Peer Community In Ecology

Integrating evolution and ecology in forests: insights from a multi species demogenetic model

Sylvie Oddou-Muratorio *based on peer reviews by* ***Silvio Shueler*** *and 3 anonymous reviewers*

Louis Devresse, Freya Way, Tanguy Postic, François de Coligny, Xavier Morin (2025) Evolutionary rescue in a mixed beech-fir forest: insights from a quantitative-genetics approach in a process-based model. HAL, ver. 4, peer-reviewed and recommended by Peer Community in Ecology. https://hal.science/hal-04575070

Submitted: 24 May 2024, Recommended: 24 April 2025

Cite this recommendation as:
Oddou-Muratorio, S. (2025) Integrating evolution and ecology in forests: insights from a multi species demogenetic model. *Peer Community in Ecology*, 100701. 10.24072/pci.ecology.100701

Published: 24 April 2025

The study of eco-evolutionary dynamics, i.e. of the inter-twinning between ecological and evolutionary processes when they occur at comparable time scales, is of growing interest in the current context of global change (Carroll, Hendry, Reznick, & Fox, 2007; Govaert et al., 2019). Demo-genetic agent-based models (DG-ABMs) have gained popularity to address this issue because of their abilities to consider feedback loops between ecological and evolutionary processes and to track populations of interacting individuals with adaptive traits variations (Berzaghi et al., 2019; Lamarins et al., 2022). This type of individual- and process-based simulation modelling where interindividual variation in fitness and hence opportunities for selection emerge from demography, which in turn affects the genetic composition of the population over successive generations (feedback loop), is only beginning to be applied to forest trees (Oddou-Muratorio, Hendrik, & Lefèvre, 2020). Examples include studies investigating the dispersal capacity of transgenes in forest landscapes using spatially explicit DG-ABMs with different demographic rates for transgenic and wild-type trees (DiFazio, Slavov, Burczyk, Leonardi, & Strauss, 2004; Kuparinen & Schurr, 2007), the effect of assortative mating and selection on genetic and plastic differentiation along environmental gradients (Soularue et al., 2023) or the interactions and feedback between tree thinning, genetic evolution, and forest stand dynamics, eventually in the context of drought-induced disturbances (Fririon, Davi, Oddou-Muratorio, Ligot, & Lefèvre, 2024; Godineau et al., 2023).

In this study, Devresse et al. (2025) extend the current DG-ABM framework for forest trees by incorporating interspecific interactions within diverse, uneven-aged forests. To this end, they adapted an existing multi-species, process-based forest dynamics model—ForCEEPS (Morin et al., 2021)—enabling the evolution of selected tree functional traits across generations. Their work focuses on three quantitative traits: drought tolerance, shade tolerance, and maximal growth rate. Using this enhanced DG-ABM, the authors investigate the conditions under which evolutionary rescue might occur in a mixed beech-fir forest facing climate change. Their results demonstrate that greater trait variability and higher heritability can mitigate short-term (century-scale) forest cover loss under climate warming. The study also shows that assisted gene flow facilitates species adaptation to climate change, while the introduction of pre-adapted species (assisted migration) may enhance post-disturbance recovery but simultaneously constrain the evolutionary rescue of local species.

This work represents a major interdisciplinary advancement in forest ecology and nicely illustrates how integrating evolutionary processes into ecology-focused models can offer novel insights into forest dynamics. The implementation of genetic variability and inheritance via the infinitesimal model of quantitative genetics, along with its limitations, is described in detail, and the various research questions explored using the coupled DG-ABM are presented as proof of concept for this successful integration. Beyond its methodological contribution, the study highlights the importance of more integrated approaches to understanding forest responses to climate change—approaches that account for both within- and between-species diversity and that promote nature-based solutions. It also underscores the urgent need for experimental studies exploring the genetic variation and architecture of adaptive traits in forest species to better anticipate and support their adaptive potential in a rapidly changing environment.

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Reviews

Evaluation round #3

DOI or URL of the preprint: `https://hal.science/hal-04575070`
Version of the preprint: 3

Authors' reply, 08 April 2025

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Decision by **Sylvie Oddou-Muratorio**, posted 03 April 2025, validated 04 April 2025

please see the text enclosed **Download recommender's annotations**

Evaluation round #2

DOI or URL of the preprint: `https://hal.science/hal-04575070`
Version of the preprint: 2

Authors' reply, 06 March 2025

Download author's reply

Decision by **Sylvie Oddou-Muratorio**, posted 12 February 2025, validated 12 February 2025

Firstly, I would like to apologize for the delay in my response, which was due to a poor sequence of manuscript reception dates, the availability of reviewers, and myself, as well as the time I wanted to dedicate to synthesizing the detailed feedback from the reviewers.

Three reviewers, who had already read the manuscript, agree that it has been significantly improved, and I congratulate the authors for their careful revision, the new supporting information, and the detailed answer to reviewers' comments. The novelty of the approach, which incorporates both evolutionary processes and multi-species interactions, is now much better justified and argued in the introduction. The description of model specifications and assumptions is clearer and more targeted to a broad audience, although Reviewer 1 still suggests some improvements. Technical and language clarity has improved, although there is still room for further refinement.

Based on these feedbacks, I am confident that we can move toward the recommendation process. However, before formally recommending this manuscript, it is important for the authors to address the sometimes very detailed comments from the reviewers. I am willing to conduct a final evaluation without necessarily having the text reviewed by the reviewers again, and I will pay particular attention to the following points:

1. Strengthening the Precision of the Genetic Component

This work represents a major interdisciplinary advancement for forest ecology, and very well illustrate how incorporating a dose of evolutionary consideration in an ecology-focused model can shed new light on the ecological dynamics. However, the precision of the text regarding population genetics concepts needs to be enhanced. For example, it is crucial at this stage not to confuse hereditary versus heritable traits (L53). "Hereditary" refers to those traits passed down from parents to offspring. They are determined by genes and can be influenced by the environment, but they do not necessarily vary within a population. For example, the number of legs in humans is a hereditary trait because it is passed down genetically, but it is not heritable because there is no variation in the number of legs among humans. By contrast, heritable traits refer to traits that exhibit variation within a population due to genetic differences. For a trait to be subject to natural selection and contribute to evolutionary rescue, it must be heritable.

Another point to improve on this topic: Evolutionary rates measured in Haldane's units always represent measures of short-term evolutionary change, whether over 100 years or 1,000 years. These timescales remain contemporary compared to other evolutionary timescales. Other measure of evolutionary change may be more appropriate for longer timescales (e.g., Darwin, often used in paleontological studies to quantify rates of morphological change over long periods; morphological disparity measures; genetic distance; or substitution rate). The text lines 356-358 leaves some doubt as to whether the same formula was used for both short-term and long-term changes. You should consider indicating "evolutionary rates" (a variable) on the Y axis Fig 5 A for instance instead of "haldanes" (a unit).

There is also an error in the equation (3), as pointed out by reviewer 3. In my opinion, the last term of the equation (1/ AMs) should be replaced by AMs/ΔT, with ΔT being the time elapsed in years. In this way, the change in trait value is correctly weighted by the number of generations.

Regarding genetic correlation among traits, I think addressing this topic is beyond the scope of this manuscript, and would require considering the pairwise relationships between traits values at the individual scale, which is not done in the manuscript (if I am correct).

2. Better link to Demography

In evolutionary ecology, the widely acknowledged metric for assessing the consequences of genetic drift, the possibility of genetic rescue of the efficacy of selection is the number of individuals (ideally the effective population size), not the Relative Basal Area (RBA). I think it is crucial to better explain why RBA is retained a the criterium evolutionary rescue in this study, why this arbitrary threshold of 5% is selected, and how RBA relates to demography. Specifically, we need to understand how many (reproductive) trees correspond to the 5% RBA criterion: depending on the distribution of tree sizes, 5% of RBA can correspond to very different population sizes. I agree with Reviewer 1's suggestion to dedicate a specific section in the methods to explain how the median minimal and final RBA values are computed, and how they relate to demography. Additionally, the suggestion by several reviewers to add supplementary figures 2' and 4' considering population size instead of RBA is valid and should be done (probably as supplementary materials).

Comments regarding how regeneration is managed by the model, and how is the number of new seedlings is defined are also relevant in this perspective (see comment by Reviewer 1 at L152-175)

3 Pay special attention to form

A careful revision of variable name consistency, typos, and grammatical errors throughout the manuscript is needed. Note that the recommended article must be as close to perfect as possible in terms of form because it is a completed final article. All three reviewers provided suggestions for improvements, and addressing these will further improve the manuscript.

I think that most of the specific comments (including the numerous comments of reviewer 3) deserve attention. The only points where I may be more reserved concerns:

— The structure of the methods section, where I think a certain degree of repetition is somewhat unavoidable. Regarding the way of describing individual-based model, the Design concepts and Details (ODD) protocol by Grimm et al. (2020) may be useful to consider in future publications (it would be too late to ask the authors to switch to this at this stage).

— The concept of resilience and recovery: as they have specific meanings depending on the disciplines, I would advise simply defining them briefly and reformulating, for example, L19-20 as: ”Evolutionary rescue is defined by a population’s ability to avoid extinction (persistence) and recover through natural selection acting on heritable variation (Bell, 2017). Recovery refers here to the population’s capacity to regain a viable size following a disturbance.”

I look forward to reading the final version of this manuscript.

Reviewed by anonymous reviewer 3, 14 January 2025

Dear recommender and authors,

I have now read the latest version of the paper “Evolutionary rescue in a mixed beech-fir forest: insights from a quantitative-genetics approach in a process-based model” by Louis Devresse, François de Coligny, Freya Way, Xavier Morin.

This version is greatly improved and the authors have addressed all of my comments thoroughly. The references and definitions missing from the introduction have been added. The first figure, which describes the model framework, has been improved and I find it more intuitive to read and clearer overall now. I find the new title appropriate. I have no further comments to make (probably because this reaches the limits of what I can evaluate), so I will leave it to the other reviewers to share their thoughts on the other technical and scientific aspects of this work. I can, however, offer some help with typos and grammatical errors that I noticed in the text. Hopefully this will be useful for your next review.

Abstract:

“most of these works” □ “most of these studies” (or: “most work focuses on...”) could be more natural in this context

“The main objective and originality of our work is” □ “The main objective and originality of our work are”

“study suggested” □ “study suggests” for consistency of the tense

“allows to test” □ “allows us to test”

Main text:

L10: “increasing evidence suggest” □ “increasing evidence suggests”

L13: “may as well raise the probability” □ “may also raise the probability”

L17: “to adapt to a rapid climate change” □ “to adapt to rapid climate change”

L45: “the development of a PBMs” □ “the development of PBMs” (plural)

L54-55: “parameters that are costly and difficult estimate in field studies” □ “parameters that are costly and difficult to estimate in field studies”

L73: “species specific parameters” □ “species-specific parameters”

L80: “the QTL model assume that” □ “the QTL model assumes that”

L82: “the phenotypes of the offsprings are drawn” □ “the phenotypes of the offspring are drawn” (offspring is both singular and plural)

L126: “our approach to model regeneration” □ “our approach to modeling regeneration”

L127: “Trees in a same patch all compete for light” □ “Trees in the same patch compete for light”

L153: “In the individual based forest PBM literature” □ “In the literature on individual-based forest PBMs”

L167: “We refer to […], “local regeneration”” □ “We refer to […], as “local regeneration””

L171: “only local the regeneration occurs” □ “only the local regeneration occurs”?

L239: “A tree is considered as reproducer if it meet two criteria” à “A tree is considered a reproducer if it meets two criteria”

L256: “constant across generation” □ “constant across generations”

L259: “to obtain those of the offspring” □ “to obtain that of the offspring”

L265: “In the present case, migrants trait” □ “In the present case, migrants’ trait”

L291: “on climates of historical periods” □ “under climates of historical periods”

L293: The statement “with beech as the dominant species.” could benefit from clarification (dominant in what sense?) □ “with beech being the dominant species in terms of density and basal area.”

L376: “[…] was due to the release from competition for light cause by the high mortality in the warming period” □ “[…] was due to the release from competition for light caused by the high mortality during the warming period.”

L396: “This result can be explained by the lifting of competition” □ “This result can be explained by the alleviation of competition”

L459-461: “It’s worth noting […] competition for light was the fiercest” is a bit awkward, it can perhaps be improved with something like “It is important to note […] competition for light was most intense”?

L485: “matter” □ “matters”

L486: “need” □ “needs”

L526: “was explicitly considered in ForCEEPS” □ ” were explicitly considered in ForCEEPS”

L528: “this work represent” □ “this work represents” (or : “constitutes”?)

Reviewed by anonymous reviewer 2, 31 January 2025

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Reviewed by anonymous reviewer 1, 13 January 2025

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Evaluation round #1

DOI or URL of the preprint: `https://hal.science/hal-04575070`
Version of the preprint: 1

Authors’ reply, 29 November 2024

Download author’s reply

Decision by **Sylvie Oddou-Muratorio**, posted 08 August 2024, validated 09 August 2024

This simulation study by Louis Devresse and colleagues investigates how evolutionary response may contribute to forest adaptation to climate change, focusing on the possibility of evolutionary rescue in mixed fir-beech forests under different scenarios involving genetic or species enrichment. This study is based on an existing multi-species, process-based, forest dynamic model, which the authors modified for this study by allowing selected tree functional traits to evolve across generations. Four reviewers have now provided overall positive feedback on the pre-print, but they have also highlighted areas for improvement. I concur with their assessment that the manuscript can be challenging to follow in some parts, and that both the clarity of the text and the quality of the figures need to be enhanced. The main issues raised regarding the manuscript can be summarized as follows:

1- Clarification of the objective and justification of novelty: As stressed by reviewers #2 and #4, this study straddles (1) a purely methodological study aiming to develop a new model and (2) a classical research study investigating evolutionary rescue in forest tree populations. A choice needs to be made between these two options. If option 2 is retained, a definition of the concept of evolutionary rescue should be included, as noted by most reviewers. The novelty of the approach, which lies in incorporating both evolutionary processes and multi-species interactions, should also be better justified in relation to key conceptual issues and within a comparative framework. The introduction should more clearly articulate how evolutionary dynamics have been incorporated into previous process-based models and distinguish the current model from these existing models. A thorough review of the literature on process-based models that incorporate evolutionary aspects would provide the necessary context and clarify the manuscript's contribution.

2- Description of model specifications and assumptions. The manuscript should describe the model specifications and assumptions in a way that is accessible to a broad audience, including forest ecologists familiar with gap models (a term that should be defined in the manuscript) and evolutionary ecologists who may require basic information on gap models, but who may question the use of the infinitesimal model. As noted by reviewer #4, the authors need to better justify the choice of the infinitesimal model, explain it and maybe discuss how results may differ from those obtained with other multilocus quantitative approaches. Reviewers #2 and #3 noted that the description of key processes, such as recruitment, growth, and mortality, was inadequate. The authors also need to clarify the time step used in the simulations (e.g., monthly, yearly), and how environmental variables change over time (monthly variations, inter-annual variations). Additionally, terms like ”recovery,” ”slow vs. fast evolutionary scenarios,” and the specific migration rates considered need to be explicitly defined and consistently used throughout the manuscript.

3- Improvement of technical and language clarity. The manuscript requires major improvements in language clarity, including syntax and grammar, especially in complex sentences, which have been highlighted by the reviewers as hindering comprehension. There are also inconsistencies between the main text and the supplementary materials.

I carefully reviewed the pre-print myself and have some additional comments that I hope will be useful for the authors in producing an updated pre-print:

L131-143: the phenotypic variance-covariance matrix Sigma$sigmaP$P 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.

L282-283: 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)

Figure 4 : on this figure, the authors grouped together their different scenario in terms of heritabilities (h^2 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 h^2 and VR on a single scale: This approach is confusing because combining $h^2$and VR in this manner is not meaningful; it is analogous to adding apples and oranges, which are fundamentally different metrics.

Figure 5B: these plots showing evolution in joint trait values are not really difficult to interpret due to the dense information and small symbols. Additionally, we miss the simple trajectory for each trait value (as mentioned in my earlier point). The legend in the main text is also incomplete compared to Figure S6 in the supplementary material. It might be better to keep only Figure 5A in the main text.

Supplementary Materials: The supplementary should be carefully revised so that they better match/complement figure in main text. I strongly advice the authors to make these supplementary materials available separately from the other material provided on the Zenodo data center, which currently hosts a single large zip file.

Reviewed by anonymous reviewer 3, 04 July 2024

Review of "A Process-based Model Approach to test for evolutionary rescue in forest ecosystems under climate change" by Louis Devresse, François de Coligny, Freya Way, Xavier Morin

Title and abstract

The title accurately represents the content of the article and the abstract is clear and well written.

Introduction

The introduction is based on relevant research in the field and clearly identifies the importance of developing these innovative models. The research questions and scenarios are clearly presented and are highly relevant and interesting. Below are just a few suggestions:

L9: It would be useful to add a simple definition of what process-based models are so that a wide audience can easily follow this paragraph.

L14-16: "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.

L31-33: You might want to add a reference for evolutionary rescue.

L37-38: typos? Reword into 'recent work suggests' 'evolutionary processes'?

Materials and methods

The method section is detailed and very clear overall.

Page 4 – Figure 1: Although aesthetically very pleasing, I have had a bit of trouble figuring this figure out. Given the size of this figure, the order at which the different parts appear are important. Here, the fact that the original model and the base of the model are at the bottom is a bit confusing because the 'species composition feedback' and 'evolution module' parts come first. Perhaps inverting the two and putting the color code for the additions at the top would make it clearer to see what has been added right away. Some of the text is also very small (the equations notably). Overall, I wonder if the authors have not put too much information on this figure, making it less comprehensible. I suggest that they consider simplifying it.

L207-208: 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?

Results & Discussion

The results are correctly interpreted and the discussion is in agreement with the results described. The latter also raises the limits of the model, though see my last point for lines L207-208.

Reviewed by anonymous reviewer 2, 14 July 2024

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Reviewed by anonymous reviewer 1, 03 July 2024

Download the review

Reviewed by Silvio Shueler, 07 August 2024

Devresse et al. provide an interesting and important study. The authors combine a multi-species forest growth/development model with evolutionary processes to test for effects on climate change on the effects on maladaptation, respectively the effects of maladaptation on forest development, as well as for testing for effects of mixture forest, genetic enrichment (could maybe also considered as assisted migration) and species enrichment on the evolutionary dynamics.

Overall, I found the study highly interesting and timely. However, the manuscript also left me a puzzled, because the abstract, the title and the described aim of the study do not really fit to the structure of the paper and the main results. In the abstract and the definition of objectives the authors explain that the aim of the study is “to propose a methodology” or “an approach that integrates….” and to use some case studies just for demonstrating this approach. According to these objectives, the paper would be rather a methodological study. 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. For a good methodological study, I would also expect that the authors make some more simple model runs, to test if basic evolutionary processes, such as drift, migration and various selection intensities results into output expected. If the study should be a purely introduction of the methodology (as the authors state in their objectives), the results of such “simple” model runs with trees would already justify its publication. Using the case of evolutionary rescue as case study would be insufficient to justify the model, because such questions were rarely addressed in other studies and therefore do not allow a comparison of the model validity.

However, I found the results of the study stronger organized around the outcomes of the simulation of climate change and evolutionary rescue and I would see these results far more important then just being examples for the new methodological development. In case, the authors decide to shift to a such a more traditional research paper, with the evolutionary rescue in its centre, the paper would need to be reorganized in the abstract and the introduction, and the discussion should be widened. I also suggest another paper title, reflecting more the research question or outcome. Moreover, shifting the focus of the paper to the case study would still require that the authors better explain the infinitesimal model. Also, the simple model runs, which probably have been done by the authors anyhow, should be documented in the supplement and mentioned at the end of the model description.

I’m convinced that the study would make a valuable scientific contribution (actually I would be happy to read it), if it would be organized around the case studies, but see that it will require a moderate major revision to do so.

Besides this major suggestion on the study direction and organization I have few more minor comments below:

Abstract: the general introduction takes more than 50% of the abstract. Please reduce this part and provide equal weight on the result and discussion.

Abstract, line 17: reduced the lost or loss?

Introduction: large parts of the introduction switch several times from a description of the general problem (i.e. climate change, forest adaptation, evolutionary rescue, etc.) and the technical feasibilities of available models, i.e. lines 3-7 are problem, lines 7-19 are model issues, lines 19-24 are problem, lines 24-28 are on models and so forth. This structure makes it difficult to differentiate between actual scientific knowledge and the open research questions. I suggest using a rather traditional structure, with one paragraph outlining the problem of climate change, forests and adaptation and evolutionary constrains and potential rescue and another one introducing the needs of forest models and their present limitations.

L31-32: better introduce and define evolutionary rescue and what we know so far about it, beyond the simple statements given in lines 43-47

L48-75: the overall description of objectives is rather long and remains vague – please reduce and stay with main objectives

L57-61: here you already involve parts of the methods section

Figure 1: consider more contrasting colours for the text and arrows within the coloured boxes: some are very hard to see

L80: revise, sentence not clear

L107-110: define age limits for the change from seedlings to adults, ate what age does the shade tolerance changes?

L118-120: extend the description of the evolutionary modul - see above

L152ff: 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!

L211-217: 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

L228-235: the genetics of the additional 8 species is not described. Please add. I also suggest moving some basic species parameters from the suppl Tabl. S3 to the paper itself. That helps understanding the large differences in drought tolerance

L249: the medial minimal RBA is an important parameter: before you show how its is driven, explain better, how its has been calculated.

L253: 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)

Fig. 2: 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

L253-256: authors comparing fir and beech, but they are actually the same? " … was reached fro minimum h2 and VR of 0.3 in fir" and "In beech … the same threshold was reached for h2 of 0.1 and VR of 0.3"… Given that h2 of 0.1 is the minimum this is actually the same for the 2 species?

L173-275: "… the evolution rates…" are this for beech or fir or both? Revise for better understanding

L282 and L 317: what is parameter "g" – I guess growth rate otherwise marked with RGR??

L293-294: is final RBA identical to the RBA and the end of the simulation? Revise for better understanding

Figure 4. use similar scales for all subfigures

L353: here the authors start to discuss some limitations of their evolutionary module. That's highly needed, but without a proper introduction of the modul in the methods is feels useless because it requires a lot of additional knowledge from the reader

L340: this chapter should be transformed into a typical discussion section.