Response to the first round of review

Dear PCI reviewers and recommenders, thank you for your constructive comments, which have helped us improving considerably the quality of our article. Below you will find a general response and a summary of the main changes we have made, followed by our point-by-point reply to each comment. As there were many comments, we only wrote a detailed response to the comments that led us to make significant changes to the text, or to comments that needed to be discussed. Other more specific suggestions (minor clarifications, rewording of sentences, etc.) not mentioned in this document have simply been applied following the suggestion by the reviewers.

General comment answer to reviewers

As suggested by our fourth reviewer and supported by our PCI recommender, the structure of the article has been considerably modified, so that it now adopts a more classic format. More precisely, we defined our objectives in clearer terms, and we have modified the title, the abstract and the introduction to support those objectives.

As requested by all reviewers, we also included definitions of the concepts at the core of this work in the introduction, such as "evolutionary rescue", "process based models" (PBM) and "gap models". Consistently with the suggestion of reviewer 4, the first two paragraphs of the introduction have been reorganized into i) a first paragraph strictly dedicated to the presentation of ecological and scientific issues and ii) a second paragraph focusing on the needs of forest models and their limitations.

Following the recommendation of reviewer 2, the introduction now includes a paragraph devoted to comparing our work with other similar approaches, and also includes a more detailed justification of the choices and assumptions made in the study. However, as our methodology has never been described before and differs from other approaches with similar aims, we have retained a solid methodological description of our work. In particular, we have kept the detailed description of the evolutionary module in the main text and added simulation results dedicated to the model validation in the supporting information.

We have also included a "Model description" sub-section in the "Methods" section in which we provide the information requested by the various reviewers concerning the ForCEEPS model. The 'Results and discussion' section has been clarified by properly defining the terms used to describe the results as requested by reviewer 4. The structure of this section has also been changed to facilitate the reader's understanding.

Figures were improved according to suggestions from all reviewer, additional figures and tables were also added in the supporting information when additional data was needed to support our interpretations.

The former section "Limits and Future Applications" was split and broadened into two sections: "Model and simulation plan limitations" and "Perspectives". A "Conclusion" with take-home messages was also added, as requested by reviewer 3.

The supporting information was carefully revised and made available separately from the rest of the code and data. Terms usage has also been homogenized throughout the manuscript to ensure better comprehension. For example, "PBM" is always preferred to "vegetation models" and other non-specific terms. Regarding the different simulation plan modalities, the terms "genetic enrichment" and "species enrichment" have been replaced by "assisted gene flow" and "assisted migration" that are more commonly used in literature and that are also more explicit in our research field. We also made sure that the term "treatment" always refers to the management options (i.e. "monospecific", "beech-fir mixture", "assisted gene flow" and "assisted migration"). Additionally, the term "period" always refers to the different time periods (with associated climatic conditions) described in the method section except in the case of the "reference period" that is defined when used. The term "scenarios" systematically refers to the 16 modalities of VR and h^2 , except when referring to the IPCC's RCP 4.5 projection, where this term is in common usage. Lastly, to improve clarity and technicality of the language, our manuscript was proofread by a native English speaker.

Section by section answer to reviewers

Abstract

• **Reviewer 4:** The general introduction takes more than 50% of the abstract. Please reduce this part and provide equal weight on the result and discussion. *Reply: The abstract was reorganized and the importance of this section was significantly reduced.*

Introduction

• L14-16: Reviewer 1: "inherent requirements": are you referring to ecological parameters / computer power / code? I suggest rewording or being more specific about which requirements you are referring to.

Reply: These requirements are now explicitly described in the second paragraph of the introduction that defines process-based models and exposes their current limitations L54.

• L21: Reviewer 3: consider making clearer which statement is based on empirical and/or simulation data. The next sentence should also be clearer about how your model is

different from the previous ones. In its current state, it sounds a little like things have already been done in previous studies (even if the rest of the introduction makes the novelty of the study very clear).

Reply: This comment led us to write a new paragraph (ie. third one) in the introduction dedicated to this topic L66-88.

- L43: Reviewer 3: We might want to have more details about the processes by which species diversity could be a buffer or reduce evolutionary rescue. *Reply: Processes by which species diversity and evolution interact such as demographic effect, sampling effect and selective pressure emerging from species interactions are now detailed L23-33.*
- L48-56: Reviewer 2: I think the aims of the paper should be explained more clearly in this paragraph. Indeed, I would say that adding "a new evolutionary module allowing species-specific parameters to evolve within the course of the simulation" (L51-52) is not the purpose of the paper, but the method. What is the objective behind adding an evolutionary module? An improvement in predictions (if so, which ones)? A better understanding of certain processes (if so, which ones)?

Reply: Developing such an evolutionary module in a multi-specific context and including it in a forest PBM was one of the aims of this study. We have rephrased this part so that it is more explicit. This being said, and in line with the main change in the structure of the manuscript, we now refer to it as the "preliminary objective" L69. Other objectives are also more clearly exposed in the fourth paragraph of the introduction L98-105.

- L57-61: Reviewer 4: here you already involve parts of the methods section Reply: Consistently with what we replied to the previous comment, as the development of our methodology is our preliminary objective and as part of the novelty of our work depends on it, we think we needed to address that point early in the introduction.
- L61: Reviewer 2: Is there a paper showing that? (ie the extinction of beech populations in ForCEEPS simulations without evolution)

Reply: We have modified the text to make it clearer. This is indeed only a prediction of the ForCEEPS model without evolution. This simply allows us to place ourselves in a context (defined by the simulations) where the study of evolutionary rescue is relevant (and possible). Therefore we do not claim that beech and fir will necessarily disappear under the climate projection we have chosen for this study, and that other works support this assertion L95.

Methods

Reviewer 4: However, for a purely methodological study, I would expect a more detailed description of the evolutionary dynamics. The authors address this issue only within a single sentence (P.6, L118-120), where they state that they use the infinitesimal model. Given that the theoretical background of the model and its assumptions are not common knowledge and differ from the more frequently used multilocus models, I strongly

recommend adding a larger paragraph on the model, its assumptions and its realization. *Reply: We agree with the reviewer, and we have thus amended the introduction to fix this issue. The requested details are now given in the third paragraph of our new introduction L79-88.*

• L96 Reviewer 2: Is this migration parameter binary or quantitative (with an infinite number of values between 0 and 1)? And when M=1, what is the proportion of local regeneration vs migration regeneration?

Reply: These informations are now provided in the "Regeneration and Species Composition Feedback" subsection L152.

• L107 Reviewer 2: When does seedlings become adults? & Reviewer 4: L107-110: define age limits for the change from seedlings to adults, ate what age does the shade tolerance changes?

Reply: This part of the text was indeed confusing. The parameters related to seedlings are not the same as those for adults to take into account that young trees have often a different sensitivity than adult ones. Yet, we only consider a different set of parameters for the first year, ie. establishment: these different parameters thus are related to the regeneration process (affecting establishment probabilities), and not growth. A new tree "appears" in the simulation at year n with a height greater than 1.3 meters, and is no longer considered a seedling at the year n+1. However, a tree can only reproduce once it reaches its speciesspecific age of maturity L185.

- Reviewer 2: I am not sure I fully understand how ΣP is obtained. I would advise making it clearer which parameters have values set at the initiation of the simulations and then that change during the simulations, which parameters have fixed values throughout the simulations, and which parameters have values based on empirical estimates from the literature. Regarding VR, where does the initial value of VR come from? Is it fixed throughout the simulation? And is it a common value for all species? I am not sure I understand what sdinter is, the interspecific standard variation of the traits? & L133: Reviewer 3: How is VR calculated when indicated at the level of the whole forest? is it an average of the species-specific VR weighted by their relative abundance?
 VR is identical for all species and all treatment in a given evolutionary scenario. \$sd{inter}\$ is an array containing the three traits standard deviation (common for all species) computed from the initial trait values of all the species calibrated in ForCEEPS. We hope that the new sentence in the method section L211-221 and the new supporting information table S.1 makes our methodology clearer.
- L131-143: Recommender: the phenotypic variance-covariance matrix (sigmaP) is a key element of the model, and requires better description and justification beyond the correlation table S1. A major assumption in the model is that the genetic variance-covariance matrix SigmaG is proportional to SigmaP (equation 2), which is a significant oversimplification, particularly for the covariance terms. Indeed, the phenotypic covariances between traits reflect the overall relationships observed in the population, but

they do not distinguish between genetic and environmental sources of covariance. Environmental covariances may either inflate or deflate the observed phenotypic covariances, meaning that the observed phenotypic covariances do not straightforwardly translate into genetic covariances. These relationships may be even more complex, because the calibration using the TRY database likely implies that the traits are measured in different populations with varying environmental conditions. While there are no simple solutions to this issue, the strong assumption made here should at least be acknowledged and discussed.

This assumption is now explicit in the main text and we added a justification for it L214.

• L152: Reviewer 4: I didn't fully understand the approach of the "slowth growth status": Is this status depending on the individual or on the population? If it is driven by the temperature I would rather expect is for population, but that does not make sense. If it is anyhow used for the population could it be considered as a variable for masting? If its is for individuals: would it then not be assign of competition and thus also correlate to its size? Please explain!

Reply: Slow growth is an individual state. In fact, it can be caused by competition. A tree whose growth is too limited by the obstruction of light by taller trees will not be able to reproduce (drawn at random as a parent). Please let us know if the "model description" section makes this point clearer L122.

• L158: Reviewer 3: consider mentioning earlier that there are evolving and non-evolving traits and why using nonevolving traits.

Reply: We now explain that choice in the "model description" section. We have chosen to restrict the number of parameters subject to evolution to keep the model within a range of behaviour that still allows us to interpret why the model outputs differ between the different treatments L73.

• L176: Reviewer 3: As h^2 and sigma_E are fixed, how do you control for sigma_G after local and migration regeneration?

Reply: We have amended the text to be more explicit about the fact that h^2 , Σ_E , and Σ_G are input parameters that determine the initial state of the simulation. As the simulation progresses, the realized heritability and genetic variance are dynamic variables that vary according to selection and drift. This is also the case in QTL approaches such as those of, Godineau et al. (2023) – cited in the manuscript L 220.

• L207-208 Reviewer 1: I wonder what the benefit would be for having fewer parameter scenarios for h2 and VR versus more replications. Have you tested the robustness of the results for more or fewer replications ?

Reply: We tested the dependence of our results to the number of repetitions (10 to 100) when developing the model and testing new features. This revealed that, despite the presence of stochastic processes, the model remains quite deterministic for the size of forest stands we simulate (i.e. hundreds of individuals). The number of replicates could even have been lower. See also the drift validation section in the supporting information.

- L213-214 Reviewer 3: I am not sure to understand the part "with the number differing in order to keep a similar number of individuals of each species." Does it mean that there is the same number of firs in the 50 mixed plots than in the 11 monospecific plots (and the same number of beeches in the 50 mixed plots than in the 11 monospecific plots)? What is proportion of beach vs fir in the mixed plots? Is the size of the patches the same across all the simulations? In L79, it is specified that the size of the patches is "usually ca. 1000 m²". I think it would be helpful to make clear which patch size was used in the case study. *Reply: Our overall simulation plan is now more detailed in the dedicated "Simulation plan" paragraph, we hope that the new version of the text clarifies these points L291-306.*
- L211-217: Reviewer 4: these and the following cases are based on measurements in real sites. Therefore, it would be needed to describe the initial state of the forest (species share, basal area, etc.) more detailed, the best would be within an additional table *Reply: We have added the initial number of trees and basal area of each species in our initial state inventories in the main text and in an additional table (Table S.3). We have also made it more explicit in the text that these inventories were generated using the ForCEEPS model without the evolution module L288-291.*
- L213: Reviewer 3: The scenario-specific patch number is confusing to me. I assume all the patches are not run together within a simulation. It is either 50 patches of mixed beech-fir or 42 patches of monospecific beech or 11 patches of monospecific fir. Could you indicate the initial number of trees? In the section about the limitations of the model, you could discuss the choice of fixing the initial number of trees. Are the densities resulting from the initial number of trees consistent with the ones in the field? Did you get a chance to explore if the results are robust to the initial number of trees? If yes, I think it would be worth mentioning. For instance, would that change the reference period basal area and thus the final relative basal area and the dynamics of evolutionary trajectories? *Reply: The "Simulation plan" subsection was amended to clarify this choice and justifications were added L291-306. We also included some elements of discussion in the "limitation" section about the number of trees L474, Table S.3.*
- L233: Reviewer 3: Were the initial values obtained from simulations in the Montagne noire? Which are the eight additional species? Are they more or less drought-tolerant than beech and fir in the simulations? What is the proportion of migrants from each species? More explanations are needed here.

Reply: We have added new additional tables to provide these informations, which are also commented in the text. Please refer to L325, table S.4 and the new table 1 respectively.

Results & Discussion

• L253: Reviewer 4: it is very difficult to see within one parameter, the median minimum RBA if a population could really be rescued: because the BA can be calculated out of many very small but dying trees or few old tree. In case the BA is only summed up from small trees

which might rarely flowering, it is questionable fi rescue really can happen. Therefore it is required to show for the median minimum RBA also the outputs of tree density and diameter (and height)

These additional details were not added to the various figures or sub-figures because they are already quite complex. Furthermore, we do not consider this information essential, given that basal area is a fairly accurate measure of forest condition in our simulations. In our study framework, a low basal area will necessarily be associated with a sparse forest with young individuals (as the older, less adapted ones do not survive climate change). Conversely, high basal areas will correspond to dense forests with diverse age classes, including old, dominant trees.

• L268: Reviewer 2: Do the initial values of drought tolerance systematically higher for beech than for fir? It would be highly interesting to run some simulations in which beech and fir have the same abundance but different initial values of drought tolerance, and some simulations in which beech and fir have different abundances but the same initial values of drought tolerance, to assess which hypothesis (monopolization vs preadaptation hypotheses) is the most likely

Reply: We thank the reviewer for this very interesting suggestion. However, as we feel that our article is already ambitious and with a lot of material, we have chosen not to run these simulations, even if it means not being able to decide between these two hypotheses. What is suggested here is an example of what we can explore theoretically with the model we developed. Yet for this present study, we recall that initial values of drought tolerance, and especially the relative difference between beech and fir, are rooted in observations. The rational for our simulations was thus to consider that the species show this difference in drought tolerance now, and considering this starting point, we explored how this difference may evolve. We have, however, reworded the text to make it more consistent with what our results allow us to assert or not L409-414.

- L281: Reviewer 3: I might not read well fig 5B but it seems to me that g evolves and fluctuates over time (like ShTol) Reply: A more detailed interpretation of this figure was provided throughout the result section and the range of fluctuation across our replicates was added to the figure to show the inconsistency of the signal L398, 428, 459.
- L282-283: Recommender: we really miss figures like Figure 5A, S4 or S5 to visualize evolutionary change (or absence of evolutionary change) in other traits than DrTol (ie, ShTol and g)

Reply: These are now included in the supporting information Figure S.9-12.

• L304: Reviewer 2: Which result or figure shows the role of trade-offs among traits in the outcome of the simulations?

Reply: We hope that the new version of the "Does assisted gene flow facilitate evolutionary rescue?" section L422-428, supported by data shown in the new figure 5.B, exposes that point more clearly.

• **Figure 2: Reviewer 2:** Can we really say that VR corresponds to trait variability? From what I understood, VR is the ratio of intra vs interspecific variance of the phenotypic traits, so I do not understand how it can correspond to "trait variability".

Reply: We have simplified the figure to make it easier to understand without having read the methods section in detail - and thus without even looking at what VR precisely stands for. We do not consider this simplification inaccurate, since VR translates directly into trait variability in the sense that increasing VR means increasing genetic and environmental trait variance. Furthermore VR is indicated in parenthesis so that the reader can know exactly what is on the "x" axis on Fig. 2.B & D.

- Figure 2: Reviewer 3: In general and on Fig2D: does the median minimal forest basal area rebound before the end of the warming period? Reply: This point was discussed in the former "Limits and Future Applications" section L483: it only happens in the 'assisted migration' treatment, otherwise species evolution lags behind the environmental change and prevents populations' recovery.
- Figure 2: Reviewer 4: the subfigures A and C also contain the numbers of rescued scenarios. However, as they are shown within the graph, there are difficult to interpret. I suggest to add another figure which shows the recovery percentages for the various scenarios

Reply: The figures in the heat maps do not represent the number of replicates undergoing evolutionary rescue, but the median RBA for specific scenarios. Please let us know if the information added in the "Data analysis and software" subsection L342-346 and the new Fig. 2 legend help to clarify this point.

- **Figure 3: Reviewer 2:** How was the mean individual relative light availability calculated? *Reply: The new legend of the Fig. 3 was amended to give more informations about the light availability. We hope that it improves the clarity of the figure.*
- Figure 4: Recommender: On this figure, the authors grouped together their different scenario in terms of heritabilities (h² ranging from 0.1 to 0.4) and trait variability (VR, ranging from ranging from 0.1 to 0.4), by simply summing the two parameters h² and VR on a single scale: This approach is confusing because combining h² and VR in this manner is not meaningful; it is analogous to adding apples and oranges, which are fundamentally different metrics.

Reply: We used a two dimensional colour palette to represent h^2 and VR, to avoid this confusion.

 Figure 4: Reviewer 2: I do not understand what the three plots on the third row represent: the community weighted ΔDrTol calculated for the reference period, the last decade of the simulations, and which period for the third plot?

Reply: Explanations on how $\Delta DrTol$ are computed are now given in the "Data analysis and software subsection", and a reminder was also made available in the figure caption L357.

• Figure 4: Reviewer 2: It's very hard to see and understand the patterns on these graphs, and the graphs are too small. What represent the gray lines? If the populations did not go

extinct, how do we see the trait values at the end of the simulation? What are these areas without any points or crosses on the bottom right of the plots on the right ? Are they areas of the parameter space that were reached by the parameters over the course of the simulations but then the parameter values moved away from these areas toward the end of the simulations? And why are there no crosses on the plots on the right? *Reply: We realized that this figure was very difficult to read, so we aimed at simplifying it considerably. We have added date labels to show the direction of evolutionary trajectories over time. Note that the former figure is still available in the supporting information (Fig. S.12), as we still find it helpful to visualize the diversity of evolutionary trajectories across replicates and treatments.*

- L340: Reviewer 4: This chapter should be transformed into a typical discussion section. Reply: The choice of the 'Results and Discussion' format has been heavily discussed among co-authors. We decided to follow our original rationale, believing that the present form of the article allows us to deal with the results and their interpretations question by question, avoiding the need to address the three questions one after the other in a results section and again the three same questions one after the other in a discussion section. This form allows us to avoid repetition and we believe it enhances the understanding of each point, as the three addressed questions are not necessarily strongly related to each other.
- L377: Reviewer 3: I am unsure why competition for water would act differently from competition for light. We might need more details here to clarify this point. *Reply: Competition for water between individuals can select individuals that are more tolerant to water stress, which goes in the same way than the selection pressure imposed by climate change (with increasing temperatures and more severe droughts). This is in contrast with our current framework, where global warming acts as an opposing selection force to competition because of the negative trade-offs between <i>DrTol* and competitive traits (*ShTol and g*). We have clarified this point in the last sentences of the perspectives section L523.

Model and simulation plan limitations

• L231: Reviewer3: A limit to this scenario is that a single migration rate has been investigated. This limit could be mentioned in the limitation section. Do you have any intuition or simulations available to predict the outcome of a lower migration rate? Would the replacement of beech and fir be avoided or just take longer, and would that lead to the extinction of the whole forest? If you don't have any intuition, I would still suggest mentioning the possible outcomes as it could inspire future work in this direction. *Reply: We now address this point in the 'Perspectives' section L516. More precisely, we now discuss the need to improve the migration component of the model to address important new issues in assisted gene flow.*

Perspective

• **Reviewer 3**: The authors could broaden the impact of their study by discussing a little further the implications of the study for forest management. I give below some points to consider. These are just suggestions, and the authors are, of course, free to decide whether they are relevant to the manuscript's discussion:

Reply: We thank the reviewer for this suggestion However, we are a bit reluctant to formulate recommendations for foresters in view of the numerous limitations mentioned above and detailed in the manuscript, and particularly because we have restricted ourselves to a single study site (and a single main composition), so far. We have, however, stressed the importance of genetic variability in helping forests to withstand global warming in the conclusion L545.

We would like to thank the reviewers for their detailed and constructive feedback. Their suggestions and dedication to the review process were deeply appreciated and and helped to refine our work.

Yours sincerely,

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