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Migration-based simulations for Canadian trees show limited tracking of suitable climate under climate change

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Abstract

Aim: Species distribution models typically project climatically suitable habitat for trees in eastern North America to shift hundreds of kilometres this century. We simulated potential migration, accounting for various traits that affect species' ability to track climatically suitable habitat.

Location: Eastern Canada, covering ~3.7 million km^2.

Methods: We simulated migration-constrained range shifts through 2100 using a hybrid approach combining projections of climatically suitable habitat based on two Representative Concentration Pathways (RCP4.5, RCP8.5) for three time periods and two species distribution modelling approaches with process-based models parameterized using data related to dispersal ability and generation time. We developed a unique "migration kernel" that uses seed dispersal traits and observed migration velocities to obtain kernel shape and dispersal probabilities for each tree species. We then calculated lags between the migration-constrained range limits obtained through simulations and limits of climatically suitable habitat.

Results: All species demonstrated northward range shifts at the leading edge of their simulated distribution through 2100, but the magnitude and rate of that shift varied by species and time period. Climatically suitable habitat limits were found to be north of simulated distribution limits across both RCPs, with lags increasing through time. On average, simulated distribution that remained within climatically suitable habitat declined more under RCP8.5 than RCP4.5, with large areas of the rear edge of the simulated distribution becoming partially or completely climatically unsuitable for many species.

Main conclusions: Climatically suitable habitat limits projected for 2100 far exceeded migration-constrained range limits for all 10 tree species, particularly for temperate species. This study underlines the limited extent to which tree species will track climate change via natural migration. Integrating observed migration velocities, seed dispersal and generation time with SDM outputs allows for more realistic evaluations of tree migration ability under climate change and may help orient forest conservation and restoration efforts.

KEYWORDS
Canada, climate change, dispersal kernels, long-distance dispersal, range shifts, species distribution modelling, tree migration ability

1 | INTRODUCTION

Species distribution models (SDMs) coupled with climate projections reveal that the climatically suitable habitat of tree species in the temperate and boreal forests of eastern North America could shift by hundreds of kilometres by the end of this century (Iverson et al., 2008; McKenney et al., 2011; Thuiller et al., 2005). These models provide valuable insights into the extent to which species would need to migrate to track their climatically suitable habitat, but they do not inform on species' ability to actually migrate. Projecting more realistic tree distributions is crucial to adapting forest conservation and management practices in a warming climate. Over the current century, climate velocity—the distance that climate is projected to shift over time (Loarie et al., 2009)—is expected to far exceed that experienced during post-glacial periods, especially at northern latitudes (Marcott et al., 2013). Organisms with low migration ability, such as trees, may be considerably challenged to keep up with the projected pace of climate change (Aubin et al., 2018; Prasad et al., 2013). If climate velocity outpaces the velocity of species' migration, mismatches between a species' distribution and its suitable climate are likely to occur, resulting in migration lags (Corlett & Westcott, 2013; Sharma et al., 2022).

Projecting more realistic tree distributions requires integrating species distribution models and climate projections with species-specific information on migration ability. Migration ability depends on a number of discrete processes including seed dispersal events, successful establishment at suitable sites and generation time that combine to result in range shift. As these processes are influenced by species-specific traits, the ability to migrate is expected to vary among tree species (Davis, 1981; Williams & Jackson, 2007). Generation time is related to age of sexual maturity, growth and seed production, whereas successful establishment depends on a species' tolerance to environmental conditions. Species-specific values for traits related to generation time are generally available from silvicultural compendiums for many tree species (e.g. Burns & Honkala, 1990), as are models of species occurrence in relation to climate (e.g. Iverson et al., 2004; McKenney et al., 2011). Evaluating tree dispersal ability, however, remains a challenge. Dispersal kernels—mathematical functions that describe the probability that a seed disperses to a given distance relative to a source (Nathan & Muller-Landau, 2000)—have been used to quantify dispersal ability, and by extension, migration ability. Yet, obtaining field information to calibrate kernels for both wind- (mostly seed traps; Bullock et al., 2006) and animal-dispersed species (Myers et al., 2004) can be problematic. As such, most tree species do not have published literature on their dispersal kernels, which limits the extent to which species-specific kernels can be incorporated into modelling (Snell et al., 2014). Consequently, proposing ways to parameterize dispersal kernels using readily available data from a variety of sources and spatial scales could help fill a data gap in climate change modelling while providing more realistic estimates of tree migration ability.

Parameterizing dispersal kernels to quantify dispersal ability, and by extension migration ability, requires information on key parameters such as common seed fall distance and migration velocity. Common seed fall distance, a metric that incorporates the effects of several seed traits (e.g. dispersal vector, seed weight), can be used to calibrate kernels and is readily available (e.g. Silvics of North America, Burns & Honkala, 1990). Migration velocity describes the distance per year by which species' distributions shift, as derived from range shift studies at broad spatial scales. Tree migration velocities have been used in process-based models to limit how far the distribution of a species can shift in a given time period (e.g. Bouchard et al., 2019; Meier et al., 2012), and have been estimated through simulations (e.g. SHIFT—Iverson et al., 2004; or TreeMig—Lischke et al., 2006). However, observational studies of migration velocity based on tree range shifts have yet to be broadly used in dispersal kernels. Observational studies could provide more realistic estimates of migration velocities because they integrate dispersal and colonization ability (Boisvert-Marsh & de Blois, 2021) as well as species' ability to respond to a changing climate (Boisvert-Marsh et al., 2019; Zhu et al., 2012). Information on range shifts is increasingly available through paleoecological range reconstructions (Ordonez & Williams, 2013) and changes in species occurrence/abundance across networks of permanent plots (e.g. Boisvert-Marsh et al., 2014; Fei et al., 2017; Zhu et al., 2012). As well, long-distance dispersal (LDD) events play a significant role in shifting range limits (Nathan et al., 2008), but are hard to detect using field-based methods (Bullock et al., 2006). Traits such as plant height, dispersal vector, seed mass and seed terminal fall velocity have been shown to relate well to maximum dispersal distances (Aubin et al., 2016; Tamme et al., 2014) and are commonly available through various sources (trait databases, e.g. TRY—Kattge et al., 2020 and TOPIC—Aubin et al., 2020), so using a trait-based approach offers a promising avenue for characterizing LDD and its effect on tree migration.

We simulated tree migration under climate change in eastern Canada (~3.7 million km^2) for 10 important species selected to represent a variety of dispersal abilities, observed migration velocities and generation times. Simulations were conducted using a hybrid modelling framework (MigClim; Engler et al., 2012) that implements parameters based on species' traits, such as dispersal (dispersal probability and long-distance dispersal) as well as growth and generation time (as it relates to reproductive potential), with projected suitable climate conditions over this century. An important aspect of this work is the development of a novel method that integrates readily available information from the scientific literature (common seed fall distance, migration velocity, and traits related to LDD) into kernels that quantify the probability of dispersal events. We simulated potential changes in distribution through migration to 2100 and compared these outcomes to projected changes in climatically suitable habitat under four combinations of Representative Concentration Pathways (RCPs) and SDMs (2 RCPs × 2 SDMs). We evaluated the magnitude of migration-constrained range shifts by quantifying shifts in the northern limits of the simulated distribution relative to northern limits of the initial distribution over time, and hypothesized that all species would exhibit modest northward range shifts. We also evaluated changes in projections of climatically suitable habitat by quantifying the limits of climatically suitable habitat and the magnitude of shifts over time and the proportion of the simulated distribution that remained within climatically suitable habitat. Because of the unprecedented rate of climate change at northern latitudes in this century and the limited migration ability of tree species, we further hypothesized that shifts in climatically suitable habitat would outpace shifts in simulated distribution limits, resulting in significant lags between the two. In addition to providing forest managers with more realistic projections of future tree distributions, our approach allows us to identify areas of consensus in climatic suitability as critical areas or refuges where conditions remain suitable for a species over time and which can be the focus of monitoring, conservation, or experimentation efforts (Stralberg et al., 2018).

2 | METHODS

2.1 | Study area

The study area covers much of the forested areas of eastern Canada, from the Ontario/Manitoba border east to Newfoundland (~3.7 million km^2 in area, Figure 1). The temperature gradient runs from warmer in the south to colder in the north and the precipitation gradient generally follows an east–west pattern from wetter to drier. According to the Köppen-Geiger climate classification system, the climate in the study area is considered Continental, mostly encompassing Dfa/Dfb (warm to hot summers and cold winters) and Dfc (boreal/subarctic with long winters) (Beck et al., 2018). The forests in this area vary from deciduous to mixed temperate forests in the southern areas of Ontario, Quebec and the Atlantic provinces to boreal forests in the northern areas (Baldwin et al., 2019). Ten tree species were selected for which the study area captures much of their current distribution as well as the leading edge, and that represent a range of dispersal abilities and observed generation times (Table 1).

2.2 | Modelling framework

We simulated migration using the MigClim package (version 1.6) in R (version 3.6.0, R Core Team, 2019), a hybrid SDM/process-based model platform that integrates dispersal ability and life history characteristics with current and projected climatic conditions and barriers to dispersal to produce a cell-based model of tree species migration (Engler et al., 2012). MigClim requires the following inputs: a series of maps indicating how the spatial distribution of climatically suitable habitat changes through time, a map of species' initial distribution and barriers to dispersal, species' dispersal parameters and life history traits related to generation time. The modelling framework is shown in Figure 1, and the model inputs are briefly described below (inputs listed in Tables S1.2–S1.5). All trait data used to parameterise the models are provided here and through the TOPIC database (Aubin et al., 2020).

2.2.1 | Determining climatic suitability

For each species, climatic suitability and the thresholds for suitability/unsuitability were defined using a recent historical period (1971–2000) and then used to project future climatically suitable/unsuitable habitat for three time periods: 2011–2040, 2041–2070 and 2071–2100. Four model combinations of climate suitability were obtained for each of these three time periods by combining two SDMs and two Representative Concentration Pathways (RCP, see Price et al., 2011 for details) –a medium (RCP4.5) and a high (RCP8.5) concentration pathway—as generated by the Canadian Earth System Model (CanESM2; Arora et al., 2011). For the recent historical period (1971–2000), SDMs (McKenney et al., 2007) were calibrated using an extensive database of actual occurrences of North American plants (http://planthardiness.gc.ca/) and by interrogating spatial climate models for that period (described in McKenney et al., 2011) to determine the climatically suitable habitat. Climatically suitable habitat for both the recent and projected future time periods was assessed at a resolution of 300 arc seconds (~10 km) using six key climate variables for tree growth and survival (McKenney et al., 2007): mean annual temperature, maximum temperature of the hottest month, minimum temperature of the coldest month, total annual precipitation, precipitation of the hottest 3 months and precipitation of the coldest 3 months. Under RCP4.5 and RCP8.5, winter temperatures are projected to increase by 3–5°C and 7–9°C, respectively, in the Canadian boreal forest and 2–4°C and 5–7°C in the eastern temperate forest. Projected summer temperature increases are more uniform across Canada (2–4°C and 5–7°C, respectively; Zhang et al., 2019).

Two distinct SDM approaches appropriate for presence-only data were used to assess climatic suitability based on each RCP, allowing us to evaluate uncertainty between SDMs that approach modelling from fundamentally different perspectives: the ANUCLIM package version 6.1 (Xu & Hutchinson, 2013) and the maximum entropy package Maxent version 3.4.3 (Phillips et al., 2006). To assess the habitat considered climatically suitable in each of the time

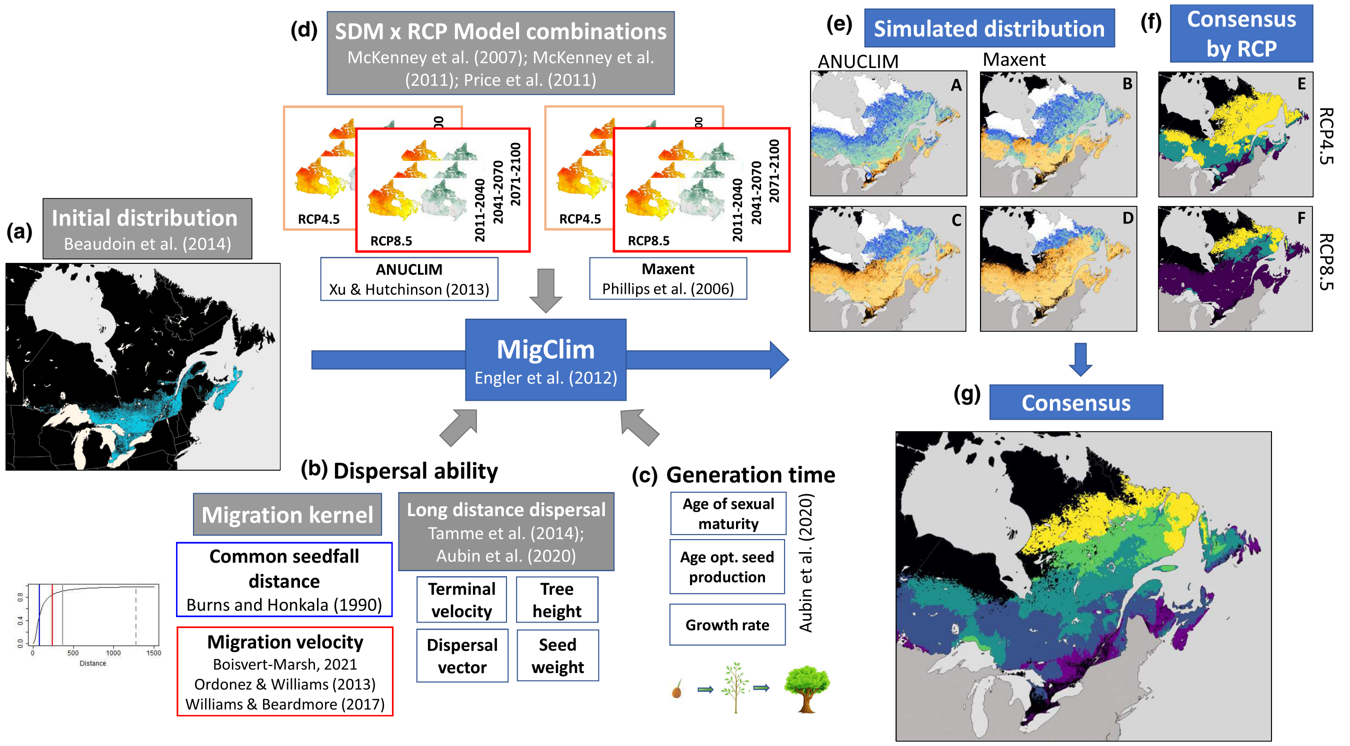

FIGURE 1 Modelling framework for simulating migration. (a) *Initial species distributions* were obtained from raster grids of forest inventory attributes, interpolated using a *k*-nearest neighbour (kNN) analysis. (b) *Dispersal ability* was assessed using *migration kernels* and *long-distance dispersal*. The migration kernel was calibrated from common seed fall distance (i.e. typical distances that seeds disperse) and observed migration velocity (i.e. observed range shift per year). Long-distance dispersal was considered as the confidence intervals of the estimated maximum dispersal distance. (c) *Life history traits* related to potential for seed production post-colonization. (d) *Climatically suitable habitat* as determined by species distribution modelling (SDM) and Representative Concentration Pathway (RCP). (e) The *Simulated distribution* (*Abies balsamea* shown here) is the output at the end of simulations (90 years, corresponding time period = 2071–2100). Four simulations were conducted, one for each SDM × RCP model combination: (A) ANUCLIM RCP4.5, (B) Maxent RCP4.5, (C) ANUCLIM RCP8.5, (D) Maxent RCP8.5 (maps shown in Appendix S3). (f) The *Consensus by RCP* maps show areas of consensus and disagreement in climatically suitable/unsuitable habitat across SDMs for (E) RCP4.5 and (F) RCP8.5 through to the end of simulations (90 years, corresponding time period = 2071–2100). (g) The *Consensus* map shows areas of agreement in climatically suitable habitat among the four model combinations.

periods, we chose cut offs that define areas of climatic suitability that align well with species' initial distributions. For ANUCLIM-based models, we employed the "core" climate profile, that is the climate space delimited by the 5th and 95th percentiles of each climate variable. For Maxent-based models, we employed the logistic threshold that balanced training omission, predicted area and the threshold value, thresholds that vary by species. In both cases, areas that did not meet these thresholds were considered unsuitable for the species. Predictive accuracy for each SDM type was assessed on the recent historical data using 10-fold cross-validation to generate a mean area under the receiver operator curve (AUC) value (Table S2.1). For ANUCLIM, 10,000 random pseudoabsence points were generated to allow AUC calculations to be carried out using the dismo package version 1.3-5 in R (Hijmans et al., 2011). For the Maxent models, we employed the cross-validation functionality built into the Maxent software, along with 10,000 random background points. Note that, since Maxent employs background points to assess predictive accuracy, this approach produces a modified AUC based on fractional predicted area rather than the standard commission rate (Phillips et al., 2006). Climatic suitability/unsuitability based on the historical period was projected for three time periods—2011–2040, 2041–2070 and 2071–2100—using the four SDM × RCP model combinations, which are hereafter called ANUCLIM RCP4.5, ANUCLIM RCP8.5, Maxent RCP4.5 and Maxent RCP8.5. Retaining these four model combinations allowed us to assess the unique effect of using different SDMs and/or of using different RCPs on areas of climatic suitability/unsuitability in the simulations (Buisson et al., 2010; Shabani et al., 2016).

2.2.2 | Simulating changes in species' distribution through migration

For each species, simulations of changes in distribution constrained by species-specific migration were conducted for each of the SDM × RCP model combinations (one simulation per model combination and four simulations in total). Migration was simulated on a 25 m resolution raster grid for 90 time steps, with each step corresponding to 1 year. The fine resolution of the grid was selected to represent a realistic scale for local dispersal processes and to

TABLE 1 List of the 10 tree species selected for this study, including their estimated *a* and *b* parameters of 2Dt migration kernels, the estimated minimum and maximum distances of long-distance dispersal (LDD_{min} and LDD_{max}), the probability of a long-distance dispersal event (LDD) and the cumulative distance at the leading edge.

			Migration kernel		Long-distance dispersal			Cumulative distance at 90 years	
Scientific name	Species code	Common name	*a*	*b*	LDD_{Min}	LDD_{Max}	Probability	Distance (m)	Rate (m/year)
Abies balsamea	ABIBAL	Balsam fir	0.6372	813.1	295.0 (275)	1011.4 (1025)	.045	2281.2	25.3
Acer rubrum	ACERUB	Red maple	0.7170	6137.1	288.4 (275)	1002.2 (1025)	.131	5203.0	57.8
Acer saccharum	ACESAC	Sugar maple	2.015	24355.4	153.2 (150)	528.0 (550)	.2622	1164.9	12.9
Betula alleghaniensis	BETALL	Yellow birch	1.052	10728.3	282.7 (275)	1007.1 (1025)	.1034	1782.1	19.8
Betula papyrifera	BETPAP	Northern white birch	0.7240	24923.7	282.7 (275)	1007.1 (1025)	.2988	3107.5	34.5
Picea mariana	PICMAR	Black spruce	0.6431	3301.9	369.3 (375)	1281.4 (1300)	.0781	3605.9	40.1
Pinus strobus	PINSTR	Eastern white pine	0.6899	2079.4	243.3 (225)	833.0 (850)	.0899	2931.2	32.6
Populus tremuloides	POPTRE	Trembling aspen	1.010	40537.7	1281.5 (1275)	5582.8 (6000)	.0222	17996.0	200.0
Quercus rubra	QUERUB	Northern red oak	0.6096	425.1	106.0 (100)	1668.1 (1675)	.1375	2859.7	31.8
Thuja occidentalis	THUOCC	Eastern white cedar	0.7195	1542.6	230.8 (225)	791.0 (800)	.0663	2600.2	28.9

Note: The migration kernel was parameterized using the median and mean using common seed fall distance and observed migration velocity (see Section S1.1 for methodology and Table S1.2 for parameters in Appendix S1). LDD was estimated using the dispeRsal function (Tamme et al., 2014) as the lower ($LDD_{min,}$ rounded down to nearest 25 m) and upper bounds ($LDD_{max,}$ rounded up to nearest 25 m) of the confidence intervals around the maximum estimated dispersal distance. The probability of LDD was estimated as the cumulative probability under the 2Dt function between LDD_{min} and $LDD_{max.}$ Cumulative distance is the distance (in metres) between an initial distribution cell and a cell colonized at year 90 and the rate (m/year), as an indication of small-scale effects of dispersal and generation time on migration. A randomized sample of the leading edge was obtained ($n = 500$) and the median of cumulative distances are shown here.

adequately reflect decreasing probability of successful dispersal with increasing distance. Initial distributions (i.e. species' distributions at year 0) were obtained from Canada-wide raster grids (250 m resolution) of forest inventory attributes, which were interpolated using a *k*-nearest neighbour analysis of both forest inventory photograph plot data and satellite data based on the 2001 inventory year (see Beaudoin et al., 2014 for details). To avoid including stands that were not at full seed production at year 0 and to minimize data quality issues related to species-level attribution of young stands, only stands over 40 years of age were included in the current study. Large bodies of water (lakes, rivers and oceans) were incorporated into the model from an existing file (1:50 m; Natural Earth, 2009+; https://www.naturalearthdata.com/downloads/50m-physical-vectors/), as strong barriers to dispersal (i.e. no possible dispersal through these areas).

Dispersal and post-dispersal generation time

A cell is considered successfully colonized if it is located in climatically suitable habitat in a given time step (year 1 to year 90) and if a seed disperses from a climatically suitable occupied cell. The probability that a seed disperses to a given distance relative to a source was assessed using what we called a migration kernel. The kernel was developed to overcome the limited availability of published dispersal kernels for our species and employs two available metrics that integrate individual and population-based processes: common seed fall distance and observed migration velocity. Common seed fall distance, or the distance to which a seed typically disperses (as obtained from Burns & Honkala, 1990), characterizes the influence of individual trees on dispersal patterns at local scales. Observed migration velocity describes the distance by which species' distributions at broad spatial scales have been reported to shift yearly (Boisvert-Marsh et al., 2014), acting as a proxy for population-level processes (e.g. abundance or prevalence). We derived measures of migration velocity from three sources based on paleoecological and contemporary observations from studies located partially or entirely within the study area (Boisvert-Marsh, 2021; Ordonez & Williams, 2013; Williams & Beardmore, 2017). Paleoecological observations were based on the pollen record of a given species, whereas contemporary observations were based on changes in presence/absence as obtained from repeated forest inventories in eastern Canada between 1970 and 2015. For each data source, migration velocity was calculated as the distance between two observations in time divided by the number of years between observations, to obtain a velocity in m/year for each species. If multiple observations were available (e.g. over time, or for different locations), a mean was first calculated for each study. The species-specific mean of migration velocity was calculated from the data sources for which values were available. The methods used to obtain observed migration velocity are detailed in Section S1.1.

To obtain dispersal probabilities, we employed the 2Dt kernel (Clark et al., 1999), a commonly used kernel for wind-dispersed species that performs well compared with other distributions (Bullock et al., 2017). The cumulative distribution function (formulation based on Greene et al., 2004) was used to calculate the probability of dispersal at *x* distance from the source cell (Equation 1).

$$\left(\frac{b}{b+x^2}\right)^a \tag{1}$$

To define the shape of the kernel, we estimated *a* and *b* using the median and mean of the function using common seed fall distance as the median and observed migration velocity as the mean respectively (shown in Tables S1.1 and S1.2). Then, the parameters *a* and *b* were solved from the median and mean using the Newton–Raphson method as implemented in the rootSolve package version 1.6 (Soetaert, 2009) to derive a unique numerical solution. The estimates for *a* and *b* are found in Table 1, and additional methods used to parameterize the 2Dt function are detailed in Appendix S2 and S4.

MigClim requires dispersal probabilities for both typical dispersal and long-distance dispersal (LDD). To obtain the distances between which LDD was considered, we used the dispeRsal regression model (Tamme et al., 2014) to estimate the maximum dispersal distance for a given species based on widely available plant traits. We used the lower (5th) and upper (95th) bounds of the confidence interval around the estimated maximum dispersal distance from the dispeRsal model as the upper cut-off for typical dispersal distance (LDD_{min}) and the upper cut-off for LDD (LDD_{max}), both rounded to the nearest 25 m. Hence, the probabilities of typical dispersal were assessed in 25 m increments up to LDD_{min} and probabilities of LDD were assessed between LDD_{min} and LDD_{max}. For this study, two different models in dispeRsal were tested and assessed against published literature values: the model for wind-dispersed species includes dispersal vector and seed terminal fall velocity and the model for animal-dispersed species includes dispersal vector, seed mass and seed release height (parameters shown in Table S1.3).

If a colonized cell remains in climatically suitable habitat, subsequent dispersal of the next generation depends on whether the minimum age of seed production has been attained. If so, the probability of seed production increases according to a sigmoid curve until the age at which optimum seed production is achieved, with growth rate used to modulate the inflection point of the curve. Once the optimum age is attained, the probability of seed production reaches 1 and is held constant. While many of the seed production parameters can vary by location and depending on their sensitivity to climate (Clark et al., 2021; Tremblay et al., 2002), suitable data are not widely available so these parameters remained fixed across the study area.

A time period lasts for 30 steps, that is steps 1–30 = climate suitability for 2011–2040; steps 31–60 = 2041–2070; steps 61–90 = 2071–2100. At the beginning of a time period, each cell, including those that are part of the initial distribution and those colonized during the simulation, is tested to assess whether it is still climatically suitable. If it is no longer suitable, cell dispersal probability is reset to 0 and the cell is reclassified to indicate the time period when it becomes unsuitable. Given the high resolution across a broad area (~14 billion cells), it was necessary to cut the raster grid into smaller blocks. Two model runs were conducted on each block, then stitched back together into a grid once simulations on all blocks were completed. Two grids were constructed, each fully overlapping the other to reduce the edge effect from each model run, for a total of four runs for each simulation.

2.3 | Post-modelling analyses

Once the simulations were complete, post hoc analyses were conducted to assess changes over time, notably in the proportion of simulated distribution that remains in climatically suitable habitat, the magnitude of migration-constrained range shifts and the lag between simulated range limits and climatically suitable habitat limits.

2.3.1 | Changes in simulated distribution and climatically suitable habitat

For each SDM × RCP model combination, we calculated the proportion of simulated distribution (i.e. all occupied cells, or the initial distribution and cells colonized through the simulations) situated in climatically suitable habitat through to the end of the time period (i.e. total cells comprising the simulated distribution after 30, 60 and 90 years). Moreover, at the end of a time period, the simulated distribution situated in climatically suitable habitat was calculated in km^2 as well as the ratio of simulated distribution within climatically suitable habitat relative to the area occupied by the initial distribution (i.e. year 0). To identify areas of agreement in climatic suitability/unsuitability for a given RCP model, we mapped areas of consensus in climatically suitable habitat by RCP (RCP4.5, RCP8.5) to highlight how SDM choice influenced model outputs. Moreover, to identify possible climatic refugia (Doxa et al., 2022; Saraiva et al., 2021), we overlaid the outputs of the four simulations to highlight areas of consensus in climatic suitability/unsuitability across all SDM × RCP model combinations. From here, for each cell, we calculated the number of climatically suitable simulations (values ranging from 0—i.e. no simulation was located in climatically suitable habitat— to 4—i.e. all simulations were located in climatically suitable habitat) as well as the proportion of the simulated distribution each occupied. Given the nature of outputs from the SDMs, these consensus maps were based on areas of climatically suitable/unsuitable habitat identified by each SDM × RCP model combination and the assumption that each combination contributed equally to the final output.

2.3.2 | Quantifying migration-constrained range shifts

To evaluate the effects of migration on constraining range shifts at smaller scales, we computed the cumulative distance n = 500 times between the initial distribution and cells colonized by year

90 using a windowed sampling approach at the leading edge (see Appendix S2 for more details and Figure S2.1 for example). We then extracted the median cumulative distance of sampled areas and used it as a proxy of potential spread in areas colonized through range-extending migration.

To assess broad-scale patterns, the magnitude of migration-constrained range shifts was calculated as the difference at the leading edge between the range limit of the initial distribution—that is the latitudinal position of the initial distribution—and migration-constrained range limits—that is the latitudinal position of all occupied cells in the simulated distribution, as obtained through the simulations—at the end of a given time period using a percentile approach (hereafter called range shifts; Boisvert-Marsh et al., 2014). Range shifts were calculated at two different percentiles to capture different dynamics at the leading edge and the predominant patterns underlying shifts. Range shifts based on the 90th percentile provide an indication of range filling at the leading edge where species' distributions become discontinuous. Conversely, range shifts based on the 99th percentile are an indicator of range extension through long-distance dispersal. Range shifts were assessed in 50 km wide bands from west to east to capture the latitudinal variation at the leading edge of species' distributions across our study area. Average range shift values were calculated as the mean differences in latitude for occupied bands weighted by the number of occupied cells in each. Positive range shift values indicate that the range limit has shifted northward (i.e. at a higher latitude) between the initial distribution and the time period of interest whereas negative values indicate a southward shift (i.e. at a lower latitude). Simulated migration velocity here was calculated as the migration-constrained range shift (in km) divided by the number of years elapsed in the simulation (30, 60 or 90 years). Range shift values and simulated migration velocity included cells that were part of the initial distribution and colonized but that became unsuitable at some point in the model runs. This was done because we assumed that the species may persist under unsuitable climate conditions, even if conditions for seed production and colonization are not met (Hampe & Jump, 2011). Range shifts were calculated for each simulation (4 in total).

2.3.3 | Lag between migration-constrained range limits and climatically suitable habitat limits

Finally, we quantified the lag through time between migration-constrained range limits and climatically suitable habitat limits—that is the latitudinal position of climatically suitable habitat, as obtained from the SDM × RCP model combinations. Lags were calculated in two ways to capture different dynamics. First, to compare the migration-constrained range limits and climatically suitable habitat limits at the northern edge, we calculated the difference between the 99th percentile of latitude of the climatically suitable habitat and the 99th percentile of latitude of the simulated distribution at each time period. Second, to compare the southern limit of climatically suitable habitat to the northern migration-constrained range limit, we calculated the difference between the 1st percentile of latitude of a species' climatically suitable habitat and the 99th percentile of latitude of the simulated distribution in each time period. In both cases, positive values indicate that the climatically suitable habitat limit is north (i.e. at a higher latitude) of the limit of the simulated distribution. Conversely, negative values indicate that the limit of the simulated distribution is at a higher latitude than the climatically suitable habitat limit. Lag was assessed in 50 km wide bands across the entire east–west distribution. Average lag was calculated as the mean difference in limits for occupied bands weighted by the number of occupied cells in each.

3 | RESULTS

3.1 | Dispersal

Parameterizing the migration kernel using common seed fall distances and observed migration velocity resulted in species-specific dispersal probabilities that were then used in simulations (Figure S2.1). Common seed fall distances (i.e. kernel median) ranged from 30 m (*Quercus rubra*) to 200 m (*Betula papyrifera* and *Populus tremuloides*) while observed migration velocity (i.e. kernel mean) ranged from 107.5 (*Quercus rubra*) to 451.6 m/year (*Populus tremuloides*) (Table S1.1). Maximum long-distance dispersal (LDD_{max}) values varied from a lower bound of 100 m (*Quercus rubra*) to an upper bound of 5575 m (*Populus tremuloides*), but most were limited to <1700 m (Table 1). The migration kernel resulted in relatively high probabilities of dispersal at both short and long distances. On average, the probability of long-distance dispersal (LDD) was 0.12 but these probabilities varied greatly among species (Table 1).

3.2 | Changes in simulated distribution and climatically suitable habitat

As might be expected, across species, more of the simulated distribution remained in climatically suitable habitat through 2071–2100 under RCP4.5 (medium concentration pathway) than under RCP8.5 (high concentration pathway) (Table 2, also see maps in Appendix S3). For most species, ANUCLIM models retained a higher proportion of their initial distribution within climatically suitable habitat (average across species: RCP4.5 – 97.4%; RCP8.5 – 47.7%) than Maxent models (average across species: RCP4.5 – 89.6%; RCP8.5 – 46.4%) (Table 2a). Patterns were similar for colonized cells (Table 2b), but generally a higher proportion of colonized cells remained in climatically suitable habitat. The proportion of simulated distribution that remains within climatically suitable habitat by the end of the simulations varies greatly among species and SDM × RCP model combinations. Across combinations, two species—*Acer rubrum* and *Acer saccharum*—retained on average more than 90% of both initial distribution and colonized area within climatically suitable habitat (Table 2). Conversely, RCP was particularly important for *Thuja occidentalis* and, to a lesser degree, *Betula alleghaniensis*. For these species, over 98% and 96% of their initial distribution remained suitable under RCP4.5; however, for *Thuja occidentalis*, only 7.2% of the initial distribution remained suitable under ANUCLIM RCP8.5 and 0.86% under Maxent RCP8.5 (Table 2a). *Betula alleghaniensis* showed a similar trend but to a lesser degree (Table 2a). The simulated distribution (i.e. initial distribution + cells colonized through the simulations) that remains in climatically suitable habitat increased for almost all species in the first time period (2011–2040), but this trend diverged across RCPs in the 2041–2070 and 2071–2100 time periods (Figure 2a,b). All species showed increases in their simulated distribution that remained suitable for one or both SDMs under RCP4.5, while six species showed decreases under one or both SDMs under RCP8.5.

Based on the consensus by RCP models, RCP4.5 tended to have smaller areas of consensus in simulated distribution that falls within climatically unsuitable habitat than RCP8.5, as well as smaller areas of disagreement between SDM approaches (panels E and F in Figures S3.1–S3.10). Specifically, climatically suitable habitat under RCP8.5 diverged for more southerly species (*Acer rubrum*, *Acer saccharum*, *Pinus strobus* and *Quercus rubra*). For these species, Maxent tended to project climatically unsuitable habitat in the western portion of the study area along the Great Lakes, while ANUCLIM projected central and eastern portions of the study area to become climatically unsuitable (Figure 3; also see maps of SDM × RCP specific results in Appendix S3). Across the SDM × RCP model combinations, an average of 61.8% among species of the simulated distribution is projected to remain in climatically suitable habitat across most (i.e. 3 or 4) model combinations (Figure 3; Table S2.2). This proportion, however, varied greatly between species, with between 7.0% (*Thuja occidentalis)* and 99.5% (*Acer rubrum*) of the simulated distribution remaining suitable across most model combinations (Figure 3, green and yellow shades). Not surprisingly, persistent climatically suitable habitat was mainly situated in the northerly portions of species' initial distributions. Generally, most of the simulated distribution projected to remain suitable in fewer than 2 SDM × RCP model combinations by 2071–2100 occurred in the southern portion of the study area (Figure 3, blue to purple shades). More northerly distributed species, such as *Abies balsamea* and *Picea mariana* as well as *Thuja occidentalis*, showed considerable proportions of their simulated distribution becoming entirely unsuitable or nearly so by 2071–2100 (purple and blue colours, respectively, in Figure 3; Table S2.2).

3.3 | Quantifying migration-constrained range shifts

At leading edge of species' simulated ranges, the median cumulative distance between the initial distribution and cells colonized at year 90 ranged from 1.2 km to 18.0 km (Table 1, Figure S2.1). With the exception of *Populus tremuloides* and *Acer rubrum*, species showed a cumulative distance at localized scales of less than 5 km over the simulations.

Average migration-constrained range shifts across the four simulations were invariably northward, but the magnitude and rate varied by species and time period (Figure 4a,b). Simulated range shifts at the 90th percentile varied between 25.8 km (*Betula alleghaniensis*)

TABLE 2 Proportion of initial distribution cells (a) and colonized cells (b) that remain in climatically suitable habitat through to the end of the simulations (2100).

	(a) Initial distribution				**(b) Colonized**			
	RCP4.5		**RCP8.5**		**RCP4.5**		**RCP8.5**	
	ANUCLIM	**Maxent**	**ANUCLIM**	**Maxent**	**ANUCLIM**	**Maxent**	**ANUCLIM**	**Maxent**
ABIBAL	87.60	52.87	24.96	12.36	93.13	78.00	38.64	27.63
ACERUB	99.97	100.00	96.18	96.09	99.90	100.00	92.02	93.42
ACESAC	99.96	97.39	82.19	85.64	99.96	99.26	84.41	83.32
BETALL	99.49	96.24	31.76	5.20	99.70	90.13	38.24	12.75
BETPAP	99.63	93.22	40.23	67.20	99.13	94.50	74.34	86.31
PICMAR	91.11	81.01	27.37	19.06	83.86	81.76	46.04	37.91
PINSTR	99.98	99.16	32.43	64.43	99.95	99.50	50.82	66.50
POPTRE	99.84	92.19	68.10	23.27	99.90	94.67	88.92	60.96
QUERUB	97.71	94.91	66.94	89.49	99.85	99.67	74.42	93.33
THUOCC	98.54	88.99	7.21	0.86	96.99	89.72	7.26	2.81

Note: Four combinations of climate suitability from SDM × RCP models are shown: ANUCLIM RCP4.5, Maxent RCP4.5, ANUCLIM RCP8.5, Maxent RCP8.5. Species are listed in the first column. Species codes: ABIBAL, *Abies balsamea*; ACERUB, *Acer rubrum*; ACESAC, *Acer saccharum*; BETALL, *Betula alleghaniensis*; BETPAP, *Betula papyrifera*; PICMAR, *Picea mariana*; PINSTR, *Pinus strobus*; POPTRE, *Populus tremuloides*; QUERUB, *Quercus rubra*; THUOCC, *Thuja occidentalis*.

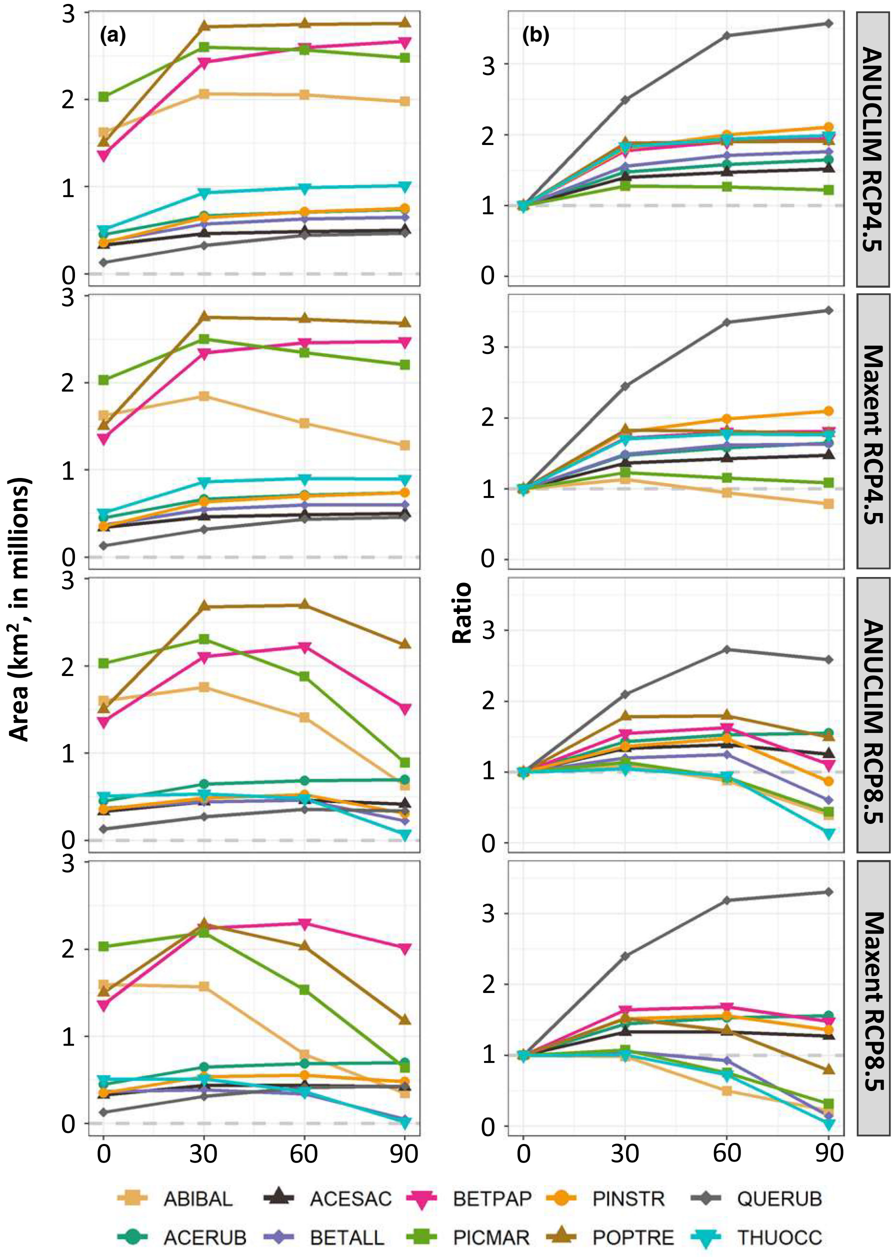

FIGURE 2 Simulated distribution that remains in climatically suitable habitat, as expressed as (a) area (in km^2) and (b) the ratio relative to the area of the initial distribution at a given time period (indicated at the bottom). Four combinations of climate suitability from SDM × RCP models are shown (from top to bottom): ANUCLIM RCP4.5, Maxent RCP4.5, ANUCLIM RCP8.5, Maxent RCP8.5. In (b), ratio values greater than 1 indicate that the simulated distribution that remains in climatically suitable habitat is greater then the area of the initial distribution. Ratio values less than 1 indicate that the simulated distribution that remains in climatically suitable habitat is less than the area of the initial distribution. The time step indicated at the bottom refers to the year at the end of the time period (model after 30 [2011–2040], 60 [2041–2071], 90 years [2071–2100], respectively). Species are listed in the legend on the bottom and refer to codes listed in Table 2.

and 342.8 km (*Betula papyrifera*) over the simulation period (i.e. all 90 years, Figure 4a), translating to velocities of ~0.29 to ~3.8 km/year. At the 99th percentile, range shifts varied from 15.3 km (*Acer saccharum*) to 185.1 km (*Betula papyrifera*) over the simulation period, translating into velocities of 0.17–2.1 km/year (Figure 4b). The largest shifts tended to occur within the first time period (steps 1–30) and decreased thereafter, but this depended on the latitudinal limit considered. Most species showed larger shifts at the 90th percentile of latitude as compared with the 99th percentile, with the exceptions of *Acer rubrum* and *Betula alleghaniensis*. Note that range shift values, which include initial distribution and colonized cells when calculating latitudinal percentiles for each time period, differ from the cumulative distances described above by specifically measuring range shift at the leading edge.

3.4 | Lag between migration-constrained range limits and climatically suitable habitat limits

The climatically suitable habitat limits exceeded migration-constrained range limits in each time period (Figure 5), but varied greatly depending on the spatial arrangement of species' initial distribution. Calculated lags were positive, even in the first time period, indicating that the limit of climatically suitable habitat was at a higher latitude than the migration-constrained range limit. The largest increase in lag occurred in 2011-2040 followed by 2041–2070, then slowing considerably towards 2071–2100 (Figure 5). Except in the first time period, lags across species were larger on average for RCP8.5 and for ANUCLIM-based model combinations (averages shown in Table S2.3). Southerly species (i.e. *Acer rubrum*, *Acer*

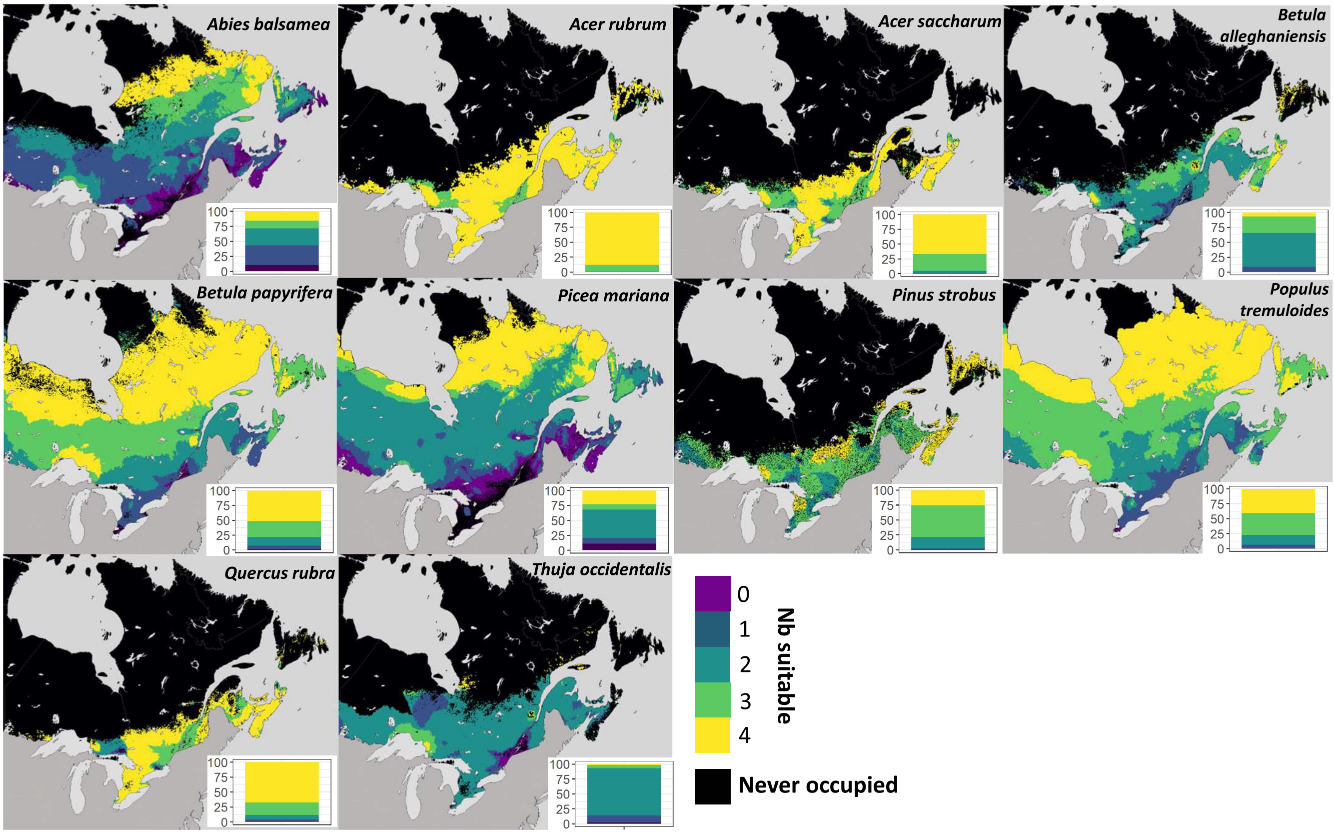

FIGURE 3 Maps of the consensus outputs from the four simulations for 10 tree species in eastern Canada. Simulations are based on four combinations of climate suitability from SDM × RCP models (ANUCLIM RCP4.5, ANUCLIM RCP8.5, Maxent RCP4.5 and Maxent RCP8.5) constrained by species-specific migration parameters. Maps show the simulated distribution, that is either part of the initial distribution or were colonized during the simulations. The colour scale (see legend) indicates the number of simulations that are projected to be located in climatically suitable habitat through to 2100, with values ranging from 0 (i.e. no simulation was located in climatically suitable habitat—shown in purple) to 4 (i.e. all simulations were located in climatically suitable habitat—yellow). The inset displays the proportion of the simulated distribution located in climatically suitable habitat based on the number of simulations. For each species, all proportions shown are cumulative and sum to 100. Proportions are also shown in Table S2.2.

saccharum, *Betula alleghaniensis*, *Pinus strobus*, *Quercus rubra* and *Thuja occidentalis*) had larger lags than more northerly species (average across SDM × RCP combinations: 871.3 km for southerly species vs. 306.6 km for northerly species; Table S2.3). When looking by longitudinal band, southerly distributed species exhibited large lags in central parts of the study area, with the limit of climatically suitable habitat surpassing the migration-constrained range limit by 900 to 1500 km by the end of the 2071–2100 time period (Figure S2.3).

4 | DISCUSSION

Species distribution models typically project considerable increases in climatically suitable habitat in this century for tree species at their northern leading edge (e.g. Iverson et al., 2004; McKenney et al., 2011; Périé & de Blois, 2016). Combining ecological information on dispersal ability and generation time with biophysical predictions from SDMs improves our ability to evaluate the extent to which tree species may colonize newly climatically suitable habitats. At the leading edge, our study shows notable differences in simulated range shifts among species when constrained by dispersal ability and generation time, but also related to the spatial arrangement of their initial distribution and the presence of geographic barriers. However, we observed considerable lags between migration-constrained range limits and the limits of their projected climatically suitable habitat (see Meier et al., 2012 for comparable work in Europe). Areas of consensus in climatically suitable/unsuitable habitat were mapped, highlighting areas of consensus and disagreement across SDM × RCP model combinations.

4.1 | Changes in climatically suitable area at the leading and rear edge

4.1.1 | Leading edge changes

Our findings support the growing consensus that tree species will not be able to keep up with the pace of climate change, even under more moderate concentration pathways (Lenoir et al., 2020; Loarie et al., 2009; Sharma et al., 2022). At the leading edge, the spatial arrangement of species' initial distributions influenced the

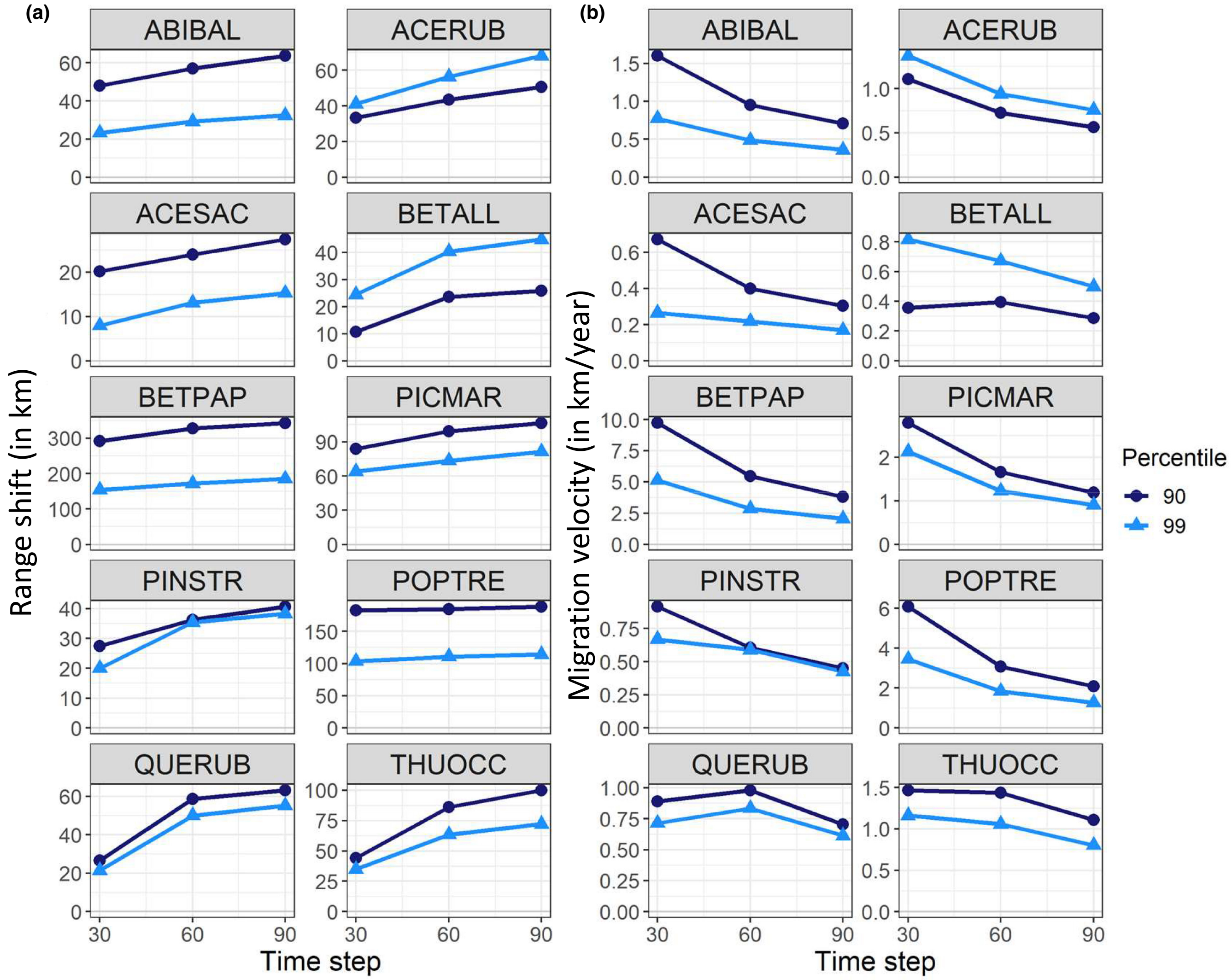

FIGURE 4 (a) Migration-constrained range shift and (b) simulated migration velocity by time period for the 10 selected tree species, as calculated as the average shift across the four simulations. Range limits are calculated as a percentile of latitude of occupied cells in the simulated distribution, whether or not they were located in climatically suitable habitat. Two range limits were calculated, 90th and 99th. The average range limit is calculated across latitudinal bands weighted by the number of cells in a given band relative to the total number of cells across bands. Range shifts are based on the difference between the average latitudinal limit of the simulated distribution as obtained through the simulations in the last year of a given time period (model after 30 years [2011–2040], 60 years [2041–2071], 90 years [2071–2100], respectively) relative to the average latitudinal limit of the initial distribution. Simulated migration velocity is calculated as the range shift divided by the number of years through to the end of a given time period. At a given percentile, positive shifts and velocities indicate that the range limit shifted northward between the initial distribution and the time period of interest. Codes refer to species names listed in Table 2. For a complete list of simulation-specific range shift values, please see Table S2.2.

magnitude of range shifts and resulting lags. Boreal species with more diffuse northern range limits (e.g. *Betula papyrifera*, *Populus tremuloides* and *Picea mariana*) showed the highest range shift values, mostly linked to infilling of their initial distributions. Mixed temperate forest species with compact leading edges such as *Acer saccharum* and *Pinus strobus* showed more moderate range shifts. Furthermore, mixed temperate forest species showed larger lags at the leading edge between migration-constrained range limits and climatically suitable habitat limits than boreal species, with lags of up to 1500 km in some longitudinal bands under high concentration pathways. While this portrait may seem less bleak for boreal species, they in fact quickly run out of room to migrate due to barriers presented by the North Atlantic and Arctic Oceans. Other modelling studies in North America that included dispersal also found that even the most optimistic dispersal scenarios did not result in appreciable leading edge range expansion by the end of the century (Bouchard et al., 2019; Miller & McGill, 2018; Prasad et al., 2020), implying that substantial range extension will take generations (Corlett & Westcott, 2013). Our results suggest that range filling will be an important process in the short term.

The magnitude of range shifts will ultimately depend on whether species can successfully colonize newly climatically suitable areas

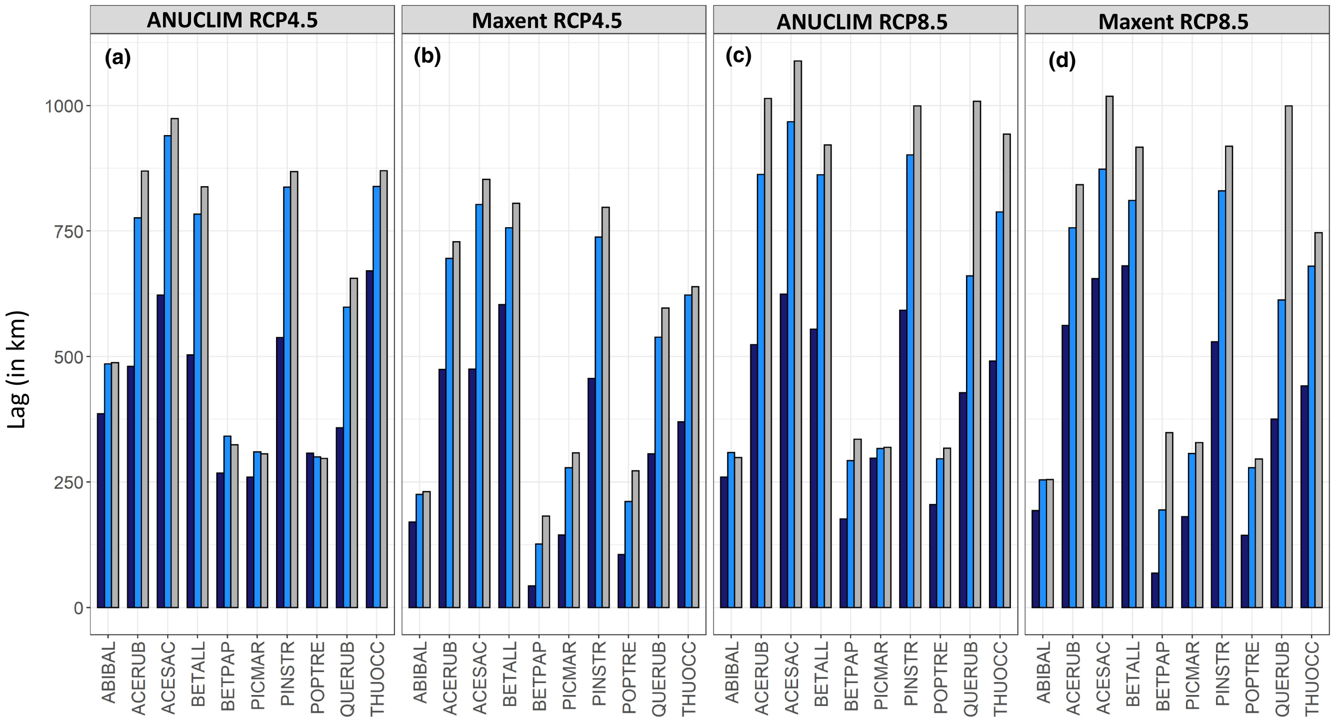

FIGURE 5 Average lag (in km) between the leading edge of climatically suitable habitat relative to the leading edge of a species' simulated distribution. The leading edge of the climatically suitable habitat here is defined as the 99th percentile of latitude of a species' climatically suitable habitat for a given time period (2011–2040—dark blue, 2041–2070—blue and 2071–2100—grey). The leading edge of a species' simulated distribution is defined as the 99th percentile of latitude of all occupied cells (i.e. initial distribution + area colonized through the simulations) through to the end of the time period (after 30, 60 or 90 years). Four combinations of climate suitability from SDM × RCP models are shown: (a) ANUCLIM RCP4.5, (b) Maxent RCP4.5, (c) ANUCLIM RCP8.5, (d) Maxent RCP8.5. Lags were calculated as the average difference across all occupied 50 km wide bands weighted by the number of cells comprising both the simulated distribution and the climatically suitable habitat relative to the total for a band. Positive values indicate that the limit of climatically suitable habitat is at a higher latitude than the limit of a species' simulated distribution in a given time period. Codes refer to species names listed in Table 2.

(Soberón & Peterson, 2005). Recent studies at the temperate-boreal ecotone in North America reported that colonization is influenced by a combination of climate, stand factors (e.g. species composition and disturbance history), biotic interactions and soil conditions (Boisvert-Marsh & de Blois, 2021; Brice et al., 2019; Fisichelli et al., 2014; Solarik et al., 2020). For species with leading edge range limits determined mainly by non-climatic factors, such constraints can effectively impose dispersal barriers and moderate tree migration, potentially exacerbating the disequilibrium between range limits and climate (Svenning & Sandel, 2013). Disturbance is another key factor in species' migration, particularly in the boreal forest (Boulanger et al., 2017; Brice et al., 2019), where frequent disturbances trigger successional changes by breaking the inertia that inhibits new species from moving in (Renwick et al., 2016; Urban et al., 2012). Indeed, observed range shifts over a 30–40 year period (Boisvert-Marsh & de Blois, 2021) for the boreal species *Betula papyrifera* and *Populus tremuloides* were much lower than those predicted by the simulations presented here (*Betula papyrifera*—71.0 km observed vs. 292.2 km simulated; *Populus tremuloides*—19.4 km observed vs. 182.6 km simulated), with observed colonization mainly associated with disturbance. Conversely, temperate species such as *Acer saccharum* and *Acer rubrum* had observed range shifts closer to our simulated shifts (17.1 km vs. 20.2 km and 23.9 km vs. 33.3 km). In this case, observed shifts were closely linked to species' ability to respond to newly suitable climatic conditions (Boisvert-Marsh et al., 2019; Tremblay et al., 2002) and to colonize sites characteristic of the boreal forest (Fisichelli et al., 2014; Solarik et al., 2020). Non-climatic factors will undoubtedly influence the rate at which species migrate, possibly leading to range expansion only when conditions become favourable (Copenhaver-Parry et al., 2020; Renwick & Rocca, 2015).

4.1.2 | Rear edge changes

Large portions of the simulated distribution at the rear edge become partially or completely unsuitable for most species by the end of the century, depending on species' initial distribution and RCP. Two species projected to retain the highest proportion of their initial distribution in Canada across all SDM × RCP model combinations, *Acer rubrum* and *Acer saccharum*, are distributed well into the United States, indicating their suitability for warmer climates than those currently found in the Canadian portion of their distribution. Even though the United States was not included in migration simulations, southern climates were used to calibrate climatically suitable habitat projections (Section 2.2.1). Some other species retained areas of suitable climate in southern parts of the study area, but only under RCP4.5. Specifically, *Betula alleghaniensis* and *Thuja occidentalis* show considerable variability in the amount of initial distribution that becomes unsuitable between RCP4.5 and RCP8.5 without much colonization at the leading edge to compensate, putting them at risk of migration failure (sensu Aubin et al., 2018). Under RCP8.5, four of the six species that showed the greatest decreases of simulated distribution in climatically suitable habitat are distributed mainly in Canada. Moreover, *Abies balsamea and Picea mariana* show large areas in the southern portion of the study area where no simulation is climatically suitable by the end of this century (purple areas in consensus maps, Figure 3). Other studies also project that much of the U.S. distribution could become climatically unsuitable for these species during this century (McKenney et al., 2007; Talluto et al., 2017).

Maxent and ANUCLIM-based models showed some divergence in spatial projections of climatically suitable/unsuitable habitat, particularly between western and eastern parts of the study area and along the rear edge of some species ranges under RCP8.5 (Figure 3). Seven species showed over 60% agreement in projections of climatically suitable/unsuitable habitat across the two SDMs (Table S2.2). Differences in future suitable habitat are likely due to fundamental differences between the two SDM types, specifically in how they project novel climate conditions. ANUCLIM employs a multivariable approach to identify a climate envelope under current conditions, but does not extrapolate beyond the current envelope limits when making future projections. Conversely, Maxent (by default) “clamps” projections such that responses are held constant to values at the limit of the training data (Phillips, 2017). Other studies have also reported significant differences between SDM approaches. Buisson et al. (2010) found that SDM type was the largest source of variation in their projections of future fish habitat in France that employed ensemble forecasting. Shabani et al. (2016) showed how the type of SDM can considerably influence the projections of modelled habitat for Australian plants. Nevertheless, we found pockets of consensus in climatically suitable habitat around the Great Lakes for a number of species (areas in green and yellow in the consensus maps, Figure 3), indicating a potential for climate refugia (see also Doxa et al., 2022; Stralberg et al., 2018). Overall, using a variety of SDMs and RCPs can highlight areas of uncertainty and areas of consensus, information that is critical for conservation planning and forest management moving forward.

While it is clear that species will not keep up with the rate of projected climate change at the leading edge, the fate of trees in climatically unsuitable areas is less certain (Aitken et al., 2008; Holt, 2009). Here, we report on changes in climatically suitable habitat at the rear edge but assume that species maintain their presence in these areas for the purpose of calculating range shifts. These decisions reflect both the risk associated with loss of climatically suitable habitat and the potential for species to persist in situ for some time under unfavourable conditions (Hampe & Jump, 2011; e.g. Decker et al., 2021). Such persistence would delay precipitous changes at the trailing edge, possibly allowing for species to adapt to novel climate conditions (Peterson et al., 2019; Royer-Tardif et al., 2021). However, persistence could also prevent better suited genotypes or even other species from becoming established, putting extant populations at risk of climate-related maladaptation and possibly leading to forest health decline (Frank et al., 2017; Gougherty et al., 2021). Alternatively, trees in these areas could experience rapid mortality, particularly in response to extreme events (Holt, 2003). This has already been reported in some locations (Michaelian et al., 2011; van Mantgem et al., 2009). We note that in the event that rapid extirpations occur at the southern range limits of the species studied here our methodology would tend to underestimate the magnitude of range shifts.

4.2 | Migration kernels and long-distance dispersal

We present here a novel method to calibrate migration kernels to describe the probability of dispersal across the landscape. Typically, process-based models employ dispersal kernels that are calibrated mainly using evidence from field-based studies (see Bullock et al., 2017 for list). However, these studies are usually limited in scale because of the logistical challenges of setting up seed traps at a high enough density to capture dispersing seeds across long distances (Bullock et al., 2006). To calibrate our kernels, we used two parameters—common seed fall distance, which reflects small-scale dynamics of individual-based dispersal, and observed migration velocity, which integrates dynamics from across the range. While a sensitivity analysis on intraspecific variation of model parameters and its effect on simulations was not done per se, our choice of species reflected the range of dispersal abilities and generation times typical for tree species in eastern Canada (see Table 1; Table S1.4). This interspecific variation is well illustrated by comparing traits of *Acer saccharum* (moderate seed fall distance, low LDD values and long generation time) with those of *Populus tremuloides* (high seed fall distance, high LDD and moderate generation time) (also see Figure S2.1). These differences, along with differences in spatial arrangement at the leading edge, resulted in considerably greater range shifts for *P. tremuloides* (1.26 km/year) relative to *A. saccharum* (0.17 km/year). Our results show that migration is an incremental process in which species-specific traits related to dispersal ability and generation time interact to produce a detectable spatial signal.

Observed migration velocity acts as a proxy for other considerations not typically captured in dispersal kernels, such as abundance within populations (Clark et al., 2001) and colonization potential (Boisvert-Marsh & de Blois, 2021). This study used observed changes in presence–absence over time across latitudinal gradients to assess migration velocity. While empirical observations of migration velocity are still scarce for plants (Lenoir & Svenning, 2015), any metric that is representative of range shift could be used (see Yalcin & Leroux, 2017 for overview). Other contemporary studies have used changes in abundance (Fei et al., 2017) or relative position of juveniles vs. mature trees (Boisvert-Marsh et al., 2014; Zhu et al., 2012) to assess changes in species' ranges and range limits. More recent assessments of paleoecological range shifts have highlighted the importance of cryptic refugia in the calculation of range shift velocities (Feurdean et al., 2013; also see description of dataset in Appendix S1). Because the mean is one of the two parameters that controls kernel shape, different migration velocities could provide different perspectives into the probability of long-distance dispersal events.

Calibrating migration kernels in the way proposed here further supports the overall consensus that tree range shifts are likely to be rather slow and that substantial movement will take generations (Corlett & Westcott, 2013). Similar to the findings from Clark et al. (1998), we found that cumulative distance was rather limited when dispersal ability and generation time were taken into consideration, with an average median distance of 48.4 m/year across our study species. Furthermore, Clark et al. (2001) reported that the cumulative distance travelled for *A. rubrum* over multiple generations was approximately 45 m/year, which is similar to our finding (median = 57.8 m/year). At larger scales, species such as *A. saccharum*, whose simulated range shifts were on the lower end (simulated average velocity of 170 m/year), tended to be closer to estimates of paleoecological range shifts (168 m/year from 12–10 kybp; Ordonez & Williams, 2013), while simulated shifts for *A. rubrum* and *Picea mariana* (simulated average velocity of 757 and 903 m/year) greatly exceeded paleoecological shifts (~1000–1500 m/decade—McLachlan et al., 2005; Ordonez & Williams, 2013). In a study that quantified changes in contemporary range limits using shifts in the centroid of abundance in the eastern United States (Fei et al., 2017), results for early successional tree species like *B. papyrifera* and *P. tremuloides* as well as *Quercus rubra* were most comparable to our findings (observed velocity of 2.65, 1.36 and 0.89 km/year respectively vs. simulated velocity of 3.81, 2.09, 0.70 km/year), but were considerably different for our other study species. This may be because shifts in abundance can occur without realized changes in range limits and incorporate both gains and losses, both of which are patterns not quantified here.

Long-distance dispersal has long been thought to explain the rapid spread of trees at the end of the Pleistocene (Clark et al., 1998; Delcourt & Delcourt, 1991; Giesecke et al., 2010). While LDD values were not used to calibrate the kernels themselves, the probability of such an event might not be as rare as expected, especially if seed fall distances have a long “fat” tail (Clark, 1998). We used a trait-based approach to bound the distances within which long-distance dispersal (LDD_{min} and LDD_{max}) occurs and ultimately obtain the probability of such events from the kernels. For comparison purposes, we set LDD_{min} to the upper confidence interval (i.e. 95th percentile) from the dispeRsal model output (ranges from 528 to 5582 m, see Table 1) and LDD_{max} to 10,000 m in test trials to examine the kernel probabilities in the long tail beyond the LDD used in our simulations. The probability of these distant dispersal events for all species were much lower than the ones we used (Figure S1.2, Table S1.5), implying that such very long distance, potentially range-extending dispersal events would indeed be rare. Considering intraspecific variation in seed trait values would undoubtedly affect dispersal probabilities (see Snell et al., 2019 for discussion), but using confidence intervals from the dispeRsal model helped to incorporate uncertainty surrounding LDD into the simulations. Overall, given the relative simplicity of the approach proposed here, parameterizing dispersal kernels with seed traits and range shift metrics offers another option to modellers looking to incorporate dispersal constraints into migration simulations or to conduct sensitivity analyses on parameters that underlie migration velocities.

4.3 | Limitations

We recognize that well documented issues with SDMs—including the concern that species' range limits are not at equilibrium with climate (Araújo & Peterson, 2012; Oldfather et al., 2020; Talluto et al., 2017)—also apply to the current study. Such mismatches have the potential to affect the response of species to climate change at both the leading and rear range edges. However, many studies have reported that northern species are cold limited at their northern range limits (Caccianiga & Payette, 2006; Graignic et al., 2014; Tremblay et al., 2002), indicating that climate is likely a key constraint to northward range expansion. Here, we generated a consensus model using outputs from a variety of SDMs and RCPs. An alternative approach would be to generate the consensus model using outputs from the *n*-fold cross-validation exercise and a variety of background datasets. Such an approach would provide another perspective on the uncertainty within a single RCP/SDM combination. While including migration velocities takes species' establishment into account, our simulations could be improved by integrating factors that directly influence species colonization, such as edaphic conditions (e.g. Périé & de Blois, 2016) and land use (e.g. Miller & McGill, 2018). More complex modelling approaches could also be used, mainly by incorporating SDMs suitable for presence/absence data, different submodels or using an integrative modelling approach, to account for the different factors that can influence species' biophysical responses to climate (e.g. Boulanger et al., 2022; Périé & de Blois, 2016; Talluto et al., 2016). To keep the model relatively simple, we used static values across the range for traits related to seed production, including growth, age of sexual maturity and probability of seed production once maturity is reached. Another option would be to introduce variability in such climate-sensitive traits into the model, such as fecundity (Clark et al., 2021), recruitment (Copenhaver-Parry et al., 2020), tree age/size in relation to seed production (Bogdziewicz et al., 2020; Viglas et al., 2013) and masting (LaMontagne et al., 2020). The detailed information required to generate such models is not available for most species or regions. However, integrating the various types of information mentioned here would likely further constrain migration-related range shifts, so our findings may be on the optimistic side. Given the complex and uncertain nature of modelling species shifts under climate change, our results could be considered a first step upon which future studies could explore how biotic and abiotic factors may interact to influence species outcomes.

4.4 | Applications

Simulations like the ones presented here not only inform on the ecological processes driving tree range shifts in a changing climate, but also provide species and spatially explicit information to support conservation and/or management decisions. For instance, our simulations and consensus maps identified rear edge populations of *Picea mariana* at high risk of maladaptation. These findings can be combined with demography-based models (e.g. Sheth & Angert, 2018) to highlight areas where in situ conservation may be feasible (i.e. climate refugia; Stralberg et al., 2018) or where seed collection for ex situ conservation efforts should be conducted (Fady et al., 2016). Our consensus maps indicate general locations that may be suitable for assisted migration efforts aimed at moving species to potential refugia within and beyond current range limits. As noted, such areas could be critical for conservation and forest management planning moving forward. Temperate species that lag considerably behind their suitable climate could be targeted for assisted migration as part of forestry operations (Pedlar et al., 2012) or non-forestry commercial purposes (Legault et al., 2019). In fact, our simulated distribution limits provide defensible targets for assisted migration efforts aimed at mimicking natural migration patterns. Like climate refugia of the past (Davis, 1983), assisted migration could provide new nuclei for range expansion by diffusion, and active measures could be taken to ensure tree survival. Range-extending assisted migration is already being practiced, either formally (e.g. Muller et al., 2019) or informally (e.g. horticultural purposes, Van der Veken et al., 2008), and tools exist to aid with decision making (e.g. McKenney et al., 1999; Pedlar et al., 2011; Swanston et al., 2016). Risk assessment frameworks originally developed for invasive species could also be adjusted to the context of range expansions of native species into newly climatically suitable habitat (Essl et al., 2019; Urban, 2020). Moreover, forest management could be adapted to favour resilience or community transition at the leading edge (sensu Millar et al., 2007). In the latter case, this could mean favouring species not just based on their commercial value for forestry, but because they serve as nurse species that facilitate northward migration of other desirable forest species (Boisvert-Marsh et al., 2020; Boisvert-Marsh & de Blois, 2021). The results for our study species suggest that mixed temperate forest species would benefit more from assisted migration than northern boreal species which may require refugia. In any case, long-term forest monitoring will remain crucial to evaluate whether migration-constrained simulations are indeed a good approximation of climate-driven range shifts into the future.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The species maps of each SDM × RCP combination and the maps of Consensus by RCP are available in Appendix S3. All data used to parameterise the migration simulations are summarized in Tables S1.1–S1.4. The R script used to obtain the 2Dt migration kernels and the files necessary to run the script are available as Supplemental material to this article (Appendices S4-S6). Additional scripts including files necessary to run an example migration simulation are available at https://github.com/laurabm/MigClim_example. The raster files of the species initial distributions are available from https://open.canada.ca/data/en/dataset/ec9e2659-1c29-4ddb-87a2-6aced147a990. Maps of climatically suitable habitat are available from http://planthardiness.gc.ca/. Raster outputs of migration simulations for each combination of species, SDM and RCP are available on Dryad at https://doi.org/10.5061/dryad.dv41ns21t.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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