

# Interactions between climate change, competition, dispersal, and disturbances in a tree migration model

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**Abstract** Potentially significant shifts in the geographical patterns of vegetation are an expected result of climate change. However, the importance of local processes (e.g., dispersal, competition, or disturbance) has been often ignored in climate change modeling. We develop an individual-based simulation approach to assess how these mechanisms affect migration rate. We simulate the northward progression of a theoretical tree species when climate change makes northern habitat suitable. We test how the rate of progression is affected by (1) competition with a resident species, (2) interactions with disturbance regimes, (3) species dispersal kernel, and (4) the intensity of climate change over time. Results reveal a strong response of species' expansion rate to the presence of a local competitor, as well as nonlinear effects of disturbance. We discuss these results in light of current knowledge of northern forest dynamics and results found in the climatic research literature.

**Keywords** Forest dynamics · Simulation model · Disturbance regime · Species range · Boreal forest · Tree colonization

## Introduction

Shifts in the geographical patterns of vegetation are an expected result of climate change. Niche-based models,

based on current plant–climate relationships, predict that northwards expansion of biomes could reach 100 km in a century (Emanuel et al. 1985; Prentice et al. 1992; Malcolm et al. 2002). These predictions, emphasizing a primary control of climate on vegetation patterns, have been questioned by empirical and simulation-based studies (Masek 2001; Gamache and Payette 2005; Ibáñez et al. 2007). In several recent studies (Solomon and Kirilenko 1997; Kirilenko and Solomon 1998; Loehle 1998, 2000; Pacala and Hurtt 1993), it has been argued that climate change research largely underestimates the importance of local processes (e.g., dispersal or competition) in determining ecological patterns. Moreover, niche-based models are based on the fact that the observed species is in equilibrium with its environment. This assumption is far from being true in many areas of the world where the system is usually in a state of transient dynamics, even at large scales (Payette 2007; Caplat et al. 2006). Some of the niches that are observed characterize forerunners or remnants of the postglacial migration (Payette 2007) and should not be used to predict future distributions. In the context of climate change, the niche-based approach does not describe the range expansion processes that species are expected to undergo before they reach the supposed new equilibrium. Taking into account the mechanisms by which species migrate could considerably change the predicted rates of distribution shifts and thus have important implications for climate change research.

Process-based models offer a good alternative to niche-based approaches by taking into account detailed ecosystem fluxes (Kumagai et al. 2004). However, their level of detail can make it difficult to apply them at large scales, especially for understanding spatiotemporal variability (Ibáñez et al. 2007). Indeed, the apparent relationship between a species range and the environment is contingent

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on many factors whose long-term influence is difficult to predict. For instance, dispersal barriers can strongly affect species distribution (Timoney 1995; Guisan and Thuiller 2005). In forest ecosystems, disturbance regimes in particular determine successional dynamics and stand regeneration (Jasinski and Payette 2005; Turner 2005). As climate changes, disturbance regimes are in turn altered through direct climatic effects (e.g., frequency or severity of windstorms) or indirect effects of climate on fire or pest outbreaks (Chapin et al. 1997). In a simulation study, Overpeck et al. (1990) showed that catastrophic disturbances (i.e., killing all individuals over a large space) tend to increase the rate at which ecosystems respond to climate change. However, disturbances due to climate change are likely to include subtle as well as catastrophic disturbances. In addition, one must consider the possibility that disturbances which target specific species (either a resident or a newcomer), such as pests, will not affect other species, changing the outcomes of migration.

In the present paper, we develop an individual-based (*sensu* Breckling et al. 2006) simulation approach to assess how local ecological processes interact with climate change and disturbance regimes to affect range expansion of tree species. The utility of individual-based models (IBMs) has been demonstrated in work from the past three decades (Botkin et al. 1972; DeAngelis and Mooij 2005), but the need for detailed parameterization has often been a cause for “narrow application” (Grimm 1999). Recent studies, however, have shown how IBMs can answer theoretical questions (see Breckling et al. 2006 for examples in different research areas), and they appear to be relevant also for studying the nonlinear interactions created by the different processes intervening in species migration (Brooker et al. 2007). Here, we approach the issue of vegetation response to climate change from a theoretical basis. Our interest is to include the key transient processes that can affect a species ability to expand its range, namely, dispersal (see Clark et al. 1998), competition (Loehle and LeBlanc 1996), and disturbance (Turner 2005). Most studies of species range expansion (for a review on niche-based approaches, see Guisan and Thuiller 2005) focus on two points in time (generally, current and postclimate change distributions). By comparison, we focus on the processes through which species distribution will evolve over time, by taking into account individual interactions. Moreover, few studies have assessed the combined effects of disturbance, biotic interactions, and climate change on species range shift, as we do here (see He and Mladenoff 1999 for an example of landscape model focussed on fire), though similar approaches focusing on different processes were developed recently (Brooker et al. 2007; Takenaka 2005), which revealed a strong interaction between species life traits (particularly dispersal ability and fecundity) and

environmental changes in species migration ability. Here, we add different mechanisms (individual growth, disturbances) that improve both the biological realism and the tractability of the model.

We base our approach on boreal–subboreal biomes, which are interesting for their high sensitivity to climate change (Chapin et al. 2004). Boreal climatic conditions are strongly limiting for tree growth (air temperature, length of the growing season, presence of permafrost, strong winds; Kittel et al. 2000), favoring only a few conifer species (e.g., black spruce, white spruce). By improving growing conditions, climate change is expected to substantially affect vegetation dynamics by allowing species located in the southern parts of boreal forests (e.g., aspen, maples, birches) to migrate northwards (Parmesan 2006). This system is then particularly adapted to the study of tree migration, and the fact that tree dynamics are dominated by a few species (Timoney 1995; Payette et al. 2001) allows simulating community dynamics with relatively simple rules, increasing the tractability of modeling outcomes.

Here, we simulate the northward progression of a theoretical tree species when climate change makes northern habitat suitable. In particular, we test how the rate of progression is affected by (1) competition with a resident species, (2) interactions with disturbance regimes, (3) species dispersal kernel, and (4) the intensity of climate change over time. We then discuss these results in light of current knowledge of temperate and boreal forest dynamics.

## Materials and methods

### Model description

FORSITE-DIS simulates competitive interactions and disturbance in a two-species system, in the context of climate change. We focus on a small area located at the “zone of interaction” between two biomes (e.g., subboreal and boreal forests). The goal of the study is not to simulate a real system but rather to show how a set of local processes changes the outcome of migration in an idealized but tractable system. For that reason, we consider a case in which only two species interact (a northern and a southern species). This simple approach allows revelation of most outcomes of tree migration, especially since boreal forests are often dominated by no more than two or three species (Payette et al. 2001). We simulate how processes like dispersal, competition, disturbances, and the rate of climate change affect the expansion of the southern species population. The model is implemented on the modeling platform CORMAS (Bousquet et al. 1998) using the Visual-Works® environment. This platform allows flexible designs and allows implementation of individual-based stochastic

dynamics in a spatial, dynamical context. Detailed UML diagrams of a more basic version of the model can be found in Caplat et al. (2008).

### Tree dynamics

Individual trees are distributed on a line of 50 hexagonal habitat cells. The choice for a one-dimensional grid (seen as a latitudinal transect) allows focus on north–south dynamics while gaining computation time. Space is cylindrical, assuming periodic boundaries on the sides (east–west) but not on the extremities (north–south). Cells are characterized by a climatic index, which is a theoretical index constituted by all the factors that might affect the relationships between latitude and habitat suitability (e.g., air temperature, precipitation, soil temperature, presence of permafrost). We defined its range of variation between 0 and 2, 0 representing conditions unsuitable for tree growth (i.e., arctic climate), to increase the tractability of the model's computations. The choice of cell diameter  $x$  (see Table 1 for a summary of the parameters and their values) depends on the modeled system. In the present study, it defines the scale of the competitive neighborhood, which we fixed at 20 m (i.e., the size of neighborhood affected by a large canopy tree). Individuals are defined by the following state variables: species, identity number, age, and height. The

model proceeds in annual time steps. Within each year, every tree consumes a theoretical resource from its habitat, grows, reproduces (if it has reached sexual maturity), and may die.

Resource uptake is a function of the density of competing individuals within the habitat cell: a tree is affected by competition with its neighbors for limited resources. For convenience, we define the maximum resource available as equal to 1 (minimum=0). Competition is asymmetric (i.e., an individual is affected only by taller neighbors) to simulate shading-like competition (Pacala et al. 1996). The resource available  $R$  for a given tree is affected by the density of taller individuals ( $N_{H>H_i}$ ) through the parameter  $h$ , the strength of taller tree competition:

$$R = e^{-C} \quad (1)$$

with

$$C = \frac{N_{H>H_i}}{h} \quad (2)$$

The growth rate ( $g$ ) is a function of resource uptake ( $R$ ) and climatic index ( $c_s$ ) and affects reproduction ability through fecundity and dispersal distance. The growth rate ( $g$ ) is defined as follows:

$$g = g_{\text{species}} \times R \times c_s^\sigma \quad (3)$$

**Table 1** Overview of the model parameters and default values used in the present analysis

Level	Parameter	Description	Mean value ( $\pm$ SD)
Model	$x$	Cell diameter	20
	$N_c$	Number of cells	50
	$M_c$	Maximum climatic index	1
	$C_r$	Rate of climatic index change	0.001
	$g_{\text{northie}}$	Optimal growth rate ( $\text{m year}^{-1}$ )	0.1 ( $\pm 0.01$ )
Northie	$H_{\text{max}}$	Maximum height (m)	20 ( $\pm 2.0$ )
	$\sigma$	Sensitivity to climatic index	2
	$H_t$	Height threshold for windfall (m)	15
	$g_{\text{southie}}$	Optimal growth rate ( $\text{m year}^{-1}$ )	0.1 ( $\pm 0.01$ )
Southie	$H_{\text{max}}$	Maximum height (m)	25 ( $\pm 2.5$ )
	$\sigma$	Sensitivity to climatic index	3
	$H_t$	Height threshold for windfall (m)	15
	$h$	Strength of taller tree competition	100
	$M_0$	Probability of mortality at zero growth	0.7
	$M_d$	Decay of growth-dependent mortality	0.8
	$M_i$	Intrinsic mortality	0.01
	$H_{\text{rep}}$	Height threshold for reproduction (m)	2
	$f_{\text{max}}$	Species maximum fecundity (seedlings per year)	5
Individual tree	$p$	Probability of short-distance dispersal	0.95
	$\alpha$	Mode of the short dispersal kernel (m)	10
	$c$	Exponent in the height–dispersal function	1.5
	$\beta$	Mode of the long dispersal kernel; defined by $D$ and $c$ .	(500)
	$D$	Distance increment (m) by height increment for the height–dispersal function	2.5

where  $g_{\text{species}}$  is the optimal growth rate of the species and  $\sigma$  is the species sensitivity to the climatic index. Growth follows a Gompertz function (Moravie and Robert 2003; Zeide 2004) defining the annual height increment  $I_h$  as:

$$I_h = H \times \ln\left(\frac{H_{\max}}{H}\right) \times g \quad (4)$$

where  $H$  is the tree height and  $H_{\max}$  the tree maximum height.

A tree becomes adult if it reaches a threshold height ( $H_{\text{rep}}$ ). An adult tree produces  $f$  seeds. The individual fecundity  $f$  is defined for a given step  $t$  as:

$$f = f_{\max} \times \frac{H}{H_{\max}} \quad (5)$$

where  $f_{\max}$  is the species maximum fecundity. Each seed is dispersed to a given habitat cell according to a dispersal kernel mitigated by the height of the seed source. The dispersal kernel is defined as a double exponential (mixed) kernel, with a typical fat-tailed shape that allows us to take account of the rare but important long-distance events (Clark et al. 1998; Higgins and Cain 2002; Katul et al. 2005; Debain et al. 2007). The density of probability for a single seed is given for  $d$  (distance from the seed source) by the following:

$$P(d) = \frac{p}{2\pi\alpha} \times e^{\left(-\frac{d}{\alpha}\right)} + \frac{(1-p)}{2\pi\beta} \times e^{\left(-\frac{d}{\beta}\right)} \quad (6)$$

The first term gives the probability of seeds being dispersed at short distance (proportion  $p$  of the seeds), while the second represents long-distance dispersal (proportion  $(1-p)$ ). The parameters  $\alpha$  and  $\beta$  define the mode of respectively short- and long-distance dispersal (SDD and LDD). A similar mixed function was shown by Higgins and Cain (2002) to allow great flexibility in dispersal modeling: with  $p=1$ , one can simulate a local dispersal case, whereas with  $p=0$  and  $\beta$  bigger than the size of the grid one can simulate a global dispersal case. In the case of long-distance dispersal, the actual dispersal distance follows a power-law relationship to the seed-source height (which is the relationship found by Greene and Johnson 1996, between wind speed and tree height; we assume that dispersal distance is directly linked to wind speed):

$$\beta = [D \times H]^c \quad (7)$$

where  $\beta$  is the mean long-distance dispersal. Parameters  $D$ ,  $c$ , and  $\alpha$  (mode of the short-distance dispersal kernel) are constants that we define following the results of Debain et al. (2007) as dispersal parameters for boreal species are not available. We assume no directionality in dispersal (Higgins and Richardson 1999). As individual height is affected by direct competition, from Eqs. 5 and 7, we see that a dense neighborhood decreases individual fecundity as well as dispersal distances. The same way, a favorable climatic

index, by increasing tree growth rate, increases fecundity and dispersal distances. Seeds germinate the following year and start to grow from an initial height of 2 cm following Eq. 4. For the sake of simplicity, growth parameters for seedlings are assumed to follow the same rules as adults (which should not affect growth trajectories as the growth curve at young age is almost linear).

Finally, trees die according to two processes: (1) intrinsic mortality represents all causes of mortality which are not related to growth (senescence, disturbances occurring at the individual level; Keane et al. 2001). Each individual dies with a constant probability  $M_i$  per year; (2) growth-dependent mortality affects trees that grow too slowly. This effect has been found in forest ecosystems due to limits in the individual ability to cope with suppressed growth (Keane et al. 2001):

$$m = M_0 e^{-M_d I_h} \quad (8)$$

where  $M_0$  is the probability of mortality at zero growth,  $M_d$  the decay of growth-dependent mortality,  $I_h$  the annual height increment, and  $m$  the probability of death per year.

We define the two species competing on the spatial grid: (1) the resident species, nicknamed “Northie”, is modeled after a typical boreal forest tree, adapted to northern habitats (e.g., black spruce). This feature is translated in the model by a low sensitivity to climatic index ( $\sigma=2$ ); (2) the invader (“Southie”) is adapted to southern habitats, meaning that it exhibits a high sensitivity to climatic index ( $\sigma=3$ ). However, in optimal conditions (climatic index  $\geq 1$ ), it grows taller than Northie (note that we adopt the standard convention for species names for Southie and Northie, thus using singular forms for the remainder of the manuscript) as would do early succession species like aspen or jack pine (Pacala et al. 1996). The choice of these two growth types was motivated by our goal: emphasizing potential contrasting dynamics occurring with different disturbance regimes. Many different tree types may be involved in climate-induced migration; however, it seemed that these two types would produce the most interesting dynamics. The interaction between growth and climatic index in Eq. 3 creates distinct habitats based on climatic index: if it is lower than 1, Northie is advantaged, if it is higher than 1, Southie is advantaged.

## Disturbance

Amongst the large variety of disturbances affecting northern forests, we choose windstorms as an example of a simple mechanism that could strongly impact forest dynamics. This choice is motivated by several points: (1) windstorms have been shown to be the dominant type of disturbances in northern forest dynamics, creating punctual tree mortality as well as large gaps (Elie and Ruel 2005); (2) since winds are driven by climate, one can expect windstorms regimes to be affected by climate change; (3)

compared to disturbances like fire or pest outbreaks, windstorms are relatively easy to simulate, making them an appropriate choice for our study.

In the model, windstorm-like disturbance can affect one patch (large canopy tree) with a probability  $P_{dis}$ . Within the patch, windthrow kills every individual higher than a threshold  $H_t$ . This approach simulates the effect of wind on trees higher than the average canopy (Caplat, personal observation) and can be viewed as a simplification of the positive size probability of windthrow relationship found by Canham et al. (2001) in northern forests. Because Southie grows taller than Northie, this disturbance is expected to affect Southie more than it affects Northie (as size-related windthrow affects more strongly early succession species than shade-tolerant species—Rich et al. 2007). This way, we expect disturbances to counteract the advantages conferred to Southie by climate change. A modified version of this disturbance creates “gaps”: a tree killed by windthrow kills shorter individuals in its neighborhood (i.e., the same cell), which should mitigate the negative influence of disturbance on Southie by also killing shorter trees.

### Simulations

We aim at testing the Southie rate of progression when climate change makes conditions more suitable for it. After a sensitivity analysis checking the qualitative consistency of model response to parameter variation (including all parameters), simulations all follow the same basic design:

1. Every cell is set with a relatively low climatic index ( $c_s=0.7$ ), except for the “southern edge,” 6% of the grid, set with high climatic index ( $c_s=1.2$ ). This design allows Northie to dominate the grid but maintains a small population of Southie at the “southern edge” of the grid, acting as seed sources.
2. Seeds of both species are uniformly distributed over the grid, and the simulation runs until a pseudo-equilibrium in population size is reached (i.e., when the coefficient of variation over a 150-year period is less than 5%)
3. We simulate climate change by increasing the climatic index  $c_s$  everywhere at an annual rate  $Cr$  until  $c_s$  reaches the climatic maximum  $Mc$ .
4. When appropriate, we also introduce a disturbance regime.

We define five scenarios based on disturbance type. We first run simulations (ten replicates each) in which Northie is absent from the grid when climate change occurs, allowing Southie trees to progress across an empty space (*Freeprog*). Then, we run simulations with both species present, but with no disturbance (*Comp*), then with windthrow or gap creation disturbances (respectively,

*Windthrow* and *Gaps*). To check the effect of scenario *Windthrow* on modeled trees, we add a scenario (“Southie-specific windthrow”) in which disturbances kill only Southie individuals.

For every scenario, we change the annual rate of climate change ( $Cr=0.001$  or  $0.002$ , for, respectively, baseline and high rate of change of the climatic index), the climatic maximum ( $Mc=1$  or  $1.3$ , for, respectively, baseline and high climatic maximum), or the shape of Southie dispersal kernel ( $p=0.95$ ,  $0.8$ , or  $1$  for, respectively, baseline dispersal, long-distance dispersal, and short-distance dispersal sets). The detailed parameter values are given in Table 2.

### Analyses

Interreplicate variation is measured with a coefficient of variation estimated from the multiple time series. Southie progression is analyzed through two measures: (1) an “expansion rate”, obtained by dividing the population size at equilibrium by the time needed to reach the equilibrium, and (2) a “colonization rate” obtained by dividing the length of the grid by the time needed for a single, viable tree to establish at the northernmost end of the grid. We chose the two

**Table 2** Simulation settings and outcomes

Scenario	$Mc$	$Cr$	$p$	Pop. Size	Time to eq
<i>Freeprog</i>	1	0.001	0.95	1,300	412
<i>Comp</i>	1	0.001	0.95	1,300	2,079
<i>Windthrow</i>	1	0.001	0.95	150	
<i>Gaps</i>	1	0.001	0.95	950	2,023
<i>Freeprog</i>	1.3	0.001	0.95	1,900	654
<i>Comp</i>	1.3	0.001	0.95	1,900	690
<i>Windthrow</i>	1.3	0.001	0.95	1,300	582
<i>Gaps</i>	1.3	0.001	0.95	1,500	634
<i>Freeprog</i>	1	0.002	0.95	1,300	244
<i>Comp</i>	1	0.002	0.95	1,300	1,903
<i>Windthrow</i>	1	0.002	0.95	150	
<i>Gaps</i>	1	0.002	0.95	950	1,803
<i>Freeprog</i>	1.3	0.002	0.95	1,900	361
<i>Comp</i>	1.3	0.002	0.95	1,900	469
<i>Windthrow</i>	1.3	0.002	0.95	1,300	370
<i>Gaps</i>	1.3	0.002	0.95	1,250	423
<i>Freeprog</i>	1	0.001	0.8	1,300	359
<i>Comp</i>	1	0.001	0.8	1,300	1,826
<i>Windthrow</i>	1	0.001	0.8	280	
<i>Gaps</i>	1	0.001	0.8	950	1,750
<i>Freeprog</i>	1	0.001	1	1,300	530
<i>Comp</i>	1	0.001	1	Unknown	>2,500
<i>Windthrow</i>	1	0.001	1	150	
<i>Gaps</i>	1	0.001	1	950	>2,500

Blank entries correspond to cases in which Southie population failed to expand (italicized rows).

Pop. size Southie population size at equilibrium (number of individuals), Time to eq time needed to reach the equilibrium (years)



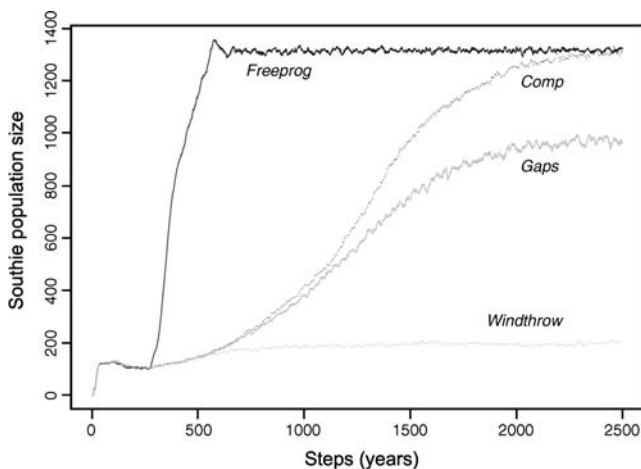
approaches as they give different insights on the outcomes of plant migration, respectively, time lag between change and equilibrium conditions and the speed of spatial expansion.

## Results

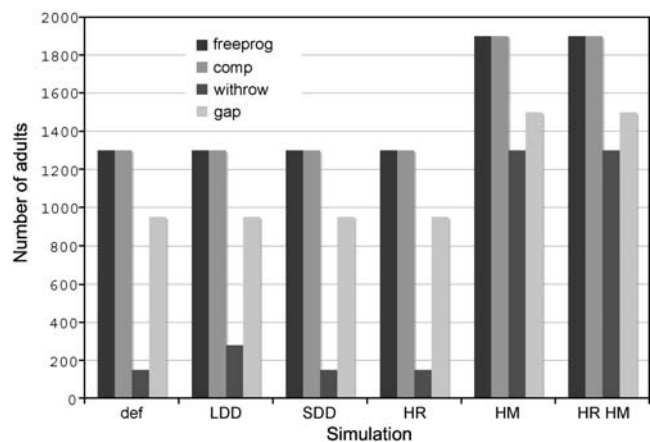
FORSITE-DIS exhibits high robustness (characterized by interreplicate coefficients of variation lower than 5%). For that reason, we illustrate the simulation outcomes with graphs plotted with average values across replicates.

### General dynamics—qualitative results

The effect of different possible scenarios on qualitative and quantitative outcomes of the model is very strong. With baseline parameters (Fig. 1), different scenarios affect the fate of the two species differently. Note that equilibrium populations lower than 400 correspond to cases in which Southie failed to expand (and remained restricted to the Southie habitat at the bottom of the grid). As expected, with the scenario *Freeprog*, Southie population expands quickly. With the scenarios *Comp* and *Gaps*, Southie takes over the grid and totally excludes Northie population. Southie expansion in scenario *Freeprog* is the baseline progression. When the resident species (Northie) is present to compete with the invader (Southie; Fig. 1, *Comp*), the rate of Southie expansion is lower, but Southie reaches the same population size at equilibrium. As expected, when disturbances kill tall trees (*Windthrow*) because Southie individuals grow taller than Northie individuals, the Southie population is disadvantaged and fails to expand. However, when this disturbance is associated with the creation of gaps, Southie population expands and excludes Northie



**Fig. 1** Effects of scenario on Southie expansion, with baseline parameters. Values are averaged across ten replicates for each simulation settings, with an average coefficient of variation <0.05



**Fig. 2** Variation of Southie population size at equilibrium between simulations. Values are averaged across ten replicates for each simulation settings, with an average coefficient of variation <0.05. *Def*: baseline settings, *LDD* (long-distance dispersal):  $p=0.8$ , *SDD* (short-distance dispersal):  $p=1$ , *HR* (high rate of change):  $Cr=0.002$ , *HM* (high maximum):  $Mc=1.3$

from the grid, but its population size at equilibrium is smaller. This occurs because gaps created by the death of tall Southie individuals clear up resident Northie trees, allowing Southie seedlings to establish. However, the negative effect of the disturbance keeps the population at a smaller size. The same pattern between scenarios can be found with most sets of parameters (Table 2). However (gray lines in Table 2), two sets of parameters ( $Mc=1.3$  with  $Cr=0.001$  or  $Cr=0.002$ ) allow Southie expansion even with the windthrow disturbance. It is likely that the benefit of increased climatic index on Southie tree height and growth rate allow the population to establish quickly and withstand the negative effects of disturbance.

### Effects of parameters on population size at equilibrium

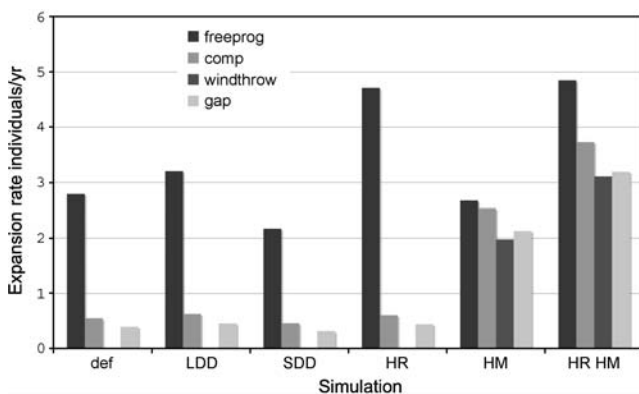
The first columns of Fig. 2 (baseline settings) describe the pattern found in Fig. 1. Without disturbance, Southie population size at equilibrium stabilizes at around 1,300. Figure 2 illustrates how the pattern exhibited in Fig. 1 is conserved when the dispersal kernel is modified (SDD and LDD) and also when the rate of change  $Cr$  increases. However, when the climatic maximum is high ( $Mc=1.3$ , HM and HR HM), the pattern is different. The equilibrium Southie population size is increased by half on average, but the most surprising result is that the third scenario (*Windthrow*) no longer prevents Southie from invading the grid. This dramatic change in the model prediction for a relatively small change in parameter value suggests that there may be a threshold, whereby the model dynamics change qualitatively and quite suddenly once a certain parameter value (in this case, climatic maximum) is

sufficiently large. In addition, replacing the scenario *Windthrow* with its alternative in which windthrows affect only Southie individuals (not shown) does not change this result, providing evidence for a control of processes over Southie dynamics but not Northie.

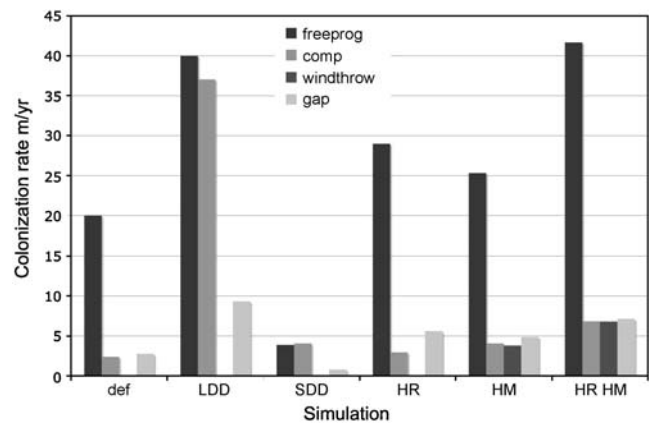
#### Effects of parameters on population expansion rate

The Southie expansion rate (Fig. 3) is, as expected, faster when the Northie population has been removed from the grid (*Freeprog*), with the Southie population growth rate reaching values of 4.6 individuals per year with baseline settings. The fact that this value is close to the average individual fecundity shows that, under the scenario *Freeprog*, Southie populations exhibit little density dependence while progressing on the empty space. When competition with the resident species occurs (*Comp*), the rate of expansion is reduced almost five times (0.6 individuals per year—more than 2,000 years needed to reach equilibrium) compared to free progression (2.7 individuals per year—equilibrium reached in 412 years on average).

The qualitative differences under the various scenarios are conserved when dispersal kernel or rate of climate change are changed. With increased long-distance dispersal ( $p=0.8$ ), the expansion rate is slightly greater than in the baseline scenario (3.2 individuals per year), whereas when trees disperse only at short distance ( $p=1$ ) the expansion rate is decreased to 2.2 individuals per year. On the other hand, a high rate of climate change produces a strong increase in the Southie expansion rate (4.7 individuals per year). When a high climatic maximum is introduced, the differences between the four scenarios are decreased. Combined with a high rate of change, it results in a surprisingly high rate of Southie expansion under *Windthrow*.



**Fig. 3** Variation of Southie population expansion between simulations. Values are averaged across ten replicates for each simulation settings, with an average coefficient of variation  $<0.05$ . Def: baseline settings, LDD:  $p=0.8$ , SDD:  $p=1$ , HR:  $Cr=0.002$ , HM:  $Mc=1.3$



**Fig. 4** Variation of Southie colonization rate between simulations. Values are averaged across ten replicates for each simulation settings, with an average coefficient of variation  $<0.05$ . Def: baseline settings, LDD:  $p=0.8$ , SDD:  $p=1$ , HR:  $Cr=0.002$ , HM:  $Mc=1.3$

#### Effects of parameters on colonization rate

Colonization rates (Fig. 4) differ from expansion rates since they do not necessarily depend on the Southie population size per se but rather on the species' ability to reach and establish few individuals at far distances. The differences between scenarios are qualitatively similar to those described above, but one can note an increased effect of the absence of disturbance (*Freeprog*), which allows the trees to progress across space without any "barrier" from the resident population. Colonization rate is also favored by increased LDD frequency under the competition scenario (*Comp*). Measuring invasion in terms of a colonization rate emphasizes the importance of dispersal, as the LDD case strongly increase colonization rate values (by a factor two) while the SDD case decreases them.

#### Discussion

Numerous biogeographical studies (Kirilenko and Solomon 1998; Malcolm et al. 2002; Heikkinen et al. 2006) have predicted changes in biomes based on infinite or fixed migration capacities for species subjected to climate change. For instance, Kirilenko and Solomon (1998) included, in a niche-based model, migration rates based on paleoecological literature. Instead of considering migration as a fixed, exogenous parameter, we chose to study the effects of key ecological processes on species migration. Brooker et al. (2007) showed in a simple model that a system of two species spatially segregated by their biotic interactions (competition vs. mutualism) exhibits various responses to climate change (i.e., northwards progression, extinction of one or the other species), depending on

dispersal distances and rate of change. Like them, we find that the explicit inclusion of local individual interactions in our model produces outcomes that have not been observed with niche-based models. In particular, we show that variation in dispersal kernel, disturbance regimes, and rate of climatic change can strongly change a population's capacity to track climate change by migrating.

#### Transient mechanisms in FORSITE-DIS

The difference between our first (free progression) and second (competition with the resident species) scenarios, for every parameter setting, shows a strong effect of the presence of a local competitor (here, the Northie population) on the favored species expansion, as the time needed to reach a new equilibrium is almost increased by a factor of 5 (from 400 to 2,000 years). The introduction of a disturbance regime, mimicking the effects of windstorm, changes the fate of the two species; in most cases, it prevents Southie from invading the grid and excluding Northie. Although disturbances have been shown to increase the sensitivity of a community to invasion (i.e., establishment of a new species; Higgins and Richardson 1998; Melbourne et al. 2007), here, we observe the opposite: This is due to the fact that the disturbance simulated here target tall trees. As climate change occurs, it favors growth but also increases the newcomer's sensitivity to disturbance. However, increasing the maximum climatic index alters this result, allowing Southie to expand for all scenarios; this is also true with the introduction of gap formation in the disturbance process. Why does the Southie population overtake the grid when the climatic change is higher, even if windstorm-type disturbance occurs? Two hypotheses can explain this: (1) Northie trees, becoming taller with less climatic change as compared to Southie trees, are also affected by the disturbances and thus allow Southie to expand; (2) Southie growth and fecundity is so advantaged that disturbance regime cannot prevent its population from expanding. The scenario in which disturbance regime affects only Southie allows us to reject the first hypothesis: the result was the same as with the disturbance affecting both species. Consequently, this result emphasizes an interesting trade-off between improvements of life traits and disturbance regimes, both mediated by climate change. A species (here, Southie) disadvantaged by disturbances at a given growth rate can overcome this disadvantage at a higher growth rate (here, driven by the species sensitivity to climate change).

Another surprising result is the weak effect of long dispersal distances on population expansion rate since several studies have shown a role for long-distance dispersal events in determining population expansion rates

(Clark et al. 1998; Higgins and Richardson 1999). Indeed, our simulations revealed a strong effect of dispersal on colonization rate. This result can be explained by the fact that an increase of the frequency of long-distance dispersal events does not change significantly the rate of population growth at a given site (i.e., filling an empty space): one seed dispersed at long distance, if establishment is successful, is enough to create a new settlement of trees as no Allee effects are simulated in the model.

#### Real-world migrations induced by climate change

Predictions about species migrations can be made in several ways. The most extensively used approach is to use niche-based models, which project current species–environment relationships to future (predicted) climatic conditions (Guisan and Thuiller 2005; Guisan et al. 2007). However, as this type of approach does not take into account transient processes, other approaches are necessary to examine the ability of species to actually reach their projected distribution. Several studies have attempted to measure tree ability to migrate, by studying paleoecological data (e.g., Kirilenko and Solomon 1998) or through simulation approaches (e.g., Malanson and Cairns 1997). However, the question of which mechanisms matter and how they can affect tree migration are still worth exploration. In the following, we relate the mechanisms explored in the study to knowledge about ecological dynamics.

#### Competition

The first key element in assessing species expansions is the inclusion of competition between the migrant species and one (or more likely, several) resident species. In FORSITE-DIS, we approach competition simply, as interspecific and intraspecific competitions follow the same rules and are purely asymmetric. Many variations in species interactions might affect the way species will be able to migrate in the presence of a resident. Competition symmetry, for instance, can strongly affect population dynamics (Pacala and Weiner 1991; Caplat et al. 2008) and in consequence may change the shape of communities. Other mechanisms, such as allelopathy (Schenk 2006) or facilitation (Brooker et al. 2008), are likely to limit or increase species abilities to expand their range. Another species trait that might change the outcome of competition between newcomers and residents is the ability to resprout. Indeed, many northern tree species reproduce asexually by layering (e.g., black spruce—Pereg and Payette 1998). Resprouting (layering) confers a competitive advantage as resprouted individuals usually grow taller and stronger than seedlings and may thus outcompete migrating species. Last, but not least, because climate changes gradually, the progression of a



moving climatic front might affect resident species before they are competing with newcomers, affecting the outcome of competition in an unpredictable way.

Some of these mechanisms have been explored in theoretical models, with or without empirical support. We believe that in order to improve our ability to predict ecological consequences of climate change, one needs to fill the gap between exploratory, theoretical models and realistic, field-based ones. Empirical data, coupled with appropriate inverse-modeling methods (Canham and Uriarte 2006), are required to design realistic models; simulation-based models that allow to test for spatial and temporal variability are required to test the consequences of interacting mechanisms. For instance, a number of forestry studies exist that would offer, if compiled, an interesting assessment of the rate of resprouting in forest ecosystems. But in order to make predictions related to climate change, one must have an idea of the consequences of resprouting on population and community dynamics (see Peterson and Squiers 1995 for a study of the consequences of vegetative reproduction on forest dynamics). The same would be true for other key mechanisms like belowground competition or allelopathy. However, some questions point to phenomena that are not yet occurring (e.g., how would [southern] species A grow in the neighborhood of [northern] species B?). For questions like these, data cannot be collected in existing ecosystems and thus require experiments (greenhouse studies and field transplantations).

### Dispersal

Dispersal and particularly long-distance dispersal (LDD) have been highlighted as a key mechanism for species migration in many theoretical and empirical studies for the past 15 years (Clark et al. 1998; Thompson and Katul 2008). We opted for a flexible version of dispersal kernel (the mixed exponential—Greene et al. 2004) that allowed us to test simple assumptions regarding the frequency of LDD events. Other kernels might be worth testing, especially since some specific dispersal strategies can favor species coexistence (Bolker and Pacala 1999) and, thus, facilitate species migration. The colonization rates we found are probably highly dependent on the values we used for the kernel. For instance, another simulation study (Malanson and Cairns 1997) produced migration rate values ranging from 160 to 1,500 m yr<sup>-1</sup>, by using very long dispersal distances (in their dispersal kernel, distances of 5,337 m occurred with a probability of 0.001, while in FORSITE-DIS such a distance would occur with a probability lower than 1e-8). We might have used other values and found results more similar to those of Malanson and Cairns. Again, we fixed some of the parameters in our study for obvious simplicity reasons, our goal being to offer

simple rules for assessing tree migration and not to cover the whole range of variation.

Dispersal interacts also with the spatial heterogeneity of the environment. For instance, it has been often suggested that spatial heterogeneity, through fragmentation of the habitat favorable for establishment, could slow down species spatial progression (Gustafson and Gardner 1996; Malanson and Cairns 1997). Such an effect is highly dependent on the species dispersal kernel (Malanson and Cairns 1997): with very long dispersal distance, potentially any favorable site can be colonized by one or few individuals. The ability to establish, however, depends on population-size dependence relationships and potential Allee effects (Lee and Hastings 2006): it is more likely that an individual would establish, grow, and act as a potential seed source (thus speeding the migration up) if it does not need conspecifics for its survival. Consequently, fragmentation seems more likely to affect migration rates for animal species than for plants, amongst which single seed source can speed up invasions considerably (Buckley et al. 2005; Caplat et al. 2006). However, while it is possible to find parameterization based on field data for many forest model components (see Pacala et al. 1996), parameterization of dispersal mechanisms is not yet fully available for modelers. Only recently, mechanisms of LDD have been modeled in a way that is satisfying for large-scale models (Katul et al. 2005). Thanks to this work and others (Higgins and Richardson 1999; Greene et al. 2004; Debain et al. 2007), we can expect to improve significantly models of tree migration in the future.

### Disturbances

In a “stable” climate, disturbances contribute strongly to shaping communities (Turner 2005). In a changing climate, disturbance regimes will as well constrain a species’ ability to adapt to new conditions. We chose for this study only a limited set of disturbances affecting range expansion, and yet this revealed quite complex interactions. We tested the effects of disturbances killing tall individuals (regardless of the species), with or without creation of gaps. We chose these cases to emphasize the contrasting effect of climate change that favors the newcomer’s growth rate while also increasing its sensitivity to disturbances. Note that we also ran simulations (not shown due to space limitation) in which disturbances targeted the resident species. As can be expected from the theory of biological invasions (Davis et al. 2000), disturbance increased Southie’s expansion rate by decreasing locally the competition with Northie (see also MacDougall et al. 2008). We did not study major disturbances (e.g., large-scale fire or pest outbreak) that were too complex to include in this study, but they are likely to strongly affect ecosystems (or are already doing

so: see Soja et al. 2007 for a review in boreal regions). More generally, real ecosystems will experience a combination of disturbances with various characteristics: target species (particularly when considering pest outbreaks), intensity, frequency, and/or extent (Pham et al. 2004). It would then be interesting to include in the model approaches that account for the variety of processes (see Pagnutti et al. 2007 for a simulation study on gap size distribution). However, disturbances are a difficult component to integrate in models (as experimental data are often lacking), and making headway in this field requires a strong modeling effort. Within one biome (e.g., the boreal forest), disturbance regimes and their impact on species dynamics are diverse; for that reason, it seems necessary to complement general approaches (like ours) with studies that focus and get insights on a specific system. Only with a two-sided approach to the generality–realism tradeoff will modeling improve our predictive ability.

## Conclusions

FORSITE-DIS provides insight into the complexity of ecosystem response to environmental changes. Designed as a model of intermediate level of detail between highly parameterized mechanistic models on the one hand and statistical niche-based models on the other hand, it allows one to test a variety of theories that need to be taken into account to improve understanding and predicting the future of forest ecosystems. FORSITE-DIS measures migration rate as an emerging property of population dynamics instead of an a priori property of the system. As such, it highlights transient mechanisms that affect species' ability to migrate and confirms the need for approaches complementary to niche-based models. It offers the possibility to define general rules of species response to climate change in a variety of situations (e.g., an increase of windthrow frequency limits the northwards expansion of a tall newcomer). Such rules are needed to disentangle the complexity of the ecological dynamics that arise in response to climate change (e.g., dramatic fires, drought-induced tree mortality, upward tree line dynamics; see Soja et al. 2007). In this context, it is complementary to experimental approaches attempting to determine species' fundamental niches by plantation experiments (e.g., Asselin et al. 2003) or highly parameterized process models (e.g., Morin et al. 2007).

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