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Abstract Invasive success of many fleshy-fruited plants has been linked to opportunistic interactions with generalist frugivores. *Prunus mahaleb* is a small tree, producing large quantities of little, bright black, sugary drupes that are consumed by vertebrates. It is native to the Mediterranean region but has become invasive in several countries. This study was carried out at a nature reserve including remnant mountain grasslands of high conservation value in the southern Argentine Pampas. Our aim is to reconstruct the colonization history of invading populations proposing a generalized model to describe the invasion process: colonization events result in the establishment of a founder tree followed by a lag phase until it reaches massive seed production and enables an increase in local recruitment and plant density. To test this hypothesis, we analyzed population age structures and contrasted them with those predicted using a Leslie matrix growth model. We found that matrix model predictions fit well to actual age structures. Our results reveal the existence of an 8–18-year lag period between the establishment of the founder tree and local effective recruitment. The end of this lag coincides with an abrupt increase in individual fruit production that may have a strong effect on bird attraction and successful seed dispersal. This lag phase represents an opportunity for preventing further spread of *P. mahaleb*. Early detection and rapid eradication of new invasion focuses should be targeted as a principal aim of an effective control strategy.

Keywords *Prunus mahaleb* · Age structure · Biological invasions · Seed dispersal · Plant-animal interactions · Leslie matrix

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Introduction

The proliferation of invasive trees and shrubs, at the expense of perennial grasses, has been one of the most striking land cover changes in grasslands and savannas worldwide over the past century (Browning et al. 2008; Jurena and Archer 2003; Van Auken 2000), driving major consequences for biodiversity and ecosystem functioning (Van Auken 2009; Barger et al. 2011; Archer et al. 2001). Fleshy-fruited, animal-dispersed species are among the most aggressive invasive plants (Buckley et al. 2006). Plants dispersed by animals seem to more easily overcome the barriers that limit spread in new habitats, enhancing their chances to become invasive (Mooney et al. 2005). For many species, this achievement seems to be related to the plasticity of their interaction networks with generalist animals (Mooney et al. 2005; Deckers et al. 2008). Many vertebrate-dispersed plants exhibit diffuse interactions with a range of dispersal agents, and this may play a key role for facilitating invasive behavior in regions outside their native range (Deckers et al. 2008). Fruits of cultivated or spontaneous exotic plants are commonly included in the diet of generalist vertebrates and thus they promote dispersal of nonnative as well as native species (Dennis et al. 2007; Gosper et al. 2005).

It has been reported that crop size is positively related to both visitation rate and fruit removal by birds for many fleshy fruited plant species (Sallabanks 1992; Jordano 1987; Herrera and Jordano 1981; Deckers et al. 2008). This relationship is expected to have implications in the colonization and spreading process of invasive fleshy-fruited plants, being a special case of propagule pressure (Simberloff 2009). Relative to other food resources, fruits are extremely aggregated in space, usually in relatively isolated patches (Jordano 2000) where local abundance might depend primarily on plant density, age structure and spatial distribution. Since invasive species can quickly enter and spread in a new habitat, it is important to understand these parameters and their implications in the colonization process (Meekins and McCarthy 2002).

The initial population dynamics of a woody plant population and its colonization history may be inferred from the present age structure. Moreover, if a clear relationship can be established between fecundity and age, historical changes in local propagule pressure can be also understood, leading to a picture of the invasion process that could be applied for preventing further spread. The colonization history of woody plants invading grasslands has been studied using present age structures in a number of situations, focused on climate, disturbance and more recently, on biotic interactions (Rice et al. 2012). Biotic interactions might be fundamental in the conversion of grassland to shrubland due to the invasion of woody plants (Halpern et al. 2010; Rice et al. 2012), and retrospective age structure analysis can give important information about the spreading of vertebrate-dispersed plants in this process (Debussche and Lepart 1992; Deckers et al. 2005).

Saint Lucie's or Mahoma's cherry (*Prunus mahaleb*), is a small, deciduous, rosaceous tree, native to central and southern Europe, northwestern Africa and west-central Asia (Herrera and Jordano 1981). Because of its showy flowers, variety of growth habits, fast growth, adaptability to a wide variety of soils and climates and resistance to pests, *P. mahaleb* is frequently used as a rootstock for orchard trees, as an ornamental plant and also for wood production (Bass et al. 2006; Grisez et al. 2008). Thus, it has been widely distributed in several countries, becoming invasive in some of them, including the United States (Swearingen 2008), Canada (Brouillet et al. 2010), Australia (Bass et al. 2006), New Zealand (Webb et al. 1988) and Argentina (Zalba 2001). Particularly, *P. mahaleb* has spread over natural grasslands in Argentine Pampas, threatening some of their valuable remnants (Zalba and Villamil 2002). Flowering, fruiting and seed dispersal of *P. mahaleb* have been extensively studied within its native range of distribution (Guitián et al. 1992; Kollmann and Pflugshaupt 2001, 2005; Pflugshaupt et al. 2002; Herrera and Jordano 1981; Jordano 1995, 1993; Jordano and Schupp 2000) but little is known about its invasive behavior (Bass et al. 2006).

In this work we study colonization history in populations of *P. mahaleb* from Sierra de la Ventana mountains, Argentina. In a previous study, we analyzed the relationship between fruit production and plant age within the same study area, finding that individuals are characterized by an abundant seed production since early ages. Fruit production starts at ages around 3 years, and individual crop size shows a remarkable increase at ages between 10 and 15 years (Zalba and Amodeo, unpublished data). Plants around that age go from producing hundreds of fruits to bearing thousands of them, and we consider this as the start of massive fruit production. We also found a considerable increase in fruit density within the crown around the same age, probably due to higher photosynthetic efficiency in leaves and/or better subterranean water up-taking by roots induced by such developmental changes. This fact may have particular implications in the dynamics of the colonization process. When a single plant colonizes a new site, local dispersal is expected to take a time to initiate because of retardations in propagule availability and disperser attraction. Within its native range of distribution, it has been demonstrated that isolated *P. mahaleb* individuals experience lower visitation rates by dispersers and a minor percentage of fruits are consumed (Jordano 1995). In order to facilitate significant recruitment around the colonizer, fruit availability might need to reach high enough levels to promote bird attraction.

The spreading of *P. mahaleb* over natural grasslands could depend primarily on a combination of long-distance colonization events and subsequent local proliferation and population growth. Long-distance dispersal agents (possibly mammals and/or large birds) may facilitate colonization events and, after a lag phase until massive fruit crop is reached, short-distance dispersal agents (small and medium sized birds) that are attracted to the founder tree enable local proliferation. In this scenario, we propose that after a single plant colonizes a new isolated site, it becomes the main source of propagules in the zone and that local dispersal predominates after a lag period during which seed production increases. Once this founder tree reaches large crown volume and crop size (thousands of fruits), we expect bird attraction to promote recruitment and nucleus expansion around the colonizer. To test this hypothesis, we analyzed population age structure of seven populations and contrasted them with those predicted using a Leslie matrix growth model.

Materials and methods

Study species

Prunus mahaleb L. is a highly light-demanding tree with a prostrate to vertical growth habit (0.5–10 m height), depending on local conditions (Kollmann and Pflugshaupt 2001). Within its native range the species can be found growing on shallow and rather poor soils, from the vicinity of streams to dry hillsides at mid-elevation altitudes (1,250–1,900 m) (Herrera and Jordano 1981; Jordano 1994). Corymbs of 3–10 small white flowers, with numerous stamens, are produced by mid spring (Jordano 1993; Guitián et al. 1992). Bees (Hymenoptera: Andrenidae, Apidae) and flies (Diptera: Calliphoridae, Tachinidae, Syrphidae) are its main pollen vectors (Guitián et al. 1992; Jordano 1993). Production and ripening of fleshy fruits take place during approximately 2 months in late spring and early summer. One-seeded drupes, bright black when ripe, 8 mm diameter and with a sugary water-rich pulp are held in auxiliary clusters of one to ten fruits (García et al. 2007; Herrera and Jordano 1981; Jordano 1995). At least 38 bird species, four mammals and one lizard have been recorded feeding on *P. mahaleb* fruits in its native range of distribution (Jordano 1995; Jordano and Schupp 2000; Herrera 1989). In our study area we recorded 20 birds, seven mammals and one ant species manipulating *P. mahaleb* fruits.

Study area

This study was carried out at Ernesto Tornquist Provincial Park (ETPP), which covers an area of approximately 6,700 ha of mountain grasslands in southern Argentine Pampas (38°3.90′S; 61°58.33′W), being one of the few protected areas of the whole eco-region (Bilenca and Miñarro 2004). The climate is temperate, with a mean annual temperature of 14 °C and wide annual and daily fluctuations. Annual precipitation is around 800 mm, mostly concentrated in spring and early summer (Burgos 1968). Vegetation is dominated by grass steppes with scattered rocky outcrops and exotic woody plants growing in small plantations, spontaneous forests or as isolated individuals (Zalba and Villamil 2002). *P. mahaleb* individuals are commonly found, scattered or aggregated in different sized populations in valleys and hillsides. Densest populations are associated with streams and canyons where dispersers' activity seems to be higher. Nevertheless, smaller stands can also be found at mid-elevation on the hill-sides.

Sampling design and data analysis

Seven stands growing at mid-elevations (between 450 and 560 m elevation) were randomly selected, providing that there were no conspecifics or any other exotic woody plant in the surroundings (100 m or more). Using a GPS, we registered the position of all individuals within each stand, and measured its area by walking around the perimeter. We also looked for the largest tree/s in each stand and identified it/them as the founder/s, recording the distance between the biggest and every other individual in the stand.

The age of all plants was estimated from basal stem diameter by means of a regression model developed in a previous work (Zalba and Amodeo, unpublished data). Following those results, basal stem diameter (*BSD*, in centimeters) appears as a good predictor of plant age (*A*, estimated by counting annual rings in cross sections of basal stem) with a different slope for plants growing on different soil types (full model $F_{(5,68)} = 99.61$, $p < 0.0001$, $R^2 = 0.87$, $N = 75$). Plants growing on dry soils with no evident root confinement, like in the case of the stands studied in the present paper, showed the following relationship between age and stem diameter: $\log(A) = 1.3292 + 0.48 * \log(BSD)$. We use frequency histograms to analyze age structures. The time between the age of the oldest tree and the oldest subsequent cohort with more than five individuals was defined as the lag period from colonization to effective recruitment. Using violin plots (Hintze and Nelson 1998), we analyzed the distribution of individual distances from founder tree for seedlings and pre-reproductives (0–3 years), transitional stage and young reproductive individuals (3–10 years) and mature reproductive trees (10–20 years) defining also the maximum population radius.

Considering the founder tree as the unique source of seeds during the establishment of the stand, we constructed a Leslie matrix for each population with as many rows as the age of the founder tree. Net fertilities were incorporated in the matrix top row, computing every year the crop of the founder at its corresponding age based on a regression model between crop size (*CS*) and plant age (*A*) that we constructed in a previous work for trees growing in dry soils with no root confinement: $\log(CS) = -5.6528 + 5.3782 * \log(A)$ (full model $F_{(3,77)} = 166.5$, $p < 0.0001$, $R^2 = 0{,}8664$, $N = 81$) (Zalba and Amodeo, unpublished data). Considering the results of field germination tests within the study area, we incorporated a general germination rate of 0.05 as a coefficient affecting the fecundity values in the matrix top row. According to previous information and field observations, annual survival probabilities (principal subdiagonal) were stated as follows: 0.03 for seedlings (1 year), 0.5 for immature pre-reproductives (2–3 years), 0.7 for transitional stage and young reproductive individuals (3–10 years), and 0.9 for mature reproductive trees (>10 years). We started the demographic simulations with one seedling (representing the arrival of the founder tree) and made it intentionally skip from mortality by summing each year one individual of the corresponding founder's age. Therefore, every year's fecundity was composed only by the crop of the founder at its corresponding age and recruitment was defined by subsequent germination and annual survival rates of its descendants. We visually compared the predicted age structure with the actual age frequency histograms. All analyses were performed using R (R-Core-Team 2012) and ggplot2 package (Wickham 2009). Log transformations are natural logarithms.

Results

All the populations included one to three trees being considerably older than the others (which are pointed as the founder and co-founders) followed by a gap in the age structure with low or null plant establishment or survival (lag phase in Table 1, black lines in Fig. 1). This lag phase ranged from 8 to 18 years among populations (mean value = 12.43; SE = 3.6; n = 7).

All the stands were composed by more than 60 individuals summing a total number of 1,556 plants. Pre-reproductive individuals (<3 years) represented the most abundant age class for all populations (more than 70 % of total population size in populations 1–6). Population 7 showed a dominance of transitional and

Table 1 Description of *Prunus mahaleb* populations studied at Ernesto Tornquist Provincial Park (Sierra de la Ventana, Argentina)

Population	1	2	3	4	5	6	7
Number of founders	1	2	3	1	1	1	2
Maximum age (years)	24	17	16	16	14	24	24
Mean age (years)	2.52	2.717	3.189	2.846	2.973	3.329	5.995
Lag phase (years)	16	12	8	11	9	18	13
Max distance (m)	34	45	66	80	107	48	98
Total area (m^2)	774	1,320	1,553	2,837	5,231	3,438	6,564
Density (ind/m^2)	0.53	0.23	0.246	0.022	0.035	0.029	0.018
Total number of plants	410	303	382	62	184	99	116

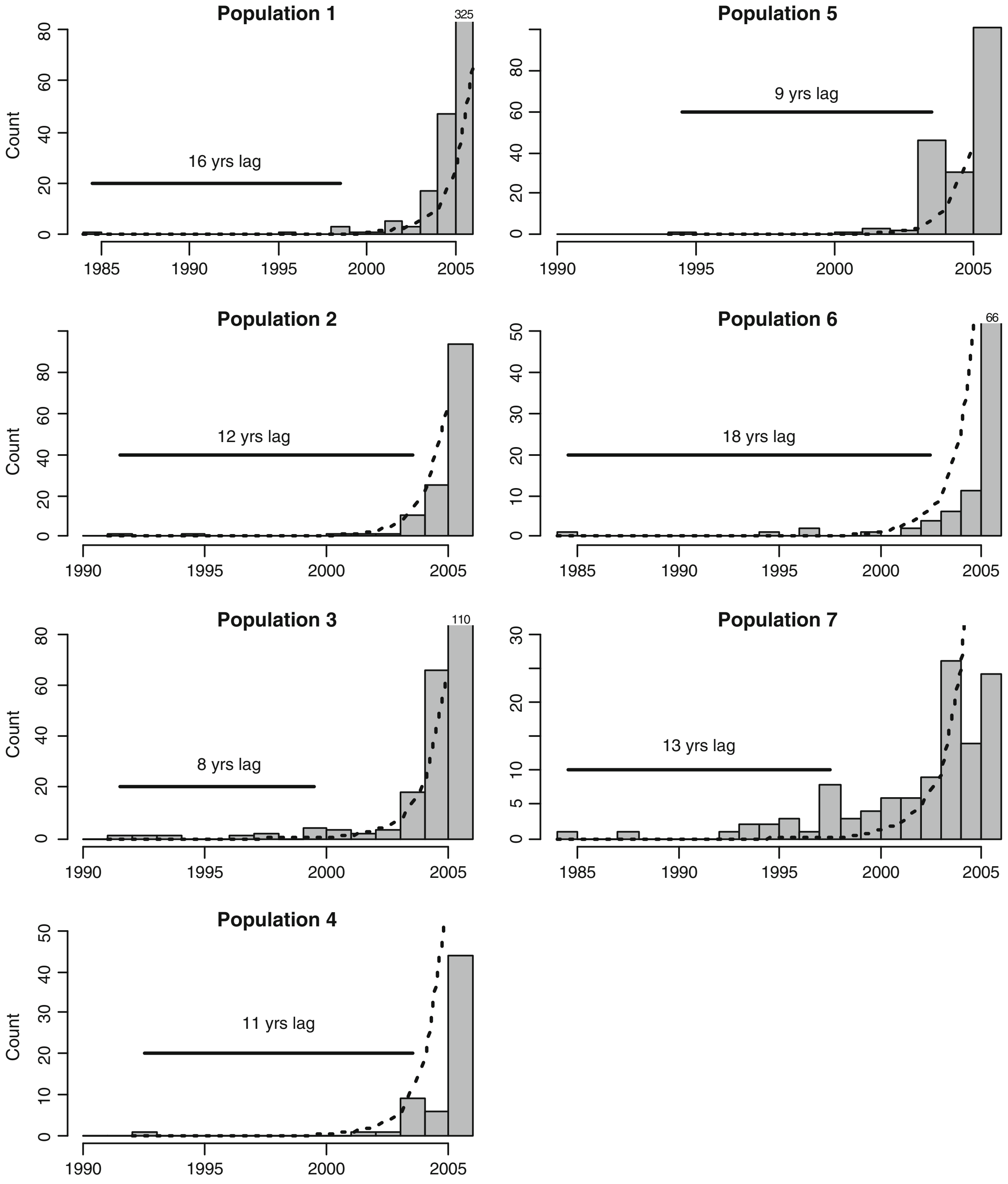

Fig. 1 Age structure of *Prunus mahaleb* isolated populations at Ernesto Tornquist Provincial Park (Sierra de la Ventana, Argentina). *Grey bars* indicate observed frequencies, *dashed lines* show frequencies predicted by Leslie matrix population growth models. *Black lines* represent lag period until effective recruitment starts

young reproductive individuals (48.7 % of total population size). In all populations, under-10-year-old individuals represented more than 80 % (mean value = 96.2 %; ES = 2.26 %; n = 7) of total population size. Tree density varied between 0.02 and 0.53 individuals/m^2 among the populations (Table 1). The area where a population was established was mostly occupied by grasslands and rocky outcrops and total canopy cover ranged from 0.03 to 10 % of total population area.

Oldest individuals occupied a central position in all populations and younger plants extended over a maximum radius of between 32 and 107 meters around the founder tree (mean value = 68.29 m; ES = 10.53 m; n = 7 populations). More than 50 % of pre-reproductive individuals were located beneath the founder canopy. However, seedlings were found throughout the entire population area, with their abundance declining until 80 m from the founder, where they became almost absent (Fig. 2). Transitional juveniles and young reproductive plants (3–10 years old) were also aggregated near the founder, but distributed over longer distances. Median distance for this category reached 19.4 m. Half of the mature plants (>10 years) were found within 33.9 m from the founder.

Discussion

The shape of age distributions and the existence of a gap after the establishment of the founder tree in all the studied populations are in concordance with the proposed colonization process. The demographic model fits to observed distributions, supporting also our colonization hypothesis. Recruitment appears to depend almost entirely on the founder's seed supply, which is the main source of propagules for the growing population. In absence of any other local source of seeds, several years are needed before local

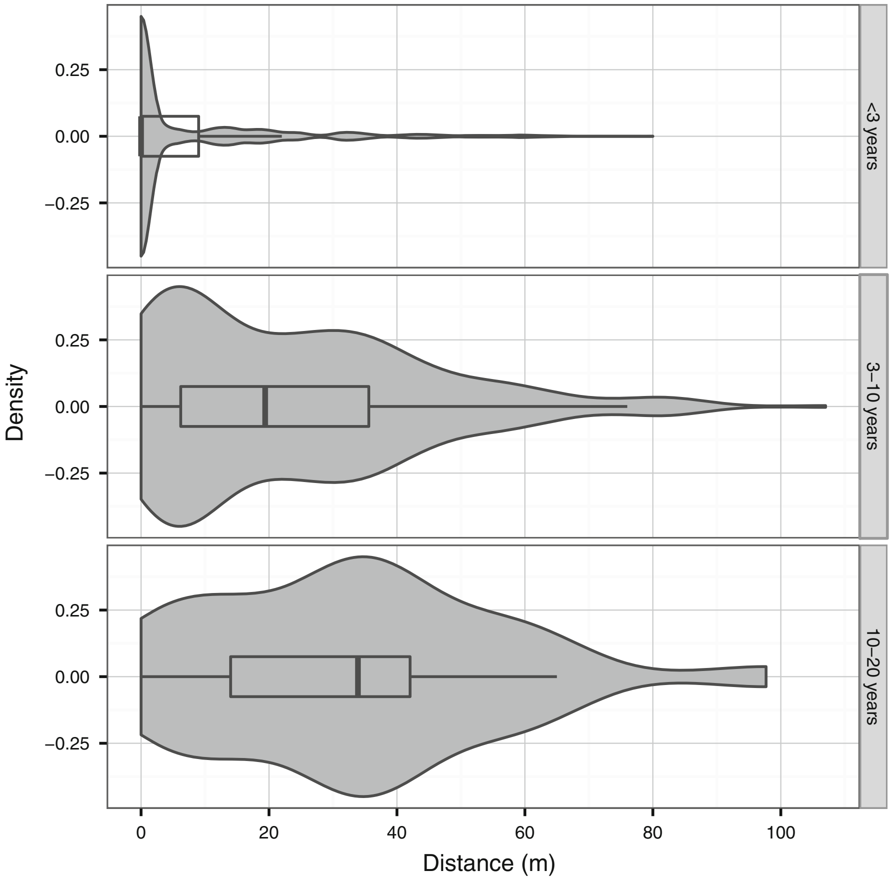

Fig. 2 Violin plots of individual distances from founder tree for plants within three age categories. All studied *P. mahaleb* populations at Ernesto Tornquist Provincial Park (Sierra de la Ventana, Argentina) are included. Data range, median and quartiles are indicated by the *inner box plot* in combination with the density trace in *dark grey*

recruitment starts. In this scenario, a few recruits might appear earlier, but dispersal into the area is insufficient to enable considerable establishment before the first colonizer starts to set seeds (Harper 1977). This pattern is also supported by the distribution of seedlings, which were mostly aggregated near the founder canopy in all the studied populations.

Age structure analysis showed a high relative abundance of seedlings in all populations, leading to what Kollmann and Pflugshaupt (2005) called L-shaped age distributions, for *P. mahaleb* populations in Switzerland. This shape of distributions suggests that studied populations are possibly in expanding processes. Populations 3 and 7 show some deviations from the expected age structure, probably because they received more than one founder tree in their early years, which lead to a slightly earlier start of the local colonization process, as can be seen in Fig. 1.

The length of the lag between founder establishment and local colonization, matches the age at which these trees exhibit a remarkable increase in their crops. We propose that the abrupt increase in fruit production found at ages around 10 years has a strong effect on avian dispersers' visitation rate and hence, on the intensity of seed consumption and dispersal around the colonizer. As we stated before, when a single plant colonizes a new site, local dispersal is expected to be delayed because of an initial scarcity of propagules. Once the founder tree reaches large crown volume and crop size, propagule pressure and bird attraction may increase rapidly, enhancing the recruitment process. The presence of co-founder trees in a colonizing nucleus may imply earlier increase on local fruit supply and a faster growth of the nucleus. This could explain why the shortest lag-phase occurred in the population that includes three co-founders, but more evidence is needed to be conclusive about this.

The relationship between fruit production and dispersal efficiency is complex, with various limitations affecting the process. As stated before, there is some evidence about dispersers' visitation rates and fruit removal being directly related with fruit availability (Sallabanks 1992; Jordano 1987; Herrera and Jordano 1981; Deckers et al. 2008). However, some studies propose that the proportion of seeds that are effectively dispersed in a visit decrease when fruit production is high, due to saturation in the disperser function by changes of behavior (Jordano 1995). Big trees attract more birds, but each visit is less effective because they stay longer in the canopy. The time a bird spends on the source tree increases the number of seeds that are deposited under the parent canopy and are thus not effectively dispersed (Abrahamson 1989). Nevertheless, Jordano (1995) proposed that growing trees can reach crop values high enough to suppress this negative effect on individual effectiveness. Although increased bird attraction and fruit removal rates with growing crop size is a reasonable assumption for our studied populations, this cannot be concluded solely from age structures data. More information on actual bird attraction and fruit removal in the area is needed.

A single colonizer might experience all these stages in its interaction with local dispersers. As a nucleus starts to grow around the colonizer, visits and dispersal efficiency might increase and, at the time, the dispersers' ensemble composition might vary considerably in response to changes in the physiognomy of the landscape, that, in turn may affect the dispersal process (Jordano 1994). Evidence from direct observation of frugivorous birds in Spain indicates that trees growing in dense patches are visited more frequently by small birds behaving as short-distance dispersers (García et al. 2005; Jordano and Schupp 2000). This situation is also compatible with our model of lag-phase/increased local colonization.

In practical terms, the detected lag phase represents an opportunity for preventing further spread of *P. mahaleb* in the study area, and probably in other ecosystems invaded by this species and other bird-dispersed trees. Early detection and rapid eradication of new invasion focuses should be targeted as a principal aim of an effective control strategy. At the same time, efforts should be devoted to the identification and control of vectors and pathways associated with the dispersal of propagules of founder trees.

Conclusions

In this work, we found evidence supporting a key relationship between the reproductive performance of colonizing trees and the establishment of new stands. The existence of a lag period and the high density of seedlings near the founder canopy support the idea that it acts as the main, and almost unique, source of propagules in early colonization. The end of the lag phase coincides with an abrupt increase in individual fruit production between the age of ten and fifteen, which may have a strong effect on seed dispersal. Further understanding of the spreading process by means of the behavior and composition of the assemblage of dispersers will help to define management options directed to control *P. mahaleb* invasion.

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