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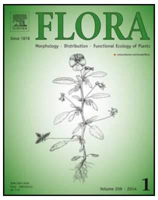

Spatio-temporal variation in seed predation by a native weevil in the invasive *Prunus serotina*

M. Vanhellemont[a,*], L. Baeten[a,b], A. Smeets[c], J. Mertens[c], K. Verheyen[a]

[a] *Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, 9090 Gontrode, Belgium*
[b] *Terrestrial Ecology Unit, Department of Biology, Ghent University, K. L. Ledeganckstraat 35, 9000 Ghent, Belgium*
[c] *Department of Applied Biosciences, Faculty of Bioscience Engineering, Ghent University, Valentin Vaerwyckweg 1, 9000 Ghent, Belgium*

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ABSTRACT

Invasive species may escape the enemies from their native range (‘enemy release’), but they can also acquire new enemies in their introduced range, which will affect the invasion process. For the invasive tree species *Prunus serotina*, seed predation by the native weevil *Furcipus rectirostris* has been reported in forests in its introduced range. In this study, we quantified how common the infestation of *P. serotina* seeds by *F. rectirostris* is in a 4000 km^2 area in northern Belgium. Seeds were sampled on *P. serotina* trees in different habitats and in two years, i.e., with low and high *P. serotina* fruit production. Infestation was found throughout the study region, in 43 and 62% of the sampled trees in the two years of the study; the maximum infestation levels of infested seed samples were 50 and 69%. Overall, predation occurred in 4.4 and 10.8% of the sampled seeds. The level of infestation differed between habitats and years, and the number of fruits per raceme was inversely related to the infestation level. Notwithstanding the rather high incidence of *F. rectirostris* infestation in our study, the impact on *P. serotina*'s invasiveness might remain low seeing the overall high seed production and dispersal capacity of the species.

Introduction

Prunus serotina Ehrh., a North American tree species, was introduced into Europe in the 17th century and planted widely, mainly in the understory of pine forests, during the first half of the 20th century (Starfinger et al., 2003). The species successfully colonized new areas, became locally abundant, and has been reported to affect biodiversity, influence abiotic site conditions, and alter the succession of invaded ecosystems in Western and Central Europe (Chabrerie et al., 2008, 2010; Godefroid et al., 2005; Starfinger, 1990; Verheyen et al., 2007). Despite many intensive and costly control programs (Starfinger et al., 2003), the species has continued to spread (Klotz, 2009). Studies on invader success often investigate the enemy release hypothesis, which states that alien species will experience less regulation by enemies in the introduced range and will thus be able to rapidly increase their distribution and abundance in the introduced range (Keane and Crawley, 2002). The competitive release of alien species in the introduced range can be the result of (1) an escape from generalist (and specialist) enemies of the native range, (2) the smaller impact of the generalist enemies of the introduced range on the alien species relative to the native species (Eschtruth and Battles, 2009; Keane and Crawley, 2002; Schierenbeck et al., 1994), and (3) pathogen spillback from alien species that are a competent host for parasites or pathogens native to the recipient ecosystem to native species (Kelly et al., 2009; Strauss et al., 2012). The smaller the phylogenetic distance between an alien species and the native species in the recipient community, the higher the probability that the present specialist natural enemies will also affect the alien species (Harvey et al., 2012), and the longer an alien species has been present, the higher the number and impact of native enemies (Castells et al., 2013). Anyhow, knowledge on the identity and characteristics of new enemies in the introduced range and the impact of these enemies on the population dynamics of the alien species is important for understanding invasion processes (Chang et al., 2011).

In its introduced range, several native species live or feed on the invasive *P. serotina*. Herbivorous insects have been observed on *P. serotina* (Halarewicz and Jackowski, 2011; Karolewski et al., 2014; Nowakowska and Halarewicz, 2006a, 2006b); a range of insect, bird, and mammal species feeds on *P. serotina* fruits (Boucault, 2009; Deckers et al., 2008; Korringa, 1947); and *P. serotina* seeds are predated by rodents (Boucault, 2009; Eijsackers and Van de

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* Corresponding author. Tel.: +32 09 264 9037; fax: +32 09 264 9092.
E-mail addresses: Margot.Vanhellemont@UGent.be (M. Vanhellemont), Lander.Baeten@UGent.be (L. Baeten), Jan.Mertens@UGent.be (J. Mertens), Kris.Verheyen@UGent.be (K. Verheyen).

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Ham, 1990) and the bird-cherry weevil (Moraal, 1988; Pairon et al., 2006). Pre-dispersal seed predation, as by the bird-cherry weevil *Furcipus rectirostris* (Linnaeus 1758), has not yet been reported in *P. serotina*'s native range (e.g., Marquis, 1990). Some recent observations in its introduced range suggest that the seed infestation level varies between sites and years (Boucault, 2009; Vanhellemont et al., 2009a). Local growing conditions may indeed affect infestation levels, seeing that the seed predation rate of host plant species has been found to be related to their growth, fruit density, and flowering phenology (Chang et al., 2011; Hornoy et al., 2011). Weather conditions, for instance, can affect flowering and seed development of the host plant, insect activity, and the timing and duration of seed availability for the predator. The vernal emergence of insect adults is also often triggered by environmental factors such as temperature (Forrest and Thomson, 2011). Seed predation rates may be further influenced by the spatial patterns of predator egg distribution, i.e., clumping, across the available seeds and hosts (Van Klinken and Flack, 2008), and the competence and abundance of the host plants (Telfer and Bown, 2012). We therefore expect differences in the susceptibility of *P. serotina* trees to *F. rectirostris* seed predation between years, due to differences in, e.g., weather conditions during flowering and seed development, and habitats, due to differences in, e.g., host abundance. As far as we know, however, no figures are available on temporal differences in the prevalence and degree of *F. rectirostris* infestation for *P. serotina* on a spatial scale larger than a few study sites or outside forest habitats.

The research questions of the present study were (1) How common is the infestation of *P. serotina* seeds by *F. rectirostris* in northern Belgium? (2) Does the infestation level differ between years differing in *P. serotina* fruit production? (3) Do the size of the *P. serotina* tree, the number of fruits per raceme, and the characteristics of the habitat in which it grows influence the infestation level?

Materials and methods

Study species

Prunus serotina Ehrh., native to North America, is a semi shade-tolerant tree species (Auclair and Cottam, 1971) that grows on a wide variety of soils (Marquis, 1990; Zerbe and Wirth, 2006). The invasiveness of the species in its introduced range has been attributed to the multiple introductions (Pairon et al., 2010) as well as the species' high potential growth rate and reproduction capacity, i.e., frequent seed production, effective seed dispersal, and the build-up of a seedling bank (Deckers et al., 2005, 2008; Pairon et al., 2006; Vanhellemont et al., 2009a, 2009b). Reinhart et al. (2003) suggested that *P. serotina* also benefits from enemy release, i.e., release of soilborne pathogens that negatively affect *P. serotina* seedlings in its native range.

Furcipus rectirostris (Linnaeus 1758), the bird-cherry weevil, is a species from the family Curculionidae that occurs in a large part of the Palearctic, i.e., from Europe through Russia to Japan (Alford, 2007; David'yan, 2009; Kojima and Morimoto, 1994). The species is a pest of cultivated cherries, and wild hosts include *Prunus* species with small fruits, e.g., *P. avium* L. and *P. padus* L. The weevil also feeds on other Rosaceae, e.g., on *Sorbus aucuparia* L. (David'yan, 2009). *Furcipus rectirostris* is a univoltine (or monovoltine) weevil (David'yan, 2009). Adult weevils appear in spring, from mid-April to mid-June; they can fly well and feed on flowers, leaves, petioles, and apical shoots. Single eggs are deposited inside immature, soft stone fruits. The egg develops in ca. 2 weeks. The larva feeds on the seed and pupates inside the stone. As the weevil's larva eats the embryo of the infested fruit, affected trees will produce less viable seeds. The affected fruits show necrotic spots on the surface, develop slowly and fall off early or grow into deformed cherries. From the end of July, beginning of August onwards, adults emerge from the infested stone fruits through an exit hole that was created by the larva. The adult weevils feed on the ripe fruit; they hibernate under the bark of trees, in litter or the soil surface layer (Alford, 2007; David'yan, 2009).

Study area and data collection

Samples of *P. serotina* fruits were collected at 60 locations in the Campine region in northern Belgium (Fig. 1), i.e., the Belgian region where *P. serotina* has been massively planted and is currently most common and abundant (Van Landuyt et al., 2006; Vanhellemont et al., 2008). The study area spanned ca. 4000 km^2 (50°55′–51°27′N, 4°27′–5°45′E). The 60 locations were selected based on the presence of forest, using topographic maps, and the presence of *P. serotina* in the forest, which was examined in the field. At every location, we searched for fruiting *P. serotina* trees in two forest habitats, i.e., (1) the forest interior and (2) a forest edge, and two habitats in the open landscape near the forest, i.e., (3) an isolated *P. serotina* tree and (4) a *P. serotina* tree in a hedgerow. We did sample different habitats as *P. serotina*'s fruit production is affected by light availability (Closset-Kopp et al., 2007) and the seed infestation rate of a species has been shown to be negatively correlated with fruit density (e.g., Hornoy et al., 2011). We sampled only one fruiting *P. serotina* per habitat type at each location because we wanted to quantify the spatial prevalence of infestation and the differences in infestation between habitat types and were not interested in the within-habitat variability in infestation between trees. As we did not find a fruiting *P. serotina* tree for each of the four habitat types at each of the 60 locations, a total of 196 *P. serotina* individuals were sampled in 2011. In 2012, the 196 trees were visited again. Due to eradication measures and low seed production (see further), only 70 individuals could be re-sampled. For the trees that could not be re-sampled, we searched for a new *P. serotina* individual close to the one sampled in 2011, i.e., with the same habitat-location combination. Eventually, 157 *P. serotina* individuals, at 59 locations, were sampled in 2012. The geographic coordinates of each sampled tree were noted.

Sampling started after the endocarp of randomly sampled test fruits appeared to be woody, i.e., when the endocarp had become too hard for *F. rectirostris* to lay any more eggs inside. Endocarp development starts around 28 days after flowering (Swain et al., 1992), and *P. serotina* flowers in May–June in its introduced range (Closset-Kopp et al., 2007; Phartyal et al., 2009). The sampling period lasted from 18 July–12 August in 2011 and 11 July–31 July in 2012. We aimed to collect 50 fruits from each *P. serotina* individual, but the samples were smaller for the least fecund trees (minimum sample size = 33 in 2011, 10 in 2012). Fruits were collected by picking entire racemes, i.e., *P. serotina*'s indeterminate inflorescences bearing flowers or fruits on short stalks, from the sample trees. In 2011, the fruit production of *P. serotina* was high: all racemes bore fruits. In 2012, the fruit production of *P. serotina* was low: many trees or many racemes on a fruit-bearing tree bore no fruits. We collected racemes from random positions in the crown in 2011, and we collected all racemes on randomly selected branches, i.e., racemes with and without fruits, in 2012. In this way, a sample could be used to calculate the mean number of fruits per raceme, a component of the tree's fecundity. The mean number of fruits per raceme was 7.3 in 2011 (range 1.4–22.3) and 1.8 in 2012 (0.3–9.5). Further in the manuscript, we will refer to 2011 and 2012 as the years with high or low fruit production. The fruits of each sample were sliced in half to check for the presence of larvae, pupae or adult weevils inside the stone.

For each sampled tree, we measured variables that might influence the habitat suitability for *F. rectirostris*, i.e., presence of