



HAL
open science

Evolutionary rescue in a mixed beech-fir forest: insights from a quantitative-genetics approach in a process-based model

Louis Devresse, François de Coligny, Freya Way, Xavier Morin

► To cite this version:

Louis Devresse, François de Coligny, Freya Way, Xavier Morin. Evolutionary rescue in a mixed beech-fir forest: insights from a quantitative-genetics approach in a process-based model. 2024. hal-04575070v2

HAL Id: hal-04575070

<https://hal.science/hal-04575070v2>

Preprint submitted on 29 Nov 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Evolutionary rescue in a mixed beech-fir forest: insights from a quantitative-genetics approach in a process-based model

Louis Devresse¹, François de Coligny², Freya Way³, and Xavier Morin¹

DOI not yet assigned

Abstract

Questions have been raised about the ability of long-lived organisms, such as trees, to adapt to rapid climate change, and to what extent forest management actions influence the evolutionary responses of tree species. Given the life history of trees and the time scales involved, these questions are often addressed through modeling approaches. Yet, most of these works focus on single-species case studies. The main objective and originality of our work is to explore the evolutionary responses of tree species to climate change using a process-based model, in a multi-species context. This approach allows us to investigate the conditions necessary for evolutionary rescue in a mixed beech-fir forest. Additionally, we explored how adaptation measures, such as assisted gene flow and assisted migration affect the conditions for evolutionary rescue in this forest. To achieve these objectives, we integrated a quantitative genetic module into a process-based forest gap model, enabling species-specific parameters to evolve as quantitative traits under selective pressure and drift. Our results show that increased trait variability and heritability reduce the loss of forest cover following climatic warming in the short term (over a century). We also found that assisted gene flow had the expected effect of aiding species in tracking climate change. Finally, our study suggested that introducing new pre-adapted species into the forest could improve recovery after climate change but could also hinder the evolutionary rescue of local species. We conclude that integrating evolutionary dynamics into process-based models significantly enhances their predictive power by incorporating genetic adaptation scenarios that would otherwise be overlooked. This approach also allows to test eco-evolutionary hypotheses and better understand the potential consequences of adaptation measures to climate change for tree species.

Keywords: Ecology, Evolution, modeling, Quantitative Genetic, Forest Ecology, Climate Change, Eco-Evolution, Process-Based modeling

¹CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France, ²botAnique et Modélisation de l'Architecture des Plantes et des végétations AMAP Parc Scientifique Agropolis, Montferrier-sur-Lez, France, ³University of Edinburgh, Ashworth Laboratories Charlotte Auerbach Road Edinburgh EH9 3FL, UK

Correspondence

xavier.morin@cefe.cnrs.fr

Introduction

2

3 There is growing concern about the viability of temperate forests in the coming years given
4 the speed at which climatic conditions are anticipated to change (Dyderski et al., 2018; Wessely
5 et al., 2024). At the global scale, a large number of forests have already experienced increased
6 mortality induced by heat waves and extreme drought events related to climate change (Hart-
7 mann et al., 2022). Among the emerging adaptation solutions to climate change, the promotion
8 of species diversity and forest structure complexity is gaining ground, supported by a growing
9 body of empirical evidence (Astigarraga et al., 2023; Hisano et al., 2018). More precisely, increas-
10 ing evidence suggest that tree species diversity can stabilize forest growth in a changing climate
11 - according to observations (Pardos et al., 2021) and modeling work (Morin et al., 2018) - and
12 also buffer the impact of disturbances in communities (Silva Pedro et al., 2015). Increasing di-
13 versity may as well raise the probability that a forest will contain species pre-adapted to future
14 environments (sampling effect) (Loreau and Hector, 2001). However, forecasting the future of
15 forest ecosystems and tree species over the coming centuries in a changing environment, neces-
16 sarily requires consideration of their evolutionary dynamics. In fact, questions are being raised
17 about potential for long living organisms such as trees to adapt to a rapid climate change (Al-
18 berto et al., 2013). More precisely, to their possibility of experiencing an evolutionary rescue.
19 The evolutionary rescue is defined by the recovery and persistence of a population through
20 natural selection acting on heritable variation (Bell, 2017). Indeed, the prospect of the evolu-
21 tionary rescue of tree species in the face of global warming is still largely unknown (Lefèvre et
22 al., 2014). The same applies to how forest management measures may affect the evolutionary
23 responses of tree species. In addition, evolution and species diversity can interact in complex
24 ways, stressing the importance of taking eco-evolutionary feedback loops into account when
25 studying the fate of forests. Specifically, in species-rich communities, certain species could be
26 prevented from adapting to a new environment because of competitive exclusion from other
27 pre-adapted species (Johansson, 2008; Price and Kirkpatrick, 2009; Thompson and Fronhofer,
28 2019). This effect is even more important for rare species, for which a reduction in population
29 size due to competition can have particularly harmful consequences on their adaptive capacity
30 by increasing genetic drift (De Mazancourt et al., 2008; Eldijk et al., 2020). Lastly, the selection
31 pressures exerted by interactions between species can act in the same or in the opposite direc-
32 tions to those imposed by an environmental change, thus accompanying or hindering species
33 adaptation (Osmond and Mazancourt, 2013).

34 Given the difficulty of experimenting on mature forests and the long term perspective of cli-
35 mate change impacts, these questions are frequently investigated through modeling approaches.
36 Among these, process-based models (PBMs) have been particularly advocated recently. Building
37 on the definition provided by Mäkelä et al. (2000), we define PBMs as simplified representations
38 of a system, characterized by functional components that interact with each other and with the
39 environment through explicitly simulated physical and mechanistic processes over time. Com-
40 pared to statistical or phenomenological models, PBMs should be more robust in predicting out-
41 comes under unprecedented conditions, as they don't need to extrapolate trends based on ob-
42 served statistical relationships between variables (Cuddington et al., 2013). Indeed, PBMs have
43 already been used to simulate, species range shifts (Keenan et al., 2011; Morin et al., 2008),
44 changes in ecosystem productivity (Guillemot et al., 2017; Morin et al., 2018) and responses

45 to drought events (Ruffault et al., 2022). However, the development of a PBMs often involves
46 the addition of new functional components with their associated parameters and more equa-
47 tions. PBMs development has therefore been limited by ecological knowledge to implement and
48 parametrize new functions, as well as (but to a lesser extent) computing power and code archi-
49 tecture. This is even truer for fine-scale models, such as individual based models that are used
50 to simulate forest dynamics. Hence, these models are often parameterized for the same domi-
51 nant species and focus mainly on monospecific and even-aged forests (see discussion in Morin
52 et al., 2021). For many of the same reasons, evolutionary processes are still rarely implemented
53 in PBMs, as it requires the simulation of new processes, such as the transmission of hereditary
54 traits or alleles from parents to offspring. This involves parameters that are costly and difficult
55 estimate in field studies such as the heritabilities and intraspecific variances of traits. As a result,
56 most predictions of the future of tree species have been made using fixed responses, without
57 incorporating evolutionary adaptation. However, authors who have incorporated evolution into
58 forest PBMs have shown for example that species-specific parameters that are subjected to
59 evolution can change significantly under the pressure of natural selection, after only two to six
60 generations (Kramer et al., 2015; Oddou-Muratorio and Davi, 2014). Furthermore, Godineau et
61 al. (2023) have shown that forest management practices such as early thinning can hinder adap-
62 tation by substituting the self-thinning process, which naturally selects better-adapted allele
63 combinations over time. Consequently, ignoring evolution can lead to inappropriate adaptation
64 and mitigation measures and can lead to an overestimation of the negative consequences of
65 climate change on forests (Gloy et al., 2023).

66 However, studies that have integrated evolution into PBMs so far have limited their scope to
67 monospecific and often even-aged forests. For this reason, here we propose a novel approach,
68 which involves considering evolutionary dynamics in a multi-species context, in order to improve
69 the robustness of PBM predictions over long time scales. Therefore, our preliminary objective
70 was to develop an evolutionary module capable of simulating the evolution of species-specific
71 parameters of a PBM through natural selection and drift in diverse and uneven-aged forests. For
72 this, we have chosen the PBM ForCEEPS (see methods for a model description and Morin et al.,
73 2021, 2020). We focused on three of its species specific parameters which were relevant regard-
74 ing our following objectives (see below): intrinsic growth rate, tolerance to shade and tolerance
75 to drought. In addition, our approach differs from those of Godineau et al. (2023), Kramer et al.
76 (2015) and Oddou-Muratorio and Davi (2014) in that we considered overlapping generations in
77 order to better represent unmanaged forests. These studies also used quantitative trait loci (QTL)
78 to simulate phenotypic variation and heredity while we have opted for the infinitesimal model
79 (Barton et al., 2017; Fisher, 1919) (see methods and limitations). To draw a parallel between
80 these two genetic models, the QTL model assume that traits are governed by a finite number of
81 loci of quantitative effect and their inheritance is explicitly modeled when reproduction occurs.
82 In the infinitesimal model, however, the phenotypes of the offsprings are drawn in a Gaussian
83 distribution around the average phenotype of two parents and this distribution is assumed to
84 result from the contribution of a large number of genes with small and additive effects. Further-
85 more, contrary to QTL approaches, the infinitesimal model does not explicitly model changes in
86 allele frequencies in the population and implies simpler (and therefore faster) calculations, while
87 retaining a certain genetic realism. This model is recommended by Romero-Mujalli et al. (2019)
88 for more ecologically-focused models that wish to take account of species evolution.

Species name	Type _s	S _s	Hmax _s	Amax _s	g _s	DDMin _s	WiTN _s	WiTX _s	Thot _s	Tco2Hot _s	<u>DrTol_s</u>	Ntol _s	Brow _s	<u>ShTolSI_s</u>	<u>ShTol_s</u>	LQ _s	AM _s
Local species																	
<i>Abies alba</i>	E5	75	50	366	350	841	-6	5	25	45	0.23	3	5	0.05	1	2	40
<i>Fagus sylvatica</i>	D3	76	50	400	260	841	-6	9	22	45	0.25	2	3	0.05	1	2	45
Imported species																	
<i>Quercus ilex</i>	E4	48	23	500	79	1121	0	14	26.5	45	0.45	1	1	0.1	5	2	30
<i>Quercus petraea</i>	D3	76	45	1000	246	981	-7	10	23.5	45	0.33	2	4	0.2	7	2	30
<i>Quercus pubescens</i>	D3	60	35	600	146	981	-4	9	23.5	45	0.33	2	4	0.3	7	2	30
<i>Quercus robur</i>	D3	66	45	1000	249	631	-10	10	23.5	45	0.3	2	4	0.3	9	2	40
<i>Pinus cembra</i>	E5	40	25	1000	115	600	-9	-2	26.5	45	0.3	1	4	0.2	5	3	30
<i>Pinus montana</i>	E5	46	25	300	138	600	-20	-3	26.5	45	0.37	1	3	0.4	9	3	30
<i>Pinus pinaster</i>	E4	69	35	300	350	1121	-1	12	26.5	45	0.4	1	3	0.25	7	1	24.5
<i>Pinus sylvestris</i>	E4	58	35	200	150	631	-20	5	26.5	45	0.37	1	3	0.3	9	3	20

Table 1 – Initial species-specific parameter values for both local and imported species at the Drôme site (France, 26). Initial values of the parameters related to the three candidate traits for evolution *i.e.* tolerance to drought (*DrTol*) or shade (*ShTol*) and intrinsic growth rate (*g*) are underlined (see method for detailed description). Additionally, *AM_s*, the age at maturity of the species is not evolving but is used for the computation of the evolutionary rates (see methods). For a full parameter description, see Morin et al. (2021). For the parameter values of other species used in ForCEEPS, see the supporting information.

89 For this first application of our method, we focused on the evolution of a beech-fir forest
90 (*Fagus sylvatica* and *Abies alba*) based on a specific site in south-eastern France, subject to RCP
91 4.5 climate warming (corresponding to an average warming of 3°C and a reduction in annual
92 rainfall of 120 mm over the century). We chose the beech-fir forest because it is a common
93 species assemblage in the European montane ecosystem (Toïgo et al., 2015). What’s more, the
94 chosen location is in the southern part of the range of both species, where they are particularly
95 vulnerable to global warming. Indeed, in this specific context, the ForCEEPS model predicts the
96 extinction of beech and fir in the absence of species evolution, making it an ideal setup for assess-
97 ing the conditions for which evolutionary rescue could emerge, and the effect of management
98 practices on these conditions. Therefore, we had three main objectives: 1) Identify the conditions
99 for evolutionary rescue of beech and fir, in monospecific (hereafter “monospecific treatment”)
100 and mixed forests (hereafter beech-fir “mixture treatment”); 2) Assess the impact of directional
101 gene flow on the prospects for evolutionary rescue and on evolutionary trajectories in beech and
102 fir populations. We explore this question by importing beech and fir individuals pre-adapted to
103 more arid conditions (hereafter “assisted gene flow treatment”) (Fady et al., 2016; Hlásny et al.,
104 2014); 3) Evaluate the consequences of introducing new species that are more tolerant of water
105 stress (Table. 1) on the evolutionary rescue conditions and evolutionary trajectories of beech
106 and fir (hereafter “assisted migration treatment”) (Hisano et al., 2018; Hlásny et al., 2014). We
107 considered the two treatments “assisted gene flow” and “assisted migration” to be human-driven
108 movement of reproductive material for climate change adaptation. Therefore, we refer to these
109 treatments as climate change adaptation measures or “management practices”. However, more
110 broadly, these treatments could also be interpreted as the natural migration of individuals from
111 an external pre-adapted population into a population maladapted to future conditions, such as
112 the natural migration of drought-tolerant species into the beech-fir forest of our focus site.

113 Methods

114 Model Description

115 We integrated our evolutionary module into the PBM ForCEEPS, a model from the gap model
116 family developed to simulate both managed and freely evolving forests (Morin et al., 2021, 2020)
117 (Fig. 1, blue, green and yellow boxes). Gap models simulate the growth, mortality and regener-
118 ation of trees in a collection of patches of land. ForCEEPS is individual based, and relies on

119 calculating an optimal growth for each tree using empirical equations from Bugmann (1996) and
120 Moore (1989). This optimal growth is then reduced according to several environmental stresses,
121 such as lack of light, water, nitrogen or browsing. Tree mortality depended on two components:
122 background mortality and growth-related mortality. The former depends on the species' maxi-
123 mum longevity, but is stochastic; the latter occurs if a tree experiences three consecutive years
124 with growth below a certain threshold (hereafter "slow growth state"). Furthermore, we modified
125 the regeneration process in ForCEEPS to account for interspecific competition. Our approach to
126 model regeneration is more precisely described later in this section. In gap models, individuals
127 are generally not spatialized within a plot for the sake of simulation time. Trees in a same patch
128 all compete for light and share the same environmental conditions, and so the carrying capacity
129 of a patch is an emergent property. The sum of several patches simulates a forest or a represen-
130 tative sample of a given forest within a forest matrix (Shugart et al., 2018). The main process in
131 the model is competition for light within these patches, considered to be the main driver of tem-
132 perate forest dynamics (Kohyama and Takada, 2012). However, tree to tree competition for light
133 is indirectly influenced by the effect of environmental conditions, (especially climate), on growth
134 (Morin et al., 2020). The ForCEEPS model operates on an annual time step, but takes into account
135 monthly climatic variations (temperature and precipitation) to calculate the water balance of the
136 patches. Species in ForCEEPS are defined by a specific set of parameters (Table. 1). In order to
137 simplify the interpretation of simulation results, we have limited our scope to the evolution of
138 three of these traits, most related to our questions of interest. We focused on the adaptive dy-
139 namics of drought tolerance (hereafter *DrTol*) as it is strongly selected by environmental change
140 and so presumably, also under selection from global warming. In order to be comprehensive
141 with our investigations, we considered the potential interactions of *DrTol* with the main traits
142 related to species competitive abilities which are shade tolerance (hereafter *ShTol*) and intrin-
143 sic growth rate (hereafter *g*). Negative trade-offs were therefore imposed between *ShTol* and
144 *DrTol*, and between *g* and *DrTol*, to account for the relationships observed between drought
145 tolerance and competitive abilities in tree species (Kattge et al., 2020; Niinemets and Valladares,
146 2006). The other species-specific parameters do not undergo evolution, and a single value per
147 parameter is assigned to all individuals of the same species. To facilitate further analysis, basal
148 area (BA) (m^2/ha) and its dynamic through time are output to describe the ecological state of the
149 simulated forests. BA is commonly used in silviculture and forest ecology as a proxy of forests
150 density and reflects the development stage of a forest. Finally, changes in the average values of
151 population traits and rates of evolution are output to enable the study of evolutionary dynamics.

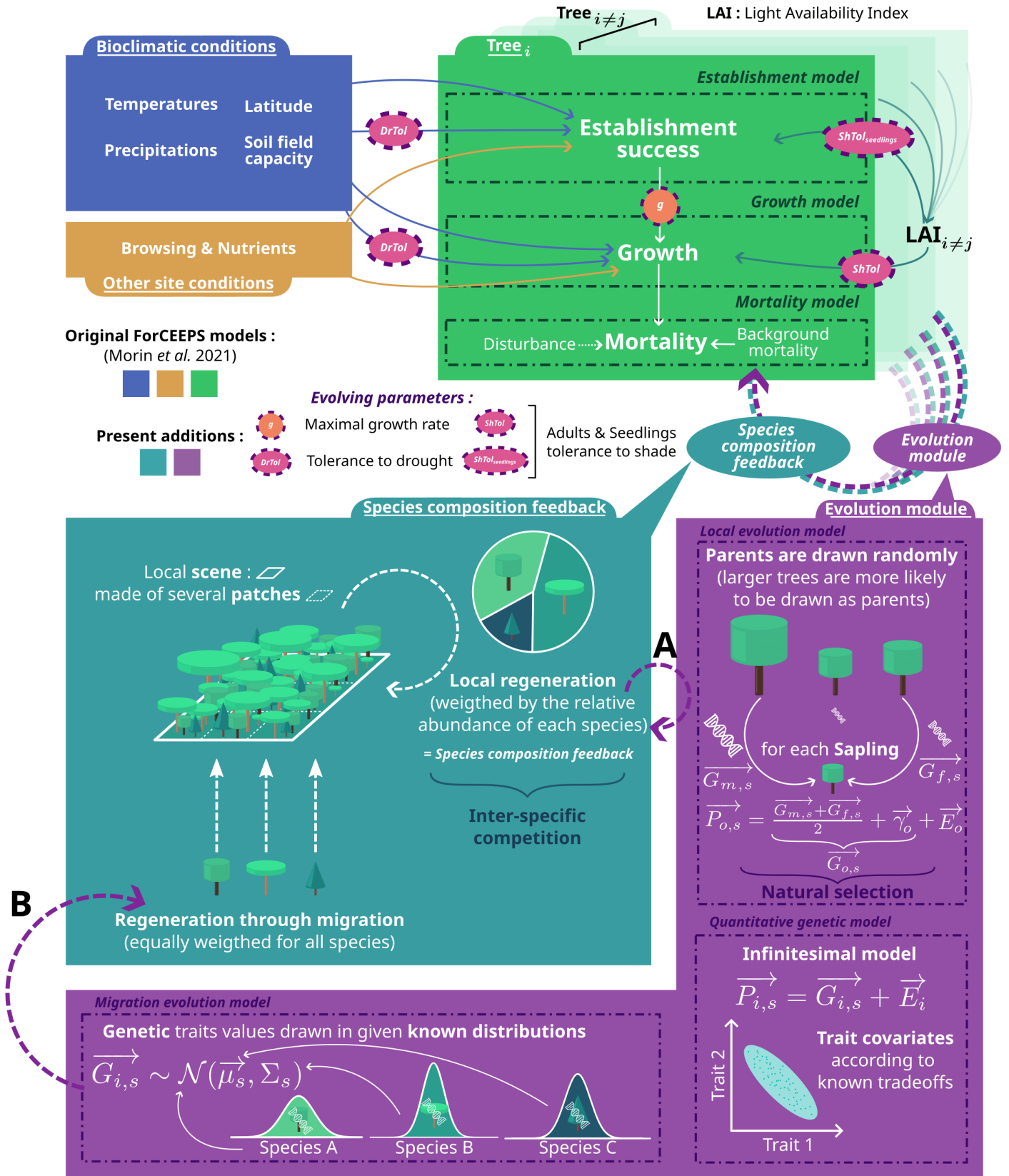


Figure 1

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 referred to here as “migration”. 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 initial trait's values (Table. 1) 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 traits along established trade-offs. The initial state of any evolution simulation is a forest inventory (see methods). We begin by randomly assigning genotypes and phenotypes using the distributions described above. Two types of individuals may then appear during the simulation: **A**) For a locally generated offspring o , its phenotype is 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 (γ_o) and environmental noise (E_o). An individual can be randomly drawn as a parent if it is older than the known age of maturity for its species (Table. 1) and if it is growing above a certain threshold (not in a “slow-growth” state). 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.

152 Regeneration and Species Composition Feedback

153 In the individual based forest PBM literature, two main approaches are used to simulate re-
 154 generation. The first one calculates the number of new seedlings as a function of the number of
 155 seeds produced by mature trees in the simulation, followed by the application of a mortality filter.
 156 The second approach, more commonly used in gap models such as ForCEEPS, involves target-
 157 ing a predefined seedling density per unit area, calibrated from inventory data (Bugmann, 1996;
 158 Didion et al., 2009; Morin et al., 2021). Among the previous examples of models that account for
 159 evolutionary processes, most have adopted the first approach. However, the second approach
 160 renders regeneration independent of the current state of the simulated forest. In a multi-species
 161 context, regeneration would therefore consist of a constant “seed rain” across time and would
 162 include all species considered as able to reproduce in the simulation. To account for the impact
 163 of interspecific competition on regeneration, and following earlier work by Vallet (*unpublished*),
 164 we incorporated a feedback mechanism from the current composition of the forest (based on
 165 the relative abundance of species in relation to their BA across all patches) on the identity of
 166 colonizing seedlings each year. We refer to this type of regeneration, based on the relative abun-
 167 dance of species, “local regeneration” (Fig. 1 teal box, arrow A). In addition, we have retained the
 168 option of using a regeneration identical to the classic gap model scheme, now called “migration
 169 regeneration” (Fig. 1 teal box, arrow B). If activated, the migration regeneration is added to the
 170 local regeneration and weighted by a parameter M . The parameter M is a continuous index rang-
 171 ing from 0 to 1, where 0 indicates that only local the regeneration occurs, and 1 indicates that
 172 the full seed rain is added to the local regeneration, effectively doubling the target number of
 173 seedlings per unit area. This last point implies that migration can only raise the seeding density.
 174 M must be maintained at a low value (< 0.2) to prevent the risk of the model operating outside
 175 its valid range.

176 Evolution Module

177 The core of this work was the incorporation of a module simulating evolutionary dynamics
 178 into the ForCEEPS model (Fig. 1 purple box). This module required species traits to be both
 179 variable and heritable, with natural selection and drift impacting the distribution of these traits
 180 through time. As stated above we specifically selected three species-specific parameters as fo-
 181 cal evolving traits, chosen for their relevance in responding to selection pressures imposed by
 182 climate change and competition:

- 183 • The individual's drought tolerance ($DrTol_{i,s}$): a continuous index ranging between 0 (in-
 184 tolerant) and 1 (tolerant).
- 185 • The individual's shade tolerance ($ShTol_{i,s}$) and its counterpart, the seedlings' shade tol-
 186 erance ($ShTolSl_{s,i}$). $ShTol_{s,i}$ is a continuous index ranging from 1 (shade tolerant) to 9
 187 (shade intolerant) that determines the impact light deprivation has on growth. $ShTolSl_{s,i}$
 188 is an index ranging from 0 (tolerant) to 1 (intolerant) that controls the availability of light
 189 required for seedling establishment.
- 190 • The individual's maximal growth rate ($g_{i,s}$), unitless.

191 The initial trait values before evolution: $DrTol_s$, $ShTol_s$ and $ShTolSl_s$ (Table. 1) come from
 192 a compilation of previous studies (Bugmann, 1996; Ellenberg and Mueller-Dombois, 1965; Ni-
 193 inemets and Valladares, 2006; Rameau et al., 2008). Initial values for g_s are inferred from actual
 194 measurements from French national forest inventory (Morin et al., 2021). The validation of drift
 195 and natural selection processes in simple contexts are available in the supporting information
 196 (Model validation section, Fig. S.1-4).

197 Initialisation phase

198 The three traits described above are treated as quantitative and are assumed to be influenced
 199 by a large number of genes with small and additive effects, each of which contributes infinitesi-
 200 mally to an individual's phenotype (infinitesimal model *sensu* Fisher, 1914) (Barton et al., 2017).
 201 Consequently, traits initially follow a normal distribution in populations. Each initial state of an
 202 evolution simulation must consist of a forest inventory derived from field observations or previ-
 203 ous simulations. From there, a phenotype is assigned to each individual in the form of an array
 204 of values for each evolving trait by means of random draws from 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, $\vec{E}_i \sim \mathcal{N}(\vec{0}, \Sigma_E)$

205 The phenotype array $P_{i,s}$ of individual i of species s , is composed of a genetic and an en-
 206 vironmental component, respectively $G_{i,s}$ and $E_{i,s}$. μ_s is an array containing the initial values of
 207 the ForCEEPS species specific parameters ($DrTol_s$, $ShTol_s$ and g_s). Consequently, $G_{i,s}$ and $P_{i,s}$ are
 208 centered around the initial species specific parameters described above whereas $E_{i,s}$ is a zero
 209 centered random non heritable noise. Σ_G and Σ_E are the genetic and environmental variance-
 210 covariance matrices as described below:

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

211 where h^2 is the heritability and Σ_P is the phenotypic variance-covariance matrix. Σ_P values
 212 depend on the initial intraspecific trait variability ratio (VR) which is the fraction of the interspe-
 213 cific variability in traits ($\overrightarrow{sd_{inter}}$) observed in the pool of species parameterized in ForCEEPS (see
 214 equation (2) and Table S.1 for the species pool) (Morin et al., 2021). This calculation requires us
 215 to assume that Σ_G is proportional to Σ_P which remain a major oversimplification of reality. This
 216 choice was necessary to reduce the number of input parameters for our evolutionary module,
 217 especially as it is extremely complicated to obtain estimates of the genetic and environmental
 218 covariances of traits. Furthermore, h^2 and VR are input parameters in the simulation, with the
 219 same initial values assigned uniformly to all traits and species within each evolutionary scenario.
 220 However the realized heritability becomes a dynamic variable as natural selection and drift act
 221 on the genetic variance of traits throughout the simulation.

$$(2) \quad \Sigma_P = \text{diag}(\overrightarrow{sd_{intra}}) \cdot \Sigma_c \cdot \text{diag}(\overrightarrow{sd_{intra}}) \quad \text{Where } \overrightarrow{sd_{intra}} = VR \cdot \overrightarrow{sd_{inter}}$$

222 Where $\overrightarrow{sd_{intra}}$ is the intraspecific traits standard deviation array and Σ_c , the trait correlation
 223 matrix. Trait correlation values were derived from interspecific correlations of proxy traits for
 224 *DrTol*, *ShTol*, and *g* found in literature and databases (Kattge et al., 2020; Niinemets and Val-
 225 ladares, 2006). We used proxies to expand the scope to include the largest possible set of species.
 226 By applying these interspecific correlations to the intraspecific scale, we assumed that the trade-
 227 offs shaping trait relationships at the macroevolutionary scale also occur at the microevolution-
 228 ary scale. We set those correlations to 0.36 between *DrTol* and *ShTol* and 0.38 between *DrTol*
 229 and *g* (Fig. S.5). For more details, please refer to the supporting information.

230 Seedling shade tolerance (*ShTolSI*) evolves only through changes in *ShTol*, making it an ex-
 231 tension of this trait. The seedling shade tolerance for an individual, *ShTolSI_{i,s}*, was linearly de-
 232 rived from the difference between the individual's shade tolerance for growth, *ShTol_{i,s}*, and the
 233 species' initial shade tolerance value (*ShTol_s*). A 1/8 ratio was applied to convert the difference
 234 *ShTol_{i,s} - ShTol_s* on a scale of 1 to 9 into the difference *ShTolSI_{i,s} - ShTolSI_s* on a scale of 0 to 1:

$$ShTolSI_{i,s} = ShTolSI_s + \frac{1}{8} \cdot (ShTol_{i,s} - ShTol_{i,s})$$

235 Evolution phase

236 After the initialization, traits are inherited through the process described below and illus-
 237 trated in (Fig. 1 purple box arrow A) as the simulation runs. For locally regenerated individuals,
 238 new seedlings of species *s* were attributed two parents randomly chosen among a pool of repro-
 239 ducer trees. A tree is considered as reproducer if it meet two criteria: 1) the tree is older than
 240 its species-specific maturity age (Table. 1) and 2) it is not in state of "slow growth". An individual
 241 tree is considered in a slow growth state if it has been growing less than a specific threshold for
 242 three consecutive years. This phenomenon occurs when environmental factors such as temper-
 243 ature or light levels are too restrictive for the tree and simulates the process of carbon starvation
 244 (Morin et al., 2021). We assume that in such conditions, trees do not invest in reproduction. The
 245 probability of each tree from the reproducer pool to be drawn as parent is weighted by its size
 246 (assessed as its relative BA in the reproducer pool, assuming that larger trees leave more off-
 247 spring). Once a seedling is attributed two parents, each of its non-evolving traits is set as equal

248 to the species' base trait value (Morin et al., 2021) while the phenotypic values of each of the
 249 three evolving traits is defined as the mean of the genetic trait values of both parents, to which
 250 a genetic (γ_o) and an environmental noise is added (e_o):

$$\vec{P}_{o,s} = \underbrace{\frac{\vec{G}_{m,s} + \vec{G}_{f,s}}{2}}_{\vec{G}_{o,s}} + \vec{\gamma}_o + \vec{E}_o, \text{Where}$$

$$\vec{\gamma}_o \sim \mathcal{N}(\vec{0}, \Sigma_G \cdot \frac{1}{2}) \text{ and } \vec{E}_o \sim \mathcal{N}(\vec{0}, \Sigma_E)$$

251 With, $P_{o,s}$ the phenotype of offspring o , for a given species s and $G_{m,s}$ and $G_{f,s}$ the genotype
 252 of the mother and father', respectively. The genetic noise γ_o originates from the within-family
 253 genetic variance, also called the segregation variance as it results from the process of Mendelian
 254 segregation of alleles. Under the infinitesimal model, assuming sufficiently large and stable an-
 255 cestral populations and dismissing inbreeding, this genetic noise variance is constant across gen-
 256 eration and normally distributed, regardless of the distributions of the parents' genetic values
 257 (Bulmer, 1971). Without selection, setting the within-family genetic variance to half the initial
 258 genetic variance keeps the overall population's genetic variance constant through generations,
 259 as computing the mean breeding value of two parents to obtain those of the offspring will re-
 260 sult in reducing population's genetic variance by half each generation. In contrast, for seedlings
 261 originating from migration (Fig. 1 purple box arrow B), phenotypes are drawn in multi-normal
 262 distributions as described in equation (1) with the difference that the means can differ from
 263 those of local seedlings. These distributions can either be set at the beginning of the simulation,
 264 or can be updated during the on-going simulation to represent at best the genetic composition
 265 of replicate populations evolving simultaneously. In the present case, migrants trait means and
 266 variances are set initially depending on the treatment and evolutionary scenario considered (see
 267 the simulation plan sub-section). Σ_E variances are fixed at the start of the simulation depending
 268 on h^2 and VR , and remain constant throughout the simulation.

269 Site and climate data

270

271 Our study is based on two sites: a central site in south-east France (hereafter "Drôme"), where
 272 beech and fir forests are common ecosystems (44°55'01.2" N; 5°17'27.6" E: 1146 mm of yearly
 273 precipitations and mean temperatures of 5.9°C), and another site with drier conditions (hereafter
 274 "Montagne Noire"), at the southern limit where beech-fir forests could be found (43°27'55.4"N;
 275 2°16'43.2"E: 983 mm of yearly precipitations and mean temperatures of 9.3°C). The model's site
 276 parameters (i.e. other than climate conditions) for the Drôme site were derived from field mea-
 277 surements, and those for the Montagne Noire site were arbitrarily set to be identical to ensure
 278 comparability between the two sites (Table S.2). Climate data consisted of monthly temperature
 279 and precipitation data available from the CHELSA (CMIP5, BCG model) (Karger et al., 2020),
 280 which were organized into three periods:

- 281 • A historical period based on records of climate conditions at the coordinates of both sites
- 282 from 1900 to 2000, repeated over 1000 years.
- 283 • A 100-year warming period including data from 2000 to 2100 for the RCP 4.5 scenario.

- A stabilization period consisting in a repetition of the previous climatic projections from years 2090 to 2100, repeated over 1000 years.

Simulation plan

In order to obtain mature, age-structured forests in a pseudo-equilibrium state to serve as the initial state for all our later simulations, we carried out 50 replicates of what we call “baseline simulations”. These simulations consist of 1000 years of ForCEEPS simulations from bare soil on climates of historical periods without the evolution module. For the beech-fir mixture treatment, the baseline simulations included 50 patches of 1,000 m² each of mixed beech-fir forest, with beech as the dominant species. These simulations produced inventories containing on average 720 beech trees at a density of 11.60 m²/ha of basal area and 90 fir trees at a density of 1.91 m²/ha (Table S.3). In order to isolate the effect of interspecific interactions between species from the effect of the maximum population size, we kept the number of individuals in the same order of magnitude between beech-fir mixtures and monospecific baseline simulations. In the Drôme site and climate, the ForCEEPS model predicts that a mixed beech-fir forest will be strongly dominated by beech. Comparing later, the evolutionary trajectories between a monospecific fir forest and a mixed forest of the same area will result in a comparison of two fir populations of significantly different sizes. The effects that interspecific interactions might have on the evolutionary trajectories of forests will then be indistinguishable from the effects caused by drift. Consequently, we reduced the number of patches in monospecific baseline simulations by running 42 patches of monospecific beech and 11 patches of monospecific fir. This yielded an average of 693 beech trees with a basal area density of 14.13 m²/ha, and 76 fir trees with a density of 8.10 m²/ha. Then, to address our three questions, we implemented the simulation framework depicted in Fig. S.6, with the evolution module activated starting from inventories produced from the baseline simulations. Each question was 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, 0.4) (thus 16 evolutionary scenarios) in order to cover cases ranging from the systematic extinction of both species in all replicates to the recovery of abundances above or close to the initial levels of both species after 1000 years of climate stabilization.

1. Does mixing fir and beech dampen evolutionary rescue?

The persistence and recovery of forests and the evolutionary trajectories of traits during and after the three climatic periods were compared between the two treatments: beech-fir mixtures and beech-fir monospecific forests. We ran 50 replicates of each of the three compositions for each evolutionary scenario at the Drôme site, with associated climate projections (a total of $50 \times 3 \times 16 = 2400$ simulations).

2. Does assisted gene flow facilitate evolutionary rescue?

Secondly, we compared the previously mentioned beech-fir mixture treatment with an “assisted gene flow” treatment. This latter was identical to the beech-fir mixtures treatment, with the difference that we added immigration of pre-adapted beech and fir individuals during the 100-year warming period. The migration parameter M was arbitrarily set to 0.1 to allow new genotypes to colonize with a marginal impact on equilibrium BA. The phenotypic distributions of migrant traits (Table S.4) are centered around the average phenotypes across 25 replicates of beech-fir mixed forests that have evolved over 1000 years in the historical climates of the Montagne Noire

327 (with values of h^2 and VR corresponding to the evolutionary scenario considered). We carried
 328 out only 25 replicates of this treatment, as computation time was significantly larger ($25 \times 16 =$
 329 400 simulations).

330 **3. Does assisted migration prevent local species' evolutionary rescue?**

331 Lastly, the assisted migration treatment was similar to the assisted gene flow treatment, but in-
 332 stead of adding beech and fir individuals during the warming period, individuals from a set of
 333 eight other species were introduced through migration ($M = 0.1$). The phenotypic values of im-
 334 ported species were drawn from multivariate normal distributions, with the means for the evol-
 335 ving traits corresponding to the initial values parameterized for these species (Table. 1). Imported
 336 species were also subject to evolution as soon as mature individuals established themselves in
 337 the simulated forests. For reasons of computational efficiency, we carried out only 25 replicates
 338 of this treatment again, starting exclusively from mixed beech-fir forests ($25 \times 16 = 400$ simula-
 339 tions).

340 Data analysis and software

341 Climate, site, and trait values were analyzed and transformed into the desired formats and
 342 figures using R software 4.3.0 (R Core Team 2023). To follow the definition of Bell (2017), we
 343 consider a population to have undergone evolutionary rescue if two criteria are met: Firstly, its
 344 BA at the end of the entire simulation is greater than 5% of its reference BA for the historical
 345 period (persistence). Secondly, if population growth is positive (recovery) during the stabilization
 346 period, which is always the case when the 5% threshold is exceeded). To describe trait evolu-
 347 tion, trait values per species s were averaged by weighting them by the BA of each individual.
 348 This approach ensures the values are representative of the population p in a given year y and
 349 prevents over-representation of a large number of unfit seedlings that will not survive several
 350 consecutive years. We refer to those weighted averages as $\overline{DrTol}_{s,p,y}$, $\overline{ShTol}_{s,p,y}$ and $\overline{g}_{s,p,y}$ for the
 351 three respective traits. For each evolutionary scenario, average trait evolutionary rates across
 352 replicates ($Nrep$) were also measured in Haldanes (H_0) according to Gingerich (1983) between
 353 the years 2000 ($y1$) and 2100 ($y2$), depending on its age at maturation (AM_s) for each species s
 354 (see equation (3)). Exact H_0 values are provided along with their 95% confidence intervals for all
 355 replicates for the h^2 and $VR = 0.3$ evolutionary scenarios as this setting led to the most realistic
 356 evolutionary rates (Bone and Farres, 2001). Haldanes rate measures the "short term" evolution-
 357 ary responses of populations. To quantify the long-term evolution of the $DrTol$ trait in species s
 358 and in population p i.e $\Delta Drtol_{s,p}$, we computed the difference between the $\overline{DrTol}_{s,p,3000}$ and the
 359 average $\overline{DrTol}_{s,p,y}$ over a reference historical period (year 1500 to 2000). The ForCEEPS model,
 360 as well as its evolution module, is available via Capsis, a simulation platform for forest growth
 361 and dynamics models (Dufour-Kowalski et al., 2012).

$$(3) \quad \overline{H_{0, Trait, s, y1, y2}} = \frac{1}{Nrep} \sum_{n=1}^{Nrep} \left(\frac{\overline{Trait}_{s, y2} - \overline{Trait}_{s, y1}}{sd(\overline{Trait}_{y1, y2})} \right) \cdot \frac{1}{AM_s}$$

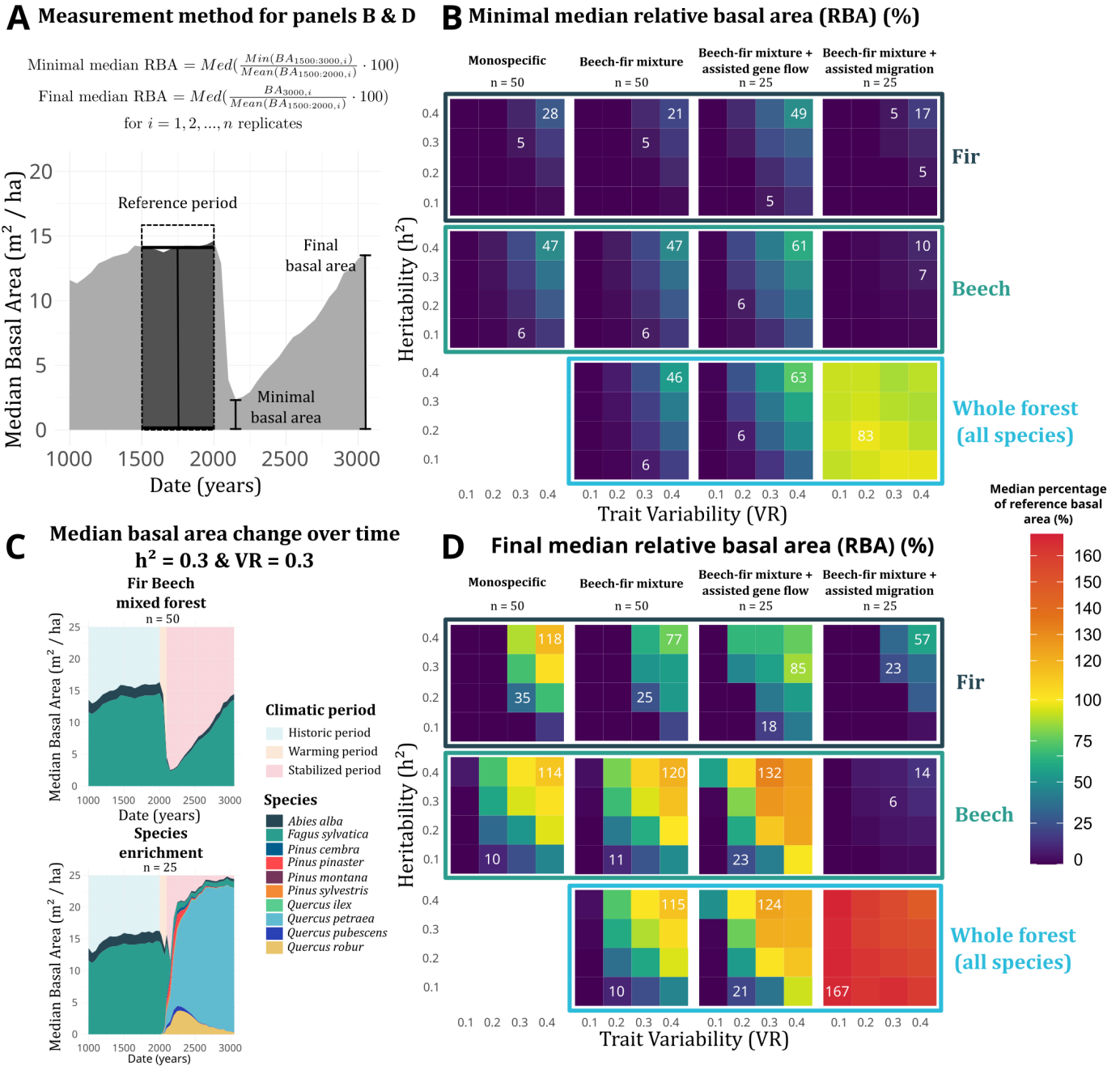


Figure 2 – **A.** Median minimal relative forest basal area (see D) at the end of the stabilization period in a forest of Drôme site for the various scenarios of heritability (h^2) and intra- to interspecific trait standard deviation ratio (VR). Number of replicates are indicated under the treatment type and numerical values of median relative basal area are indicated for maximum and for minimum value above 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 assisted migration 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).

Results & Discussion

362

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

364 The median minimal Relative Basal Area (RBA) (Fig. 2) can be interpreted as the population's
 365 safety margin for persistence. VR and h^2 had a strong impact on minimal RBA (Fig. 2.B), highlight-
 366 ing the relevance of the evolutionary processes even in the short term, as minimal RBA typically
 367 occurs soon after the end of the warming phase (year 2150-2200) (Fig. 2.C, Fig. 3 & Fig. S.7).
 368 We use the terms "slower evolutionary scenarios" for cases with lower h^2 and VR values, and
 369 "faster evolutionary scenarios" for those with higher h^2 and VR values, for which we expect
 370 lower and higher evolution rates, respectively. The 5% threshold of median minimal RBA was
 371 reached for minimum h^2 and VR of 0.3 in fir in both monospecific and beech-fir mixture treat-
 372 ment populations. In the monospecific beech treatment however, the 5% threshold was reached
 373 for "slower" evolutionary scenarios of h^2 of 0.1 and VR of 0.3 (Fig. 2.B). The most pre-adapted
 374 species encountered the lowest risks of extinction, i.e. beech with $DrTol_s = 0.25$ as opposed to
 375 fir with $DrTol_s = 0.23$. The lack of differences between the monospecific and mixture treatments
 376 in terms of safety margin was due to the release from competition for light cause by the high
 377 mortality in the warming period (Fig. 3 & Fig. S.7). Therefore, mixing did not impact the chances
 378 of persistence for both species. We used the final RBA to assess the population's ability to re-
 379 cover its pre-warming basal area by the end of the 1000-year stabilization period in a warmed
 380 climate. In contrast to the short term response, the recovery of fir populations at the end of the
 381 simulations showed differences between the monospecific and mixture treatments. Fir recovery
 382 was generally lower in the beech-fir mixture treatment than in the monospecific treatment for
 383 the fastest evolution scenario (h^2 and $VR = 0.4$, Fig. 2.D), with a median final RBA of 77% and
 384 120%, respectively.

385 An analysis of trait evolutionary trajectories is necessary to understand why evolution tends
 386 to favor beech populations over fir ones. Firstly, $DrTol$ evolution toward higher values was criti-
 387 cal for population recovery, with populations that reached higher $\Delta DrTol$ showing the strongest
 388 recoveries. As expected, higher $\Delta DrTol$ values were observed for higher h^2 and VR scenarios
 389 (Fig. 4). However, interspecific interactions between beech and fir had no impact on the evo-
 390 lutionary trajectories of the three traits in the short term, as there were no differences in fir
 391 and beech evolutionary rates between the monospecific and the beech-fir mixture treatment
 392 (Fig. 5.A), regardless of the evolutionary scenario (Fig. S.8). Fir $DrTol$ evolutionary rates were 0.23
 393 H_0 [0.22; 0.25] in the monospecific treatment compared with 0.23 H_0 [0.20; 0.25] in the mixture.
 394 For beech, the rates were 0.35 H_0 [0.34; 0.36] for monospecific and beech-fir mixture treatments.
 395 The same observations can be made for the two other traits ($ShTol$ and g) (Fig. 5.A). This result
 396 can be explained by the lifting of competition following the massive mortality episodes that
 397 accompany climate change. More surprisingly, long-term evolutionary trajectories were also un-
 398 affected by competitive interactions between beech and fir individuals. This is evidenced by the
 399 overlap of evolutionary trajectories and destinations of monospecific and the beech-fir mixture
 400 treatments for both species (Fig. 5.B). Populations of both species showed an increase in \overline{DrTol}
 401 throughout the simulations, accompanied by a decrease in \overline{ShTol} and \overline{g} over time due to the
 402 negative trade-off between $DrTol$ and the two competitive traits (Fig. 5.B; Fig. S.9-11). Lower
 403 recoveries were observed in fir population in the beech-fir mixture treatment compared to the
 404 monospecific one for equivalent $\Delta DrTol$ evolution (see the curvature of the final RBA to $\Delta DrTol$

405 relationship in Fig. 4). We interpreted this result as the return of competition for light as the main
 406 process shaping the community composition in the beech-fir mixture treatment, preventing fir
 407 recovery despite its tolerance to drought. In beech-fir mixtures, evolution favored the dominant
 408 species, which is in line with our expectations and theoretical works (De Mazancourt et al., 2008;
 409 Eldijk et al., 2020; Thompson and Fronhofer, 2019). We propose two non-exclusive interpreta-
 410 tions of this phenomenon: 1) beech was favored because its populations were initially larger,
 411 reducing drift and increasing the probability of the population to host more drought tolerant in-
 412 dividuals explaining the faster evolutionary rates in beech populations overall (Fig. 5.A); and/or
 413 2) beech was initially fitter due to its higher $DrTol_s$ allowing its populations to reach higher final
 414 \overline{DrTol} values (Fig. 5.B).

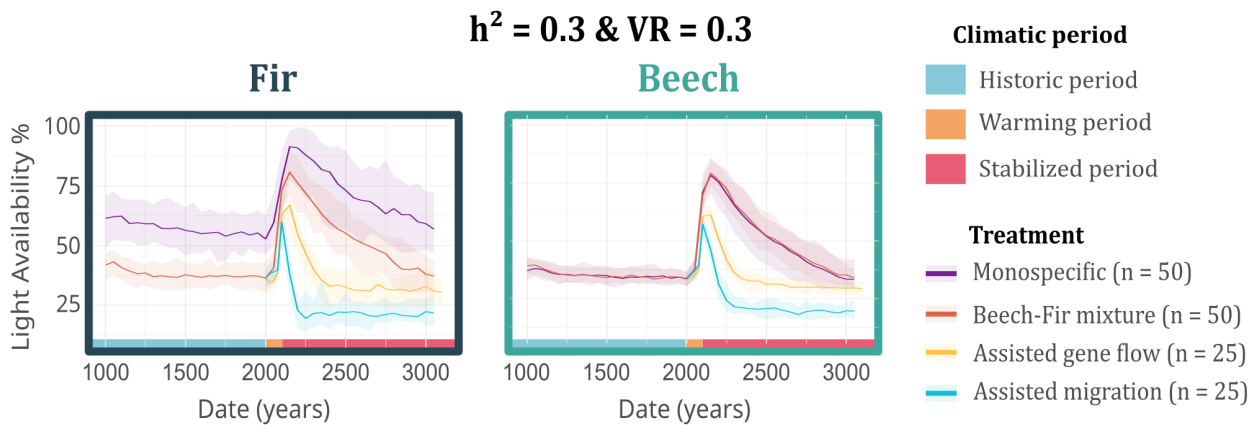


Figure 3 – Median across 25 to 50 replicates of the mean relative light availability perceived by individuals of beech and fir (model output) across replicates in the four treatments for the evolutionary scenario with $h^2 = 0.3$ and $VR = 0.3$. The envelopes show the quantiles 0.025 and 0.975 over all repetitions of light availability. Bottom stripe color indicates different climatic periods (see Methods for details). Results for other evolutionary scenarios are presented in Fig. S.7.

415 2. Does assisted gene flow facilitate evolutionary rescue?

416 As expected, the assisted gene flow treatment led to the highest $DrTol$ evolutionary rates
 417 during the warming period, with beech $H_0 = 0.50$ [0.46; 0.51] and fir $H_0 = 0.39$ [0.35; 0.43]
 418 for the h^2 and $VR = 0.3$ scenario (Fig. 5.A). These values are within the largest known H_0 for
 419 plant adaptation to abrupt changes in natural populations (Bone and Farres, 2001). Therefore,
 420 assisted gene flow led to a higher safety margin (minimal RBA) for both species and to a larger
 421 number of evolutionary scenarios in which both beech and fir experienced evolutionary rescue
 422 (Fig. 2.B & D). While assisted gene flow helped both species track climate change in the short
 423 term (minimal RBA around 2100 years), it led to more complex relationships between evolution-
 424 ary rates (h^2 and VR) and recovery (final RBA) in the long term. In contrast with the beech-fir
 425 mixture treatment, highest recoveries (final RBA) no longer occurred for the fastest evolutionary
 426 scenarios (h^2 and $VR = 0.4$) for fir and beech populations individually and at the whole forest
 427 scale (Fig. 2.D). In the assisted gene flow treatment, higher evolutionary rates led to even lower
 428 values of \overline{ShTol} and \bar{g} in beech (Fig. 5.B). These reduced \overline{ShTol} values resulted in slower effective
 429 growth rates as shading intensified during forest recovery (Fig. 3). Additionally for fir, lower
 430 recoveries occurred for equivalent $\Delta Drtol$ in the assisted gene flow treatment compared to the
 431 simple mixture (flatter $\Delta Drtol$ to final RBA recovery curve) (Fig. 4). This result can be explained

432 by the fact that assisted gene flow may have asymmetrically favored the dominant species of the
 433 mixture (beech). Altogether, this treatment showed that beyond a certain point, stronger evolu-
 434 tionary responses regarding the *DrTol* no longer guaranteed better recoveries. In this context,
 435 trait coevolution and interspecific competition played a more decisive role on the fate of forests.

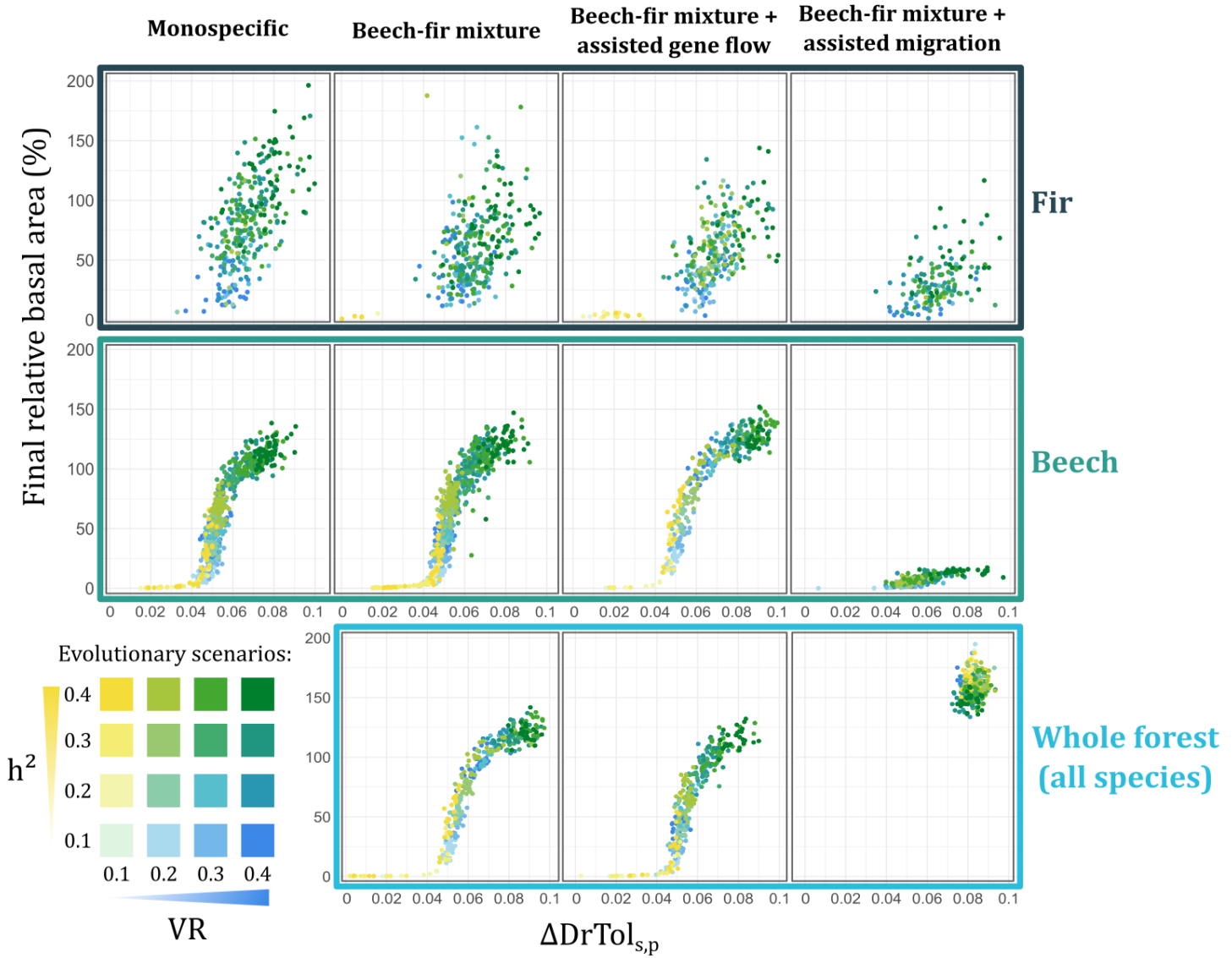


Figure 4 – Final relative basal area (see Fig. 2.A) as a function of evolutionary change in tolerance to drought ($\Delta Drtol$) for fir and beech species, and for the whole forest (all species confounded). $\Delta Drtol$ is computed as the difference between the weighted mean trait value in the year 3000 and the weighted mean value of the trait averaged over a reference period (1500 to 2000 years). The weights correspond to the basal area of the individuals in relation to the basal area of their species or that of the forest as a whole (all species combined). Each point represents a population of a given replicate, species (or community) and treatment.

436 **3. Does assisted migration prevent local species' evolutionary rescue?**

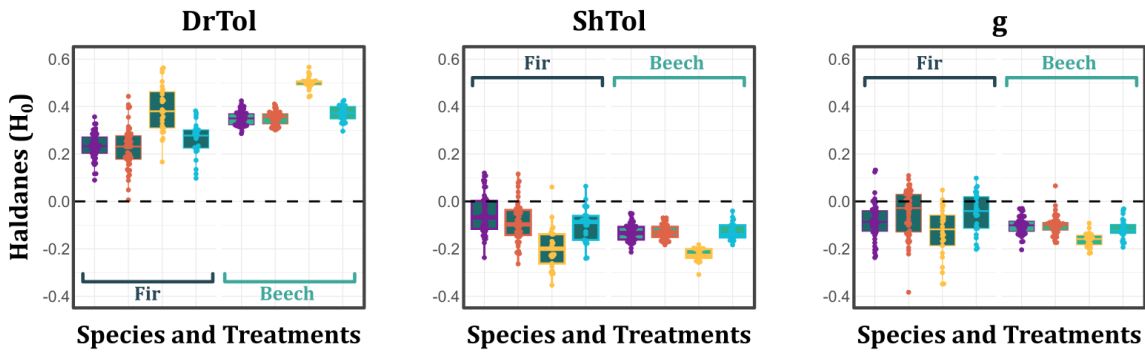
437 In the assisted migration treatment, fir and beech became extinct in the majority of evolu-
 438 tionary scenarios, including those where both species experienced evolutionary rescue in the

439 beech-fir treatment (Fig. 2.B & D). This result is consistent with our expectations and the lit-
440 erature on the subject. The arrival of newly pre-adapted species can endanger local evolving
441 ones (De Mazancourt et al., 2008). We observed a turnover between beech and sessile oak
442 (*Quercus petraea*), a more thermophilous species (higher $DrTol_s$ see Table. 1). Contrary to the
443 previous treatments, in all evolutionary scenarios, fir populations decreased relatively less than
444 beech ones (Fig. 2.B & D). It is important to note that changes in BA are expressed in relative
445 terms, so the fact that beech populations are no longer the dominant species largely explains
446 this result. Secondly, if both beech and fir populations are subjected to a similar shading regime
447 (Fig. 3), beech is expected to grow more slowly due to its lower g_s . Furthermore, fir and beech
448 populations recoveries (final RBA) were lower in the assisted migration treatment for equivalent
449 $\Delta Drtol$ in comparison with the two-species mixture treatment. The difference between the two
450 treatments was greater for beech populations for which +0.07 in $\Delta Drtol$ allowed to reach over
451 100% of final RBA in the beech-fir mixtures against 25% or less in the assisted migration treat-
452 ment (Fig. 4). $DrTol$ evolutionary rates were unaffected by species introduction in the short term
453 (during the warming period) with $H_0 = 0.26$ [0.23; 0.29] in fir and $H_0 = 0.37$ [0.36; 0.38] in beech
454 for the assisted migration treatment against respectively: 0.23 [0.20; 0.25] in fir and 0.35 [0.34;
455 0.36] in beech for the beech-fir mixture treatment (Fig. 5.A). Assisted migration tended to slow
456 down $DrTol$ evolution only in beech populations over the long term (Fig. 5.B & Fig. S.9). Slower
457 evolution in beech \overline{DrTol} was associated with a maintenance of higher \overline{ShTol} compared to the
458 beech-fir mixture (Fig. 5.B & Fig. S.10). This result is in line with the view of a niche conservatism
459 induced by interspecific interactions (Peterson et al., 1999; Wiens et al., 2010). It's worth not-
460 ing that forests with assisted migration had the highest leaf cover and, consequently, were the
461 forests where competition for light was the fiercest (Fig. 3. & Fig. S.7). Altogether, these results
462 indicate that assisted migration induces a faster return to a light competition driven regime in
463 forests as new species colonize. At the whole forest scale (sum of all species BA), assisted mi-
464 gration allowed for the most significant recoveries and the highest minimal RBA, with all final
465 recoveries over 130% and all minimal RBA above 75% (Fig. 2.B & D). Therefore, our case study
466 tends to confirm the view that species range shifts could mitigate the impact of climate change
467 on forest ecosystems in some scenarios, but at the risk of losing local species, provided migration
468 rates are sufficiently high (Hisano et al., 2018).

469 Model and simulation plan limitations

470 The initial-state forest densities (resulting from baseline simulations in historical climates) at
471 the Drôme site (table S.3) can be considered low compared with the forests that actually grow
472 in this region (IGN | *Institut national de l'information géographique et forestière* 2024). This is due
473 to the fact that our study sites are located in the southern part of the range of the two focal
474 species and that our model was calibrated for a single value of $DrTol_s$ per species for their range
475 throughout Europe. The $DrTol$ of the Drôme populations has therefore most certainly been un-
476 derestimated, resulting in smaller populations and consequently an overestimation of the drift in
477 our simulations. On a different topic, the arbitrary choice of stabilizing the climate after 100 years
478 of warming (at the end of the predictions available in climate projections), limits conclusions on
479 any long-term effects. In fact, we noticed that in all treatments but the assisted migration one,
480 populations started to recover only once the climate had stabilized (Fig. 2.C & Fig. 3). This result
481 is consistent with evolutionary theory. When a population undergoes a change of environment,

A Short term evolutionary rates between 2000 and 2100 ($h^2 = 0.3$ & $VR = 0.3$)



Treatments

■ Monospecific
 ■ Beech-fir mixture
 ■ Assisted gene flow
 ■ Assisted migration

B Long term evolutionary trajectories ($h^2 = 0.3$ & $VR = 0.3$)

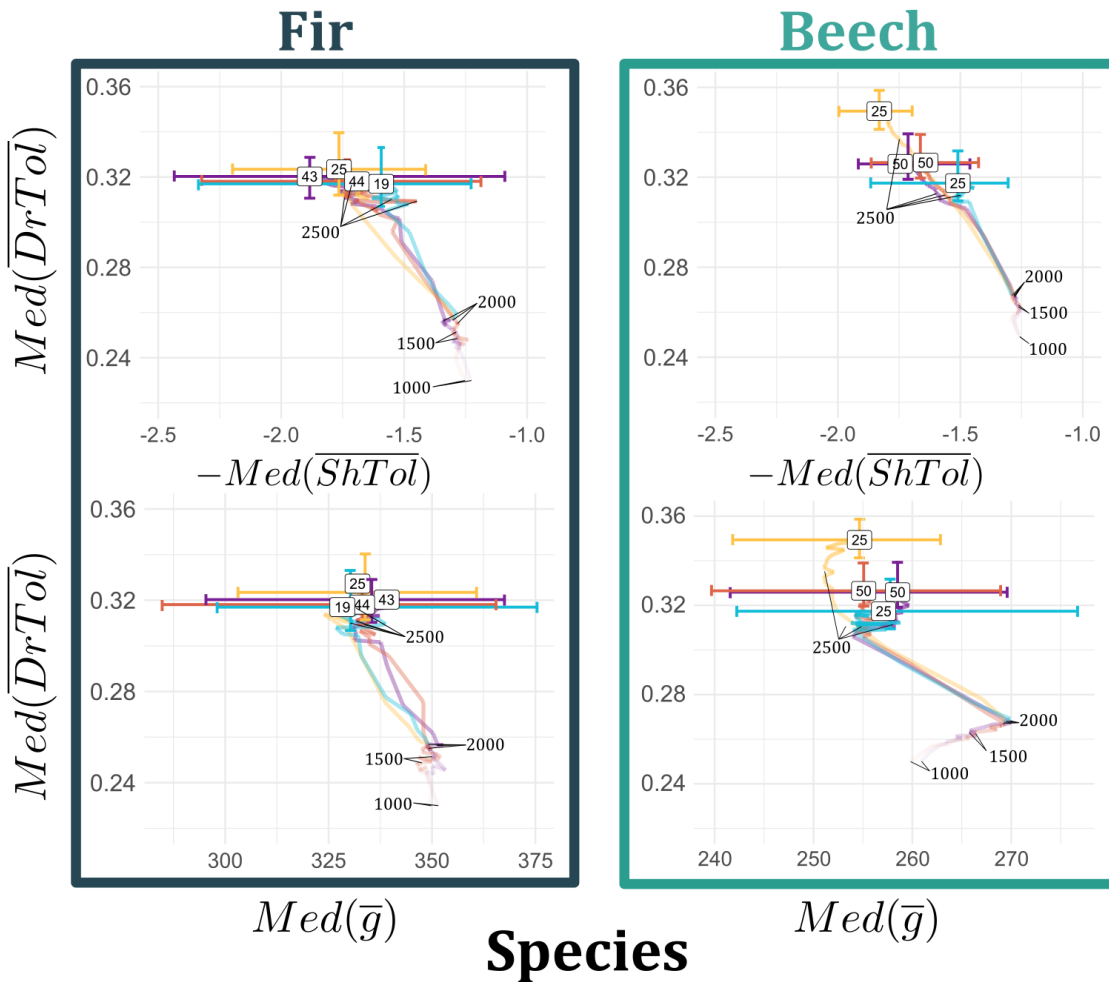


Figure 5

482 we expect the evolution of its traits to always lag behind a moving optimal value (Bürger and
 483 Lynch, 1995). This principle remained applicable even in the fastest evolutionary scenarios we
 484 explored. This shows that to simulate long-term impacts of climate change on species evolution,
 485 not only the speed and the absolute values of changing climate matter, but also the duration of

Figure 5 – A. Evolutionary rates in Haldanes (see Methods) for the three evolving traits before and after the warming period in beech and fir across the four treatments. The grey dashed line marks the 0 evolutionary rate threshold. Only the h^2 and $VR = 0.3$ evolutionary scenario is presented here; other scenarios are available in the supporting information (Fig. S.8). **B.** Median across replicates of the weighted average trait values in two dimensions over time. Line transparency reflect time progression also highlighted by date labels. Framed numbers represent the number of replicates in which populations survived until the last simulation year (3000), with a maximum of 50 for the monospecific and beech-fir mixture treatments, and 25 for the assisted gene flow and assisted migration treatments. Vertical and horizontal error bars show the 0.025 and 0.975 quantiles around the median weighted average trait values across replicates at the simulation's end for each treatment. For the individual evolutionary trajectories of populations, please refer to the supporting information.

486 the simulated change. The time scales over which we have observed trait evolution also need to
487 be discussed. Moreover, rapid climate change induces significant decreases in population sizes,
488 thus increasing the likelihood of kinship between individuals. However, inbreeding has the effect
489 of eroding genetic variance between siblings (within-family variance) Barton et al., 2017. As a
490 result, overall genetic variance and therefore, evolutionary speed may have been overestimated
491 by considering within-family variance constant. Finally, it is worth noting that only two selective
492 forces operate in our simulations: 1) climate change which will positively select *DrTol* and 2)
493 competition between individuals for light which will select for higher *ShTol* and *g*. Given that
494 we have imposed negative trade-offs between *DrTol* and the traits related to competition ability
495 (*ShTol* and *g*), intra- and interspecific interactions could only hinder the evolution of *DrTol*, conse-
496 quently preventing evolutionary rescue. Introducing pre-adapted species to future environments
497 in this context leads to a competitive hierarchy for light, ultimately resulting in the dominance of
498 imported species over local ones. This has imposed two strong and opposing selection pressures
499 on local species creating particularly stringent conditions for evolutionary rescue.

500

Perspectives

501 The erosion of genetic variance discussed earlier could be accounted for in the future by
502 tracking the pedigree of individuals (Barton et al., 2017). That being said, this effect is counter-
503 balanced by gene flow, which generally keeps inbreeding at low levels in natural forest ecosys-
504 tems (Petit and Hampe, 2006) except in the case of isolated populations (Mimura and Aitken,
505 2007). Tracking pedigrees between reproducers and reducing the within-family variance accord-
506 ing to the kinship of the two parents in the present context would however result in assuming
507 that the simulated forest is a completely closed system. The best solution we can think of would
508 be to simulate realistic migration processes and assume that immigrants share no ancestry with
509 the local individuals. Genetic variation would then be reduced by inbreeding and replenished
510 by migration, with the balance between these processes depending on effective population size.
511 However, tracking pedigree would also be computationally expensive for large populations. Im-
512 plementing this solution could then be relevant for simulations of small populations where higher
513 inbreeding is expected and tracking pedigree is less costly. Another reason to improve the inte-
514 gration of migration into models is to explore its demographic impact on populations. In our case,
515 we have deliberately limited these impacts to highlight the genetic consequences of the arrival of
516 pre-adapted individuals. Nevertheless, assisted gene flow is also advocated for the demographic
517 support it offers (Aitken and Whitlock, 2013). Studying the consequences of different migration
518 intensities on evolutionary rescue remains a crucial step towards a better understanding of the

519 consequences of assisted gene flow. Beyond improving a model's realism and predictive capa-
520 bilities, our priority is to better understand how species' adaptation to a new environment is
521 impacted by ecological interactions. We therefore think it is urgent to explore the case where
522 intra- and interspecific interactions are at the origin of selection pressures that accompany envi-
523 ronmental change. With moderate competitive selection pressure, a positive effect of competi-
524 tion on evolutionary rescue could be observed (Osmond and Mazancourt, 2013). The conditions
525 for this to occur in the context of global warming could be explored within our framework, for
526 instance, if competition for water between individuals was explicitly considered in ForCEEPS.

527

Conclusions

528 To our knowledge, this work represent the first attempt to simulate the evolution of multiple
529 interacting species using a functional and mechanistic framework (PBM). Most importantly, we
530 showed that both trait variability and heritability had a major impact on the model's predictions,
531 even over a time scale of one or two centuries. Our results support the view that increasing
532 genetic variability within stands is a key lever to enhance forests' capacity to cope with climate
533 change. More broadly, they highlight the necessity of accounting for the evolutionary responses
534 of tree species when projecting the impacts of climate change on forests. In addition, "assisted
535 gene flow" enabled species to keep pace with climate change without any apparent drawbacks
536 emerging in our framework. We also showed that abiotic factors, such as climate, are not the
537 only dynamic forces influencing species' evolution. Population dynamics also shape species' evo-
538 lutionary trajectories through competitive interactions. However, interspecific competition did
539 not lower the chances of evolutionary rescue in the short term (century) in the beech-fir mix-
540 ture as the two focal species were primarily affected by climate change. The evolutionary tra-
541 jectories of these two species were only affected by competition in the long term (millennium),
542 particularly in the assisted migration treatment when more arid-tolerant species colonized the
543 forests. In this treatment, more intense competition reduced the likelihood of evolutionary res-
544 cue for beech and fir. Nevertheless, assisted migration allowed for the fastest forest recoveries.
545 Given the ecological issues highlighted in this study, we argue that our approach represents an
546 important step towards understanding the interactions between competition and evolutionary
547 dynamics. It also paves the way toward more robust predictions of the impacts of climate change
548 on forests.

549

Acknowledgements

550 We are particularly grateful to the various developers of the Capsis platform and to Nogoye
551 Diouf, who worked on the trait data from the TRY database.

552

Fundings

553 The authors declare that they have received no specific funding for this study.

554

Conflict of interest disclosure

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

Data, script, code, and supplementary information availability

557

558 The version of ForCEEPS used to produce the data presented here, the R scripts for data
559 analysis and figure production, as well as the supporting information are available online (<https://doi.org/10.5281/zenodo.14197821>; Devresse et al., 2024)

561

562

References

563 Aitken SN, Whitlock MC (2013). *Assisted Gene Flow to Facilitate Local Adaptation to Climate Change*.
564 *Annual Review of Ecology, Evolution, and Systematics* **44**, 367–388. <https://doi.org/10.1146/annurev-ecolsys-110512-135747>.

566 Alberto FJ, Aitken SN, Alía R, González-Martínez SC, Hänninen H, Kremer A, Lefèvre F, Lenor-
567 mand T, Yeaman S, Whetten R, Savolainen O (2013). *Potential for evolutionary responses to*
568 *climate change – evidence from tree populations*. *Global Change Biology* **19**, 1645–1661. <https://doi.org/10.1111/gcb.12181>.

570 Astigarraga J, Calatayud J, Ruiz-Benito P, Madrigal-González J, Tijerín-Triviño J, Zavala MA, Andi-
571 via E, Herrero A (2023). *Forest structural diversity determines tree growth synchrony in response*
572 *to climate change*. <https://doi.org/10.1101/2023.03.17.532989>.

573 Barton NH, Etheridge AM, Véber A (2017). *The infinitesimal model: Definition, derivation, and im-*
574 *PLICATIONS*. *Theoretical Population Biology* **118**, 50–73. <https://doi.org/10.1016/j.tpb.2017.06.001>.

576 Bell G (2017). *Evolutionary Rescue*. *Annual Review of Ecology, Evolution, and Systematics* **48**, 605–
577 627. <https://doi.org/10.1146/annurev-ecolsys-110316-023011>.

578 Bone E, Farres A (2001). *Trends and rates of microevolution in plants*. *Genetica* **112**, 165–182.
579 <https://doi.org/10.1023/A:1013378014069>.

580 Bugmann HKM (1996). *A Simplified Forest Model to Study Species Composition Along Climate Gra-*
581 *dients*. *Ecology* **77**, 2055–2074. <https://doi.org/10.2307/2265700>.

582 Bulmer MG (1971). *The Effect of Selection on Genetic Variability*. *The American Naturalist* **105**, 201–
583 211. <https://doi.org/10.1086/282718>.

584 Bürger R, Lynch M (1995). *EVOLUTION AND EXTINCTION IN A CHANGING ENVIRONMENT: A*
585 *QUANTITATIVE-GENETIC ANALYSIS*. *Evolution* **49**, 151–163. <https://doi.org/10.1111/j.1558-5646.1995.tb05967.x>.

587 Cuddington K, Fortin MJ, Gerber LR, Hastings A, Liebhold A, O'Connor M, Ray C (2013). *Process-*
588 *based models are required to manage ecological systems in a changing world*. *Ecosphere* **4**, art20.
589 <https://doi.org/10.1890/ES12-00178.1>.

590 De Mazancourt C, Johnson E, Barraclough TG (2008). *Biodiversity inhibits species' evolutionary*
591 *responses to changing environments*. *Ecology Letters* **11**, 380–388. <https://doi.org/10.1111/j.1461-0248.2008.01152.x>.

593 Devresse L, Coligny F, Morin X (2024). *Evolutionary rescue in a mixed beech-fir forest: insights from*
594 *a quantitative-genetics approach in a process-based model - Model, Data, Scripts and Supporting*
595 *Information*. <https://doi.org/10.5281/zenodo.14197821>.

596 Didion M, Kupferschmid AD, Bugmann H (2009). *Long-term effects of ungulate browsing on forest*
597 *composition and structure*. *Forest Ecology and Management*. IUFRO Conference on Biodiversity
598 in Forest Ecosystems and Landscapes **258**, S44–S55. <https://doi.org/10.1016/j.foreco.2009.06.006>.

599

- 600 Dufour-Kowalski S, Courbaud B, Dreyfus P, Meredieu C, Coligny F (2012). *Capsis: an open soft-*
601 *ware framework and community for forest growth modelling. Annals of Forest Science* **69**, 221–
602 233. <https://doi.org/10.1007/s13595-011-0140-9>.
- 603 Dyderski MK, Paž S, Frelich LE, Jagodziński AM (2018). *How much does climate change threaten*
604 *European forest tree species distributions? Global Change Biology* **24**, 1150–1163. <https://doi.org/10.1111/gcb.13925>.
- 605
- 606 Eldijk TJB, Bisschop K, Etienne RS (2020). *Uniting Community Ecology and Evolutionary Rescue*
607 *Theory: Community-Wide Rescue Leads to a Rapid Loss of Rare Species. Frontiers in Ecology and*
608 *Evolution* **8**. <https://doi.org/10.3389/fevo.2020.552268>.
- 609 Ellenberg H, Mueller-Dombois D (1965). *Tentative physiognomic-ecological classification of plant*
610 *formations of the earth. https://doi.org/10.5169/SEALS-377650*.
- 611 Fady B, Aravanopoulos FA, Alizoti P, Mátyás C, Wühlisch G, Westergren M, Belletti P, Cvjetkovic
612 B, Ducci F, Huber G, Kelleher CT, Khaldi A, Kharrat MBD, Kraigher H, Kramer K, Mühlethaler
613 U, Peric S, Perry A, Rousi M, Sbay H, et al. (2016). *Evolution-based approach needed for the con-*
614 *servation and silviculture of peripheral forest tree populations. Forest Ecology and Management*
615 **375**, 66–75. <https://doi.org/10.1016/j.foreco.2016.05.015>.
- 616 Fisher RA (1919). XV.—*The Correlation between Relatives on the Supposition of Mendelian Inheri-*
617 *tance. Earth and Environmental Science Transactions of The Royal Society of Edinburgh* **52**, 399–
618 433. <https://doi.org/10.1017/S0080456800012163>.
- 619 Gingerich PD (1983). *Rates of Evolution: Effects of Time and Temporal Scaling. Science* **222**, 159–
620 161. <https://doi.org/10.1126/science.222.4620.159>.
- 621 Gloy J, Herzs Schuh U, Kruse S (2023). *Evolutionary adaptation of trees and modelled future larch*
622 *forest extent in Siberia. Ecological Modelling* **478**, 110278. <https://doi.org/10.1016/j.ecolmodel.2023.110278>.
- 623
- 624 Godineau C, Fririon V, Beudez N, De Coligny F, Courbet F, Ligot G, Oddou-Muratorio S, Sanchez
625 L, Lefèvre F (2023). *A demo-genetic model shows how silviculture reduces natural density-dependent*
626 *selection in tree populations. Evolutionary Applications* **16**, 1830–1844. <https://doi.org/10.1111/eva.13606>.
- 627
- 628 Guillemot J, Francois C, Hmimina G, Dufrêne E, Martin-StPaul NK, Soudani K, Marie G, Ourcival
629 JM, Delpierre N (2017). *Environmental control of carbon allocation matters for modelling forest*
630 *growth. New Phytologist* **214**, 180–193. <https://doi.org/10.1111/nph.14320>.
- 631 Hartmann H, Bastos A, Das AJ, Esquivel-Muelbert A, Hammond WM, Martínez-Vilalta J, McDow-
632 ell NG, Powers JS, Pugh TA, Ruthrof KX, Allen CD (2022). *Climate Change Risks to Global Forest*
633 *Health: Emergence of Unexpected Events of Elevated Tree Mortality Worldwide. Annual Review of*
634 *Plant Biology* **73**, 673–702. <https://doi.org/10.1146/annurev-arplant-102820-012804>.
- 635 Hisano M, Searle EB, Chen HYH (2018). *Biodiversity as a solution to mitigate climate change im-*
636 *pacts on the functioning of forest ecosystems. Biological Reviews* **93**, 439–456. <https://doi.org/10.1111/brv.12351>.
- 637
- 638 Hlásny T, Mátyás C, Seidl R, Kulla L, Merganičová K, Trombik J, Dobor L, Barcza Z, Konôpka
639 B (2014). *Climate change increases the drought risk in Central European forests: What are the*
640 *options for adaptation? Forestry Journal* **60**, 5–18. <https://doi.org/10.2478/forj-2014-0001>.
- 641
- 642 IGN | Institut national de l'information géographique et forestière (2024).

- 643 Johansson J (2008). *EVOLUTIONARY RESPONSES TO ENVIRONMENTAL CHANGES: HOW DOES*
644 *COMPETITION AFFECT ADAPTATION?* *Evolution* **62**, 421–435. [https://doi.org/10.1111/](https://doi.org/10.1111/j.1558-5646.2007.00301.x)
645 [j.1558-5646.2007.00301.x](https://doi.org/10.1111/j.1558-5646.2007.00301.x).
- 646 Karger DN, Schmatz DR, Dettling G, Zimmermann NE (2020). *High-resolution monthly precipita-*
647 *tion and temperature time series from 2006 to 2100.* *Scientific Data* **7**, 248. [https://doi.org/](https://doi.org/10.1038/s41597-020-00587-y)
648 [10.1038/s41597-020-00587-y](https://doi.org/10.1038/s41597-020-00587-y).
- 649 Kattge J, Bönsch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA, Aakala
650 T, Abedi M, Acosta ATR, Adamidis GC, Adamson K, Aiba M, Albert CH, Alcántara JM, Alcázar
651 C C, Aleixo I, Ali H, Amiaud B, et al. (2020). *TRY plant trait database - enhanced coverage and*
652 *open access.* *Global Change Biology* **26**, 119–188. <https://doi.org/10.1111/gcb.14904>.
- 653 Keenan T, Maria Serra J, Lloret F, Ninyerola M, Sabate S (2011). *Predicting the future of forests*
654 *in the Mediterranean under climate change, with niche- and process-based models: CO2 matters!*
655 *Global Change Biology* **17**, 565–579. [https://doi.org/10.1111/j.1365-2486.2010.02254.](https://doi.org/10.1111/j.1365-2486.2010.02254.x)
656 [x](https://doi.org/10.1111/j.1365-2486.2010.02254.x).
- 657 Kohyama TS, Takada T (2012). *One-sided competition for light promotes coexistence of forest trees*
658 *that share the same adult height.* *Journal of Ecology* **100**, 1501–1511. [https://doi.org/10.](https://doi.org/10.1111/j.1365-2745.2012.02029.x)
659 [1111/j.1365-2745.2012.02029.x](https://doi.org/10.1111/j.1365-2745.2012.02029.x).
- 660 Kramer K, Werf B, Schelhaas MJ (2015). *Bring in the genes: genetic-ecophysiological modeling of*
661 *the adaptive response of trees to environmental change. With application to the annual cycle.*
662 *Frontiers in Plant Science* **5**.
- 663 Lefèvre F, Boivin T, Bontemps A, Courbet F, Davi H, Durand-Gillmann M, Fady B, Gauzere J,
664 Gidoïn C, Karam MJ, Lalagüe H, Oddou-Muratorio S, Pichot C (2014). *Considering evolutionary*
665 *processes in adaptive forestry.* *Annals of Forest Science* **71**, 723–739. [https://doi.org/10.](https://doi.org/10.1007/s13595-013-0272-1)
666 [1007/s13595-013-0272-1](https://doi.org/10.1007/s13595-013-0272-1).
- 667 Loreau M, Hector A (2001). *Partitioning selection and complementarity in biodiversity experiments.*
668 *Nature* **412**, 72–76. <https://doi.org/10.1038/35083573>.
- 669 Mäkelä A, Landsberg J, Ek AR, Burk TE, Ter-Mikaelian M, Ågren GI, Oliver CD, Puttonen P (2000).
670 *Process-based models for forest ecosystem management: current state of the art and challenges*
671 *for practical implementation.* *Tree Physiology* **20**, 289–298. [https://doi.org/10.1093/](https://doi.org/10.1093/treephys/20.5-6.289)
672 [treephys/20.5-6.289](https://doi.org/10.1093/treephys/20.5-6.289).
- 673 Mimura M, Aitken SN (2007). *Increased selfing and decreased effective pollen donor number in pe-*
674 *ripheral relative to central populations in Picea sitchensis (Pinaceae).* *American Journal of Botany*
675 **94**, 991–998. <https://doi.org/10.3732/ajb.94.6.991>.
- 676 Morin X, Bugmann H, Coligny F, Martin-StPaul N, Cailleret M, Limousin JM, Ourcival JM, Pre-
677 vosto B, Simioni G, Toigo M, Vennetier M, Catteau E, Guillemot J (2021). *Beyond forest succes-*
678 *sion: A gap model to study ecosystem functioning and tree community composition under climate*
679 *change.* *Functional Ecology* **35**, 955–975. <https://doi.org/10.1111/1365-2435.13760>.
- 680 Morin X, Damestoy T, Toigo M, Castagneyrol B, Jactel H, Coligny F, Meredieu C (2020). *Using*
681 *forest gap models and experimental data to explore long-term effects of tree diversity on the pro-*
682 *ductivity of mixed planted forests.* *Annals of Forest Science* **77**, 1–19. [https://doi.org/10.](https://doi.org/10.1007/s13595-020-00954-0)
683 [1007/s13595-020-00954-0](https://doi.org/10.1007/s13595-020-00954-0).
- 684 Morin X, Fahse L, Jactel H, Scherer-Lorenzen M, García-Valdés R, Bugmann H (2018). *Long-term*
685 *response of forest productivity to climate change is mostly driven by change in tree species com-*
686 *position.* *Scientific Reports* **8**, 5627. <https://doi.org/10.1038/s41598-018-23763-y>.

- 687 Morin X, Viner D, Chuine I (2008). *Tree species range shifts at a continental scale: new predictive*
688 *insights from a process-based model. Journal of Ecology* **96**, 784–794. [https://doi.org/10.](https://doi.org/10.1111/j.1365-2745.2008.01369.x)
689 [1111/j.1365-2745.2008.01369.x](https://doi.org/10.1111/j.1365-2745.2008.01369.x).
- 690 Niinemets Ü, Valladares F (2006). *TOLERANCE TO SHADE, DROUGHT, AND WATERLOGGING OF*
691 *TEMPERATE NORTHERN HEMISPHERE TREES AND SHRUBS. Ecological Monographs* **76**, 521–
692 547. [https://doi.org/10.1890/0012-9615\(2006\)076\[0521:TTSDAW\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2).
- 693 Oddou-Muratorio S, Davi H (2014). *Simulating local adaptation to climate of forest trees with a*
694 *Physio-Demo-Genetics model. Evolutionary Applications* **7**, 453–467. [https://doi.org/10.](https://doi.org/10.1111/eva.12143)
695 [1111/eva.12143](https://doi.org/10.1111/eva.12143).
- 696 Osmond MM, Mazancourt Cd (2013). *How competition affects evolutionary rescue. Philosophical*
697 *Transactions of the Royal Society B: Biological Sciences.* [https://doi.org/10.1098/rstb.](https://doi.org/10.1098/rstb.2012.0085)
698 [2012.0085](https://doi.org/10.1098/rstb.2012.0085).
- 699 Pardos M, Río M, Pretzsch H, Jactel H, Bielak K, Bravo F, Brazaitis G, Defossez E, Engel M, God-
700 vod K, Jacobs K, Jansone L, Jansons A, Morin X, Nothdurft A, Oreti L, Ponette Q, Pach M,
701 Riofrío J, Ruíz-Peinado R, et al. (2021). *The greater resilience of mixed forests to drought mainly*
702 *depends on their composition: Analysis along a climate gradient across Europe. Forest Ecology and*
703 *Management* **481**, 118687. <https://doi.org/10.1016/j.foreco.2020.118687>.
- 704 Peterson AT, Soberón J, Sánchez-Cordero V (1999). *Conservatism of Ecological Niches in Evolution-*
705 *ary Time. Science* **285**, 1265–1267. <https://doi.org/10.1126/science.285.5431.1265>.
- 706 Petit RJ, Hampe A (2006). *Some Evolutionary Consequences of Being a Tree. Annual Review of Ecol-*
707 *ogy, Evolution, and Systematics* **37**, 187–214. [https://doi.org/10.1146/annurev.ecolsys.](https://doi.org/10.1146/annurev.ecolsys.37.091305.110215)
708 [37.091305.110215](https://doi.org/10.1146/annurev.ecolsys.37.091305.110215).
- 709 Price TD, Kirkpatrick M (2009). *Evolutionarily stable range limits set by interspecific competition.*
710 *Proceedings of the Royal Society B: Biological Sciences* **276**, 1429–1434. [https://doi.org/](https://doi.org/10.1098/rspb.2008.1199)
711 [10.1098/rspb.2008.1199](https://doi.org/10.1098/rspb.2008.1199).
- 712 Rameau JC, Institut pour le Developpement Forestier Pf, Mansion D, Dume G, Gauberville C,
713 Bardat J, Bruno E, Keller R, Ministere de l'Agriculture et de la Peche Pf (2008). *Flore forestiere*
714 *francaise: guide ecologique illustre.*
- 715 Romero-Mujalli D, Jeltsch F, Tiedemann R (2019). *Individual-based modeling of eco-evolutionary*
716 *dynamics: state of the art and future directions. Regional Environmental Change* **19**, 1–12. [https:](https://doi.org/10.1007/s10113-018-1406-7)
717 [//doi.org/10.1007/s10113-018-1406-7](https://doi.org/10.1007/s10113-018-1406-7).
- 718 Ruffault J, Pimont F, Cochard H, Dupuy JL, Martin-StPaul N (2022). *SurEau-Ecos v2.0: a trait-*
719 *based plant hydraulics model for simulations of plant water status and drought-induced mortality*
720 *at the ecosystem level. Geoscientific Model Development* **15**, 5593–5626. [https://doi.org/](https://doi.org/10.5194/gmd-15-5593-2022)
721 [10.5194/gmd-15-5593-2022](https://doi.org/10.5194/gmd-15-5593-2022).
- 722 Shugart HH, Wang B, Fischer R, Ma J, Fang J, Yan X, Huth A, Armstrong AH (2018). *Gap models*
723 *and their individual-based relatives in the assessment of the consequences of global change. En-*
724 *vironmental Research Letters* **13**, 033001. <https://doi.org/10.1088/1748-9326/aaaacc>.
- 725 Silva Pedro M, Rammer W, Seidl R (2015). *Tree species diversity mitigates disturbance impacts on*
726 *the forest carbon cycle. Oecologia* **177**, 619–630. [https://doi.org/10.1007/s00442-014-](https://doi.org/10.1007/s00442-014-3150-0)
727 [3150-0](https://doi.org/10.1007/s00442-014-3150-0).
- 728 Thompson PL, Fronhofer EA (2019). *The conflict between adaptation and dispersal for maintain-*
729 *ing biodiversity in changing environments. Proceedings of the National Academy of Sciences* **116**,
730 21061–21067. <https://doi.org/10.1073/pnas.1911796116>.

- 731 Toïgo M, Vallet P, Perot T, Bontemps JD, Piedallu C, Courbaud B (2015). *Overyielding in mixed*
732 *forests decreases with site productivity. Journal of Ecology* **103**. Ed. by Charles Canham, 502–
733 **512**. <https://doi.org/10.1111/1365-2745.12353>.
- 734 Wessely J, Essl F, Fiedler K, Gattringer A, Hülber B, Ignateva O, Moser D, Rammer W, Dullinger
735 S, Seidl R (2024). *A climate-induced tree species bottleneck for forest management in Europe.*
736 *Nature Ecology & Evolution*, 1–9. <https://doi.org/10.1038/s41559-024-02406-8>.
- 737 Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Jonathan
738 Davies T, Grytnes JA, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010).
739 *Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters*
740 **13**, 1310–1324. <https://doi.org/10.1111/j.1461-0248.2010.01515.x>.