



Original article

Long-term scenarios of the invasive black cherry in pine-oak forest: Impact of regeneration success

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ABSTRACT

The spread of invasive tree species in forests can be slow because of their long life span and the lag phases that may occur during the invasion process. Models of forest succession are a useful tool to explore how these invasive species might affect long-term forest development. We used the spatially explicit individual tree model SORTIE-ND to gain insight into the long-term development of a gap-dependent invasive tree species, *Prunus serotina*, in a pine-oak forest on sandy soil, the forest type in which *P. serotina* occurs most often in its introduced range. Forest inventory data, tree ring data, and photographs of the tree crowns were collected in a forest reserve in the Netherlands, characterized by high game densities. The collected data were then combined with data from literature to parameterize the model. We ran the model for two different scenarios in order to evaluate the impact of differences in the regeneration success of the native *Quercus robur* and the invasive *P. serotina*. The outcome of the simulations shows two differing courses of forest development. The invasive *P. serotina* became the dominant species when the regeneration of *Q. robur* was hindered, e.g., because of high herbivore densities. When both *Q. robur* and *P. serotina* were able to regenerate, *Q. robur* became the most abundant species in the long-term. We hypothesize that the relatively short life span of *P. serotina* may preclude its dominance if other long-lived tree species are present and able to regenerate.

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1. Introduction

Shade-tolerant invasive plant species can have adverse and long-lasting effects on forest ecosystems worldwide (Martin et al., 2009). Yet, biological invasions in forests have received little attention compared to invasions in, e.g., herbaceous communities (cf. Levine et al., 2004), probably because the rates of invasion of shade-tolerant species in forests are comparatively slow, which makes their invasion less perceivable (Martin et al., 2009). Perennial woody invaders may indeed experience prolonged establishment phases between initial introduction and subsequent spread because of their long generation times and the multiple lag phases that can occur during the invasion process (Wangen and Webster, 2006). These lag phases partly result from the temporal scarcity of canopy gaps. Seedlings and saplings of gap-dependent woody species can survive in the shaded conditions of forest understories, but they can only recruit into the canopy layer if a canopy gap is

formed and the subsequent higher light availability enables them to regain growth (Martin et al., 2009). Studying the patterns and consequences of tree species invasion in forests obviously requires long-term data, which are, however, rarely available. Model simulations of long-term forest development represent an additional tool for gaining insight into the possible outcomes of various scenarios of forest development with invasive species, but most models require a lot of data to be parameterized and validated.

We used the invasive tree species *Prunus serotina* Ehrh., a typical gap-phase species native to North America (Auclair and Cottam, 1971), as a case to explore the long-term invasion patterns of a gap-dependent invasive tree species. *P. serotina* was introduced into Europe in the 17th century for ornamental reasons. During the first half of the 20th century, the species was also frequently planted in forests, mainly in or next to pine (*Pinus sylvestris* L.) and larch (*Larix* spp.) stands on sandy soils in Western and Central Europe. Afterwards, the species spread rapidly to neighbouring forest stands as well as grass- and heathlands. Because the dense shrub layers of *P. serotina* were thought to have an adverse effect on biodiversity, the regeneration of native tree species, and forest management, control of the species started as early as the 1950s

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and is still ongoing (Starfinger et al., 2003). High densities of *P. serotina* have been found to affect abiotic soil conditions, alter biodiversity, and change succession (Chabrierie et al., 2008; Starfinger et al., 2003; Verheyen et al., 2007). *P. serotina* has not yet reached its potential range in Europe (e.g., Verheyen et al., 2007) and shows a clear range expansion (Klotz, 2009). Both forest managers and nature conservationists might therefore benefit from insights into the future role of the species in European forests. Yet, the relatively short period in which *P. serotina* has been present in European forests and the widespread attempts to control the species have largely precluded the investigation of long-term, spontaneous development of *P. serotina* in its introduced range (but see Vanhellemont et al., 2009b, 2010b). Efforts to model the spread of *P. serotina* are also scarce, and these models focused on the demography of the invader, not explicitly taking into account the establishment and growth of other species (Sebert-Cuvillier et al., 2007, 2008). The results of these recent studies suggest that ecosystem disturbances, e.g., wind storms (Sebert-Cuvillier et al., 2007) or grazing by large herbivores (Vanhellemont et al., 2010b), may facilitate *P. serotina* invasion.

We used SORTIE-ND (www.sortie-nd.org), a spatially explicit individual tree model of forest dynamics, to simulate the long-term development of a pine-oak (*P. sylvestris*, *Quercus robur* L.) forest in which the studied species, *P. serotina*, was present. The original version of SORTIE was developed in the 1990s for forests in the northeastern part of the United States (Pacala et al., 1996), but the model has been successfully parameterized and used for modelling forest development in, e.g., northern British Columbia (see Coates et al., 2003) and southern New Zealand (Kunstler et al., 2009). We focused on a pine forest on sandy soils because this is the forest type in which *P. serotina* occurs most often in its introduced range (Starfinger et al., 2003). The Ossenbos forest reserve, located in the Netherlands, represented a unique opportunity for this study because it is a pine forest in which *P. serotina* has spread and developed spontaneously for almost 70 years, opposite to most other forests in Western Europe where *P. serotina* has been planted or managed. In a prior study on the colonization patterns of *P. serotina* in the Ossenbos (Vanhellemont et al., 2010b), we found that the establishment and growth of *P. serotina* were mainly related to light availability. Besides, the high density of large herbivores in the forest reserve appeared to favour *P. serotina* above native species. *P. serotina* successfully recruited into the shrub and tree layer, while native deciduous species, e.g., the palatable *Q. robur*, were unable to outgrow the seedling stage (Vanhellemont et al., 2010b). The regeneration of *Q. robur* can indeed be hampered by high densities of animal species that consume acorns and browse on small seedlings (Gómez et al., 2003; Groot Bruinderink et al., 1994) whereas *P. serotina* has been found to dominate seedling and sapling layers in areas with high deer densities in its native range (Horsley et al., 2003).

In the present study, we wanted to examine the possible further development of the Ossenbos forest reserve. Our main objectives were (1) investigating whether SORTIE-ND can be a useful tool to simulate the development of an invasive woody species, (2) predicting the long-term development of the invasive *P. serotina* and the invaded forest reserve, and (3) exploring the impact of differences in the regeneration success of the native *Q. robur* and the invasive *P. serotina*.

2. Materials and methods

2.1. Study species

P. serotina is a gap-dependent tree species that grows on a wide variety of soils (Marquis, 1990). In shaded conditions, seedlings

survive in a short-lived seedling bank (Vanhellemont et al., 2009a). In high light conditions in open landscapes, seedlings grow fast and start producing seeds from the age of four years (Deckers et al., 2005). Fruit production is high, even in forest understories, i.e., 1500–6000 fruits per tree (Pairon et al., 2006a), and most fruits (up to 95%) fall within 5 m of the parent tree (Pairon et al., 2006b). Birds and mammals account for seed dispersal over distances >100 m (Boucault, 2009). Seeds remain viable for 3 up to 5 years (Wendel, 1977). The resprouting capacity of *P. serotina* is high, and the stump sprouts grow rapidly, especially in full light (Closset-Kopp et al., 2007).

2.2. Study area

The Ossenbos forest reserve (54 ha) is situated within the 3600 ha artillery training camp De Harskamp in the Natura 2000 site Veluwe, the Netherlands (N52°08' E005°48'), in a landscape matrix that includes forest patches, heathlands, and bare sand. The forest reserve is a spontaneously developed forest on dry sandy soils. Scots pine (*P. sylvestris*) and pedunculate oak (*Q. robur*) establishment started around 1850 and 1900. Around 1940, the first *P. serotina* established in the pine-oak forest, probably as a result of seeds brought in by birds coming from nearby heathland afforestations (Table 1; Vanhellemont et al., 2010b). The minimum and maximum monthly mean temperatures are 2 °C in January and 17 °C in July, and the mean annual precipitation is 850 mm (www.knmi.nl). In 1989, the deer fence around the training camp was removed, which allowed large game species to enter. The forest reserve is the only area within the training camp in which hunting is prohibited and therefore acts as a safe site, which has resulted in a high game density, i.e., around 1 ha⁻¹ (A. Varkevisser, personal communication). The large herbivore species that occur in the area are red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*). Data were collected in a study plot of 70 m × 140 m in March 2003 and August 2007. A detailed description of the study area, study plot, and data collection can be found in Vanhellemont et al. (2010b); below, we only mention the collection of the data used for the parameterization of the model in this study.

For trees with a diameter at breast height (dbh) > 5 cm, the position (x,y-coordinates), species, dbh, height, crown radius, and crown length were measured in 2003. In 2007, additional data were collected on age and crown openness for the three main tree species. For 49 *P. sylvestris* trees, 33 *P. serotina* trees, and 25 *Q. robur* trees, we measured dbh and height and took a stem cross section (for small individuals) or tree core (for large individuals) at 20–30 cm above the root collar. The age of the sampled trees was determined by counting the growth rings using a stereomicroscope (Olympus SZX12). We made photographs of the crown for 20 trees of each of the three species using a Nikon D70S with an AF-S Zoom-Nikkor ED 18–70 mm f/3.5–4.5G IF DX lens and following the methods of Beaudet et al. (2002). In addition, for each of the three

Table 1

Stem density (N, ha⁻¹) and basal area (BA, m² ha⁻¹) for the tree species in the study area (the Ossenbos forest reserve; Vanhellemont et al., 2010b). Percentages of the total stem density or basal area are given between brackets.

Species ^a	N (ha ⁻¹)		BA (m ² ha ⁻¹)	
<i>Pinus sylvestris</i> L.	188	(23)	23.5	(72)
<i>Prunus serotina</i> Ehrh.	586	(71)	6.7	(20)
<i>Quercus robur</i> L.	46	(6)	2.5	(8)
Total	821	(100)	32.8	(100)

^a *Sorbus aucuparia* L. (0.01 m² ha⁻¹) and *Betula* spp. (0.03 m² ha⁻¹), i.e., *Betula pendula* Roth and *Betula pubescens* Ehrh., were not included in the table because of their low contribution to the basal area.

main tree species, we randomly chose 25 trees with dbh < 5 cm and measured their dbh, height, and diameter at 10 cm above the root collar (diam10).

2.3. Model

We used the model SORTIE-ND version 6.10 (www.sortie-nd.org), which is based on the earlier SORTIE model (Pacala et al., 1996). SORTIE-ND is (1) individual-based – the basic unit of data is a tree, (2) spatially explicit – each tree has a unique location, (3) dynamic – the model shows how a forest changes during a certain time span, and (4) empirical – the model functions are fitted based on field data (Tremblay et al., 2005). The original, basic version of SORTIE consisted of four submodels with species-specific equations that calculate (1) the local light availability (Canham et al., 1994); predict (2) the growth and (3) mortality of individual seedlings, saplings, and adults (Kobe et al., 1995; Pacala et al., 1994); and determine (4) seedling recruitment (Ribbens et al., 1994). SORTIE-ND simulates the life cycle of individual trees during a certain number of 5-year time steps. Light is considered the limiting resource, and for each time step in a simulation or model run, SORTIE-ND first calculates an index of light availability for each tree. This Global Light Index (GLI) is based on the tree's neighbourhood, i.e., the density, size, position, and species of all the neighbouring trees, which illustrates the neighbourhood dynamics ('ND') in SORTIE-ND. The calculated light availability is subsequently used to determine the growth of the subject tree, which is then translated into probability of mortality. Living trees with a dbh above the Minimum DBH for Reproduction produce seedlings that will be dispersed according to a given dispersal kernel.

2.4. Parameterization

We determined parameters for the allometry relationships for *P. sylvestris*, *P. serotina*, and *Q. robur* and for the four submodels, i.e., light, growth, mortality, and dispersal, based on the data collected in the Ossenbos forest reserve (see 2.2) and on literature. We performed a sensitivity analysis to determine to which parameters the model output was most sensitive. Following the methods described in Steppe et al. (2006), we calculated (1) a sensitivity measure of the model output for the individual parameters based on a parameter perturbation of 10% and (2) parameter correlations. High sensitivity measure values indicate that the value of the tested parameter has a large impact on the model output; a zero sensitivity measure value means that the output does not depend on the parameter. For highly correlated parameters, small changes in the value of one

parameter can be compensated by changes in other parameters with no impact on the model output (Brun et al., 2002). The model output was sensitive to all the parameters tested, but the correlation between most parameters was high. The calculated sensitivity measures are not shown, but they are discussed in the following sections.

The complete parameter file used for the simulations is provided in the Appendix; in the following sections, we indicate how we derived the parameter values.

2.4.1. Allometry

In SORTIE-ND, each tree is a discrete individual with a given spatial location and with attributes that describe its size and shape. Allometry refers to the relationships between the different components of the size and shape of a tree. We used the standard SORTIE-ND functions for the relationships crown radius–dbh, crown length–height, height–dbh for saplings and adults; dbh–diam10 for saplings; and height–diam10 for seedlings (see Table 2). For each of these relationships, the parameters were estimated based on the 2003 data for the study area (Table 2). Non-linear and linear regressions were performed in R 2.8.0 (R Development Core Team, 2008). For the parameter Maximum Tree Height (see Appendix), we used the maximum tree height as reported in Brzeziecki and Kienast (1994) in combination with data from prior studies on *P. serotina* (Vanhellemont et al., 2009b, 2010b). Sensitivity of the model output was lowest for changes in the allometry parameter values of *P. sylvestris* and the crown radius function; model sensitivity was highest for the *P. serotina* parameter values.

2.4.2. Light

For each individual, SORTIE-ND simulates a hemispherical photograph and uses this simulated photograph to calculate GLI, i.e., the percentage of full light received by the tree. We adjusted the region-specific light parameters that determine the local sky brightness and the seasonality to the local situation. The Beam Fraction of Global Radiation (0.32; Hemming et al., 2007) and the First and Last Day of Growing Season (81 and 284; Jacobs et al., 2008) were taken from literature; the Clear Sky Transmission Coefficient (0.526) was calculated for a clear summer day in Wageningen (N51°58' E005°38'), close to the study area (A. Jacobs, personal communication). We then determined the crown openness for each of the three species, based on our photographs of the tree crowns and following the methods described in Beaudet et al. (2002). The mean crown openness, with the standard error between brackets, was 29.9% (2.0) for *P. sylvestris*, 23.8% (1.7) for *P.*

Table 2

Estimates of the parameters (α and β) in the allometry relationships for the *Pinus sylvestris*, *Prunus serotina*, and *Quercus robur* in the Ossenbos forest reserve.

Relationship ^a	<i>Pinus sylvestris</i>				<i>Prunus serotina</i>				<i>Quercus robur</i>			
	α	β	R^2	n^b	α	β	R^2	n	α	β	R^2	n
crown radius (m) – dbh (cm) $y = \alpha x^\beta$	0.35	0.64	0.23	183	0.78	0.50	0.40	573	0.55	0.62	0.71	46
crown length (m) – h (m) $y = \alpha x^\beta$	0.71	0.78	0.24	183	0.42	1.13	0.78	573	0.56	1.06	0.27	49
h (m) – dbh (cm) $y = 1.35 + \alpha [1 - \exp(-\beta x)]$	18.6	0.06	0.45	183	22.7	0.03	0.61	573	16.9	0.05	0.51	49
dbh (cm) – diam10 (cm) $y = \alpha x$	0.78	–	0.99	25	0.80	–	0.93	25	0.75	–	0.97	25
h (m) – diam10 (cm) $y = 0.1 + 30 [1 - \exp(-\alpha x)]$	0.021	–	0.77	25	0.024	–	0.90	25	0.022	–	0.73	25

^a dbh, diameter at breast height; h, tree height; diam10, diameter at 10 cm height. The relationships with diam10 are based on data for individuals with a dbh < 5 cm.

^b n, the number of sample trees.

serotina, and 25.1% (1.7) for *Q. robur*. Crown openness differed between species (one-way ANOVA: $F = 5.7$, $p < 0.005$). The crown openness of *P. sylvestris* was higher than that of *P. serotina* (Tukey post-hoc: $p = 0.006$) and *Q. robur* ($p = 0.036$); the crown openness of *P. serotina* and *Q. robur* did not differ ($p = 0.796$). The other parameters for the calculation of GLI (see Appendix), which are not region-specific, were taken from the standard parameter file (www.sortie-nd.org).

2.4.3. Dispersal

The dispersal submodel creates seedlings and disperses them across the plot according to a given seed dispersal kernel.

The Minimum DBH for Reproduction for *P. sylvestris* and *Q. robur* was calculated based on the minimum age for first reproduction reported by Brzeziecki and Kienast (1994) and the relationships between age and dbh based on the data for the study area (see 2.4.4) and another forest reserve in the Netherlands (see Goris et al., 2007). For *P. serotina*, we used the minimum diameter at which 90% of the *P. serotina* set seed in the understory of pine forests on sandy soils in Flanders (Vanhellemont et al., unpublished results).

The Standardized Total Recruits (STR) is defined as the number of new seedlings that would be produced by a tree with a dbh of 30 cm. Because we did not have good long-term data on seed rain and recruitment for the three species, we determined STR based on mean annual fecundity, seed germination and 1-year seedling survival following Papaik and Canham (2006). Mean annual fecundity was calculated with the empirical relationship between seed mass and seed number formulated by Greene and Johnson (1994, 1998) and using seed mass data from Brzeziecki and Kienast (1994) for *P. sylvestris* and *Q. robur* and from Grisez (1974) for *P. serotina*. Seed germination and 1-year seedling survival were determined based on literature for *P. sylvestris* (Castro et al., 2004), *P. serotina* (Pairon et al., 2006a; Vanhellemont et al., 2009a), and *Q. robur*, for which we used the data on *Quercus pe-traea* (Matt.) Liebl. in Degen (2006).

For the spatial placement of the seedlings around the seed trees, we chose the Weibull probability density function with the parameters provided by C. Canham (personal communication). We used the North American parameters provided for *Pinus strobus* L., *Quercus rubra* L., and *P. serotina* for the *P. sylvestris*, *Q. robur*, and *P. serotina* in the Ossenbos forest reserve. *P. strobus* and *P. sylvestris* are both wind-dispersed, their seeds have similar dimensions, but the seeds of *P. strobus* are somewhat heavier than those of *P. sylvestris* (Brzeziecki and Kienast, 1994; Noland et al., 2006). Both *Quercus* species are mainly barochorous, and the weight and dimensions of their seeds are similar (Brzeziecki and Kienast, 1994; Kostel-Hughes et al., 2005).

Similar to the allometry parameters, the model output was least sensitive to the dispersal parameter values for *P. sylvestris* and most sensitive to the *P. serotina* parameter values, most notably STR.

2.4.4. Growth and mortality

The parameters for the submodels growth and mortality were optimized manually, based on the data collected in 2003/2007 and a reconstruction of the forest in 1953. First, we counted the number of tree rings to estimate the age of the sampled trees. Second, we determined the relationships between age (y) and dbh (x) for the three species: $y = 8.85 + 2.15x$ for *P. sylvestris* ($R^2 = 0.71$, $n = 49$), $y = 10.90 + 10.80 \ln(x)$ for *P. serotina* ($R^2 = 0.68$, $n = 33$), and $y = 35.3 + 1.09x$ for *Q. robur* ($R^2 = 0.65$, $n = 25$). Third, we used these relationships together with the 2003 inventory of living and dead trees to reconstruct the 1953 forest. Fourth, we ran SORTIE-ND for 10 time steps, i.e., 50 year, with the 1953 situation as the model input and the parameters for allometry, light, and dispersal set as in sections 2.4.1, 2.4.2, and 2.4.3. We adjusted the parameters

for growth and mortality iteratively so that the output of the simulation approximated the real 2003 situation. For that purpose, we compared the maximum age and dbh as well as the diameter distribution (see Fig. 1) for the model output and the 2003 inventory data. Seeing the high impact of large herbivores on the regeneration of *Quercus* species (Gómez et al., 2003; Groot Bruinderink et al., 1994), we used different parameter values for the Juvenile Background Mortality Rate for *Q. robur* for the period 1953–1993 (with a low density of large herbivores) and 1993–2003 (with a high density of large herbivores). The growth values calculated based on the estimated parameters were in concordance with growth ranges that are reported in literature for the three species in this study (see Table 3). The sensitivity of the model output to the growth and mortality parameter values was similar for the three species and for the different parameters.

2.5. Model input and scenarios

We used the 2003 inventory data for the Ossenbos forest reserve to define the initial tree population parameters for the SORTIE-ND simulations. The Minimum Adult DBH was set to 5 cm. The initial seedling densities were set to the densities in the shrub layer (tree height < 10 m) because working with the high seedling densities that occur in reality (cf. Vanhellemont et al., 2010b) slows down SORTIE-ND and most of these seedlings will die anyway (C. Canham, personal communication). The model input, which is called the 'tree map', i.e., the x,y -coordinates, the species, the dbh, and height for all trees, was also based on the 2003 inventory data.

We ran the model for 100 time steps, i.e., 500 years, to study the long-term development of the pine-oak forest with *P. serotina* for two scenarios that differed in the regeneration success of the invasive *P. serotina* and the native *Q. robur*. Since the extremely high

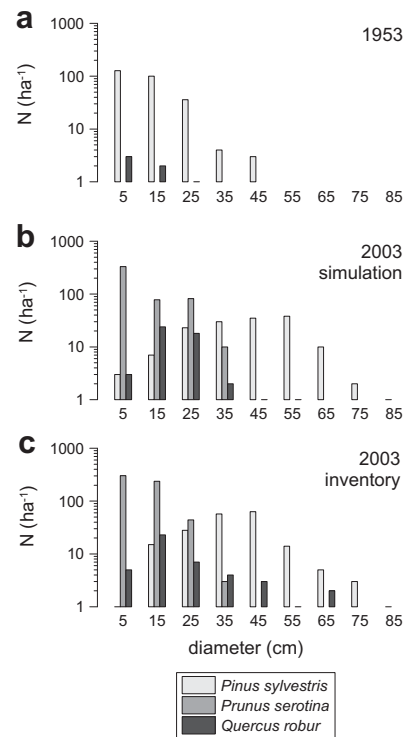


Fig. 1. Diameter distribution for (a) the reconstructed 1953 situation, (b) the simulated 2003 situation, and (c) the real 2003 situation in the Ossenbos forest reserve. Note that the stem densities (N, ha⁻¹) for the different diameter classes are depicted on a logarithmic scale.

Table 3

The range of radial growth rates, i.e., minimum and maximum radial growth in mm yr^{-1} , calculated based on the growth functions in this study compared to ranges of radial growth rates reported in the literature for *Pinus sylvestris*, *Prunus serotina*, and *Quercus robur* on sandy soils in the Netherlands or Flanders (the northern part of Belgium).

Species	This study (mm yr^{-1})	Literature data (mm yr^{-1})	Reference
<i>Pinus sylvestris</i>	0.5–2.7	0.9–3.2	Goris et al. (2007)
<i>Prunus serotina</i>	0.5–4.1	0.1–4.3	Vanhellemont et al. (2010a)
<i>Quercus robur</i>	0.1–3.4	0.1–6.4	Haneca (2005)

herbivore densities in the Ossensbos forest reserve (see 2.2) seemed to hamper the regeneration of *Q. robur* and facilitate the regeneration of *P. serotina* (Vanhellemont et al., 2010b), we regarded the regeneration differences between the two scenarios as a proxy of a difference in large herbivore densities. We distinguished between (1) a scenario with high densities of large herbivores, in which *Q. robur* showed no successful regeneration and (2) a scenario with low densities of large herbivores, in which *Q. robur* was able to regenerate. The two scenarios were implemented by changing the parameters that describe seedling establishment and juvenile mortality (see 2.4.3, 2.4.4). The juvenile mortality rates for the two scenarios were taken from the optimizations in 2.4.4. The seedling establishment parameter, i.e., the STR values derived in 2.4.3, was lowered for *Q. robur* and *P. serotina* in the scenario with high densities of large herbivores (see Appendix), according to the seedling and sapling densities recorded for the two species in a previous study in the Ossensbos forest reserve (Vanhellemont et al., 2010b). For *P. sylvestris*, we used the same values for the two scenarios because *P. sylvestris* is less affected by herbivory and is not able to recruit below a canopy anyhow. We repeated the simulation ten times for each scenario to account for the stochasticity in the mortality and dispersal submodels in SORTIE-ND (cf. Deutschman et al., 2000; Ménard et al., 2002). Based on the output of the ten simulations, we then calculated mean stem density (N , ha^{-1}) and mean basal area (BA , $\text{m}^2 \text{ha}^{-1}$) for each species and each time step.

3. Results

Fig. 2 depicts the output of the 500-year SORTIE-ND simulations for the scenarios with high densities of large herbivores in which *Q. robur* showed no successful regeneration (Fig. 2a,c) and with low densities of large herbivores in which *Q. robur* was able to regenerate (Fig. 2b,d). The changes in stem density (N) and basal area (BA) of *P. sylvestris* were similar for the two scenarios: N and BA both decreased until no *P. sylvestris* stems were left after 200 years. For *P. serotina*, N showed a sharp initial decline (Fig. 2a,b). Between year 100 and 200, *P. serotina* N and BA remained relatively stationary, and they were similar for the two scenarios. After the year 250, the changes in N and BA of *P. serotina* differed between the scenarios: both N and BA increased steadily in the scenario with many large herbivores (Fig. 2a,c) whereas they decreased in the scenario with few large herbivores (Fig. 2b,d). For *Q. robur*, the two scenarios resulted in clearly differing patterns for the changes in N and BA . In the scenario with high densities of large herbivores, *Q. robur* was not able to regenerate, N showed a steady decline (Fig. 2a), and BA followed a bell-shaped curve (Fig. 2c). In the scenario with few large herbivores, N and BA of *Q. robur* both showed a steady increase after year 100 (Fig. 2b,d). After 200 years, the difference in N and BA of *Q. robur* between the two scenarios became apparent.

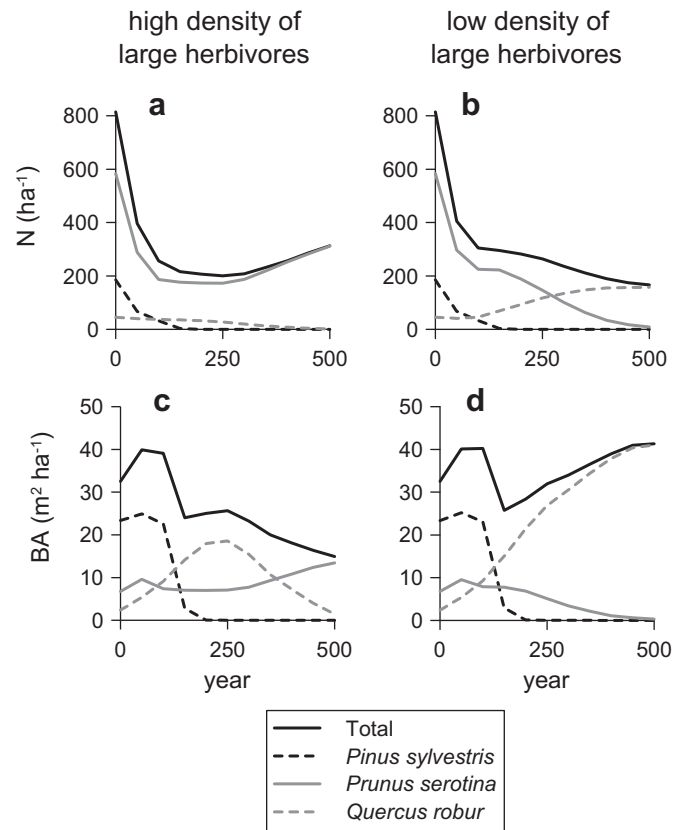


Fig. 2. Output of the SORTIE-ND simulations for the Ossensbos forest reserve over a 500-year simulation period showing the stem density (N , ha^{-1}) and basal area (BA , $\text{m}^2 \text{ha}^{-1}$) of the adult trees ($\text{dbh} > 5 \text{ cm}$) of *Pinus sylvestris*, *Prunus serotina*, and *Quercus robur*. The mean stem density and basal area of 10 model runs are given for the scenario with high densities of large herbivores in which *Q. robur* showed no successful regeneration (a and c) and for the scenario with low densities of large herbivores in which *Q. robur* and *P. serotina* were both able to regenerate (b and d).

4. Discussion

4.1. Modelling *P. serotina* invasion

The spatially explicit individual-based model SORTIE-ND enabled us to explore the future development of a highly invaded, unmanaged forest reserve in which *P. serotina* occurred in the tree, shrub, and herb layer (Vanhellemont et al., 2010b). Due to the neighbourhood dynamics ('ND') incorporated in SORTIE-ND, the course of the simulated development of one of the species in the forest and of the entire forest stand is affected by the simulated development of all the species and their mutual interactions. Thus, SORTIE-ND simulates the development of a *P. serotina* tree in association with the development of the neighbouring trees. This approach clearly differs from the models that have been used previously to better understand and predict the spread of *P. serotina*. These models only looked at *P. serotina* and did not account for changes in the invaded vegetation. Pairon (2007), for instance, used a spatially explicit individual-based model that included both demographic patterns and the spatial genetic structure of a *P. serotina* population to predict the local spread of *P. serotina* in patches of heathland and dry grassland. Sebert-Cuvillier et al. (2007) used a stage-classified demographic matrix population model to explore the local population dynamics of *P. serotina* in a forest stand and identified the life history stages with the greatest impact on population growth using elasticity analysis. This matrix model was

then used to model the spatial spread of *P. serotina* in a heterogeneous landscape (Sebert-Cuvillier et al., 2008). In the matrix model of Sebert-Cuvillier et al. (2007), all *P. serotina* individuals in a certain life stage were considered equal, e.g., each seedling has the same chance to die, to remain in the seedling stage, or to become a sapling. In addition, once a forest patch got invaded, it remained invaded for the rest of the simulation run (Sebert-Cuvillier et al., 2008). Although Sebert-Cuvillier et al. (2007) did include disturbances that changed the environmental conditions from 'shade' to 'light', canopy gaps created by the model only affected *P. serotina*. In SORTIE-ND, changes in light availability affect all the species present. Moreover, each seedling, sapling, or tree is treated as a separate individual with its growth and mortality dependent on its neighbourhood, and, as shown by the model output in Fig. 2, an invaded forest patch does not have to remain invaded. SORTIE-ND may thus provide a useful addition to the models that predict the spread of *P. serotina* as it enables to explore the future development of forest stands that get invaded, taking into account the changes in the invader as well as in the invaded stand.

4.2. Does herbivory matter?

Simulating forest development with SORTIE-ND made it possible to depict the long-term development of the Ossenbos forest reserve according to two specific scenarios that differed in the regeneration success of the invasive *P. serotina* and the native *Q. robur*. We called those the scenarios with low or high herbivore densities because the extremely high herbivore density in the study area is probably the most important factor influencing the regeneration of the tree species in the Ossenbos forest reserve. We simulated the impact of high herbivore pressure on tree seedlings and saplings by lowering the establishment of seedlings and by increasing the mortality of juveniles in SORTIE-ND. The outcome of the simulations for the two scenarios clearly differed. In the scenario in which the regeneration of *Q. robur* was hindered, *P. serotina* became the dominant species. When *Q. robur* was also able to regenerate, e.g., because of low herbivore densities, *Q. robur* became more abundant than *P. serotina* on the long-term, which resulted in an oak-dominated forest, the expected outcome of forest development in ageing, unmanaged pine forests with oak seed trees on sandy soils (Kint et al., 2004). Factors that limit the regeneration of native tree species such as *Q. robur*, e.g., a high density of large herbivores, may thus increase the invasibility of a particular ecosystem for *P. serotina* (cf. Vanhellemont et al., 2010b).

The observation that *Q. robur* gained ascendancy over *P. serotina* in the scenario in which both species were able to regenerate might be the result of the longer life span of *Q. robur*. Von Holle et al. (2003) proposed biological inertia within a plant community as a component of the community's resistance to invasion and considered the longevity of tree species as a component of the biological inertia of forests. The life span of *P. serotina* in forests in its introduced range is relatively short, i.e., 50–80 years (Sebert-Cuvillier et al., 2007; Wallis de Vries, 1987), as compared to the life span of *Q. robur*, i.e., several centuries and even up to 500 years (Brzeziecki and Kienast, 1994). The life span of *P. sylvestris* is similar to that of *Q. robur* (Brzeziecki and Kienast, 1994), but *P. sylvestris* is less shade-tolerant than *Q. robur* (Niinemets and Valladares, 2006) and is not able to regenerate in forest understories. In addition, the shade-casting ability of *Q. robur* is higher than that of *P. sylvestris* (cf. Baeten et al., 2009), which makes the invasion of *P. serotina* in *Q. robur* forests less likely (cf. Sebert-Cuvillier et al., 2008). In a model simulation for a developing, mixed deciduous forest in its native range, the basal area of *P. serotina* also declined (Deutschman et al., 2000). Thus, the relatively short life span of *P. serotina* might

preclude its dominance in the course of forest succession when other tree and shrub species are also able to regenerate, e.g., because large herbivores are absent.

The two scenarios used in our study simulated the effects of a continuously low or high impact of large herbivores on tree species regeneration and forest development. However, fluctuations in herbivore densities can be expected over time due to, e.g., harsh versus mild winter conditions (Melis et al., 2009) or differences in hunting effort (Klopcic et al., 2010). These fluctuations in herbivore densities may affect the regeneration of particular tree species and influence the structure and species composition of forests (Klopcic et al., 2010). Yet, the ungulate densities in the Ossenbos forest reserve are so high that even a moderate decrease in ungulate density might not have significant impacts on the course of succession seeing that *Q. robur* did not even show successful regeneration at ungulate densities of one tenth of the present densities (Kuiters and Slim, 2002).

4.3. Improving the present model

Although forest succession models such as SORTIE-ND are a valuable tool for exploring the possible outcomes of long-term forest development (cf. Royo and Carson, 2006), some ecological mechanisms have not yet been implemented. Two issues that might be important with regard to simulations of *P. serotina* invasion are (1) its ability to delay mortality by building up a seedling bank or by resprouting when its crown dies back (Closset-Kopp et al., 2007; Vanhellemont et al., 2009a) and (2) the negative impact of dense herb layers on *P. serotina* seedling survival (Horsley, 1993; Royo and Carson, 2008; Vanhellemont et al., 2009b). Similarly, Beaudet et al. (2002) and Tremblay et al. (2005) pointed out that integrating a herb layer in the submodel 'light' of SORTIE-ND will improve the predictions for forests with dense understory vegetation, and Caplat and Anand (2009) recently showed the importance of incorporating the resprouting ability of tree species in individual-based forest development models.

In addition, including a submodel on harvest and disturbance (see www.sortie-nd.org) might be essential for a gap-dependent species such as *P. serotina*. In this study, we simulated the development of an unmanaged forest reserve and saw that *P. serotina*'s abundance might decrease on the long-term if the long-lived, native *Q. robur* can recruit successfully. Yet, Sebert-Cuvillier et al. (2007) showed that disturbances opening up the canopy layer may speed up the *P. serotina* invasion. Management measures, such as regular thinning, may therefore continue to trigger growth and reproduction of *P. serotina*, which will enable the invasive species to remain abundant in managed forests.

Including plant–soil interactions in a model on community dynamics might also be interesting, particularly when dealing with exotic or invasive species. The soil community in invaded areas and the native range may differ greatly. The absence of certain soil pathogens in the invaded range can favour the exotic species above the natives (cf. Keane and Crawley, 2002), while the absence of beneficial soil biota, e.g., mycorrhiza, can put the exotic species at a disadvantage (Molina, 2007). For instance, Reinhart et al. (2003) suggested that the soil community in Europe facilitates *P. serotina* invasion whereas soilborne pathogens negatively affect *P. serotina* seedlings in the native range. Yet, implementing facilitation processes in a model such as SORTIE-ND is not straightforward.

A lot of data are required to parameterize SORTIE-ND and simulate forest development over large areas. Further parameterization efforts should focus on the parameters with the highest sensitivity value, such as STR, and an elaborate data collection

focused on the parameterization of the growth and mortality functions for the three species will be desirable.

5. Conclusion

Although the simulations in this study were based on one specific site and the parameters were mostly derived indirectly, our results clearly show the usefulness of spatially explicit individual tree models such as SORTIE-ND in exploring possible outcomes of long-term development in forests in which (invasive) alien species are present. Based on the output of the simulations, it seems that the relatively short life span of *P. serotina* prevents its overall dominance in unmanaged forests if other tree species are also able to regenerate. Starfinger et al. (2003) have already indicated that 'wait and see' might be an efficient strategy for managing *P. serotina* in European forests characterized by a low degree of disturbance because *P. serotina*'s dominance will decrease, even in forests without shade-tolerant trees. Indeed, next to differences in shade tolerance, differences in life span also play a part in the coexistence of species over the course of forest development (Lusk and Smith, 1998). Likewise, Cunard and Lee (2009) stated that managing the invasive *Frangula alnus* P. Mill. in forests in New Hampshire will be less effective than allowing the natural forest succession to run its course.

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Appendix

Parameter values used for the SORTIE-ND simulations in the Ossenbos forest reserve

Species: *Pinus sylvestris* L. (PISY), *Prunus serotina* Ehrh. (PRSE), *Quercus robur* L. (QURO).

For the meaning of the different parameters, see www.sortie-nd.org. The superscript characters indicate whether a parameter was (a) set according to the characteristics of the model runs given in section 2.5, (b) estimated based on own data as described in 2.4.1 and 2.4.2, (c) based on the calibration of the submodels discussed in 2.4.4, (d) derived from literature or via personal communication, or (e) taken from the sample parameter file provided on www.sortie-nd.org

Plot parameters

Parameter	
Number of timesteps ^a	100
Random Seed ^a	0
Number of years per time step ^e	5
Plot Length in the X (E–W) Direction, in meters ^a	280
Plot Length in the Y (N–S) Direction, in meters ^a	280
Plot Latitude, in decimal degrees ^a	52.13

Allometry parameters

Parameter	PISY	PRSE	QURO
New Seedling Diameter at 10 cm, in cm ^e	0.2	0.2	0.2
Maximum Tree Height, in meters ^{b/d}	26	25	22
Slope of Asymptotic Crown Radius ^b	0.347	0.777	0.547
Crown Radius Exponent ^b	0.638	0.503	0.617
Slope of Asymptotic Crown Height ^b	0.709	0.417	0.559
Crown Height Exponent ^b	0.772	1.132	1.058
Slope of DBH to Diameter at 10 cm Relationship ^b	0.766	0.799	0.751
Intercept of DBH to Diameter at 10 cm Relationship ^e	0	0	0
Slope of Asymptotic Height ^b	0.061	0.029	0.053
Slope of Height-Diameter at 10 cm Relationship ^b	0.021	0.024	0.022

Tree population parameters

Parameter	PISY	PRSE	QURO
Minimum Adult DBH ^a	5	5	5
Seedling Height Class 1 Upper Bound, in cm ^a	20	20	20
Seedling Height Class 2 Upper Bound, in cm ^a	120	120	120
Initial Density (#/ha) – Seedling Height Class 1 ^a	0	503	16
Initial Density (#/ha) – Seedling Height Class 2 ^a	0	503	16

Light parameters

Parameter	
Beam Fraction of Global Radiation ^d	0.32
Clear Sky Transmission Coefficient ^d	0.526
First Day of Growing Season ^d	81
Last Day of Growing Season ^d	284
Number of Altitude Sky Divisions for Quadrat Light Calculations ^e	18
Number of Azimuth Sky Divisions for Quadrat Light Calculations ^e	12
Minimum Solar Angle for Quadrat Light, in rad ^e	0.779
Height at Which GLI is Calculated for Quadrats, in meters ^e	0.675
Height of Fisheye Photo ^e	Mid-crown
Number of Azimuth Sky Divisions for GLI Light Calculations ^e	18
Number of Altitude Sky Divisions for GLI Light Calculations ^e	12
Minimum Solar Angle for GLI Light, in rad ^e	0.779
Light Transmission Coefficient – PISY ^b	0.299
Light Transmission Coefficient – PRSE ^b	0.238
Light Transmission Coefficient – QURO ^b	0.251

Dispersal parameters.

The STR values were different for the scenario with low herbivore densities (*L*) and with high herbivore densities (*H*).

Parameter	PISY	PRSE	QURO
Minimum DBH for Reproduction, in cm ^{b/d}	6.7	11.5	26.7
Canopy Function Used ^d	Weibull	Weibull	Weibull
Weibull Canopy Annual STR (<i>L</i>) ^d	0.005	0.15	0.05
Weibull Canopy Annual STR (<i>H</i>) ^{b/d}	0.005	0.1	0.001
Weibull Canopy Beta ^d	2.0	2.0	2.0
Weibull Canopy Theta ^d	3.0	3.0	3.0
Weibull Canopy Dispersal ^d	1.03E-05	7.75E-05	1.46E-04

Growth parameters.

Parameter	PISY	PRSE	QURO
Shaded Linear – Diam Intercept in mm/yr ^{c/d}	4.4	5.53	4.8
Shaded Linear – Diam Slope ^{c/d}	–0.016	–0.06	–0.029
Shaded Linear – Diam Shade Exponent ^{c/d}	0.7	0.4	0.5

Mortality parameters.

The Juvenile Background Mortality Rates were different for the scenario with low herbivore densities (*L*) and with high herbivore densities (*H*).

Parameter	PISY	PRSE	QURO
Senescence Mortality Alpha ^c	–20.0	–5.0	–25.0
Senescence Mortality Beta ^c	0.7	0.45	0.65
DBH at Onset of Senescence, in cm ^c	85.0	50.0	85.0
Juvenile Background Mortality Rate (<i>L</i>) ^c	0.25	0.015	0.06
Juvenile Background Mortality Rate (<i>H</i>) ^c	0.25	0.015	0.9
Mortality at Zero Growth ^c	0.35	0.2	0.3
Light-Dependent Mortality ^c	1.0	1.5	5.0
Adult Background Mortality Rate ^c	1.0E-4	0.018	1.0E-4
Juvenile Self-Thinning Slope ^c	–	0.008	0.012
Juvenile Self-Thinning Intercept ^c	–	0.001	0.0015

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