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Simulating migration in dynamic vegetation models efficiently using LPJ-GM

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Abstract

Dynamic vegetation models are a common tool to assess the effect of climate and land use change on vegetation. While the current development aims to include more processes, e.g. the nitrogen cycle, the models still typically assume an ample seed supply allowing all species to establish once the climate conditions are suitable. A number of species have been shown to lag behind in occupying climatological suitable areas (e.g. after a change in the climate) as they need to arrive and establish at the newly suitable areas. Previous attempts to implement migration in dynamic vegetation models have allowed simulating either only small areas or have been implemented as post process, not allowing for feedbacks within the vegetation. Here we present two novel methods simulating migrating and interacting tree species which have the potential to be used for continental simulations. Both distribute seeds between grid cells leading to individual establishment. The first method uses an approach based on Fast Fourier transform while in the second approach we iteratively shift the seed production matrix and disperse seeds with a given probability. While the former method is computationally marginally faster, it does not allow for modification of the seed dispersal kernel parameters with respect to terrain features, which the latter method allows.

We evaluate the increase in computational demand of both methods. Since dispersal acts at a scale no larger than 1 km, all dispersal simulations need to be performed at least at that scale. However, with the current available computational power it is not feasible to simulate the vegetation dynamics of a whole continent at that scale. We present an option to decrease the required computational costs, reducing the number of grid cells where the local dynamics is computed by simulating it only along migration transects. Evaluation of species patterns and migration speeds shows that although the simulation along transects reduces the migration speed slightly, both methods are reliable. Furthermore, both methods are sufficiently computationally efficient to allow large scale DGVM simulations with migration on entire continents.

1. Introduction

A large suite of dynamic global vegetation models (DGVMs) is currently used to simulate the effects of climate and / or land use change on vegetation and ecosystem properties. These simulations result in projections (or hind-casts) of species ranges as well as changes in ecosystem properties such as carbon stocks and fluxes. Examples of these DGVMS include ORCHIDEE (Yue et al., 2018), LPJ-GUESS (Sitch et al., 2003), IBIS (Foley et al., 1998), (Sato et al., 2007), for a review of DGVM features see (Quillet et al., 2010).

These models typically assume that species can establish at any site once the environmental conditions become suitable. However, in real ecosystems species need not only to establish and replace existing vegetation – the processes gap models describe successfully – but they also need to have sufficient

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amount of seeds at a given location to successfully establish. Implicitly, current DGVMs assume that ample amounts of seeds of all species are present in every location.

While this approach might seem reasonable in cases where the vegetation can keep up with climate change (i.e. moving sufficiently fast to occupy areas which become suitable), there have been a number of instances reported where a considerable migration lag occurred. For instance *Fagus sylvatica* has been shown to have a considerable migration lag and is currently still in the process of occupying its climatological optimum (Bradshaw and Lindbladh, 2005).

Inclusion of migration is not only of interest to simulate species migration in the past. For the projection of ecosystem properties in the future (with projected climate), migration lags might lead to uncertainties in projected ecosystem properties if the wrong species community is predicted to occur at a certain site. Especially, given that the speed at which environmental conditions change currently is unprecedented at least over the last centuries, effects of the migration lag of key species should be evaluated when projecting ecosystem properties.

Migration lags can be caused by different factors. Seed transport might only occur over limited distances. But also low seed amounts and in particular long generation times can slow down migration. Seed amount and generation time depend on the competition with other trees: a free standing tree starts earlier to produce seeds and produces more than a tree of the same age in the closed forest. The competitors, however, are also migrating, which leads to feedbacks between the species.

Thus, for simulations over large areas covering long time spans, species migration – consisting of a) local dynamics influenced by the environment, b) competition between species, and c) of seed dispersal – has to be taken into account simultaneously for several species.

Species migration has been implemented successfully in dynamic vegetation models working on smaller extents and finer scales than DGVMs typically use, e.g. forest landscape models (FLMs; review in Shifley et al, 2017), such as TreeMig, (Lischke et al., 2006), Landclim (Schumacher *et al.*, 2004), Landis (Mladenoff, 2004), or Iland (Seidl et al., 2012).

In these models, seed dispersal is modelled in a straightforward way: seeds are distributed from each producing to each receiving cell with a distance dependent probability. However, transferring these approaches to DGVMs is problematic, due to a number of conceptual and technical difficulties. DGVMs usually operate on a coarse spatial resolution to reduce computational load and input data requirements. This neglects the spatial heterogeneity within the grid cells. Additionally, and even more critical for implementing migration, it leads to discretization errors: if it is assumed that the forest representing the grid cell is located in the centre of the cell, the seeds cannot move far enough to leave the cell (given a typical cell size of 50km by 50km). If it is assumed that the simulated forest is

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uniformly distributed in the cell, with each time step some of the seeds reach the neighbour cell, leading to a resolution dependent speed up of the migration.

Additionally specifics of model implementations might complicate the inclusion of migration in some DGVMs. Many DGVM implementations are done in a way that for each grid cell all years are simulated before the simulation of the next cell is started. This is done to minimize input-output effort since the whole climate data for each cell is read in at once and it also eases parallelisation for multi-core computer since in this case each node is assigned a number of grid cells which the node calculates independently of the other nodes with no required communication. However, for simulating seed dispersal, all cells need to be evaluated in each time step.

There have been a number of attempts to integrate species migration in DGVMs (cf. Snell *et al.*, 2014, and Discussion section). For example, Sato and Ise (2012) developed a DGVM where species could potentially migrate between neighbouring cells with a fixed rate of about 1km/year.

However, to the knowledge of the authors, there is no implementation into a DGVM which allows simulations at continental scale, takes into account the migration within the grid cell and includes feedbacks between all simulated species.

Here we present two methods to fill this gap, i.e. allow simulating species migration of several species simultaneously. The methods are implemented into the LPJ-GUESS DGVM but can potentially also be implemented into other DGVMs. Though they are tested here using a virtual landscape they can be applied for continental simulations given current computing resources.

2. Methods

2.1 The dynamic vegetation model LPJ-GUESS

LPJ-GUESS is a flexible framework for modelling the dynamics of terrestrial ecosystems from landscape to global scales (Sitch et al., 2003; Smith et al., 2001). This DGVM consists of a number of sub-modules containing formulations of subsets of ecosystem processes at defined spatial and temporal scales. A large body of publications describes the features of LPJ-GUESS in detail; here we concentrate on the changes that were applied to LPJ-GUESS version 4.0. To differentiate between the original version of LPJ-GUESS and our extended version (where we implemented the migration module) we refer to the extended version as LPJ-GM (short for LPJ-GUESS-MIGRATION).

2.2 Technical implementation

Standard LPJ-GUESS simulations are typically performed at a computing cluster with cells running on different nodes of the cluster without any interaction of the nodes. We implemented a distributed simulation using MPI (Clarke et al., 1994) with the grid cells communicating with a master process.

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Seeds are produced potentially in each grid cell at the end of each migration year. The number of seeds produced is sent to the node computing the dispersal while all nodes wait for this node to finish the calculation. This node sends the number of seeds that arrive at each grid cell back to all nodes to continue the calculation.

Similar to the standard version of LPJ-GUESS (Sitch et al., 2003; Smith et al., 2001), in the first 100 years no seed dispersal is performed and all plant types are allowed to establish and grow without N-limitation to equilibrate the soil pools with carbon and nitrogen. This time period is used to sample NPP given a certain N deposition and climate to subsequently equilibrate the N pools of the soil and a fast spin-up of 40000 years approximated using the sampled rates of C assimilation (Smith et al., 2014). After this initialisation period all vegetation is killed and succession starts from a bare soil and now seed limitation is active.

In LPJ-GM seed dispersal is done on an annual basis which corresponds to the temporal resolution of seed production. The amount of seeds produced is communicated to the master node at the end of each year. The master node re-distributes seeds over the whole spatial domain according to the dispersal algorithm and communicates the amounts of arriving seeds back to each grid cell. Seeds transferred to the grid cells are added to the seed bank which determines establishment probability in environmentally-suitable cells. All communications between the processes are done via MPI protocol (Clarke et al., 1994).

LPJ-GUESS is a gap model with the typical successional vegetation changes. To even out successional based fluctuations in ecosystem properties and to be able to simulate disturbances a certain number of replicate patches are simulated per grid cell. All patches share the same climate but potentially differ in their successional stage due to different timing of disturbances and stochastic mortality. Conceptually, each patch has a size of 1000 m^2 but represents an area depending on the resolution of the grid cell. Patches have no spatial position with respect to each other and do not interact (Smith et al., 2001). In LPJ-GM we reduced the number of patches to one but achieved the representative averaging by using explicitly placed small grid cells instead of statistical units (replicate patches). For each large grid cell in the climate grid we simulate a large number of cells of 1km^2 area resulting in a more than sufficient averaging of successional stages. LPJ-GUESS simulations are typically performed with patch numbers around 10 (e.g. Smith *et al.*, 2001) but depending on the aim of the simulation patch numbers have been increased even to 500 (e.g. Lehsten *et al.*, 2016). In our setup even with 50 km corridors (see below) LPJ-GM represents a 0.5x0.5degree cell with 200 simulation cells ranging at the higher end of the patch number per area compared to previous simulations.

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2.3 Migration processes

2.3.1 Seed production

Similar to TreeMig (Lischke et al., 2006) we implemented seed production (depending on leaf area index; LAI) and seed bank dynamics.

The seed number produced within each grid cell is calculated as the product of the maximum fecundity multiplied by the proportion of the current LAI to the maximum LAI and multiplied by the area per grid cell (Lischke et al., 2006). No specific age of maturity is taken into account.

All seeds of a species produced S(x',y') at a location (x',y') within a year are available for seed dispersal. Once seeds have entered the seed bank, no further dispersal is possible (they remain in the seed bank). Though LPJ-GUESS keeps track of carbon allocated to the main plant compartments and even allocates a certain amount of carbon to seeds (which is transferred to the litter pool, the soil pool and finally the atmosphere), for simplicity we decided not to relate the seed production to the carbon accounting at this point. Allocation rules including seed production and even mast fruiting effects could be included in the future.

2.3.2 Seed dispersal

The produced seeds are distributed according to

$$S_d(x,y) = \int S(x',y') k_s(x-x', y-y')\, dx'\, dy' \qquad \text{(eq. 1)}.$$

$S(x',y')$ is the seed production, and $k_s(x-x', y-y')$ the seed dispersal kernel in euclidean coordinates. The seed distribution $S_d(x,y)$, i.e. the input of seeds in location x, y is then obtained by integrating over all possible locations x', y' for arriving at x, y.

Thus, the seed distribution is given by the convolution of the seed production and the seed dispersal kernel:

$$S_d = S ** k_s. \qquad \text{(eq. 2)}$$

For this study we used the seed dispersal kernel and parameterization from TreeMig (Lischke *et al.*, 2006). The seed dispersal kernel defines the probability of seeds arriving at a sink cell (x,y) from the source cell (x', y') with a certain distance $z = \sqrt{(x-x')^2 + (y-y')^2}$.

The kernel is specified in a polar coordinate system,

$k_s(z,\theta) = k_s(z|\theta)k_s(\theta)$, with the radial distance z. The seeds follow a mixture of two exponential distributions, the short and the long term dispersal, while the angular dispersion, θ, is uniform in all directions (in our case the angular dispersion θ is uniform, but if one is interested in implementing wind directions this can be changed). Thus, the radial component of the kernel is given by

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$$k_s(z|\theta) = (1-\kappa)\frac{1}{\alpha_{s,1}} e^{-\frac{z}{\alpha_{s,1}}} + \kappa \frac{1}{\alpha_{s,2}} e^{-\frac{z}{\alpha_{s,2}}}, \kappa \in (0,1) \quad \text{(eq. 3)}$$

while the angular term is given by

$$k_s(\theta) = \frac{1}{2\pi} 1_{\{\theta \in [0,2\pi]\}}. \quad \text{(eq. 4)}$$

The dispersal kernel is defined by the species specific values for the proportion of long term dispersal κ and the species expected dispersal distances $\alpha_{s,1}$ and $\alpha_{s,2}$ for the two kernels.

The species specific values for these parameters were roughly estimated by Lischke *et al.* (2006) to be 0.99 for κ_s and 25m and 200m for the two mean dispersal distances k_s for *Fagus sylvatica*.

2.3.3 Seed bank dynamics

The number of the seeds in the seed bank is increased by the influx S_d of seeds according to (eq. 1) , and reduced by the yearly loss of germinability and the amount of germinated seeds at the end of each simulated year, similar to TreeMig (Lischke et al., 2006).

A year is defined for each species and grid cell before which seed bank constraints are ignored (hence free establishment happens). This way we can specify in which areas each species is already potentially established at the beginning of the simulation and this defines thereby the location of the refugia. This parameter can also indicate that a species is not hindered in its establishment by migration.

2.3.4 Germination

LPJ-GUESS is a gap model and in the original version the number of newly established saplings only depends on the amount of light reaching the forest floor (given that the cell has a suitable climate). In LPG-GM we additionally limit the establishment of seedlings depending stochastically depending on the number of available seeds. The probability that a species establishes is proportional to the seed number in the seed bank multiplied by the seed germination proportion and an extra parameter which (implicitly) takes the area of each grid cell into account. In our case we fixed this parameter to 0.01 after initial testing. Hence if in a certain year 100 seeds are in the seed bank per and the germination rate is 0.71 (value for *Fagus sylvatica*) the probability of an age cohort establishing is 0.01*100*0.71=0.71.

2.4 Enhanced dispersal simulation

One way to simulate seed dispersal is to calculate the convolution of all seeds produced of the matrix containing the seed production and the seed dispersal kernel (specified in eq. 1 and eq. 3). However, evaluating the convolution explicitly can be computationally expensive for seed dispersal kernels with long range.

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2.4.1 Fast Fourier transformation method (FFTM)

An alternative is based on the convolution theorem and the Fast Fourier Transformation (FFT), a technique commonly used in physics, image processing and engineering (Strang, 1994).

This approach carries out the computations in the frequency domain, see Gonzales & Woods (2002). Here we use the notation $F\{S\} = \int e^{-iux-ivy} S(x,y)\, dx\, dy$ to denote the two dimensional Fourier transform of S and correspondingly $F\{k_s\}$ the two dimensional Fourier transform of k_s. It then follows that the Fourier transform of the convolution equals the product of the Fourier transforms

$$F\{S \ ** \ k_s\} = F\{S\}F\{k_s\} \qquad \text{(eq. 5)}$$

Thus, it is possible to compute the convolution by applying the inverse Fourier transform to the products of the Fourier transforms

$$S \ ** \ k_s = F^{-1}\{F\{S\}F\{k_s\}\} \qquad \text{(eq. 6)}$$

This equation must be discretized before evaluating it on a computer. The discrete Fourier transform is computed using the Fast Fourier Transform (Cooley and Tukey, 1965), which has a computational cost of $O(N^2 log^2(N))$ in two dimensions. The discrete approximation of S_d is then given by

$$S_d = F^{-1}\{F\{S\} \odot F\{k_s\}\} \qquad \text{(eq. 7)}$$

where $\odot$ is the element-wise (Hadamard product) multiplication of matrices.

Nowadays, software packages for FFT typically only compute positive frequencies. That means that we have to shift the frequencies prior to the element-wise multiplication of $F\{S\}$ and $F\{k_s\}$. This is illustrated in Fig.1 see also supplementary material S.2.

<Figure 1 to be placed here>

While this method allows including different wind distributions by changing the seed dispersal kernel, it does not allow to use different seed dispersal kernels at different locations, e.g. due to prevailing wind directions in valleys, due to barriers to animal transport like a motorway, or due to lower transport permeability in already forested areas.

2.4.2 Seed matrix shifting method (SMSM)

Another way to simulate seed dispersal is to simulate the seed movement between the cells explicitly by shifting the matrix containing the produced seeds by one position (repeatedly in all directions of the Moore neighbourhood) and simulating seed transport of a certain proportion of the seeds into the next cell. Each move can be viewed as an independent random variable. Repeating these moves thus

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corresponds to a random walk process. The Lindeberg's condition for sequences for sums of independent random variables ensures that the kernel will be Gaussian under general conditions (Shiryaev, 2016), with the expected value given by the sum of expected values for each random variable and similarly for the variance (see supplementary material S.1 for a formal proof and a derivation of the parameters of the resulting normal distribution).

If this is done repeatedly it allows an easy implementation of spatial explicit differences in seed dispersal kernel distributions, by adjusting the proportions of seeds being transported into the next cell according to a similarly sized matrix containing the area roughness or permeability. By this approach, barriers and even wind speeds in latitudinal and longitudinal directions can be implemented by adjusting the dispersal probabilities accordingly.

<Figure 2 placed here>

After the distribution of the dispersed seeds is calculated, the seeds are added to the seed bank.

2.5 Corridors

Seed dispersal acts at a rather fine scale compared to the usual scale at which DGVMs are run (LPJ-GUESS is typically run at a 0.5 to 0.1 degree longitude / latitude scale). Given that the average long distance seed dispersal for example for *Fagus sylvatica* is 200 m, simulations at such a coarse scale will not be able to capture this process.

As a compromise between currently available computing resources and required simulation detail we choose a 1km scale at which we performed our simulations. However, even at this scale, simulating for example the European continent would result in an extreme computational effort.

Given that in some areas the landscape is rather homogenous while other areas have a variable terrain (or land use conditions), we test whether for the homogenous landscapes it is sufficient to simulate the local dynamics only in latitudinal, longitudinal and diagonal transects (corridors) and how this will influence the migration speed. The corridors are 1 grid cell wide and regularly placed in the simulation domain. Their density can be chosen by defining the distance between the latitudinal and longitudinal corridors.

Although LPJ-GM only simulates local dynamics in the cells along the corridors, the seed matrix needed to be filled for the dispersal calculation using the FFTM or the SMSM algorithm. We applied a nearest neighbour interpolation of the seed production before performing the seed dispersal calculation (theoretical considerations show that a distance weighted average would strongly speed up the migration).

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2.6 Simulation experiments

To test our newly developed migration module we simulated the spread of a single late successional species (*Fagus sylvatica*) through an area covered by an early successional species (*Betula pendula*). All grid cells and all years in the simulated area had a static climate suitable for both species. For a specific simulation using the SMSM method we assumed differences in the dispersal ability (e.g. more or less permeable areas or physical barriers) while the climate on all grid cells is still static and favourable. Given the uniformity of the climate, there should be no variability in the migration speed caused by differences in climatic conditions. We simulated the spread of *F. sylvatica* from a single grid cell in the corner of the study area which represents the refugium. We tested several corridor distances (between the parallel and between the diagonal corridors) for their effect on the migration speed. We calculated the migration speed as the distance between the start point of the migration and the 95 percentile farthest point in the virtual landscape where the leaf area index (LAI) of *F. sylvatica* is larger than 0.5 divided by the simulated time elapsed since the start of the migration. To avoid founder effects we neglected the points within the first 5 km of the refugium. The simulations were performed over 3000 years and over an area of 100 by 100 cells of 1 km^2. Finally we ran one simulation where we did not calculate the seed dispersal (but performed all communication between cells), hence allowing us to estimate the computation time demand for the seed dispersal calculation.

3. Results

3.1 Explicit seed dispersal

Pre-studies have shown that both the FFTM as well as the SMSM are performing much faster than an explicit dispersal from each grid cell to each other within the range of the dispersal. This is especially pronounced if the area to be simulated is increased. Instead of comparing the explicit seed exchange with the FFTM using LPJ-GM we demonstrated this with a small Matlab™ script in the supplementary material S.2 which also allows demonstrating both the transformation of the seed dispersal kernel as well as the FFTM in detail.

3.2 FFTM simulations

Using the parameterization from TreeMig in a complete (no corridors) simulation area of 100 by 100 grid cells results in a migration speed of 34 m per year for *Fagus sylvatica* (Fig. 3).

<Figure 3 placed here>

Though the establishment is stochastic, the spread is relatively smooth. Using at a distance of 10 km, 20 km and 50 km results in a somewhat reduced migration rate of 26, 28 and 28 m/year (compared to a simulation without corridors), respectively (Fig 3, lower three rows of panels). While in the simulation without corridors the variability of the migration speed is relatively low (dots under the red line in upper left panel of Fig 3), this variability is strongly increased when corridors are simulated.

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310 This is caused by *F. sylvatica* migrating along the diagonal, reaching the end point of the diagonal and
311 then migrating along the longitudinal and latitudinal corridors into cells which have actually a shorter
312 distance to the refugia than the endpoint of the diagonal.

313 The calculation time per grid cell in the whole area (range for which the seed dispersal is computed) is
314 increased by 12% by simulating the FFT, but by using the corridors it is reduced to 36%, 22% and
315 12%, compared to simulating the full area (Tab. 1, col. 7). The proportion of computation time used
316 to perform the FFT increases from 11% without corridors to 18%, 29% and 29% for simulations with
317 corridors every 10, 20 and 50 km. This estimate only includes the required time for computing the
318 FFT-based seed dispersal since the control run without seed dispersal still contained all
319 communication between cells. For the control run seeds were produced and send to the master but the
320 master did not compute the seed dispersal, though still communicated with all other nodes to allow a
321 fair assessment of the computation time demand of the two methods (see Tab. 1).

322 ### 3.3 Shifting seed simulations

323 Initial testing of the probability parameter for the SMSM suggested a value of $p=5 *10^{-7}$ to generate a
324 migration speed comparable to the migration speed for the FFTM based on the TreeMig
325 parameterization.

326 This resulted in a migration speed of 39 m/year for the filled area and 27m/year respective 29 m/year
327 and 30m/year for the 10 km, 20 km and 50km corridors (Fig. 4).

328 <Figure 4 placed here>

329 Similarly to the FFTM simulations, the migration speed is reduced (see table 1 for a summary). Also
330 comparable to the FFTM based seed dispersal computation, calculation time per grid cell in the whole
331 area (range for which the seed dispersal is computed) is increased by 16% by the simulation of
332 dispersal, but reduced to 35%, 19% and 11% by using the corridors. The proportion of calculation
333 time spend for simulating the seed dispersal is comparable to the proportion using the FFT, it is 16%,
334 19%, close to 23% and 32% (see Tab. 1).

335 Since the SMSM allows adjusting the probability depending on the seed transport permeability of the
336 terrain we also simulated the migration within a non-homogenous dispersal area. The results of this
337 simulation are displayed in Fig 5.

338

339 <Figure 5 placed here>

340 Though all cells of the virtual landscape have a similar climate, some cells will never be occupied (see
341 Fig. 5) because the seeds are not able to reach them (which might not be reasonable for real world

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simulations but demonstrates the method). Migration speed is different in different parts of the simulated area.

<Table 1 placed here>

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4. Discussion

To our knowledge we are the first that manage to implement (tree-) species migration in a DGVM in a way that allows continental simulations of simultaneously migrating and interacting species.

4.1 Performance of new migration methods

The presented new methods for simulating migration in DGVMs show a promising performance in different aspects.

The first is the gain of efficiency by the FFTM and the SMSM methods as compared to the traditional, straightforward approach to evaluate the seed transport from each cell to each other (last Fig in S.2). A two dimensional FFT can be obtained by successive passes of the one dimensional FFT, hence the complexity will be the one-dimensional complexity squared (Gonzalez and Woods, 2002).The computational complexity for the FFTM is $O(N^2 log^2(N))$ for a $N \times N$ grid discretizing the seed distribution, while the complexity of the direct implementation of the convolution approach in the SMSM is $O(2KRN^2)$ for a $N \times N$ grid discretizing the seed distribution and $R \times R$ kernel (for the derivation see supplementary material S.1). This can be computationally comparable to the FFTM for kernels with short range of R. Secondly, simulating the local dynamics only along the corridors instead of in the full area resulted in a very similar migration pattern, and the simulated migration speed is similar to that of the simulation with full grid cell cover (it is slightly slower, caused by the stochasticity of the establishment), but needs much less computing time (reduction of 88% for the corridors every 50km).

4.2 Comparison of the two dispersal methods

In this study we present two alternative methods for simulating dispersal, which differ in their properties. While the FFTM allows any type of seed dispersal kernel, the SMSM corresponds to a normal distribution kernel. Although other shapes of dispersal kernels can be approximated by weighted sums of normal distributions, of which each of them has to be simulated by an own SMSM, which will cause strong increases in computational demand.

On the other hand, the advantage of the SMSM lies in its ability (contrary to the FFTM) to modify the parameters of the seed dispersal kernel spatially depending on the terrain. If instead of applying a single permeability for all directions, different permeability is applied for each of the 8 directions (e.g. north, northeast, east, etc.) this method also allows a spatially explicit consideration of wind directions (which is not possible for the FFTM, as it relies on a universal kernel applied to the whole entire area). Hence, depending on the aim of the analysis either one of the algorithms most suitable.

4.3 Comparison to other approaches

Our new species migration submodule FFTM uses for the first time (to our best knowledge) in ecology an algorithm based on Fast Fourier Transformation to simulate dispersal in a DGVM, which due to its

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efficiency is one of the "workhorses" in mathematics, physics and signal processing (Strang, 1994). The SMSM, in turn, mimics the seed transport process itself in a simple and straightforward way, which to our knowledge has also not been implemented in DGVMs either.

Both approaches are combined with features of modelling species migration that are already used in other DGVMSs (cf . Snell, 2014).

The cellular automaton KISSMig (Nobis & Normand, 2014), e.g. simulates the spread of single species driven by a spatio-temporal grid of suitability, and by transitions to the nearest neighbour cells, which is similar to one iteration in the SMSM. The suitability based models CATS (Dullinger *et al.*, 2012) or MigClim (Engler and Guisan, 2009) simulate a simple demography of single species and explicitly the spread based on a seed dispersal kernel.

To also account for ecophysiology, the CATS model was combined with LPJ-GUESS in a post-processing approach (Lehsten et al., 2014) which used a spatio-temporally explicit suitability estimated from LPJ-GUESS simulated productivity of a single species, assuming the presence of the other species. This suitability was subsequently used within CATS to simulate migration spread rates. Such a post-processing approach however does not include interactions between several migrating species.

Forest landscape models have been developed to integrate such feedbacks between species as well as dispersal (He et al., 2017; Shifley et al., 2017). These models simulate local vegetation dynamics with species interactions, and dispersal by explicit calculation of seed or seedling transport probabilities with dispersal kernels of different shapes (e.g. LandClim (Schumacher *et al.*, 2004), Landis (Mladenoff, 2004), Iland (Seidl et al., 2012)). To capture spatial heterogeneity, they run at a comparably fine spatial resolution (about 20-100m grid cells), allowing only the simulation of relatively small areas due to computational demands.

To overcome such computational limits, several approaches for a spatial upscaling of the models have been put forward. For example, the forest landscape model TreeMig can operate at a coarser resolution (grid cell size 1000m) because it aggregates the within-stand- heterogeneity by dynamic distributions and height classes (Lischke et al., 1998), which allows applications at a larger scale, e.g. over entire Switzerland (Bugmann et al., 2014) or on a transect through Siberia (Epstein et al., 2007). Another upscaling of TreeMig was achieved by the D2C method (Nabel, 2015; Nabel and Lischke, 2013) which simulates local vegetation dynamics only in a subset of cells that are dynamically determined as representative for classes of similar cells. This method led to a computing time reduction of 30-85% as compared to the full simulation similar to our transect methods which resulted in 85 % gain of computing time.

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In dynamic global vegetation models (DGVMs), the discretization problem is even more pronounced, because they are designed to operate on very large extents (continents or the entire globe). Given the computational demands of the simulations, they are therefore typically running at a coarse resolution for example 0.5 or 0.1 degree longitude / latitude, and simulate the vegetation dynamics at the centre of each of these grid cells, assuming this point to be representative for the entire cell.

Snell (2014) approached the discretization problem for the DGVM LPJ-GUESS by also using a reduced number of representative units (here patches) within each grid cell. She assumed that the numerous replicates of the vegetation dynamics on a patch are randomly distributed over the area of the grid cell. Migration within the grid cell is treated similar to an infection process, where the probability of a patch becoming infected (e.g. of the migrating species being able to establish) depends only on the number of already invaded patches within the grid cell. Only once a migrating species managed to establish in a certain proportion of the patches of the simulated grid cell, further dispersal (explicit via a dispersal kernel) into surrounding grid cells is possible. Yet, there is no spatial orientation of the patches within the grid cell and all simulations in this approach are strongly resolution dependent. Simulations of large areas such as continents remain computational challenging with this approach.

Our transect approach, similarly to the approach of Snell (2014), uses smaller representative spatial units, 1km-cells, for a spatial upscaling. Since these small grid cells are arranged in contiguous corridors, the migration along these corridors can be simulated without or with only a small discretization error. The results indicate that also the error potentially introduced by the interpolation to the rest of the area is small.

Thus, with our approaches, we have combined several advantages of the before mentioned approaches: the seed dispersal from forest landscape models, improved by the novel FFTM or SMSM and the ecophysiology, structure and community dynamics of LPJ-GUESS. We furthermore found a compromise between discretization and efficiency by the corridor method.

4.4 Potential further improvements

Despite the satisfying performance of the new methods in these first tests some aspects suggest further development.

4.4.1 Computation time

Even with the computing time reduction by the corridor approach using a corridor of 50km distance, the computing time required for the simulations including dispersal is still considerable. This is caused by the number of cells on the corridors where the local dynamics is simulated being larger than the number of replicates usually used in all the 1 or 0.5 degree grid cells simulated in traditional DGVMs. For large-scale applications, the approach should be further optimized, e.g. by choosing corridors even further apart from each other in homogenous areas and adapting the corridor density to the large

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scale (between grid-cell) heterogeneity of the terrain. The within grid-cell heterogeneity in turn can be accounted for by deriving seed dispersal permeability, that can be used in the SMSM approach. Another area of improvement lies in the technical implementation of the seed dispersal algorithm. In the current implementation the seed dispersal is performed at a single cpu, while all other cpus wait until they receive the seeds. There are certainly ways to perform the seed dispersal computation on several nodes to decrease the waiting time. Furthermore, in multi-species simulations the dispersal has to be calculated for each migrating species. In this case, the dispersal of different species should be calculated on separate nodes. When evaluating the run times needed for the simulated areas in the supplementary material it becomes obvious that sometimes larger areas resulted in shorter runtimes for the FTTM (last Fig. in S.2). The differences are quite pronounced given that the time axis is logarithmic. These decreases are caused by the effect that the calculation of a fft can be optimised in case the domain has a size of 2^n.

4.4.2 Migration speed reduction by corridor approach

As expected, any sub-cell assumption results in discretisation errors. In our case the assumption of a corridor slightly reduced the migration speed. This needs to be taken into account when evaluating the result of such studies. The design of the corridors might also not be optimal, maybe a corridor wider than a single cell might result in less decrease of migration speed. However, these types of analysis are outside the scope of this study.

4.4.3 Parameterisation of dispersal kernels

In this study the focus is on developing and testing the novel methods, i.e. we do not attempt to correctly simulate the spread of *F. sylvatica* over a defined time period. The calculated spread rates are well below most of the spread rates in the literature. *F. sylvatica* has been estimated to migrate with ca 100 m per year based on pollen analyses by Bradshaw and Lindbladh (2005). Although such estimated high migration speeds could also be the result of glacial refugia located further north than assumed (Feurdean et al., 2013), our estimates of the migration speeds of 20-30 m/year still seem rather low. However, in this paper we aimed to implement tree migration by using the parameterisation of TreeMig in a DGVM and thereby allow continental scale simulations. Our estimated migration rates of 20-30 m per year are very close to the migration rates estimated for this parameterisation for TreeMig by Meier *et al.*, (2012) which estimated a value of 22 m per year. Hence, though we implemented the migration module into a conceptually very different model, the resulting migration rate remains comparably similar.

To perform modelling runs estimating the migration speed of any species would require a fine tuning of the seed production and dispersal parameters (which are both very rough estimates in TreeMig (Lischke et al., 2006) to generate the observed migration e.g. by comparing to migration rates based on pollen records.

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4.5 Potential for applications

The test simulations were performed at a virtual landscape of 100km by 100km, but eventually the method is aimed to allow continental simulations over several millennia. Regarding memory requirements, this is possible of currently available hardware: Test runs with landscapes of 4000 by 4000 grid cells (i.e. the size of Europe) performed without technical problems at least regarding the memory requirement (given 62 GB of RAM). The considerable computational costs however require a relatively high amounts of computing time, which might be reduced by efforts for speeding up (due to efficient parallelisation) of the FFT as the local simulations, e.g. by even further apart corridors.

5. Conclusions

The presented novel approaches offer a high potential to simulate the spatiotemporal dynamics of species which are migrating and interacting with each other simultaneously. The approaches are not restricted to LPJ-GUESS, but can in in principle be applied to other DGVMs or FLMs which simulate seed (or seedling) production and explicit regeneration. While the presented methods will allow in future to simulate tree migration at continental scale and over paleo time scales, our study also shows that the estimates for seed dispersal kernels for the major tree species need to be revised to allow truly mechanistic simulations of forest development for example over the Holocene.

6. Author contributions

VL, DL and HL designed the study, VL performed the simulations and the statistical analysis. MM and EL contributed to the study design, MM also performed large parts of the coding. EL developed the formal proof in Supplementary material S.1 and the computation performance related estimates the Conclusion section. All authors contributed to the writing of the article.

7. Competing interests

The authors declare that they have no conflict of interest.

8. Acknowledgements

This study was funded by the Swiss National Science Foundation project CompMig, Nr . 205321_163223 .

9. Code and Data availability

The code generating the figures in Supplementary material 2 are part of the material. The used DGVM LPJ-GUESS containing the migration module can be requested from the author.

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The data behind all figures will be published on the DataGURU server (dataguru.lu.se) with an own DOI upon acceptance of the paper.

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10. Contents of the supplementary material

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11. Figures and tables

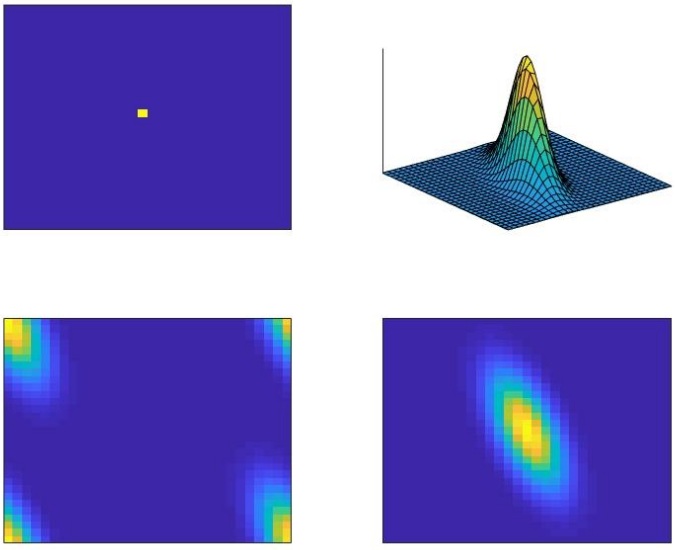

Fig. 1. Upper left panel: seed source. Upper right panel: example of a seed dispersal kernel (here a non-symmetric kernel is assumed), lower left panel: transformed seed dispersal kernel, lower right panel: seed distribution after convolution.

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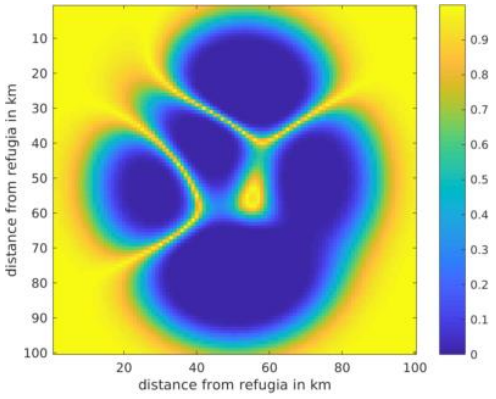

Fig. 2: Seed dispersal permeability for SMSM simulation tests. Each time the seed matrix is shifted, the probability of entering the new cell (which in our test is set to $5*10^{-7}$) is multiplied with the seed dispersal permeability of the new potentially entered cell.

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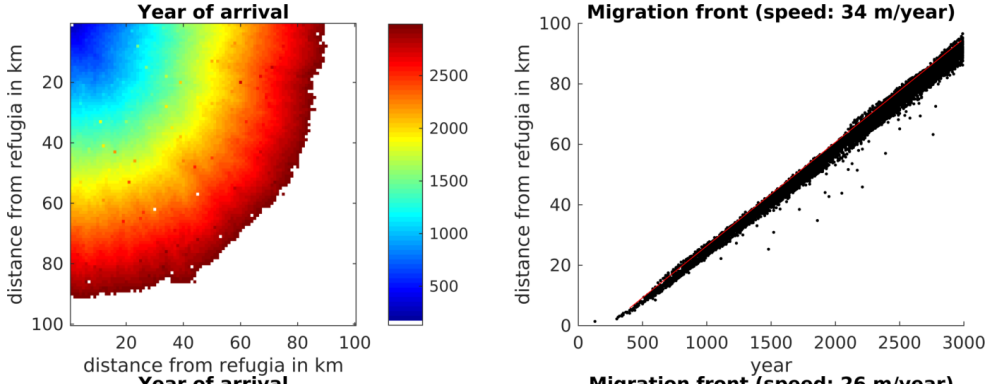

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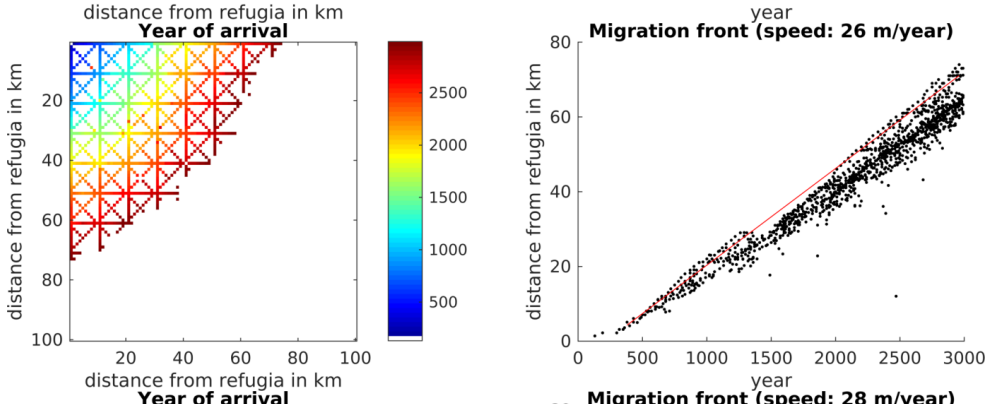

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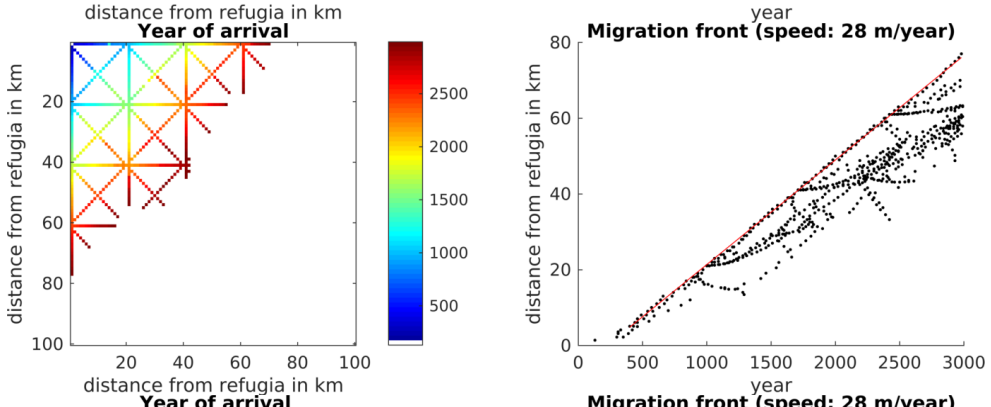

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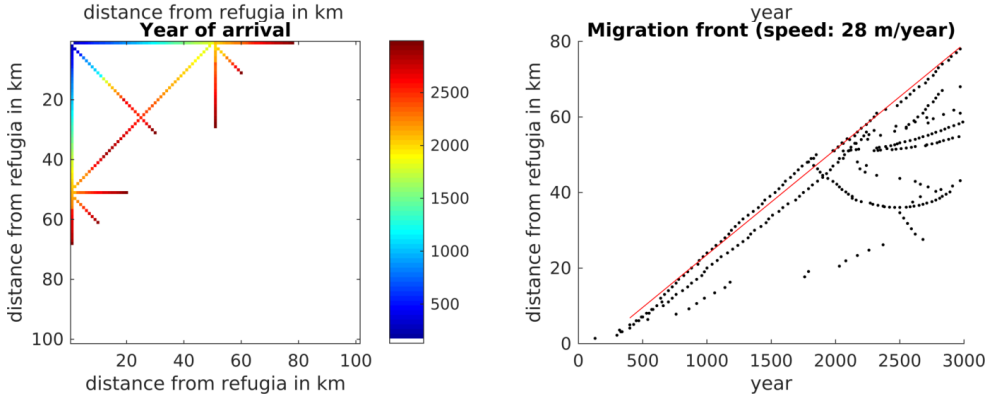

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642 Fig. 3 Spread of *Fagus sylvatica* through an area of 100 * 100 grid cells with static climate using the
643 FFTM algorithm with no corridors or corridors every 10km, 20km or 50km. The left panels display
644 the time when *F. sylvatica* first reached an LAI of 0.5. *F. sylvatica* is allowed to establish freely only
645 in the upper left corner. The right panels show the distance of the grid cells with LAI 0.5 for *F.*
646 *sylvatica* from the starting point. The red line indicates the 95 percentile of the grid cells farthest away
647 from the starting point. The migration speed is calculated as slope of this line, taking only for grid
648 cells at least 5 km away from the starting point into account to avoid some initial establishing effects.

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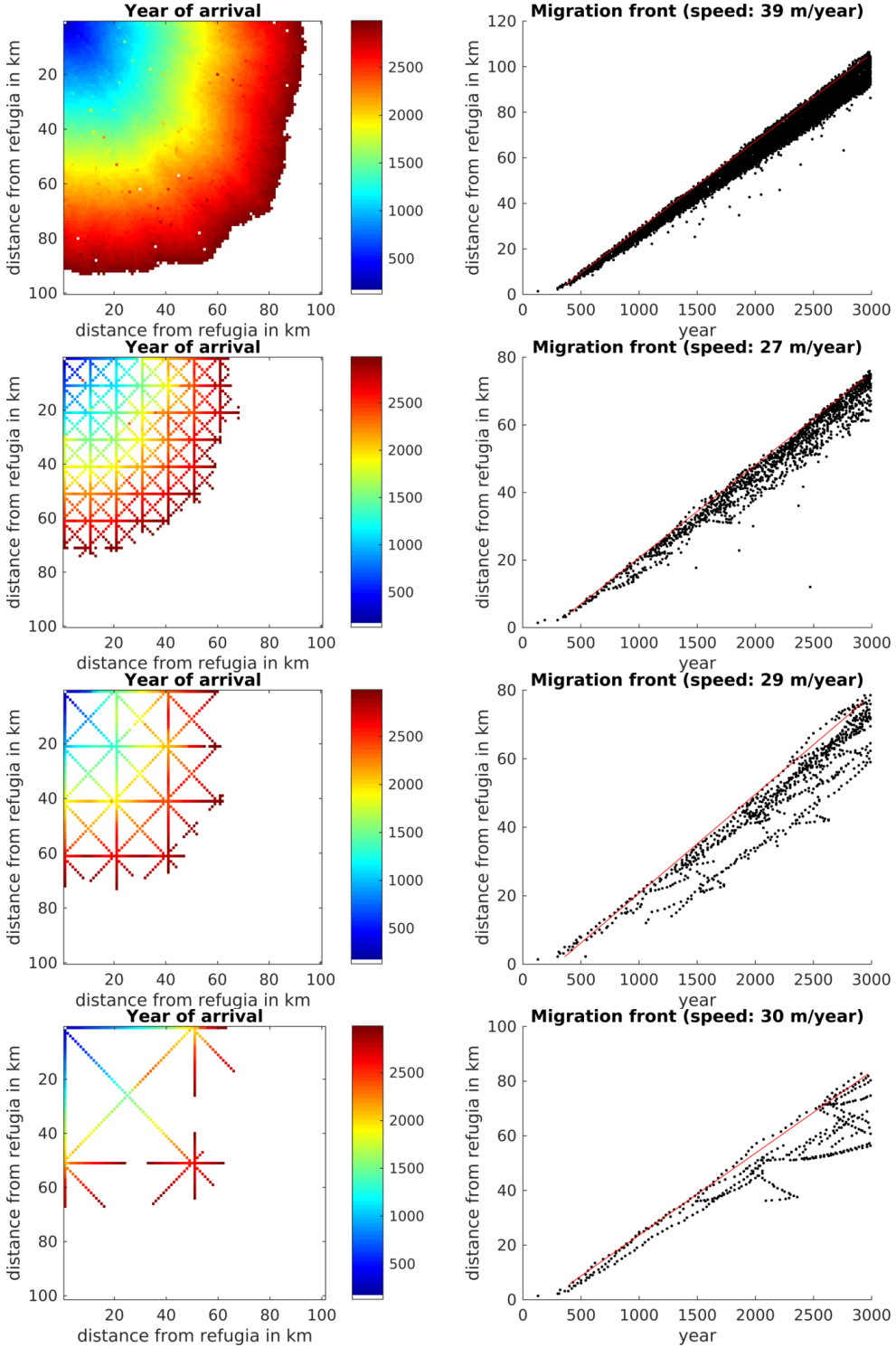

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654 Fig. 4 Spread of *Fagus sylvatica* using the SMSM through an area of 100 * 100 grid cells with
655 identical climate, using the full area (upper row of panels) or corridors every 10^{th}, 20^{th} or 50^{th} cell. For
656 more explanation see Fig. 3.

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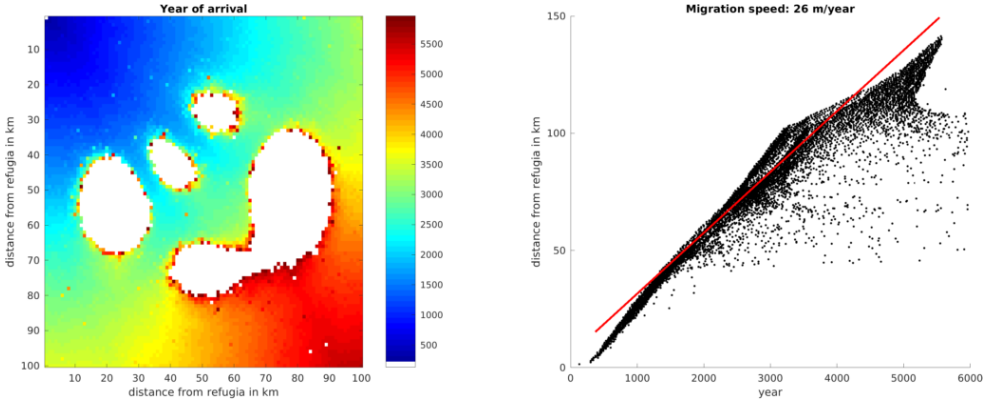

Fig. 5 Spread of *Fagus sylvatica* using the SMSM method through an area of 100 * 100 grid cells with identical climate but probability of seed fall is set to 0.00005 multiplied with the spatially explicit seed dispersal permeability value as shown in Fig. 2. Note that we increased the simulation time to 6000 years in order to have F. sylvatica establishing in all areas.

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Table 1. Summary of migration speeds and calculation time. A corridor distance of 0 indicates no corridors but an area completely filled with grid cells. The simulated grid cells column lists the number of cells for which LPJ-GM calculates the population dynamics, in all simulations the simulation domain (for which the seed dispersal was calculated) had a size of 10000 grid cells and all simulations were performed over 3000 years. The last line lists a simulation identical to the others except that no seed dispersal was calculated to allow estimating the computation time demand for this operation.

Seed dispersal mode	Corridor distance (cells)	Simulated grid cells (corridor cells)	Migration speed, m/year	Computation time (cpu* h)	Comp. time change per corridor grid cell compared to sim. without dispersal (CPU h)	Total comp. time change for whole domain compared to sim. without dispersal (CPU h)	Percentage of CPU time for dispersal	Decrease due to corridor simulation
FFTM	0	10000	34	1800	+12%	+12%	11%	
FFTM	10	3330	26	650	+22%	-59%	18%	67%
FFTM	20	1765	28	400	+41%	-75%	29%	78%
FFTM	50	977	27	220	+41%	-86%	29%	88%
SMSM	0	10000	39	2000	+25%	+19%	16%	
SMSM	10	3330	27	700	+31%	-59%	19%	65%
SMSM	20	1765	29	400	+41%	-77%	23%	81%
SMSM	50	977	30	220	+41%	-86%	32%	89%
Non	0	10000	0	1600	0%	0%	0%	