Landscape Ecol (2008) 23:787–801
DOI 10.1007/s10980-008-9237-4

RESEARCH ARTICLE

Spatial spread of an alien tree species in a heterogeneous forest landscape: a spatially realistic simulation model

Emmanuelle Sebert-Cuvillier · Valérie Simon-Goyheneche · Frédéric Paccaut · Olivier Chabrerie · Olivier Goubet · Guillaume Decocq

Received: 4 May 2007 / Accepted: 6 June 2008 / Published online: 27 June 2008

Abstract The effect of environmental heterogeneity on spatial spread of invasive species has received little attention in the literature. Altering landscape heterogeneity may be a suitable strategy to control invaders in man-made landscapes. We use a population-based, spatially realistic matrix model to explore mechanisms underlying the observed invasion patterns of an alien tree species, *Prunus serotina* Ehrh., in a heterogeneous managed forest. By altering several parameters in the simulation, we test for various hypotheses regarding the role of several mechanisms on invasion dynamics, including spatial heterogeneity, seed dispersers, site of first introduction, large-scale natural disturbances, and forest management. We observe that landscape heterogeneity makes the invasion highly directional resulting from two mechanisms: (1) irregular jumps, which occur rarely via long-distance dispersers and create new founder populations in distant suitable areas, and (2) regular, continuous diffusion toward adjacent cells via short- and mid-distance vectors. At the landscape scale, spatial heterogeneity increases the invasion speed but decreases the final invasion extent. Hence, natural disturbances (such as severe storms) appear to facilitate invasion spread, while forest management can have contrasting effects such as decreasing invasibility at the stand scale by increasing the proportion of light interception at the canopy level. The site of initial introduction influences the invasion process but without altering the final outcome. Our model represents the real landscape and incorporates the range of dispersal modes, making it a powerful tool to explore the interactions between environmental heterogeneity and invasion dynamics, as well as for managing plant invaders.

Keywords Compiègne forest (France) · Connectivity · Disturbance · Environmental heterogeneity · Forest management · Invasibility · Long-distance dispersal · *Prunus serotina* · Population-based matrix model · Resource availability

Introduction

Biological invasions have become a primary concern for conservation biologists and land managers

---

Electronic supplementary material The online version of this article (doi:10.1007/s10980-008-9237-4) contains supplementary material, which is available to authorized users.

E. Sebert-Cuvillier · V. Simon-Goyheneche ·
O. Chabrerie · G. Decocq (✉)
Dynamiques des Systèmes Anthropisés, Université de
Picardie Jules Verne, 1 rue des Louvels,
Amiens Cedex 80037, France
e-mail: guillaume.decocq@u-picardie.fr

E. Sebert-Cuvillier · V. Simon-Goyheneche ·
F. Paccaut · O. Goubet
Laboratoire Amiénois de Mathématiques Fondamentales
et Appliquées (UMR 6140 CNRS), Université de Picardie
Jules Verne, 33 rue Saint Leu, Amiens Cedex 80039,
France

because of their deleterious ecological consequences (Lodge 1993; Williamson 1999) and large costs to society (Pimentel et al. 2000), Developing effective strategies for invasion management requires an ability to predict the rate and pattern with which an invasive species will spread (Higgins et al. 2000). Mathematical models are flexible tools allowing the study of both current and potential invasive species over a wide range of environmental conditions (Higgins and Richardson 1996). Hypotheses about key processes or abiotic factors affecting invasion can be tested and the consequences of different management strategies can be explored prior to expensive and time-consuming field tests (Buckley et al. 2003).

Invasion depends on a sequence of complex interactions between an invader and the recipient ecosystem (Richardson and Pyšek 2006). Habitat quality, including both abiotic (e.g., soil properties) and biotic (e.g., the resident plant community) factors, as well as resource availability are key components to explain ecosystem invasibility. These interactions fluctuate over time, especially in response to disturbances that temporarily release both space and resources ('window concept' sensu Johnstone 1986; Davis et al. 2000). For management purposes, it is easier to act on invasibility than on invasiveness.

Invasibility also depends on spatial heterogeneity, particularly at large spatial scales (Davies et al. 2005). This has recently led to the environmental heterogeneity hypothesis (EHH), which postulates that spatio-temporal heterogeneity both increases invasion success and reduces the impact to native species (Melbourne et al. 2007). Compared to homogeneous environments where invaders would need to be superior competitors to establish by displacing natives, heterogeneous environments would provide more niche opportunities for invaders, promoting both establishment and species coexistence.

Thus, assessing plant invasions inherently involves a landscape perspective (With 2002) and models should integrate environmental heterogeneity. Classical diffusion or integro-difference equation models are not appropriate because often they are spatially implicit (e.g., they track percentage of habitat invaded rather than spatial locations invaded). Even if they can also be spatially explicit, they generally consider space to be homogeneous (e.g., they deal with mean-field approximations instead of the spatial structure of real landscapes, assuming that spatial correlations play an insignificant role) (Hanski 1999). Such models are limited but have led to important insights, especially regarding the spread rate of various species (Shigesada and Kawasaki 1997), the importance of dispersal mechanisms (Neubert et al. 2000) and the role of propagule pressure, immigration rate and Allee effect (Drake and Lodge 2006). Alternatively, spatially explicit, individual-based models include detailed information about individual fecundity, dispersal, and landscape structure (Pulliam and Dunning 1995; Hanski 1999; Westerberg and Wennergren 2003). A population-based model is more appropriate for abundant organisms such as invasive plants, (Cannas et al. 2003; Sebert-Cuvillier et al. 2007). Such models can also incorporate invasion history (i.e., previous recipient ecosystem and invader distributions), as well as landscape composition (percent of suitable habitat) and configuration (habitat fragmentation), which have been shown to act as key controls on the invasion spread at a landscape scale (Chabrerie et al. 2007b). These advantages are also drawbacks, since these models are species-specific (Hastings et al. 2005) and the data needed to parameterize the model may be difficult to attain.

Here, we use a spatially explicit ('spatially realistic' *sensu* Hanski 1999; see also Westerberg and Wennergren 2003; Westerberg et al. 2005), population-based, density-independent matrix model to simulate the invasive spread of an alien tree species throughout a man-made, heterogeneous forest landscape. We focus on the American black cherry (*Prunus serotina* Ehrh.), which is currently the most problematic invader in European temperate forests (Chabrerie et al. 2007a; Verheyen et al. 2007). We use a lognormal kernel to reproduce seed dispersal, and the real landscape is transformed into a lattice of cells, each associated with an invasibility index. We address the following research questions:

1. When dispersion is incorporated as a nondirectional process, does landscape heterogeneity explain the invasion patterns?
2. What are the relative importances of local (common) and long-distance (rare) dispersal events for black cherry?
3. How much does the site of initial introduction influence the invasion outcome?

4. Do historical episodes of large-scale natural disturbances increase invasion rates for this gap-dependent species?
5. How would different management scenarios have influenced current distributions of black cherry?

Methods

Case study and study area

The American black cherry is a gap-dependent tree species native to North America that was introduced into many European forests for ornamental, timber production, and soil amelioration purposes (Starfinger 1997). For at least three decades it has been spreading throughout temperate forests of Western and Central Europe, particularly on well-drained, nutrient-poor soils (Starfinger 1997; Chabrerie et al. 2007a; Verheyen et al. 2007; Chabrerie et al. 2008). Its population dynamics have been studied in detail in the study area (Closset-Kopp et al. 2007). *P. serotina* seeds are able to enter closed-canopy forests to form a long-living sapling bank ('Oskar syndrome': no height growth, diameter increment <0.06 mm.yr^{-1}, longevity > several decades). When a canopy gap occurs, saplings are released from suppression and grow rapidly (>56 cm.yr^{-1}) to reach the canopy and fill in the gap. In clearcuts and large gaps *P. serotina* often forms a low, closed carpet of small trees, which impedes natural regeneration (Starfinger 1991; Chabrerie et al. 2007a).

After establishment, *P. serotina* can persist locally by resprouting from roots and stumps. Individuals become fertile at the age of 8 years on average and produce numerous seeds (6,011 per tree on average), of which 42% are able to germinate (Closset-Kopp et al. 2007). Several studies have shown that *ca.* 95% of the seeds are dispersed by gravity or after local regurgitation by birds in a radius of 5 m around the parent tree (Starfinger 1997; Deckers et al. 2005; Pairon et al. 2006). For the remainder (*ca.* 5%), long-distance dispersal events are likely to occur, via birds and mammals (especially foxes in the study area). The mean dispersal distances are 100 m for birds and 918 m for foxes.

To develop a 'spatially realistic' model that can be used to study existing populations in real landscapes, we collected data in the forest of Compiègne, located in northern France (49°22′N; 2°54′E; 32–148 m altitude). Compiègne forest contains a wide range of habitat conditions and is currently the most heavily invaded by *P. serotina* in France. It is also representative of ecosystems that are likely to be invaded by *P. serotina* in temperate Europe. This is a mixed forest covering 14,417 ha (Fig. 1), which is currently managed as even-aged plantations of common beech (*Fagus sylvatica*), oaks (*Quercus robur, Q. petraea*) and Scots pine (*Pinus sylvestris*). The clearcut-return interval for the forest is 180 yr for *Q. robur* and *Q. petraea*, 110 yr for *F. sylvatica* and 100 yr for *P. sylvestris*. During this time interval, thinnings are conducted every 4–10 years. Natural disturbances mainly consist of windthrows. In the past 30 years, two strong storms affected the Compiègne forest, in 1984 (364 m^3.ha^{-1}, i.e., 129,075 trunks over 933 ha) and in 1990 (227 m^3.ha^{-1}, i.e., 134,451 trunks over 1,199 ha), which are thought to have promoted *P. serotina* invasion.

P. serotina was probably introduced to the Compiègne forest around 1850 ($t = 0$ in the simulations hereafter) from a nearby pheasantry ('La Faisanderie', corresponding to cell $i = 388$ in Fig. 1). Other potential locations for the first introduction (Gardens of a neighbouring castle: $i = 178$, and 'Les Beaux Monts': $i = 228$), as well as a possible second introduction in the 1950s (at 'La Muette': $i = 639$) have been questioned.

The model

Using Geographic Information System (GIS) technology, we first superimpose a lattice of 500 × 500 m cells over the forest map. This generates a grid of 41 × 29 cells, numbered consecutively from 1 (top, left corner) to 1,189 (bottom, right corner), among which 696 and 493 correspond to forest and non-forest cells, respectively. Each forest cell i thus consists of a patch mosaic (PM) to which we assign an invasibility index $c(i)$, ranging from 0 (resistant to invasion whatever the diaspore pressure) to 2 (would be invaded with certainty if the invader disperses into it). The invasibility index is computed following the method by Chabrerie et al. (2007b). Cells (i.e., PMs) are first characterized on the basis of their habitat (i.e., patch) composition. Correlations between *P. serotina*

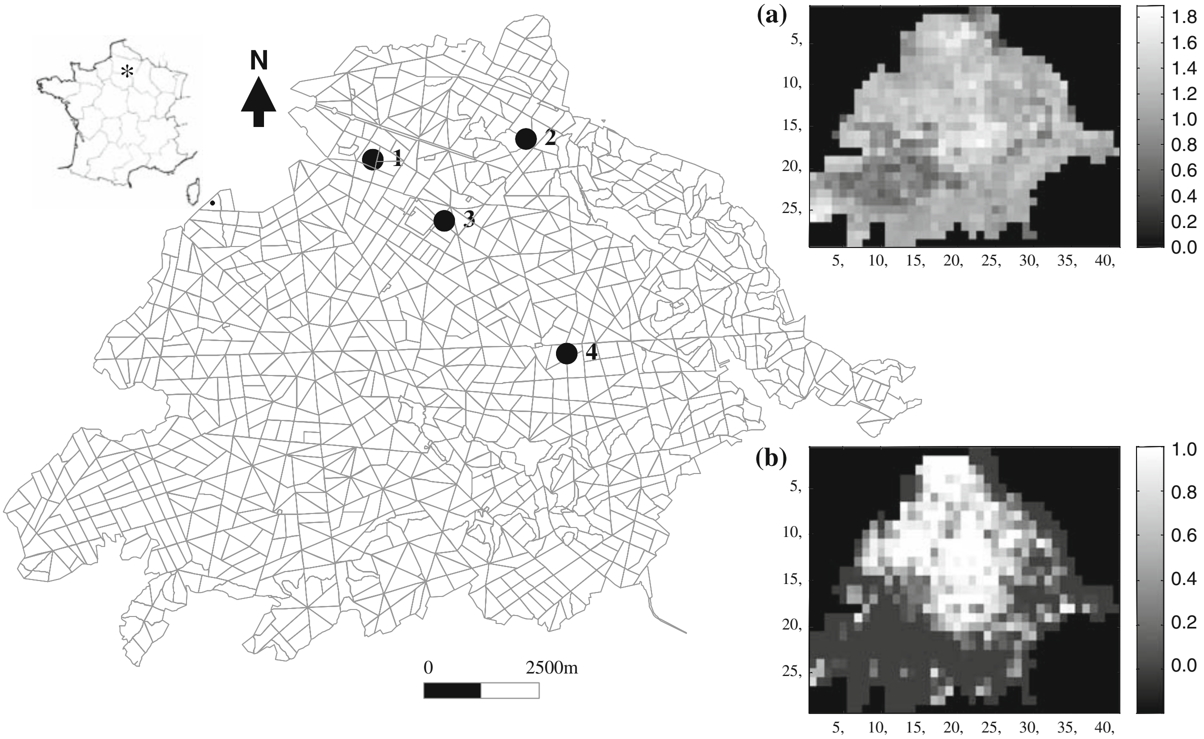


Fig. 1 The Compiègne forest and its conversion into an invasibility map (**a**), to be compared with the current invasion state (**b**). Numbered locations indicate the sites of introduction used for simulations (1: edge of the castle gardens, i = 178; 2: 'Les Beaux Monts', i = 228; 3: 'La Faisanderie', i = 388; 4: 'La Muette', i = 639). The scale on the right of the maps indicates (**a**) the invasibility index or (**b**) the proportion of a cell which is currently invaded; non forest cells are in black

abundance and habitat factors (e.g., soil type, soil moisture, dominant tree species) are then extracted from a Principal component analysis to define habitat invasibility indices, and a weighted, averaged invasibility index is finally derived for each PM. The 1189 invasibility indices defined a vector c, referred as the 'invasibility vector'.

Secondly, we incorporate seed dispersal using a dispersal kernel. We consider three types of dispersal: short-distance dispersal resulting from gravity and local regurgitation (corresponding to seeds staying inside the same cell as the mother tree), mid-distance dispersal (corresponding to birds exporting seeds in the 8 cells that are contiguous to a given cell) and long-distance dispersal (corresponding to mammals, especially foxes, transporting seeds into cells that are distant from a given cell), that amounts respectively to 98% (including the 95% dispersed within 5 m around the mother tree, and 3 of the 5% that are dispersed beyond 5 m but stay in the same cell), 1.5% and 0.5% of the total dispersal. These odds were obtained from field measures. Mid- and long-distance dispersals are described by two lognormal functions. The long-distance dispersal, although typically rare, is crucial to population spread (Kot et al. 1996; Clark et al. 1998; Trakhtenbrot et al. 2005). A complete dispersal matrix M is derived, describing all possible transitions between the cells.

The probability for a given cell to be invaded is then determined by a suitable nonlinear Markov chain using the dispersal matrix M. Hence, the model is deterministic and runs on an 8 yr time-step to match the average time lag between the release of saplings from suppression and the first seed production. At each time step t, the vector $X^t = (X_i^t)$ contains the probability for the forest to be invaded. For each cell i ($i = 1 \ldots 1189$), X_i^t gives the probability for cell i to be invaded at time t. Instead of computing the risk of invasion by a classical linear Markov chain as $X^{t+1} = M \cdot X^t$, we add two extra steps, the first one taking into account the invasibility index of the cell, the second one describing that, once a cell is invaded with probability 1, it remains as such until the end of the simulation run. This reads, for each entry:

$$\text{If } X_i^t = 1 \text{ then } X_i^{t+1} = 1, \text{ else}$$
$$X_i^{t+1} = \min\left(1, c(i)(M \cdot X^t)_i\right)$$

Note that, although $c(i)$ ranges from 0 to 2, X_i^{t+1} does vary between 0 and 1 as we take the minimum between 1 and $c(i)(M \cdot X^t)_i$. Therefore, the numbers X_i^t may be viewed as probabilities.

The model also accounts for historical large-scale natural disturbances. To incorporate the effects of the two severe storms of 1984 and 1990 (see study area description), we assign to each cell i and for each storm event ($t = 16, 17$) a disturbance coefficient d_i^t, which equals the proportion of the cell area disturbed by storm. The disturbance vector d^t is included into the establishment phase; hence, in the equation above, at $t = 16$ and $t = 17$, $c(i)$ is replaced by $c(i)(1 + d_i^t)$.

The validation of the model was done by comparing the predicted distribution maps (i.e., presence/absence binary maps) of *P. serotina* in the Compiègne forest with the actual distribution (Fig. 1b), after having introduced the invader in cell $i = 388$ at $t = 0$ (i.e., 'La Faisanderie' in 1850) and run the model for 19 iterations (152 years). Goodness-of-fit measures gave the best results for the maps considering 'presence' and 'absence' for output probabilities to be invaded $P = 1$ and $P \neq 1$, respectively. We found an overall agreement of 81% (i.e., 81% of the 696 forest cells were correctly predicted for presence/absence by the model), with a Kappa statistic (overall agreement corrected by chance) of 62% and a proportion of agreement due to location of 74%. The underestimation error (i.e., the percent of invaded cells which were not predicted as such) reached 13%.

Full information about the model, invasibility indices, dispersal kernel, and model validation is given in Appendix S1.

Simulations and data analysis

All simulations use MATLAB® software. Hereafter, i_k refers to a cell where *P. serotina* is introduced at the kth iteration; hence i_0 is the cell of first introduction at $t = 0$ (calendar year 1850). To visualize the results, we extract maps of the forest at different times k of the simulation run and plot the probability X_i^t for invasion for each cell i. We also plot the three following quantitative measures against time:

(1) Propagation distance P_t, i.e., the Euclidian distance between i_0 and the furthest cell from i_0 which is invaded with probability 1. For $t = 0$, $P_t = 0$;

(2) Invasion speed D_t, i.e., the maximal distance covered at each time step. It is defined as:

$$D_t = P_t - P_{t-1}$$
$$D_0 = 0$$

The invasion speed is expressed in grid unit per time unit but can easily be converted in m.yr^{-1} by the operation $500{*}D_t/8$.

(3) Invasion extent, i.e., the percentage of the 696 forest cells that are invaded with probability 1 at time t.

Influence of spatial heterogeneity

To evaluate the influence of forest landscape composition and configuration on the invasion process, we introduce *P. serotina* at 'La Faisanderie' ($i_0 = 388$) and run the model for 19 iterations (corresponding to the 1850–2002 interval, i.e., 152 years). Then, to predict the future spread of *P. serotina* in Compiègne forest for the next 152 years (to year 2154), we continue simulations for 19 time units. To better analyze the influence of landscape heterogeneity and $c(i)$ values on the invasion dynamics, we compare the results to those obtained with a 'mean field model', where a same $c(i)$ value equalling 1.16 (corresponding to the average value of the 696 forest cells) is attributed to all forest cells (see Appendix S1 for further details about the mean field model).

Respective importance of seed-dispersers

To assess the relative importance of birds and foxes in the invasion pattern, simulations are performed separately without foxes and without birds, starting from 'La Faisanderie' ($i_0 = 388$) and running 19 iterations.

Influence of the site of first introduction

To test whether different scenarios of introduction would result in different outcomes, we run four simulations over the 1850–2002 period (19 iterations) with exactly the same set of parameters except for the cell of introduction. Alternative introductions were i_0 = 228 ('Les Beaux Monts'), $i_0 = 178$ (edge of the castle gardens), i_0 = 388 ('La Faisanderie'), and i_0 = 178 followed by $i_{12} = 639$ (i.e., first introduction in 1850 at the edge of the castle gardens followed by a second one in 1950 at 'La Muette'; see Fig. 1).

Importance of large-scale natural disturbances

We run the same set of simulations as above but exclude natural disturbances (by deleting Eq. 11 in the computation, see Appendix S1) to account for the influence of storm-induced natural tree falls on *P. serotina* spread.

Influence of forest management

We are studying the invasion process in a man-made forest landscape, therefore we test different management options that might have changed the current situation. *P. serotina* is introduced in cell i_0 = 388. At the 19th iteration, we compare output maps, propagation distance, invasion speed, and invasion extent with those obtained in the absence of two common management options:

(1) replacing the actual dominant canopy tree species by another one, by introducing virtual invasibility indices that were obtained by replacing the real partial index for land cover by the one associated with the dominant tree species for each cell i. We first simulate *P. serotina* spread in a forest landscape entirely dominated by one of the three main commercial species in northern France, Scots pine, common beech, and oak. The virtual coefficients are then applied to the whole forest. Common beech is expected to be the strongest competitor against *P. serotina*, therefore we analyse the influence of a virtual 3,500 m-wide pure beech plantation, crossing the forest along an east-west band. In the latter case, the virtual coefficients were applied only to the 171 cells corresponding to the E-W band (i.e., all cells from row 8 to 14).

(2) early eradication of all *P. serotina* individuals that were present on the leading edge of the invasion wave, by fixing the probability of all cells of the lines 15, 16 and 17 equal to 0 at the 8th iteration (corresponding to the year 1914). At that time, none of the cells located to the south of this band were invaded with a probability greater than 0.1.

Results

Influence of spatial heterogeneity

Seventy-two years after the first introduction at 'La Faisanderie' ($i_0 = 388$), only a few neighbouring cells around i_0 are likely to be invaded (Fig. 2a); a compact zone with a rough border composed of cells with a high probability of being invaded has developed toward both the north and the south-east of i_0. The invader has progressed toward the south along the narrow corridor of moderately invasible cells to reach the second most invasible zone (see Fig. 1a). Conversely, the cells exhibiting a low invasibility index at the west of i_0 remain uninvaded. After 96 years, the first two most invasible parts of the forest, at the north-west and the centre, are invaded with probability 1 (Fig. 2b). These core zones are surrounded by cells showing a lower probability of invasion. This probability of invasion progressively decreases from the centre to the edge of the core zone. After 152 years, the invader has dispersed everywhere (i.e., all cells have received seeds) and more than half of the forest is invaded with probability 1 (Fig. 2c). The third most vulnerable zone, in the far south-west, is colonized by *P. serotina* but remains disconnected from the already heavily invaded parts of the forest. The large resistant area composed of cells with a low invasibility index remains uncolonized.

Simulations over the 2002–2154 period show that the invasion has not yet reached a steady state (Fig. 2d). The future spread of *P. serotina* will mainly affect the southern and eastern margins of the forest. Only the area of hydromorphic soils of the south-east will remain relatively safe while being surrounded by invaded cells.

The invasive spread only starts 80 years after the first introduction (10th iteration), with a sudden increase of propagation distance corresponding to a first peak of invasion speed (Fig. 2e). The

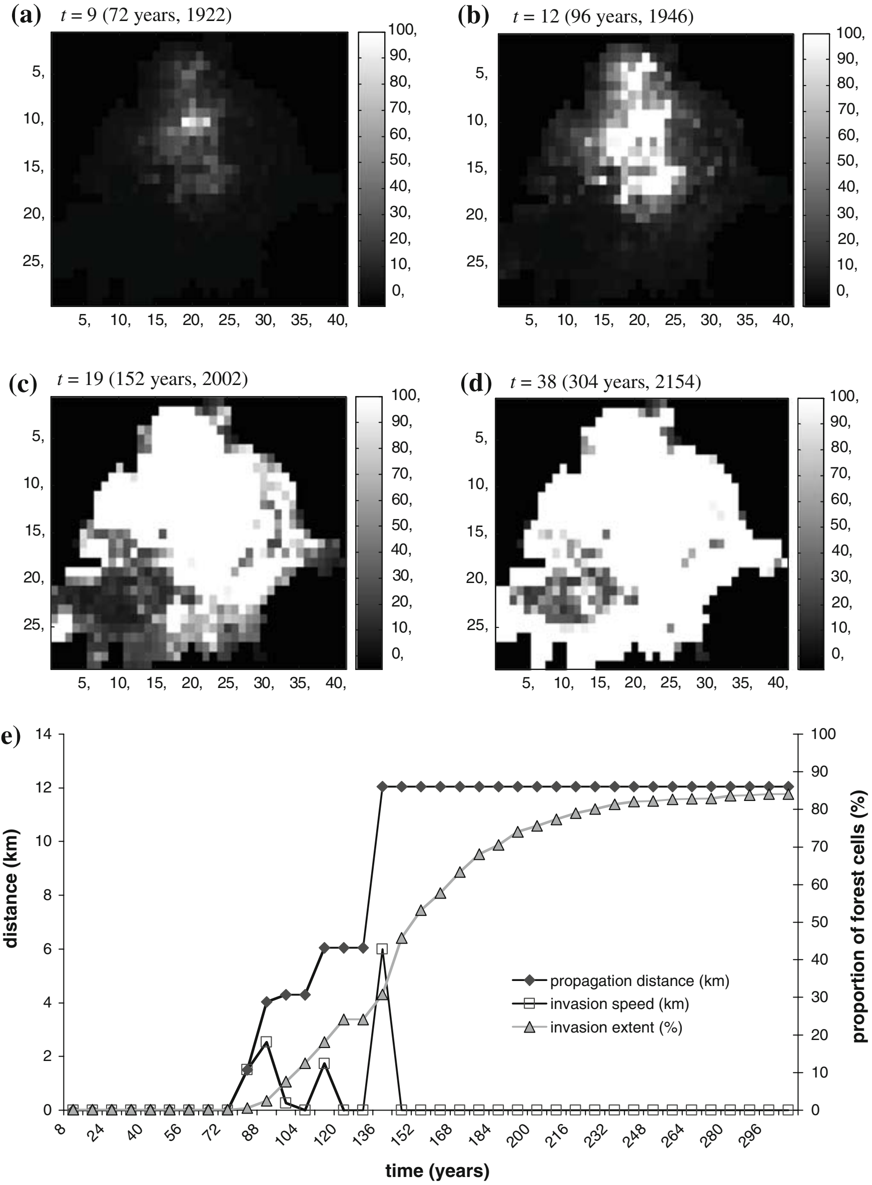


Fig. 2 Spatial spread of *Prunus serotina* in the Compiègne forest following its introduction at 'La Faisanderie' (i_0 = 388) at t = 0 (= year 1850). (**a**)–(**d**), distribution maps extracted at different times t of the simulation run (one time unit = 8 years). The scale on the right of each map gives the risk for a cell to be invaded (in %). (**e**), Quantitative descriptors of the invasion plotted against time: cumulative distance (propagation distance), maximal distance per time unit (invasion speed) and proportion of invaded cells (invasion extent)

propagation distance increases stepwise until 136 years, which corresponds to the main peak of invasion speed (12 grid units in 8 years or 750 m.yr^{-1}). After 136 years the propagation distance becomes constant and the invasion speed is null, indicating that the furthest cells from i_0 are reached. The invasion extent increases linearly from the 80th to the 200th year, with an average of 5% of the cells invaded at each time step (4.3 cells.yr^{-1}). This indicates a regular diffusion from the core invaded zones towards neighbouring cells. After 208 years, an asymptote is reached at 83% and the invasion pattern is stable in both space and time until the end of the simulation run.

Respective importance of seed-dispersers

The invasion extent does not vary until the 128th year for simulations omitting long-distance dispersal by foxes. A sudden increase in invasion extent occurs after the 128th year (instead of the 72nd year with foxes), suggesting that the invader has reached a more vulnerable zone. After 152 years, only 0.43% of the cells are invaded with probability 1 (instead of 43% with foxes), mainly towards the south-east of i_0. In contrast, when mid-distance dispersion is neglected by omitting birds, the distribution map does not differ from the one obtained with the full model (see Fig. 2c).

Influence of the site of first introduction

Invasion spatial patterns (Fig. 3), propagation distance, invasion speed and invasion extent (Fig. 4) clearly depend on the site of initial introduction. For example, for a first introduction at the edge of the castle gardens ($i_0 = 178$) and at 'Les Beaux Monts' ($i_0 = 228$), the maximal invasion speed is 563 and 969 $\mathrm{m.yr^{-1}}$ respectively. After 152 years, the invasion extent is the highest when *P. serotina* has been first introduced at 'La Faisanderie' (*ca.* 53%). A second introduction at 'La Muette' ($i_{12} = 639$), does not change the outcome of a single introduction one hundred years prior at the edge of the castle gardens ($i_0 = 178$), because *P. serotina* has already reached this part of the forest by the 96th year.

Whatever the site first introduction, propagation distance starts to increase only between the 72nd and the 80th year (Fig. 4a). Then, it increases stepwise rather than linearly, explaining why invasion speed shows several peaks (Fig. 4b). Conversely, invasion extent increases more regularly (Fig. 4c).

Importance of large-scale natural disturbances

Large-scale disturbances clearly lead to higher probabilities of invasion for a number of cells located along the south-eastern and eastern forest edges (Fig. 5). Propagation distance and speed also increase earlier, i.e., at the 16th instead of the 17th iteration, and the final invasion extent is higher (53% vs. 50%) when past storms are included.

Influence of forest management

A forest dominated by Scots pines facilitates invasion (Fig. 6a). The forest is almost entirely invaded at the end of the simulation run, with a regular invasion speed averaging 187 $\mathrm{m.yr^{-1}}$ between the 64th and the 104th year, after which the maximal propagation distance is reached (Fig. 7). Conversely, a beech-dominated forest strongly inhibits invasion (Fig. 6b). The propagation distance starts to increase only at the 112th year, to reach 5,000 m after 152 years, when

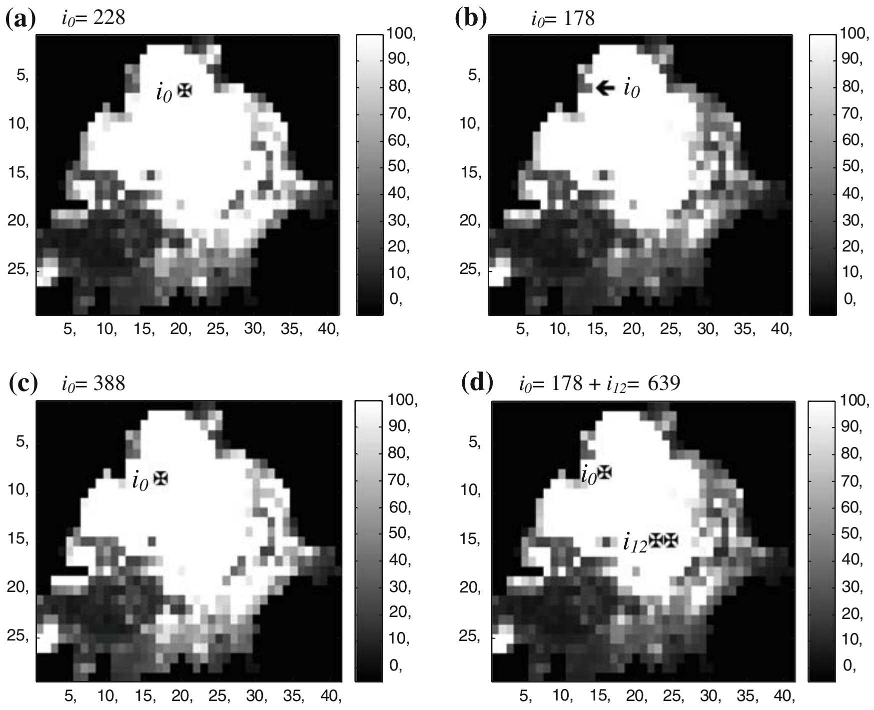


Fig. 3 Invasion pattern at the 19th iteration (152 years = calendar year 2002) when *Prunus serotina* is first introduced in 1850 at (**a**) 'Les Beaux Monts', (**b**) the edge of the castle gardens, (**c**) 'La Faisanderie' and (**d**) both the edge of the castle gardens and 'La Muette' 100 years later. The scale on the right of each map gives the risk for a cell to be invaded (in %)

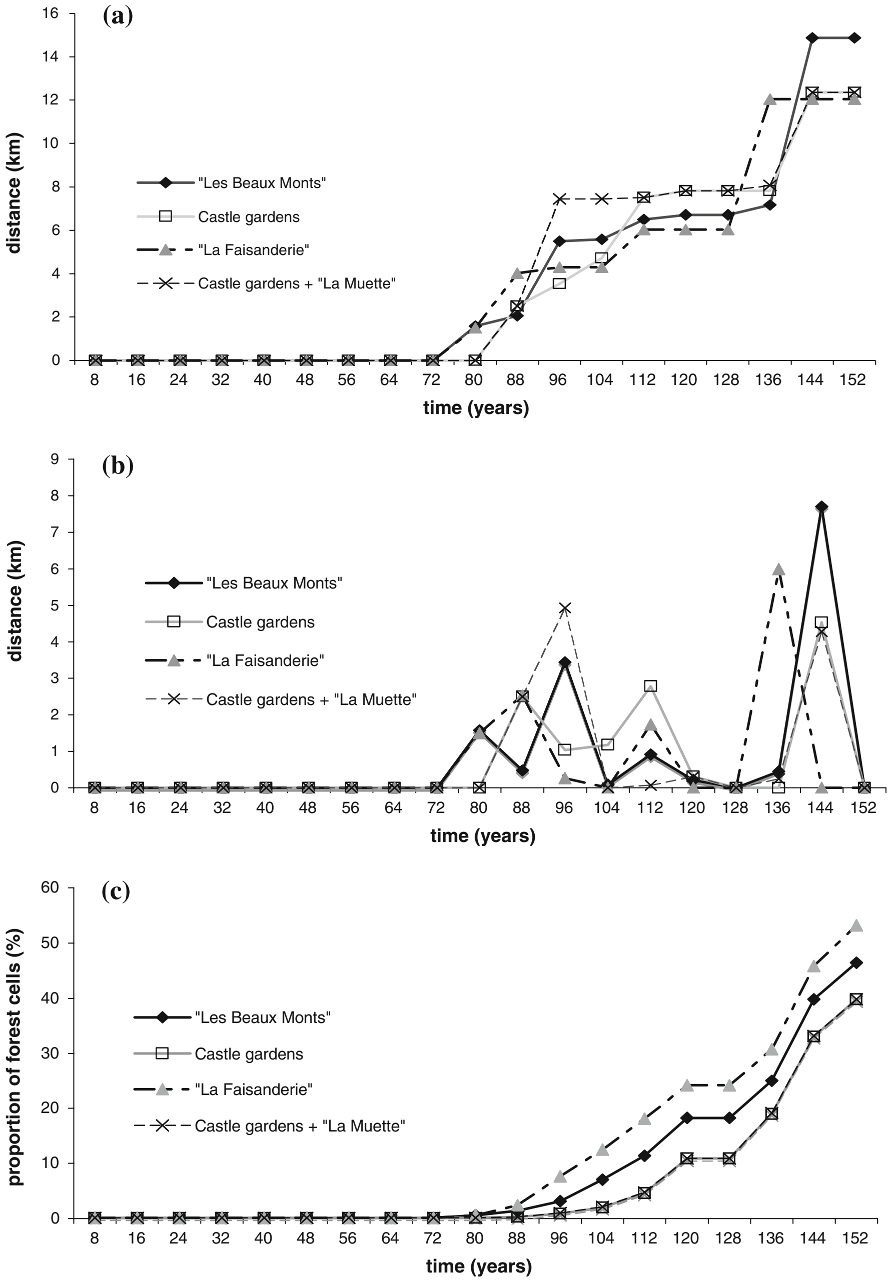


Fig. 4 Comparison of (**a**) propagation distance, (**b**) invasion speed and (**c**) invasion extent, plotted against time for the four scenarios of introduction (see also Fig. 3)

only 20% of the cells are invaded (Fig. 7). Even when beech is restricted to an E-W band across the real forest landscape (Fig. 6d), it significantly reduces the invasion extent (35% instead of 50%), making the spatial spread one time unit (i.e., 8 years) slow. An oak-dominated canopy exhibits intermediate patterns (Fig. 6c), with 65% of the cells invaded after 152 years. Except for beech, the forest dominated by a single tree species is predicted to be more heavily invaded than the real heterogeneous forest landscape.

The eradication of all adult *P. serotina* present on the leading edge at the 64th year significantly slows down the invasion, with the extent reaching 38% instead of 50% after 152 years (results not shown). Again, the spatial spread is only one time unit slow.

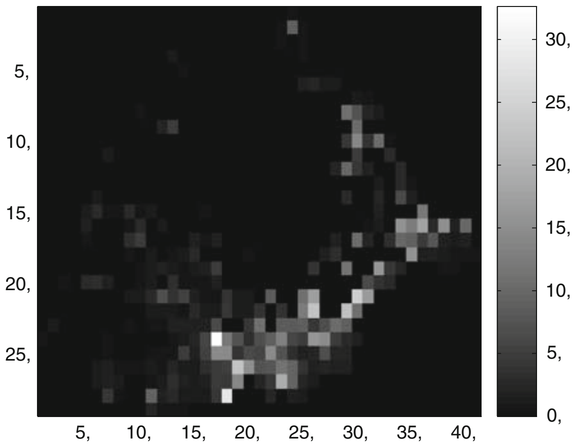


Fig. 5 Map obtained by subtracting the output map neglecting the two storm events from the output map including them (see Fig. 3c); i_0 = 388, 19 iterations. The scale on the right gives the risk for a cell to be invaded (in %)

Discussion

The invader-vectors-landscape interplay

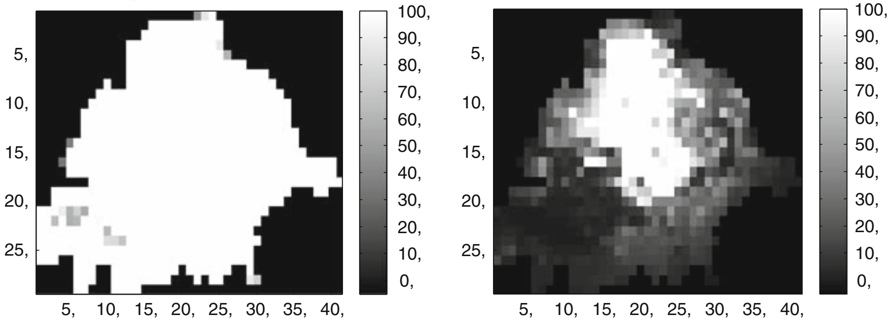
Our model allows the exploration of the whole gradient of invasibility by *Prunus serotina.* Rather than being limited to describing individual effects of landscape variables on invasibility, our model includes the interactions between spatial spread of an invasive species and both landscape composition and configuration.

We found a maximum invasion rate of 750 m.yr^{-1} in the real landscape, which is much faster than the 375 m.yr^{-1} found with the mean field model (i.e., homogeneous landscape in which the same invasibility index was attributed to all cells; see Appendix S1, Figs S4 and S5). However, the final invasion extent was lower (83 vs. 100%). These results are not fully consistent with the predictions of the EHH that environmental heterogeneity increases invasibility (Melbourne et al. 2007). Our results suggest that real landscapes experience faster invasions that cover less area as compared to homogeneous environments, especially when the species is initially introduced close to an area of high invisibility, as in our case study. Further theoretical work is needed to generalize this result and obtain more insight for the complex relationships between landscape heterogeneity and invasibility.

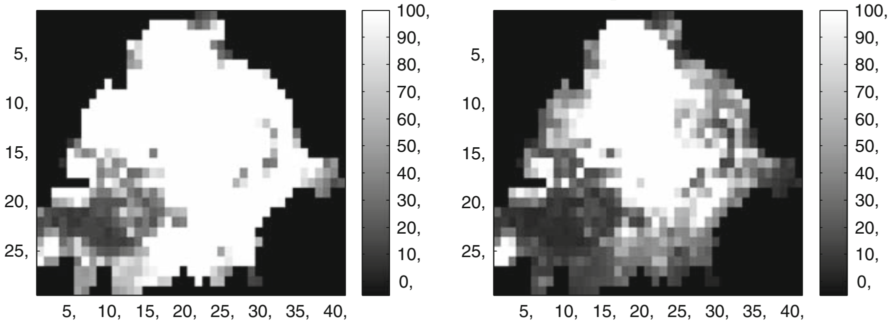
The invasion speed varied among directions, revealing a highly directional process. Propagation

Fig. 6 Simulated invasion patterns after 152 years (19 iterations) when the forest matrix is (**a**) a pure Scots pine plantation, (**b**) a pure common beech plantation, (**c**) a pure oak plantation, and (**d**) the real landscape crossed by a 3,500 m-wide pure beech plantation (i.e., all cells from row 8 to 14). The scale on the right of each map gives the risk for a cell to be invaded (in %)

(a) Scots pine **(b)** Common beech



(c) Oak **(d)** E-W strip of beech



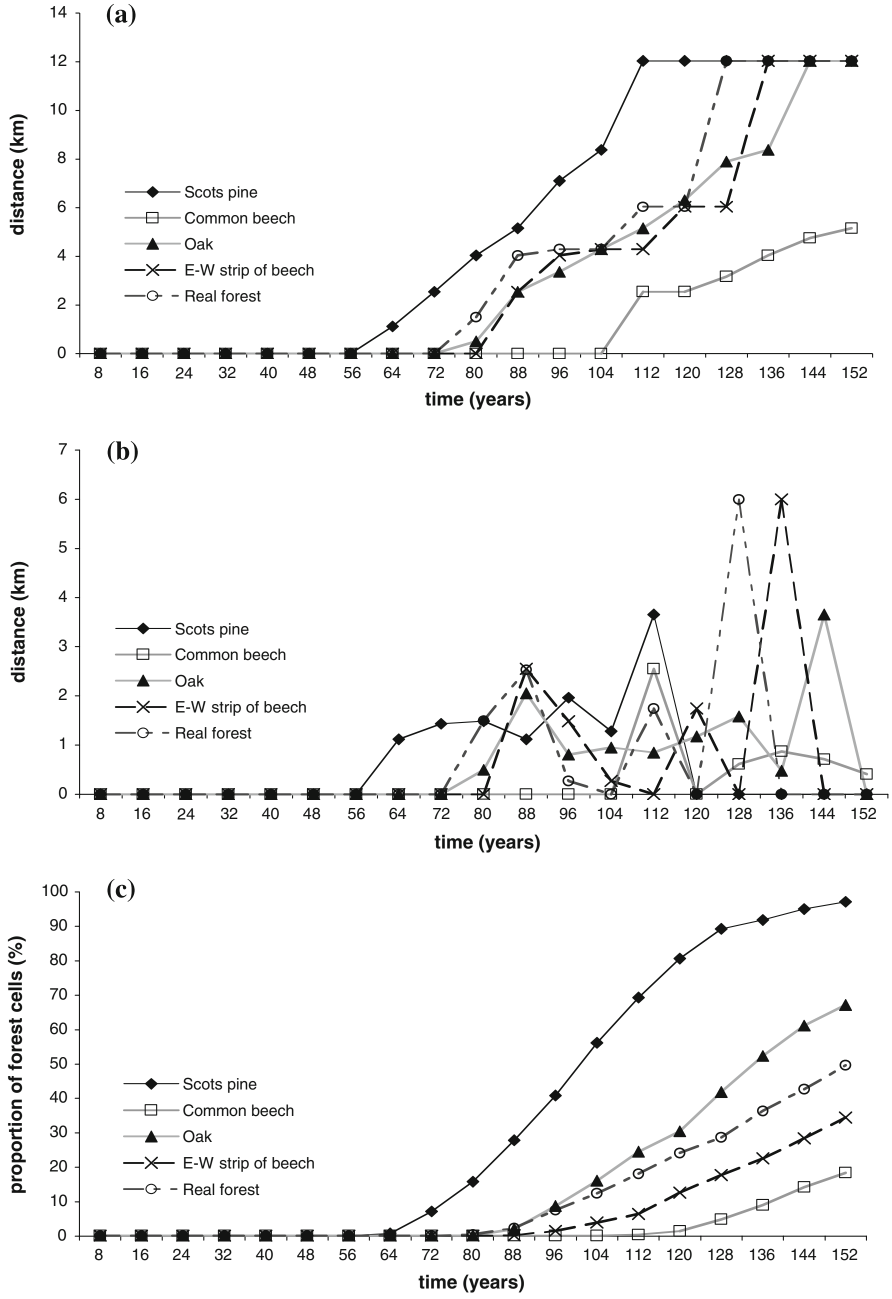


Fig. 7 Propagation distance (**a**), invasion speed (**b**) and invasion extent (**c**) of *Prunus serotina* throughout the real and virtual forest landscapes (see also Fig. 6)

distance increased irregularly through a process of sudden increases in invasion speed alternating with periods of stasis. This indicates that connectivity (i.e., the degree to which the landscape facilitates or impedes movement of the organisms among resource patches, Tischendorf and Fahrig 2000) between invasible cells controls both invasion speed and direction. Those depend not only on the distance between suitable habitats, but also on the presence of corridors and stepping stones (Fahrig and Merriam 1994). For example, once the invasion had started from 'Les Beaux Monts' ($i_0 = 228$), it took only 16 years for the invader to reach the central vulnerable zone from the northern one, both being linked by a corridor (*ca.* 315 m.yr^{-1}), while it took 48 years to reach the south-western vulnerable zone from the central one, both being separated by an area of resistant cells (*ca*. 260 $\mathrm{m.yr}^{-1}$).

Simulations omitting recent storm events show that large-scale disturbances increase invasion rates in parts of the forest that were previously at low risk of invasion. Disturbance has often been reported to enhance invasibility by increasing heterogeneity and resource availability, thus providing a number of regeneration niches for a range of species (Johnstone 1986; Davis et al. 2000; Melbourne et al. 2007). This is particularly true for the gap-dependent *P. serotina* whose saplings require light penetration in the understory to be released from suppression. Our results also demonstrate that environmental factors interact with disturbance events, as previously suggested by Higgins and Richardson (1998). Environment type can locally increase or override the effect of large-scale disturbances on invasion events, altering their direction and speed.

Invasion differed in rate and spatial patterns according to the site of first introduction, but tended to converge towards the same 'final' spatial pattern where all suitable areas are invaded. The propagation distance became constant after 144 years, indicating that the species had time to invade the whole forest and the origin of invasion is irrelevant beyond this time. In other words, the invader's realized distribution matches the potential range (Wilson et al. 2007). The differing rates of invasion indicate that environmental managers will be given more or less time to implement effective control operations depending on the site of initial establishment.

Introducing *P. serotina* in a distant place one century after the first introduction did not influence the invasion process. This suggests that the impact of repeated introductions in a heterogeneous landscape depends on both the time elapsed since earlier establishments ('residence time') and their position in relation with already established populations ('range size'; Wilson et al. 2007). At a landscape scale, propagule pressure becomes less crucial to invasion as the residence time and/or the range size are increasing.

Although invasion speed was very irregular, invasion extent experienced a linear increase, indicating a regular diffusion phenomenon from invaded cells to their formerly uninvaded neighbours. Simulations conducted by separating short- and mid-distance dispersers (gravity and birds) from long-distance dispersers (foxes) confirm these assumptions. The mass action of local dispersal maintains high propagule pressure on neighbouring cells, increasing the chance for the invader to successfully establish in cells with low invasibility indices (Snyder and Chesson 2003; Lockwood et al. 2005; Wilson et al. 2007). Each cell contains a mosaic of patch types and mass dispersion allows the invader to locate a suitable patch from which it can colonize the entire cell. This explains why the invasion extent was continuously increasing, even when the invasion speed was null. This also demonstrates the inextricable link between ecosystem invasibility and species invasiveness (Richardson and Pyšek 2006).

In contrast to the mass action of local dispersion, foxes alone accounted for the entire invasion pattern at the landscape scale, despite dispersing a very small proportion of available seeds (0.5%). This is consistent with previous studies, which have shown that long-distance dispersal, even when it is rare, governs the invasion speed (Kot et al. 1996; Clark et al. 1998; Suarez et al. 2001; Trakhtenbrot et al. 2005; Garnier and Lecomte 2006). Consequently, *P. serotina* invasion may be very sensitive to fluctuations in fox population densities and invasion models should emphasize long-distance dispersal and vector movement patterns (foxes in our case study).

We conclude that the invasion dynamics of *P. serotina* at the landscape scale rely on two simultaneous mechanisms that can be enhanced by disturbances in a deterministic (management-related disturbances) and/or stochastic (natural disturbances) way: (1) irregular, dramatic jumps in distribution caused by long-distance dispersers; and (2) regular, continuous diffusion toward the adjacent, more or less invasible cells, via short- and mid-distance vectors. Rare long-distance dispersal events are responsible for the creation of new founder populations in distant suitable areas, resulting in increased invasion speed. To reach these suitable areas the invader follows directional corridors or stepping stones of invasible cells that are embedded in a matrix of more resistant cells. Even when dispersal is incorporated as an unrestricted (i.e., multidirectional) process, landscape heterogeneity makes the invasion highly directional. Following the establishment of founder populations by long-dispersal events, diffusion via short- and mid-distance dispersal mechanisms is responsible for the continuous, centrifugal growth of invader populations.

Overall, our results from real landscapes support the theoretical results previously obtained in studies addressing habitat connectivity in virtual landscapes (e.g., Söndgerath and Schröder 2002). Our results are consistent with Cannas et al. (2006) who reported that short-distance dispersion mainly accounts for the growing area of the main patch (i.e., the founder population) with a constant velocity, while long-distance dispersal produces an invasion front that grows exponentially with time.

Management implications

Forest management strongly influences the spatial pattern of the landscape by creating patches of distinct size, composition and arrangement (Franklin and Forman 1987). By virtually altering landscape patterns, our model can easily explore the effects of several alternative management strategies on invader populations. Our simulations support the predictions of Chabrerie et al. (2007b) that changing the dominant tree species greatly influences the invasion process. We found a gradient of decreasing invasibility from Scots pine plantations to beech and oak stands that strongly correlates with a gradient of increasing light availability within the canopy. Higher proportions of beech in the forest canopy resulted in slower invasion rates. Managers could reduce light availability in our study area by increasing the proportion of shade-providing tree species, such as beech and hornbeam and/or extending the harvesting rotation time. Our results also show reduced invasion rates following annual removal of *P. serotina* along the invasion leading edge. Hence, a second strategy would be to reduce seed dispersal by removing fertile individuals, especially along the leading edge.

Our model can be easily applied to other European forests exposed to *P. serotina* invasion because it mainly requires a map of landscape invasibility and information about disturbances, data that are usually available for managed forests as GIS technology has become a common tool for forest management. However, the proportion of seeds subjected to long-distance dispersal should be calibrated according to regional fox densities. Especially in forests where the species has recently spread, our model may be a flexible tool that can help identify where control operations would be most efficient and to prioritize monitoring efforts on sites where the invader is most likely to be successful.

Beyond the special case of *P. serotina* in forest ecosystems, our model could be extended to other systems. Depending on the study species, the time-step used for simulation has to be adapted (e.g., 1 year for most perennial and annual herb species) as well as the size and grain of the lattice. Incorporating a probability of local extinction may be necessary for species that establish only transiently in a succession. Individual- or population-based models often have limited applicability because of the large amount of information needed for model parameters (Hastings et al. 2005). However, our results suggest that invasion patterns can be predicted once three key components of the system are known: spatial heterogeneity, disturbance regime, and long-distance dispersal. Spatial heterogeneity can be represented as an invasibility map for any type of landscape. Once located in space and time, disturbances can be incorporated into the invasibility index of a given cell at a given time of the simulation run. Long-distance dispersal is undoubtedly the most difficult parameter to quantify (Trakhtenbrot et al. 2005). Accurate mechanistic models are available for wind-dispersed seeds (e.g., Nathan et al. 2005) and can be easily incorporated into our model. But in most other cases, long-distance dispersal estimates require dispersal kernels or models of vector movements. Alternatively, when data about invasion history are available (i.e., time and place of first introduction, distribution map of the invader at a given time), simulations can test a range of values for long-distance dispersal to determine the most likely value.

Consistent with Higgins and Richardson (1998), we conclude that despite their species-specificity, individual- and population-based models incorporating interactions and mechanisms instead of individual factors can potentially reduce the amount of data needed to predict plant invasion, and thus serve as useful tools for management purposes.

Acknowledgements We thank Marie Pairon (Université catholique de Louvain) for her help in parameterizing the model and Jérôme Jaminon (Office National des Forêts) for facilities during field data collection. We also thank Kirk Moloney, David Richardson and the three anonymous referees for their helpful comments on the initial manuscript, and Sharon Stanton for having reviewed the English writing. This study was financially supported by the French 'Ministère de l'Ecologie et du Développement Durable' (INVABIO II program, CR No. 09-D/2003).

References

Buckley YM, Briese DT, Rees M (2003) Demography and management of the invasive plant species *Hypericum perforatum*. II. Construction and use of an individual-based model to predict population dynamics and the effects of management strategies. J Appl Ecol 40:494–507. doi:10.1046/j.1365-2664.2003.00822.x

Cannas SA, Marco DE, Paez SA (2003) Modelling biological invasions: species traits, species interactions, and habitat heterogeneity. Math Biosci 183:93–110. doi:10.1016/S0025-5564(02)00213-4

Cannas SA, Marco DE, Montemurro MA (2006) Long range dispersal and spatial pattern formation in biological invasions. Math Biosci 203:155–170. doi:10.1016/j.mbs.2006.06.005

Chabrerie O, Hoeblich H, Decocq G (2007a) Déterminisme et conséquences écologiques de la dynamique invasive du cerisier tardif (*Prunus serotina* Ehrh.) sur les communautés végétales de la forêt de Compiègne. Acta Bot Gallica 154:383–394

Chabrerie O, Roulier F, Hoeblich H, Sebert E, Closset-Kopp D, Leblanc I et al (2007b) Defining patch mosaic functional types to predict invasion patterns in a forest landscape. Ecol Appl 17:464–481. doi:10.1890/06-0614

Chabrerie O, Verheyen K, Saguez R, Decocq G (2008) Disentangling relationships between habitat conditions, disturbance history, plant diversity and American Black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest. Divers Distrib 14:204–212. doi:10.1111/j.1472-4642.2007.00453.x

Clark JS, Fastie C, Hurtt G, Jackson ST, Johnson C, King GA et al (1998) Reid's paradox of rapid plant migration. Bioscience 48:13–24. doi:10.2307/1313224

Closset-Kopp D, Chabrerie O, Valentin B, Delachapelle H, Decocq G (2007) When Oskar meets Alice: does a lack of trade-off in r/K-strategies make *Prunus serotina* a successful invader of European forests? For Ecol Manage 247:120–130. doi:10.1016/j.foreco.2007.04.023

Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ (2005) Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. Ecology 86:1602–1610. doi:10.1890/04-1196

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–536. doi:10.1046/j.1365-2745.2000.00473.x

Deckers B, Verheyen K, Hermy M, Muys B (2005) Effects of landscape structure on the invasive spread of black cherry *Prunus serotina* in an agricultural landscape in Flanders, Belgium. Ecography 28:99–109. doi:10.1111/j.0906-7590.2005.04054.x

Drake JM, Lodge DM (2006) Allee effects, propagule pressure and the probability of establishment: risk analysis for biological invasions. Biol Invasions 8:365–375. doi:10.1007/s10530-004-8122-6

Fahrig L, Merriam G (1994) Conservation of fragmented populations. Conserv Biol 8:50–59. doi:10.1046/j.1523-1739.1994.08010050.x

Franklin JF, Forman RTT (1987) Creating landscape patterns by forest cutting: ecological consequences and principles. Landsc Ecol 1:5–18. doi:10.1007/BF02275261

Garnier A, Lecomte J (2006) Using a spatial and stage-structured invasion model to assess the spread of feral populations of transgenic oilseed rape. Ecol Modell 194:141–149. doi:10.1016/j.ecolmodel.2005.10.009

Hanski I (1999) Metapopulation ecology. Oxford University Press, Oxford

Hastings A, Cuddington K, Davies KF, Dugaw CJ, Elmendorf S, Freestone A et al (2005) The spatial spread of invasions: new developments in theory and evidence. Ecol Lett 8:91–101. doi:10.1111/j.1461-0248.2004.00687.x

Higgins SI, Richardson DM (1996) A review of models of alien plant spread. Ecol Modell 87:249–265. doi:10.1016/0304-3800(95)00022-4

Higgins SI, Richardson DM (1998) Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. Plant Ecol 135:79–93. doi:10.1023/A:1009760512895

Higgins SI, Richardson DM, Cowling RM (2000) Using a dynamic landscape model for planning the management of alien plant invasions. Ecol Appl 10:1833–1848. doi:10.1890/1051-0761(2000)010[1833:UADLMF]2.0.CO;2

Johnstone IM (1986) Plant invasion windows: a time based classification of invasion potential. Biol Rev Camb Philos Soc 61:369–394. doi:10.1111/j.1469-185X.1986.tb00659.x

Kot M, Lewis M, van den Driessche P (1996) Dispersal data and the spread of invading organisms. Ecology 77:2027–2042. doi:10.2307/2265698

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasion. Trends Ecol Evol 20:223–228. doi:10.1016/j.tree.2005.02.004

Lodge DM (1993) Biological invasions: lessons for ecology. Trends Ecol Evol 8:133–137. doi:10.1016/0169-5347(93)90025-K

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL et al (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecol Lett 10:77–94. doi:10.1111/j.1461-0248.2006.00987.x

Nathan R, Sapir N, Trakhtenbrot A, Katul GG, Bohrer G, Otte M et al (2005) Long-distance biological transport processes through the air: can nature's complexity be unfolded *in silico?*. Divers Distrib 11:131–137. doi:10.1111/j.1366-9516.2005.00146.x

Neubert GN, Kot M, Lewis MA (2000) Invasion speeds in fluctuating environments. Proc R Soc Lond B Biol Sci 267:1603–1610. doi:10.1098/rspb.2000.1185

Pairon M, Jonard M, Jacquemart AL (2006) Modeling seed dispersal of black cherry (*Prunus serotina* Ehrh.) an invasive tree: how microsatellites may help? Can J Res 36:1385–1394. doi:10.1139/X06-018

Pimentel DL, Lach L, Zuniga R, Morisson D (2000) Environmental and economic costs of nonindigenous species in the United States. Bioscience 50:53–65. doi:10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2

Pulliam HR, Dunning JB (1995) Spatially explicit population models. Ecol Appl 5:3–11. doi:10.2307/1942044

Richardson DM, Pyšek P (2006) Plant invasions—merging the concepts of species invasiveness and community invasibility. Prog Phys Geogr 30:409–431. doi:10.1191/0309133306pp490pr

Sebert-Cuvillier E, Paccaut F, Chabrerie O, Endels P, Goubet O, Decocq G (2007) Local population dynamics of an invasive tree species with a complex life-history cycle: a stochastic matrix model. Ecol Modell 201:127–143. doi:10.1016/j.ecolmodel.2006.09.005

Shigesada N, Kawasaki K (1997) Biological invasions: theory and practice. Oxford University Press, Oxford

Snyder RE, Chesson P (2003) Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. Ecol Lett 6:301–309. doi:10.1046/j.1461-0248.2003.00434.x

Söndgerath D, Schröder B (2002) Population dynamics and habitat connectivity affecting the spatial spread of populations. A simulation study. Landsc Ecol 17:57–70. doi:10.1023/A:1015237002145

Starfinger U (1991) Population biology of an invading tree species-*Prunus serotina*. In: Seitz A, Loeschcke V (eds) Species conservation: a population-biological approach. Birkhaüser Verlag, Basel, pp 171–184

Starfinger U (1997) Introduction and naturalization of *Prunus serotina* in Central Europe. In: Brock JH, Wade M, Pyšek P, Green D (eds) Plant invasions: studies from North America and Europe. Backhuys Publishers, Leiden, pp 161–171

Suarez AV, Holway DA, Case TJ (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proc Nat Acad Sci USA 98:1095–1100. doi:10.1073/pnas.98.3.1095

Tischendorf L, Fahrig L (2000) On the usage and measurement of landscape connectivity. Oikos 90:7–19. doi:10.1034/j.1600-0706.2000.900102.x

Trakhtenbrot A, Nathan R, Perry G, Richardson DM (2005) The importance of long-distance dispersal in biodiversity conservation. Divers Distrib 11:173–181. doi:10.1111/j.1366-9516.2005.00156.x

Verheyen K, Vanhellemont M, Stock T, Hermy M (2007) Predicting patterns of invasion by black cherry (*Prunus serotina* Ehrh.) in Flanders (Belgium) and its impact on the forest understorey community. Divers Distrib 13:487–497. doi:10.1111/j.1472-4642.2007.00334.x

Westerberg L, Wennergren U (2003) Predicting the spatial distribution of a population in a heterogeneous landscape. Ecol Modell 166:53–65. doi:10.1016/S0304-3800(03)00118-2

Westerberg L, Östman Ö, Wennergren U (2005) Movement effects on equilibrium distributions of habitat generalists in heterogeneous landscapes. Ecol Modell 188:432–447. doi:10.1016/j.ecolmodel.2005.02.004

Williamson M (1999) Invasions. Ecography 22:5–12. doi:10.1111/j.1600-0587.1999.tb00449.x

Wilson JRU, Richardson DM, Rouget M, Proches S, Amis MA, Henderson L et al (2007) Residence time and potential range: crucial considerations in modelling plant invasions. Divers Distrib 13:11–22. doi:10.1111/j.1366-9516.2006.00302.x

With KA (2002) The landscape ecology of invasive spread. Conserv Biol 151:1192–1203. doi:10.1046/j.1523-1739.2002.01064.x