one hand, and  
374 drought tolerance on the other hand, species enrichment could only hinder the evolution of  
375 drought tolerance in local species, consequently affecting their evolutionary rescue. In other  
376 words, the emerging selection pressures from species enrichment and those arising from climate  
377 change have acted in opposed directions. However, if these selection pressures were aligned,  
378 such as through explicit competition among individuals for water, with a moderately competitive  
379 selection pressure, a positive effect of species enrichment on the evolutionary rescue of local  
380 species could have been observed (Osmond and Mazancourt, 2013). Similarly, using a demo-  
381 genetic model in a monospecific even-aged high forest, (Godineau et al., 2023) showed that  
382 lowering competition by reducing forest density at an early stage decreased adaptation speed  
383 for tolerance to drought. Therefore, future works should extend this framework to consider other  
384 competitive processes, and especially competition for water.

385 Very little is known about the interactions between species diversity, competition and evolu-  
386 tion in forests, especially in future conditions. A major strength of our approach is to be able to  
387 simulate reasonable evolutionary dynamics (Bone and Farres, 2001) for several tree species inter-  
388 acting through explicit competition in a context of climate change. To the best of our knowledge  
389 and in view of the ecological issues mentioned above, our approach proposes a significant step  
390 to test hypotheses about the interaction among species richness, intra- and inter-specific com-  
391 petition, and evolutionary dynamics (Cuddington et al., 2013; De Meester et al., 2019; Donohue  
392 et al., 2015; Franklin et al., 2020).

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393

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396

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### Conflict of interest disclosure

398

399 The authors declare that they comply with the PCI rule of having no financial conflicts of  
400 interest in relation to the content of the article.

### Data, script, code, and supplementary information availability

401

402 The version of ForCEEPS used to produce the data presented here, the R scripts for data  
403 analysis and figure production, and supplementary figures and tables are available online (10.  
404 5281/zenodo.10978643; Devresse et al., 2024 )

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