ORIGINAL PAPER

Prunus serotina unleashed: invader dominance after 70 years of forest development

**Margot Vanhellemont · Lotte Wauters ·
Lander Baeten · Rienk-Jan Bijlsma ·
Pieter De Frenne · Martin Hermy · Kris Verheyen**

Abstract Propagule pressure and disturbance have both been found to facilitate invasion. Therefore, knowledge on the history of introduction and disturbance is vital for understanding an invasion process, and research should focus on areas in which the invasive species has not been deliberately introduced or managed to study unconfounded colonization patterns. Comparing the outcome of such spontaneous colonization processes for different ecosystems might provide a useful framework for setting management priorities for invasive species that enter new, uninvaded areas. We focused on the 70-year spontaneous spread of the invasive tree species *Prunus serotina* in a pine forest in the Netherlands. To reconstruct the invasion pattern, we combined historical maps, tree ring analysis, spatially explicit tree inventory data, seed density data, and regeneration data for both native and non-native species. *Prunus serotina* was the only species that showed successful regeneration: the species was present throughout the forest in the tree, shrub, and herb layer. Native species were not able to outgrow the seedling stage. Our data demonstrate that *P. serotina* is a gap-dependent species with high seed production that builds up a seedling bank. We also compared the results of this study with a similar study on *P. serotina* colonization in a deciduous forest in Belgium, where *P. serotina* invasion was not successful. The sharp contrast between the outcomes of the two invasion processes shows the importance of studying an invasive species and the recipient ecosystem jointly and made us raise the hypothesis that herbivore pressure may facilitate *P. serotina* invasion.

Keywords Biological invasions ·
Demography · Ripley's L · Dispersal kernel ·
Pine forest · Sandy soils

M. Vanhellemont (✉) · L. Wauters · L. Baeten ·
P. De Frenne · K. Verheyen
Laboratory of Forestry, Ghent University,
Geraardsbergsesteenweg 267, 9090 Gontrode, Belgium
e-mail: Margot.Vanhellemont@UGent.be

R.-J. Bijlsma
Centre for Ecosystem Studies, Alterra Wageningen UR,
P.O. Box 47, 6700 AA Wageningen, The Netherlands

M. Hermy
Division Forest, Nature and Landscape, K.U.Leuven,
Celestijnenlaan 200e, 3001 Leuven, Belgium

Introduction

The rate of biotic invasions has increased dramatically over the past 200 years due to the expansion in human mobility and trade (e.g., Lambdon et al. 2008). Moreover, the impact of invasive species on the functioning and biodiversity of native ecosystems has become readily apparent throughout the world (Mack et al. 2000), and both the adverse effects of biotic invasions and the efforts to control invasive species have resulted in huge economic losses (Pimentel et al. 2005). Many researchers have sought

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to identify sets of species traits that account for invasiveness and the habitat characteristics that contribute to the invasibility of native communities. Despite these efforts, the traits of successful invaders often appear to be idiosyncratic and context-dependent (Moles et al. 2008), and habitat invasibility is difficult to predict. Actual rates of invasion often appear to be largely a function of propagule pressure (Von Holle and Simberloff 2005).

Invasive woody plant species that alter the vegetation structure and the species composition of native communities pose conservation problems world-wide, both in forest and non-forest ecosystems (e.g., Martin 1999; Richburg et al. 2001; Tassin et al. 2006; Meiners 2007; Martin et al. 2009). Shade-tolerant woody species are a particular challenge because they typically have long generation times as well as multiple lag phases during the invasion process (Martin and Marks 2006; Wangen and Webster 2006). This makes the early detection of the invasiveness of shade-tolerant species difficult, and may allow a species to consolidate its position (and its impact on the ecosystem) long before the need for control measures becomes obvious. To gain insight into the patterns and ecosystem consequences of such protracted invasion processes, it would be interesting to study the colonization of invasive species in areas where the history of introduction and ecosystem disturbance are known. Because high propagule pressure and ecosystem disturbance have both been found to facilitate invasion processes (Lozon and MacIsaac 1997; Křivánek et al. 2006), research should focus on areas in which the invasive species has not been planted or managed. The widespread control measures in highly invaded regions often preclude the study of the ecological processes that govern the rate of invasion.

Prunus serotina Ehrh., a North American tree species introduced into Europe in the seventeenth century and planted widely during the first half of the twentieth century (Starfinger et al. 2003), has been considered an aggressive invasive species because its presence complicates forest management, hampers the regeneration of native deciduous species, and suppresses the development of a diverse herb layer (Starfinger 1990). Despite many intensive and costly control programs (Starfinger et al. 2003), the species has continued to spread, and has become one of the most frequently regenerating plant species in forests in Flanders, the northern part of Belgium (Waterinckx

and Roelandt 2001). There has been considerable recent research on the ecology of *P. serotina* in its introduced range (e.g., Deckers et al. 2005, 2008; Closset-Kopp et al. 2007; Pairon 2007; Verheyen et al. 2007), but most studies have focused on areas that are already heavily invaded. Studies on long-term population dynamics of *P. serotina* in areas where the species had not been planted intentionally remain scarce (e.g., Vanhellemont et al. 2009). *Prunus serotina* has clearly not yet fully occupied its potential range in Europe and its spread is believed to be limited by dispersal (Zerbe and Wirth 2006; Verheyen et al. 2007). Identification of the factors that control the rate of colonization of new sites by *P. serotina* and the consequences of the establishment of *P. serotina* for native populations and ecosystem processes will be critical to the development of appropriate management strategies.

In this study, we wanted to gain insight into the patterns of *P. serotina* colonization in a developing forest located in an area with an initially low propagule pressure of *P. serotina*. The Ossenbos forest, located in the Veluwe (the Netherlands), provided a unique opportunity for our study since it has not been managed for over 70 years, and *P. serotina* has not been planted nor managed; it is a pine forest on poor sandy soils, which represents the habitat in which *P. serotina* occurs most frequently in the introduced range. The specific research questions of our study were: (1) which factors are related to the patterns of *P. serotina* seedling, sapling, and tree abundance, (2) which factors affected the growth of *P. serotina*, (3) what is the pattern of *P. serotina* seed dispersal, and (4) how does the demography of *P. serotina* compare to the other tree species in the Ossenbos? Because the Ossenbos forest is characterized by a high herbivore pressure, we also compared the observed *P. serotina* colonization patterns for the Ossenbos with the *P. serotina* colonization in a forest without ungulates in Belgium (Vanhellemont et al. 2009).

Methods

Study species

Prunus serotina Ehrh. is a semi shade-tolerant opportunistic gap-phase species (Auclair and Cottam 1971) that grows on a wide variety of soils (Marquis

1990; Zerbe and Wirth 2006). Fruit production is high, even in forest understories (Pairon et al. 2006b), and variable between years (Starfinger 1990). Fruit production is strongly correlated with tree size in open landscapes (Deckers et al. 2008), but not in forest understories (Pairon et al. 2006b). Most fruits fall within 5 m of the parent tree; birds and mammals account for long-distance dispersal (>100 m; Pairon 2007). Many bird species disperse the fruits non-randomly to focal points within the landscape (Deckers et al. 2008). A short-lived seed bank (Wendel 1972) and a seedling/sapling bank (Starfinger 1990) occur at many sites. Under favorable conditions, seedlings grow rapidly and can produce seeds from the age of 4 years (Deckers et al. 2005). Moreover, the resprouting capacity is high, and stump sprouts grow rapidly, especially in full light (Closset-Kopp et al. 2007). The species is allotetraploid and has high genetic diversity (Pairon 2007).

Study area

The Ossenbos forest reserve (54 ha) is situated within the 3,600 ha artillery training camp De Harskamp in the Natura 2000 site Veluwe, the Netherlands (N52°08′ E005°48′), in a landscape matrix which includes forest patches, heathlands, and bare sand (Fig. 1). The site lies 39 m above sea level on poor wind-borne sand deposits. Minimum and maximum monthly mean temperatures are 2°C in January and 17°C in July, and mean annual precipitation is 850 mm (www.knmi.nl). The Ossenbos developed spontaneously around an east–west running mound that had been installed around 1832 to protect the heathlands, south of the mound, from the drifting sands north of the mound (Fig. 1). Pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L.) establishment close to the mound started around 1850 and 1900, respectively. Further tree colonization of the former heathland occurred between 1926 and 1965, while the former drift sand did not appear as forested until 1976. The first *P. serotina* plantings at De Harskamp, at 3 km from the Ossenbos, occurred in 1973 (A. Varkevisser, personal communication). Yet, *P. serotina* first became established in the Ossenbos around 1940, which indicates that the earliest colonization came from outside De Harskamp. By 2003, the mean basal area (BA) of the forest was 26.6 ± 1.3 m^2 ha^{-1}, and the mean stem density (N) was $1,169 \pm 81$ ha^{-1}, with *P. sylvestris* (85% of BA, 53% of N) and *P. serotina* (11% of BA, 44% of N) as the main tree species. Other tree and shrub species, present in low densities, were *Betula pendula* Roth, *Betula pubescens* Ehrh., *Q. robur*, *Quercus rubra* L., *Sorbus aucuparia* L., and *Frangula alnus* Mill. The forest reserve is the only area within the Harskamp in which hunting is prohibited and therefore acts as a safe site, which results in a high game density, i.e., around 1 ha^{-1} (A. Varkevisser, personal communication). The three species of large herbivores that occur in the area are red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*).

Data collection

Forty circular plots of 500 m^2 were located randomly on a 50 m × 50 m grid in the entire forest, and, in
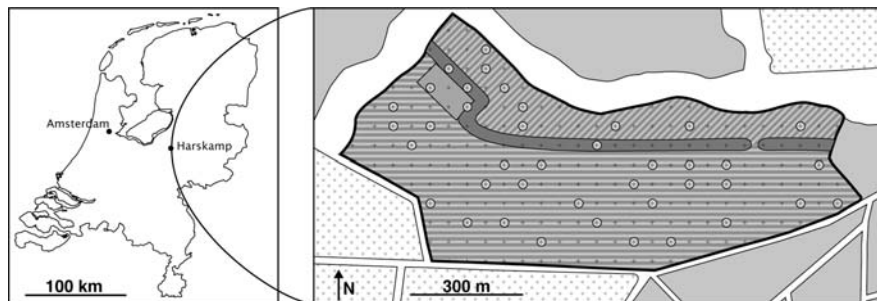

Fig. 1 *Left* location of Harskamp and the Ossenbos forest reserve (54 ha) in the Netherlands; *right* the Ossenbos (*black contour line*) with the 40 *circular* plots and the core area (*plain grey*), surrounded by open sand and sandy tracks (*white*), heathlands (*grey dots*), and forest patches (*dark grey*). The northern part of the Ossenbos, which developed on drift sand (shaded with *right-slanting lines*), is separated from the southern part, which developed on heathland (shaded with *horizontal lines*), by a mound that runs from west to east through the forest (*deep dark grey*)

addition, a study area of 70 m × 140 m, i.e., the core area, was installed in the oldest part of the forest reserve (Fig. 1). In the 40 circular plots, dendrometric and regeneration data were collected for each tree species in March 2003: position, diameter at breast height (dbh), and height (h) were measured for all living trees (dbh > 5 cm) in a circle with radius 12.6 m; and the height and number of saplings (dbh < 5 cm, h > 0.5 m) were recorded in an inscribed square plot of 18 m × 18 m.

In the core area, position (x, y-coordinates), dbh, and height were measured for all living and dead trees with a dbh larger than 5 cm in March 2003. In addition, in August 2007, further data were collected on *P. serotina* growth and establishment as well as on regeneration of other tree and shrub species. To study the growth of *P. serotina* in the core area, we selected 33 *P. serotina* individuals, distributed within the diameter range of *P. serotina* in the inventory data and located below the intimately mixed native tree species *P. sylvestris* and *Q. robur* (13 individuals), below the non-native *P. serotina* (11), or in a canopy gap (9). Diameter and height were measured, and stem cross sections (for small individuals) or tree cores (for large individuals) were taken at 20–30 cm above the root collar. Ring widths were measured to the nearest 0.01 mm using a positioning table (LINTAB) with associated software (TSAPWin; www.rinntech.com) and a stereomicroscope (Olympus SZX12). For each individual, competition was calculated with Daniels' competition index (Eq. 1; Daniels 1976), based on the diameter of and the distance to all neighboring trees that meet the criterion in Eq. 2:

$$CI_i = \sum_{j=1}^{N} \frac{dbh_j / dbh_i}{dist_{ij}} \tag{1}$$

$$\text{for} \quad \frac{dbh_i + dbh_j}{8} \geq dist_{ij}, \tag{2}$$

with CI_i the competition index of subject tree i, dbh_i the diameter at breast height for subject tree i (cm), dbh_j the diameter at breast height for competitor j (cm), $dist_{ij}$ the distance between subject tree i and competitor j (m), and N the number of competitors for subject tree i.

The core area was subdivided into 96 squares of 10 m × 10 m. At the centre of each square, we took a hemispherical photograph (Nikon D70S with a Sigma 8 mm fisheye lens), which was processed with Gap Light Analyzer (GLA version 2.0; www.ecostudies.org/gla) to calculate canopy openness over the zenith angle 0–63°. The central 60 squares were used to study regeneration of tree and shrub species. In the centre of each of these plots, a 4 m × 4 m regeneration plot and a 0.4 m × 0.4 m litter plot were defined. Since the forest reserve is located in an artillery training camp and fieldwork was only possible during a 2-week shooting-free period in summer, we could not quantify the seed rain of *P. serotina* directly. Instead, we collected litter in the 60 litter plots, measured the volume of the litter samples, and sorted out the seeds. Both intact seeds, representing a potential seed bank, and seed halves, representing germinated seeds, were counted. Since seeds of *P. serotina* found in the litter layer of forests have been shown to have a low germinability (O'Hanlon-Manners and Kotanen 2006), we only used the data for the germinated seeds for further analysis. In addition, the spatial position of the seed-bearing *P. serotina* trees in the core area was noted. For all tree and shrub species, regeneration was counted in the 60 regeneration plots. Seedlings were divided into four classes (classification after Closset-Kopp et al. 2007): seedlings resulting from seeds germinated in 2007 (stage I), seedlings < 20 cm (stage II), 20 cm < seedlings < 120 cm (stage IIIa), and seedlings > 120 cm (stage IIIb).

Data analysis

For our analysis of the colonization patterns and the demography of *P. serotina*, we focused on the core area, located in the oldest part of the forest, where *P. serotina* was present in the tree, shrub, and herb layer. In addition, the regeneration data for the circular plots were used to check whether the regeneration patterns that were observed in the core area also held for the younger portions of the forest. First, we analyzed the spatial patterns of trees and shrubs in the core area to determine the past establishment of *P. serotina* in the developing pine forest. Second, to examine the demography of *P. serotina*, we successively studied growth and seed densities of *P. serotina* in the core area, and the presence and abundance of seedlings and saplings in the core area and the circular plots. Third, we also studied the regeneration of native tree and shrub species, in the core area and in the circular plots, to compare the colonization potential of *P. serotina* with that of the native species. Data

analysis was performed in SPSS 15.0 (SPSS 2006) and R 2.7.0 (R Development Core Team 2008).

Spatial patterns

The 2003 data for individuals with a dbh > 5 cm were used to calculate basal area (m^2 ha^{-1}) and stem density (ha^{-1}) for living and dead trees in the core area. Based on the frequency histogram of the tree height data, the dataset was divided into trees ($h > 10$ m) and shrubs ($h < 10$ m). The frequency histograms for the dbh data of the *P. serotina* trees and shrubs were studied to gain further insight into the structure of the *P. serotina* tree and shrub layer. Using the add-on R library spatstat version 1.14-4 (Baddeley and Turner 2005), we evaluated the stem density for the main tree and shrub species spatially with isotropic Gaussian smoothing kernels, and analyzed the patterns of interactions between the spatial point patterns of the different tree species in the shrub and tree layer with bivariate Ripley's K (Ripley 1977). We calculated Ripley's L, a square root transformed Ripley's K, using Ripley's isotropic edge correction. The pointwise 5% upper and lower critical envelopes for testing the hypothesis of complete spatial randomness, i.e., $L(d) = 0$, were based on 999 Monte Carlo simulations of a uniform Poisson process. Observed $L(d)$ values lying within the envelopes indicate a random spatial association; observed $L(d)$ values larger than the upper envelope indicate a positive spatial association; $L(d)$ values smaller than the lower envelope indicate a negative spatial association.

Growth of *Prunus serotina*

For the sampled *P. serotina* trees and shrubs, multiple linear regressions were used to analyze the mean radial growth for the years 2001–2006 as a function of dbh, height, age, canopy openness, and competition. Next, the curve estimation procedure in SPSS was used to study the relationships between age and dbh and between age and height for *P. serotina* growing below *Q. robur* and *P. sylvestris*, below *P. serotina*, or in gaps. Interactive effects between the canopy tree neighborhood and the age of the studied *P. serotina* on the achieved dbh or height were investigated with ANCOVA analysis (Scheiner and Gurevitch 2001).

Dispersal kernels for *Prunus serotina*

We used inverse modeling (Ribbens et al. 1994) to relate our data on the seed and seedling densities in each plot to data on the location of seed-bearing trees. Overlapping seed shadows were used to model the density of seeds or seedlings with distance from the source tree, calculated as the product of fecundity, i.e., seed production, and the dispersal kernel, i.e., the probability density describing the scatter of seeds/seedlings about the source tree (Clark et al. 1999). Since Greene et al. (2004) found the lognormal dispersal kernel to be the best fit to observed dispersal curves, which was confirmed for *P. serotina* by Pairon et al. (2006b), we used the lognormal seed dispersal kernel (Eq. 3), multiplied by the seed production (Eq. 4), which was modeled as a function of the dbh of the source tree:

$$\frac{1}{(2\pi)^{1.5} S \, \text{dist}_{pt}^2} \exp\left(-\frac{(\ln(\text{dist}_{pt}/L))^2}{2S^2}\right) \qquad (3)$$

$$a(\text{dbh}_t)^b \qquad (4)$$

with S the shape parameter, L the scale parameter, dist_{pt} the distance between plot p and source tree t, dbh_t the dbh of source tree t, and a and b translating the dbh of the source tree into seed production. We determined kernels for seeds, for seedlings smaller than 20 cm (stage I and stage II), and for seedlings taller than 20 cm (stage IIIa and stage IIIb) in order to evaluate the local efficiency of the seed rain with regard to the subsequent regeneration stages. Calculating the dispersal kernels was done with maximum likelihood methods, using the R packages neighlikeli and likelihood version 1.0 (Murphy 2006a, b). Pearson correlations and the slope between observed and predicted seed/seedling densities were used to estimate the goodness of fit of the models.

Regeneration of tree and shrub species

We used the same approach for the study of the regeneration patterns for the seedlings in the core area and for the saplings in the circular plots. First, presence/absence of a species was modeled with binary logistic regressions based on the plot characteristics, i.e., basal area of the tree and shrub layers (m^2 ha^{-1}), stem density (ha^{-1}), and, for the core area, canopy openness (%). For *Q. robur* in the core area,

we also used the minimum distance to a seed tree (m) because *Q. robur* seed trees were present in the core area and local *Quercus* dispersion is mainly barochorous (Johnson et al. 2002). Next, to explain the abundance of the seedlings/saplings of a species, we performed a data reduction (PCA) on the plot characteristics, and calculated Pearson correlations between the seedling/sapling densities and the principal components. For the circular plots, we used the data on basal area of the tree and shrub layer, stem density, and maximum tree height (m). For the regeneration plots in the core area, we additionally used data on canopy openness and, for *P. serotina*, seed density (m^{-2}).

Results

Spatial patterns and forest structure in the core area

In the core area, *Pinus sylvestris* accounted for ca. 70% of the basal area, both for living and dead trees, while *Prunus serotina* showed the highest stem densities for living trees (71%) and for standing dead trees (79%) (Table 1). The tree layer was made up of *P. sylvestris* (62%, 177 ha^{-1}), *P. serotina* (28%, 82 ha^{-1}), and *Quercus robur* (10%, 29 ha^{-1}), while the shrub layer consisted almost completely of *P. serotina* (97%, 503 ha^{-1}), with only a few *Q. robur* (3%, 16 ha^{-1}) present. Shrubs (h < 10 m) of *P. serotina* showed a reverse J-shape frequency distribution across dbh classes, and had a dbh between 5 cm (62% of the shrubs) and 25 cm (1%). The histogram for the dbh of

P. serotina trees (h > 10 m) was bell-shaped and ranged from a dbh of 5 to 35 cm, with 60% of the trees having a dbh between 15 and 25 cm.

Figure 2 shows the spatial patterns of stem density for the main tree and shrub species in the core area. Areas with high densities of *P. serotina* trees (Fig. 2b) corresponded to areas with low densities of *P. sylvestris* and *Q. robur* trees (Fig. 2a) whereas *P. serotina* shrubs (Fig. 2c) were more abundant below *P. sylvestris* and *Q. robur* trees (Fig. 2a) than below *P. serotina* trees (Fig. 2b). These observations are further demonstrated in Fig. 3. Negative spatial dependence occurred between *P. serotina* trees and the two most common native species—*P. sylvestris* and *Q. robur*—for distances larger than 1.8 m (Fig. 3a), and between *P. serotina* shrubs and *P. serotina* trees for distances larger than 1 m (Fig. 3c). The positions of shrubs of *P. serotina* were independent of the positions of *P. sylvestris* and *Q. robur* trees at distances up to 16.3 m, but showed a positive spatial association for larger distances (Fig. 3b). Spatial associations between living and dead trees were random for all distances and all species, except for dead pines/oaks and shrubs of *P. serotina*, which showed clustering between 3.7 and 18.2 m (figures not shown).

Growth of *Prunus serotina*

Radial growth of *P. serotina* showed a significant relationship with dbh: ln growth = 0.083 + 0.491dbh ($R^2 = 0.66$, $P < 0.001$). Adding height, age, competition, or canopy openness did not improve the regression. *Prunus serotina* growing in gaps and

Table 1 Stem density (N, ha^{-1}) and basal area (BA, m^2 ha^{-1}) for the main tree species in the core area: living trees, standing dead trees, and lying dead trees

Species	Living		Dead			
			Standing		Lying	
	N (ha^{-1})	BA (m^2 ha^{-1})	N (ha^{-1})	BA (m^2 ha^{-1})	N (ha^{-1})	BA (m^2 ha^{-1})
Pinus sylvestris L.	188 (23)	23.5 (72)	54 (20)	3.6 (65)	89 (51)	2.1 (74)
Prunus serotina Ehrh.	586 (71)	6.7 (20)	215 (79)	1.9 (34)	83 (47)	0.7 (24)
Quercus robur L.	46 (6)	2.5 (8)	4 (1)	0.03 (1)	4 (2)	0.05 (2)
Total	821 (100)	32.8 (100)	273 (100)	5.5 (100)	176 (100)	2.8 (100)

Percentages of the total stem density or basal area are given between brackets

Sorbus aucuparia L. (0.01 m^2 ha^{-1}) and *Betula* spp. (0.03 m^2 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
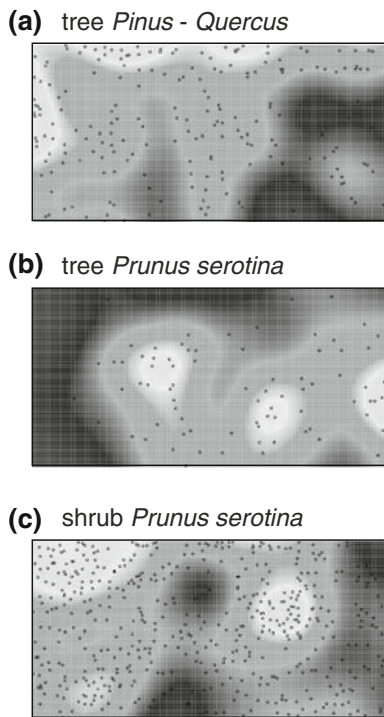
(a) tree *Pinus - Quercus*

(b) tree *Prunus serotina*

(c) shrub *Prunus serotina*

Fig. 2 The spatial position (*black dots*) and stem density (background color from *dark grey* for low densities to *light grey* for high densities) of *Pinus sylvestris* and *Quercus robur* trees (**a**), *Prunus serotina* trees (**b**), and *P. serotina* shrubs (**c**) in the 70 m × 140 m core area

below *P. serotina* showed a clear relationship between age and dbh ($R^2 = 0.94$ and 0.83) and between age and height ($R^2 = 0.96$ and 0.86). For *P. serotina* below *P. sylvestris*/*Q. robur*, the fits were worse: $R^2 = 0.61$ for dbh—age and $R^2 = 0.37$ for height—age (Table 2). Interactions between the growing situations

and age on the achieved dbh and height were significant ($P = 0.013$ and $P = 0.034$): the increases of dbh and height with age were higher in gaps than below *P. serotina* (Fig. 4).

Dispersal kernels for *Prunus serotina*

In the entire core area, 347 *P. serotina* trees and shrubs were found to be bearing fruits, of which 208 were in the central 60 plots. In the litter samples, we found 2,374 intact *P. serotina* seeds (247.3 m^{-2}) and 1,996 germinated seeds (207.9 m^{-2}). The observed mean seed production per tree was 6,984 for intact seeds and 5,872 for germinated seeds. Figure 5 shows the dispersal kernels for *P. serotina* seeds ($r = 0.27$, slope $= 0.97$), small seedlings (stage I and stage II; $r = 0.43$, slope $= 0.96$), and large seedlings (stage IIIa and stage IIIb; $r = 0.17$, slope $= 0.95$). Seeds and small seedlings both displayed maximum probability densities close to the source tree, while large seedlings showed a maximum around 13 m from the source tree.

Regeneration of tree and shrub species

Table 3 shows the seedling data for the tree and shrub species in the core area. *Prunus serotina* was by far the most abundantly regenerating species and the only species with stage IIIb seedlings, i.e., seedlings taller than 120 cm. For *P. sylvestris*, only stage I seedlings, i.e., resulting from seeds germinated in the year of sampling, were found. *Prunus serotina*, *Sorbus aucuparia*, and *Q. robur* showed the highest
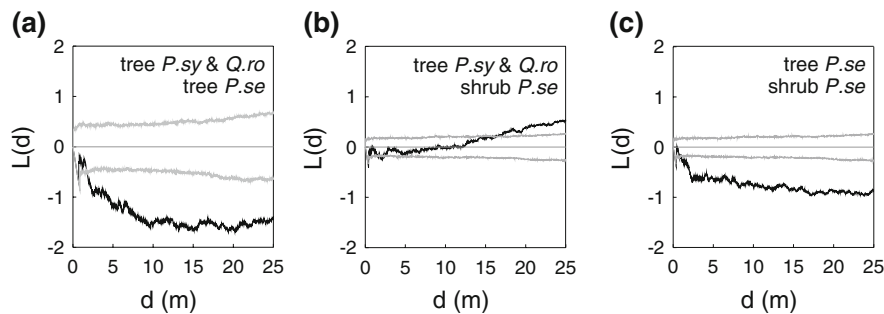

Fig. 3 Bivariate Ripley's L for the point patterns of *Pinus sylvestris* (*P.sy*) and *Quercus robur* (*Q.ro*) trees on the one hand and *Prunus serotina* (*P.se*) trees (**a**) or *P. serotina* shrubs (**b**) on the other hand, and for *P. serotina* trees and shrubs (**c**).

The observed *L(d)* values are indicated in *black*, the 5% upper and lower critical envelopes for the hypothesis of complete spatial randomness are indicated in *grey*

Table 2 Equations of the linear and power regressions for the relationships dbh—age and height—age for *Prunus serotina* growing in gaps, below *Pinus sylvestris* or *Quercus robur*, and below *P. serotina*

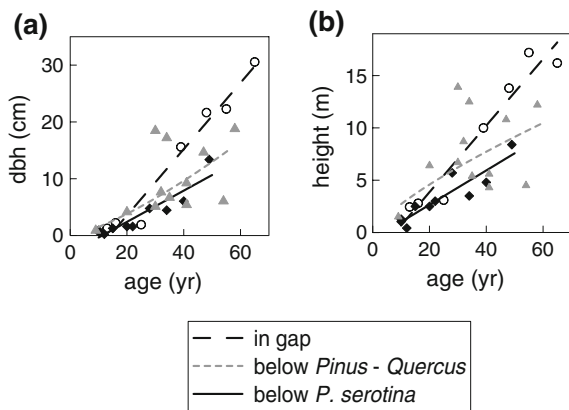|	Equation	R^2	P
dbh—age			
In gap	$-8.149 + 0.584 \times age$	0.96	<0.001
Below *P. sylvestris*–*Q. robur*	$0.070 \times age^{1.335}$	0.61	0.003
Below *P. serotina*	$-3.1 + 0.275 \times age$	0.86	<0.001
height—age			
In gap	$-2.498 + 0.318 \times age$	0.94	<0.001
Below *P. sylvestris*–*Q. robur*	$0.482 \times age^{0.752}$	0.37	0.037
Below *P. serotina*	$-0.625 + 0.164 \times age$	0.83	<0.001

Fig. 4 Relationships between dbh—age (**a**) and height—age (**b**) for *Prunus serotina* in gaps (*open circles*), below *Pinus sylvestris* or *Quercus robur* (*grey triangles*), and below *P. serotina* (*black diamonds*)
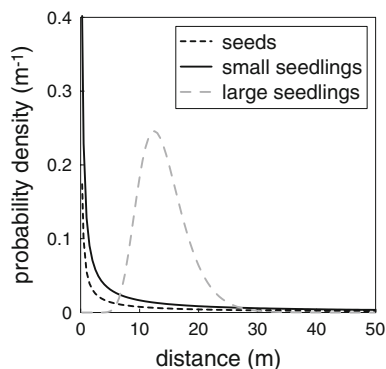

Fig. 5 Probability density of seeds (*dashed black line*), seedlings smaller than 20 cm (*solid black line*), and seedlings taller than 20 cm (*dashed grey line*) of *Prunus serotina* in the core area as a function of the distance from the source tree

densities for stage II seedlings: most seedlings of these species were smaller than 20 cm. Logistic regressions for presence/absence of the species'

regeneration, based on the characteristics of the tree and shrub layer, were not significant. The abundance of *P. serotina* seedlings smaller than 20 cm increased with seed density (stage I: $r = 0.50$, $P < 0.001$; stage II: $r = 0.44$, $P = 0.001$), and the abundance of *P. serotina* seedlings taller than 20 cm (stage IIIa: $r = -0.50$, $P < 0.001$; stage IIIb: $r = -0.42$, $P = 0.001$) was correlated with the principal component 'competition' (eigenvalue = 1.352), which contrasted basal area ($r = 0.77$) and stem density ($r = 0.73$) with canopy openness ($r = -0.48$). Thus, the abundance of the seedlings taller than 20 cm was higher in plots with high canopy openness and a low basal area and stem density. No significant correlations were found for the other species.

Saplings were found in all circular plots. The most frequently present species were, with the number of plots and mean density in these plots between brackets: *P. serotina* (40 plots, 5,477 ha^{-1}), *S. aucuparia* (23 plots, 168 ha^{-1}), *P. sylvestris* (10 plots, 762 ha^{-1}), *Frangula alnus* (9 plots, 158 ha^{-1}), and *Q. robur* (9 plots, 65 ha^{-1}). Saplings of *Betula* spp. and *Ilex aquifolium* L. occurred in only three plots and in very low numbers. We found no significant relationships between presence/absence and abundance of tree species regeneration on the one hand and the characteristics of the tree and shrub layer of the circular plot on the other hand, except for *P. serotina*. Ln-transformed abundances of *P. serotina* saplings smaller than 2 m ($r = 0.35$, $P = 0.037$) and taller than 2 m ($r = 0.55$, $P = 0.001$) were significantly correlated with the principal component (eigenvalue = 1.166) that combined maximum tree height, basal area of tree and shrub layers, and stem density. *Prunus serotina* saplings were more abundant in plots with a high stem density and with a high basal area for both the tree and the shrub layer.

Table 3 Regeneration of tree and shrub species in the 60 regeneration plots in the core area: density (ha^{-1}) and the number (*n*) and percentage (%) of plots

Species	Density	Plots	
	(ha^{-1})	*n*	%
Prunus serotina Ehrh.	182,646	60	100
Stage I	10,875	60	100
Stage II	149,656	60	100
Stage IIIa	20,771	59	98
Stage IIIb	1,344	38	63
Pinus sylvestris L.	7,844	56	93
Stage I	7,844	56	93
Sorbus aucuparia L.	1,833	44	73
Stage I	42	3	5
Stage II	1,396	39	65
Stage IIIa	396	21	35
Quercus robur L.	542	31	52
Stage I	83	7	12
Stage II	385	23	38
Stage IIIa	73	7	12
Frangula alnus Mill.	323	18	30
Stage I	10	1	2
Stage II	135	9	15
Stage IIIa	177	12	20
Ilex aquifolium L.	73	7	12
Stage II	73	7	12

Total regeneration per species is subdivided into seedlings resulting from seeds germinated in 2007 (stage I), seedlings smaller than 20 cm (stage II), seedlings between 20 and 120 cm (stage IIIa), and seedlings taller than 120 cm (stage IIIb)

Regeneration of *Taxus baccata* L. (stage II), *Betula pendula* Roth (stage II), and *Amelanchier lamarckii* F.G. Schroed. (stage IIIa) did only occur in one or two plots and in densities between 10 and 20 ha^{-1}

Discussion

Studies on spontaneous invasion patterns in areas characterized by an initially low propagule pressure can provide insight into the ecological mechanisms associated with invasion processes while ruling out possibly confounding effects of control measures or deliberate introduction events. Our study on the spontaneous invasion of *Prunus serotina* in the Ossenbos forest reserve shows that spatial abundance data for different life stages are a powerful tool to unveil the factors influencing the invasion process of a long-lived invasive species.

Prunus serotina colonization and demography

The first *P. serotina* establishment in the Ossenbos in 1940 was most probably the result of long-distance dispersal by birds because by that time, the pine and oak trees in the developing Ossenbos were large enough to have acted as focal trees in the open heathland landscape (cf. Deckers et al. 2008). By 2003, the Ossenbos had developed into a *Pinus sylvestris*—*P. serotina* forest, with high *P. serotina* abundances in well-structured forest plots characterized by a high basal area and stem density. *Prunus serotina* was the only species present in the tree and shrub layer as well as in (extremely) high seedling and sapling densities.

Prunus serotina trees occurred mainly in gaps of the pine/oak canopy, and the growth of *P. serotina* was highest in gaps, which supports the gap-dependence of *P. serotina* as reported in both its native (Auclair and Cottam 1971) and introduced range (Starfinger 1990; Closset-Kopp et al. 2007). The semi-shade tolerance of *P. serotina* was further illustrated by the high density of *P. serotina* shrubs below light-demanding *P. sylvestris* and *Quercus robur* trees, the relatively low density of *P. serotina* shrubs below shade-casting *P. serotina* trees, and the positive correlation between canopy openness and the abundance of *P. serotina* seedlings taller than 20 cm.

Seed production per tree and seed densities in the litter layer were high and similar to other studies in forests in the introduced range (Pairon et al. 2006a, b; Closset-Kopp et al. 2007), but much higher than values observed in the native range (Smith 1975). The extremely high densities of *P. serotina* seedlings smaller than 20 cm indicate the build-up of a persistent seedling bank (cf. Closset-Kopp et al. (2007) for the introduced range and Marquis (1990) for the native range), and the higher abundance of *P. serotina* seedlings taller than 20 cm in plots with a higher canopy openness suggests that the height of suppressed *P. serotina* seedlings depends on the light level (cf. Knight et al. 2008). The observed increase in mean distance from the source tree for taller seedlings fits in with the Janzen-Connell hypothesis (Janzen 1970; Connell 1971), which has already been

shown to hold for *P. serotina* in its native range (e.g., Packer and Clay 2000). Our data also suggest some kind of 'shrub bank', with *P. serotina* trees of up to 60 years old and still less than 10 m high growing below *P. sylvestris* or *Q. robur*.

The herbivory hypothesis

Prunus serotina was omnipresent in the forest reserve whereas native deciduous species occurred only sporadically and most native seedlings did not grow taller than 20 cm. Consequently, one would be tempted to consider *P. serotina* as a prolific and successful invasive species. Nonetheless, in a similar study in a mixed deciduous forest in Belgium, *P. serotina* did not act as a prolific invader (data shown in Vanhellemont et al. 2009). For both the Ossenbos (this study) and the Liedekerke forest reserve (Vanhellemont et al. 2009), the propagule pressure was low at the beginning of the invasion process. Ungulates were absent in the Liedekerke forest reserve whereas game densities were exceptionally high in the Ossenbos (i.e., 1 ha^{-1}). The two non-native species that occurred in both forests, i.e., *P. serotina* and *Quercus rubra*, showed contrasting colonization patterns. *Prunus serotina* successfully invaded the Ossenbos, but did not show a rapid spread in Liedekerke. *Quercus rubra* did not show successful regeneration in the Ossenbos although seed trees were present in the forest and *Q. rubra* had been planted next to the forest in 1914 (A. Varkevisser, personal communication). In the Liedekerke forest reserve, on the other hand, *Q. rubra* regeneration was locally abundant and the species had been able to triple its basal area during the 20-year study period (Vanhellemont et al. 2009).

Seeing the differences in colonization for *P. serotina* and *Q. rubra* in these two forests, we hypothesize that the high herbivore pressure in the Ossenbos forest reserve has favored *P. serotina* colonization above colonization of the tree and shrub species that would naturally occur on the poor sandy soils of the Ossenbos, i.e., *Betula* spp., *Q. robur*, and *Sorbus aucuparia* (Van der Werf 1991). First, even at much lower ungulate densities, i.e., ca. 0.15 ha^{-1}, in similar forests in the Veluwe ecoregion, Kuiters and Slim (2000, 2002) found equally low regeneration densities for native species, with almost no seedlings growing above the height of the herb layer, i.e.,

30–50 cm. Second, although wild boar feed on *P. serotina* fruits (Starfinger 1990), most *P. serotina* seeds are defecated unharmed. Acorns, on the other hand, are consumed completely and are a preferred food source for red deer and, particularly, wild boar (Groot Bruinderink et al. 1994; Gómez et al. 2003), which might explain the low densities of *Q. robur* (and *Q. rubra*) seedlings despite the presence of seed trees. Third, in its native range, *P. serotina* is less affected by deer browsing than its associated species, with the result that the species may dominate seedling and sapling layers (Marquis 1990; Horsley et al. 2003). Fourth, Eschtruth and Battle (2009) recently showed that a generalist native herbivore, i.e., white-tailed deer (*Odocoileus virginianus*), can facilitate, and even accelerate, the invasion of an exotic shrub species in forests.

Implications for management and suggestions for further research

The comparison of the *P. serotina* colonization patterns in this study and the forest reserve in Vanhellemont et al. (2009) illustrates that invasion processes may differ between ecosystems and stresses the importance of studying an invasive species in combination with the resident community in the recipient ecosystem (cf. Facon et al. 2006). Our study also shows that *P. serotina* is able to thrive under extremely high ungulate densities when other sources of food, e.g., the surrounding heathlands, are available. Although grazing has been suggested as a control measure for *P. serotina*, it is clear from this study that large herbivores may facilitate *P. serotina* invasion.

In order to investigate the possible impact of positive feedback mechanisms associated with herbivory on *P. serotina*, it would be interesting to study spontaneous *P. serotina* colonization at sites with different ungulate densities. In the Ossenbos forest reserve, the forest development in the absence of ungulates might be studied by means of exclosures in patches where seed sources or large saplings of other species are already present. Are native tree and shrub species able to compete with *P. serotina* in the absence of herbivory? Will *P. serotina* continue to recruit below *P. serotina*? Particular attention should be dedicated to patches in which both *P. serotina* and the native shrub species *S. aucuparia* are present

because the ecology of these species is similar and they often co-occur (Verheyen et al. 2007; Vanhellemont et al. 2009). Since seedlings and saplings of *S. aucuparia* cannot grow into the tree/shrub layer under high grazing pressure (Linder et al. 1997), the species might profit from a decrease in herbivore pressure. Besides, *S. aucuparia* seedlings are shade-tolerant (Raspé et al. 2000), which might enable *S. aucuparia* to survive in shaded conditions, e.g., below *P. serotina*. Thus, a decrease in herbivore pressure in areas with *S. aucuparia* might lead to a change in the further development of the forest.

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