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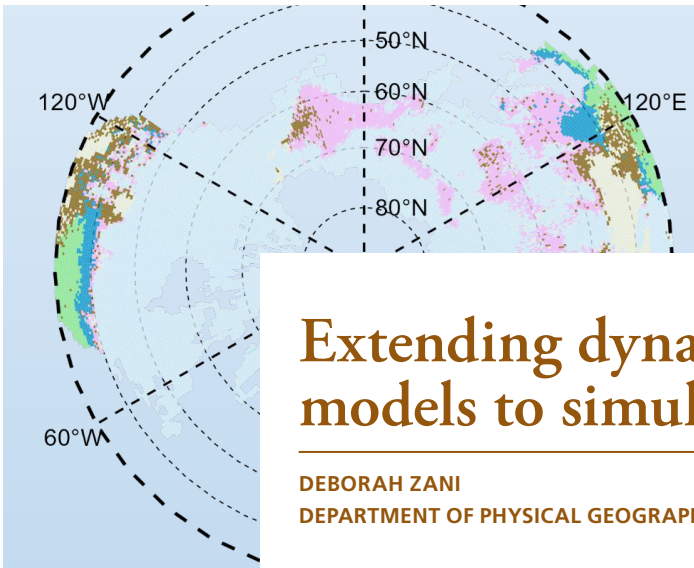
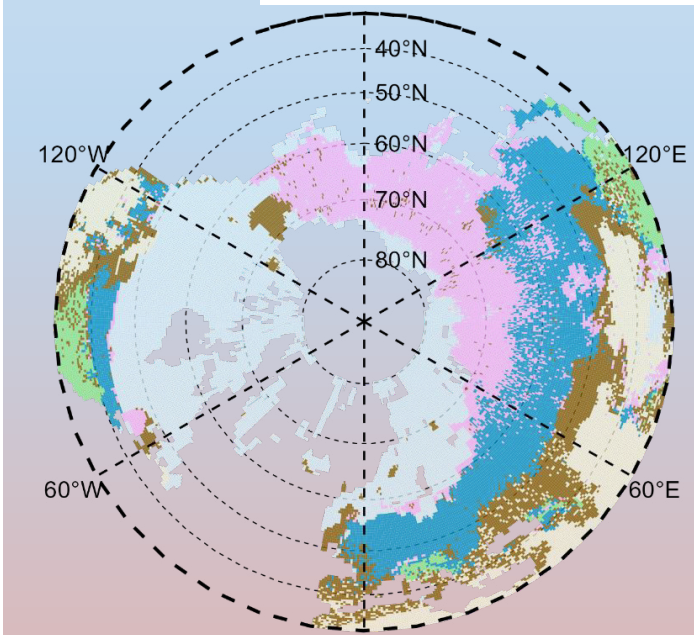
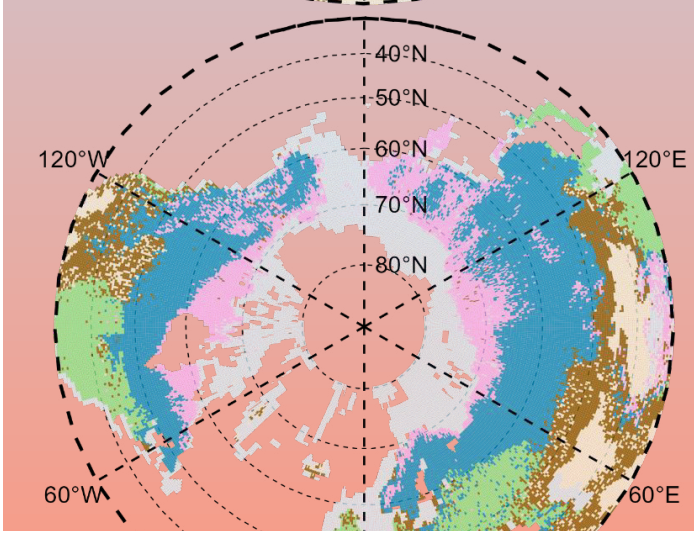


Extending dynamic vegetation models to simulate range shifts

DEBORAH ZANI
DEPARTMENT OF PHYSICAL GEOGRAPHY AND ECOSYSTEM SCIENCE | LUND UNIVERSITY





LUNDS UNIVERSITET

Department of Physical Geography
and Ecosystem Science
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Extending dynamic vegetation models to simulate range shifts

Extending dynamic vegetation models to simulate range shifts

Deborah Zani

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DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Science at Lund University to be publicly defended on date 30th of November at 13.00 in Pangea Hall, Department of Physical Geography and Ecosystem Science, Sölvegatan 12, Lund

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Abstract:

In response to rapid climate change and increasing human pressure, a wide variety of taxa have shifted their distribution in the past decades (range shift), with important consequences for ecosystem services and human health and economy. However, it is not yet clear whether most species will be able to track their favourable habitats or lag behind the climate signal (migration lag). Studying the paleo-vegetation response to past climatic fluctuations may help to understand the ecological processes underlying range shift dynamics. This thesis aims to implement an efficient model to hind- and fore-cast the range shift of the vegetation at large temporal and spatial scales. To this end, we used the dynamic global vegetation model (DGVM) LPJ-GM, which couples a migration module to the widely-used DGVM LPJ-GUESS, thus allowing plant species to migrate while interacting with each other. First, we assessed and calibrated the migration module of LPJ-GM 1.0 by using estimates of migration rates derived from pollen records of major European tree species, resulting in the parametrized model LPJ-GM 1.1. In agreement with previous modelling studies and ecological theory (Reid's paradox), long-distance dispersal events were found to be crucial in realizing the high spreading rates of migrating trees during the last deglaciation. Next, we upgraded the existing migration routine of LPJ-GM 1.1 (henceforth the SEEDISP option) and implemented a second migration routine (henceforth the FIXSPEED option) to decrease the computational cost of range shift simulations at larger scales. These implementations resulted in the model LPJ-GM 2.0. We then applied LPJ-GM 2.0 to simulate the paleo-vegetation dynamics during the last (inter-)stadial cycles (Europe after the Last Glacial Maximum and the Northern Hemisphere, NH, for the last 50 ky) under two dispersal modes, where plant establishment was determined by: (1) the standard LPJ-GUESS routine (free dispersal), or (2) additionally constrained by "seed" availability (dispersal limitation of LPJ-GM 2.0; SEEDISP for Europe and FIXSPEED for the NH). Applying migration constraints to vegetation dynamics altered the paleo-vegetation distribution at points of rapid climate change. A number of tree taxa and forested biomes experienced multi-millennia migration lags during the sudden warming events following the cold spells of the Older Dryas (around 14.5 ka) and the Younger Dryas (around 11.5 ka). We found the highest migration lags (>3 millennia) in the boreal forests colonizing Central Siberia across the Holocene, and in the post-glacial expansion of European temperate forests. The magnitude of migration lags of forested biomes and tree taxa depended on the presence of dispersal barriers, distance to glacial refugia, the configuration of the migrant population, thermal requirements for establishment and species-specific dispersal ability (and subsequent competition). The performance of both SEEDISP and FIXPSEED was higher than "free dispersal" simulations when compared with pollen reconstructions. Altogether, our results suggest that accounting for migration processes in vegetation models will increase our confidence in future projections of plant range shifts and thus, of ecosystem services and climate-vegetation feedback.

Key words: dynamic vegetation models, migration, paleovegetation, range shift

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Extending dynamic vegetation models to simulate range shifts

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Abstract

In response to rapid climate change and increasing human pressure, a wide variety of taxa have shifted their distribution in the past decades (range shift), with important consequences for ecosystem services and human health and economy. However, it is not yet clear whether most species will be able to track their favourable habitats or lag behind the climate signal (migration lag). Studying the paleo-vegetation response to past climatic fluctuations may help to understand the ecological processes underlying range shift dynamics. This thesis aims to implement an efficient model to hind- and fore-cast the range shift of the vegetation at large temporal and spatial scales. To this end, we used the dynamic global vegetation model (DGVM) LPJ-GM, which couples a migration module to the widely-used DGVM LPJ-GUESS, thus allowing plant species to migrate while interacting with each other.

First, we assessed and calibrated the migration module of LPJ-GM 1.0 by using estimates of migration rates derived from pollen records of major European tree species, resulting in the parametrized model LPJ-GM 1.1. In agreement with previous modelling studies and ecological theory (Reid's paradox), long-distance dispersal events were found to be crucial in realizing the high spreading rates of migrating trees during the last deglaciation.

Next, we upgraded the existing migration routine of LPJ-GM 1.1 (henceforth the SEEDISP option) and implemented a second migration routine (henceforth the FIXSPEED option) to decrease the computational cost of range shift simulations at larger scales. These implementations resulted in the model LPJ-GM 2.0.

We then applied LPJ-GM 2.0 to simulate the paleo-vegetation dynamics during the last (inter-)stadial cycles (Europe after the Last Glacial Maximum and the Northern Hemisphere, NH, for the last 50 ky) under two dispersal modes, where plant establishment was determined by: (1) the standard LPJ-GUESS routine (free dispersal), or (2) additionally constrained by "seed" availability (dispersal limitation of LPJ-GM 2.0; SEEDISP for Europe and FIXSPEED for the NH). Applying migration constraints to vegetation dynamics altered the paleo-vegetation distribution at points of rapid climate change. A number of tree taxa and forested biomes experienced multi-millennia migration lags during the sudden warming events following the cold spells of the Older Dryas (around 14.5 ka) and the Younger Dryas (around 11.5 ka). We found the highest migration lags (>3 millennia) in the boreal forests colonizing Central Siberia across the Holocene, and in the post-glacial expansion of European temperate forests. The magnitude of migration lags of forested biomes and tree taxa depended on the presence of dispersal barriers, distance to glacial refugia, the configuration of the migrant population, thermal requirements for establishment and species-specific dispersal

ability (and subsequent competition). The performance of both SEEDISP and FIXPSEED was higher than “free dispersal” simulations when compared with pollen reconstructions. Altogether, our results suggest that accounting for migration processes in vegetation models will increase our confidence in future projections of plant range shifts and thus, of ecosystem services and climate-vegetation feedback.

Populärvetenskaplig sammanfattning

Som respons på snabba klimatförändringar och ökande mänsklig påverkan har en mängd olika taxa förändrat sin distribution och utbredning under de senaste decennierna (s.k. förskjutning av artutbredningsgräns), vilket i sin tur medfört betydande konsekvenser för ekosystemtjänster (t.ex. kolbindning i växande skogar) och människors hälsa och ekonomi (t.ex. invasion av zoonotiska sjukdomsvektorer och trädskadegörare). Det är ännu inte klarlagt om de flesta arterna kommer förmå att följa med förskjutningen av sina gynnsamma livsmiljöer, eller dröja kvar och hamna efter klimatsignalen (s.k. migrationsfördröjning). Att studera paleo-vegetationens svar på tidigare klimatfluktuationer kan bidra till att förstå de ekologiska processer som ligger bakom dynamiken för artutbredningsförskjutningar. Denna avhandling syftar till att implementera en effektiv modell för att både bak- och förutsäga vegetationens utbredningsförskjutning i stora tids- och rumsmässiga skalor. För detta ändamål använde vi den globala dynamiska vegetationsmodellen (DGVM) LPJ-GM (LPJ-GUESS+MIGRATION) 1.0, som kopplar samman en migrationsmodul till den mer allmänt använda DGVM LPJ-GUESS 4.0, vilket gör att växtarter kan migrera medan de interagerar med varandra.

Först utvärderade och kalibrerade vi migrationsmodulen för LPJ-GM 1.0 genom att använda uppskattningar av migrationshastigheter härledda från pollenregister från stora europeiska trädarter, vilket resulterade i den parametriserade modellen LPJ-GM 1.1. I överensstämmelse med tidigare modelleringsstudier och ekologisk teori (Reids paradox), visade sig långdistansspridningshändelser vara avgörande för att realisera de höga spridningshastigheterna för migrerande träd under den senaste deglaciationen.

Därefter uppgraderade vi den befintliga migreringsrutinen för LPJ-GM 1.1 (hädanefter alternativet SEEDISP) för att simulera fröspridning mer effektivt. Alternativet SEEDISP simulerar migration årligen genom att explicit beräkna fröproduktion, fröspridning, frögroning och planteringsetablering. Dessutom implementerade vi ytterligare en migreringsrutin för att minska beräkningskostnaden för artutbredningssimuleringar i större skalor (hädanefter alternativet FIXSPEED). Till skillnad från SEEDISP, beräknar FIXSPEED inte den explicita utspridningen av fröer och spårar inte heller utsädesmängd spatialt. Istället simuleras artspridningsbegränsningen implicit, genom att begränsa artetableringen baserat på en taxaspecifik maximal migrationshastighet, samtidigt som den tar hänsyn till tidsfördröjningar i mognad och uthållighet av jordens fröbank. Dessa implementeringar resulterade i modellen LPJ-GM 2.0.

För att undersöka effektiviteten och validera våra implementeringar, tillämpade vi LPJ-GM 2.0 i stora tids- och rumsmässiga skalor och simulerade därefter paleo-vegetationsdynamiken under de senaste (inter-)stadiala cyklerna. Vi körde

paleosimuleringar under två spridningslägen, där växtetablering bestämdes av: (1) klimatförhållanden (fritt spridningsläge; standard LPJ-GUESS-rutin), eller (2) dessutom begränsad av "frö"-tillgänglighet (spridningsbegränsning; SEEDISP eller FIXSPEED-alternativ för LPJ-GM 2.0). Specifikt tillämpade vi alternativet SEEDISP i en högupplöst skala (0,01 grader) i Europeisk kontext efter den sista istidens maximum (>18,5 ka). Alternativet FIXSPEED tillämpades istället på grövre skalor (0,5 grader) över hela norra halvklotet (NH) och under de sista 50 ky.

Tillämpningen av migrationsbegränsningar på vegetationsdynamiken förändrade särskilt paleo-vegetationsfördelningen vid tidpunkter med snabba pågående klimatförändringar. Ett antal trädtaxa och skogbevuxna ekosystem uppvisade flera årtusendens migrationsfördröjningar under de plötsliga uppvärmningsskeenden som uppstod efter kylan i äldre dryas (cirka 14,5 ka) och yngre dryas (cirka 11,5 ka). Vi fann de största migrationsfördröjningarna (>3 årtusenden) i de boreala skogarna som då koloniserade centrala Sibirien under holocen, och i den postglaciala expansionen av europeiska tempererade skogar och deras mer värmekrävande och långsamt spridande trädarter. Över hela NH berodde storleken på migrationsfördröjningen av skogbevuxna ekosystem främst på förekomsten av spridningsbarriärer (inlandsisar eller berg), avståndet till glacial refugia och konfigurationen av migrerande artpopulation (breda spridande fronter och angränsande ockuperade livsmiljöer minskar migrationsfördröjningen). För europeiska trädarter var det temperaturmässiga krav på etablering och artspecifik spridningsförmåga (och efterföljande konkurrens) som avgjorde den tidsmässiga fördröjningen av etablering, då köldtoleranta och snabbt spridande pionjärtaxa knappast upplevde någon migrationsfördröjning. Simuleringsresultaten för både SEEDISP och FIXPSEED överenstämde bättre med biom- och marktäckesrekonstruktioner från pollenregister, jämfört med standardsimuleringar med "fri spridning". Sammantaget tyder våra resultat på att hänsynstagande till migrationsprocesser i vegetationsmodeller kommer att öka vår precision för framtida prognoser av växtutbredningsförskjutningar och därmed även för prognoser av ekosystemtjänster och klimat-vegetationsåterkoppling.

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List of Papers

Paper I

Zani, D., Lehsten, V., & Lischke, H. (2022). Tree migration in the dynamic, global vegetation model LPJ-GM 1.1: efficient uncertainty assessment and improved dispersal kernels of European trees. *Geoscientific Model Development*, 15(12), 4913-4940.

Paper II

Zani, D., Lehsten, V., & Lischke, H. (2023). The role of dispersal limitation in the forest biome shifts of Europe since the last 18,000 years. Manuscript submitted to *Journal of Biogeography*, Manuscript.

Paper III

Zani, D., Lehsten, V., & Lischke, H. (2023). Post-glacial spread velocities and directions of major European tree species under free and limited dispersal. Manuscript submitted to *Frontiers in Ecology and Evolution*.

Paper IV

Zani, D., Lischke, H, Huntley, B., Lister, A., & Lehsten, V. (2023). The role of migration in the change of Northern Hemisphere vegetation for the past 50,000 years. Manuscript unpublished.

Author's contribution to the papers

Paper I

DZ and VL designed the study, **DZ** performed the simulations and the statistical analysis, VL provided support with the coding, and VL and HL provided statistical support. All authors contributed to the writing of the paper.

Paper II

HL and VL conceived the initial idea of applying LPJ-GM to paleo-vegetation changes, and provided the funding. **DZ**, HL and VL designed the simulation experiments. **DZ** implemented, fine-tuned, ran and analysed the simulations. **DZ** wrote the paper with assistance from VL and HL.

Paper III

With support by VL and HL, **DZ** conceived the study, obtained the computational resources, performed the model simulations, data analysis, and interpreted the results (on drivers of post-glacial species establishment in European tree species). **DZ** wrote the paper with assistance from VL and HL.

Paper IV

DZ conceived the study with BH and AL. BH and AL provided the climate data, model setting and parameters. **DZ** performed the model modifications (more efficient migration routine) and simulations, and data analysis. **DZ** interpreted the results with the support of BH, AL, VL and HL. **DZ** wrote the manuscript, with reviewing and editing support by BH and HL.

Abbreviations

ABIO	Abiotic envelope
BA	Bølling-Allerød interstadial (15–12.9 ka)
BIO	Biotic interactions
BP	Before Present
D(G)VM	Dynamic (Global) Vegetation Model
DISP	Dispersal limitation
EH	Early Holocene (11.7–8.236 ka)
FLM	Forest Landscape Model
IS	Isothermal shift
ka	1000 years ago
ky	1000 years
LDD	Long Distance Dispersal
LGM	Last Glacial Maximum (26–19 ka)
LGI	Late Glacial Interstadial (19–15 ka)
LH	Late Holocene (4.25–0 ka)
MH	Mid Holocene (8.236–4.25 ka)
NH	Northern Hemisphere
NL	Niche Limits
OD	Older Dryas (14 ka)
PFT	Plant Functional Type
RL	Range Limits
YD	Younger Dryas (12.9–11.7 ka)

1.Introduction

1.1 Species range shifts under climate change

How does biodiversity change and persist under fast environmental changes?

Studies on the paleo-vegetation under past climatic fluctuations and plant distributions in the last decades have highlighted two main mechanisms by which species respond to environmental change: 1) niche shift or evolution, i.e. species adapt their climatic tolerance to the new climate (Corlett & Westcott, 2013; Loarie et al., 2009); 2) range shift, i.e. species migrate to track their former climatic niche (Jezkova & Wiens, 2016; Jump & Peñuelas, 2005); or a combination of both (Berg et al., 2010; Román-Palacios & Wiens, 2020). However, the unprecedented rapidity of anthropogenic environmental change makes it unlikely that niche evolution alone would provide a successful survival strategy for slow-growing and long-generation taxa such as most tree species (Berg et al., 2010). The ability of plants to track their optimal environment is thus considered their primary response to rapid ongoing climate change (Berg et al., 2010; P. L. Thompson & Fronhofer, 2019). Indeed, global change—either as climate warming or humans acting as intentional or accidental spreading vectors—has already caused the redistribution of a substantial number of plant (and non-plant) species during the last decades (Pecl et al., 2017). Specifically, climate warming has driven a worldwide isotherm shift (IS) towards the poles and upslope in previously cooler latitudes and elevations, respectively (Lenoir et al., 2020). Following IS, the majority of vascular plants in the Northern Hemisphere responded by shifting their ranges towards the summits of mountains (40%) and the North Pole (38%) (Fig. 1). However, this trend does not necessarily mean that trees will be able to track their optimal environments. In their comprehensive study on worldwide range shifts, Lenoir et al. (2020) showed that though plants are migrating after IS, their migration rates are overall lower than IS velocity. This phenomenon is known as migration lag, i.e. the delayed establishment in a climatically suitable habitat due to the limited dispersal capacity of the species or other processes slowing down migration (Section 1.2). In other words, the climate is changing too fast for some species to keep pace. A number of studies on the paleo-vegetation have also hypothesized that migration lag played an important role in the vegetation dynamics of the last interglacial cycles, especially during the forest expansion in the Northern Hemisphere following the Last Deglaciation (Dallmeyer et al., 2022; Greve Alsos et al., 2022; Ordonez & Williams, 2013; Svenning & Skov,

2004). However, the time and magnitude of the migration lag and its variation among taxa and geographical areas are still debated.

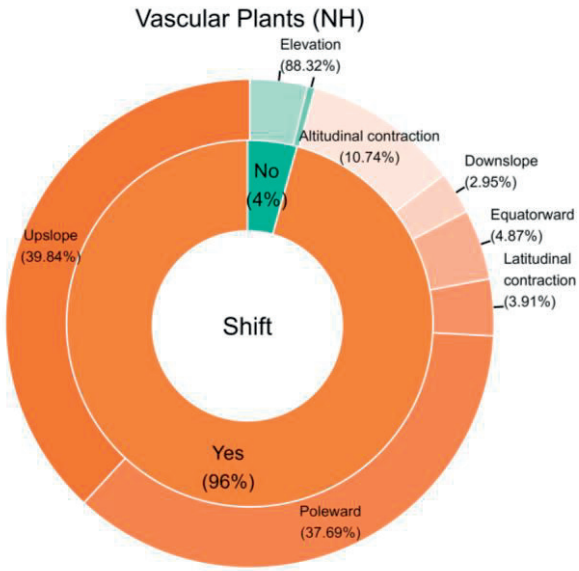

Figure 1. Range shift of vascular plants (Kingdom: Plantae, Phylum: Tracheophyta) in the Northern Hemisphere over the last decades (>1950). The direction of the range shift has been calculated as follows: no shift = null values of range shift estimates; contraction = positive values at the trailing edge or negative values at the leading edge; equatorward/downslope = negative values at the trailing edge (for latitudinal and elevation gradient, respectively); poleward/upslope = positive values at the leading edge (for latitudinal and elevation gradient, respectively). Sample size: 4,172 vascular plant species. All data reported were compiled from the BioShifts database (Lenoir et al., 2020).

Both contemporary and past evidence seems to suggest that accounting for migration lag may increase our confidence in the predictions or hindcasts of plant redistribution under climate change. For example, a failure to account for migration lag in range shift expansion may lead to the over-prediction of vegetation cover, which in turn can cause wrong assessments of potential ecosystem properties (e.g. terrestrial carbon storage) and/or feedbacks to the climate. Finally, the inclusion of migration processes in cost-effective tools for range shift prediction, such as dynamic models, can help to provide more reliable projections of future ecosystem services, and support plant conservation, tree assisted migration, and risk management (Iverson et al., 2019; Iverson & McKenzie, 2013; Urban, 2020).

In this thesis, we aimed to implement a large-scale dynamic model for the effective simulation of range shifts in plant species (Section 2). As a first step, we identified the key drivers of range shift dynamics and migration lag (Section 1.2).

1.2 Drivers of range shift dynamics

Range-limit theory (Boulangeat et al., 2012; Sirén & Morelli, 2020) identifies three main ecological drivers of range limits: 1) abiotic factors forming the environmental envelop or potential niche within which a species can persist given its physiological limits (ABIO); 2) dispersal limitation (DISP), i.e. the ability of individuals to move their propagules (seeds for vascular plants) beyond their current position; and 3) biotic interactions (BIO).

The "niche-driven hypothesis" posits that species' range limits (RL) are the spatial reflection of their niche limits (NL), where niche limits are defined by ecological gradients that decline from the centre of the range towards its edges (Pearson & Dawson, 2003). This means that populations in the interior are expected to be denser than populations at the range edge ("abundant centre" hypothesis) (Gaston et al. 2000). The principal ecological gradients are assumed to be abiotic (ABIO), though biotic interactions (BIO) may also shape NL via negative interactions in the species-rich or less stressful parts of the niche (usually around the centroid of the range or at lower edges) (Ettinger & HilleRisLambers, 2017). These hypotheses consider RL largely at equilibrium, i.e. species' ranges remain more or less spatially stable, though minor and temporary fluctuations are possible (RL$\sim$NL). For example, species may contract their ranges along the edges during rare bad years (RL<NL) and then start dispersing (DISP) as soon as the climate ameliorates until the edges are fully recolonized (RL=NL). Therefore, equilibrium requires that the response of species to environmental change (range shift or adaptation) be faster than the rate of environmental change itself. On the other hand, if rapid environmental changes occur on a large scale and continue over time, RL might enter into a disequilibrium state so that range limits almost never overlap with the niche of a species (permanent disequilibrium, RL$\neq$NL) (Hargreaves et al., 2014). This condition implies that species shift their ranges too slowly to keep pace with environmental change (i.e. migration lag; RL<NL), as appears to be the case for most plants under current climate change (see Section 1.1).

Finally, the three main drivers of range limits (ABIO, DISP, and BIO) interact to define the realized niche of a species (the effective RL), where ABIO determines the potential climate niche to occupy and DISP and BIO determine the ability of a species to track the climate niche (i.e. the magnitude of migration lag). Specifically, the process underlying migration lag can be subdivided into two components: 1) dispersal lag at the leading edge and 2) establishment lag in newly occupied habitats

(Alexander et al., 2018). 1) Dispersal lag happens when dispersal limitation (DISP) prevents a species from reaching a potentially suitable habitat that lies outside of its range limits (RL<NL). Dispersal limitation determines the degrees to which trees can move their seeds into new habitats (propagule pressure) and is directly linked to the plant's functional traits (e.g. tree fecundity, germination rate, tree height, age to maturity) (Beckman et al., 2020). For example, slow-maturing species with low seed production are expected to have far slower dispersal rates than fast-growing and highly fecund species (Parolo & Rossi, 2008). Dispersal lag can also be affected by both BIO (e.g. for species relying on animal vectors, or frugivores, for dispersal) and ABIO (directly via habitat continuity, wind speeds, dispersal barriers, or indirectly via altering dispersal traits such as the length of the juvenile period or plant fecundity) (Svenning & Sandel, 2013). 2) Following dispersal, a minimum number of propagules is required for successful establishment as individuals grow towards the population carrying capacity (establishment lag). Low establishment rates are linked to suboptimal environmental conditions (ABIO, extreme irradiance, extreme temperatures, drought, and limited soil development) (Bertrand et al., 2016) and/or high competitive pressure and altered interaction networks with other plants (BIO) (Alexander et al., 2015). For example, increased competition following niche expansion of multiple species is expected to limit the establishment of less competitive species (e.g. shade-intolerant) in favourable areas (Shabani et al., 2020).

Together, these findings suggest that including the effects of climate, dispersal limitation, and biotic interactions in a dynamic way will help models capture the climate-vegetation disequilibrium (RL<NL) that may result from rapid environmental change (due to migration lag). However, most of the large-scale models commonly used for global predictions tend to assume a quasi-state of range equilibrium (RL~NL), e.g. the dynamic global vegetation models (DGVMs) ORCHIDEE (Yue et al., 2018) and LPJ-GUESS (Sitch et al., 2003). These models typically simulate the distribution of species as being mainly driven by the climate through species-specific bioclimatic limits (ABIO) and competition between species for space and light (BIO). Thus, it is implicitly assumed that seeds are available across the whole simulation domain at any time and that species can potentially establish as soon as climatic (and biotic) conditions are favourable (i.e. free dispersal). So far, the efficient implementation of dispersal limitation has mostly succeeded in species distribution models (SDMs; e.g. MigClim) (Engler & Guisan, 2009) or mechanistic age-structured models (also hybrid SDM; e.g. CATS) (Gattringer et al., 2023) by using dispersal potential to adjust the range of environmental suitability given by the main algorithm. Here, we are interested in the implementation of migration processes (resulting in dispersal limitation) in dynamic, process-based vegetation models (DVMs). These models can provide complementary advantages to SDMs in the simulation of species range shifts, such as the explicit representation of processes relevant for plant migration and the ability to account for feedbacks among different range shift drivers in space and time (for

a more comprehensive list, see Snell et al., 2014). On the other hand, dispersal limitation is challenging to include in large-scale dynamic models due to a number of reasons, including the high computational cost (Section 1.3.2). To address this challenge, we searched for up-to-date DVMs that include migration processes in their framework (Section 1.3.1), identified limitations, and discussed possible developments in the use of DVMs for the simulation of plant range shifts (Section 1.3.2).

1.3 Migration processes in dynamic vegetation models

1.3.1 State-of-the-art in migration modelling

Forest landscape models (FLMs) are DVMs that can simulate forest dynamics across a grid-based landscape, where the growth, mortality, and regeneration of trees are implemented as a function of the abiotic environment (ABIO) and competition for resources (BIO). The sub-model for regeneration may also include the processes underlying the migration of trees. Specifically, a tree can migrate through the production of seeds from mature individuals, the dispersal of seeds to suitable sites, the persistence of seeds in the soil seed bank and subsequent germination, and finally the survival and growth of saplings in new habitats (Hanbury-Brown et al., 2022). Here we list and describe up-to-date FLMs with an explicit implementation of (some) migration processes and ongoing application (see also Petter et al. (2020)): ***LandClim*** (Schumacher et al., 2004), ***LANDIS-II*** (Scheller et al., 2007), ***TreeMig*** (Lischke et al., 2006), and ***iLand*** (Seidl et al., 2012).

LandClim (Schumacher et al., 2004) is a FLM operating at the landscape scale with a focus on European forests, though it has been extended to include North American species. The model simulates the demographic processes (growth, regeneration, and mortality) of tree cohorts in a spatially explicit domain of cells driven by input environmental conditions (mediated by species-specific parameters defining the potential niche) and intra-specific competition for light. Migration processes associated with regeneration include dispersal and establishment. Seed dispersal is represented by a cell-based dispersal probability, which decreases from the source cell (a cell containing a mature tree) according to a negative exponential function. A sink cell is marked as containing seeds if the dispersal probability of that cell is higher than a randomly drawn number (from a uniform distribution between 0 and 1). Next, the establishment of new trees in seeded cells is calculated based on the number of favourable years for establishment in a decade (in turn determined by temperature, drought, browsing, and stochastically by randomly sampling a 0-1 value against an establishment coefficient), light conditions, and the relative growth performance at the cell level (with respect to other potentially occurring tree

species). Seed production, the number of dispersed seeds, and seed bank dynamics (persistence in the soil and seed germination) are not explicitly simulated.

The FLM ***LANDIS-II*** (Scheller et al., 2007) simulates the forest dynamics of North America (now extended to Asia, Europe, and South America) over medium spatial and temporal scales (104–107 ha and 105 years, respectively). The landscape domain is subdivided into grid cells, where each cell belongs to an ecoregion defined by climatic and soil conditions (or other user-defined characteristics). Ecophysiological processes of species-specific age cohorts are simulated at the cell level and integrated over space and time to simulate forest succession, with growth being a function of light, soil moisture, and climate, and tree cohorts competing for light and water. Similarly to ***LandClim***, the processes of natural regeneration in ***LANDIS-II*** include seed dispersal and establishment, and do not explicitly model the production of seeds. Seed dispersal is simulated based on species-specific dispersal kernels (the probability of a seed to reach a sink cell) starting from source cells containing mature cohorts (i.e. above a species-specific maturity age). Differently from ***LandClim***, the number of dispersed seeds is simulated through the dispersal kernel as a double negative exponential function defined by species-specific effective and maximum seed dispersal distances. In the event that seeds manage to reach a sink cell, new cohorts can stochastically establish if the species establishment probability (SEP) exceeds a variate (0–1), where SEP is a function of suboptimal temperature, soil moisture, and light conditions.

The FLM ***TreeMig*** (Lischke et al., 2006) was developed to simulate the forest dynamics of Central Europe (now including North American and Chinese species) at larger scales, i.e. from a landscape to continental spatial domains and spanning decades up to millennia. ***TreeMig*** simulates the local demographic processes of tree species (germination, survival, and growth) driven by climatic conditions (mediated by species-specific potential niches) and interactions among trees (inter-specific competition for light and space, and carrying capacity of seeds in the soil bank). The migration processes implemented in ***TreeMig*** include dispersal, establishment, and, in addition to ***LandClim*** and ***LANDIS-II***, seed production and seed bank dynamics. The number of produced seeds is based on an input parameter of maximum fecundity and scaled by the leaf area of the individual. Similarly to ***LandClim*** and ***LANDIS-II***, only mature trees can produce seeds, and specifically only when a critical tree height is reached (maturation height). The seeds produced by all individuals in a species are then summed up for each cell and dispersed through a dispersal kernel. The dispersal kernel in ***TreeMig*** corresponds to a weighted mean of two negative exponential functions for species-specific short- and long-distance dispersal (LDD), where LDD is assumed to be rare (weight = 0.01). The dispersed seeds can then enter the soil seed bank of each sink cell, where seeds die annually by a fixed fraction (0.13) and surviving seeds can germinate. A generic carrying capacity is also added to the soil seed bank to avoid an excessive accumulation of

seeds. Finally, germinated seeds can establish as seedlings depending on light conditions at the soil level, minimum temperature, and degree-day sum.

The FLM ***iLand*** (Seidl et al., 2012) can simulate the demographic processes (regeneration, growth, mortality) of individual tree species, where individuals grow based on the forcing climate (light use efficiency approach) and compete for resources (e.g. light, water). Migration is simulated annually at each 20 x 20 m grid cell through seed dispersal from mature trees and establishment based on seed availability, environment, and light conditions. The dispersal approach in ***iLand*** uses concepts from the above-described models. Similarly to ***TreeMig***, the default dispersal kernel is a two-part negative exponential function (although different functions can be tested). Differently from ***TreeMig***, the dispersal process does not keep track of the number of seeds per individual tree in an explicit way but uses dispersal probabilities (cf. ***LandClim***) from cells occupied by mature trees above a critical age (cf. ***LANDIS-II***). Nevertheless, seed production can be implicitly included by scaling the probability kernel with species-specific fecundity, where fecundity can be adjusted at different years (for non-seed and seed years, which are randomly drawn based on a mean interval for seed years). Overlapping probability kernels are summed at each cell to determine the establishment probability along with environmental conditions (e.g. winter temperature, growing degree-days, soil moisture, light conditions). Newly established saplings grow and compete as cohorts and enter the individual-based approach after reaching a height threshold (4 m, where shorter saplings are cleared out of the cell). In ***iLand***, seed bank dynamics are not simulated explicitly.

Dynamic Global Vegetation Models (DGVMs) are generally considered state-of-the-art modelling frameworks for the estimation of species range shifts under climate change as they can dynamically implement many relevant physiological and biochemical processes at a large (global) scale and thus potentially cover the whole spatial domain of multiple species and track the redistribution of global biomes (Snell et al., 2014). Additionally, DGVMs can be coupled to General Circulation Models to include climate-vegetation feedbacks for the prediction of the global climate, which can be significantly affected by the vegetation extent and distribution (A. J. Thompson et al., 2022). One of the most commonly used DGVMs for the hind- and fore-casting of vegetation distribution and services is LPJ-GUESS (Sitch et al., 2003; Smith et al., 2001, 2014). To our knowledge, only two LPJ-GUESS-based models have attempted to integrate migration processes into their framework: ***LPJ-DISP*** (Snell, 2014) and ***LPJ-GM*** (Lehsten et al., 2019).

Snell (2014) implemented dispersal limitation in LPJ-GUESS (***LPJ-DISP***) by representing the spread of the vegetation between and within grid cells. As in the default LPJ-GUESS framework, each grid cell contains multiple patches as statistical replicates for stochastic processes of local vegetation dynamics (e.g. disturbances and mortality). Vegetation spread is represented by the probability of transmission of seeds (and patch adjacency) as a function of the number of patches

containing the spreading species and of a species-specific seed dispersal kernel derived from published observations (so far, three boreal PFTs). Specifically, seeds are dispersed between grid cells at discrete time steps (each 500 m) via a generalized dispersal kernel, whose parameters (shape and scale) can be adjusted to simulate local dispersal (leptokurtic kernel) or LDD events (fat-tailed kernel). Seed production in ***LPJ-DISP*** is implicitly included via the variable of total carbon allocated to reproduction, which is scaled by the proportion of patches located at the edge of each grid cell. This approach assumes a coarse spatial scale, where the large size of grid cells (ca. 18 km in the study) allows the spread of seeds to other cells only from patches at the edge. Since patches are not spatially placed within the grid cell (as in the default LPJ-GUESS), patches are assumed to be randomly located, and the number of patches at the edge is calculated based on the size of the grid cell and the total number of replicate patches. Finally, spread within the grid cells (i.e. among patches) is calculated as the probability of having a neighbouring patch with seeds (i.e. new patches that are available to receive seeds) based on a logistic growth curve where the total number of replicate patches represents the carrying capacity. Seed bank dynamics and the subsequent establishment of saplings are not explicitly simulated.

More recently, Lehsten et al. (2019) extended LPJ-GUESS in ***LPJ-GM*** (LPJ-GUESS-MIGRATION) 1.0 by using a two-dimensional landscape (cf. ***LPJ-DISP***) to simulate the migration process similarly to Lischke et al. (2006). Namely, at the start of each year, seed production is calculated by scaling an input maximum fecundity with the leaf area index of each migrating species at the stand-level. Similarly to ***TreeMig***, seeds are produced only when individuals exceed a given and species-specific "maturity height" and subsequently summed up across the grid cell (default 1 km^2) for the same species. Differently from LPJ-DISP, each grid cell has only one patch, which is spatially placed at the centre of the cell, and thus only one seed reservoir per species. The total amount of seeds produced per species is then distributed from each source cell across the spatial domain based on a seed dispersal kernel. In the default version of LPJ-GM, the dispersal kernel follows the formulation of ***TreeMig*** (and ***iLand***) with a two-part negative exponential function. Next, distributed seeds in the sink cells are transferred to the soil seed bank, where they germinate according to an input species-specific rate. Finally, the number of potential new establishments (saplings) is calculated by the LPJ-GUESS code (based on light conditions, resource allocation to reproduction, and maximum establishment rate) and modified by the number of germinating seeds. Newly established saplings then compete for resources and grow according to the default LPJ-GUESS code (for further details, see Section 3.1). In conclusion, LPJ-GM 1.0 simulates all main migration processes in an explicit way and allows the simultaneous spread of multiple species (in principle, all PFTs implemented in LPJ-GUESS) and their dynamic interactions at a relatively fine resolution (for DGVMs).

1.3.2 Key challenges in migration modelling

While it is possible to update the model structure of DVMs to improve the representation of range shift processes, there are drawbacks linked to this added complexity. Here, we list the main challenges of implementing migration processes in large-scale DVMs and some possible solutions.

High computational cost and parallelization. The study of range shifts in plant species usually requires both large spatial extents to cover the whole range of species and long periods of time to allow sessile and slow-spreading organisms, such as plants, to shift their distributions in a marked way (compared to animal taxa) (Lenoir et al., 2020). In addition, relatively high spatial resolutions are often needed to accurately represent the movement of seeds between the cells of the simulated grid (at least 1 km) (Snell et al., 2014). Furthermore, migration algorithms can be computationally expensive, especially in the evaluation of seed dispersal, by e.g. the convolution of seed production and dispersal kernel (from all source cells to all sink cells) (Lehsten et al., 2019). Together, large spatial and temporal extents, fine spatial resolutions, and expensive dispersal algorithms result in a high computational load, which may be beyond the capacity of even strong High Performance Computing (HPC) clusters. Besides optimizing the code (e.g. by applying the convolution and the Fast Fourier Transform theorem), one common solution to decrease the computational load is to apply parallel processing to DVM simulations in HPC clusters, such as message-passing interface (MPI) (Decker & Rehmann, 1994). Unfortunately, the application of parallel processing can also be constrained by the spatial connectivity required for the simulation of migration. That is, the grid structure of most D(G)VMs is spatially implicit, with grid cells being simulated separately and in parallel to enhance the computational efficiency of the simulation for large spatial and temporal extents. For instance, LPJ-GUESS uses MPI parallelization by simulating grid cells separately until the total number of simulation years is reached. Thus, the dispersal of seeds between grid cells or within grid cells (among patches) is not possible in the default structure of LPJ-GUESS. LPJ-GM managed to overcome this limitation by spatially placing single patches within grid cells and by using MPI distributed parallelism to simulate tree migration via seed dispersal among grid cells (Lehsten et al., 2019). Nevertheless, the default MPI routine of LPJ-GM 1.0 may be inadequate for simulations at large spatial scales (>100,000 cells) due to a risk of MPI knotting (for more details, see Section 3.3).

Coarse spatial resolutions and less mechanistic algorithms. To decrease the computational load, we can also simulate large spatial extents with large grid cells (coarse resolution; >5 km), which is often the case in the default structure of most DVMs (see Section 1.3.1). In this case, we have to deal with possible discretization errors for the simulation of seed dispersal in large cells. That is, seeds that arrive in a large cell are assumed to be spread across the area, i.e. they immediately cover a distance equal to the size of the cell, which can be unrealistic in the case of >5 km

cells. One solution is to implement implicit intra-grid seed dispersal as done by LPJ-DISP (see Section 1.3.1). Alternatively, we can use a simpler dispersal algorithm where we do not track the effective distance covered by seeds but an overall spreading front as the probability of having seeds (and thus of new establishments) in a grid cell (cf. ***LandClim*** approach). Nevertheless, the use of coarse resolutions has drawbacks, such as the homogenization of the environment within large areas, which may exclude (micro-)habitats relevant to the species' survival and establishment from the simulation domain. Less mechanistic representations of plant migration via simpler algorithms should also take into account the scale (and resolution) of the simulation domain and the biological entity under study. For example, simulating the shifts of plant biomes over large areas allows the use of coarser resolutions and less mechanistic algorithms than simulating the migratory patterns of single species across a landscape with high topographic variability. Additionally, complex representations of dispersal are challenging to parametrize (for lack of data and computational cost) and may introduce uncertainty in the model structure without effectively improving the simulation output (Snell et al., 2014). For instance, a mechanistic model of plants dispersed by animals would require information on animal movement, gut retention, and interactions with other competing animals or predators, which might be unavailable for large-scale settings (Nathan et al., 2008, 2012). On the other hand, these local stochastic processes tend to be less relevant in large spatial domains (above the landscape level) and can be effectively ignored in large-scale simulations as they would likely occur within a grid cell (and thus the fine-scale movements would be lost in the homogeneous cell; see above). In this sense, a phenomenological approach (i.e. without any explicit representation of dispersal processes) would be more convenient to simulate species spread at large spatial scales. An example is the use of a "total dispersal kernel", which allows reducing all possible dispersal vectors (animals, winds, etc.) to a single probability function (Nathan et al., 2008). Overall, a less mechanistic approach (as long as it can reasonably capture the migration front) requires less parametrization effort and may decrease the inherent uncertainty of the model and the computational cost by having a more efficient dispersal algorithm (compared to explicit calculations of seed movement) and by allowing to upscale the spatial and taxonomic resolution of the simulation domain.

Model assessment. No matter the algorithm used to represent migration processes, it is always necessary to parametrize and evaluate the model uncertainty and validate newly implemented solutions. The predictive power of DVMs can be enhanced by including more detailed and mechanistic representations of ecological processes. On the other hand, increasing model complexity may also lead to higher uncertainty in predictions as each additional equation and/or parameter carries its own inherent uncertainty (Snowling & Kramer, 2001). Specifically, uncertainty in migration modelling in DVMs is attributed to:

- model uncertainty, i.e. the appropriate (mathematical) representation of the ecological processes underlying the model (e.g. representation of rare long-distance dispersal events or multiple agents of dispersal such as water and wind);
- parameter uncertainty, which is linked to the estimation of parameters carried under limited observations and/or biases in measurements (e.g. shape of seed dispersal);
- inherent uncertainty, which is determined by the inclusion of highly unpredictable (near random) processes in the model (e.g. animal movement mediating seed dispersal).

Model uncertainty can be controlled by incorporating up-to-date ecological information on the processes underlying migration (demographic and dispersal processes) and its key drivers (e.g. climate, landscape, species interactions) into the model (Alexander et al., 2018; Tomiolo & Ward, 2018). Parameter uncertainty can be quantified with a sensitivity analysis (SA) by systematically changing the value of the input parameter and measuring the related response of the model output (Saltelli et al., 2000). Next, non-relevant parameters (and their inherent uncertainty) may be excluded from the modelling framework, and/or the representation of relevant parameters may be refined by combining ecological information with the interpretation of SA results ("model reduction") (Loehle, 2004). Finally, the overall assessment is achieved by comparing model outputs with independent observations.

Data availability. Ecological information and data are required for both model evaluation and parametrization. This information should be ideally large-scale, as site-specific data can be biased by local conditions and fail to capture general ecological patterns of migration processes (across different biomes and continents; Nabel et al. 2012), which would be needed for a less biased parametrization of process-based models. Similarly, the validation of simulated range shifts requires independent spatio-temporal data at multiple time steps and across wide areas. A possible solution is the use of paleo-records (pollen and/or macrofossils) to calibrate migration parameters (e.g. against paleo-derived migration rates) and validate the model. Paleo-records over continental and millennial scales can better represent the long spatio-temporal dynamics of migration and are more suitable to capture possible multi-millennia migration lags than small-scale contemporary distribution (Fordham et al., 2020). For instance, paleo-reconstructions of climate and vegetation from fossil records have highlighted marked changes in both temperature regime and plant cover across a number of Quaternary glacial-interglacial cycles (Allen et al., 2020; Huntley et al., 2013, 2023). Specifically, paleo-vegetation reconstructions from pollen and macrofossil records show a forest expansion across the Northern Hemisphere after the ice sheet retreat of the Last Deglaciation (ca. 19–15 ka) (Cao, Tian, Dallmeyer, et al., 2019; Cao, Tian, Li, et al., 2019; Dallmeyer et al., 2022; Githumbi et al., 2022; Harrison, 2017). However, the role that migration

lag played in this vegetation shift is not yet clear, with studies observing a fast response to climate amelioration in North American woody taxa (Ordonez & Williams, 2013; Williams et al., 2002), while others argue for an ongoing range filling (i.e. range still lagging behind the post-glacial climate niche) in some tree taxa (Svenning & Skov, 2004). Unfortunately, the spatial, temporal, and taxonomic unevenness of fossil records might impair the complete reconstruction of climate-vegetation dynamics in the long past. In this sense, large-scale simulations with DGVMs have already been used to explore the effect of millennial climatic fluctuations on the paleo-vegetation (for LPJ-GUESS simulations, see Allen et al., 2010, 2020; Huntley et al. 2013, 2023), although none have assessed the effect of dispersal limitation on the paleo-vegetation dynamics.

To sum up, we aimed to address the following challenges (C):

I. Assess the uncertainty and parametrize the migration module of a large-scale DVM by using paleo-records (C1).

II. Simulate migration processes at large extents and with a relatively low computational cost by implementing more efficient dispersal algorithms (C2).

III. Validate and assess the efficiency of the updated model by simulating the migration of multiple species at large spatial and temporal extents (C3).

IV. Clarify the role of dispersal limitation (and migration lag) in the post-glacial vegetation (C4).

2.Aims

The main aim of this thesis is to implement a dynamic model for the effective simulation of range shifts in plant species, starting with the widely used DGVM, LPJ-GUESS. The final model aims to explicitly include the migration of vegetation and feedbacks from interacting plant species. This will allow us to evaluate the effects of climate change and migration processes, both in terms of carbon fluxes and stocks as well as species distributions and spreading patterns.

This thesis is divided into successive steps with implementations of new functionalities in the model and tests of applicability through simulations (case studies), where each step aims to address a challenge (C) of Section 1.3.2:

I. the uncertainty assessment of the spatially explicit DGVM, LPJ-GM 1.0, which couples a dynamic migration module of explicit seed dispersal (SEEDISP) with LPJ-GUESS (LPJ-GUESS-MIGRATION), resulting in LPJ-GM 1.1 (Paper I) (C1);

II. the implementation of a more efficient MPI protocol in SEEDISP and an additional migration mode with higher computational efficiency (FIXSPEED) in LPJ-GM 1.1, resulting in LPJ-GM 2.0 (C2);

III. the evaluation of LPJ-GM 2.0 in large-scale simulations of the paleo-vegetation: Europe, 18.5–0 ka (SEEDISP; Papers II, III) and the Northern Hemisphere, 51–0 ka (FIXSPEED; Paper IV) (C3 and C4).

3.Methods

3.1 LPJ-GUESS and LPJ-GM 1.0

The LPJ-GUESS DGVM allows simulating eco-physiological processes and the structural dynamics of forests in response to input climate forcing (e.g. temperature, precipitation, short-wave radiation, and nitrogen deposition) (Smith et al., 2001, 2014). Simulated plants are classified in plant functional types (PFTs) based on specific attributes, such as growth form, life-history strategy, physiology, and bioclimatic limits. Population dynamics (establishment, growth, and mortality) of plants are simulated annually as local communities of PFTs (patches), which share the same climatic conditions within each grid cell constituting the spatial domain of simulation. Plant dynamics are affected by climate forcing and local competition for light, water, and nutrients among and within PFTs. Plant biometrics, such as canopy heights and root fraction per soil layer, and PFT-specific shade tolerances determine the outcome of PFT competition. On the other hand, the climate niche of simulated plants is defined by PFT-specific bioclimatic limits (e.g. minimum temperature for survival and establishment). Thus, the establishment of PFTs is mainly determined by the presence of suitable environmental conditions at the grid cell level, whereas patches within grid cells represent statistical replicates experiencing potentially different stochastic processes (disturbance and mortality). In LPJ-GUESS, seeds are therefore assumed to be always available across all patches, with plant establishment not depending on seed availability, i.e. the model assumes free dispersal.

In LPJ-GM 1.0 (Lehsten et al., 2019), LPJ-GUESS is combined with a dynamic migration module with explicit seed dynamics and dispersal across space to limit seed availability. Thus, the model explicitly simulates the spread of species via seed dispersal while allowing species to interact with each other. Contrary to LPJ-GUESS, the establishment of plants in LPJ-GM 1.0 is a function of seed abundance at the patch level, given that environmental conditions within the grid cell are suitable for survival and establishment. In this sense, patches are spatially placed to allow the explicit simulation of the dispersal process with the exchange of seeds among cells. The model also allows for an initialization phase of free dispersal where establishment is exclusively dependent on bioclimatic limits by providing a cell- and PFT-specific starting date to restrain establishment with seed availability. Overall, the migration module of LPJ-GM 1.0 follows the TreeMig model

implementation (Lischke et al., 2006), with migration being simulated at the start of each year through four processes: (1) seed production depending on leaf area index; (2) seed dispersal via a dispersal kernel; (3) seed bank dynamics including germination and soil longevity; and (4) sapling establishment based on the number of viable seeds in the soil bank (Fig. 3.1).

For more details on the migration module, see Lehsten et al. (2019) and Appendix A of **Paper I**.

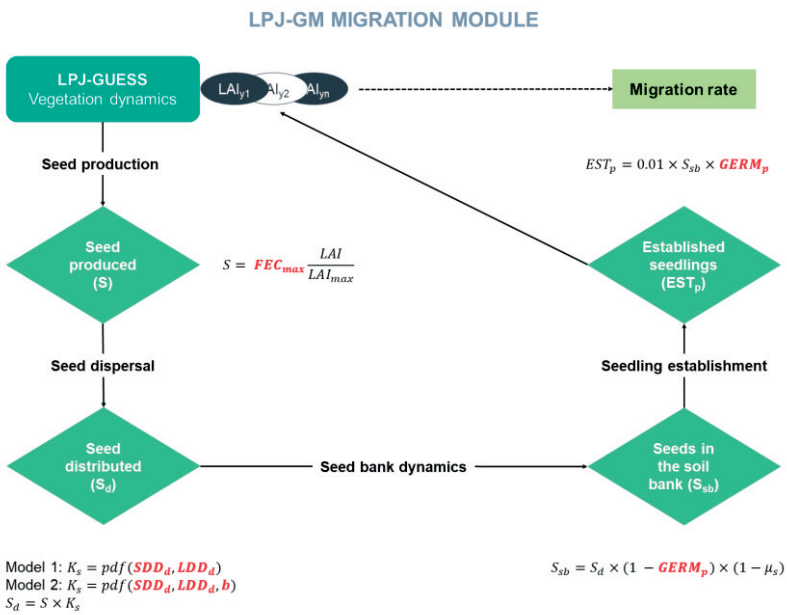

Figure 3.1. Migration module of the model LPJ-GM. Migration parameters are highlighted in red: maximum fecundity (FEC_{max}), average short (SDD_d) and long (LDD_d) dispersal distance, and seed germination rate ($GERM_p$). Model 1 (LPJ-GM 1.0) and Model 2 (LPJ-GM 1.1) refer to the default and modified model structures employing negative exponentials or species-specific fat-tailed kernels, respectively, for seed dispersal. Source: **Paper I**.

3.2 Uncertainty assessment of LPJ-GM 1.1 (Paper I)

In **Paper I**, we conducted an efficient uncertainty assessment of model selection and parameter estimates for the newly implemented migration module of LPJ-GM 1.0 (Section 3.1). Since vegetation metrics of the underlying LPJ-GUESS model have already been validated (Morales et al., 2007; Pappas et al., 2013), we focused

our parametrization on the newly added migration parameters of LPJ-GM 1.0: maximum fecundity (i.e. number of seeds produced per tree per year; FEC_{max}), seed germination rate ($GERM_p$), and the average short and long dispersal distances of seeds (SDD_d and LDD_d, respectively) (Fig. 3.1). We tested different parameter sets and model structures against observed migration rates for 17 major European tree taxa, where observed migration rates were estimated by paleo-records of pollen distribution in post-glacial Europe (i.e. starting from 18,000 BP until today) (Huntley, 1983). Simulated migration rates were obtained by allowing each species to spread in a 100º x 100º terrain for a total of 500 years under non-limiting environmental conditions and competing exclusively with the early-successional *Betula pendula* and C3 grass. We first conducted a species-specific local sensitivity analysis (LSA) to quantify the importance of each migration parameter with respect to the output, i.e. migration rate. Next, we performed an extreme value analysis (EVA) based on the LSA interpretation, where the EVA quantifies the change in model output after all parameters are set to extreme range values (minimum and maximum) collectively. Thus, EVA can be used to reduce the performance landscape and later inform a more efficient parametrization routine. Next, we evaluated the effect of alternative seed dispersal kernels (model structures) on migration rates and model uncertainty. Finally, we retained the model structure with higher utility (model selection) and the set of parameter values that minimized the most the error between observed and simulated migration rates for each species (parametrization). For more details on the model assessment routine (and formulae), see Material and Methods of **Paper I**.

The optimized model structure and parameter sets resulted in the model LPJ-GM 1.1.

3.3 Implementation of LPJ-GM 2.0

After the successful parametrization of the original migration module of LPJ-GM 1.1 (hereafter, the SEEDISP option; Section 3.2), we made two modifications to the model in order to improve its efficiency at large scales.

(1) We upgraded the MPI routine of SEEDISP to parallelize the seed dispersal routine more efficiently at large spatial scales. Namely, the spatial domain of LPJ-GM is represented by an ensemble of grid cells (corresponding to 1 km^2), which are divided among the MPI tasks. The amount of seeds produced by trees in each grid cell is communicated to a set of master-ranks at the end of each year. Following a dispersal algorithm, these master-ranks redistribute the seeds over the whole spatial domain and communicate the amounts of arriving seeds back to each grid cell (slave-ranks), where the main LPJ-GUESS code simulates local vegetation dynamics (Lehsten et al., 2019). However, the MPI protocol implemented in LPJ-

GM 1.0 and 1.1 may also have limitations concerning the ratio between the total number of simulated cells (spatial extent) and the number of available nodes (or processes per CPU), which is an inherent characteristic of the HPC cluster available for the simulation. That is, in the case of great spatial extents, it is necessary to use multiple master-ranks to optimize the calculation of seed dispersal (convolution with FFT). According to the default MPI protocol of LPJ-GM 1.0 and 1.1, the slave-ranks have to wait for all master-ranks to finish the calculation (i.e. to receive the seeds from the respective master) before proceeding with the simulation on their rank. However, with a high number of simulated cells, it might happen that a master-rank would be assigned as a slave to another master-rank (and vice versa). This would result in a deadlock in the simulation (MPI knot). To solve this issue, we added non-blocking asynchronous communication (MPI_Ibsed and MPI_Recv), which can also increase the overall performance of the MPI parallelization.

(2) We implemented an additional routine to simulate migration in a less explicit but more computationally efficient way (hereafter, the FIXSPEED option). Differently from the expensive algorithm of SEEDISP with explicit inter-grid seed exchange, the FIXSPEED option simulates plant migration by calculating the time delay to full establishment at the patch level based on a 1) PFT-specific maximum migration rate (given as an input parameter derived from pollen records) (Huntley, 1983). To correct the time to establishment based on vegetation dynamics, two additional parameters are given: 2) the number of years for which seeds are able to survive in an environment not suitable for plant establishment or survival (seed bank longevity), and 3) a leaf area index threshold above which individual plants are able to become seed donors. As a further improvement on computational efficiency, the FIXSPEED option allows the use of coarser spatial (>1 km) and taxonomic (parametrization possible above the species level) resolutions. Finally, to control for the coarse spatial scale (see Section 1.3.2), we modified the seed bank longevity based on the topographic heterogeneity of the cell so that seeds can survive longer in environments with a higher elevation difference (conceptually mid-elevation refugia). For more details on the FIXSPEED option, see Methods in **Paper IV**.

The upgrading of the MPI routine of SEEDISP and the implementation of the FIXSPEED option in LPJ-GM 1.1 resulted in the model LPJ-GM 2.0.

3.4 Modelling of paleo-vegetation dynamics with LPJ-GM 2.0 (Papers II-IV)

In order to validate the newly-implemented and parametrized migration module of LPJ-GM 2.0 (Section 3.2 and Section 3.3), we conducted historical simulations of the paleo-vegetation change in Europe and in the Northern Hemisphere with the SEEDISP and FIXSPEED options, respectively.

For **Papers II** and **III**, we defined our simulation domain in Europe at a resolution of 0.01º, and starting with the ice sheet retreat after the LGM (18.5 ka) and until the current time (0 ka). We allowed for 100 years of nitrogen and carbon build-up in the soil to start the plant succession (18.5–18.4 ka) as recommended by the default LPJ-GUESS (Sitch et al., 2003; Smith et al., 2001), followed by 400 years (18.4–18 ka) of free establishment given suitable climatic conditions. For **Paper IV**, the spatial domain of simulation was divided into grid cells of 0.5º resolution and spanned the Northern Hemisphere (NH) between 30°N and 80°N. Simulations were performed for a total of 51 ky with 1 ky of free establishment. The initialization phase of free dispersal was used to locate potential glacial refugia, i.e. isolated areas where (mostly tree) species managed to survive cold periods. Then, we applied two alternative dispersal modes across the remaining years (18–0 ka for **Papers II** and **III**, and 50–0 ka for **Paper IV**): 1) free dispersal (plant establishment independent of seed availability and dispersal, as in LPJ-GUESS) and 2) dispersal limitation (plant establishment following the migration module of LPJ-GM 2.0; SEEDISP for **Papers II** and **III**, and FIXSPEED for **Paper IV**). For **Papers II** and **III**, the 24 simulated taxa follow the set of species selected by Hickler et al. (2012) as representative of European vegetation, with the addition of *Alnus glutinosa*, *Acer campestris*, and *Larix decidua*. In **Paper IV**, we selected representative global taxa following Allen et al. (2020) for a final set of 20 PFTs, including 11 tree PFTs, 7 shrub PFTs, and 2 grass PFTs. General model settings follow previous large-scale paleo-simulations performed with LPJ-GUESS (Allen et al., 2020; Huntley et al., 2013). We used the pollen-derived estimates of migration rates by Huntley (1983) either to calibrate the migration parameters in the SEEDISP option (approach described in **Paper I** and Section 3.2) or directly as input parameters in the FIXSPEED option (PFT-specific maximum migration rate; see Section 3.3).

3.5 Analysis of the paleo-vegetation (Papers II-IV)

Simulations were validated with paleo-records:

- Biome reconstructions and species presence and absence from the fossil pollen data of the Neotoma database (http://www.neotomadb.org) (Fyfe et al., 2009; Giesecke et al., 2014) (**Papers II**).
- Species-specific maximum range shift velocity after the LGM derived from fossil pollen analyses of major European tree taxa (Huntley, 1983) (**Papers III**).
- Boreal and temperate tree cover (%) across the Holocene (after 12 ka) based on fossil pollen interpolations of the REVEALS product (Regional Estimates of Vegetation Abundance from Large Sites) (Githumbi et al., 2022) (**Papers IV**).

In **Paper II**, we first inferred biomes from pollen abundance and from the output of LPJ-GM 2.0 simulations under both dispersal modes (Allen et al., 2010; Prentice et al., 1996). We then located time periods of fast climate warming (maxima of gradient-based temperature velocity; Garcia Molinos et al., 2019) and estimated the onset of forest expansion according to pollen records and LPJ-GM 2.0 simulations. Thus, we were able to evaluate the ability of each dispersal mode to capture the temporal trend of the post-glacial forest expansion in Europe and to detect possible migration lags (the temporal difference between the forest onset under free dispersal and dispersal limitation). Additionally, we compared the performance of each dispersal mode in simulating the overall distribution and temporal trend of biomes and single taxa (as presence and absence) against pollen records. To this end, we used a common similarity metric (kappa statistics) and newly-developed point-to-grid (Fractional Score, FS; based on Dallmeyer et al., 2019) and dissimilarity metrics (Earth Movers' Distance, EMD; Chevalier et al., 2023).

In **Paper III**, we first calculated the gradient-based spatial (each 0.5º) and temporal (each 100 years) pattern of temperature velocity after the European LGM and then derived the maxima across time (also used in **Paper II**). Next, we calculated the species-specific range shift velocities obtained from the two dispersal modes and compared them with the thermal velocity at points of maxima to assess whether (and which) tree species could keep up with climate change in both dispersal modes. We estimated the year of earliest establishment (post-glacial arrival) for each species and each simulated cell (0.01º) and compared the year of arrival between the two dispersal modes to obtain the dispersal lag, i.e. delay in establishment caused by the limited dispersal capacity of a species. We estimated the thermal lag for each simulated species as the temporal mismatch between the minimum temperature year (i.e. the earliest year at which the species-specific minimum temperature for establishment was reached) and the year of arrival for both dispersal modes (thus, thermal lag≈migration lag). Additionally, we calculated a proxy for competition at establishment by summing the leaf area index of all non-grass taxa at the year of arrival. In order to evaluate the performance of the SEEDISP option of LPJ-GM 2.0 (free dispersal vs. dispersal limitation), we compared the simulated range shift velocities and spreading patterns (year of arrival in space) with reconstructions from pollen records and phylogenetic studies. Altogether, these analyses allowed us to disentangle the relative effect of the main drivers of post-glacial vegetation change (temperature, inter-specific plant competition, and dispersal limitation).

In **Paper IV**, (mega-)biomes and land cover types were inferred from the model outputs using the approach by Allen et al. (2020) for both dispersal modes. We then calculated the temperature anomaly and average forest cover for the last 50 ky across the whole NH and for three separate areas (North America, Europe, and Asia), along with the change of temperature and forest cover between the LGM (26–

19 ka) and the Late Holocene (4.25–0 ka; LH). Additionally, we calculated the first year of post-LGM establishment (arrival) at each 0.5º cell for the temperate and boreal forest mega-biomes. Temporal differences in forest establishment between the two dispersal modes were interpreted as dispersal lags, while differences in Holocene maxima (time-points of stable forest cover after expansion or shrinking) were interpreted as delays in range filling after establishment. Finally, we evaluated the performance of the two dispersal modes in predicting the cover (%) of European boreal and temperate forests against reconstructions from the REVEALS product (Githumbi et al., 2022).

4.Results and Discussion

4.1 The importance of long-distance dispersal in tree migration (Paper I)

Sensitivity and uncertainty analyses performed on the migration module of LPJ-GM agreed on the greater importance of seed dispersal parameters (average distance for local dispersal and rare long-distance dispersal LDD events) for the accurate simulation of migration rates (Fig. 4.1).

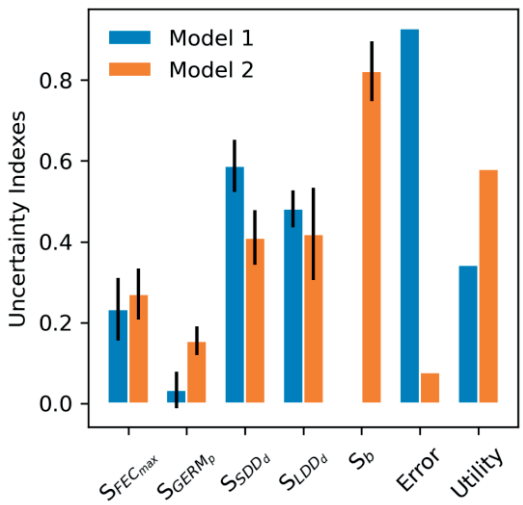

Figure 4.1. Comparison of parameter-specific sensitivities (S), model error, and utility between two structures of the migration module of LPJ-GM: Model 1 = LPJ-GM 1.0 (negative expontential kernel); Model 2 = LPJ-GM 1.1 (species-specific fat-tailed kernels). For parameters' acronyms, see the legend of Fig. 3.1. S_b: model sensitivity to the shape parameter *b* of fat-tailed kernels. Note that the kernel formulation of Model 1 has no shape parameter (hence, S_b is NA). Source: **Paper I**.

As shown in previous studies (Bullock et al., 2017; Clark et al., 1999; Nathan et al., 2008; Powell & Zimmermann, 2004), fat-tailed dispersal kernels are able to represent LDD events more realistically than exponentially bounded functions. In

our case, fitted species-specific fat-tailed kernels solved the systematic underestimation of migration rates that we found associated with the use of negative exponential functions in the default structure of LPJ-GM 1.0. This was especially the case for species with animal- or water-related mechanisms of seed dispersal. From an ecological point of view, these species may be expected to have shorter dispersal distances on average than wind-dispersed species (lower SDD_d), but they can additionally rely on rare LDD events (e.g. river transport or a migratory animal) to rapidly expand their migration front. This seemed to suggest that tree migration relies more on occasional LDD events (than local dispersal) to reach high spreading velocities, or at least the values derived from the post-glacial pollen records used in **Paper I**. Indeed, LDD events have already been identified as a likely solution to Reid's paradox, i.e. the mismatch between high post-glacial migration rates derived from pollen records and lower values observed in contemporary plant dispersal (Cain et al., 1998). Namely, observed values in contemporary settings may be interpreted as local dispersal (SDD_d). On the other hand, the fast spreading rates observed in the post-glacial period relied more on rare LDD events where plants were able to occupy newly available and distant habitats after ice retreat via less common LDD vectors (Birks, 2019; Higgins et al., 2003; Vittoz & Engler, 2007).

Although we parametrized the migration module of LPJ-GM 1.1 with Early and Mid-Holocene observations, the results can be relevant to predict future trees' range shifts. The high thermal velocity projected across the 21st century (Lenoir et al., 2020; Svenning & Sandel, 2013) indicates that the range shift of some tree taxa will be limited by their dispersal ability (i.e. migration lag), as we are already observing in the temperate-boreal forest ecotone (Vissault et al., 2020). This is especially true in a contemporary or future context where suitable habitats for establishment may be disturbed by human activities, and LDD events will become crucial to spread across a fragmented landscape. Thus, the efficient inclusion of LDD events in the modelling framework (e.g. with fat-tail dispersal kernels) can increase our confidence in the prediction of species range shift (Boisvert-Marsh et al., 2022).

4.2 Range shifts in the post-glacial forests of the Northern Hemisphere (Papers II-IV)

Large-scale simulations of paleo-vegetation change produced similar results under the simulation with limited dispersal as implemented by the SEEDISP (**Papers II, III**) and the FIXSPEED (**Paper IV**) options of LPJ-GM 2.0. Specifically, we observed a marked delay in the simulated forest expansion along with a lower forest cover under dispersal limitation if compared to the default setting of unconstrained establishment and expansion (free dispersal in LPJ-GUESS).

Figure 4.2. Change of (a) total forest, (b) boreal (blue) and temperate (green) forest coverage and temperature anomaly (grey) in the Northern Hemisphere and for each region. Forest change simulated under the free dispersal [yellow in (a), and solid in (b)] and dispersal limitation [blue in (a), and dashed in (b)] modes is calculated as the fraction of ice-free land area occupied by tree-dominated biomes. (a) Average temperatures of the Last Glacial Maximum (LGM) and Late Holocene (LH) are reported in grey, along with the difference of LGM-LH temperature (lower-right corner). Cold events [LGM (26–19 ka), Older Dryas (14 ka) and Younger Dryas (YD, 12.9–11.7 ka)] and warming periods [Bølling-Allerød (BA) interstadial (14.8–12.9 ka)] are shaded in blue and red, respectively. Source: **Paper IV**.

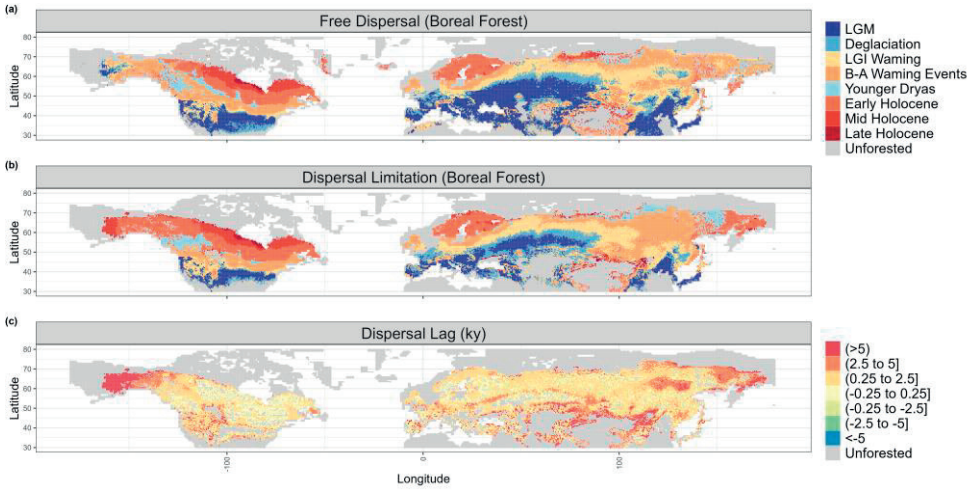

Figure 4.3. Post-LGM arrival of boreal forests under (a) the free dispersal and (b) dispersal limitation modes, and (c) dispersal lag [difference between (a) and (b) in ky]. (a-b) Years of arrival (ky) are classified as follows: the Last Glacial Maximum (26–19 ka); the Late Glacial Interstadial (19–15 ka; LGI); the Bølling-Allerød interstadial (15–12.9 ka; BA); the Younger Dryas (12.9–11.7 ka; YD); the Early Holocene (11.7–8.236 ka; EH); the Middle Holocene (8.236–4.25 ka; MH); and the Late Holocene (4.25–0 ka; LH). (c) Positive values (yellow-red) indicate a delayed forest establishment in the dispersal limitation mode [and negative values (green-blue) vice versa]. Grey indicates unforested areas. Source: **Paper IV**.

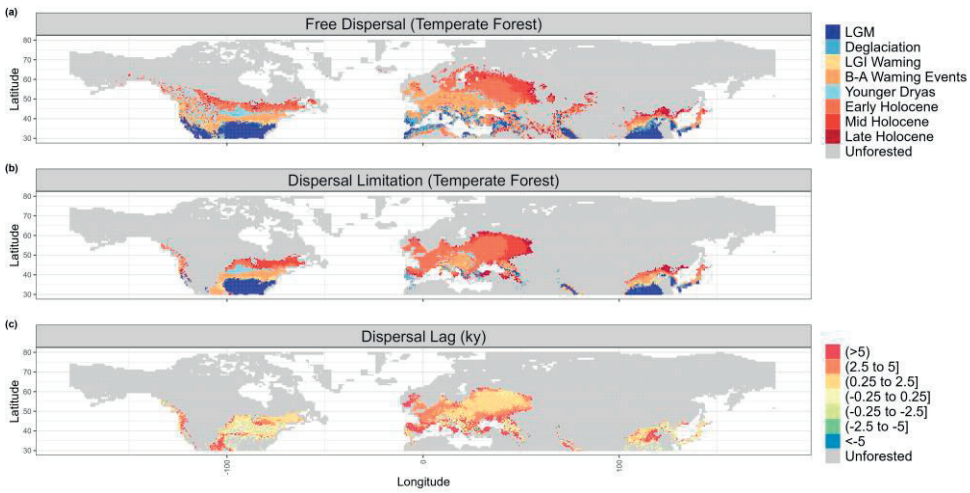

Figure 4.4. Post-LGM arrival of temperate forests under (a) the free dispersal and (b) dispersal limitation modes, and (c) dispersal lag [difference between (a) and (b) in ky]. (c) Positive values (yellow-red) indicate a delayed forest establishment in the dispersal limitation mode [and negative values (green-blue) vice versa]. Grey indicates unforested areas. See legend of Fig. 4.3 for chronozone classification. Source: **Paper IV**.

Differences in forest cover between the two dispersal modes tended to be greater at points of rapid climate change that usually follow cold periods, such as during the Bølling-Allerød interstadial following the LGM (around 14.5 ka; P-BA) or the warming Holocene after the cold spell of the Younger Dryas (around 11.5 ka; P-YD) (Fig. 4.2). Across the Northern Hemisphere (NH), the mismatch of simulated forest coverage between dispersal modes is overall higher in Europe (Fig. 4.2), and especially in the case of temperate trees at points of rapid warming (Fig. 4.2 and Fig. 4.6; **Papers II** and **IV**).

We observed multi-millennia delays of post-glacial tree establishment (dispersal lags) in the boreal forests of Central Siberia (Fig. 4.3) and in European temperate forests (Fig. 4.4). Additionally, scattered areas with similar (multi-millennial) dispersal lags were located close to mountain chains, i.e. the Rocky Mountains in North America and north of Himalaya in Asia (Fig. 4.3). We argued that the magnitude of post-glacial migration lag depended on the rate of change of the climate signal, the forest type (more warmth-demanding tree taxa or forest types lagging behind a rapidly warming climate), the presence of dispersal barriers (ice sheets or mountains), and the distance to and spatial configuration of the glacial refugia (wide spreading fronts and adjacent occupied habitats reduce migration lag). (**Paper IV**).

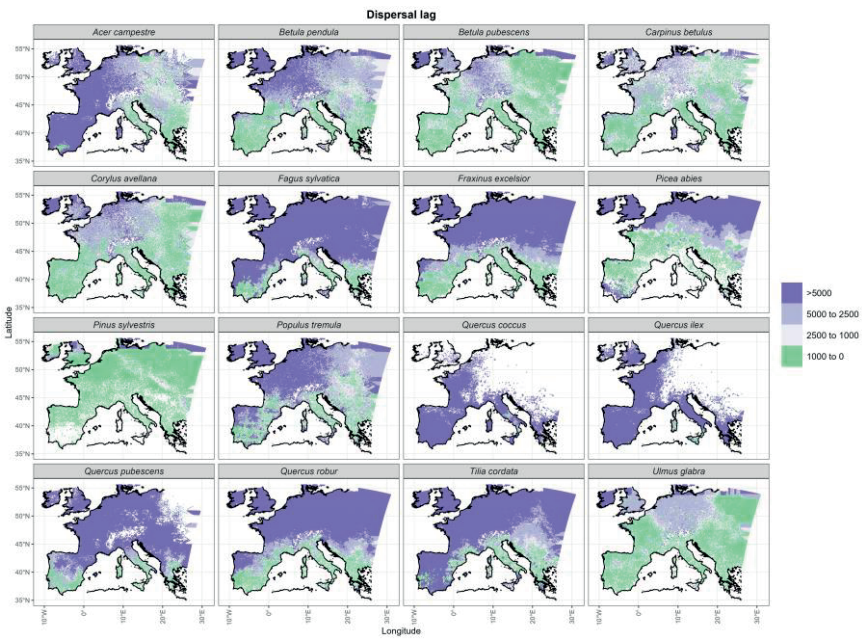

Figure 4.5. Dispersal lags as represented by the temporal delay (in years) between the year of arrival under free dispersal (LPJ-GUESS) and dispersal limitation (SEEDISP in LPJ-GM 2.0). Source: **Paper III**.

Results at a finer taxonomic scale across Europe showed a marked delay in the post-glacial establishment of more warm-demanding and relatively slow-spreading temperate species (e.g. *Fraxinus excelsior*), with estimated migration lags of several millennia (Fig. 4.5). Specifically, the dispersal limitation mode simulated a northward expansion over the Mid- and Late Holocene, whereas range filling was overall completed by the end of the first post-LGM warming period (BA) under the free dispersal mode. On the other hand, we observed far lower dispersal lags in pioneer species (e.g. *Betula pubescens* and *Pinus sylvestris*; Fig. 4.5), with almost no difference between the range shift velocities calculated under free dispersal and dispersal limitation (Fig. 4.7).

This suggested that the velocity with which European tree species managed to track their niche (and therefore the magnitude of their migration lag) likely depended on their bioclimatic tolerance (thermal minima in our case) and dispersal ability (with pioneer species being overall faster and more thermal tolerant spreaders), which in turn determined the order of arrival at newly available habitats and therefore the degree of competition for establishment (with late-successional species experiencing higher competition) (**Paper III**).

4.3 Model comparisons with fossil records (Papers II-IV)

When validating our simulations against pollen records of post-glacial Europe, we found that the lower cover and the delayed expansion of temperate forests simulated under dispersal limitation were more in agreement with pollen reconstructions than the simulations assuming free dispersal (**Paper II** and **Paper IV**). Specifically, the mismatch in model performance between the two dispersal modes was higher at points of rapid warming, i.e. P-BA (around 14.5 ka) and P-YD (around 11.5 ka) for both the SEEDISP (Fig. 4.6 and Fig. 4.7) and the FIXSPEED (Fig. 4.8) options.

Species-specific velocity of range shifts simulated under dispersal limitation were closer to pollen estimates, whereas simulated velocities under free dispersal overestimated observed values and were markedly higher for some European late-successional species (Fig. 4.7). Similarly, spreading patterns simulated under dispersal limitation better approached reconstructions from fossil pollen and phylogenetic studies (Giesecke & Brewer, 2018), although some taxa (*Fagus sylvatica* and *Quercus robur*) showed a marked underestimation of migration speed and/or range filling compared to pollen reconstructions (see Section 4.4 for a discussion on model biases) (**Paper III**).

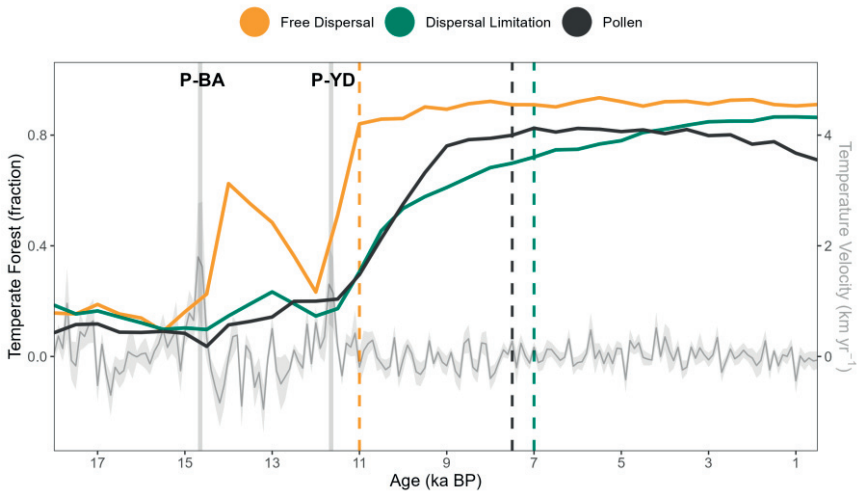

Figure 4.6. Post-glacial temperature (light grey, ±S.D.) and temperate forest change in Europe. Temperate forest fraction is the sum of cool mixed and temperate deciduous forests vs. all biomes, where dominant biomes were reconstructed either by model simulations with free dispersal (yellow) or dispersal limitation with the SEEDISP option of LPJ-GM 2.0 (dark green) or by pollen samples (black). Vertical dashed lines indicate the time when the post-glacial expansion of temperate forests slowed down or stopped (Free Dispersal: 11 ka; Dispersal Limitation: 7 ka; Pollen: 8 ka). Source: **Paper II**.

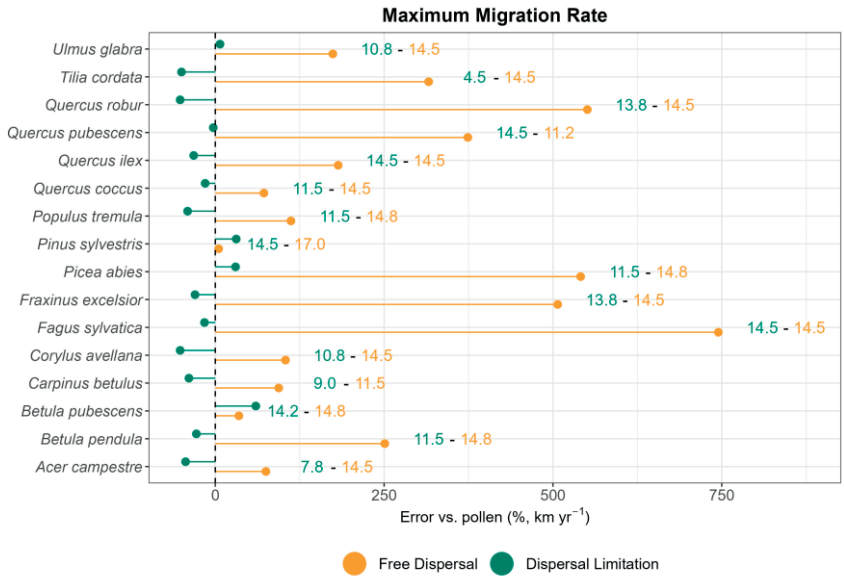

Figure 4.7. Error (percentage difference, Δ%) against pollen-derived estimates of maximum migration rate (leading edge) under free dispersal (yellow; LPJ-GUESS) and dispersal limitation (green; SEEDISP in LPJ-GM 2.0). Years of recorded maxima (ka BP) are reported on the right for each species and colored according to dispersal mode. Source: **Paper III**.

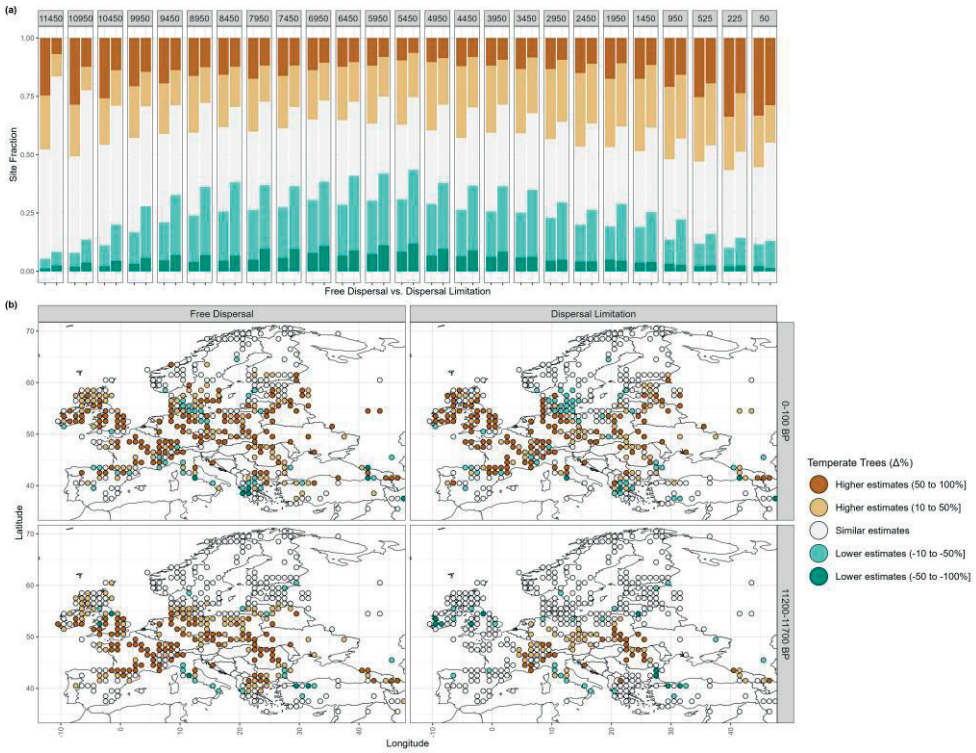

Figure 4.8. Differences in temperate tree coverage (Δ%) between pollen-derived REVEALS products and estimates from LPJ-GM 2.0 simulations under two dispersal modes: simulations with free dispersal (LPJ-GUESS) or dispersal limitation (FIXSPEED option of LPJ-GM 2.0). (a) Fraction of REVEALS sites for all time slices (mid-points, year BP, in the grey strips) with higher (orange colours), similar (white), and lower LPJ-GM estimates (green colours) of forest coverage for the free dispersal (left bars) and dispersal limitation (right bars) modes. (b) Maps of site-specific REVEALS-LPJ-GM differences for the free dispersal (left panels) and dispersal limitation (right panels) modes at two time slices: the most recent LH period [upper panels; 50 in (a)] and immediately after the YD [lower panels; 11450 in (a)]. The colour code of differences (higher, lower, similar estimates) based on % values is indicated in the legend of panel b. Temperate trees in REVEALS: *Abies alba* + *Alnus glutinosa* + *Carpinus* spp. + *Castanea* + *Corylus avellana* + *Fagus sylvatica* + *Fraxinus* + *Quercus* deciduous + *Tilia* + *Ulmus*. Temperate trees in the model: TeNE + TeBS + TeIBS. Source: **Paper IV**.

These results suggest that our simulated mismatches in forest cover (between dispersal modes) can be interpreted as migration lags in the post-glacial forest expansion of the Northern Hemisphere. In support of the "postglacial forest conundrum" (Dallmeyer et al., 2022), we argued that migration lags cannot be simulated with high accuracy by models lacking drivers of climate-vegetation disequilibrium, such as biotic interactions and dispersal limitation (see Section 1.2). Thus, a vegetation model such as LPJ-GM 2.0, which simulates plant establishment

constrained by dispersal limitation and competition for resources and space, is more likely to capture potential migration lags in forest range shift under rapid climate change. This has implications for both past ecosystems (e.g. hypotheses on the Quaternary megafauna extinction; Monteath et al., 2021) and over-predictions of forest cover under future climate change, which in turn would affect the projections of ecosystem services and vegetation-climate feedbacks.

4.4 Potential biases in the model simulation (Papers II-IV)

We detected some possible biases in our simulations under dispersal limitation: (1) the range shift was underestimated for some late-successional species (Fig. 4.5 and 4.7, **Paper III**), and (2) some contemporary taxa went extinct before the end of the simulation (**Papers II, IV**).

(1a) The simulated slow spread of some late-successional species may be attributed to an oversimplified parametrization setting for the migration parameters, namely assuming only a single and relatively weak competitor (**Paper I**). In this case, we suggested a more realistic parametrization setting with species-specific climatic conditions and competition derived from the paleo-simulations with free dispersal. (1b) Additionally, we observed that mountain chains (e.g. Alps in the European simulation) acted as dispersal barriers to northward spread, thus likely delaying the range filling of some taxa (e.g. *Fagus sylvatica* and *Quercus robur*). This is in disagreement with pollen evidence, where the Alps acted as glacial refugia for a number of tree species. We argued that this bias might be caused by the use of a coarse spatial resolution (that failed to capture micro-climatic conditions in cells with high topographic variability) and/or the wrong parametrization of the bioclimatic limits of some species (see point 2 below). (1c) Alternatively, the underestimation of the migration rates might be caused by a missing process or driver favouring the spread of late-successional species, such as anthropogenic landscape clearance and alteration of the fire regime (Bradley et al., 2013; Bradshaw & Lindbladh, 2005) (**Papers II, III**). In this sense, the inclusion of human activity in the simulations could potentially speed up the expansion of late colonizers by eliminating already established trees (competitors). Biome-wide, the overestimation of tree cover after the Mid-Holocene could be explained by increasing human deforestation (**Paper IV**). To account for human impact across the Holocene, we proposed to use databases on past anthropogenic land-cover (e.g. HYDE 3.2) (Klein Goldewijk et al., 2017) as inputs or to introduce a simple parameter for anthropogenic disturbance (cf. Berzaghi et al., 2019) in LPJ-GM.

(2) On the other hand, the simulated extinction of some contemporary taxa (**Papers II-IV**) might have been caused by the wrong parametrization of bioclimatic limits

based on contemporary distributions. Using current species distributions to reconstruct species-specific climatic niches in paleo-periods may be inadequate if (2a) species changed their climatic tolerances to past climatic conditions compared to significantly different current conditions (niche evolution) and/or (2b) current distributions are in climate-vegetation disequilibrium. As previously argued (Section 1), niche evolution is less likely in long-lived organisms such as trees, although an adaptation to colder and drier conditions (e.g. during LGM) might have occurred for taxa with limited dispersal capacity across millennia of fluctuating conditions (Wang et al., 2023). (2b) More likely, it was argued that contemporary species distributions might deviate significantly from the potential niche due to biotic and anthropogenic interactions and/or dispersal limitations. Thus, even assuming a static niche, the parametrized bioclimatic limits from contemporary observations may represent underestimations of potential physiological tolerances. Thus, we suggested parametrizing the bioclimatic niche in the temporal domain of the intended simulation. In the case of paleo-simulations, we suggested overlaying pollen data of species presence and absence with the paleo-climate at time points of minimum vegetation-climate disequilibrium (and low thermal velocity) (see also Section 6.1).

5.Conclusions

In this thesis, we developed and evaluated a dynamic vegetation model for the efficient simulation of plant migration. Specifically to our aims (Section 2):

I. We implemented an efficient uncertainty assessment for LPJ-GM 1.0, which allowed us to parametrize the migration module and explore the importance of parameters as drivers of migration. We found that the inclusion of LDD events in the model structure significantly improved the model performance. This is in agreement with ecological theory (Reid's paradox) and has implications for the mechanistic formulation of seed dispersal in models and the prediction of plant spread in future settings (**Paper I**).

II. We implemented (a) an asynchronous MPI routine to improve the efficiency and tractability of explicit seed dispersal simulations (SEEDIP, LPJ-GM 2.0) and (b) a less mechanistic and less costly algorithm to constrain plant establishment based on migration potential (FIXSPEED, LPJ-GM 2.0).

III. We tested the new model LPJ-GM 2.0 in paleo-simulations at large spatial and temporal scales and evaluated model outputs against pollen reconstructions. By comparing different dispersal modes (free dispersal and dispersal limitation), we found a climate-vegetation disequilibrium in the post-glacial forests of the Northern Hemisphere, with the highest migration lags localized in the boreal forests of Central Siberia and the temperate forests of Europe (**Paper II-IV**). Migration lags were mainly driven by the presence of dispersal barriers, the spatial configuration and size of migrant populations, and distance from glacial refugia (**Paper IV**). Specifically for Europe, a number of temperate trees appeared to have lagged behind the ameliorating climate by several millennia due to minimum thermal requirements for establishment, limited dispersal ability, and increased competition for late-successional species (**Paper III**). The model performance was overall higher when assuming migration constraints on plant establishment (dispersal limitation; SEEDISP or FIXSPEED in LPJ-GM 2.0) than when assuming unlimited availability of "seeds" for plant establishment (free dispersal; standard LPJ-GUESS), especially at points of rapid climate change (**Paper II, IV**).

The occurrence of migration lag in forest range shifts may affect (a) our understanding of paleo-ecosystems (e.g. megafauna extinction), (b) (paleo-)climate modelling when considering climate-vegetation feedbacks, and (c) the projected vegetation cover under future scenarios with implications for ecosystem services.

6.Outlooks

Although the inclusion of migration processes in LPJ-GM helped to improve our model predictions of species range shifts, we identified two possible developments: (1) parametrization of paleo-niches and (2) inclusion of more biotic interactions.

6.1 Parametrization of paleo-niches

We hypothesized that one of the reasons for the disappearance of some taxa in our simulations with limited dispersal was the biased estimation of bioclimatic parameters based on contemporary tree distribution. This parametrization approach assumes that species-specific bioclimatic limits stay constant or change relatively slowly across simulation time and that contemporary species distribution is mostly in equilibrium with the climate. While the first assumption may be partially true (at least on the scale of a few millennia) (Wang et al., 2023), the current mismatch between the potential and realized niche of most tree species has likely widened due to anthropogenic activities (forest management and agriculture), competition, or even the legacy of post-glacial migration lag (as shown in our thesis for some taxa), which is further increased by the fast ongoing climate change (the concept of 'no-analogue communities') (Birks, 2019).

In our studies' discussion, we suggested estimating the envelope parameters by relating past species distributions to paleo-climatic conditions. In a preliminary study, we used presence-absence data derived from two pollen databases (Neotoma and REVEALS product) to re-estimate the LPJ-GUESS parameter of minimum winter temperature for survival (tcmin_surv) and compared with estimations based on the contemporary distributions of 21 species. In agreement with our hypothesis, we found that paleo-estimations yield a wider minimum thermal tolerance for almost all species (Fig. 6.1). Based on this initial result, we aim to re-parametrize the bioclimatic limits of the 21 species based on their paleo-distributions, where the final potential occurrence is the union of all envelopes for the following LPJ-GUESS parameters: growing degree days, drought tolerance, minimum temperature of the coldest month for establishment and survival, maximum (minimum) temperature of the coldest (warmest) month for establishment.

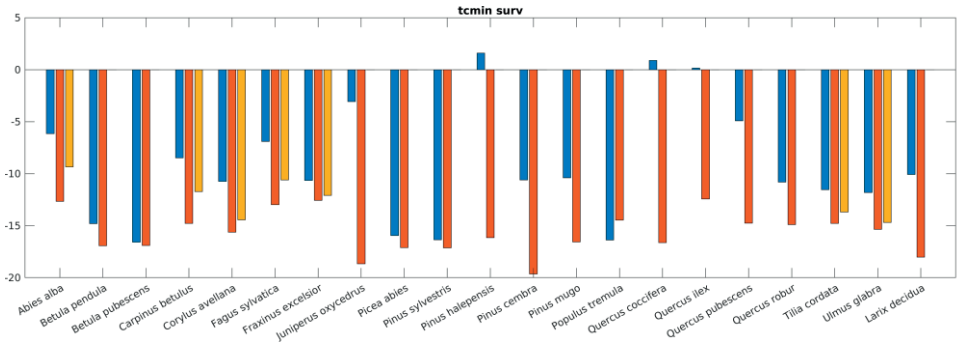

Figure 6.1. Comparison of the tcmin_surv parameter estimation for 21 species based on current species distributions (Caudullo et al., 2017, blue) or paleo-distributions derived from the Neotoma pollen database (after 18 ka, red) and from the REVEALS product (after 12 ka, yellow). Species-specific parameters were estimated as the value at which 95% of all recorded presences are realized (95th quantile).

6.2 Inclusion of additional biotic interactions

In most DVMs, including LPJ-GM, biotic interactions (BIO) are implemented simply as competition for resources among plants. However, there are other types of BIO that may affect the vegetation at different trophic levels and not only in a negative [-] but in a neutral [0] or positive [+] way (Morales-Castilla et al., 2015). In this sense, we can distinguish five types of BIO based on their effect on trees, the interacting species and the symmetry of the effect (i.e. whether the interaction signs differ between the two species) (Morales-Castilla et al., 2015):

1) competition [-/-], when negative impacts are incurred by both species (e.g. leaf competition for light and root competition for water and nutrients);
2) exploitation [-/+], when the interacting species obtains a benefit [+] while suppressing the tree [-] (e.g. large-animal browsing and forest pests and pathogens);
3) amensalism [-/0], when the interacting species affects the tree negatively but stays indifferent to the interaction (e.g. animal and human trampling);
4) facilitation [+/0], when the tree benefits from the presence of the interacting species without affecting it (e.g. climate amelioration and soil formation by nurse plants);

5) mutualism [+/+], when both trees and interacting species benefit from the association (e.g. pollination, animal-mediated seed dispersal, and beneficial soil biota such as decomposers and root symbionts).

A number of LPJ-GUESS-based models have already been implemented to include additional biotic interactions with feedbacks to the vegetation by coupling a BIO module to the main algorithm of plant dynamics. Some examples are: the spruce bark beetle (*Ips typographus*) module to predict pest outbreaks in Swedish forests (Jönsson et al., 2012); the general population dynamic module for large mammalian grazers (Pachzelt et al., 2013); and the more general animal dynamic module, Madingley, which is able to represent the population dynamics of herbivores, omnivores, and carnivores of any size class, along with animal-vegetation feedbacks and heterotrophic food webs (Krause et al., 2022). We found only one example of a LPJ-GUESS-coupled model that incorporates both biotic interactions (ungulates, with the same approach as Pachzelt et al., 2013) and migration (Stratmann et al., 2023).

In LPJ-GMINT 1.0, we aim to couple a module for biotic interactions (INT) to LPJ-GM 2.0. LPJ-GMINT 1.0 will include spatially explicit interactions between migrating plants (plant functional types, PFTs) and interacting functional species (IFTs). We will use the concept of a stage-based model to represent IFTs in six possible life history stages (from inactive juvenile to mature adult). IFTs will be defined by: (a) bioclimatic envelopes; (b) functional groups (i.e. species groups that have a similar physiological impact on plants, e.g. “defoliators”); (c) food/host preference; (d) population dynamics based on nutrition uptake and metabolic cost (cf. Krause et al., 2022); and (e) migration potential (cf. the FIXSPEED approach) optionally based on food availability (cf. Stratmann et al., 2023). With this model, we aim to implement a biotic interaction module that is sufficiently generic to include different types of biotic interactions (as described in the five BIO types above) but still account for the diversity of interacting species.

7.References

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