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RESEARCH ARTICLE

A spatially independent seed dispersal design for forest landscape models

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Abstract

Context Seed dispersal is a spatially continuous process occurring over areas ranging from tens to thousands of square meters. Current seed dispersal designs (CDD) in forest landscape models (FLMs) have notable limitations. CDD may fail to disperse seeds outward when cell size exceeds dispersal distance and commonly assumes seed sources are centrally located within cell. The problems can accumulate spatially and temporally leading to large prediction errors.

Objectives We propose a spatially independent dispersal design (SID) that overcomes the pitfalls of CDD. SID assumes seed sources occur anywhere in a cell and tracks the time required for a tree species to traverse a cell. This technically allows SID to operate at any cell sizes in FLMs.

Methods We validated the SID approach using artificial landscapes to isolate dispersal patterns from confounding factors such as environmental heterogeneity and competition, ensuring that dispersal patterns solely reflect SID and species attributes. We applied SID to a temperate forest landscape to evaluate the uncertainties in predicted tree species distributions.

Results We demonstrated that the SID algorithm achieves spatial independence when predicting tree species distributions and their changes. In simulations of the temperate forest landscape, the average difference in percent cover across spatial resolutions ranging from 100 to 400 m was less than 5% under SID, compared to over 12% under CDD. Previous prediction studies using the CDD algorithm at coarse resolutions may result in deviations exceeding 20% in predicting the percent cover of mid- and late-successional species.

Conclusions The SID algorithm enhances the simulation realism of seed dispersal in FLMs, especially at coarse spatial resolutions. The design flexibility makes it suitable for integration into broader terrestrial biosphere models, improving predictions under climate change and disturbances.

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Keywords Seed dispersal · Spatial scale dependent dispersal · Forest landscape model · Landis Pro · Tree species distribution

Introduction

Seed dispersal is a spatially continuous process that occurs over an area from tens to thousands of square metres. It facilitates establishment and expansion of species to suitable habitats and creates new plant assemblies (Turner et al. 2022; Zani et al. 2024). It is a crucial mechanism for tree species range shift in response to environmental change (Nathan and Muller-Landau 2000; Beckman and Rogers 2013; Liang et al. 2018). Seed dispersal process is determined by species traits characterized by seed size and quantity, seed source location and abundance, and external factors including dispersal agents (e.g., wind, animals, water flow) and landscape heterogeneity (Howe and Smallwood 1982; McConkey et al. 2012; Travis et al. 2012; Green et al. 2022). Seed dispersal intrinsically links population dynamics at the site scale, environmental heterogeneity at the landscape scale, and climate at the regional scale to which tree species distribution respond (Wang et al. 2018a).

Distribution ranges of tree species in response to climate change are primarily predicted using terrestrial biosphere models (Fisher et al. 2014), in which species distribution models (SDMs) (Zimmermann et al. 2009; Thuiller et al. 2014; Ehrlén and Morris 2015; Iverson et al. 2017; Franklin 2023), dynamic global vegetation models (DGVMs) (Cramer et al. 2001; Smith et al. 2001; Sitch et al. 2003; Hickler et al. 2012; Case and Lawler 2017), and forest landscape models (FLMs) (Scheller et al. 2007; He 2008; Shifley et al. 2017) are the main tools. SDMs and DGVMs typically operate at relatively coarse spatial resolutions, with grid cell size ranging from several kilometres to tens of kilometres (Thuiller et al. 2008; Pagel and Schurr 2012; Maréchaux et al. 2021), which are beyond the scale of seed dispersal process. Early SDMs and DGVMs often assumed either unlimited seed dispersal or no dispersal (Guisan and Thuiller 2005; McMahon et al. 2011; Briscoe et al. 2019). Recent SDMs and DGVMs attempted to incorporate the seed dispersal effects using various approaches. For example, Lehsten et al. (2019) constructed corridors around the diagonals and border of a grid cell in the LPJ-GM 1.0 to simulate seed dispersal. Snell (2014) used random and repetitive patches within a grid cell in the LPJ-DISP model to simulate seed dispersal between grids. Many studies have noted that these advances improved simulations realism of tree species distribution compared to earlier DGVMs (Sato and Ise 2012; Miller and Holloway 2015; Franklin et al. 2016; Holloway et al. 2016; Urban et al. 2016).

Forest landscape models (FLMs) operate at spatial resolutions from 30 to 500 m and are designed to specifically simulate seed dispersal process (He et al. 2017; Shifley et al. 2017). In FLMs, a landscape is divided into raster cells, each recording information of parent trees (location, abundance, and age) and habitats (landscape configuration and heterogeneity). FLMs simulate seed dispersal based on tree species biological traits (e.g., number of seed produced, dispersal distance, and maturity age), and the abundance and location of parent trees. Current FLMs (e.g., LANDIS, landClim, treeMig), commonly use (Clark 1998) one-dimensional probability function to calculate seed-dispersal probabilities ($P_{one\text{-}dimension}$):

$$P_{one-dimension} = \frac{c}{2\alpha\Gamma(1/c)} \exp\left(-\left|\frac{d}{\alpha}\right|^{c}\right) \quad (1)$$

where d is the distance from the focal to target site within the species-specific maximum dispersal distance (DD), $\Gamma()$ is the Gamma function that has a shape (c) and species-specific dispersal parameter (α), which can reflect species-specific dispersal modes (gravity, wind, or animal) and various dispersal probability distributions such as a fat-tailed curve for long-distance, low probability dispersal events.

The current dispersal design (CDD) in FLMs has been commonly used in predicting forest landscape change under various disturbance and climate change scenarios (Duveneck and Thompson 2017; Duan et al. 2021; Olson et al. 2021; Sebald et al. 2021; Remy et al. 2024; Huang et al. 2023). However, applying the Clark's one-dimensional dispersal function to a raster-based two-dimensional landscape to calculate dispersal probability must use the discrete cell size instead of integration. Thus, the sum of dispersal probabilities within the dispersal radius exceeds 1.0 (Ward 2004). In addition, because long distance dispersal species having more discrete cells in calculations than short distance dispersal species,

the sum of the probabilities for the former will be greater than the later. Therefore, CDD has biased predictions under above circumstances. Pitfalls also exist when applying CDD to variable cell sizes. Current FLMs using CDD assume that seed sources are centrally located within the cell. This may not be a problem when cell size is small or well within the dispersal distance but can be erroneous when cell size is large or larger than seed dispersal distance. The above problems can accumulate spatially and temporally leading to large prediction errors (shown in the evaluation section). Furthermore, CDD exhibits spatial dependency, in that simulation results vary with spatial resolution. As the spatial resolution decreases, CDD algorithms may fail to disperse seeds outwards when cell size exceeds species' maximum dispersal distance. One solution to this problem is to utilize the neighbour dispersal method, in which each cell disperses seeds exclusively to its neighboring cells (He et al. 2005). This results in an overestimation of the dispersal rates, as seeds are assumed to spread to other cells immediately after maturing within a cell (Bocedi et al. 2012).

In this study, we present a novel seed dispersal design to address the shortcomings of CDD in current FLMs. The new design is the spatially independent dispersal (SID) that can produce consistent results across different cell sizes and accommodate the situation when the cell size is larger than the dispersal distance. We verify the SID design using artificial landscapes that exclude compounding factors, such as environmental heterogeneity and species competition, so that the simulated dispersal patterns are solely driven by the algorithm and species attributes. We apply SID to a temperate forest landscape to assess the uncertainties in predicted tree species distributions by comparing simulation results from CDD and SID. We further examined the potential uncertainties in the previous predictions using CDD.

Design of the SID algorithm

The SID algorithm assumes that the parent tree (seed source) is randomly distributed within a cell when calculating the seed dispersal probability. By rotating the one-dimensional function derived from Eq. (1), we derived a two-dimensional function to calculate the probability of seed dispersal,

$$P_{two-dimension} = \frac{c}{2\pi\alpha^2\Gamma(2/c)} \exp(-\left(\frac{d}{\alpha}\right)^c) \quad (2)$$

The SID algorithm integrates the two-dimensional seed dispersal probability formula (Eq. 2) to calculate the probability of seeds dispersing from the parent tree's position (0,0) to any points within a cell within the dispersal radius (DD):

$$P_{SID} = \int_{x_1}^{x_2}\int_{y_1}^{y_2} \frac{c}{2\pi\alpha^2\Gamma(2/c)} \exp\left(-\left(\frac{\sqrt{x^2+y^2}}{\alpha}\right)^c\right))dxdy \quad (3)$$

where (x_1, y_1), (x_1, y_2), (x_2, y_1), and (x_2, y_2) are the four cell corners of the dispersed cell ($|x_1|$, $|x_2|, |y_1|, |y_2| \le DD$). The integral method (Eq. 3) addressed the issue of using discrete cell size calculations in CDD, ensuring that the sum of probabilities for short-distance dispersers exceeds that of long-distance dispersers, while the total dispersal probability within the dispersal radius approaches 1.0. The SID algorithm estimates the seed dispersal probability for a grid cell by aggregating the dispersal probabilities for all points within that cell (Eq. 3) using the monte carlo method. The probability matrices are then averaged, which results in a more accurate probability of seed dispersal to other cells (Fig. 1). To avoid excessive computation time when generating the seed dispersal probability matrix in the SID algorithm, we implemented a Monte Carlo method with an adaptive number of random iterations. The number of iterations scales with cell size, and was determined to be 0.8×cell size for this study.

We found that the time required for a tree species to traverse one cell and reach the next is governed by a temporal factor that regulates the interplay of cell size, dispersal distance, and maturity age.

$$T_{tree\ pass\ through\ cell} = \frac{Cellsize}{Dispersaldistance} \times Maturityage \quad (4)$$

Translating to the number of time steps required for a tree species to traverse one cell is therefore determined by

$$N_{tree\ pass\ through\ cell} = T_{tree\ pass\ through\ cell}/Time\ step \quad (5)$$

where timestep is the time step of the model simulation (1 to 10 years) and $N_{treepassthroughcell}$ is a

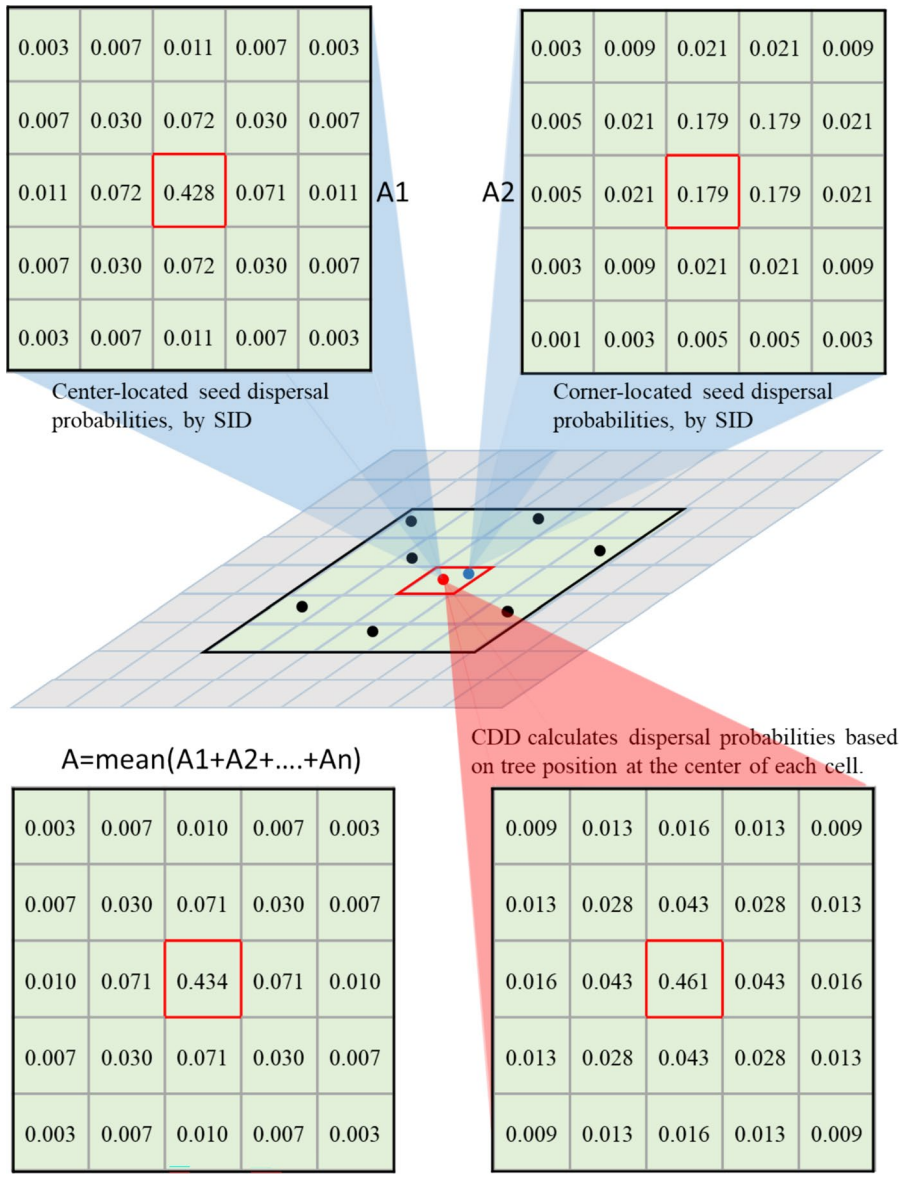

Fig. 1 **A** seed dispersal algorithm that considers the position of seed sources within the grid cell. The red dot represents the seed source at the centre of the grid cell, the blue dot represents a seed source at a non-central position, and the black dots represent seeds that have dispersed and landed within the maximum dispersal distance (black box). The probability of dispersing seeds from this grid cell (within the red box) to neighbouring grid cells decreases from the centre outward. Different seed sources have different probability matrices (the two upper matrixes). The dispersal probability matrix calculated by the SID algorithm (with all source locations considered) is different from that calculated by the CDD algorithm (the two bottom matrixes)

dimensionless number. This design made the simulation results spatially independent to cell size (Fig. 2-SID).

Evaluating the SID algorithm

Artificial landscape

To verify whether the SID algorithm can perform the objectives, we designed three artificial landscapes of varied spatial resolutions. The three landscapes are 260×260 cells at resolutions of 100 m, 130×130 cells at resolution of 200 m, and 65×65 cells at resolution 400 m, respectively. We placed one mature tree species at each corner of each landscape. The four tree species have distinct dispersal distances or maturity ages: *Pinus koraiensis*, *Quercus mongolica*, *Betula costata*, and *Betula dahurica*) (Appendix S1). We kept the rest of the landscape open under uniform environmental conditions to allow seedling establishment. We conducted simulations for the landscapes for 200 years at a 10-year time step using the LANDIS PRO forest landscape model. Under these

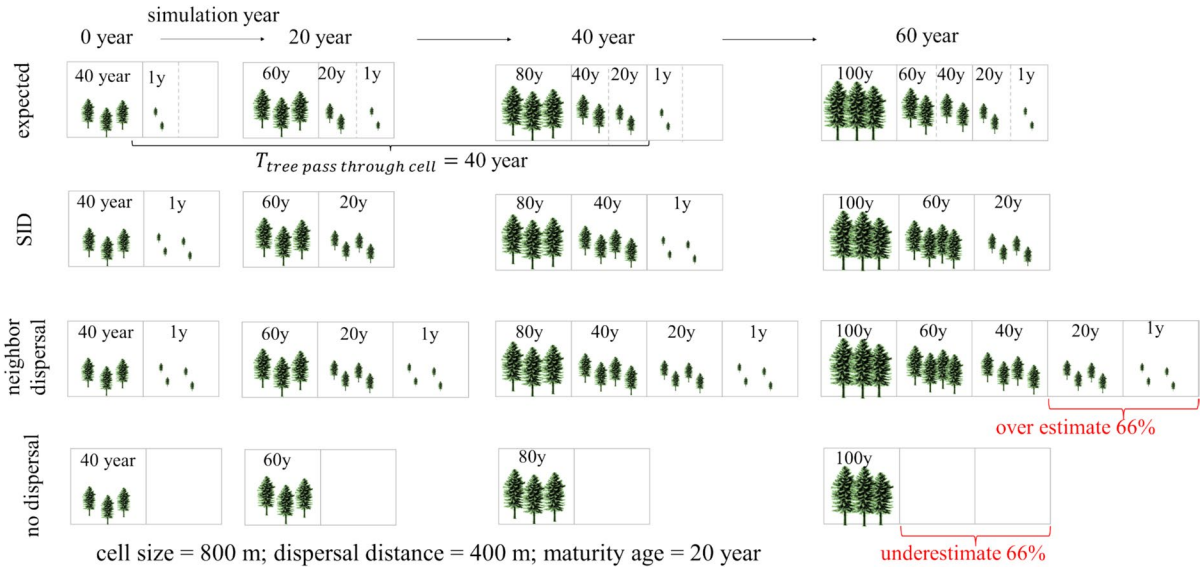

Fig. 2 Illustration of the spatially independent dispersal (SID) and current dispersal design (CDD) algorithm at low resolution (cell size lager than seed dispersal distance). The expected (top row) is to emulate actual seed dispersal and is only affected by the seed dispersal distance and the maturity age of the species. The SID algorithm (second row) approximates the expected. CDD (neighbor dispersal) (third row) only allows seed dispersal to adjacent cells during simulation; however, once the seedlings in the new cell mature, they continue to disperse to new adjacent cells, thereby overestimating the dispersal range. CDD (no dispersal) (bottom row) does not allow seeds to disperse to other cells during seed dispersal simulation at low resolution, resulting in an underestimation of the seed dispersal range

conditions, the artificial landscapes excluded compounding factors, such as environmental heterogeneity and species competition (four tree species did not interact). Thus, the simulated dispersal patterns are solely driven by the algorithm and species attributes.

Simulation results from SID showed that tree species with longer seed dispersal distances and younger maturity age exhibited faster rates of spread. After a 200 year simulation, Dahur birch, which had the longest dispersal distance (800 m) and youngest maturity age (15 years), had the largest distribution area in the landscapes, followed by Ribbed birch with the same dispersal distance but second youngest mature age (20 years), Mongolian oak with second shortest dispersal distance (200 m), and Korean pine with shortest dispersal distance (100 m) (Fig. 3).

Simulations based on the SID algorithm showed that species could disperse regardless of dispersal distance or cell size. There were no significant differences in simulated species distribution (percent cover) (p>0.1, Online Appendix S2.) among all three resolutions for each species based on the repeated measure analysis of variance (Fig. 3-SID). In contrast, simulations based on the CDD algorithm showed that, for species with seed dispersal distances smaller than cell size, Mongolian oak did not disperse under 400 m resolution and Korean pine did not disperse under 200 m and 400 m resolution (Fig. 3-CDD).

Temperate forest landscape

To evaluate how species interaction (competition) may skew the dispersal pattern found in the artificial landscapes, we chose a temperate forest landscape in Northeast China. The temperate forest landscape covered approximately 1.5 million hectares in the Small Khingan Mountains of Northeast China, with longitude and latitude ranging from 127°50′E-130°10′E, 47°05′N-49 10′N, and an elevation between 139 m and 1429 m. The study area was stratified into eight land types based on factors of climate, terrain, and soil characteristics to characterize environmental heterogeneity (Liu et al. 2020). Forest composition at each cell (age/size, abundance by species) was derived from the contemporary forest

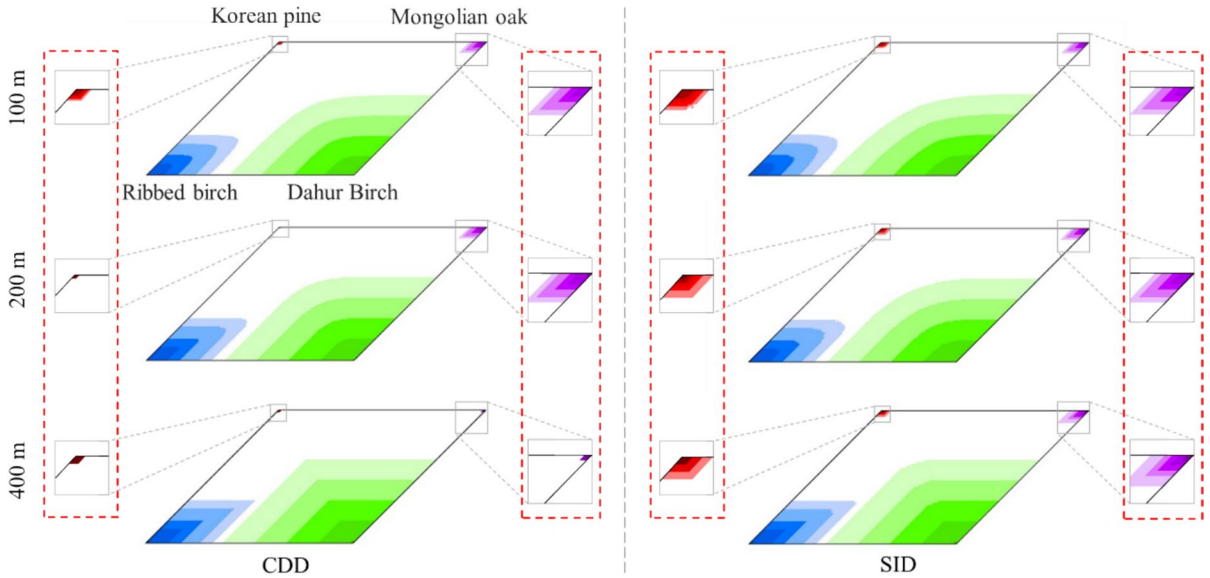

Fig. 3 Spatial distribution of Korean pine, Mongolian oak, Ribbed birch, and Dahur birch under artificial landscapes with resolutions of 100 m, 200 m, and 400 m, based on CDD and SID algorithms. Different shades of the same color represent different tree ages (0, 50, 100, 150, 200 year)

stand inventories that mostly comprised 15 main tree species (Online Appendix S1). For this study, we selected the four tree species that matched those used in the artificial landscapes for better comparison. Korean pine is a climax species in this region and Mongolian oak is a mid-to-late successional species. In the absence of logging and other disturbances, the distribution areas of Korean pine and Mongolian oak are expected to expand. Ribbed birch and Dahur birch are mid-successional species. Due to their strong seed dispersal abilities, they can maintain a significant level of percent cover in the landscape (Zhou 1994).

The temperate forest landscapes were also resampled at 100 m, 200 m, and 400 m resolution corresponding to the artificial landscapes. Direct resampling of tree species distribution and composition (the number of trees for each species age cohort) from a resolution of 100 m to resolutions of 200 and 400 m could result in disparities in the spatial information. These disparities carried over into the species distribution simulations at different resolutions, making it difficult to determine whether differences in simulated species distributions stem from the resolution itself or from the disparities during resampling. To address this, we first resampled the tree species composition map from 100 to 400 m. Then, we resampled from the 400 m resolution back to 100 m and 200 m to use as the initial model input data.

Since simulated species distributions at different resolutions could not be directly compared, we resampled the simulation results from 100 to 200 m resolutions to 400 m resolution. Traditional resampling tools, such as majority, mean, or nearest neighbour methods, can distort species distribution information. For example, in the majority method, less-common species may disappear in the resampled results, because they were present in only a few high-resolution cells and could disappear when aggregated by majority (He et al. 2002). Hence, we customised a resampling method: if any smaller high-resolution cell (100 m or 200 m in this study) contained a specific species, then the resampled 400 m resolution cell was also considered to contain that species. The number of trees in the higher resolution cells (100 m or 200 m) was evenly distributed across the larger cells. For instance, when resampling data from 100 to 400 m resolution, each 400 m cell included 16 individual 100 m cells. If any of these 16 cells had 100 korean pines, the 400 m cell was also assigned 100 korean pines. This approach minimized information loss during resampling and ensured comparability of simulation results across different resolutions.

The simulated results from the CDD and SID algorithms at different resolutions were almost identical for the first 80 years for the temperate forest landscape. As the simulation extended into the middle and later stage, the difference from the two algorithms gradually increased (Fig. 4).

The spatial distributions simulated using the SID algorithm at year 200 showed only small differences among the three spatial resolutions for each of the four species, with differences between the 100 and 400 m resolutions ranging from 2.9% for koren pine to 7.2% for ribbed birch (Fig. 5). The small difference reinforces the results from the artificial landscapes. In contrast, spatial distribution based on the CDD algorithm showed large variations among the three resolutions with the differences from: 8.0% for Mongolian oak to 28.4% for ribbed birch. For species with seed dispersal distances smaller than cell size, for example, Korean pine at 200 and 400 m resolution, they could not disperse, with their respective spatial distributions significantly lower than that at 100 m resolution ($p < 0.01$, Online Appendix S3.), also reinforcing the results from the artificial landscapes. For species with seed dispersal distances greater than cell size (e.g. two birch species), the spatial distribution at 200 and 400 m resolutions was larger than that at 100 m resolution (Fig. 4). The percent cover differences between the 100 and 400 m resolution for the remaining 12 tree species under the SID algorithm were all lower than those under the CDD algorithm except for Khingan fir, Amur cork tree, and Amur linden (with the differences for Amur cork tree and Amur linden

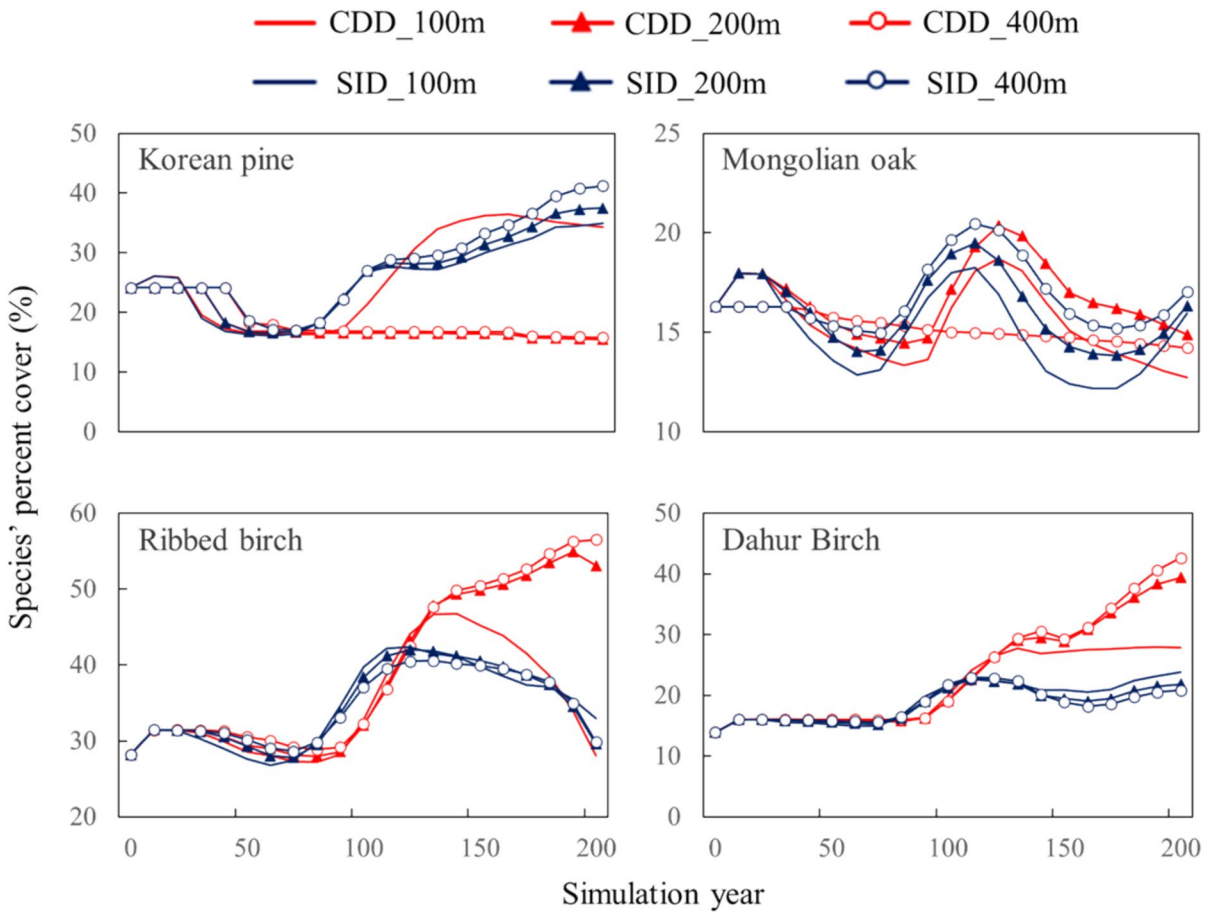

Fig. 4 Simulation of the percent cover change trends over time for Korean pine, Mongolian oak, Ribbed birch, and Dahur birch based on the CDD algorithm (red) and the SID algorithm (blue) at (a) 100 m (solid line), 200 m (solid line with solid triangle markers), and 400 m resolution (solid line with hollow circle markers)

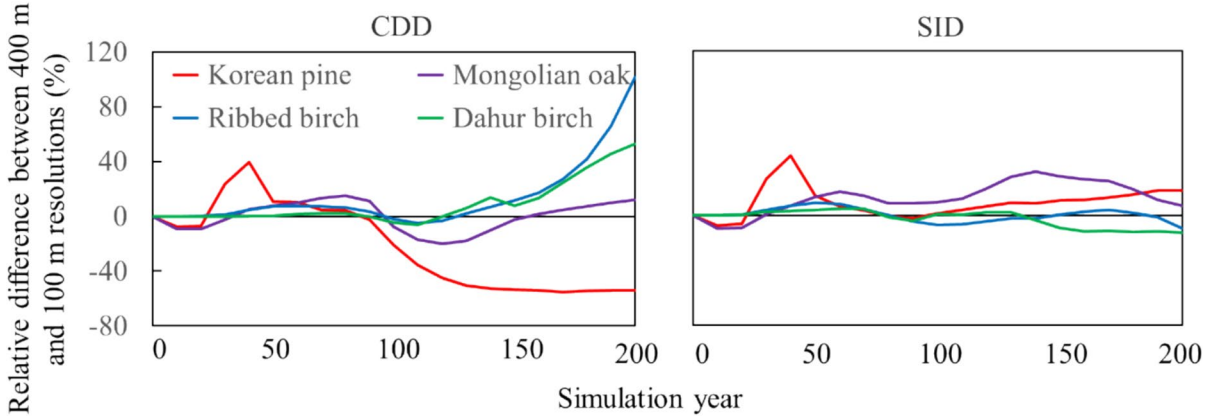

Fig. 5 Relative difference in percent cover of Korean pine, Mongolian oak, ribbed birch, and Dahur birch over time between 400 and 100 m resolutions based on CDD and SID algorithms (calculated as [(% cover at 400 m resolution− % cover at 100 m resolution)/% cover at 100 m resolution×100%])

being very small between the two algorithm). Under the CDD algorithm at coarse spatial resolution, species whose seed dispersal distance is smaller than the cell size cannot disperse into neighbouring cells. Therefore, CDD tends to produce lower percent cover at low resolution than at high resolution for these species. Khingan fir, however, is a late-successional species with short dispersal distance. Under coarse spatial resolution with the CDD algorithm, Khingan fir cannot disperse outside but persists in the occupied cells. Thus, percent cover of Khingan fir is almost identical between high and low spatial resolutions. By contrast, SID allows seeds to disperse outside the cell, resulting in the simulated percent cover of Khingan fir is higher at low resolution than at high resolution.

The average percent cover difference for all species simulated by the SID algorithm between the 100 and 400 m resolutions was 4.9%, which was significantly lower than the 12.0% observed with the CDD algorithm (online Appendix S4).

Compared to the SID algorithm, the relative difference in percent cover between 400 and 100 m resolutions under the CDD algorithm for Korean pine, Ribbed birch, and Dahur birch significantly increased over simulation time, reaching 50% for Korean pine and Dahur birch, and up to 100% for Ribbed birch (Fig. 5).

The differences in the spatial distribution of tree species simulated by the CDD algorithm at 100 and 400 m resolutions appeared to be more clustered (especially for Dahur birch) because of system errors introduced by the deficiencies of the CDD algorithm at low spatial resolutions (Fig. 6). In contrast, the differences in the spatial distributions of tree species simulated by the SID algorithm at different spatial resolutions were more dispersed and random, reflecting the stochasticity in seed dispersal.

Discussion

Simulations of seed dispersal under various cell sizes have not been previously evaluated. Our results showed that for species with dispersal distance smaller than cell size (e.g. Korean pine and Mongolian oak), the percent cover simulated by the CDD algorithm was significant different among the three spatial resolutions ($P < 0.01$), larger in the artificial landscapes (up to 75%) and smaller in the temperate forest landscape (up to 55%). The differences among the three resolutions or between the CDD and SID algorithm are minimal in the short term (e.g. the first 80 years) but become significant larger over long term (> 80 years). These results indicate that in a real forest landscape, environmental heterogeneity and stand-scale processes (e.g. competition) mediate seed dispersal process (John et al. 2007; Wang et al. 2018a), which makes the pitfalls of CDD initially less pronounced than those in the artificial landscapes. However, since seed dispersal is a fundamental process, its cumulative effects will eventually manifest as a driving force in tree species distribution over a long

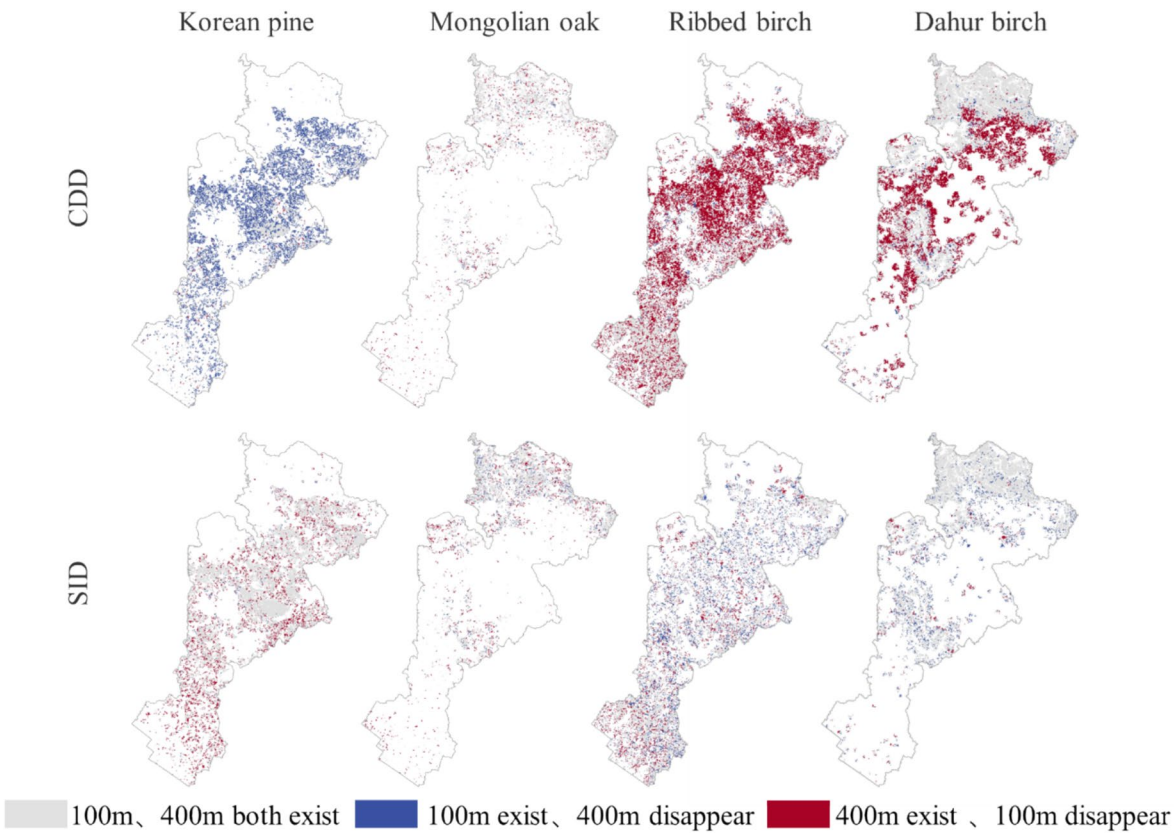

Fig. 6 The spatial distribution differences of Korean pine, Mongolian oak, Ribbed birch, and Dahur birch based on CDD and SID algorithms after 200 years of simulation between 400 and 100 m resolution (resampled to 400 m resolution)

period of time (Fig. 5). In contrast, the SID algorithm showed no significant differences in the simulated percent cover for all species under different spatial resolutions regardless the artificial or temperate forest landscape ($p > 0.1$, Online Appendix S2 & S3.).

Comparing simulation results from CDD and SID highlights the extent of discrepancies in previous predictions of tree species distributions by LANDIS (Fig. 7). Comparisons of CDD and SID algorithms suggest that the percent cover of mid-successional and late- successional species could be over predicted by 30–50% (mean). Early successional species tend to exhibit even greater prediction uncertainties under coarser spatial resolutions, primarily because the CDD algorithm in the LANDIS framework overestimates long-distance dispersal events. This results in unrealistically high colonization probabilities for distant sites, programmatically expanding the predicted distribution and dominance of early-successional species. Consequently, the competitive pressure exerted on mid- and late-successional species may be underestimated, ultimately biasing projections of the community composition and succession trajectories. In general, the CDD dispersal algorithm may conflate climate-driven range shifts with demographic or dispersal constraints, obscuring the true drivers of species distribution.

In forest landscape modeling, reducing grid cell size leads to an exponential rise in computational demand (He 2008). Over the past decades, this growth in computational load has often outpaced improvements in technological advances of computing capacity, which has limited the spatial extent and resolution that forest landscape models could achieve. For instance, only a few studies have used FLMs to simulate areas larger than one million hectares at resolutions of 60–270 m (He and Mladenoff 1999; Thompson et al. 2011; Wang et al. 2018b; Xu et al. 2020; Duan et al. 2021; Liang et al. 2023). The SID could help ease this trade-off by allowing

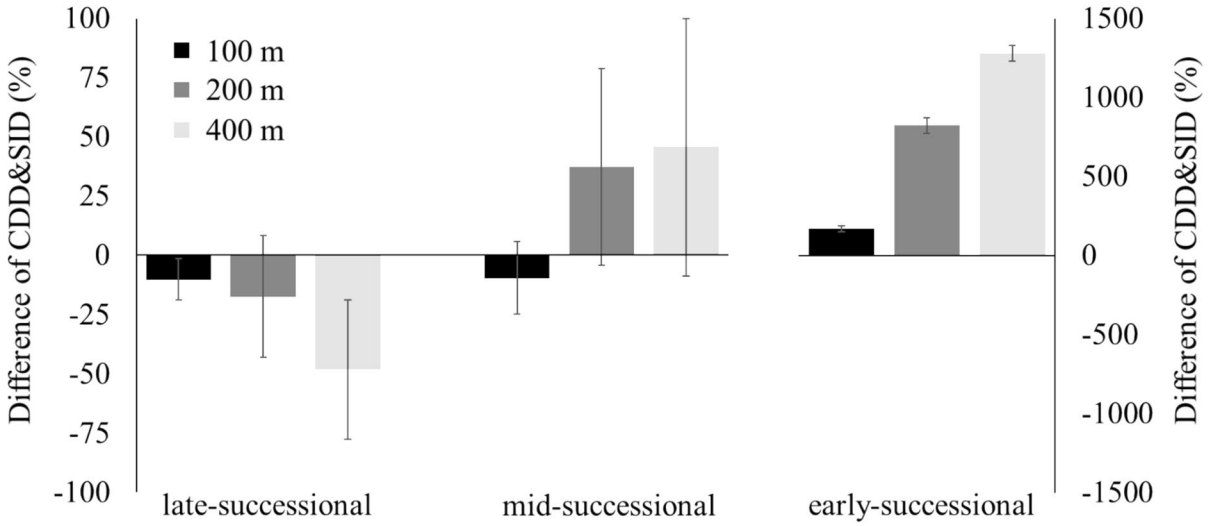

Fig. 7 Mean differences (± 1 standard deviation) in simulated distribution (% cover) between CDD and SID algorithms for late-, mid-, and early-successional species in the temperate forest landscape under three spatial resolutions at year 200 (calculated as [(% cover by CDD algorithm− %cover by SID algorithm)/% cover by SID algorithm×100%]). Early-mid-and late-stage tree species classifications are provided in Online Appendix S1

forest landscape models to cover larger areas using coarser cells. In this study, under the CDD algorithm at coarse spatial resolution, species whose seed dispersal distances are smaller than the cell size behave effectively as in a no dispersal scenario. Our results suggest that using no seed dispersal approach in terrestrial biosphere models could lead to substantial prediction uncertainties, as the unlimited seed dispersal approach has been proposed in other studies (Iverson et al. 2011; Bateman et al. 2013; De Kort et al. 2020). The no dispersal approach directly underestimates the percent cover of some species capable of dispersing across cells, while the unlimited dispersal approach overestimates the percent cover of species with poor dispersal abilities. Although many studies have attempted to incorporate seed-dispersal processes into dynamic global vegetation models or species distribution models (Snell 2014; Lehsten et al. 2019; Shipley et al. 2022), these methods have been developed based on fixed spatial resolutions, making them difficult to achieve spatial independence in simulating seed-dispersal under variable cell sizes.

Our proposed SID algorithm demonstrates spatial independence in simulating seed dispersal, which can be included in terrestrial biosphere models to improve simulating tree migration at regional and continental scales. Since SID tracks the time required for a tree species to traverse a cell as the interplay of cell size, dispersal distance, and maturity age, it can technically handle cells of any size. This advance provides opportunities for comparing predictions from FLMs with those of terrestrial biosphere models, which are rarely explored (Bugmann and Seidl 2022; König et al. 2022; Decocq et al. 2023, Díaz–Yáñez et al. 2024). Our work improves the ability of forest landscape models to run simulations at cell sizes used in dynamic global vegetation models, which have not previously been attempted. The SID algorithm improves ecological realism in simulation of forest dynamics at a low spatial resolution and therefore can benefit predicting forest landscape dynamics under disturbance and climate change. In grid-based models, dispersal kernels describe distance- and direction-dependent movement probabilities across the landscape; errors introduced by spatial discretization can compound and markedly degrade predictive performance, and quantifying and mitigating these discretization effects should be a priority for future research (Slone 2011; Zani et al. 2022).

Overall simulation runtimes for the SID and CDD algorithms are comparable. Only at low spatial resolution (i.e., when the seed dispersal distance is smaller than the cell size) does SID, during the model preparation stage, consume about 1/1000

more computing time than the CDD algorithm. The SID approach can be readily integrated into other forest landscape or dynamic vegetation models. The C++implementations of SID and LANDIS PRO are available as open-source at: https://github.com/landispro/LANDIS_PRO_8.

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Author contributions Hang Sun and Hong S. He conceived the ideas and designed methodology; Kai Liu collected the data; Xianghua Zou, Wen J. Wang and Jacob S. Fraser compiled the code; Hang Sun analysed the data; Hang Sun led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability The code and data supporting this study are available at an anonymous GitHub repository: https://anonymous.4open.science/r/LANDIS_PRO_8-8AEF/.

Declarations

Competing interests The authors declare no competing interests.

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