

**Revision of: *Upscaling with the dynamic two-layer classification concept (D2C): TreeMig-2L, an efficient implementation of the forest-landscape model TreeMig***

J. E. M. S. Nabel

I thank the referees for their reviews and their suggestions which helped to clarify the manuscript. I addressed all referee comments in point-by-point replies and inserted according text changes into the manuscript.

Because both referees had questions to the pre-structuring of the simulation area, I added a figure to the manuscript that gives an example for the pre-structuring. The new figure (Figure 3) is an adapted version of the previous Figure A.2 from the Supplementary Material. Furthermore, the new Figure already includes the information contained in the previous manuscript-Figure 4, which I therefore removed from the manuscript.

In this document I duplicated the referees comments followed by my individual responses, and attached a marked-up version (latexdiff) of the manuscript and of the supplementary.

## **Response to review RC\_C1640**

Thank you for your review and comments that help to clarify the manuscript. Below I duplicate your comments and respond to them point by point followed by the modifications that will be adopted in the revised manuscript.

### **(1) P5537 L23**

**I cannot understand what "thematical" means here**

*Response:*

*Thematical means the represented content, i.e. how the objects of the real world are represented in the model, i.e. the modelled entities. For clarification, thematical has been replaced in the sentences. The sentences now state:*

Aggregations can thereby be temporal, spatial or with regards to the representation of the modelled entities, i.e. the simulated processes and state variables. When the fine spatio-temporal resolution should be maintained (as recommended by Bocedi et al. 2012), remaining possibilities for cost reductions thus can only change the representation of the modelled entities.

### **(2) P5537 Para2**

**Following work should be adequately addressed here, as it is a pioneer work that adapted an approximation method on a forest dynamic model. Moorcroft, P.**

R., et al. (2001). A method for scaling vegetation dynamics: The ecosystem demography model (ED). *Ecological Monographs* 71(4): 557-586.

*Response:*

*The work has been cited. The second part of the paragraph now reads:*

One example finding broad application in DVMs is the aggregation of individuals with similar properties into cohorts (e.g. Scheller and Mladenoff, 2004; Smith et al. 2014). With cohorts solely one representative calculation, instead of multiple replicate calculations, needs to be conducted. Another more comprehensive example is the approximation of entire grid cell populations. Height-structured distributions (Lischke et al. 1998), as well as size- and age-structured approximations (Moorcroft et al., 2001), can be applied to upscale individual-based, stochastic models. By aggregating individuals of forest patches influenced by small scale stochastic processes, such approximations allow to dramatically reduce the number of calculations required to determine the vegetation dynamics in a grid cell. Both examples, cohorts and structured approximations, utilise similarities for within grid cell aggregations. The upscaling method presented in this paper – the dynamic two-layer classification concept (D2C) – is based on a more extensive similarity approach aiming to combine different grid cells with similar properties.

### **(3) P5542 L7-11 and L25-28**

**I cannot understand these sentences, where author try to explain how D2C organizes grid cells of the TreeMig-2L.**

*Response:*

*Following the suggestion of the second referee, the sentence L25-28 has been removed. Furthermore, because the second referee also had questions to this section, I did not only adapt the text, but also adapted the previous supplementary Figure A.2 and moved it to the main text (see Fig. 3). This Figure gives an example for the pre-structuring. It shows the discretisation of the minimum winter temperature with the set E3 of bioclimate bins for one cell and how the bioclimate driver is then calculated from all associated cells. The new Figure includes the information of the previous Fig. 4, which I therefore removed. The sentence L7-11 and subsequent sentences were rephrased for clarification and now state:*

One of the challenges for an efficient organisation of the elements on the non-spatial layer was that the number of elements is not known in advance, because it is an emergent property of the simulation. To allow for an arbitrary number of elements on the non-spatial layer, the elements are stored in linked lists, instead of using an array structure with a predetermined fixed size, as usually done in space discrete DVMs. However, using one large linked list, and comparing all elements with each other, would be very inefficient and would lead to a large organisational overhead. To reduce the organisational overhead required for the comparison of elements during runtime, TreeMig-2L uses several linked lists, and only elements in the same list are compared. To define the number of linked lists, the fact is used that the bioclimate drivers are an input to TreeMig and can thus be used to pre-structure a simulation area (see Fig. 3 for an example, and Supplement Sect. A.2 for additional information). To pre-structure a simulation area, grid cells are classified into "bioclimate types". Each bioclimate

driver is thereby discretised according to a set of pre-defined "bioclimate bins" (see e.g. Table 2). To limit the number of possible bioclimate types and to save computation time, the discretisation is only applied for temporal averages of the bioclimate drivers on a pre-defined set of "supporting periods". For each cell, one average per driver and supporting period is calculated. Two cells are classified into the same bioclimate type, if their averages fall into the same bioclimate bin for each driver and supporting period, whereby the bioclimate bins can differ in between supporting periods. For each existing bioclimate type, i.e. each type with which at least one cell is associated, an own linked list is used. The bioclimate drivers for a bioclimate type are calculated as the averages of all associated cells.

#### **(4) P5547 Para2**

**The model versions 2 and 3 would be explained more. It is very difficult to understand what they are at first reading.**

*Response:*

*The paragraph has been adapted and now states:*

To disentangle the effects of the pre-structuring into bioclimate types and of dynamic associations between the layers, simulations of four model versions with increasing complexity were compared (Table 3). (1) 1L-ORG: the original one-layer approach with the original bioclimate driver. Simulations with this version were conducted to obtain reference values for the comparisons. (2) 1L-PB: a model version in which bioclimate types were used to derive averaged bioclimate drivers, but in which all processes were still simulated on one layer. Simulations with this version thus isolate the loss in accuracy due to the averaging of the bioclimate drivers. (3) 2L-NDA: a model version using bioclimate types and two layers but no dynamic associations, i.e. in this version each bioclimate type has only one element. Because dynamic associations are switched of, differences in the number of germinated seeds between cells associated with the element do not lead to splits, and a species introduced in one of the cells will thus occur in all associated cells. Therefore, simulations with this version can elucidate if there is a necessity to track species. Furthermore, having no costs for splitting and merging, this version can be used to derive the maximum CPU time reduction that can be achieved. (4) 2L: the full TreeMig-2L model with two layers and with dynamic associations.

#### **(5) P5548, L15-17**

**The term "peak element-cell ratio" is not defined anywhere in the manuscript. Also, please provide brief explanation for the "callgrind".**

*Response:*

*The paragraph was extended to incorporate the suggested changes:*

Two further measurements were taken to assess the applicability of D2C in view of the three aspects listed at the end of Sect. 2. Firstly, the maximum number of elements reached during a simulation was tracked, here referred to as the peak element-cell ratio. Secondly, the ratio of the time spent on different processes was profiled with callgrind, a tool which records

function calls in a program during runtime (Weidendorfer, 2008).

**(6) P5564, caption of the table 3**

**Need more words. According to GMD's "manuscript preparation guidelines for authors", tables should be self-explanatory and include a concise, yet sufficiently descriptive caption.**

*Response:*

*The caption of the table has been improved. Furthermore, the model versions in the table have been re-ordered to better reflect the changes in reaction to comment (4). See Table 3.*

## **Response to review RC\_C1723**

Thank you for your review and the suggestions that help to clarify the manuscript. I have duplicated your comments in full below, each followed by a point-by-point response including the modifications that will be adopted in the revised manuscript.

**P5536 L25: I think a comment on the nature of DVM's according to Snell 2014 would be useful here.**

*Response:*

*I am not sure if I understood your comment correctly. The second sentence comments on the shared view on the nature of DVMs in this manuscript and in the Snell et al. (2014) paper. To make this more clear, I moved the Snell et al. (2014) reference to the end of the second sentence. The sentences now state:*

Impact studies of climatic changes on spatio-temporal vegetation dynamics are often conducted with so-called dynamic vegetation models (DVMs). DVMs are mainly implemented as time- and space-discrete models, simulating ecological processes that are key to vegetation dynamics, such as establishment, growth and mortality, usually under consideration of biotic and abiotic influences (see e.g. Snell et al., 2014).

**P5537 L27: Could do with references to models that use cohorts. I am not sure that it is very useful to refer so heavily to another paper here.**

*Response:*

*References to two example models using cohorts were added and the reference to Snell et al. (2014) removed, the sentences now read:*

One example finding broad application in DVMs is the aggregation of individuals with similar

properties into cohorts (e.g. Scheller and Mladenoff, 2004; Smith et al. 2014). With cohorts solely one representative calculation, instead of multiple replicate calculations, needs to be conducted.

**P5541 L17: I think it is perhaps better to be explicit that you are referring to avalanches.**

*Response:*

*The sentence has been adapted according to the suggestion and now states:*

Other processes which would require information on the neighbourhood are, for example, spatially connected disturbances such as snow avalanches (e.g. Zurbriggen, 2013).

**P5542 L17: ‘Supporting period’ is not a very intuitive descriptive term here. Could the the need for the definition of the period be described more clearly?**

**P5542 L20: What happens if the bioclimate bins change between supporting periods? Is there an accommodation for a changing climate?**

*Response:*

*I rewrote the paragraph on the pre-structuring of the simulation area to clarify that one average is calculated for each supporting period and that the bioclimate bins can thus change between supporting periods. The paragraph now expresses that the supporting periods have the function to sample the bioclimate for each cell in time. To accommodate for a changing climate more than one supporting period is required. The more supporting periods, on the other hand, the more bioclimate types can theoretically result. More supporting periods will, furthermore, also lead to higher costs in the pre-clustering step.*

*The first referee also had clarification questions to this section, and I therefore not only adapted the text but also adapted a figure from the supplementary (previous Figure A.2) and moved it to the main text (see Fig. 3). This Figure gives an example for the pre-structuring. It shows the discretisation of the minimum winter temperature with the set E3 of bioclimate bins for one cell and how the bioclimate driver is then calculated from all associated cells. The new Figure includes the information of the previous Fig. 4, which I therefore removed.*

*The adapted paragraph now states:*

One of the challenges for an efficient organisation of the elements on the non-spatial layer was that the number of elements is not known in advance, because it is an emergent property of the simulation. To allow for an arbitrary number of elements on the non-spatial layer, the elements are stored in linked lists, instead of using an array structure with a predetermined fixed size, as usually done in space discrete DVMs. However, using one large linked list, and comparing all elements with each other, would be very inefficient and would lead to a large organisational overhead. To reduce the organisational overhead required for the comparison of elements during runtime, TreeMig-2L uses several linked lists, and only elements in the same list are compared. To define the number of linked lists, the fact is used that the biocli-

mate drivers are an input to TreeMig and can thus be used to pre-structure a simulation area (see Fig. 3 for an example, and Supplement Sect. A.2 for additional information). To pre-structure a simulation area, grid cells are classified into "bioclimate types". Each bioclimate driver is thereby discretised according to a set of pre-defined "bioclimate bins" (see e.g. Table 2). To limit the number of possible bioclimate types and to save computation time, the discretisation is only applied for temporal averages of the bioclimate drivers on a pre-defined set of "supporting periods". For each cell, one average per driver and supporting period is calculated. Two cells are classified into the same bioclimate type, if their averages fall into the same bioclimate bin for each driver and supporting period, whereby the bioclimate bins can differ in between supporting periods. For each existing bioclimate type, i.e. each type with which at least one cell is associated, an own linked list is used. The bioclimate drivers for a bioclimate type are calculated as the averages of all associated cells.

**P5542 L25-30: Maybe too much detail? Defer to editorial advice on how much description of the actual code is desirable.**

*Response:*

*I removed the sentence. For interested readers this information is still contained in the supplementary material.*

**P5543 L2 : Is this sentence “The communication between the layers is asymmetric.” needed? I found it rather inhibited my understanding of this paragraph.**

*Response:*

*I rephrased the sentence. The important point here was that the cell starts the communication. The paragraph now starts with:*

The information exchange between the layers is induced by the cells.

**P5543 L6: Are the light conditions those of the under-storey, above the canopy, or in gaps?**

*Response:*

*In TreeMig, each height class has its own frequency distribution of light which is calculated from the tree distribution of all higher height classes (see Lischke et al., 1998; Löffler and Lischke, 2001; Lischke et al., 2006). I added more information to the sentence, which now states:*

For regeneration, additionally, the current bioclimatic conditions and the light distribution of the lowest height-class need to be accessed, because they influence the density of newly germinated seeds (see Lischke et al., 1998, 2006).

**P5543 L13: Averaged densities of what?**

*Response:*

*Added 'of germinated seeds':*

Averaged densities of germinated seeds falling below a pre-specified presence threshold are thereby set to zero.

**P5544 L4: The concept of ‘tracked’ and ‘untracked’ species I find confusing. Can it be elaborated on slightly?**

*Response:*

*I added further explanation, the according sentences of the paragraph now state:*

In TreeMig-2L this trade-off between accuracy and possible splits is approached by not considering splitting for all species, but only for a set of species previously specified as species to be tracked. I.e. for tracked species differences in the number of germinated seeds among grid cells associated with the same element can lead to splits. For untracked species, in contrast, the number of germinated seeds is not compared among grid cells and deviations can thus not lead to splits. Apart from the splitting step, all species are treated the same, in particular the number of germinated seeds on an element is calculated as the average over all associated cells for each species, no matter if tracked or untracked. As a consequence, untracked species might be represented less accurately, which can feedback on the tracked species via competition. Therefore, species that are expected to change their distribution in the course of the simulation should be defined as tracked species.

**P5545 L6: ‘influenced’, not ‘influence’.**

*Response:*

*Thank you for spotting this typo, I corrected the sentence and it now states:*

The number of bioclimate types will also be influenced by the spatial extent of a simulation area:...

**P5545 L 26: Maybe add some brief context here, like ‘the scenarios pertain to different regions of Switzerland’.**

*Response:*

*The suggested context was added to the sentence, which now states:*

TreeMig-2L simulations were conducted for two different application scenarios (A1 and A2), pertaining to different regions of Switzerland.

**P5546: Again, perhaps some context might be of use here, in terms of ‘scenario A1, in the flatter areas of Northern Switzerland’ vs scenario B, a N-S transect across the whole of the Swiss Alps’.**

*Response:*

*Thank you, I added the suggested text to the application scenario descriptions, which now state:*

Scenario A1, in the flatter areas of Northern Switzerland, stems from a study with a preliminary TreeMig-2L version without dynamic associations between the layers (Nabel and Lischke, 2013). Scenario A2, a north-south transect across the Swiss Alps, stems from a study investigating the influence of interannual bioclimate variability in simulations of the northwards migration of *Ostrya carpinifolia* Scop. (European Hop Hornbeam) with TreeMig-Netcdf 1.0 (Nabel et al., 2013).

**P5546 L16: I am not sure what happens to the other species. Are there other species? How many? Do their dynamics not affect the distributions of the ‘tracked’ species?**

*Response:*

*The number of competing species was so far only contained in Table 1. This information has now been added to the main text and further text has been added for clarification. I hope that, together with the explanation to comment P5544 L4 above, it is now clear what happens to the other species and that they indeed compete with the tracked species.*

The tracked species in scenario A2 is naturally the investigated migrating species (*O. carpinifolia*). The other 21 competing species simulated in this application scenario were not tracked. For A1 four out of the 31 simulated competing species were selected as tracked species: *Quercus pubescens*, *O. carpinifolia*, *Larix decidua* and *Pinus sylvestris*. These species were selected because they have the highest drought tolerance indices in TreeMig. With increasing drought severity (and increasing temperatures), these species are therefore expected to extend their spatial distributions, whilst the other species might be less effected or have declining distributions.

**P5546 L25: This idea of ‘stochastic extrapolation’ could do with some more explanation. What is the timespan of the simulation compared to the availability of the driving data? Why does the extrapolation need to be stochastic?**

*Response:*

*I agree that this is an important topic. However, I suggest that this discussion is not in the scope of the current manuscript and I would like to refer to the publications Nabel et al. (2013, 2014) in which different extrapolation methods are discussed in detail on the example of application scenario A2.*

**P5547 L1: I am confused about the need to use/define these three sampling periods? Are they ‘supporting periods’? Why not use the whole time series?**

*Response:*



*Thank you very much for spotting this relict. These are of course the supporting periods and this sentence as well as a sentence in the supplementary have been corrected accordingly. Regarding the question why not using the whole time series: I hope that the text change in response to the comments P5542 L17 and P5542 L20 above clarified that several supporting periods are required to accommodate for a changing climate.*

*The changed sentence state:*

For both scenarios three supporting periods were averaged: the first 30 (A1: 1961–1991; A2: 1901–1931) and the last 30 years (both: 2071–2100), as well as the whole time span (A1: 1961–2100; A2: 1901–2100).

**P5547 L7: Suggest adding “Simulations with scenario A2, a much smaller land area required one-tenth...”**

*Response:*

*I adapted the sentence which now states:*

Simulations with scenario A2, having much less grid cells and requiring only one-tenth of the CPU time of scenario A1, were repeated 100 times.

**P5547 L10: Are there not four versions, including the control 1L-ORG?**

*Response:*

*The original intention was to refer to three model versions in addition to the original model. However, I agree that this is cumbersome and adapted the sentence which now states:*

To disentangle the effects of the pre-structuring into bioclimate types and of dynamic associations between the layers, simulations of four model versions with increasing complexity were compared (Table 3).

**L5549 L15: To what extent is the 2L approximation dependent upon how the model is driven? In the nomenclature I am most used to, metrics of bioclimate are not used as drivers, e.g. annual/daily/hourly meteorology is the main driving data set. Longer ‘bioclimate’ averages are more often used to define the ranges of vegetation, not their driving data. Is there some confusion over the use of the term ‘bioclimate’ here that requires further clarification?**

*Response:*

*Using ‘bioclimate’ as a driver: TreeMig simulations require time series of three different annual bioclimate drivers, which are derived deterministically from monthly averaged meteorology (temperature and precipitation). Because for TreeMig, the bioclimate is derived in advance in a data pre-processing step, the number of required calculation steps during runtime is reduced, which is especially beneficial for stochastic replicate simulations. However, TreeMig could also be formulated as a model directly driven by temperature and precipitation.*

*Up to now the information on the meteorology data was only contained in the supplementary and I added this information to Sect. 3.1.1, now stating:*

TreeMig simulations require time series of three different annual bioclimate drivers: the minimum winter temperature, the sum of daily mean temperatures above 5.5°C, and an index denoting the severity of droughts (Lischke et al., 2006; Nabel et al., 2014). These drivers are derived from monthly averaged temperatures and monthly precipitation sums (see e.g. Supplement Sect. B).

*Additionally the commented sentences have been slightly rephrased:*

Averaging of the bioclimate drivers of associated cells to obtain the drivers for the bioclimate types led to small but visible deviations (e.g. Fig. 3 and Supplement Sect. C). These deviations in the bioclimate driver entail deviations in the simulation results when comparing to results from one layer simulations, i.e. simulations with the original grid cell-based bioclimate driver (see column 1L-PB in Table 5 and Sect. 4.2). Using bioclimate bins with a coarser resolution thereby led to larger deviations in the driving bioclimate and, thus, to larger deviations in the simulation results (Table 5).

*Regarding your first question: Following my experiences, the pre-structuring of the simulation area is fundamental for the efficiency of TreeMig-2L (which I do state in Sect. 4.1). Thus, for an efficient 2L approximation of any model, there needs to be some pre-structuring of the simulation area enabling to define a fixed set of linked-lists, among which the elements of the non-spatial layer can be organised. This means that it is e.g. not important, if the drivers of the model are precipitation and temperature or some derived bioclimate variables, but it is important that there is some sort of information which can be used for the pre-structuring. While this will be the case for most DVMs, it would be difficult, for example, to approximate a model with interactive climate, as e.g. in coupled land-atmosphere models. For such a model one could try a pre-structuring of the land area based on a short time-span simulated with the original model. Since in such a case the driving climate time series is not known in advance, the averaging of the driver in the pre-structuring step would definitively need to be replaced by a dynamic approach in order to accommodate for a changing climate. However, as I also mentioned in Sect. 4.1, such a dynamic approach has not been tested with TreeMig-2L so far and would certainly require more computations and could thus lead to less CPU time reductions.*

**P5549: L10-30: This discussion is interesting, but slightly breaks the flow of the text. Might it be relegated to the supplementary information?**

*Response:*

*I would prefer to keep this discussion in the main text, also with respect to your question above, regarding the dependence of the method on how the model is driven. This discussion underlines the importance of the pre-structuring, explains that the pre-structuring is not necessarily coupled to the 'in advance averaging' of the bioclimate driver, and discusses some of the consequences of replacing the averaging in the pre-structuring step by a dynamic approach at runtime.*

**P5551 L9: Suggest replacing ‘selected set’ with ‘resolution’.**

*Response:*

*Thank you for this suggestion. Several sentences in the manuscript and the supplementary were adapted according to the suggestion. The sentence referred to now states:*

The level of the SC was thereby largely determined by the resolution of the applied set of bioclimate bins, the coarser the resolution, the smaller the SCs for all variables (differences in the SCs of up to 0.14 – Table 5).

**P5551 L 25-30: Could you add a sentence here about why adding more tracked species reduces the error?**

*Response:*

*The trade-off between accuracy and computation costs related to the number of tracked species is described in Sect. 3.1.4. I hope that with the additional information introduced there as a reaction on the comment to P5544 L4 it is now more clear why tracking more species can reduce the error.*

**P5555 L2-5: Not sure I understand this sentence (Most importantly...). Is there a word missing?**

*Response:*

*The sentence has been corrected and now states:*

The main determinant for the non-reducible base load is the number and complexity of processes requiring information on the neighbourhood of a grid cell, i.e. spatially linked processes.

**P5555 L14: Updated reference for LPJ-GUESS:**

Smith,B., Warlind,D., Arneth,A., Hickler,T., Leadley,P., Siltberg,J., & Zaehle,S. (2014). Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences*, 11, 2027-2054.

ED references should probably include:

Medvigy, D., & Moorcroft, P. R. (2012). Predicting ecosystem dynamics at regional scales: an evaluation of a terrestrial biosphere model for the forests of northeastern North America. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1586), 222-235.

and/or

Moorcroft, P. R., Hurtt, G. C., & Pacala, S. W. (2001). A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecological monographs*, 71(4), 557-586.

*Response:*

*Thank you. The references for LPJ-GUESS (Smith et al., 2014) and for ED (Moorcroft et al., 2001) have been added.*

## References

- Lischke, H., Löffler, T. J., and Fischlin, A.: Aggregation of Individual Trees and Patches in Forest Succession Models: Capturing Variability with Height Structured, Random, Spatial Distributions, *Theoretical Population Biology*, 54, 213–226, 1998.
- Lischke, H., Zimmermann, N. E., Bolliger, J., Rickebusch, S., and Löffler, T. J.: TreeMig: A forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale, *Ecological Modelling*, 199, 409–420, 2006.
- Löffler, T. J. and Lischke, H.: Incorporation and influence of variability in an aggregated forest model, *Natural Resource Modeling*, 14, 103–137, 2001.
- Moorcroft, P. R., Hurtt, G. C., and Pacala, S. W.: A Method for Scaling Vegetation Dynamics: The Ecosystem Demography Model (ED), *Ecol. Monogr.* 71, 557–586, 2001.
- Smith, B., Wårlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., and Zaehle, S.: Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model, *Biogeosciences*, 11, 2027–2054, 2014.

Table 3: Simulations of four model versions with increasing complexity were compared. The model versions differ in whether they (1) use the pre-structuring to bioclimate types, (2) do simulations on two layers and (3) apply dynamic associations between the two layers, i.e. allow for splitting and merging of elements on the non-spatial layer. 1L-ORG refers to the original one-layer approach with the original bioclimate driver. 1L-PB introduces the averaging of the bioclimate drivers according to the bioclimate types, but still runs on one layer. 2L-NDA applies the averaging and runs on two layers, albeit without dynamic associations. 2L, finally, refers to the full TreeMig-2L model with two layers and with dynamic associations.

	Bioclimate types	Two layers	Dynamic associations
1L-ORG	no	no	–
1L-PB	yes	no	–
2L-NDA	yes	yes	no
2L	yes	yes	yes

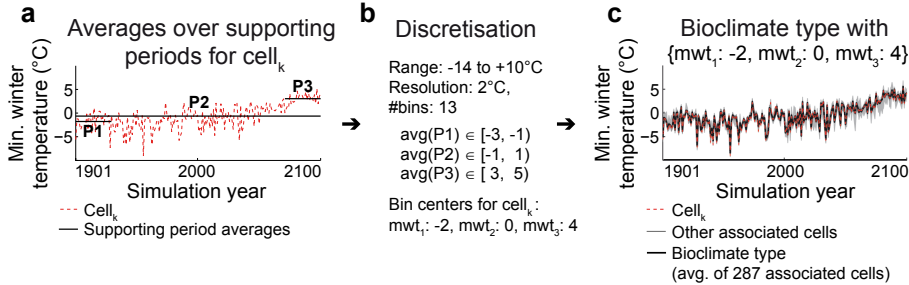


Figure 3: Visualisation of the pre-structuring into bioclimate types on the example of the minimum winter temperature (Min. winter temperature), one of TreeMig’s three bioclimate drivers. **(a)** The minimum winter temperature driving cell<sub>k</sub> is averaged for each of the supporting periods (here P1: 1901–1930, P2: 1901–2100, P3: 2071–2100). **(b)** The range of the minimum winter temperature (−14°C to +10°C) is discretised into 13 bins with a resolution of 2°C (as e.g. done for E3, the set of bioclimate bins with the coarsest resolution – see e.g. Table 2). The averages of the supporting periods P1–P3 for cell<sub>k</sub> are classified according to these bins. **(c)** Cells whose averages fall into the same bin in each of the supporting periods for each of the bioclimate drivers are classified into the same bioclimate type. The bioclimate driver (here the minimum winter temperature) of the bioclimate type is calculated as the average (black line) of its 287 associated cells (grey lines).

# Upscaling with the dynamic two-layer classification concept (D2C): TreeMig-2L, an efficient implementation of the forest-landscape model TreeMig

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## Abstract

Models used to investigate impacts of climatic changes on spatio-temporal vegetation dynamics need to balance required accuracy with computational feasibility. To enhance the computational efficiency of these models, upscaling methods are required that maintain key fine-scale processes influencing vegetation dynamics. In this paper, an adjustable method – the dynamic two-layer classification concept (D2C) – for the upscaling of time- and space-discrete models is presented. D2C aims to separate potentially repetitive calculations from those specific to single grid cells. The underlying idea is to extract processes that do not require information about a grid cell's neighbourhood to a reduced-size non-spatial layer, which is dynamically coupled to the original two-dimensional layer. The size of the non-spatial layer is thereby adaptive and depends on dynamic classifications according to pre-specified similarity criteria.

I present how D2C can be used in a model implementation on the example of TreeMig-2L, a new, efficient version of the intermediate-complexity forest-landscape model TreeMig. To discuss the trade-off between computational expenses and accuracy, as well as the applicability of D2C, I compare different model stages of TreeMig-2L via simulations of two different application scenarios. This comparison of different model stages demonstrates that applying D2C can strongly reduce computational expenses of processes calculated on the new non-spatial layer. D2C is thus a valuable upscaling method for models and applications in which processes requiring information about the neighbourhood constitute the minor share of the overall computational expenses.

## 1 Introduction

Impact studies of climatic changes on spatio-temporal vegetation dynamics are often conducted with so-called dynamic vegetation models ([DVMs](#)). DVMs are mainly implemented as time- and space-discrete models, simulating ecological processes that are key to vegetation dynamics, such as establishment, growth and mortality, usually under consideration

of biotic and abiotic influences (see e.g. Snell et al., 2014). As all models do, DVMs need to balance accuracy with computational feasibility and parametrisation requirements (Huntley et al., 2010; He et al., 2011). Modelled processes and their level of detail vary among DVMs, with a close link to the trade-off between spatial resolution and spatial extent of the simulation area. DVMs simulating small-scale processes with a fine spatial resolution ( $< 1 \text{ km}^2$ ) often have large computational expenses. Therefore, they can only operate on much smaller spatial extents than models with coarser resolution that neglect small-scale heterogeneity (see examples listed in Snell et al., 2014). Although there is a steady increase in the spatial extents that small-scale models can be applied on, due to increasing computational capacities and cost reductions via pure computational methods (e.g. parallelisation techniques), there is still a gap in what can be studied with small- and with large-scale models. One of the main problems is that the spatial resolution on which a process is simulated can markedly influence simulation results. Using a coarser spatial resolution to enable an increase in the spatial extent therefore risks introducing strong biases, such as replacing rare with dominant forest types (He et al., 2011), or overestimating dispersal distances and population sizes (Bocedi et al., 2012). Thus, there is a need to develop upscaling methods that maintain the required fine resolution for key small-scale processes (Bocedi et al., 2012).

Many upscaling methods have been proposed and applied in the context of ecological modelling (see e.g. Urban et al., 1999; Lischke et al., 2007; Auger et al., 2012). Most of these methods seek to aggregate small-scale information to a coarser scale. Aggregations can thereby be temporal, spatial or thematical with regards to the representation of the modelled entities, i.e. regarding simulated processes or the simulated processes and state variables. When the fine spatio-temporal resolution should be maintained (as recommended by Bocedi et al., 2012), remaining possibilities for cost reductions are thus thematical thus can only change the representation of the modelled entities. One example finding broad application in DVMs is the aggregation of individuals with similar properties into cohorts (e.g. Scheller and Mladenoff, 2004; Smith et al., 2014). With cohorts solely one representative calculation, instead of multiple replicate calculations, needs to



be conducted. Another more comprehensive example is the approximation of entire grid cell populations. Height-structured distributions (Lischke et al., 1998), as well as size- and age-structured approximations (Moorcroft et al., 2001), can be applied to upscale individual-based, stochastic models. By aggregating individuals of forest patches influenced by small scale stochastic processes, such approximations allow to dramatically reduce the number of calculations required to determine the vegetation dynamics in a grid cell. Both examples, cohorts and structured approximations, utilise similarities for within grid cell aggregations. The upscaling method presented in this paper – the dynamic two-layer classification concept (D2C) – is based on a more extensive similarity approach aiming to combine different grid cells with similar properties.

The motivation for D2C stems from the assumption that spatially independent locations experiencing similar environmental conditions likely accommodate similar vegetation compositions. Similar vegetation compositions, in turn, can lead to similar, potentially redundant calculations in simulations with DVMs. Especially time- and space-discrete DVMs will entail replicate calculations when different grid cells share similar state variables and drivers for long periods of time. D2C aims to avoid replicate calculations while still allowing for diverging and novel vegetation compositions. For this purpose, grid cells are dynamically classified into groups with similar properties, for which subsequently only one representative calculation is conducted. The fact that time- and space-discrete DVMs can entail replicate calculations for similar vegetation compositions has already been used to decrease computational expenses in finite state individual based models with a simple age based succession (Yang et al., 2011) and for spatially-explicit models without spatial linkage (Nabel and Lischke, 2013). These two cases can be regarded as restricted application cases and will be picked up in the discussion.

In the following I will first outline the basic principles of D2C. Afterwards, I present how D2C can be applied on the example of TreeMig-2L, a new, efficient implementation of the intermediate-complexity DVM TreeMig (Lischke et al., 2006). Subsequently, the usefulness of this D2C implementation is examined by means of two different application scenarios.

## 2 The dynamic two-layer classification concept (D2C)

The target models for D2C are complex, two-dimensional, spatially linked time- and space-discrete DVMs. The aim of D2C is to increase the computational efficiency of a DVM through identification and elimination of redundant calculations. Redundant calculations can occur in simulations with a DVM because grid cells with comparable species' composition and abundances, i.e. comparable values in the cells' state variables, tend to follow the same successional paths, provided that (1) their abiotic drivers follow the same temporal pathways and (2) none of the grid cells is subject to any cell-specific deviations (e.g. caused by immigration). To identify and eliminate redundant calculations in a DVM, D2C uses two different layers (Fig. 1) onto which the processes of the DVM are divided. The first layer is the original two-dimensional layer containing all grid cells. On this layer only those processes of the model are simulated that use information on the spatial position of a cell relative to other cells in the simulation area. One example for such a spatial process is seed dispersal using source and sink positions. The second layer is a new associated non-spatial layer, on which all other processes are simulated, for example, competition, growth and seed production. Each element on the non-spatial layer represents a certain type of cells on the two-dimensional layer, characterised by prevailing abiotic conditions and momentary species' composition and abundances. Each cell on the two-dimensional layer is thus associated with one element on the non-spatial layer (visualised in Fig. 1 with numbers). The size of the non-spatial layer is adaptive and depends on a dynamic classification according to similarity criteria on abiotic and biotic properties. These similarity criteria need to be pre-specified and are key to D2C because they define a discretisation of the abiotic drivers and the biotic state-space. Spatial processes simulated on the two-dimensional layer can lead to violations of the similarity criteria because they can entail cell-specific deviations from otherwise similar grid cells, for example, when a new species is dispersed to some but not all cells represented by one element. Thus, spatial processes can lead to changes in associations and can necessitate adding new elements to the non-spatial layer (see e.g. Fig. 1).

Elements on the non-spatial layer, on the other hand, can be merged when they satisfy all similarity criteria.

To apply D2C, the processes of a model and its state variables need to be separated onto the two layers. Additionally, the exchange of status information between cells on the two-dimensional layer and their associated elements on the non-spatial layer needs to be specified. The assignment of processes and the definition of the interface between the two layers are critical steps because the information directed from different cells to their associated element is used to test if the biotic similarity criteria are violated which would necessitate a split of the element.

The potential for reductions of computational expenses with D2C will be influenced by three aspects: (1) the non-reducible base load due to processes simulated on the two-dimensional layer; (2) the ratio of cells on the two-dimensional layer and elements on the non-spatial layer, which is strongly influenced by the specified similarity criteria; (3) the overhead introduced for managing elements on the non-spatial layer, associations between the two layers and the exchange of status information between the layers.

### **3 Methods**

#### **3.1 Implementation of TreeMig-2L**

In this section I outline how D2C can be applied on the example of TreeMig-2L, a two-layer implementation of the forest-landscape model TreeMig. Further, and more detailed information on the implementation of TreeMig-2L is given in Supplement Sect. A.

##### **3.1.1 TreeMig**

TreeMig is an intermediate-complexity DVM simulating local stand dynamics of multiple competing tree species. In addition to local dynamics, TreeMig allows for the explicit simulation of tree species' migration, with the rare advantage of including seed production, seed dispersal and subsequent regeneration processes (Thuiller et al., 2008). TreeMig simula-

tions require time series of three different annual bioclimate drivers: the minimum winter temperature, the sum of daily mean temperatures above 5.5 °C, and an index denoting the severity of droughts (Lischke et al., 2006; Nabel et al., 2014). [These drivers are derived from monthly averaged temperatures and monthly precipitation sums \(see e.g. Supplement Sect. B\).](#) TreeMig's state variables are population densities of tree species in a constant number of height classes per grid cell (Lischke et al., 2006). Additionally, TreeMig stores the density of currently available seeds per tree species, representing the seed bank of a cell.

The TreeMig two-layer implementation described in the following – TreeMig-2L – is implemented in Fortran and based on TreeMig-Netcdf 2.0 (Nabel et al., 2014). TreeMig-Netcdf 2.0 includes all processes described in the original TreeMig version (Lischke et al., 2006) with the growth response curve amendments described in Rickebusch et al. (2007), the minimum population density thresholds described in Nabel et al. (2013) and the climate extrapolation method preserving spatial autocorrelation described in Nabel et al. (2014).

### 3.1.2 Assigning processes to the two layers

Most of the processes simulated with TreeMig do not require information on the position of the cell relative to other cells on the grid: competition for light, growth, mortality and production of seeds in a cell only use information that is independent of other cells. Therefore, these processes can be simulated on the new non-spatial layer (see Fig. 2). In TreeMig-Netcdf 2.0, the only process which requires information on the position of a cell is seed dispersal. Other processes which would require information on the neighbourhood are, for example, spatially connected disturbances, [such as snow avalanches](#) (e.g. Zurbriggen, 2013). In TreeMig-Netcdf 2.0, however, spatially connected disturbances are not represented. Thus, seed dispersal is the only process in TreeMig-2L that has to be simulated on the two-dimensional layer. Yet, to enable efficient simulations on two layers, associations between cells on the two-dimensional layer and elements on the non-spatial layer need to be as long-lived as possible. This means that re-merging of elements that resulted from a very recent split needs to be prevented, and splits should only be conducted if they entail

actual changes in species' compositions. The availability of seeds of a species does not necessarily have to lead to changes in the species' composition, because a species might not be able to regenerate in a cell. Therefore, the entire regeneration process was assigned to the two-dimensional layer (Fig. 2) in order to only induce splits when newly dispersed seeds actually establish.

### 3.1.3 Architecture of TreeMig-2L

When designing the architecture of TreeMig-2L the two main requirements were an efficient organisation of the elements on the non-spatial layer and a fast exchange of status information between the two layers.

One of the challenges for an efficient organisation ~~was that the number of of the~~ elements on the non-spatial layer was that the number of elements is not known in advance ~~but, because it~~ is an emergent property of the simulation. ~~Therefore, the~~ To allow for an arbitrary number of elements on the non-spatial layer, the elements are stored in linked lists, instead of using an array structure with a predetermined fixed size, as usually done in space discrete DVMs. However, using one large linked list, and comparing all elements ~~would presumably with each other, would~~ be very inefficient ~~. Thus, to and would lead to a large organisational overhead.~~ To reduce the organisational overhead required for ~~element comparison~~ the comparison of elements during runtime, TreeMig-2L uses several linked lists ~~are used~~, and only elements in the same list are compared. To ~~pre-define which element is stored in which list~~ define the number of linked lists, the fact is used that the bioclimate drivers are an input to TreeMig and can thus be used ~~in advance~~ to pre-structure a simulation area (~~for a detailed example see see~~ Fig. 3 for an example, and Supplement Sect. A.2 for additional information). To pre-structure a simulation area, grid cells ~~with comparable bioclimate drivers are clustered to~~ are classified into "bioclimate types". Each bioclimate driver is thereby discretised according to a set of pre-defined "bioclimate bins" (see e.g. Table 2). ~~In addition to the bins, a~~ To limit the number of possible bioclimate types and to save computation time, the discretisation is only applied for temporal averages of the bioclimate drivers on a pre-defined set of "supporting periods" ~~has to be defined. For~~

the clustering to bioclimate types, one average for. For each cell, each supporting period and each bioclimate driver is calculated and compared among all cells of the simulation area. Cells whose one average per driver and supporting period is calculated. Two cells are classified into the same bioclimate type, if their averages fall into the same bioclimate bins for all supporting periods are clustered into the same bioclimate type. The resulting bioclimate types constitute the static structure of the non-spatial layer bin for each driver and supporting period, whereby the bioclimate bins can differ in between supporting periods. For each bioclimate type existing bioclimate type, i.e. each type with which at least one cell is associated, an own linked list is used to store elements on the non-spatial layer. The bioclimate influence drivers for a bioclimate type is thereby are calculated as the average averages of all associated cells for each point in time.

For organisation and information exchange, each bioclimate type has a pointer—a data type allowing direct access—to the first element in its list. In addition, each cell on the two-dimensional layer has a pointer to the element with which it is currently associated; to allow for a direct, and thus fast, exchange of status information. Because an An element can be associated with a changing number of cells, elements only track therefore, an element only tracks how many but not which cells are currently associated with it (see Fig. 2). The communication information exchange between the layers is asymmetric induced by the cells. Each cell on the two-dimensional layer accesses required information from its currently associated element. For seed dispersal calculations the density of produced seeds per species is required. For regeneration, additionally, the current light and bioclimatic conditions bioclimatic conditions and the light distribution of the lowest height class need to be accessed, which because they influence the density of newly germinated seeds per species (see Lischke et al., 1998, 2006). Newly germinated seeds are used to determine if splits are necessary (see Sect. 3.1.4). After possibly required dynamic changes in associations between the layers, cells push their germinated seed densities to the currently associated element and each element on the non-spatial layer calculates the average of the germinated seed densities received from its associated cells. Averaged densities of germinated seeds falling below a pre-specified presence threshold are thereby set to zero.

### 3.1.4 Dynamic associations

In order to account for spatial processes resulting from seed dispersal, associations between the two-dimensional and the non-spatial layer need to be dynamic. In a TreeMig-2L simulation, elements on the non-spatial layer can be split up or merged. For details on the execution sequence of a TreeMig-2L simulation see Supplement Sect. A.3.

Splitting, and thus introduction of new elements on the non-spatial layer is required as soon as the density of germinated seeds among any two cells associated with the same element is considered not similar enough. In TreeMig-2L, similarity in the density of germinated seeds can be defined by a set of thresholds. The simplest possible set consists of a single threshold which defines presence, i.e. species with a germinated seed density below this threshold are assumed to not have germinated. However, other thresholds are also possible, for example dividing sparse occurrences from more frequent ones. If the density of germinated seeds of any two cells associated with the same element fall on different sides of any of these thresholds for a single species, a split is required. One determinant for the efficiency of a TreeMig-2L simulation is assumed to be the number of considered splits. When  $k - 1$  thresholds are specified and  $n$  species are simulated,  $k^n$  different combinations could possibly entail splits. In TreeMig-2L this trade-off between accuracy and possible splits is approached by only not considering splitting for all species, but only for a set of species previously specified as species to be tracked. Deviations in the germinated seed densities of species which are not tracked are thus not tested in a simulation i.e. for tracked species differences in the number of germinated seeds among grid cells associated with the same element can lead to splits. For untracked species, in contrast, the number of germinated seeds is not compared among grid cells and deviations can thus not lead to splits. Apart from the splitting step, all species are treated the same, in particular the number of germinated seeds on an element is calculated as the average over all associated cells for each species, no matter if tracked or untracked. As a consequence, untracked species might be represented less accurately, which can feedback on other species via

competition. Therefore, species that are expected to change their distribution in the course of the simulation should be defined as tracked species.

Merging of elements is possible as soon as two elements belonging to the same bioclimate type are similar enough. The state variables stored in the elements on the non-spatial layer are population densities per species for a fixed set of height classes. In TreeMig-2L, two elements belonging to the same bioclimate type are regarded similar enough, when deviations between each pair of their population densities do not exceed a similarity threshold pre-specified for each of the height classes. To avoid immediately re-merging of elements that were recently split up, newly germinated seed densities are also compared. As opposed to splitting, merging of elements on the non-spatial layer potentially decreases accuracy. Moreover, there is a trade-off between computational expenses involved with merging and the reduction of repetitive calculations caused by similar elements. Therefore, merging is only performed after a pre-defined number of iterations in TreeMig-2L.

## 3.2 Simulations with TreeMig-2L

### 3.2.1 Expected benefit of the D2C implementation

Previous TreeMig simulations were conducted with spatial resolutions ranging from cell side lengths of 25 m to 1 km and spatial extents ranging from single cells up to 77 000 km<sup>2</sup>. The number of simulated interacting tree species ranged from ~~1~~one up to 31 species and simulation areas had differing spatio-temporal complexity (see e.g. Epstein et al., 2007; Nabel et al., 2013; Nabel and Lischke, 2013; Zurbruggen et al., 2014). Such differences in the simulation settings are expected to influence the benefit of the D2C implementation, because they control two of the three aspects assumed to be most important (see Sect. 2): (1) the non-reducible base load due to processes simulated on the two-dimensional layer, and (2) the ratio of grid cells and elements on the non-spatial layer, whereby the latter is strongly influenced by the number of bioclimate types.

The number of bioclimate types is, for example, expected to be large when the simulation area has a high spatio-temporal complexity, i.e. a high heterogeneity in its bioclimate



drivers. The number of bioclimate types will also be ~~influences~~-influenced by the spatial extent of a simulation area: a larger extent, up to a certain point, potentially leads to a larger number of types, however, there might be a threshold beyond which the number of already contained bioclimate types exceeds the number of newly added types. A similar effect is expected for the spatial resolution: bioclimate drivers in a cell are always averages and with finer resolution fewer bioclimate extremes might be smoothed out, leading to a larger number of required bioclimate types. However, especially in areas with a homogeneous bioclimate, a finer resolution might entail a larger number of similar grid cells, increasing the expected benefit of a D2C implementation. A finer resolution, on the other hand, will increase the computational expenses for seed dispersal. In TreeMig, seed dispersal is simulated from the perspective of the source cell, providing seeds to sink cells according to a pre-calculated truncated probabilistic density function (see Supplement of Lischke et al., 2006). The number of sink cells thereby depends on the spatial resolution. A fine resolution implies a large number of sink cells, causing large computational expenses on the two-dimensional layer, and therefore a large base load. A fine resolution thus can diminish the benefit of a D2C implementation. Further aspects which can influence the benefit of the D2C implementation are the number of tracked species, the splitting and merging thresholds, and the number of iterations after which merging is considered.

### 3.2.2 Application scenarios

TreeMig-2L simulations were conducted for two different application scenarios  $\div$  (A1 and A2), pertaining to different regions of Switzerland. Figure 4 shows the location of their simulation areas. Scenario A1, in the flatter areas of Northern Switzerland, stems from a study with a preliminary TreeMig-2L version without dynamic associations between the layers (Nabel and Lischke, 2013). Scenario A2, a north-south transect across the Swiss Alps, stems from a study investigating the influence of interannual bioclimate variability in simulations of the northwards migration of *Ostrya carpinifolia* Scop. (European Hop Hornbeam) with TreeMig-Netcdf 1.0 (Nabel et al., 2013). An in-depth description of the scenarios can be found in Supplement Sect. B.

The two scenarios were selected because they strongly differ in their simulation settings (see Table 1 for their main characteristics). Application scenario A1 has a more homogeneous simulation area and a finer spatial resolution than A2. Therefore, on one hand, a more beneficial ratio between the number of cells on the two-dimensional layer and the number of bioclimate types is expected for A1. On the other hand, due to the finer spatial resolution a higher base load is expected for A1 than for A2.

The tracked species in scenario A2 is naturally the investigated migrating species (*Ostrya O. carpinifolia*). The other 21 competing species simulated in this application scenario were not tracked. For A1 four out of the 31 simulated competing species were selected as tracked species: *Quercus pubescens*, *O. -carpinifolia*, *Larix decidua* and *Pinus silvestris**sylvestris*. These species were selected because they have the highest drought tolerance indices in TreeMig. With increasing drought severity (and increasing temperatures), these species are therefore expected to extend their spatial distributions, whilst the other species might be less effected or have declining distributions. For both scenarios, merging was considered every 100 simulation years and the same splitting and merging thresholds were used (for further details and sensitivity tests see Supplement Sect. C).

Both application scenarios were driven by bioclimate time series derived from SRESA1B (Nakicenovic et al., 2000) scenario projections, though from different models and down-scaled with different observational data (see Supplement Sect. B). To cover the entire simulation time span of the examples, a stochastic extrapolation method accounting for the spatial correlation of bioclimate fluctuations was used (Nabel et al., 2014).

### 3.2.3 Pre-structuring of the simulation areas

Bioclimate types for both application scenarios were derived with the same sets of bioclimate bins: E1, E2 and E3 (Table 2). For both scenarios three sampling supporting periods were averaged: the first 30 (A1: 1961–1991; A2: 1901–1931) and the last 30 years (both: 2071–2100), as well as the whole time span (A1: 1961–2100; A2: 1901–2100).

### 3.2.4 Conducted simulations

Simulations were conducted with all three sets of bioclimate types (Table 2). To account for the stochasticity involved with the extrapolation of the bioclimate drivers multiple repetitions of the simulations were performed. Simulations with application scenario A1 were repeated five times. Simulations with scenario A2, ~~requiring having much less grid cells and requiring only~~ one-tenth of the CPU time of scenario A1<sup>1</sup>, were repeated 100 times. To disentangle the effects of the pre-structuring ~~to into~~ bioclimate types and of ~~the dynamic association dynamic associations~~ between the layers, ~~three different model versions were used simulations of four model versions with increasing complexity were compared~~ (Table 3): (1) ~~the full TreeMig-2L model with two layers and with dynamic associations (2L);~~ 1L-ORG: the original one-layer approach with the original bioclimate driver. Simulations with this version were conducted to obtain reference values for the comparisons. (2) 1L-PB: a model version ~~with in which~~ bioclimate types were used to derive averaged bioclimate drivers, but in which all processes were still simulated on one layer. Simulations with this version thus isolate the loss in accuracy due to the averaging of the bioclimate drivers. (3) 2L-NDA: a model version using bioclimate types and two layers but ~~without dynamic associations(2L-NDA)no dynamic associations~~, i.e. ~~with only one element for in this version~~ each bioclimate type ; (3) a model version using the pre-structured bioclimate driver but ~~simulating all processes on one layer (1L-PB)~~. Finally, to obtain reference values, also ~~simulations with the original bioclimate driver and the original one-layer approach were conducted (1L-ORG)~~ has only one element. Because dynamic associations are switched of, differences in the number of germinated seeds between cells associated with the element ~~do not lead to splits~~, and a species introduced in one of the cells will thus occur in all associated cells. Therefore, simulations with this version can elucidate if there is a necessity to track species. Furthermore, having no costs for splitting and merging, this version can

<sup>1</sup>The average ~~CPU time CPU time~~ with the original one-layer approach (1L-ORG) was 50 353 s for A1 (average of five simulations with  $\sigma = 784$  s) and 5195 s for A2 (average of 100 simulations with  $\sigma = 38$  s).

be used to derive the maximum CPU time reduction that can be achieved. (4) 2L: the full TreeMig-2L model with two layers and with dynamic associations.

### 3.2.5 Applied performance measures

The performance of the D2C implementation was assessed by two means: an accuracy measure and the required CPU time<sup>2</sup>. To measure accuracy, different output variables were compared with a similarity coefficient (SC – Eq. 1) already used for intra-model comparisons in previous studies (e.g. Lischke et al., 1998; Nabel et al., 2013).

$$SC_y = 1 - \frac{\sum_i^{\text{cell}} |D_{\text{sum}_i}|}{\sum_i^{\text{cell}} S_{\text{sum}_i}} \quad (1)$$

$SC_y$  for a year  $y$  ranges from 0.0 (no similarity) to 1.0 (identical output) and is reciprocally dependant on the ratio of the sum of an output variable of two simulations  $S_{\text{sum}_i}$  and their differences  $|D_{\text{sum}_i}|$  summed over all cells of the simulation area. The SC was used to compare different variables among simulations with the 1L-ORG model version and model versions using bioclimate types (Table 3). Each comparison was thereby conducted with simulations using the same pseudo-random number stream to extrapolate the bioclimate driver. For both application scenarios, the SC for the sum of the biomass of all species ( $SC_{\text{sum}}$ ) and the SC of the biomass per species ( $SC_{\text{spec}}$ ) were calculated, for A1 every century and for A2 every 50 years. For A2 simulations, furthermore, the SC of the biomass of *O. carpiniifolia* ( $SC_{\text{OC}}$ ) was calculated for each year.

Two further measurement were taken to assess the applicability of D2C in view of the three aspects listed at the end of Sect. 2. Firstly, the maximum number of elements reached during a simulation was tracked, here referred to as the peak element-cell ratio~~was tracked in each simulation~~. Secondly, the ratio of the time spent on different processes was profiled with callgrind, a tool which records function calls in a program during runtime (Weidendorfer, 2008).

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<sup>2</sup>CPU time was measured with the intrinsic Fortran procedure CPU\_TIME. All simulations were conducted on 2.8 GHz AMD Opteron CPUs.

## 4 Results and discussion

### 4.1 Pre-structuring of the simulation areas

For both application scenarios the number of bioclimate types resulting from the pre-structuring was considerably smaller than the number of grid cells. However, the resulting number of types differed in absolute as well as relative terms (Table 4). The simulation area of application scenario A1 always contained fewer bioclimate types than A2 (E1:  $\sim$  factor 2; E2 and E3:  $\sim$  factor 4). Moreover, the resulting ratio of bioclimate types to grid cells was much smaller (E1:  $\sim$  factor 20; E2 and E3:  $\sim$  factor 40). As suggested in Sect. 3.2.1, this is due to the higher spatial homogeneity, the finer spatial resolution and the smaller spatial extent (and thereby smaller bioclimatic range) of the simulation area of scenario A1 compared to the simulation area of A2. A2's simulation area is divided in a larger number of bioclimate types, with two-thirds as many bioclimate types as cells for the ~~finest~~ set of bioclimate bins with the finest resolution (E1). For this set, thus, more than half of the cells end up with their own bioclimate type. For an example of the distribution of numbers of cells to bioclimate types see Supplement Fig. C-4.3.

Averaging of the bioclimate drivers of associated cells to obtain the drivers for the bioclimate types led to small but visible deviations ~~in the bioclimate~~ (e.g. Fig. ??-3c and Supplement Sect. C). These ~~bioclimate deviations~~ deviations in the bioclimate driver entail deviations in the simulation results when comparing to results from one layer simulations, i.e. simulations with the original grid cell-based bioclimate driver (see column 1L-PB in Table 5 and Sect. 4.2). ~~Coarser discretisation into bioclimate bins~~ Using bioclimate bins with a coarser resolution thereby led to larger ~~bioclimate deviations~~ deviations in the driving bioclimate and, thus, to larger deviations in the simulation results (Table 5). In the current implementation of TreeMig-2L these deviations can only be reduced using a finer discretisation into bioclimate bins or more supporting periods. The dynamic association of cells to elements on the non-spatial layer cannot reduce this error, because the bioclimate driver is not processed on the single elements but on the bioclimate types. The pre-structuring of the simulation area is fundamental for the efficiency of TreeMig-2L, because the thereby obtained

static structure is used for the organisation and maintenance of the elements on the non-spatial layer (see Sect. 3.1.3). However, averaging of the bioclimate in the pre-structuring step could potentially be replaced by a dynamic approach. In a dynamic approach, pre-processing of the bioclimate drivers could be re-transferred to the two-dimensional layer. In each time step of the simulation the bioclimate drivers of each element could then be calculated by averaging the bioclimate of the presently associated cells. Whilst this could reduce deviations in the simulation results compared to original one-layer simulations, it would also require more computations and thus could lead to less CPU time reductions (see Sect. 4.2.2).

Applying bioclimate types in their current static form is reminiscent of the stratified sampling methods used in explicit spatial upscalings of single site models (Bugmann et al., 2000), and is comparable to the ecoregions used in the forest-landscape model LANDIS (see e.g. Mladenoff and He, 1999; Scheller and Mladenoff, 2004). Similarly to cells associated with the same bioclimate type in TreeMig-2L, cells associated with the same ecoregion in LANDIS share important process rates influencing establishment and biomass development (e.g. Scheller and Mladenoff, 2004). Like bioclimate types in TreeMig-2L, ecoregions in LANDIS do not need to be contiguous but can be distributed in space (He et al., 1999). Not demanding contiguousness is an important advantage over other upscaling methods, which are often based on local spatial aggregations, such as naive upscalings that decrease the spatial resolution of a simulation area (as described in Bocedi et al., 2012). The possibility for bioclimate types, which are defined over similarity and not over spatial proximity, to be arbitrarily distributed in space, potentially reduces the number of required types and, even more important, prevents errors involved with inappropriate averaging of neighbouring grid cells. Thus, as opposed to local spatial aggregations, bioclimate types have the advantage that they conserve the spatio-temporal heterogeneity to a large degree. Supplement Fig. C-7-6 gives an example for the conservation of spatial variability; Figs. ~~???~~3, C-5-4 and C-6-5 give examples for the conservation of temporal variability.

## 4.2 Performance of TreeMig-2L simulations

To evaluate the performance of TreeMig-2L, different performance measures (Sect. 3.2.5) were used to compare two-layer simulations using different bioclimate discretisations (Table 2) to one-layer simulations using the original bioclimate. To assess to what extent different approximations involved with D2C led to performance decreases, further simulations were conducted using two different pre-stages of the 2L implementation (Table 3). In addition, sensitivity test for splitting and merging thresholds, merging intervals and tracked species were conducted (see Supplement Sect. C).

### 4.2.1 Accuracy

The accuracy of TreeMig-2L was evaluated by comparing biomass distributions from simulations using different model versions with a similarity coefficient (SC) ranging from 0.0 (no similarity) to 1.0 (identical biomass distributions in space). Comparisons generally led to SCs in the upper range for all output variables (ranging from about 0.8 to about 1.0 – Table 5) and for both application scenarios. The level of the SC was thereby largely determined by the ~~selected resolution of the applied~~ set of bioclimate bins, ~~with coarser sets leading to smaller~~ the coarser the resolution, the smaller the SCs for all variables (differences in the SCs of up to 0.14 – Table 5).

To be able to assess the relevance of deviations from 1.0 in the SCs, results from 1L-ORG simulations using different pseudo-random number streams to extrapolate the bioclimate driver were compared with each other, i.e. the deviation from 1.0 in the SC due to interannual bioclimatic variability was calculated (see Supplement Sect. C.2). The only SCs which were markedly larger than the SCs resulting from these 1L-ORG intra-comparisons were SCs from comparisons with E3 bioclimate types (compare Table 5 and Table C.1).

In all cases, SCs from comparisons between 1L-ORG and 2L simulations were very close to SCs from comparisons of 1L-ORG and 1L-PB simulations (differences in the SCs  $\leq 0.01$ ). This indicates that the deviation in 2L simulations are mainly due to the averaging of the bioclimate drivers. SCs comparing 2L and 1L-ORG were, in particular, larger than

SCs comparing 2L-NDA and 1L-ORG (differences in  $SC_{\text{spec}}$  up to 0.04 and in  $SC_{\text{OC}}$  up to 0.21), indicating the importance to track migrating species. The four tracked drought tolerant species in application scenario A1 and *Ostrya carpinifolia* in application scenario A2 seem to be good indicators to test for required splits. Sensitivity tests showed that fewer tracked species increased the error (up to 0.03 smaller  $SC_{\text{spec}}$  values) and more species only slightly decreased it (only  $\sim 0.01$  larger  $SC_{\text{spec}}$  values – see Supplement Fig. C.14.13). The sensitivity tests further showed that the choice of merging and splitting thresholds had only limited impact on the SCs. Strong differences in the SC were only observed for simulations that tested elements for merging after a decade instead of after a century (see Supplement Sect. C).

The temporal development of  $SC_{\text{spec}}$  was comparable among simulations with the three sets of bioclimate types (E1–E3) for all model versions (2L, 1L-PB and 2L-NDA) and for both application scenarios.  $SC_{\text{spec}}$  decreased in the transient phase of climate change (from around 2000 on) and stabilised after a few centuries (Fig. 5 and Supplement Sect. C). The stabilisation on a lower level is mainly due to a stronger impact of differences in the drought index between bioclimate types and single cells due to overall larger drought indices in the second half of the 20th century (see Supplement Figs. C.5.4 and C.6.5). A comparable effect resulted for inter-comparisons of 1L-ORG simulations (see Supplement Sect. C.2). While the temporal development in  $SC_{\text{spec}}$  was comparable among all model versions, trajectories resulting from 2L-NDA simulations differed from those resulting from 2L and 1L-PB simulations for  $SC_{\text{OC}}$  (Fig. 6). Having no dynamic associations,  $SC_{\text{OC}}$  for 2L-NDA simulations mainly reflects changes in the bioclimate over time (see Supplement Sect. C.2 for details).

Being a single index for the whole simulation area, the SC is a rough indicator for the similarity between two simulations and could in particular conceal biases in the spatial biomass distribution. Furthermore, depending on the research question, other aspects could be more important than absolute biomass values per grid cell, especially when studying the migration of a species. Therefore, simulations of application scenario A2 were additionally compared focussing on the migration of the tracked species. Comparisons of the spatial spread



of *O. carpinifolia* showed a reasonable approximation of 1L-ORG simulations by 2L simulations with all bioclimate discretisations (Fig. 7 and Supplement Fig. C-12.11).

In summary, SCs comparing 2L and 1L-ORG simulations were within the magnitude of deviations due to interannual bioclimatic variability and deviations were smaller than reported for previous upscalings (e.g. Lischke et al., 1998). Furthermore, comparisons of the spatial spread of *O. carpinifolia* between 1L-ORG and 2L simulations did not indicate spatial biases and comparisons with 2L-NDA simulations underlined the necessity to track migrating species.

#### 4.2.2 Computational expenses

Simulations with two layers led to considerable reductions in CPU time for both application scenarios (Table 5). When considering the ratio between the number of bioclimate types and the number of cells in the simulation areas (Table 4), larger CPU time reductions could have been expected for scenario A1 than for A2. Yet, the actual reductions are not systematically larger for A1 (E1: 52.9%, E2: 56.0%, E3: 57.8%) than for A2 (E1: 32.6%, E2: 65.6%, E3: 84.7%). To a small part this is due to increased dynamics in the number of elements on the non-spatial layer in A1 compared to A2 (Fig. 8), leading to a comparable magnitude in the peak element-cell ratio for both application scenarios (Table 5). However, sensitivity tests for the application scenario A1 showed that changes in the number of tracked species and in the merging interval leading to large changes in the peak element-cell ratio did not lead to notable changes in CPU time reductions (see Supplement Sect. C.3.1). Moreover, the small difference in CPU time reductions among A1 simulations with the three sets of bioclimate types in combination with notable differences in the peak element-cell ratio (Table 5) also indicates that the peak element-cell ratio is not the main cause for the limitation in the CPU time reduction for A1.

The actual main cause is revealed when looking at the percentage of executed instructions for the different processes (Table 6): the percentage of instructions spent on seed dispersal was simply much larger for A1 than for A2. 1L-ORG simulations for application scenario A1 spent about 45% of executed instructions on seed dispersal and only about

50 % on adult dynamics, i.e. on processes simulated on the non-spatial layer. A2 1L-ORG simulations, in contrast, only spent about 6 % of the executed instructions on seed dispersal and about 86 % on adult dynamics (Table 6). Differences in the execution ratios were already expected (see Sect. 3.2.1) because of the increased number of sink cells considered in seed dispersal calculations for the grid with 200 m cell side length in A1 compared to the grid with 1 km cell side length in A2. As a consequence, the base load that cannot be reduced with D2C was more than seven times larger for A1 than for A2.

For A2 differences in CPU time reductions were strongly driven by the applied set of bioclimate types. Sensitivity tests showed that splitting and merging thresholds as well as the merging interval were far less influential (Supplement Sect. C.3.2).

### 4.3 Applicability of D2C

In Sect. 2 three different aspects were hypothesised to influence the benefit of a D2C implementation: (1) the non-reducible base load, (2) the element-cell ratio, and (3) the organisational overhead. The implementation and the applications of TreeMig-2L confirmed the importance of these aspects. Differences in the benefit comparing application scenarios A1 and A2 demonstrated the key role of the first aspect – the non-reducible base load due to time spent with spatially linked processes (Table 6). The key role of this aspect is also underlined when comparing simulations including spatial linkages in this study to the simulations with a predecessor of TreeMig-2L in a study without spatial linkages by Nabel and Lischke (2013): simulations without spatial linkages entailed much larger reductions in CPU times. The second aspect – the number of elements on the non-spatial layer – was on one hand controlled by the number of bioclimate types derived in the pre-structuring (particularly for A2) and, on the other hand, by the number of tracked species (for A1). The number of bioclimate types, as well as the number of tracked species influenced the reductions in CPU time via the number of elements on the non-spatial layer. Compared to the first aspect, the second aspect played a minor role. The third aspect – the organisational overhead – only had a small contribution in TreeMig-2L (see Table 6), which was mainly possible due to the developed architecture: the pre-structuring ~~to~~ [te-into](#) bioclimate types and the asymmet-

ric relationship communication between cells and associated elements enabled an efficient maintenance of the dynamic non-spatial layer and the pointers kept in each cell enabled the direct access of the associated elements.

The three aspects can be used to assess the applicability of D2C for other dynamic vegetation models. ~~Most importantly will~~ The main determinant for the non-reducible base load ~~of a model be influenced by~~ is the number and complexity of processes requiring information on the neighbourhood of a grid cell, i.e. spatially linked processes. The number and complexity of spatially linked processes might also influence the number of required elements due to induced splits and will thereby also influence the organisational overhead for the maintenance of the non-spatial layer, not only due to the required splits but also due to the required information exchange between the layers. Thus, D2C might be less suitable for models with many complex and interacting spatially linked processes, such as LANDIS-II (Scheller et al., 2007), if used with several spatially linked extensions (e.g. Sturtevant et al., 2012). It should, however, be applicable for most models with few and simple spatially linked processes, such as TreeMig (provided a relatively coarse spatial resolution is used) and for spatially independent one-dimensional DVMs (sensu Fisher et al., 2010), such as ED (Moorcroft et al., 2001; Fisher et al., 2010) and most implementations of LPJ-Guess (e.g. Hickler et al., 2012; Smith et al., 2014). An upscaling of a one-dimensional DVM with D2C could perhaps free computational resources for the inclusion of a simple seed dispersal algorithm, which would be an important step towards the explicit simulation of migration. Simulating migration explicitly would be highly desirable (Neilson et al., 2005; Thuiller et al., 2008), which is also underlined by the results of this study comparing 1L-ORG and 2L-NDA simulations (see e.g. Supplement Fig. C-12.11).

Besides the number and complexity of the spatially linked processes, also properties of the local processes will influence the applicability of D2C: the concept will be suitable for a model in which local processes are rather deterministic, as in TreeMig, or in which the stochasticity in local processes is realised as patch replicates calculated and averaged for each iteration within a grid cell, as for example done in LPJ-Guess (Smith et al., 2001). For models with such properties, grid cells with similar values in the climatic drivers will tend to

also have comparable species' compositions, and these grid cells can thus be represented by the same element. D2C will be less suitable for a model in which stochasticity in the local processes is realised on the level of the grid cell, as in LANDCLIM (Schumacher et al., 2004), because stochasticity on the cell level entails diverging species' compositions and thus frequent splits of elements.

The implementation of D2C in a specific model will ultimately depend on the modelled processes, the model drivers and its state variables. Besides the assignment of the processes to the two layers and the specification of the exchanged information, various similarity criteria need to be specified controlling the composition and the dynamics of the non-spatial layer. For merging, for example, criteria need to be specified to determine when the state variables that are stored for an element are similar enough. Because TreeMig's state variables are real-valued population densities on a constant number of height classes, a set of similarity thresholds for the density in each height class was required for merging. A model with, for example, continuous height values for each individual (or cohort) and a discrete but arbitrary number of individuals would require the specification of similarity thresholds on both the continuous heights and the discrete individuals. For the special case of a model with bounded discrete state variables Yang et al. (2011) showed a very efficient technical solution with hash maps – data structures with unique key-value pairs enabling a fast lookup of associations – having a similar approach as D2C. Because the state variables are discrete and bounded, this method can aggregate cells with identical states (identical keys) and thus, no similarity criteria need to be specified. This method, however, will not be applicable whenever any state variable is continuous or unbounded because then possible states ~~can not~~ cannot be uniquely represented with a finite set of elements on the non-spatial layer. An infinite number of possible states necessitates the specification of similarity criteria and an active management of the associations between the two layers as provided by D2C.

## 5 Conclusions

The implementation of TreeMig-2L and the example simulations demonstrated that D2C can be applied to strongly reduce computational expenses for processes which do not require information on the spatial position of a grid cell relative to other grid cells. D2C is adaptable regarding the criteria used to define similarity for the drivers of a model and for its state variables. The implementation and application with TreeMig-2L indicated that these similarity criteria can be used to adjust the resulting discretisation errors. In the applications, no strong spatial biases were detected. Differences between the original one-layer model and the D2C implementation were in the magnitude of differences among simulations with the original model using different pseudo-random number streams to extrapolate the bioclimate driver, i.e. differences due to interannual bioclimate variability. A large advantage of D2C as opposed to static upscaling techniques is the possibility to track a migrating species and to account for novel vegetation compositions. Finally, D2C maintains the spatio-temporal resolution of the driver and the simulated processes (as recommended by Bocedi et al., 2012).

D2C is applicable for a broad range of DVMs and under certain conditions probably also for time- and space-discrete models simulating other organisms. D2C might, for example, be applicable for models simulating (predominantly) sessile organisms; organisms for whom spatial processes take place on a coarser time scale than local processes (e.g. only in certain life stages or once per year), or organisms with a few migration corridors.

The expected benefit when using D2C to upscale a model depends on different model properties, in particular the ratio of spatially linked to spatially unlinked processes, but also the scale on which the model applies stochasticity and the numerical properties of the state variables. With regards to currently applied DVMs an implementation of D2C together with an efficient seed dispersal algorithm could strongly improve the extent-resolution trade-off, enabling new applications on larger extents or greater numbers of stochastic repetitions to better capture important uncertainties.

## Code availability

The source code of TreeMig-2L can be requested from [jemsnabel@gmail.com](mailto:jemsnabel@gmail.com) or [heike.lischke@wsl.ch](mailto:heike.lischke@wsl.ch) (please also refer to [http://www.wsl.ch/fe/landschaftsdynamik/projekte/TreeMig/index\\_EN](http://www.wsl.ch/fe/landschaftsdynamik/projekte/TreeMig/index_EN)).

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**Table 1.** Main characteristics of the two application scenarios A1 and A2. Scenario A1 stems from a study with a preliminary TreeMig-2L version (Nabel and Lischke, 2013), scenario A2 from a study on the influence of interannual bioclimate variability on the simulated migration of *Ostrya carpinifolia* (Nabel et al., 2013). For an in-depth description of the scenarios see Supplement Sect. B.

	Spatial complexity	Spatial resolution <sup>a</sup>	Spatial extent	Number of grid cells (stockable cells <sup>b</sup> )
A1	Rather homogeneous	200 m	5000 km <sup>2</sup>	125 000 (110 789)
A2	Very heterogeneous	1 km	14 700 km <sup>2</sup>	14 700 (12 230)

	Competing species	Tracked species	Simulated time span	Number of repetitions
A1	31	Four most drought resistant	1400–2500	5
A2	22	<i>Ostrya carpinifolia</i>	1400–3000	100

<sup>a</sup> Cell side length.

<sup>b</sup> Stockable cells denote grid cells in which trees can grow in a TreeMig simulation (trees cannot grow in cells covered with water and cells with solid rock surfaces).

**Table 2.** Three sets of bioclimate bins (E1, E2 and E3) were used to pre-structure the simulation areas. The bioclimate bins resulted from discretising the bioclimate variables with different granularity (E1: fine, E2: moderate, E3: coarse). Minimum and maximum values of the bioclimate variables cover the bioclimate ranges of both application scenarios.

Bioclimate variable	Range		Resolution (number of bioclimate bins)		
	min	max	E1	E2	E3
DDsum <sub>&gt;5.5°C</sub> <sup>a</sup>	0	4200	50 (85)	100 (43)	200 (22)
Min. wtemp. <sup>b</sup>	-14	10	0.5 (49)	1.0 (25)	2.0 (13)
Drought index	0.0	0.7	0.025 (29)	0.05 (15)	0.1 (8)

<sup>a</sup> DDsum<sub>>5.5°C</sub>: sum of daily mean temperatures above 5.5 °C.

<sup>b</sup> Min. wtemp.: minimum winter temperature [°C].

**Table 3.** Model Simulations of four model versions with increasing complexity were compared. The model versions differ in whether they (1) use the pre-structuring to bioclimate types, (2) do simulations on two layers and (3) apply dynamic associations between the two layers, i.e. allow for splitting an merging of elements on the non-spatial layer. 1L-ORG refers to the original one-layer approach with the original bioclimate driver. 1L-PB introduces the averaging of the bioclimate drivers according to the bioclimate types, but still runs on one layer. 2L-NDA applies the averaging and runs on two layers, albeit without dynamic associations. 2L, finally, refers to the full TreeMig-2L model with two layers and with dynamic associations.

	Bioclimate types	Two layers	Dynamic <del>association</del> associations
<del>2L</del> 1L-ORG	yes <del>no</del>	yes <del>no</del>	yes <del>—</del>
2L-NDA <del>yes</del> 1L-PB	yes	no	—
<del>1L</del> PB-2L-NDA	yes	<del>no</del> yes	— <del>no</del>
<del>1L</del> ORG-2L	<del>no</del> yes	<del>no</del> yes	— <del>yes</del>

**Table 4.** Number of bioclimate types resulting from the three different sets of bioclimate bins (E1–E3 – Table 2). For both application scenarios (A1 and A2), absolute numbers of bioclimate types and percentages relative to the number of stockable cells of the simulation area (see Table 1) are listed.

	Application scenario A1		Application scenario A2	
	#Bioclimate types	%	#Bioclimate types	%
E1	3460	3.1 %	7941	64.9 %
E2	798	0.7 %	3424	28.0 %
E3	213	0.2 %	884	7.2 %

**Table 5.** Performance measures for simulations with both application scenarios (A1 and A2) and with all three sets of bioclimate types (E1–E3). For both scenarios, the table lists the mean similarity coefficients (SC) comparing results of the last simulation year from the three model versions (1L-PB, 2L and 2L-NDA) to 1L-ORG simulations for different target variables (biomass sum over all species, biomass per species and, for scenario A2, biomass of *Ostrya carpinifolia*). In addition to the SCs, average peak element-cell ratios and mean CPU time reductions relative to 1L-ORG simulations are listed. All means for A1 stem from five repetitions, for A2 from 100 repetitions. SCs from 2L simulations were always very close to SCs from 1L-PB simulations, indicating that the dynamics in 2L simulations follow the dynamics in 1L-ORG simulations and that most of the deviations are due to the averaging of the bioclimate drivers for the bioclimate types. SCs from 2L-NDA are smaller, in particular for SC<sub>OC</sub>, underlining the importance to track migrating species.

		Application scenario A1 (5 repetitions)				Application scenario A2 (100 repetitions)				
		Avg. SCs <sup>a</sup>		Avg. peak	Avg. CPU time <sup>c</sup>	Avg. SCs <sup>a</sup>		SC <sub>OC</sub> <sup>e</sup>	Avg. peak	Avg. CPU time <sup>c</sup>
		SC <sub>sum</sub>	SC <sub>spec</sub>	e-c ratio <sup>b</sup>	reduction [% <sup>d</sup> ]	SC <sub>sum</sub>	SC <sub>spec</sub>	SC <sub>OC</sub> <sup>e</sup>	e-c ratio <sup>b</sup>	reduction [% <sup>d</sup> ]
E1	1L-PB	0.98	0.90	–	∅	0.99	0.95	0.97	–	∅
	<b>2L</b>	<b>0.98</b>	<b>0.89</b>	<b>56.5 %</b>	<b>52.4 %</b>	<b>0.99</b>	<b>0.95</b>	<b>0.96</b>	<b>71.2 %</b>	<b>32.6 %</b>
	2L-NDA	0.97	0.85	3.1 %	59.6 %	0.98	0.92	0.71	64.9 %	33.7 %
E2	1L-PB	0.97	0.86	–	∅	0.96	0.88	0.89	–	∅
	<b>2L</b>	<b>0.97</b>	<b>0.85</b>	<b>39.9 %</b>	<b>56.0 %</b>	<b>0.96</b>	<b>0.87</b>	<b>0.88</b>	<b>38.3 %</b>	<b>65.6 %</b>
	2L-NDA	0.96	0.82	0.7 %	61.0 %	0.96	0.85	0.67	28.0 %	68.3 %
E3	1L-PB	0.96	0.78	–	∅	0.94	0.82	0.83	–	∅
	<b>2L</b>	<b>0.96</b>	<b>0.78</b>	<b>29.4 %</b>	<b>57.8 %</b>	<b>0.94</b>	<b>0.81</b>	<b>0.82</b>	<b>18.1 %</b>	<b>84.7 %</b>
	2L-NDA	0.96	0.75	0.2 %	61.4 %	0.94	0.80	0.63	7.2 %	87.0 %

<sup>a</sup> SC comparisons were conducted for the last year of the simulations, i.e. for the simulation year 2500 in case of A1 simulations and 3000 in case of A2 simulations. Simulations of the listed model versions (1L-PB, 2L, 2L-NDA – see Table 3) were compared with 1L-ORG simulations using the same pseudo-random number streams to extrapolate the bioclimate driver. Examples of the temporal development of the SCs are given in Fig. 5, Fig. 6 and in Supplement Sect. C. Standard deviations for A1 simulations were always smaller than 0.02. Standard deviations for A2 simulations with the model version 2L-NDA were much larger and reached up to 0.04.

<sup>b</sup> Peak ratio between the number of elements on the non-spatial layer and the number of stockable cells in the simulation area of the application scenario (Table 1).

<sup>c</sup> Standard deviations of CPU times were always smaller than 1.5%, therefore, only average CPU times are shown.

<sup>d</sup> Reduction relative to the average CPU time required for 1L-ORG simulations (see footnote 1).

<sup>e</sup> OC: *Ostrya carpinifolia*, the tree species whose northwards migration is simulated in application scenario A2.

**Table 6.** Percentage of instructions executed for selected computation tasks. Shown are results from a callgrind (Weidendorfer, 2008) profiling of 1L-ORG simulations and of 2L simulations with all three sets of bioclimate types (E1–E3). The measured percentage of instructions executed for selected computation tasks is a performance measure comparable to the relative amount of CPU time spent with the tasks. Measures stem from simulations using the same pseudo-random number stream to extrapolate the bioclimate driver.

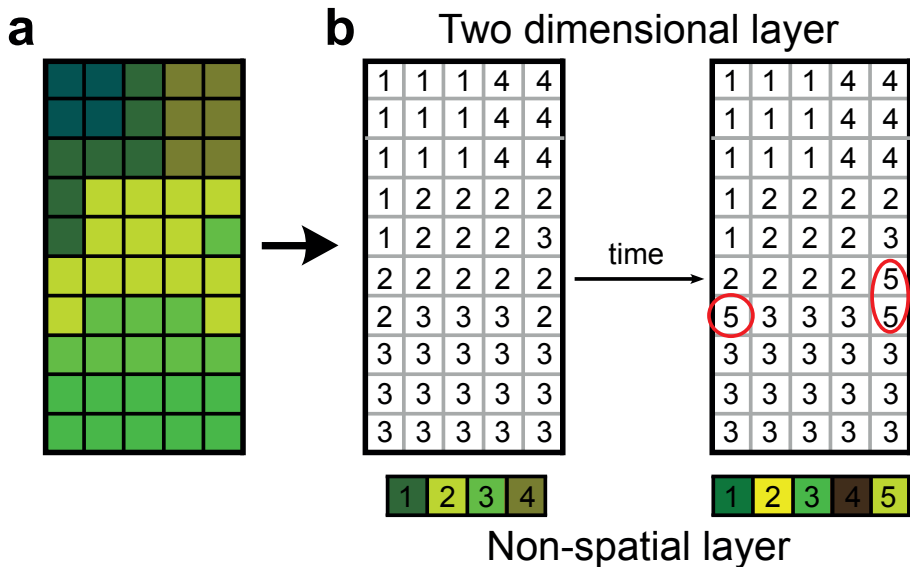
Application scenario A1				
	Seed dispersal	Bioclimate prep. <sup>a</sup>	Adult dynamics	Overhead <sup>b</sup>
1L-ORG	44.31 %	3.75 %	49.61 %	–
2L: E1	83.71 %	0.21 %	14.66 %	0.11 %
2L: E2	88.40 %	0.05 %	10.19 %	0.10 %
2L: E3	91.80 %	0.01 %	6.84 %	0.10 %

Application scenario A2				
	Seed dispersal	Bioclimate prep. <sup>a</sup>	Adult dynamics	Overhead <sup>b</sup>
1L-ORG	6.03 %	4.80 %	85.97 %	–
2L: E1	9.02 %	4.62 %	83.04 %	0.15 %
2L: E2	17.69 %	3.84 %	74.16 %	0.24 %
2L: E3	39.52 %	2.20 %	51.42 %	0.47 %

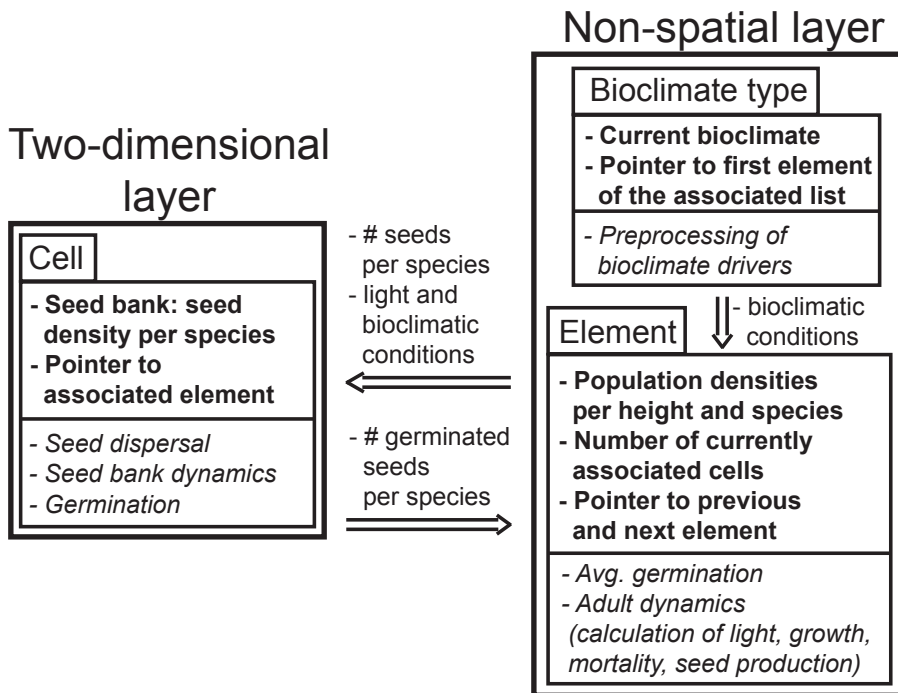
<sup>a</sup> Bioclimate prep.: Preprocessing of the bioclimate driver, which involves reading of the current values from a NetCDF file and derivation of species-specific coefficients for later calculations with bioclimate dependencies, such as growth, mortality and establishment.

<sup>b</sup> Overhead: Organisation of dynamic associations between the two-dimensional and the non-spatial layer.

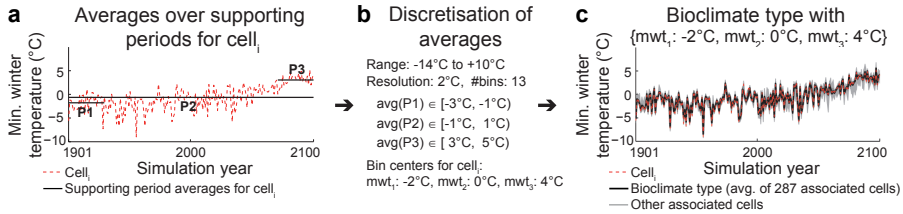


**Figure 1.** Visualisation of the dynamic two-layer classification concept. **(a)** Pre-defined similarity criteria (on abiotic drivers and biotic state variables) are used to classify similar grid cells to distinct types. Cells of the same type are coloured with the same shade of green. **(b)** For each type of cells one element is required on the non-spatial layer (coloured row, bottom). Cells on the two-dimensional layer (2-D-grid, top) are associated to these elements (numbers). Species' compositions can change over time due to processes simulated on both layers (changes in the coloured row). Furthermore, associations between the layers can change (changed numbers highlighted by red circles), for example, when processes simulated on the spatial-layer (e.g. seed dispersal) lead to differences among cells associated with the same element which violate one of the similarity criteria.

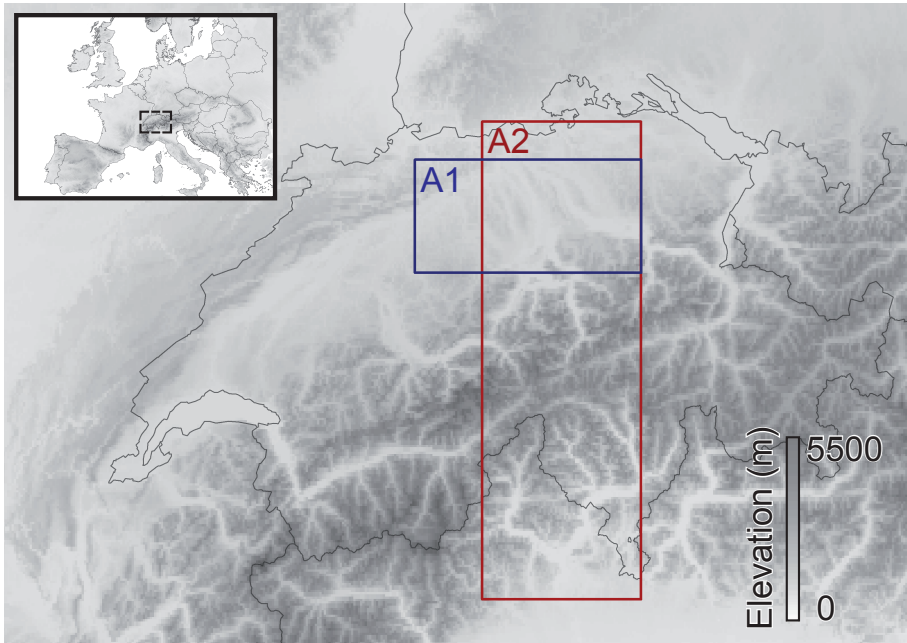




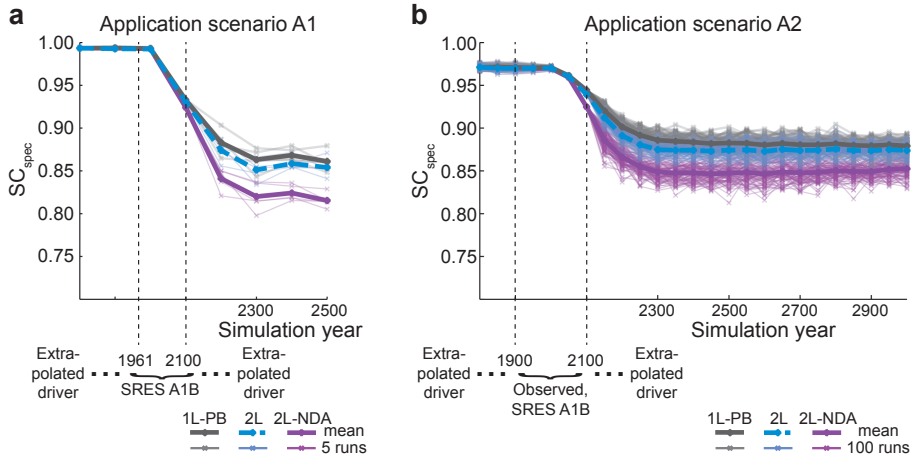
**Figure 2.** Outline of the architecture of TreeMig-2L. The two-dimensional layer consists of single cells whose state variables are seed densities per species in the seed bank. Additionally, each cell has a pointer – a data type allowing direct access – to the element on the non-spatial layer with which the cell is currently associated. The non-spatial layer consists of bioclimate types and linked lists of associated elements (for more information see Supplement Sect. A.1). State variables are printed in bold, processes in italic type. Items listed on the arrows represent information exchanged between the layers and between bioclimate types and elements of their associated list.



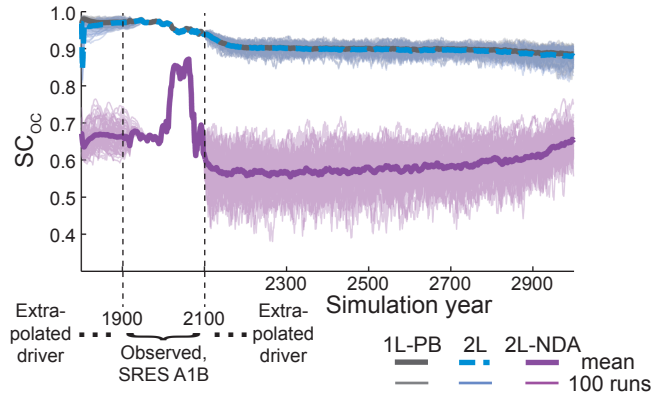
**Figure 3.** Visualisation of the pre-structuring into bioclimate types on the example of the minimum winter temperature (Min. winter temperature), one of TreeMig's three bioclimate drivers. **(a)** The minimum winter temperature driving cell<sub>i</sub> is averaged for each of the supporting periods (here P1: 1901–1930, P2: 1901–2100, P3: 2071–2100). **(b)** The range of the minimum winter temperature (–14°C to +10°C) is discretised into 13 bins with a resolution of 2°C (as e.g. done for E3, the set of bioclimate bins with the coarsest resolution – see e.g. Table 2). The averages of the supporting periods P1–P3 for cell<sub>i</sub> are classified according to these bins. **(c)** Cells whose averages fall into the same bin in each of the supporting periods for each of the bioclimate drivers are classified into the same bioclimate type. The bioclimate driver (here the minimum winter temperature) of the bioclimate type is calculated as the average (black line) of its 287 associated cells (grey lines).



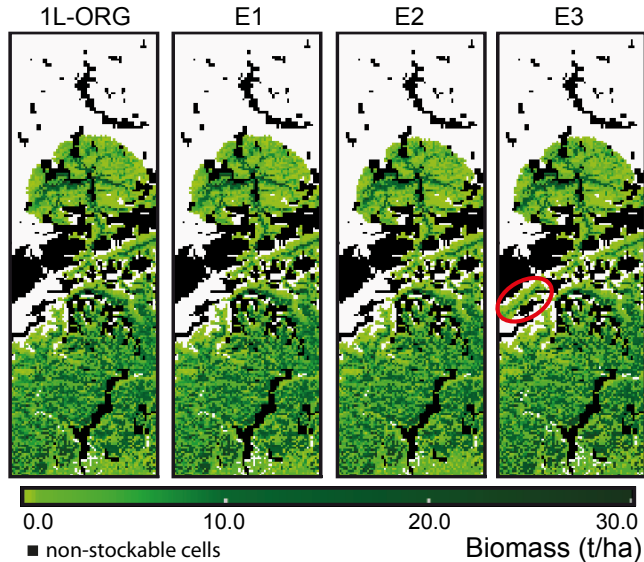
**Figure 4.** Location of the two simulation areas in Switzerland and in Europe. The map illustrates the differences in elevational heterogeneity (digital elevation model by Jarvis et al., 2008) between the simulation area of scenario A1 and of scenario A2.



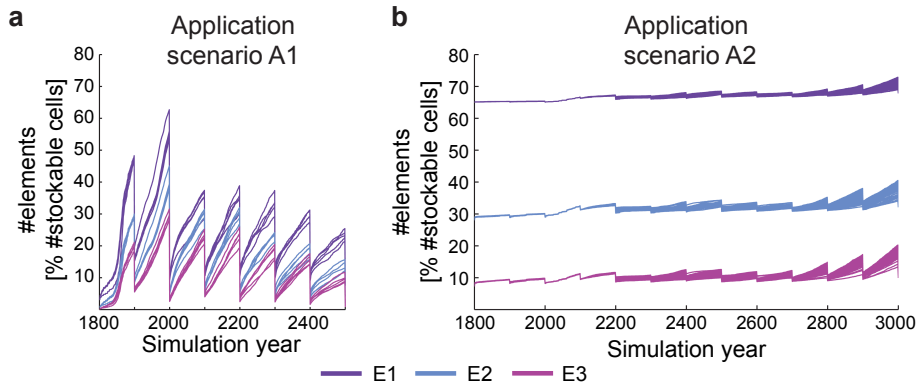
**Figure 5.** Temporal development of  $SC_{\text{spec}}$  comparing the biomass per species. Depicted is the comparison of 1L-ORG simulations to two-layer simulations with and without dynamic associations (2L and 2L-NDA, respectively) and simulations on one layer but with the bioclimate of the associated bioclimate types (1L-PB). For both application scenarios (A1: **a**, A2: **b**) bioclimate types were derived with the moderate set of bioclimate bins [with moderate resolution](#) (E2; for other bioclimate types see Supplement Sect. C).  $SC_{\text{spec}}$  values for A1 were calculated every 100 years, values for A2 every 50 years. For each setting several repetitions were compared, which were simulated using different pseudo-random number streams to extrapolate the bioclimate driver before 1961 (A1) or 1901 (A2) and after 2100. Five simulations were conducted for A1, 100 for A2. Single simulations and their means are printed half-transparent and bold, respectively. All depicted  $SC_{\text{spec}}$  time series decline in the transient phase of climate change and continue to decline for about 200 years after which  $SC_{\text{spec}}$  stabilises. Over the whole simulated time span  $SC_{\text{spec}}$  values of 2L simulations are much closer to  $SC_{\text{spec}}$  values from 1L-PB simulations than to  $SC_{\text{spec}}$  values from 2L-NDA simulations, indicating that the deviations are mainly due to the averaging of the bioclimate drivers.



**Figure 6.** Temporal development of  $SC_{OC}$  comparing the biomass of *Ostrya carpinifolia* in simulations of application scenario A2. Depicted  $SC_{OC}$  values stem from comparisons of 1L-ORG simulations to two-layer simulations with and without dynamic associations (2L and 2L-NDA, respectively) and simulations on one layer but with the bioclimate of the associated bioclimate types (1L-PB). Bioclimate types were derived with the moderate set of bioclimate bins with moderate resolution (E2; for other bioclimate types see Supplement Sect. C). For each setting 100 repetitions were compared, which were simulated using different pseudo-random number streams to extrapolate the bioclimate driver before 1901 and after 2100. Single simulations and their means are printed half-transparent and bold, respectively. Comparable to  $SC_{spec}$  values (Fig. 5),  $SC_{OC}$  values of comparisons between 1L-ORG and 2L simulations are very close to  $SC_{OC}$  values from comparisons with 1L-PB simulations over the whole simulated time span. These  $SC_{OC}$  time series thus reflect differences due to the averaging of the bioclimate driver.  $SC_{OC}$  values from comparisons of 1L-ORG simulations with 2L-NDA simulations, in contrast, mainly reflect the reaction of *O. carpinifolia* to climatic changes on the whole simulation area (see Supplement Sect. C.2), since 2L-NDA simulations were conducted without dynamic associations. 2L-NDA simulations get closer to 1L-ORG simulations towards the end of the simulation due to the northwards spread of *O. carpinifolia* in 1L-ORG over time.



**Figure 7.** Spatial spread of *Ostrya carpinifolia* in simulations with application scenario A2. Depicted are maps of the biomass distribution of *O. carpinifolia* from the last simulation year (3000) of a 1L-ORG simulation and 2L simulations with the three sets of bioclimate types (E1–E3). The maps are hardly visually discernible and the only notable difference between the depicted maps is one valley in the west of the transect, which is inhabited by *O. carpinifolia* in E3 (red circle), but not in the other depicted simulations. The absence of notable spatial biases indicates that a large share of the differences in the biomass of *O. carpinifolia* between 2L and 1L-ORG simulations (i.e.  $SC_{OC}$  values) stem from small variations in the local biomass. All depicted maps stem from simulations using the same pseudo-random number streams to extrapolate the bioclimate driver and led to  $SC_{OC}$  values (E1: 0.97, E2: 0.88, E3: 0.82) close to the means (Table 5). Maps of the biomass of *O. carpinifolia* were created with Paraview (Ahrens et al., 2005).



**Figure 8.** Ratio of the number of elements on the non-spatial layer to cells in the simulation area over time from simulations with all three sets of bioclimate types (E1–E3) and for both application scenarios (A1: **a**, A2: **b**). For A1 five repetitions using different pseudo-random number streams to extrapolate the bioclimate driver are depicted; for A2 100 repetitions are shown. The number of elements in A1 simulations increased strongly in between the merging intervals with smaller increases in the course of the simulation. For A2 simulations, in contrast, the number of elements increased faster towards the end of the simulation time, due to the growing perimeter of the migration front of the tracked species *Ostrya carpinifolia* (see Supplement Fig. C-12.11).

## A. Additional details on the implementation of TreeMig-2L

### A.1. Data structures

The architecture of TreeMig-2L comprises different data structures (Fig. A.1 and Fig. 2, main text). Processes on the two-dimensional layer require information on the spatial location of a grid cell relative to other grid cells. State variables required for these spatial processes are therefore stored in an array data structure. Processes on the non-spatial layer do not require information on the spatial location of a grid cell relative to other grid cells. Furthermore, the number of elements on the non-spatial layer, as opposed to the number of grid cells, is not pre-determined by the considered simulation area but emerges during the simulation. Therefore, the elements on the non-spatial layer need to be stored in a dynamic data structure. The dynamic data structure used for TreeMig-2L is a doubly linked list. A doubly linked list is a data structure in which each element is connected to two other elements of the list, its predecessor and its successor. Therefore, such a list can dynamically grow or shrink only changing local information instead of global information and allows for efficient traversal. The dynamic character of the non-spatial layer, i.e. splitting and merging of its elements induces an overhead required for the maintenance of its elements. To pre-constrain this overhead, multiple small lists are used instead of one large list. This enables efficient splitting and merging operations which only apply to a single list, but not to the whole non-spatial layer. In particular the comparison of elements would induce a larger overhead if all elements would be compared to all other elements, instead of restricting comparison to the other elements in one of the small lists. To pre-define which element is stored in which list, the fact is used that for grid cells to be similar not only species' compositions need to satisfy the given similarity criteria but also bioclimatic influences need to be comparable. As opposed to species' compositions which develop during runtime, bioclimate drivers are an input to TreeMig. Information about the bioclimate drivers can therefore be used in advance to pre-structure a simulation area. In this pre-structuring bioclimate types are derived from the bioclimate drivers according to a [given-pre-specified](#) set of bioclimate bins (see [Section-Sect. A.2.](#) and [Section-Sect- 3.1.3,](#) main text). Each of the derived bioclimate types is associated with one list (Fig. A.1). Because the number of the bioclimate types is known in advance, information about the bioclimate types can be stored in a one dimensional array structure.

The different data structures, i.e. the array for the two-dimensional layer, the one-dimensional array for bioclimate types and the linked lists for elements on the non-spatial layer, are asymmetrically connected (Fig. A.1). Each bioclimate type has a pointer – a data type allowing direct access – to the first element in its list. Furthermore, each cell of the two-dimensional layer has a pointer to the element with which it is currently associated, to allow for a direct and thus fast exchange of the status information.

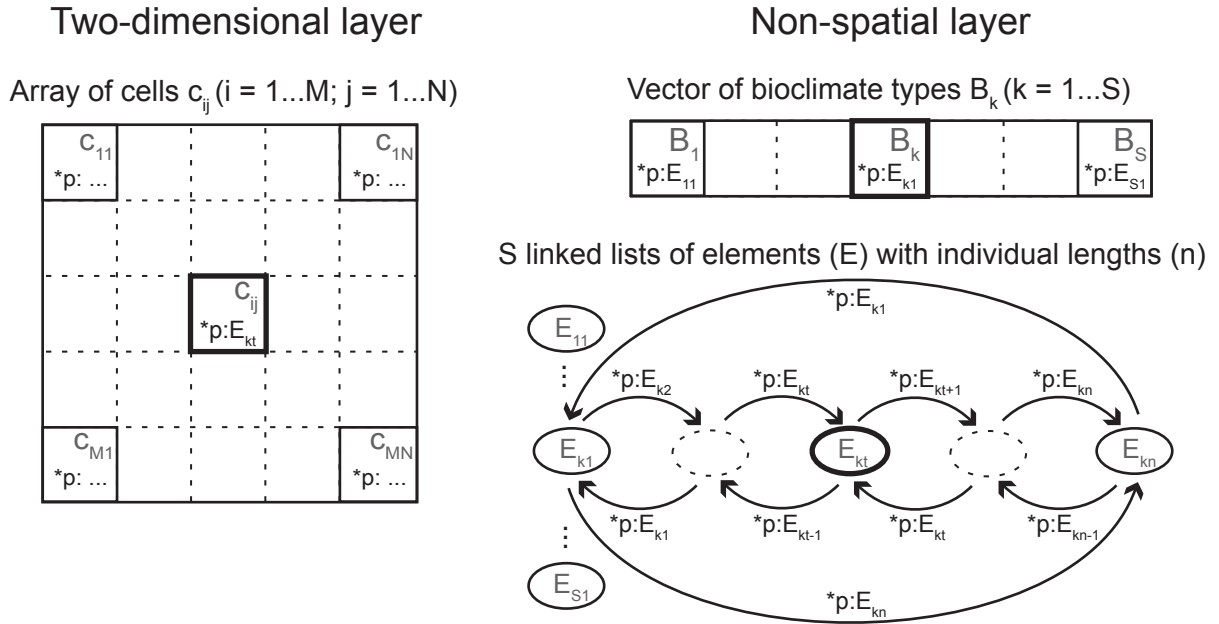


Fig. A.1: Data structures used in TreeMig-2L and their connections. State variables required for processes simulated on the two-dimensional layer (see Fig. 2, main text) are kept in cells stored in an  $M \times N$  array structure (size according to the simulation area). The non-spatial layer comprises different data structures: a vector of bioclimate types (length  $S$ ) and associated linked lists for each of these types containing the actual elements on the non-spatial layer. The bioclimate types are derived in a pre-processing (see [Section-Sect A.2.](#) and [Section-Sect. 3.1.3,](#) main text). Connections between the different data structures are asymmetric and defined with pointers. A pointer is a data structure holding the memory location of another data structure and therefore allowing direct access. Each cell ( $c_{ij}$ ) on the two-dimensional layer holds a pointer ( $*p:E_{kt}$ ) to the element on the non-spatial layer it is currently associated with ( $E_{kt}$ ). Each bioclimate type ( $B_k$ ) holds a pointer ( $*p:E_{k1}$ ) to the first element of its associated list ( $E_{k1}$ ). Elements stored in the linked lists do not contain pointers to their associated cells because the number of associated cells can change during simulation time. For explanatory reasons, list  $k$  is depicted containing several elements and  $c_{ij}$  points to element  $E_{kt}$ . However, a list can also consist of only one element which then points to itself.



## A.2. ~~Pre-structuring~~ Additional information on the pre-structuring of a simulation area

~~A In TreeMig-2L a simulated area is pre-structured to bioclimate types according to the bioclimate drivers, i.e. grid into bioclimate types using the three bioclimate drivers that are an input to TreeMig-2L. Grid cells are classified into bioclimate types according to their bioclimate drivers. The underlying idea of the pre-structuring is that the spatial correlation in the bioclimate among cells of the simulation area is rather persistent (see Nabel et al., 2014). Due to this correlation, two cells having similar bioclimate drivers for a certain time span have a good chance to have similar bioclimate drivers beyond this time span (see the examples in Fig. C.5 and C.6.4 and C.5). With this in mind, similarity of cells is not tested for each point in the entire time span covered by the bioclimate driver, but only for the averages of the pre-defined 'supporting periods' supporting periods (see Fig. A.2.3 in the main text for an example). For each of the supporting periods and for each of the bioclimate drivers one average per cell is calculated (Fig. A.2a). For each bioclimate driver, the according averages are then classified according to pre-defined bioclimate bins (Fig. A.2b). Each actually occurring set of classes defines one bioclimate type (Fig. A.2c). The number of possible bioclimate types will therefore be is influenced by the number of supporting periods and the number of bioclimate bins (see for example Fig. C.4.3). A small number of supporting periods and of bioclimate bins will lead to a coarser discretisation to into bioclimate types, whilst more periods and more bins will lead to a finer discretisation. After associating each cell with one bioclimate type, the bioclimate influence for this type is calculated as the average of all associated cells for each point in time and each bioclimate variable (e.g. Fig. A.2c).~~

~~Visualisation of the pre-structuring to bioclimate types on the example of the minimum winter temperature (Min. winter temperature), one of TreeMig's three bioclimate drivers. (Panel a) For each of the supporting periods (here P1-P3) the minimum winter temperature driving cell<sub>i</sub> is averaged. (Panel b) In the example the minimum winter temperature in the simulation area is assumed to range from -14 °C to +10 °C discretised with a resolution of 2 °C into 13 bins (as e.g. done for the set E3 of bioclimate bins in Table 2, main text). The averages of the supporting periods P1-P3 for cell<sub>i</sub> are clustered according to these bins. (Panel c) All cells with supporting periods clustered into the same bins are associated with the same bioclimate type and the bioclimate influence for a bioclimate type is calculated as the average of all associated cells for each point in time.~~

Bioclimate types receive a unique ID (see e.g. Fig. C.6) and are stored in a NetCDF file (Unidata - <http://www.unidata.ucar.edu/software/netcdf/>) used in two-layer simulations to read the bioclimate driver. Depending on the ratio of the number of bioclimate types to the number of cells in the simulation area, this NetCDF file is much smaller than the original NetCDF file which stores bioclimate input data for each single cell (e.g. the NetCDF file for the E1 version of the application scenario A1, having a 1:33 ratio of bioclimate types to cells, has a size of 9MB instead of the 400MB required for the original file).

Most TreeMig simulations start with an initialisation phase from bare ground with a reduced number of simulated processes, in particular without simulating seed dispersal (cf. Lischke et al., 2006; Nabel et al., 2013). Thus, the linked list of each bioclimate type (see Fig. A.1) will contain exactly one element over the whole time span of this initialisation phase. Simulations not starting from bare-ground but with given species' abundances would require an additional pre-processing step, introducing appropriate numbers of elements according to the different species' abundances occurring for the different bioclimate types.

### A.3. Execution sequence in TreeMig-2L

The implementation of TreeMig-2L is based on TreeMig-Netcdf 2.0 (Nabel et al., 2014) and the gross of the program structure was adopted from there. However, besides the changes in data structures (see [Section Sect. A.1](#)) also some changes in the execution sequence were required (see Fig. A.2).

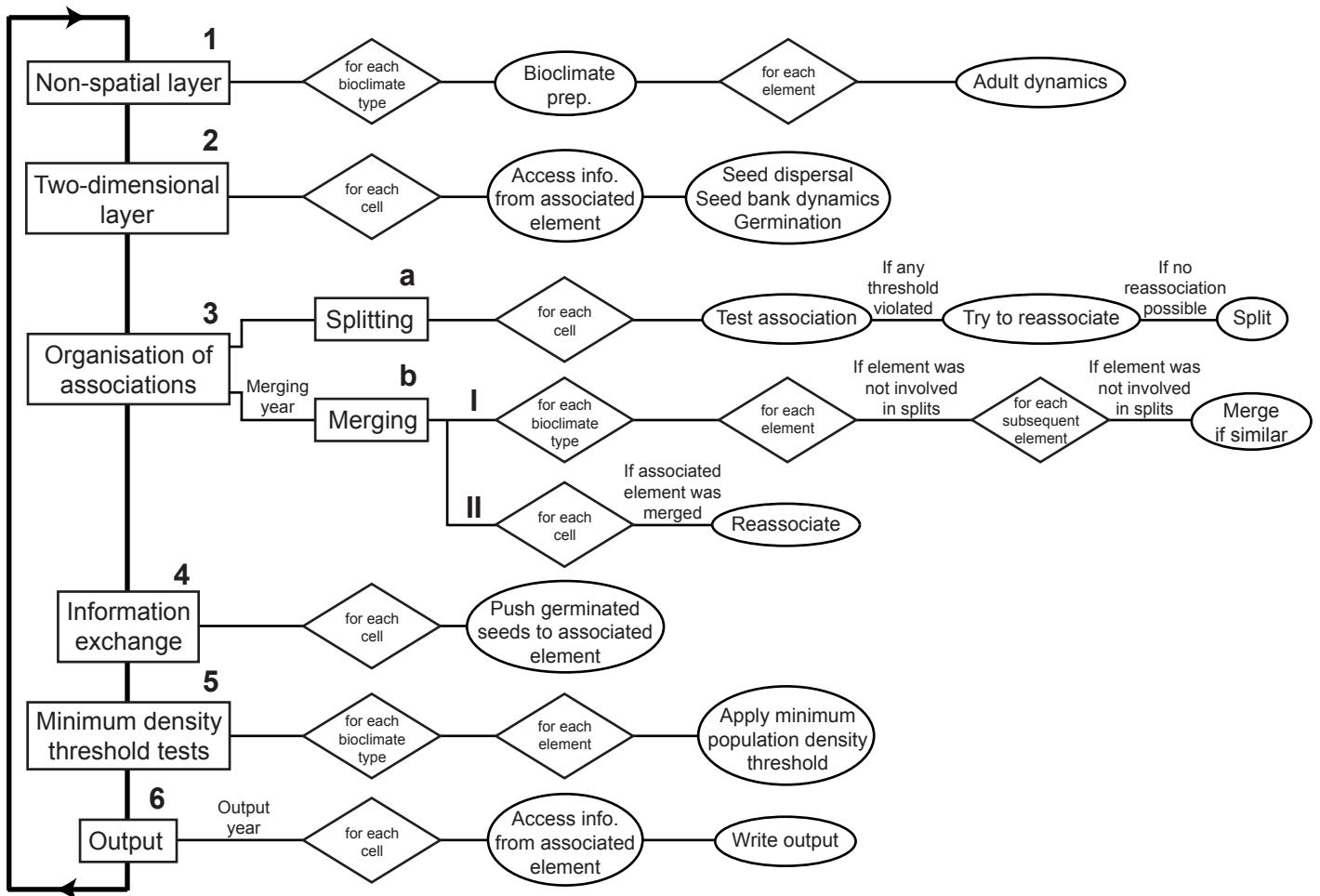


Fig. A.2: Execution sequence per time step in TreeMig-2L. (1) Each time step begins with the execution of the processes simulated on the non-spatial layer. For each bioclimate type the current bioclimate driver is read (or drawn in case of extrapolations), species-specific influences are derived and they are used for simulations of adult dynamics (described in detail in Lischke et al., 2006) in each element of the linked list of the bioclimate type. (2) Subsequently, processes simulated on the two-dimensional layer are conducted. Since each cell has a pointer to the element it is currently associated with (Fig. A.1 and Fig. 2, main text), it can access required information for seed dispersal and germination. (3a) Seeds germinated in the current time step can necessitate splitting of elements. Therefore, current associations are tested for each cell and if any threshold on the density of germinated seeds for any tracked species is violated the association is no longer valid. In case that the current associated element already had splits in the current time step, the cell can be reassociated to an element from a previous split if the thresholds on the germinated seed densities are met. If not, the current element is split up and the cell is associated with the new element. (3b) Merging is only done after a pre-defined number of time steps. (3b.I) In a merging year, all elements in the list of a bioclimate type are compared and similar elements are merged. Two elements are thereby only merged if none of them was involved in any splits in this time step. (3b.II) After merging was conducted, cells whose associated elements were merged need to be reassociated. (4) After the associations are reorganised, cells can push the number of seeds germinated in this time step to their associated elements. (5) To prevent infinitesimal values, the population densities per height class kept in each element on the non-spatial layer are tested for adherence of a pre-specified minimum density threshold (see Nabel et al., 2013). Values falling below the threshold are added to lower height classes or removed, in case of the lowest height class. (6) The output of TreeMig-2L is written at the end of each time step for each cell, provided the current time step is an output year.

## B. Additional information about the application scenarios

For this study, TreeMig-2L simulations were conducted for two application scenarios with different simulation settings which are briefly characterised in Table 1 in the main text. The location of the simulation areas in Switzerland are depicted in Fig. 3-4 in the main text. In this supplementary material, additional information for the two application scenarios is provided.

As described in [Section Sect. 3.1.1](#) in the main text, TreeMig simulations require time series of three annual bioclimate drivers. The bioclimate [influences-drivers](#) used for the two application scenarios were derived from monthly averaged temperatures and monthly precipitation sums from different SRESA1B (Nakicenovic et al., 2000) scenario projections with a program based on ForClim-E (Bugmann and Cramer, 1998; Lischke et al., 2006) – for more details on the actual climate time series see below (B.1 and B.2). Bioclimate types for both application scenarios were derived with the same set of bioclimate bins (see Table 2, main text) using three [sampling-supporting](#) periods: (1) the first 30 years (A1: 1961-1991; A2: 1901-1931), (2) the whole time span (A1: 1961-2100; A2: 1901-2100) and (3) the last 30 years (both: 2071-2100). Because the simulated time spans of both application scenarios exceeded the available bioclimate data, a stochastic method was used to extrapolate the bioclimate driver (see B.3 for further information). Simulations with both scenarios started in 1400 with an initialisation phase lasting 400 years. In this initialisation phase only a restricted set of processes was simulated assuming that saplings of all species are available in all elements (with one restriction in application scenario A2, see B.2 below) instead of simulating seed production, dispersal and germination (cf. Lischke et al., 2006; Nabel et al., 2013).

The two-layer simulations discussed in the main text all applied the same set of splitting and merging thresholds. These thresholds were defined on a unit area, the so-called patch area (cf. Bugmann, 1994), because TreeMig's state variables represent means of Poisson distributions of tree densities per species and height class on this unit area (Lischke et al., 1998, 2006). For the splitting of elements two thresholds were used, namely 0.005 and 0.5 germinated seeds per patch area. These two thresholds were used to divide the number of germinated seeds in three bins: absence of germinated seeds, scattered germinates seeds and more than one seed on every second patch. Elements on the non-spatial area were split if the germinated seeds of any of the species tracked in the application scenario fell on different sides of these thresholds for at least two associated cells. Merging was considered every 100 simulation years and elements were merged if the difference in the densities for all occurring species and height classes did not exceed a height-specific similarity threshold (50.0, 25.0, 20.0, 15.0, 10.0, 7.5, 5.0, 2.5 individuals per patch for the lowest eight height classes, respectively, and 1.0 for all other height classes).

In addition to the simulations discussed in the main text, some sensitivity tests were conducted with different splitting and merging thresholds and a different merging interval. Results for these sensitivity tests are shown and discussed in [Section Sect. C](#). For A1 and A2, tests were conducted only considering presence and absence of germinated seeds for splitting, i.e. with only one splitting threshold (0.05). For A2, additional tests with a larger set of splitting thresholds were conducted (0.0005, 0.005, 0.05, 0.5, 5.0 and 50.0 germinated seeds per patch area). For both application scenarios, a merging interval of 10 simulation years and merging conditional on smaller differences for the densities in the height classes were tested (5.0 individuals per patch area for the first seven height classes and 1.0 individuals for all other height classes).

All simulations were conducted without disturbances (other than climatically caused) and the boundaries of the simulation areas were assumed to be absorbing, i.e. seeds dispersed beyond the boundaries were lost. In both application scenarios a minimum population density threshold (see Nabel et al., 2013) of one individual per [grid-cell-grid cell](#) was applied.

### B.1. Application scenario A1

Application scenario A1 has already been used in a previous study to test the performance of a preliminary version of TreeMig-2L in simulations without dynamic associations between the layers (Nabel and Lischke, 2013). The bioclimate [influences-drivers](#) used for A1 simulations were derived from an SRESA1B scenario simulation calculated with RCA3 (1961-2100 – Kjellström et al., 2005) and downscaled to 200 m cell side length based on a grid of MeteoSwiss weather stations interpolated with daymet (Thornton et al., 1997). In addition to the monthly climate data, static data for the simulation area on slope, aspect and water holding capacity was used to calculate the bioclimate drivers. Slope and aspect were averaged from the 25 m digital elevation model of the Swiss Federal Office of Topography (DHM25 (c)1994 Bundesamt für Landestopographie). The water holding capacity was derived from data on water retention potential and soil wetness found in the Swiss soil suitability map (Frei et al., 1980) by means of a linear regression based on soil profiles at test sites according to (Löffler and Lischke, 2001).

A1 simulations were conducted for 1100 years (1400-2500) and simulated for 31 species occurring in Switzerland. These species were parameterised for previous TreeMig applications. Parameters for 30 species were taken from Lischke et al. (2006) altered according to the findings in Rickebusch et al. (2007), namely *Abies alba*, *Larix decidua*, *Picea abies*, *Pinus cembra*, *P. montana*, *P. sylvestris*, *Taxus baccata*, *Acer campestre*, *A. platanooides*, *A. pseudoplatanus*, *Alnus glutinosa*, *A. incana*, *A. viridis*, *Betula pendula*, *Carpinus betulus*, *Castanea sativa*, *Corylus avellana*, *Fagus sylvatica*, *Fraxinus excelsior*, *Populus nigra*, *P. tremula*, *Quercus petraea*, *Q. pubescens*, *Q. robur*, *Salix alba*, *Sorbus aucuparia*, *Tilia cordata*, *T. platyphyllos* and *Ulmus scabra*. Parameters for the 31<sup>th</sup> species *Ostrya carpinifolia* were taken from Nabel et al. (2012).

For the A1 simulations with two layers discussed in the main text, four species were used to decide if an element on the non-spatial layer needs to be split: *Q. pubescens*, *O. carpinifolia*, *L. decidua* and *P. [silvestris-sylvestris](#)*. These four species were selected

as tracked species because of their high drought tolerance indices in TreeMig. With increasing drought severity (and temperature), these species are expected to increase their distributions. In addition to simulations with these four tracked species, simulations with two tracked species (*P. sylvestris* and *Q. pubescens*) and simulations with six tracked species (the four species already listed and the two species most abundant in the simulation area *P. abies* and *F. sylvatica*) were conducted to assess the sensitivity of the simulation results to the choice of tracked species.

### B.2. Application scenario A2

Application scenario A2 was used in previous studies to investigate the influence of interannual bioclimate variability on the northwards migration of *O. carpinifolia* (Nabel et al., 2012, 2013). Bioclimate ~~influences~~ drivers were derived from CRU data (1901-2000 – Mitchell et al., 2003) followed by an SRESA1B scenario simulation calculated with CLM (2001-2100 – Lautenschlager et al., 2009 which was downscaled to 30'' with WorldClim data (Hijmans et al., 2005) and projected to 1 km<sup>2</sup> with FIMEX-0.28 (Klein, 2012). In addition to the monthly climate data, static data for the simulation area on slope, aspect and water holding capacity was used (see supplementary material to Nabel et al. (2013) for more details).

A2 simulations were conducted for 1600 years (1400-3000) and in addition to *O. carpinifolia* 20 other species were simulated: *A. alba*, *L. decidua*, *P. abies*, *P. cembra*, *P. sylvestris*, *Taxus baccata*, *A. platanoides*, *A. pseudoplatanus*, *A. incana*, *B. pendula*, *C. betulus*, *C. sativa*, *F. sylvatica*, *F. excelsior*, *P. tremula*, *Q. petraea*, *Q. pubescens*, *S. aucuparia*, *T. cordata*, *T. platyphyllos* and *U. scabra*.

As opposed to all other species, saplings of *O. carpinifolia* were restricted to the southern part of the transect up to the 65<sup>th</sup> transect km north in the initialisation phase (1400-1800) of the A2 simulations. From the simulation year 1800 on the northwards migration of *O. carpinifolia* was simulated. For the A2 simulations discussed in the main text the optimistic end of the range of plausible species parameters for *O. carpinifolia* (see Nabel et al., 2012) was used because the migration through the transect was not restricted for this parameter set in a previous simulation study (Nabel et al., 2013).

### B.3. Extrapolation of the bioclimate time series

To extrapolate the available bioclimate time series for the entire simulated time spans a stochastic method was used. Nabel et al. (2014) recommended that a method used to extrapolate time series for spatially explicit simulations should account for the spatial correlation of climatic fluctuations in the extrapolated data. Therefore, the simple method of drawing complete bioclimate maps from a set of base years used in Nabel et al. (2014) was also used in this study. For extrapolation of past simulation years the first 30 years of the input data for each of the two application scenarios (A1: 1961-1990 and A2: 1901-1930) were used to derive a set of detrended base years (see supplementary material to Nabel et al. (2013) for more information on the detrending). For extrapolations of future simulation years the last 30 years (2071-2100 for both application scenarios) were used to derive a second set of detrended base years.

In the pre-structuring of the simulation area, required for two-layer simulations with TreeMig-2L, the bioclimate information is transferred from the cell level to the bioclimate types. This does not affect the applicability of the extrapolation method: The only difference to simulations on one layer is that in each year a bioclimate map for all bioclimate types is drawn instead of a bioclimate map for all single cells.

## C. Additional information on the pre-structuring, the influence of the bioclimate and conducted sensitivity tests

### C.1. Pre-structuring of the simulation areas

The number of cells associated with the bioclimate types is influenced by the number of supporting periods, the number of bioclimate bins and the heterogeneity of the simulation area. Bioclimate types representing bins with frequent occurrences in the simulation area will end up with more cells than bioclimate types representing rare bioclimatic conditions. The distribution of cells to bioclimate types for the two application scenarios (A1 and A2) and the three sets of bioclimate bins (E1-E3) reflect this (see Fig. C.3, Fig. C.4 and Fig. C.5).

In the pre-structuring of the simulation area, each bioclimate type receives a unique ID (see [Section Sect. A.2](#)). This ID is theoretically arbitrary, however, the underlying algorithm in TreeMig-2L assigns the IDs in a specific order. When searching for similarities among cells, one supporting period after the other is processed and the three bioclimate variables are considered in the order: (1) sum of daily mean temperatures above 5.5 °C ( $DD_{sum>5.5^{\circ}C}$ ), (2) minimum winter temperature, and (3) drought index; each increasing from the smallest to the largest occurring value. Thus, the IDs of the bioclimate types are monotonous increasing with the  $DD_{sum>5.5^{\circ}C}$  of the first supporting period and allow some insights into the distribution of IDs for the  $DD_{sum>5.5^{\circ}C}$  in the simulation area (Fig. C.3 and Fig. C.6). For example, the tendency for bioclimate types with most associated cells to have IDs in the middle of the ID-ranges, i.e.  $DD_{sum>5.5^{\circ}C}$  values in the moderate range of the simulation area.

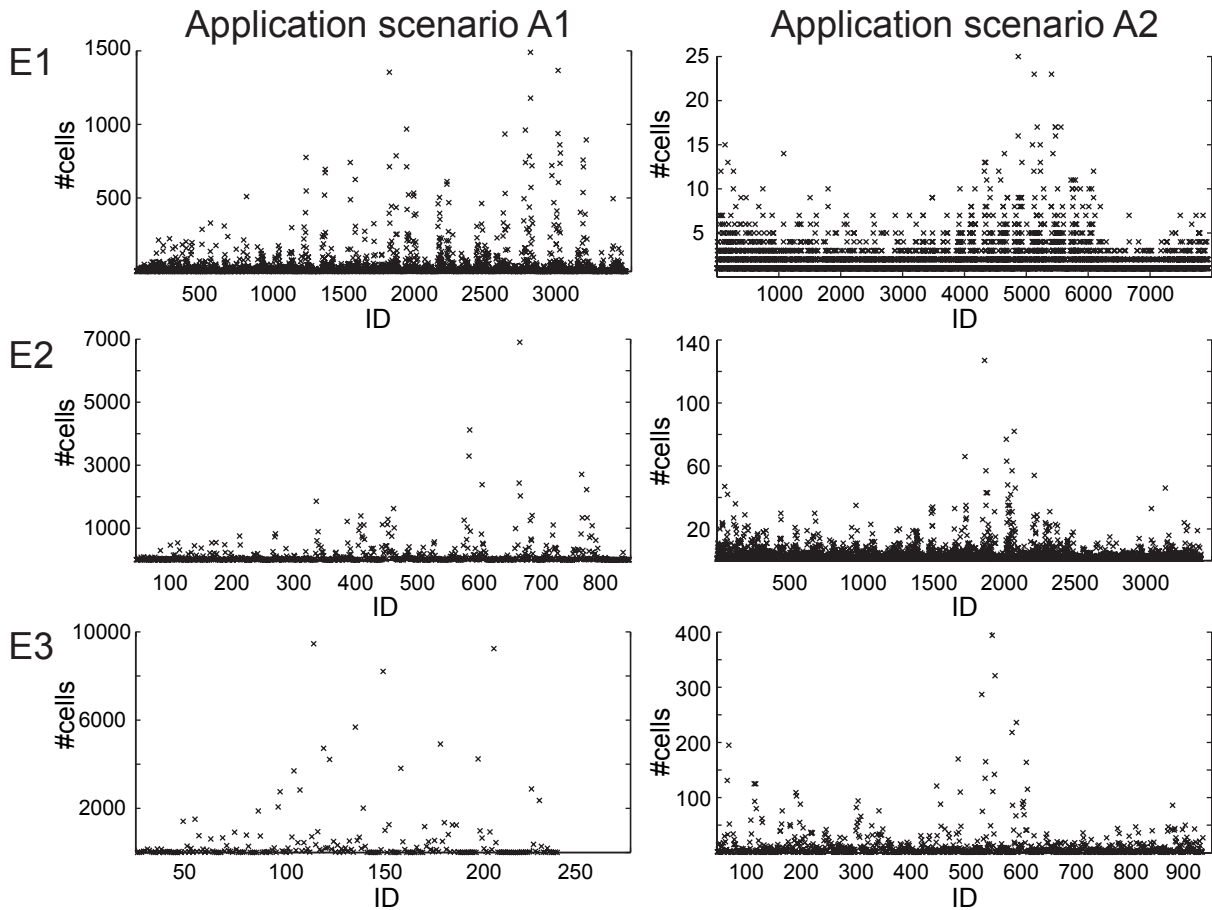


Fig. C.3: Number of cells associated with all three sets of bioclimate types (E1-E3) for the simulation areas of application scenario A1 and A2. The number of cells per bioclimate type varies strongly among the three sets and the simulation areas (note the different scales).

A finer discretisation by means of smaller bioclimate bins in the pre-structuring of the simulation area tends to lead to a smaller number of cells associated with the bioclimate types (Fig. C.3) and to smaller deviations between the averaged bioclimate and the bioclimate of the single associated cells (Fig. C.4 and Fig. C.5). This is also supported by the differences among the bioclimate variables. For all sets of bioclimate bins the  $DD_{sum>5.5^{\circ}C}$  was discretised into more bins (see Table 2, main text) leading to smaller maximum differences between  $DD_{sum>5.5^{\circ}C}$  time series of bioclimate types and their associated cells than for the other variables (Fig. C.4 and Fig. C.5).

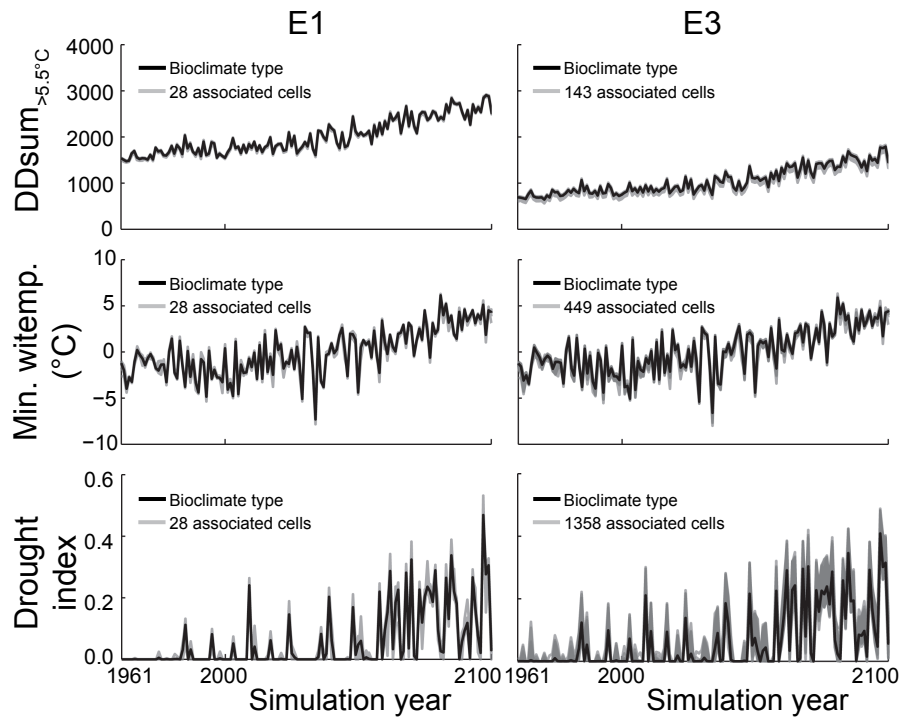


Fig. C.4: Average bioclimate for the bioclimate types (black lines) and for their associated cells (grey half-transparent lines). Depicted are those bioclimate types which averages deviated the most from one of their associated cells for pre-structurings of the simulation area of application scenario A1 with the [sets of bioclimate bins with fine](#) (E1) and [the with coarse](#) (E3) [bioclimate bins resolution](#) for each of TreeMig's bioclimate drivers (DDsum<sub>>5.5°C</sub>: Sum of daily mean temperatures above 5.5 °C; Min. witemp.: Minimum winter temperature; and the drought index).

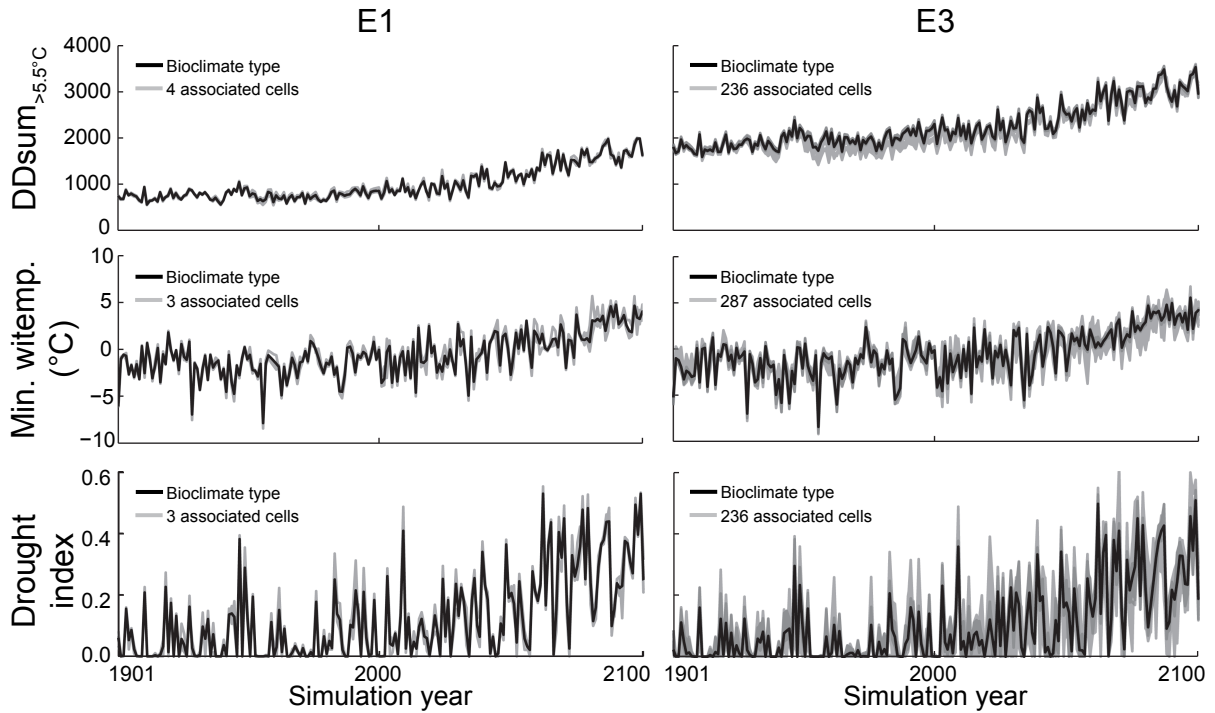


Fig. C.5: Average bioclimate for the bioclimate types (black lines) and for their associated cells (grey half-transparent lines). Depicted are those bioclimate types which averages deviate the most from one of their associated cells for pre-structurings of the simulation area of application scenario A2 with the [finer sets of bioclimate bins with fine](#) (E1) and [the coarser with coarse](#) (E3) [bioclimate bins resolution](#) for each of TreeMig's bioclimate drivers (DDsum<sub>>5.5°C</sub>: Sum of daily mean temperatures above 5.5 °C; Min. witemp.: Minimum winter temperature; and the drought index).



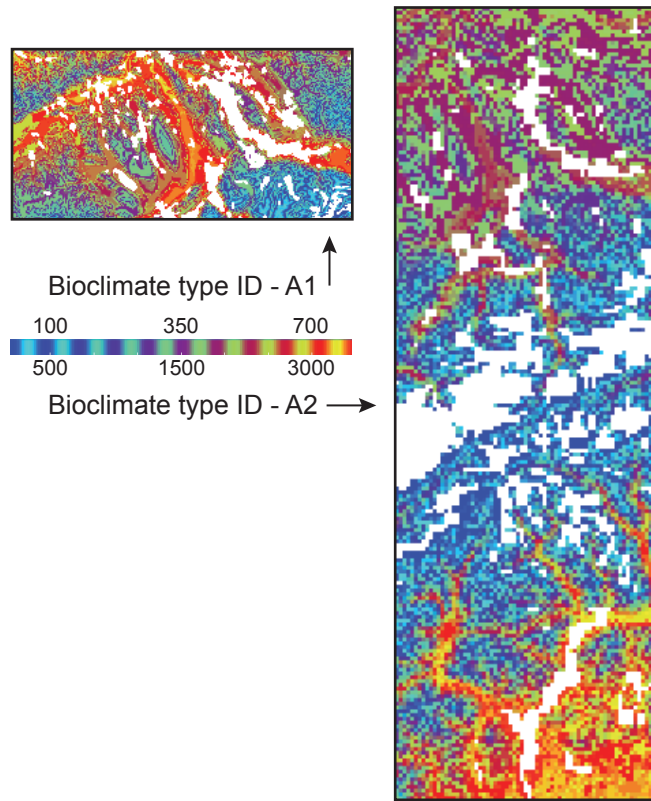


Fig. C.6: Distribution of the IDs of the bioclimate types in space for the two application scenarios A1 and A2. Depicted are bioclimate type IDs for the moderate set of bioclimate bins with moderate resolution (E2 – see Table 2, main text). Although the IDs of the bioclimate types are theoretically arbitrary they allow some insights into the distribution of IDs for the  $DD_{sum>5.5^{\circ}C}$ , due to the algorithm used to derive the bioclimate types (see text of Section Sect. C.1). For both simulation areas close IDs (i.e. IDs with close  $DD_{sum>5.5^{\circ}C}$  values) visibly cluster in space, following elevations in the transect area (see Fig. 2.4, main text). ID-maps were created with nview (Pierce, 2012).

## C.2. Influence of interannual bioclimate variability and of changes in the bioclimate over time

To assess the relevance of deviations from 1.0 in the different similarity coefficients (SCs), results from 1L-ORG simulations using different pseudo-random number streams (PRNSs) to extrapolate the bioclimate driver were compared among each other. Since these simulations only differ in the stochastically extrapolated bioclimate (before 1961 for A1, before 1901 for A2, and after 2100 for both application scenarios – see Section Sect. B.3) deviation from 1.0 in their SCs (Table C.1 and Fig. C.7) are due to the interannual variability in the bioclimate driver.

Table C.1: The similarity coefficient (SC) was used to compare different output variables among 1L-ORG for simulations applying different pseudo-random number streams (PRNSs) to extrapolate the bioclimate driver. These SCs thus show the influence of the interannual bioclimate variability on the similarity among simulations with otherwise similar conditions. SC means and standard deviations stem from comparisons among simulations with different PRNSs – five for A1 (ten comparisons) and 20 for A2 (190 comparisons).

	Avg. SC ( $\sigma$ )		
	$SC_{sum}$	$SC_{spec}$	$SC_{OC}$
A1	0.95 (0.02)	0.87 (0.04)	–
A2	0.92 (0.03)	0.86 (0.03)	0.79 (0.05)

Inter-comparisons of 1L-ORG simulations led to  $SC_{spec}$  (Fig. C.7a) and  $SC_{sum}$  (not shown) values close to 1.0 until 2100 for the homogeneous simulation area of application scenario A1. For the more heterogeneous simulation area of application scenario A2 there were small deviations from 1.0 in the SCs (Fig. C.7b and c), which vanished during the time span simulated with a deterministic bioclimate driver (1901-2100). Directly after 2100 the SCs rapidly decreased and quickly stabilised on a lower level for both application scenarios. The lower levels in the SCs after 2100 were mainly due to the larger drought index values and the higher interannual variability in the drought index (see e.g. Fig. C.4 and Fig. C.5) which entail larger fluctuations in the simulated species' abundances.

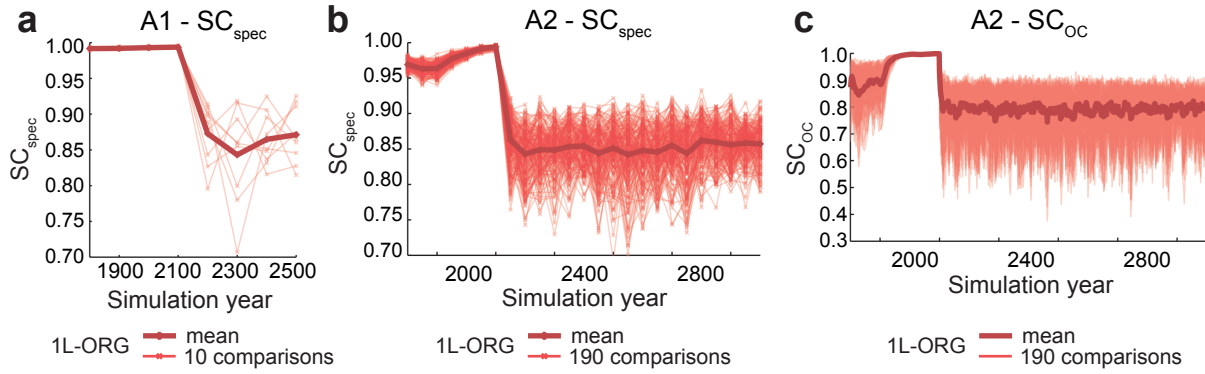


Fig. C.7: Temporal development of  $SC_{spec}$  for application scenario A1 and A2 and of  $SC_{OC}$  for A2 from comparisons among 1L-ORG simulations applying different pseudo-random number streams to extrapolate the bioclimate driver.  $SC_{spec}$  values were calculated every 100 years for A1 and every 50 years for A2 simulations;  $SC_{spec}$  was calculated for every simulation year.  $SC_{spec}$  for A1 stems from comparisons among five simulations (ten comparisons); SCs for A2 stem from comparisons among 20 simulations (190 comparisons). Single simulations and their means are printed half-transparent and bold, respectively. Since the depicted simulations only differ in the stochastically extrapolated bioclimate (before 1961 for A1, before 1901 for A2, and after 2100 for both application scenarios – see [Section Sect. B.3](#)) deviation from 1.0 in their SCs are due to the interannual variability in the bioclimate driver.

For both application scenarios, and the three different model versions (2L, 1L-PB and 2L-NDA – see Table 3, main text), the development over time of  $SC_{spec}$  (Fig. C.8 and Fig. C.9) and  $SC_{sum}$  (not shown) were comparable among simulations conducted with all three sets of bioclimate types (E1-E3) and most simulation settings: the SCs decreased in the transient phase of climate change (from around 2000 on) and stabilised after a few centuries. Comparable to 1L-ORG simulations (Fig. C.7) the SCs stabilised on a lower level than before the transient phase, which is again mainly due to the larger drought index values and TreeMigs non-linear reaction on drought indices. Deviations resulting from simulations with the original drought indices and the averaged drought indices have a stronger impact for larger than for smaller drought indices.

Trajectories for  $SC_{OC}$  measured for application scenario A2 with 2L-NDA simulations (Fig. C.10) differ from the other trajectories. 2L-NDA simulations were conducted without dynamic associations. Because no splits were conducted *Ostrya carpinifolia* quickly covered the whole simulation area after the spin-up since seeds germinated in any of the cells associated with one element contributed to the average number of germinated seeds in that element. In 1L-ORG simulations, 1L-PB simulations and in 2L simulations with dynamic associations, in contrast, *O. carpinifolia* was initially absent in the northern parts of the transect and only slowly migrated through the transect (Fig. C.11). Therefore,  $SC_{OC}$  is much smaller for 2L-NDA simulations than for 2L simulations (maximum differences in the SC of more than 0.3 – Fig. C.10). Because 2L-NDA simulations were conducted without dynamic associations they mainly reflect the changes in the bioclimate over time. In application scenario A2, the bioclimate driver was deterministic from 1901-2100 (see [Section Sect. B](#)) and a changing climate following the SRESA1B scenario was simulated. After 2000 the temperatures in the southern part of the transect got more and more favourable for *O. carpinifolia* leading to an increase in the biomass of *O. carpinifolia* by the year 2025 for simulations with all simulation settings (Fig. C.11). Because the SC is calculated as the ratio of differences compared to similarities over all cells of a simulation area (see Eq. 1, main text) an increase of the abundances in the south for all simulation settings and stable abundances in the north led to a rapid increase in  $SC_{OC}$  for 2L-NDA simulations (Fig. C.10, Fig. C.11). However, after only some decades the bioclimate in the north of the transect also got warm enough to allow for an increase in the biomass of *O. carpinifolia* in 2L-NDA simulations (Fig. C.11). This led to a sharp decrease in  $SC_{OC}$  because now the difference in biomass amounts of *O. carpinifolia* in the north of the transect compared to 1L-ORG simulations increased (Fig. C.10). After 2100  $SC_{OC}$  stayed on a stable level for some centuries and started to slowly increase again by the time *O. carpinifolia* started to also spread on the northern side of the Alps in 1L-ORG simulations (Fig. C.10, Fig. C.11).



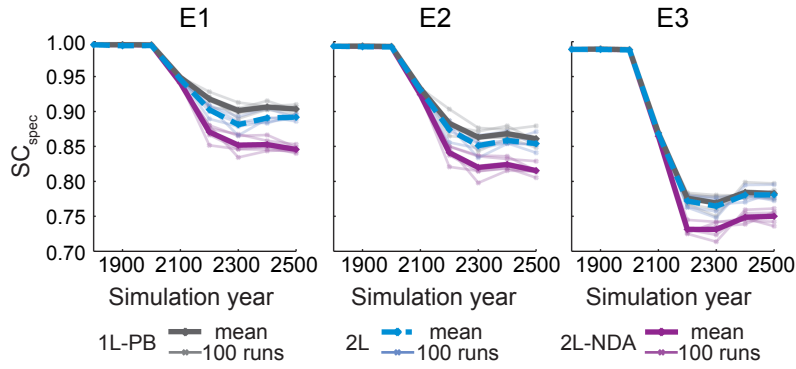


Fig. C.8: Temporal development of  $SC_{spec}$  for application scenario A1 from comparisons of 1L-ORG simulations to simulations with all three sets of bioclimate types (E1-E3).  $SC_{spec}$  values were calculated every 100 years for two-layer simulations with and without dynamic associations (2L and 2L-NDA, respectively) and simulations on one layer but with the bioclimate of the associated bioclimate types (1L-PB). For each setting five repetitions were compared, which were simulated using different pseudo-random number streams to extrapolate the bioclimate driver before 1961 and after 2100. Single simulations and their means are printed half-transparent and bold, respectively.

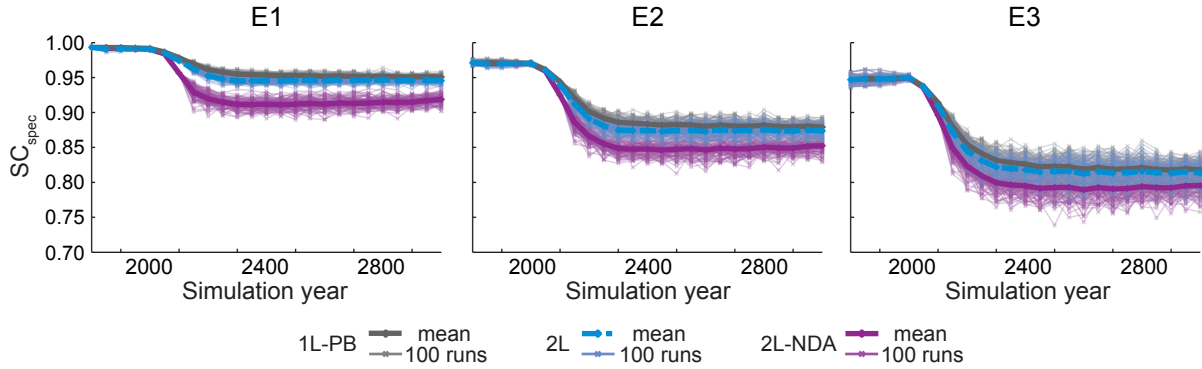


Fig. C.9: Temporal development of  $SC_{spec}$  for application scenario A2 from comparisons of 1L-ORG simulations to simulations with all three sets of bioclimate types (E1-E3).  $SC_{spec}$  values were calculated every 50 years for two-layer simulations with and without dynamic associations (2L and 2L-NDA, respectively) and simulations on one layer but with the bioclimate of the associated bioclimate types (1L-PB). For each setting 100 repetitions were compared, which were simulated using different pseudo-random number streams to extrapolate the bioclimate driver before 1901 and after 2100. Single simulations and their means are printed half-transparent and bold, respectively.

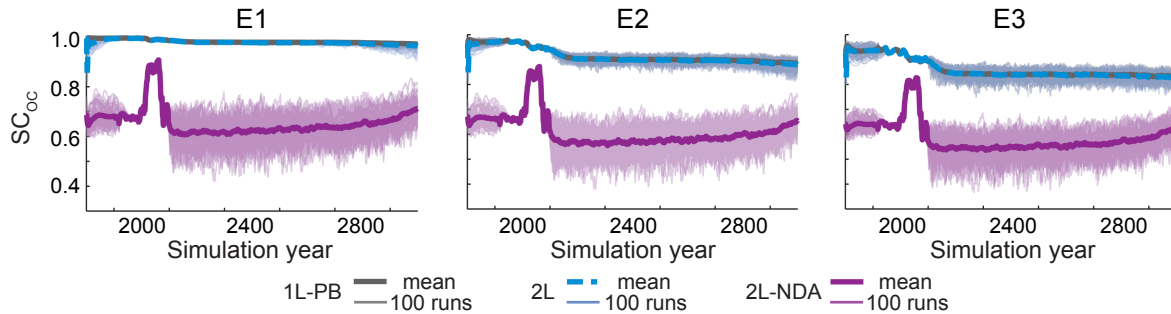


Fig. C.10: Temporal development of  $SC_{Oc}$  comparing simulations of application scenario A2. Depicted  $SC_{Oc}$  values stem from comparisons of 1L-ORG simulations to simulations with all three sets of bioclimate types (E1-E3). Simulations were conducted with two-layers with and without dynamic associations (2L and 2L-NDA, respectively) and with one layer but with the bioclimate of the associated bioclimate types (1L-PB). For each setting 100 repetitions were compared, which were simulated using different pseudo-random number streams to extrapolate the bioclimate driver before 1901 and after 2100. Single simulations and their means are printed half-transparent and bold, respectively.

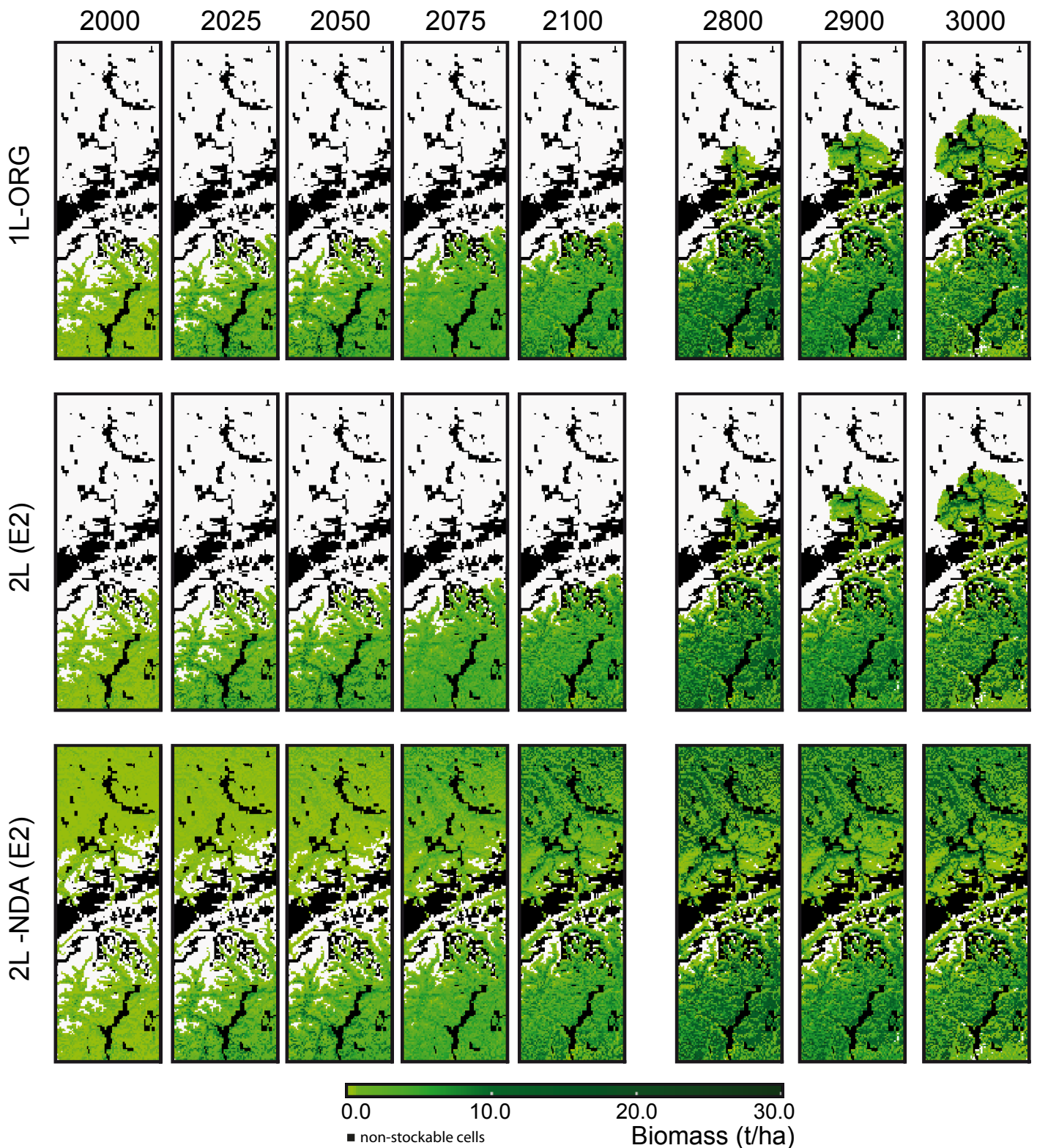


Fig. C.11: Maps of the biomass of *Ostrya carpinifolia* for different simulation years resulting in one-layer simulations with the original bioclimate driver (1L-ORG) and simulations with bioclimate types derived with the moderate-set of bioclimate bins with moderate resolution (E2 – Table 2, main text) and simulated with and without dynamic associations between cells on the two-dimensional layer and elements on the non-spatial layer (2L and 2L-NDA, respectively). Differences in the spatial spread of *O. carpinifolia* between 1L-ORG and 2L simulations on one side and the 2L-NDA simulation on the other side demonstrate the problem of simulations with a general availability of seeds for all species – as assumed in many dynamic vegetation models (see e.g. Snell et al., 2014) – and underline the importance to simulate migration explicitly. Maps of the biomass of *O. carpinifolia* were created with Paraview (Ahrens et al., 2005).

### C.3. Sensitivity tests

In addition to the simulations discussed in the main text, several sensitivity tests were conducted using different splitting and merging thresholds, two different merging intervals and, for scenario A1, different numbers of tracked species.

#### C.3.1. Sensitivity tests for application scenario A1

For application scenario A1, each combination of the variants listed in Table C.2 was simulated with all three sets of bioclimate types (E1-E3) and with five different pseudo-random number streams used to extrapolate the bioclimate driver, i.e. 360 simulations were conducted.

Table C.2: Simulated variants of tracked species, splitting and merging thresholds and merging intervals.

Tracked species	<b>2</b> : <i>P. silvestris</i> / <i>sylvestris</i> and <i>Q. pubescens</i>	<b>4</b> <sup>*</sup> : The two and <i>O. carpiniifolia</i> and <i>L. decidua</i>	<b>6</b> : The four and <i>P. abies</i> and <i>F. sylvatica</i>
Splitting thresholds	<b>1</b> : 0.05 germinated seeds per patch area	<b>2</b> <sup>*</sup> : 0.005 and 0.5 germinated seeds per patch area	
Merging accuracy	<b>c</b> <sup>*</sup> : Coarse merging thresholds <sup>a</sup>	<b>f</b> : Fine merging thresholds <sup>b</sup>	
Merging interval	<b>decade</b>	<b>century</b> <sup>*</sup>	

<sup>\*</sup> Options used in the experiments in the main text.

<sup>a</sup> Similarity thresholds of 50.0, 25.0, 20.0, 15.0, 10.0, 7.5, 5.0, 2.5 individuals per patch for the lowest eight height classes, respectively, and 1.0 for all other height classes.

<sup>b</sup> Similarity thresholds of 5.0 individuals per patch area for the first seven height classes and 1.0 individuals for all other height classes.

The different combinations simulated for scenario A1 led to dramatic differences in the number of elements on the non-spatial layer over the simulated time span. The extremes of these combinations resulted in peak ratios of the number of elements compared to the number of cells in the simulation area from below 2% to around 70% (Fig. C.12). Despite the dramatic differences in the number of elements on the non-spatial layer over time, maximum differences in CPU time reductions were only around 12% (Fig. C.13). Largest differences in CPU time reductions were found among simulations with different number of tracked species when merging was conducted every century. The number of tracked species combined with the merging interval even had a stronger effect on CPU time reductions than the set of bioclimate types (E1-E3). In contrast to CPU time reductions, the level of  $SC_{spec}$  was mainly determined by the applied bioclimate types. In summary, simulations with application scenario A1 showed that the only notable increases in CPU time reductions were achieved by tracing less species or by shortening the merging interval from centuries to decades. Both changes slightly decreased the  $SC_{spec}$ , however, always depending on the other options selected.

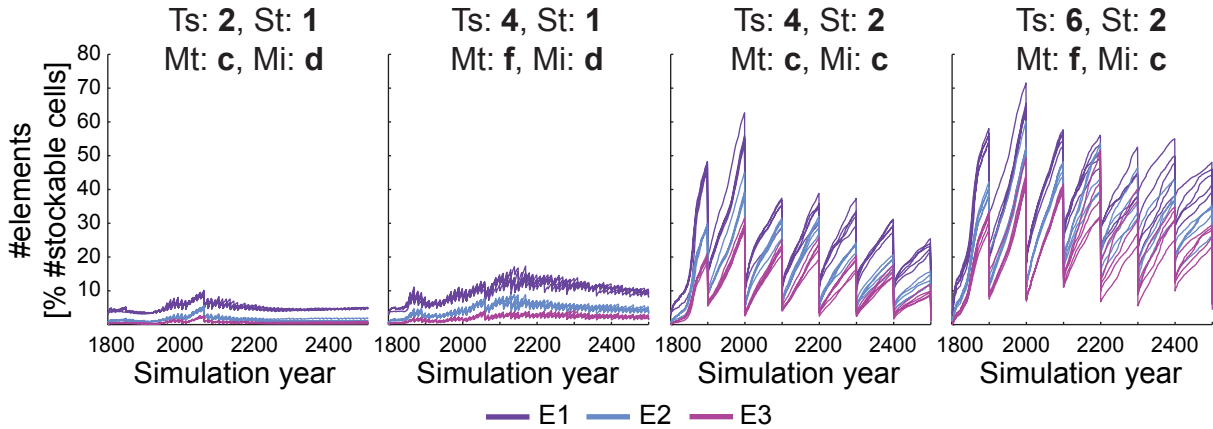


Fig. C.12: Temporal development of the elements on the non-spatial layer relative to the number of cells in the simulation area. Depicted are simulations using all three sets of bioclimate types (E1-E3) and different combinations of the options listed in Table C.2: tracked species (Ts), splitting thresholds (St), merging accuracy (Ma) and merging intervals (Mi). On the left and on the right the extreme combinations are shown. On the left the 'coarsest': tracking absence and presence (St: 1) of two species (Ts: 2) and merging every decade (Mi: d) with coarse merging thresholds (Ma: c). On the right the 'finest': tracking six species (Ts: 6) with two splitting thresholds (St: 2) and merging every century (Mi: c) with finer merging thresholds (Ma: f). In the middle two moderate combinations are shown, of which the second is the combination used in the main text, namely tracking four species (Ts: 4) with two splitting thresholds (St: 2) and merging every century (Mi: c) with coarse merging thresholds (Ma: c). For CPU times and  $SC_{spec}$  values of these and other combinations see Fig. C.13.

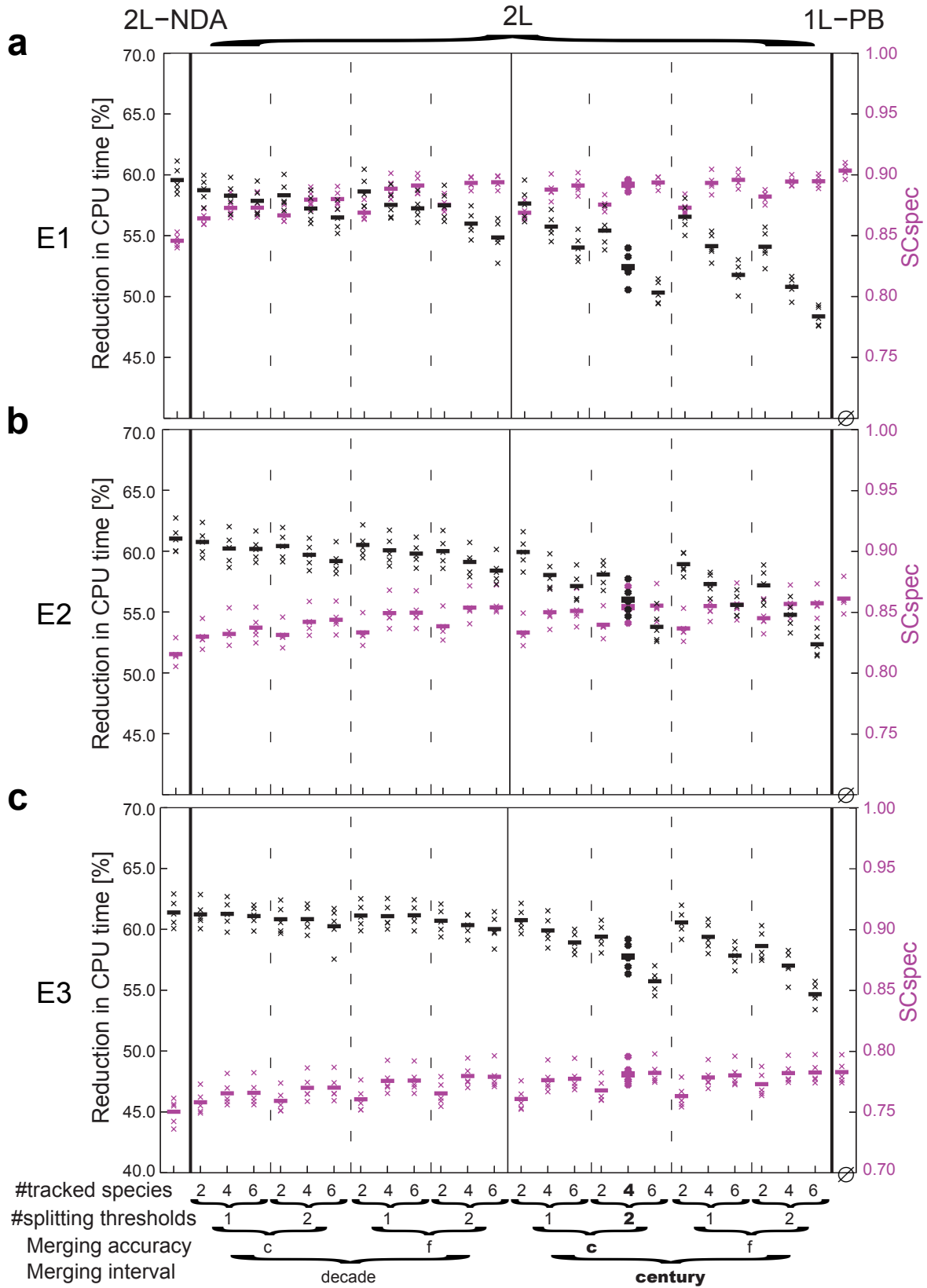


Fig. C.13: CPU time reductions and  $SC_{spec}$  values resulting from simulations of scenario A1 with each set of bioclimate types (E1-E3) using different splitting and merging settings (symbols on the x-axis are according to Table C.2). Additionally, CPU time reductions and  $SC_{spec}$  values resulting from two-layer simulations without dynamic associations (2L-NDA) and one-layer simulations with bioclimate types (1L-PB) are depicted. 1L-PB simulations did not lead to reductions in CPU times (indicated by the empty set sign). Each simulation setting was repeated five times using different pseudo-random number streams to extrapolate the bioclimate driver. The CPU times for single simulations and the resulting  $SC_{spec}$  values in the last simulation year are depicted as crosses, the mean of the five simulations as a dash for each setting. The combination shown in the main text is depicted in bold.

### C.3.2. Sensitivity tests for application scenario A2

For application scenario A2, the same splitting and merging threshold and the same merging intervals as for A1 were used (Table C.2). In addition, all combinations were simulated with a larger set of splitting thresholds (6: 0.0005, 0.005, 0.05, 0.5, 5.0 and 50.0 germinated seeds per patch area). Simulations were conducted using all three sets of bioclimate types (E1-E3) and 20 different pseudo-random number streams for the extrapolation of the bioclimate driver, i.e. in total 720 simulations were conducted.

Opposed to the large differences among A2 simulations with different bioclimate types, changes in other settings showed only tiny differences in the resulting mean CPU time reductions (maximum differences smaller than 3%) and the resulting mean  $SC_{spec}$  values (max differences smaller than 0.01 – Fig. C.14). The same was observed for most settings for mean  $SC_{OC}$  values (Fig. C.15), however, merging intervals of a decade in combination with the coarse merging thresholds led to stronger decreases in the mean  $SC_{OC}$  (maximum differences of about 0.08).

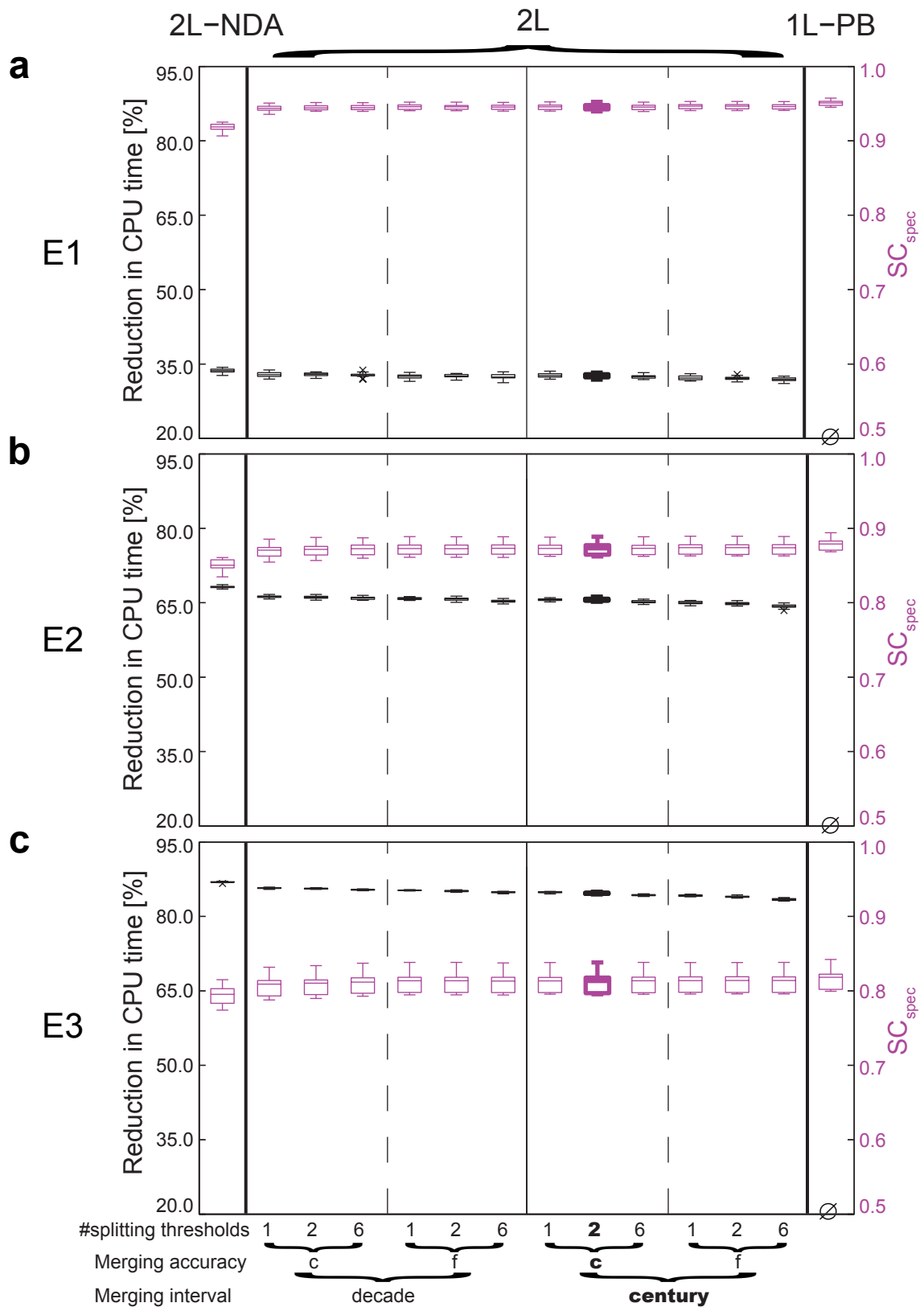


Fig. C.14: CPU time reductions and  $SC_{spec}$  values resulting from simulations of scenario A2 using different splitting and merging settings (symbols on the x-axis are according to Table C.2; for '6' splitting thresholds see text to Section Sect. C.3.2) and each of the three sets of bioclimate types (E1-E3). Additionally, CPU time reductions and  $SC_{spec}$  values resulting from two-layer simulations without dynamic associations (2L-NDA) and one-layer simulations with bioclimate types (1L-PB) are depicted. 1L-PB simulations did not led to reductions in CPU times (indicated by the empty set sign). Each simulation setting was repeated using 20 different pseudo-random number streams to extrapolate the bioclimate driver. The combination shown in the main text is depicted in bold.

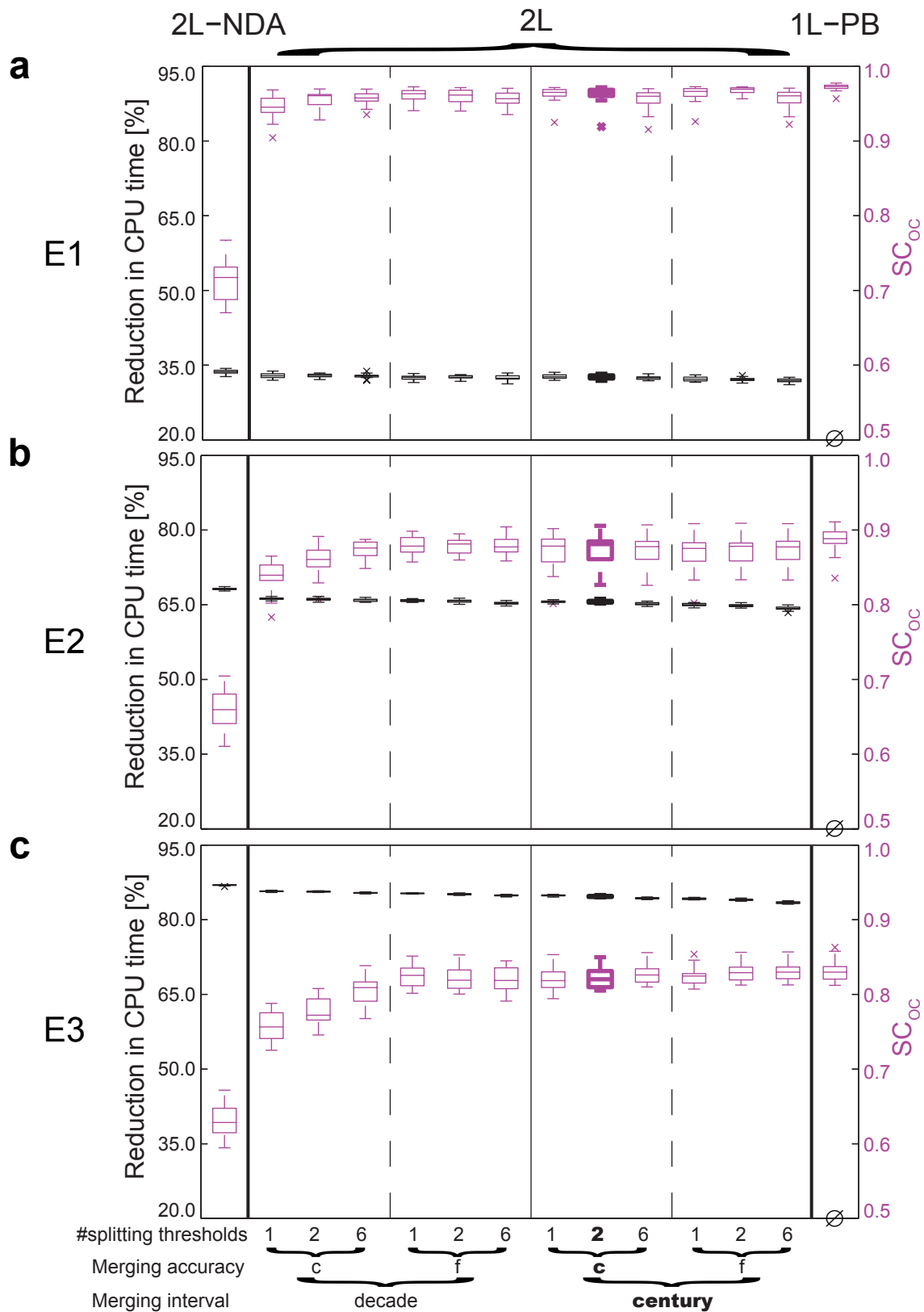


Fig. C.15: CPU time reductions and  $SC_{oc}$  values resulting from simulations of scenario A2 using different splitting and merging settings (symbols on the x-axis are according to Table C.2; for '6' splitting thresholds see text to [Section-Sect. C.3.2](#)) and each of the three sets of bioclimate types (E1-E3). Additionally, CPU time reductions and  $SC_{oc}$  values resulting from two-layer simulations without dynamic associations (2L-NDA) and one-layer simulations with the bioclimate driver from the bioclimate types (1L-PB) are depicted. 1L-PB simulations did not lead to reductions in CPU times (indicated by the empty set sign). Each simulation setting was repeated using 20 different pseudo-random number streams to extrapolate the bioclimate driver. The combination shown in the main text is depicted in bold.

## References

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