

Effects of landscape structure on the invasive spread of black cherry *Prunus serotina* in an agricultural landscape in Flanders, Belgium

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Analysing invasive spread from a landscape ecological perspective forms an important challenge in plant invasion ecology. The present study examines the effects of landscape structure on the spatial and temporal dynamics of an expanding black cherry *Prunus serotina* population within a rural landscape in Flanders, Belgium, carrying a dense network of interconnected hedgerows. The study area, 251 ha in size, harboured a total of 2962 *P. serotina* individuals. The population was characterised by a negative exponential age distribution, a high growth rate and an early and continuous reproduction throughout the species' life cycle. The historical rate of spread of the species through the hedgerow network progressively increased with time, especially during the last decade. Spatial point pattern analysis revealed that the individuals had a significantly clustered distribution pattern and were spatially aggregated around seed sources, hedgerow intersections and roosting trees. Logistic regression analysis confirmed the effect of landscape structure on *P. serotina* occurrence, suggesting directional long distance dispersal by avian dispersal vectors, resulting in a differential seed pressure throughout the hedgerow network due to the preference of dispersing birds for roosting in structurally rich hedgerow with large trees near hedgerow intersections. Hence, the distribution of *P. serotina* in agricultural landscapes was strongly mediated by dispersal processes. Furthermore, decreasing spatial aggregation along the species life cycle, with especially seedlings and saplings being significantly aggregated while adult individuals were mostly distributed at random, and a relative outward shift of seedling recruitment curves with time indicate density dependent mortality, probably caused by intraspecific competition.

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Ecosystem invasion by introduced species forms a major threat to biodiversity worldwide (Lodge 1993, Lake and Leishman 2004). By altering the availability of nutrients and physical resources, invasive species can affect both ecosystem structure and functioning (cf. the concept of ecosystem engineers by Crooks 2002). Basic ecosystem processes, such as hydrological buffering, biogeochemical cycling and disturbance dynamics, may be modified with effects at both the community and population scale (Gordon 1998, Mack and D'Antonio 1998). A decrease

in habitat complexity and heterogeneity associated with the proliferation of introduced species often leads to a decline in native species richness (Lodge 1993, Hanowski et al. 1997).

The invasion success of a non-native species depends on the characteristics of the introduction events, species attributes and ecosystem properties (Kolar and Lodge 2001, Lake and Leishman 2004). Escape from natural enemies (e.g. competitors, pathogens and predators) often enhances species spread within a new region (Wolfe 2002,

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Keane and Crawley 2002, Mitchell and Power 2003). In addition, landscape structure – or spatial pattern more in general – may affect the various stages of the invasion process, both directly and indirectly through effects on the species' dispersal vectors (With 2002). Although landscape ecology (i.e. the study of the effect of spatial pattern on ecological process, cf. Turner 1989) emerged as a scientific discipline more than two decades ago, until now little research explicitly addressed the effect of landscape structure on species invasion (With 2002).

As a model species to analyse invasive spread from a landscape ecological perspective, black cherry *Prunus serotina* was chosen. Black cherry, a bird-dispersed tree native to North and Central America, is a typical opportunistic gap species colonising openings in mixed, temperate forests and is often temporally dominant during secondary succession (Fowells 1965, Auclair and Cottam 1971, Smith 1975). The species was widely introduced in west and central Europe for timber production and soil amelioration purposes, mainly during the first half of the 20th century (Bakker 1963, Muys et al. 1993). While silvicultural expectations remained largely unfulfilled, the species expanded strongly and spontaneously during the last few decades, invading both forest fragments and linear woody habitat patches within European agricultural landscapes (Wallis de Vries 1986, Muys and Maddelein 1993). Especially on poorer soils, it often impedes nowadays natural regeneration of less competitive native species (Muys et al. 1993). Although large-scale, costly eradication programmes exist (Van den Meersschaut and Lust 1997), the success of these symptomatic treatments remains highly variable and further insight in the invasion process is needed to develop a more holistic black cherry management strategy.

For several bird dispersed species, a strong link between landscape structure and population dynamics has been demonstrated. While bird communities are strongly affected by landscape structure and composition (Lichstein et al. 2002), spatial patterns of seed deposition by birds often have a lasting impact on the population dynamics of the species dispersed (Herrera et al. 1994). Frequently, recruitment patterns of ornithochorous species peak around specific bird-attracting landscape structures such as forest edges and perches or roosting trees (McClanahan and Wolfe 1993, Wenny 2000). Hence, the question arises to what extent the population dynamics of *P. serotina*, as a bird-dispersed species, is affected by landscape structure.

The reason for the invasive character of the species within its non-native range needs further clarification as well. Evidence exists that the expansion of *P. serotina* within its region of introduction can be explained by the enemy-release hypothesis (cf. Keane and Crawley 2002). While in its native range a negative feedback between plant and soil community (more specifically *Pythium*

spp.) impedes *P. serotina* proliferation and promotes species coexistence (Packer and Clay 2000, 2003), the soil community in its introduced range seems to enhance the growth of *P. serotina* seedlings near conspecific individuals (Reinhart et al. 2003).

According to the Janzen-Connell hypothesis (Janzen 1970, Connell 1971), seedling recruitment success increases with distance from parent tree because of density- or distance dependent predation or pathogen attack on seeds and seedlings, resulting in a relative outward shift of seedling recruitment curves with time (Barot et al. 1999a, Peters 2003). However, escape from host-specific soil pathogens within its region of introduction (as reported by Reinhart et al. 2003) may lead European *P. serotina* populations to depart from this model, with no detectable outward shift of seedling cohorts with age.

Given the ecological and economic importance of black cherry invasion, disentangling the basic processes governing *P. serotina* spread forms an important challenge in present-day ecological research. This study analyses the spatial and temporal dynamics of an expanding black cherry population within a rural landscape in Flanders, Belgium, characterised by the presence of a dense network of interconnected hedgerows. The following objectives are addressed explicitly: 1) The age structure of the *P. serotina* population is determined and age-size and age-reproduction relationships established, using tree ring analysis and allometric data. 2) A detailed reconstruction of the invasion process is made and the historical rate of spread of the species through the hedgerow network is assessed. 3) The spatial distribution of *P. serotina* individuals within the hedgerow network is analysed for the entire population and different life stages separately, with a focus on the spatial clustering of individuals and spatial association with specific landscape elements, using spatial point pattern analysis. 4) The effect of landscape structure on *P. serotina* invasion is assessed, with special attention for detecting dispersal-mediated distribution patterns, using logistic regression analysis. 5) Seedling recruitment curves are constructed and evaluated against predictions by the Janzen-Connell hypothesis.

Methods

Study area and data collection

The study area, 251 ha in size, is located in an ancient agricultural landscape within the municipality of Meerhout, in the south of the province of Antwerp, Flanders, Belgium (51°7'31 N–5°2'24 E). The landscape has a typical bocage structure with small fields surrounded by hedgerows (linear strips of woody vegetation, cf. Forman and Baudry 1984). Average hedgerow density is ca 150 m ha⁻¹ (Deckers et al.

2004). Different types of grassland and corn for silage production dominate present land use. Soils are moist to moderately dry with a sand to sandy loam texture and the landscape is flat with a maximum elevation difference of only 6 m (Tavernier and Maréchal 1972). Hedgerow tree and shrub layer is typically dominated by the following species: *Quercus robur*, *Frangula alnus*, *Betula pendula* and *Sorbus aucuparia* (nomenclature follows De Langhe et al. 1988). However, *P. serotina* is rapidly invading the hedgerow network. At present, about one third (33.5%) of the hedgerows harbour black cherry individuals (Deckers et al. 2004). The absence of tree planting and the large-scale abandonment of traditional management practices during the last few decades ensure that the *P. serotina* population under study is representative for a naturally expanding population in a rural landscape context, with few individuals having been introduced or removed actively. More details about the study area and hedgerow network can be found in Deckers et al. (2004).

The exact location (x-y coordinates) of all *P. serotina* individuals present within the study area was determined. Each hedgerow (i.e. discrete segment between two different nodes of the hedgerow network) was surveyed systematically over its entire length with all *P. serotina* individuals being mapped. Individuals were grouped in four different life stages: seedlings (height <0.3 m), saplings (height 0.3–1.5 m), non-reproducing adults (height >1.5 m, no fruit production) and reproducing adults (height >1.5 m, fruit production). Height and circumference were measured and the occurrence of sexual reproduction recorded for all individuals. Age was determined for a random subset of 100 individuals, using tree ring analysis. Distance to the nearest seed source (i.e. *P. serotina* tree reproducing at time of establishment of individual, see data analysis section for computational details) and distance to the nearest hedgerow intersection (i.e. node connecting two or more segments within the hedgerow network) were quantified in a GIS-environment using ArcView 3.2a (Anon. 2000). Presence of a roosting tree (i.e. any tree >7 m) was registered in the field. Field work was done during flowering season from May to June 2003.

Data analysis

Regression analysis was used to determine age-height and age-circumference relationships, based on the subset of individuals with established age. The curve estimation procedure in SPSS 11.0 for Windows (Anon. 2002) was employed to evaluate different types of models (linear, quadratic, logarithmic, ...). The model with the best fit was retained and applied to all registered individuals to assess their age based on height and circumference data (i.e. a predictive modelling approach, sensu Mac Nally

2000), allowing the age structure of the *P. serotina* population to be constructed. Presence/absence of reproduction was modelled as a function of tree age using logistic regression analysis (Hosmer and Lemeshow 1989), enabling the average age of first reproduction to be established. Next, potential seed sources were determined for each age class separately as all individuals with an estimated age higher than the average age of first reproduction, augmented with the age of the respective cohort. Furthermore, a combination of the age and location of all individuals allowed an historical reconstruction to be made of the invasion process and the species' rate of spread through the hedgerow network, defined as the yearly fraction of hedgerows colonised by *P. serotina*. Quadratic regression was used to model the temporal evolution of this rate of spread.

The spatial distribution of *P. serotina* individuals within the hedgerow network was analysed with second-order spatial point pattern analysis, using the variance of interpoint distances to describe two-dimensional point distribution patterns (Dale et al. 2002, Perry et al. 2002). More specifically, network K-function analysis (Okabe and Yamada 2001, Spooner et al. 2004a, b), a network based adaptation of Ripley's K-function (Ripley 1976) was applied, using SANET 2.0 (Okabe et al. 2004). Analyses were done for the entire *P. serotina* population and for the different life stages (seedlings, saplings, non-reproducing adults and reproducing adults) separately. While spatial clustering of points was determined with the univariate network K-function, spatial association between groups of points (for example *P. serotina* individuals and roosting trees) was assessed with the bivariate or cross network K-function (procedures according to Spooner et al. 2004b). The network K-function is a cumulative function which can be interpreted as the total number of points located within a given shortest network distance d of each point, corrected for the overall point density of the network. The observed function $\hat{K}(d)$ was compared with the expected function $K(d)$, following a binomial distribution for a finite connected network, allowing a 95% confidence interval envelope to be constructed. Significant clustering or association of points (for respectively univariate or bivariate analyses) occurs if $\hat{K}(d)$ exceeds the confidence interval upper limit. A drop of $\hat{K}(d)$ below the confidence interval lower limit reveals significant regularity or repulsion. If $\hat{K}(d)$ lays within the boundaries of the confidence interval, no significant departure from spatial randomness or independence can be demonstrated.

Multiple logistic regression analysis (Hosmer and Lemeshow 1989) was used to examine the effect of landscape structure on *P. serotina* distribution. First, the studied hedgerow network was divided in 36 726 one-meter segments and *P. serotina* point data rearranged to presence/absence data at the segment level. Next, the

occurrence of *P. serotina* was modelled as a function of the distance to the nearest seed source, distance to the nearest hedgerow intersection and presence of a roosting tree. Logistic regression models were constructed for each variable separately and the three variables combined. Moreover, analyses were done for the entire *P. serotina* population and for the different life stages separately. Finally, the effect of distance to the nearest hedgerow intersection was examined in more detail by fitting models separately for different types of intersections (O, L, T and X-type intersections, i.e. hedgerows with a dead-end and connected with respectively one, two and three or more adjacent hedgerows).

Age-specific distance data were used to assemble seedling recruitment curves. More specifically, histograms representing the percentage of individuals as a function of the distance to the nearest seed source were constructed for each age class. Linear regression analysis was used to explore the relationship between seedling age and distance to nearest seed source in more detail. Except if stated otherwise, all analyses were done with SPSS 11.0 for Windows (Anon. 2002).

Results

Basic population characteristics

Within the study area, a total of 2962 *P. serotina* individuals were recorded, of which 40% (1177) were seedlings, 35% (1049) saplings, 10% (285) non-reproducing adults and 15% (451) reproducing adults. Both height and circumference strongly differed between individuals, with plant height ranging from 0.1 to 18.0 m (average: 0.99 m) and circumference from 0.4 to 107.0 cm (average: 5.20 cm). More than one third of the hedgerows (171 out of 511) harboured black cherry individuals. An overview of the spatial distribution of the *P. serotina* individuals within the studied hedgerow network landscape is presented in Fig. 1.

Age structure, age-size and age-reproduction relationships

The curve estimation procedure revealed that age-size relationships were described most accurately using quadratic regression models. The final model retained predicted tree age (Y) based on a combination of plant height (X_1) and circumference (X_2), using the following relationship: $Y = 1.33X_1 - 0.16X_1^2 + 0.32X_2 - 0.01X_2^2 + 0.03X_1X_2$ ($R^2 = 0.99$, $p < 0.001$). Based on this model, the age of all registered individuals was calculated. Ages obtained ranged from 1 to 35 yr, with an average of 2.91. In general, the population's age structure exhibited an exponential decline in the number of individuals with age, although the first two age classes (containing ca 70%



Fig. 1. Spatial distribution pattern of the *P. serotina* individuals recorded within the studied hedgerow network (not all individuals are visible due to overlap of adjacent points).

of the total population) were somewhat over-represented (Fig. 2).

Tree age strongly affected *P. serotina* reproduction (logistic regression: $\chi^2 = 2077.27$, $p < 0.001$; Nagelkerke $R^2 = 0.88$). Fruit production started at the age of 4 yr (with ca 10% of the individuals actively reproducing) and increased steeply between 4 and 7 yr (from 10 to >90% reproduction). The average age of first reproduction was equal to 5.2 yr. Almost all individuals older than 7 yr reproduced sexually.

Historical rate of spread

The species' rate of spread through the hedgerow network progressively increased during history (Fig. 3,

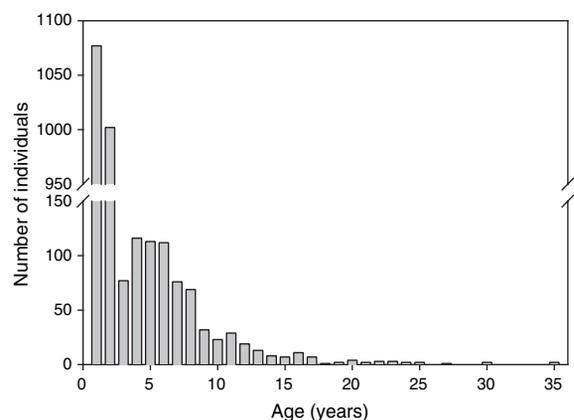


Fig. 2. Age structure of the entire *P. serotina* population.

quadratic regression: $R^2 = 0.92$, $p < 0.001$). While the average rate of spread was quite low from 1970 to 1980 (with $< 1\%$ of the hedgerows being colonised each year), it was somewhat higher, but more variable between 1980 and 1990. After 1990, the fraction of hedgerows colonised yearly rose sharply. At present, $> 5\%$ of the hedgerows within the study area is colonised by *P. serotina* each year.

Spatial patterns of *P. serotina* individuals

Univariate network K-function analysis revealed that the *P. serotina* individuals were not randomly distributed within the hedgerow network habitat (Fig. 4a, Table 1). Significant spatial clustering was demonstrated for the entire *P. serotina* population and for three of the four different life stages separately (more specifically seedlings, saplings and non-reproducing adults). Only the group of the reproducing adults followed a random distribution pattern.

Significant spatial association among life stages and between *P. serotina* individuals and focal landscape points was demonstrated with bivariate network K-function analysis (Table 1). Both the occurrence of seedlings and saplings was strongly associated with the nearby presence of reproducing adults (Fig. 4b). The distribution of non-reproducing adults however was independent from the spatial pattern of reproducing adults. The entire *P. serotina* population, as well as the seedlings and saplings separately, were significantly aggregated around hedgerow intersections. Moreover, *P. serotina* individuals (especially seedlings) were spatially associated with roosting trees.

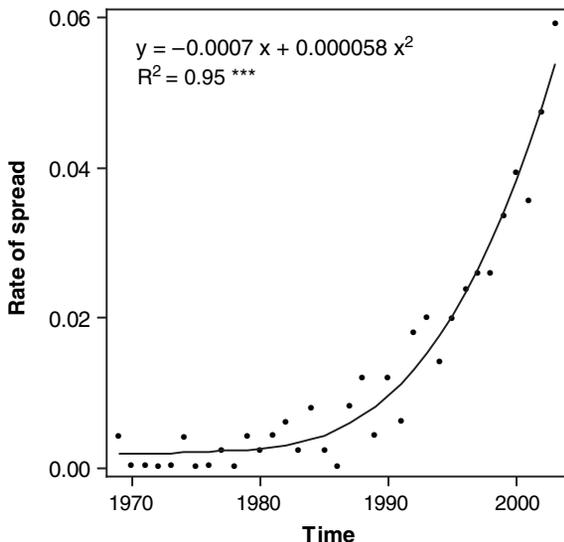


Fig. 3. *Prunus serotina* rate of spread (i.e. fraction of hedgerows colonised yearly) as a function of time (curve fitted using a quadratic regression model).

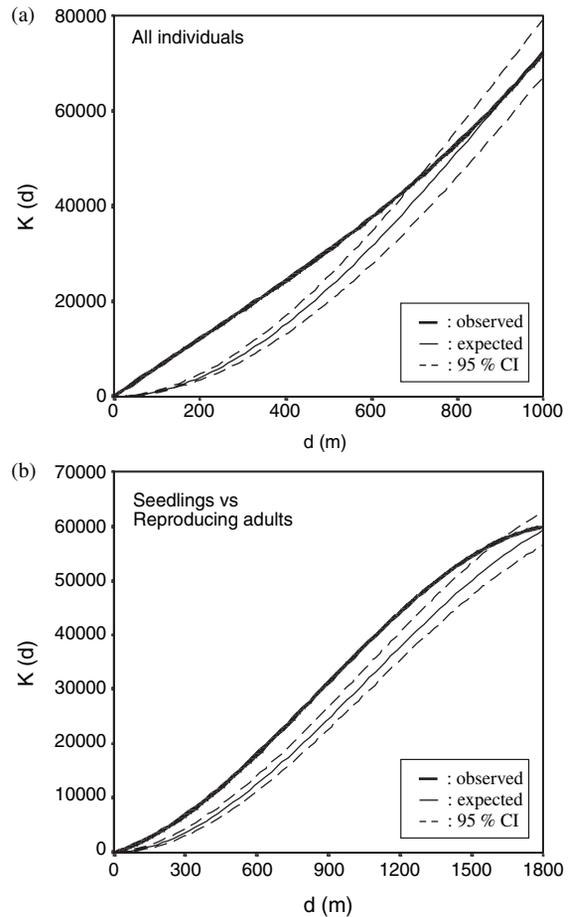


Fig. 4. Example of univariate (a) and bivariate (b) network K-function analysis. Both the observed function $\hat{K}(d)$ and the expected function $K(d)$ as well as the 95% confidence interval envelope are presented as a function of the shortest network distance d . A rise of $\hat{K}(d)$ above the confidence interval upper limit demonstrates significant spatial clustering (a) or spatial association (b).

Landscape structure and species invasion

The occurrence of *P. serotina* within the hedgerow network was strongly affected by landscape structure. The species' probability of occurrence significantly decreased with increasing distance to the nearest seed source, with hardly any hedgerow being colonised beyond 300 m from the nearest source tree (Fig. 5a). A clear decrease in probability of occurrence with increasing distance to the nearest hedgerow intersection could be observed as well (Fig. 5b). For distances exceeding 100 m, colonisation probability rapidly dropped to almost zero. In addition, the presence of a roosting tree strongly affected *P. serotina* occurrence (Fig. 5c). A nearly two-fold increase in probability of occurrence was demonstrated for hedgerow segments situated under the canopy of a large tree. An overview of the results of the multiple logistic regression analyses, exploring the combined effect of these three variables, for all

Table 1. Analysis of the spatial distribution of *P. serotina* individuals within the hedgerow network landscape using spatial point pattern analysis.

	Spatial clustering	Spatial association		
		Reproducing adults	Hedgerow intersections	Roosting trees
Seedlings	C	A	A	A
Saplings	C	A	A	N
Non-reproducing adults	C	N	N	N
Reproducing adults	N	n	N	N
All individuals	C	n	A	A

Spatial clustering determined using univariate network K-function analysis, spatial association using bivariate network K-function analysis. Significant departures from spatial randomness (univariate analysis) or spatial independence (bivariate analysis) are considered at the $p < 0.05$ significance level: C = spatial clustering, A = spatial association, N = no pattern (randomness or independence), n = not applicable. Characters in bold refer to the examples presented in Fig. 4.

P. serotina individuals and the different life stages separately, is given in Table 2. Highly significant models were obtained for all groups of plants, with a negative effect of distance to the nearest seed source and distance to the nearest hedgerow intersection and a positive effect of the presence of a roosting tree on *P. serotina* occurrence.

The effect of the distance to the nearest hedgerow intersection differed between distinct types of intersections (Fig. 6). While no significant effect was found for O-type intersections, stronger relationships were found for the more complex types. In general, the probability of occurrence (at an equal distance) rose considerably with increasing intersection complexity (i.e. from O over L and T to X-type intersections). For instance, at a distance of 25 m from the hedgerow intersection, the chance of finding black cherry was more than four times higher for X-type in comparison with O-type intersections (Fig. 6).

Seedling recruitment curves

Age-specific seedling recruitment curves demonstrated a decrease in the percentage of individuals with increasing distance to the nearest seed source (Fig. 7). Moreover, a comparison of the curves obtained for different age classes revealed a progressive outward shift of seedling cohorts with age (see Fig. 7a–d). The observed pattern was confirmed by a significant effect of *P. serotina* age on distance to the nearest seed source, with the average distance to the nearest seed source gradually increasing with seedling age (linear regression: $R^2 = 0.31$, $p < 0.001$).

Discussion

Prunus serotina growth, reproduction and spread in agricultural landscapes

The strong age-size relationship is probably linked with the high availability of nutrients and physical resources

(especially light and water) within the agricultural landscape under study (Deckers et al. 2004), causing *P. serotina* individuals to follow quite uniformly the maximum growth rate curve. This hypothesis is confirmed by a close correspondence between the observed average diameter growth rate (0.629 cm yr^{-1}) and the results of Fowells (1965), mentioning an average diameter growth rate of 6.35 cm per decade for a *P. serotina* stand under ideal growth conditions on the Allegheny plateau in Pennsylvania.

The number of individuals within each age class followed approximately a negative exponential function, as demonstrated by the reversed J-shape of the population's age structure (Fig. 2). This indicates a strongly expanding population, especially if the invasion history of the species within the study area (Fig. 3) is taken into account. Comparable age structures were observed by Debussche and Lepart (1992) for a population of *Buxus sempervirens* colonising an abandoned agricultural field and by Prévosto et al. (2004) for the first stages of colonisation by *Cytisus scoparius* of open areas after grazing abandonment.

Analysis of the age-reproduction relationship revealed that the *P. serotina* population is characterised by an early start of the reproductive phase and an abundant and continuous seed production during adulthood. The observation that *P. serotina* individuals growing in hedgerow habitats are characterised by copious flowering and seed production is confirmed by van den Tweel and Eijsackers (1987) and is probably due to the suitable growth conditions and high light availability. Moreover, the observed average age of first reproduction (5.2 yr) is in good correspondence with the work of Muys et al. (1993) and van den Tweel and Eijsackers (1987), who mention an abundant annual seed production for black cherry within its introduced region from the age of five and six respectively. This is in contrast with the situation in its native region, where reproduction starts on average only at the age of 10 yr (Fowells 1965, Wallis de Vries 1986). The species' potential to reproduce early and abundantly may form an important reason for its invasion success in Europe (Starfinger 1997).

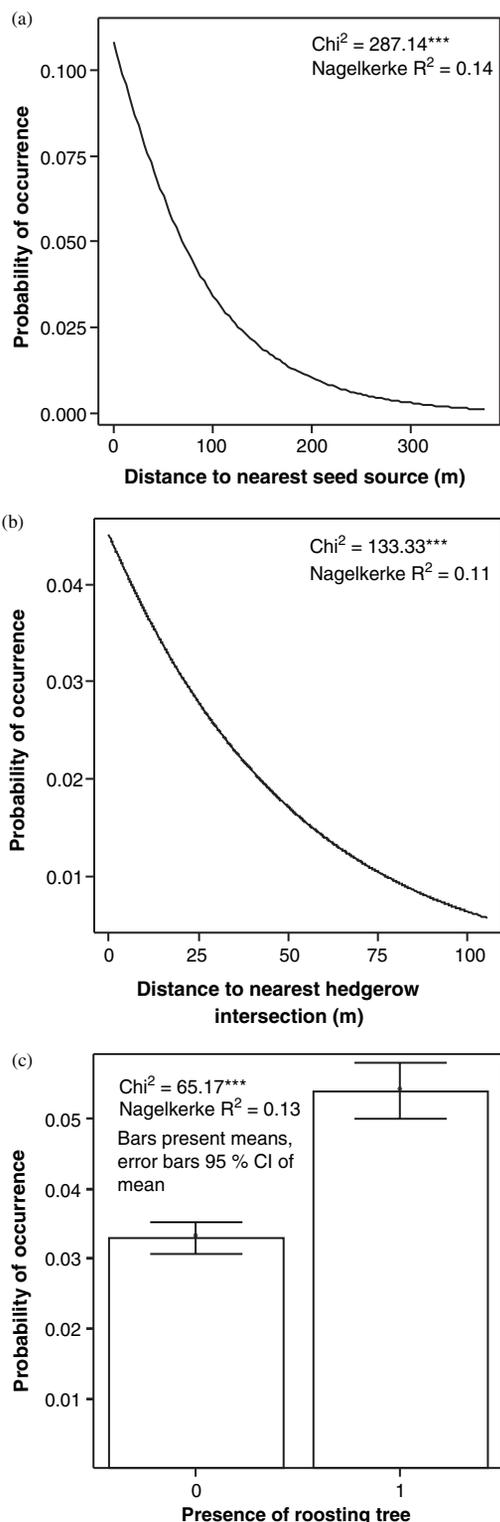


Fig. 5. Results of separate logistic regression analyses modeling the occurrence of *P. serotina* as a function of the distance to the nearest seed source (a), distance to the nearest hedgerow intersection (b) and presence of a roosting tree (c).

Historical reconstruction of the invasion process revealed a progressive increase in the species' rate of spread through the hedgerow network with time (Fig. 3), probably linked with the increasing amount of potential colonisation sources (i.e. reproductively mature trees) present within the hedgerow network as new black cherry individuals start reproducing each year (see also Bakker 1963, Muys et al. 1993). Comparing these results with literature, one has to bear in mind that, while our study considers invasive spread at the landscape scale, most other work addressed biological invasions at a larger (i.e. regional or continental) scale. Although traditionally linear models of spread received most attention (e.g. the simple reaction-diffusion model, cf. Holmes et al. 1994), several examples of non-linear spread due to environmental heterogeneity and/or a combination of different dispersal vectors can be found in literature (Williamson 1996, Hengeveld and Hemerik 2002, Bullock et al. 2002). In our case, non-linear spread is probably caused by a combination of one-dimensional diffusion along the hedgerows and two-dimensional spread by frugivorous birds to more distant roosting places.

Spatial aggregation and density dependent mortality

Spatial data analysis forms a major challenge in present day ecological research (Liebhold and Gurevitch 2002). As pointed out by Dale et al. (2002) and Perry et al. (2002), an appropriate method to analyse spatial patterns of individuals described by point-referenced data (x, y coordinates) is offered by Ripley's K-function (Ripley 1976). Especially tree and shrub spatial patterns were studied extensively using this method (see for instance Szwagrzyk and Czerwczak 1993, Haase et al. 1996, Pélissier 1998 and Barot et al. 1999b). Since the potential location of the *P. serotina* individuals was essentially restricted to the hedgerow network and not the entire surface of the study area, a network based adaptation of Ripley's K-function (i.e. network K-function analysis, cf. Okabe and Yamada 2001) was used to analyse the spatial point data (analogous to Spooner et al. (2004a, b) who studied the spatial distribution of *Acacia* populations along a road network in Australia).

A decreasing spatial aggregation of *P. serotina* individuals was found with increasing age of the trees (Fig. 4a, b, Table 1). This confirms the findings of Husch (1954), who observed the densest black cherry regeneration in the immediate surrounding of seed-bearing trees, while the proximity of a seed source had little influence on the density of the established population. The overall tendency towards less aggregated patterns along the life cycle has been found for other tree species as well (see for instance Haase et al. 1996, He et al. 1997 and Barot et al.

Table 2. Analysis of the effect of landscape structure on *P. serotina* occurrence using multiple logistic regression analysis. Results are presented for models using the entire *P. serotina* population and the different life stages separately.

	Model summary (Nagelkerke R ²)	Regression coefficients		
		Distance to nearest seed source (m)	Distance to nearest hedgerow intersection (m)	Presence of roosting tree (0/1)
Seedlings	0.173	-0.010***	-0.036***	0.661***
Saplings	0.125	-0.021***	-0.026***	0.521**
Non-reproducing adults	0.315	-0.004***	-0.003 ^{ns}	0.519***
Reproducing adults	0.291	-0.008***	-0.005 ^{ns}	0.440***
All individuals	0.156	-0.018***	-0.024***	0.617***

***: $p < 0.001$, **: $0.001 < p < 0.01$, *: $0.01 < p < 0.05$, ^{ns}: not significant.

1999b). Density dependent mortality, probably linked with strong intraspecific competition, is thought to be responsible for this trend (McCanny and Cavers 1989, Barot et al. 1999b).

The existence of density or distance dependent mortality is confirmed by the relative outward shift of seedling cohorts with age (Fig. 7), consistent with the Janzen-Connell hypothesis (see also Barot et al. 1999a, Peters 2003). The evidence of release from host-specific soil pathogens within its introduced region (Reinhart et al. 2003) indicates that this density dependent mortality may rather be linked with intraspecific competition instead of pathogen attack, in contrast with the situation in its native range (Packer and Clay 2000, 2003).

Dispersal mediated distribution patterns

Prunus serotina spread within the hedgerow network landscape was modelled using logistic regression analysis, with plant-environment interactions described by empirically derived constants (i.e. a spatial-phenomenological approach, sensu Higgins and Richardson 1996). The models obtained identify key factors affecting non-native species spread and provide a framework for the quantitative prediction of *P. serotina* invasion in agricultural landscapes.

Two important conclusions arise from the results of the logistic regression models. First, the strong effect of the distance to nearest seed source on *P. serotina* occurrence (Fig. 5a, Table 2) indicates a strong association between the spatial distribution of seedlings and the species' seed shadow, with the majority of seeds dispersed over short distances around the mother tree (McCanny and Cavers 1989, Debussche and Lepart 1992). The fact that propagule pressure is a key factor controlling biological invasions is confirmed clearly by the work of Rouget and Richardson (2003). Analogously, Plotkin et al. (2002) found evidence for dispersal-limited processes producing spatial patterns of tree species within tropical forests. Second, the important impact of landscape structure on species invasion (Fig. 5b, c and 6, Table 2) suggests directional long distance dispersal by bird vectors resulting in a differential seed pressure throughout the hedgerow network due to the preference of dispersing birds for roosting in structurally rich hedgerows with large trees near hedgerow intersections. While the functioning of roosting trees as focal points of seed dispersal and seedling establishment is approved by McClanahan and Wolfe (1993), Holl (1998) and Toh et al. (1999), the role of hedgerow intersections in the attraction of birds and the occurrence of bird-dispersed species is mentioned by Forman and Baudry (1984) and Sarlöv-Herlin and Fry (2000). The effect of intersection complexity corroborates the findings of Riffell and Gutzwiller (1996), who found a significantly higher

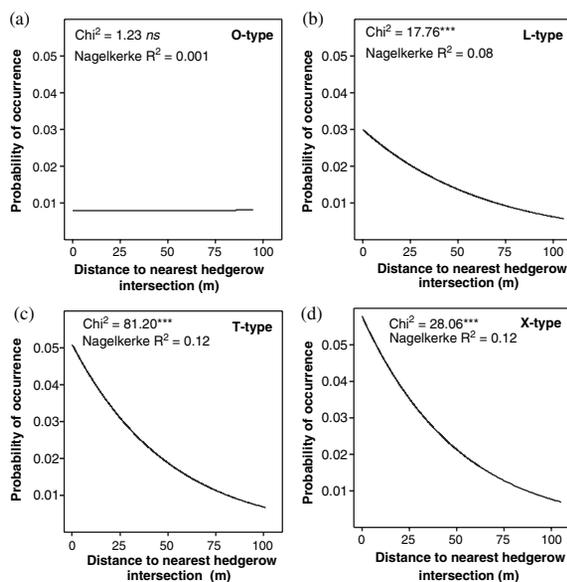


Fig. 6. Results of separate logistic regression analyses modeling the occurrence of *P. serotina* as a function of the distance to the nearest hedgerow intersection for different types of intersections: (a) O-type, (b) L-type, (c) T-type and (d) X-type intersections.

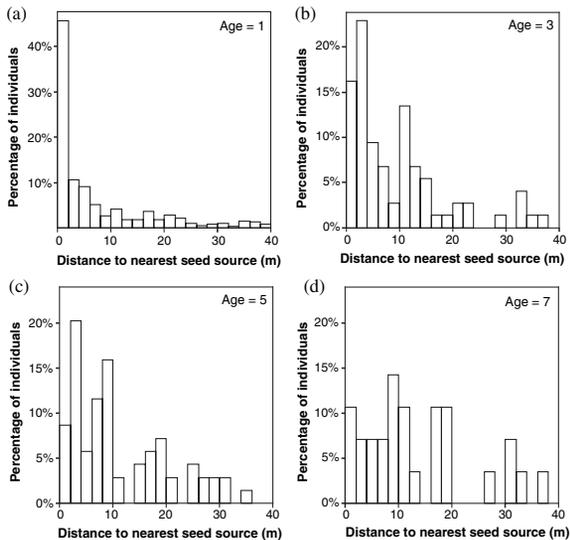


Fig. 7. *Prunus serotina* seedling recruitment curves for cohorts with age = 1 yr (a), age = 3 yr (b), age = 5 yr (c) and age = 7 yr (d).

number of animal-dispersed plant species in more complex types of intersections.

The results of the spatial pattern analysis confirm that the distribution of *P. serotina* in agricultural landscapes is strongly mediated by dispersal processes. The strong association of seedlings and saplings with reproducing adults (Fig. 4b, Table 1) supports the role of short distance dispersal (seed shadow effect), whereas the significant aggregation of plants around hedgerow intersections and roosting trees (Table 1) endorses the hypothesis of directional long distance dispersal by avian dispersal vectors.

Although evidence was found for dispersal distances of up to ca 300 m (Fig. 5a), these distances probably reflect the small-scaled nature of the studied landscape, while much larger dispersal distances could be achieved within other types of landscapes, strongly affecting the invasion process. An in-depth discussion of the importance of long distance dispersal for invasive species spread is provided for instance by Higgins and Richardson (1999) and Cain et al. (2000).

Conclusions

A high growth rate and an early and abundant seed production form basic attributes associated with invasion success of an expanding *P. serotina* population within its introduced region. The invasive spread of this species within an agricultural landscape context is the result of a combination of extensive local dispersal around the seed source, consistent with the classic seed shadow model, and a more limited amount of

directional, bird-mediated long distance dispersal events, with especially the latter process being strongly affected by landscape structure. This results in a spatially aggregated population structure, with juvenile individuals clustered around maternal trees and focal landscape points preferably visited by the avian dispersal vectors, such as hedgerow intersections and roosting trees. Subsequently, density dependent mortality, probably caused by intraspecific competition, leads to a decreasing spatial aggregation with time, resulting in the absence of spatial clustering for adult *P. serotina* individuals.

Opportunities for further research lie in comparing black cherry population dynamics and invasive spread between regions with different landscape characteristics. Future studies should focus as well on the effects of landscape structure on the foraging behaviour of dispersing birds. Additionally, the relative importance of intraspecific competition versus predation or pathogen attack as primary causes of density dependent mortality in non-indigenous *P. serotina* populations needs further clarification.

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References

- Anon. 2000. ArcView 3.2a. – Environmental Systems Research Inst.
- Anon. 2002. SPSS 11.0 for Windows. – SPSS.
- Auclair, A. N. and Cottam, G. 1971. Dynamics of black cherry (*Prunus serotina* Ehrh.) in southern Wisconsin oak forests. – *Ecol. Monogr.* 41: 153–177.
- Bakker, J. 1963. De ontwikkelingsgeschiedenis van *Prunus serotina* Ehrh. in Nederland. – *Nederlands Bosbouw tijdschrift* 35: 201–206.
- Barot, S., Gignoux, J. and Menaut, J.-C. 1999a. Seed shadows, survival and recruitment: how simple mechanisms lead to dynamics of population recruitment curves. – *Oikos* 86: 320–330.
- Barot, S., Gignoux, J. and Menaut, J.-C. 1999b. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. – *Ecology* 80: 1987–2005.
- Bullock, J. M. et al. 2002. Plant dispersal and colonization processes at local and landscape scales. – In: Bullock, J. M., Kenward, R. E. and Hails, R. S. (eds), *Dispersal ecology*. Blackwell, pp. 279–302.
- Cain, M. L., Brook, M. G. and Strand, A. E. 2000. Long-distance seed dispersal in plant populations. – *Am. J. Bot.* 87: 1217–1227.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. – In: Den Boer, P. J. and Gradwell, G. (eds), *Dynamics of numbers in populations*. Centre for Agricul-

- tural Publication and Documentation, Wageningen, pp. 298–312.
- Crooks, J. A. 2002. Characterising ecosystem-level consequences of biological invasions: the role of ecosystem engineers. – *Oikos* 97: 153–166.
- Dale, M. R. T. et al. 2002. Conceptual and mathematical relationships among methods for spatial analysis. – *Ecography* 25: 558–577.
- Debussche, M. and Lepart, J. 1992. Establishment of woody plants in Mediterranean old fields: opportunity in space and time. – *Landscape Ecol.* 6: 133–145.
- Deckers, B., Hermy, M. and Muys, B. 2004. Factors affecting plant species composition of hedgerows: relative importance and hierarchy. – *Acta Oecol.* 26: 23–37.
- De Langhe, J. E. et al. 1988. Flora van België, het Groothertogdom Luxemburg, Noord-Frankrijk en de aangrenzende gebieden. – Patrimonium van de Nationale Plantentuin van België.
- Forman, R. T. T. and Baudry, J. 1984. Hedgerows and hedgerow networks in landscape ecology. – *Environ. Manage.* 8: 495–510.
- Fowells, H. A. 1965. Silvics of forest trees of the United States. – U.S. Dept of Agriculture.
- Gordon, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. – *Ecol. Appl.* 8: 975–989.
- Haase, P. et al. 1996. Spatial patterns in a two-tiered semi-arid shrubland in southeastern Spain. – *J. Veg. Sci.* 7: 527–534.
- Hanowski, J. M., Niemi, G. J. and Christian, D. C. 1997. Influence of within-plantation heterogeneity and surrounding landscape composition on avian communities in hybrid poplar populations. – *Conserv. Biol.* 11: 936–944.
- He, F., Legendre, P. and LaFrankie, J. V. 1997. Distribution patterns of tree species in a Malaysian tropical rain forest. – *J. Veg. Sci.* 8: 105–114.
- Hengeveld, R. and Hemerik, L. 2002. Biogeography and dispersal. – In: Bullock, J. M., Kenward, R. E. and Hails, R. S. (eds), *Dispersal ecology*. Blackwell, pp. 303–324.
- Herrera, C. M. et al. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. – *Ecol. Monogr.* 64: 315–344.
- Higgins, S. I. and Richardson, D. M. 1996. A review of models of alien plant spread. – *Ecol. Modell.* 87: 249–265.
- Higgins, S. I. and Richardson, D. M. 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. – *Am. Nat.* 153: 464–475.
- Holl, K. D. 1998. Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? – *Restor. Ecol.* 6: 253–261.
- Holmes, E. E. et al. 1994. Partial differential equations in ecology: spatial interactions and population dynamics. – *Ecology* 75: 17–29.
- Hosmer, D. W. and Lemeshow, S. 1989. *Applied logistic regression*. – Wiley.
- Husch, B. 1954. The regeneration of *Prunus serotina* in northwestern Pennsylvania following cutting. – *Ecology* 35: 9–21.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. – *Am. Nat.* 104: 501–528.
- Keane, R. M. and Crawley, M. J. 2002. Exotic plant invasions and the enemy release hypothesis. – *Trends Ecol. Evol.* 17: 164–170.
- Kolar, C. S. and Lodge, D. M. 2001. Progress in invasion biology: predicting invaders. – *Trends Ecol. Evol.* 16: 199–204.
- Lake, J. C. and Leishman, M. R. 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. – *Biol. Conserv.* 117: 215–226.
- Lichstein, J. W., Simons, T. R. and Franzreb, K. E. 2002. Landscape effects on breeding songbird abundance in managed forests. – *Ecol. Appl.* 12: 836–857.
- Liebholt, A. M. and Gurevitch, J. 2002. Integrating the statistical analysis of spatial data in ecology. – *Ecography* 25: 553–557.
- Lodge, D. M. 1993. Biological invasions: lessons from ecology. – *Trends Ecol. Evol.* 8: 133–137.
- Mack, M. C. and D'Antonio, C. M. 1998. Impacts of biological invasions on disturbance regimes. – *Trends Ecol. Evol.* 13: 195–198.
- Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and recognition of – ‘predictive’ and ‘explanatory’ models. – *Biodiv. Conserv.* 9: 655–6714.
- McCanny, S. J. and Cavers, P. B. 1989. Parental effects on spatial patterns of plants: a contingency table approach. – *Ecology* 70: 368–378.
- McClanahan, T. R. and Wolfe, R. W. 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. – *Conserv. Biol.* 7: 279–288.
- Mitchell, C. E. and Power, A. G. 2003. Release of invasive plants from fungal and viral pathogens. – *Nature* 421: 625–627.
- Muys, B. and Maddelein, D. 1993. Amerikaanse vogelkers: van troefkaart tot bospest. – *Groene Band* 91–92: 1–23.
- Muys, B., Maddelein, D. and Lust, N. 1993. Ecology, practice and policy of black cherry (*Prunus serotina* Ehrh.) management in Belgium. – In: Gjerstad, D. H. (ed.), *Proc. of the International Conference on Forest Vegetation Management-Ecology, practice and policy*. Auburn Univ., pp. 86–93.
- Okabe, A. and Yamada, I. 2001. The K-function method on a network and its computational implementation. – *Geogr. Anal.* 33: 271–290.
- Okabe, A., Okunuki, K. and Shiode, S. 2004. SANET: a toolbox for spatial analysis on a network-ver. 2.0. – Centre for Spatial Information Science, Univ. of Tokyo.
- Packer, A. and Clay, K. 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. – *Nature* 404: 278–281.
- Packer, A. and Clay, K. 2003. Soil pathogens and *Prunus serotina* seedling and sapling growth near conspecific trees. – *Ecology* 84: 108–119.
- Pélissier, R. 1998. Tree spatial patterns in three contrasting plots of a southern Indian tropical moist evergreen forest. – *J. Trop. Ecol.* 14: 1–16.
- Perry, J. N. et al. 2002. Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. – *Ecography* 25: 578–600.
- Peters, H. A. 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. – *Ecol. Lett.* 6: 757–765.
- Plotkin, J. B., Chave, J. and Ashton, P. S. 2002. Cluster analysis of spatial patterns in Malaysian tree species. – *Am. Nat.* 160: 629–644.
- Prévosto, B., Robert, A. and Coquillard, P. 2004. Development of *Cytisus scoparius* L. at stand and individual level in a mid-elevation mountain of the French Massif Central. – *Acta Oecol.* 25: 73–81.
- Reinhart, K. O. et al. 2003. Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. – *Ecol. Lett.* 6: 1046–1050.
- Riffell, S. K. and Gutzwiller, K. J. 1996. Plant-species richness in corridor intersections: is intersection shape influential? – *Landscape Ecol.* 11: 157–168.
- Ripley, B. D. 1976. The second-order analysis of stationary point processes. – *J. Appl. Prob.* 13: 255–266.
- Rouget, M. and Richardson, D. M. 2003. Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. – *Am. Nat.* 162: 713–724.
- Sarlöv-Herlin, I. L. and Fry, G. L. A. 2000. Dispersal of woody plants in forest edges and hedgerows in a southern Swedish

- agricultural area: the role of site and landscape structure. – *Landscape Ecol.* 15: 229–242.
- Smith, A. J. 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. – *Ecology* 56: 19–34.
- Spooner, P. G. et al. 2004a. Spatial analysis of anthropogenic disturbance regimes and roadside shrubs in a fragmented agricultural landscape. – *Appl. Veg. Sci.* 7: 61–70.
- Spooner, P. G. et al. 2004b. Spatial analysis of roadside *Acacia* populations on a road network using the network K-function. – *Landscape Ecol.* 19: 491–499.
- Starfinger, U. 1997. Introduction and naturalisation of *Prunus serotina* in central Europe. – In: Brock, J. H. et al. (eds), *Plant invasions: studies from North America and Europe*. Backhuys Publ., pp. 161–171.
- Szwagrzyk, J. and Czerwczak, M. 1993. Spatial patterns of trees in natural forests of east-central Europe. – *J. Veg. Sci.* 4: 469–476.
- Tavernier, R. and Maréchal, R. 1972. Carte des Associations des Sols 1/500.000. – IGN.
- Toh, I., Gillespie, M. and Lamb, D. 1999. The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. – *Restor. Ecol.* 7: 288–297.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. – *Annu. Rev. Ecol. Syst.* 20: 171–197.
- Van den Meersschaut, D. and Lust, N. 1997. Comparison of mechanical, biological and chemical methods for controlling black cherry (*Prunus serotina*) in Flanders (Belgium). – *Silva Gandavensis* 62: 90–109.
- van den Tweel, P. A. and Eijssackers, H. 1987. Black cherry, a pioneer species or ‘forest pest’? – *Proc. Roy. Dutch Acad. Sci.* 90: 59–66.
- Wallis de Vries, M. F. 1986. De Amerikaanse vogelkers (*Prunus serotina*): ecologie van een exoot in nederlandse bossen. – Landbouwhogeschool Wageningen.
- Wenny, D. G. 2000. Seed dispersal, seed predation and seedling recruitment of a neotropical montane tree. – *Ecol. Monogr.* 70: 331–351.
- Williamson, M. 1996. The process of spread. – In: Williamson, M. (ed.), *Biological invasions*. Chapman and Hall, pp. 80–114.
- With, K. A. 2002. The landscape ecology of invasive spread. – *Conserv. Biol.* 16: 1192–1203.
- Wolfe, L. M. 2002. Why alien invaders succeed: support for the escape-from-enemy hypothesis. – *Am. Nat.* 160: 705–711.