

Potential contribution to the invasion process of different reproductive strategies of two invasive roses

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Abstract The type of reproductive system may be an important trait for the establishment and maintenance of populations of invasive plant species in new areas, as it can influence their demography and genetics. We studied the breeding system of two exotic invasive species, *Rosa rubiginosa* and *R. canina*, in a natural reserve in Argentina, using a combination of pollination experiments. We asked how the different reproductive modes of these species affect the quantity and quality of the fruits and seed produced. Our results show that both invasive rose species have an array of reproductive strategies, and that they are able to invade without pollinators, as they can produce seeds in the same quantity and quality through wind-pollination, self-pollination, and apomixis. Such lack of dependence on pollinators and pollination for reproduction should enhance colonization into new areas, suggesting the need of intensive monitoring of

spread and dispersal. Considering that both species are successful invaders in the region, our results are in line with Baker's rule, which posits that plants capable of uniparental reproduction are more likely to invade new areas.

Keywords Apomixis · Breeding system · Pollination · *Rosa canina* · *Rosa rubiginosa* · Seed production

Introduction

Introduced alien species can become invasive only if they manage to reproduce (Richardson et al. 2000; Blackburn et al. 2011). Plants display an enormous diversity of reproduction modes, and the reproductive system is an especially important life history trait for invasive species, because it is crucial for the establishment and maintenance of populations in new areas and therefore for the invasion process itself (Barrett 2010; Torres et al. 2013; Correia et al. 2014; Moodley et al. 2015). Reproductive systems have the potential to influence greatly the population dynamics of invasive plant species through determining propagule supply in terms of both quality and quantity of seeds. It follows that providing knowledge of plant breeding systems is crucial for understanding biological invasions (Ward et al. 2012). However, little quantitative information is available on the breeding system and

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pollination requirements of most alien plants, even for the most invasive species (Parker 1997; Traveset and Richardson 2014).

Sexual reproduction and, more specifically, pollination play an important role in the invasion process of many plants. For introduced plants that require pollinators, their reproductive success depends on their ability to attract the services of resident pollinators that can provide adequate pollen transfer in their new range. Many of the world's most invasive woody plants are likely to be biotically pollinated, as their flowers are visited by animals (Traveset and Richardson 2014). Many successful exotic woody species are obligate outbreeders, because longevity reduces the risk of reproductive failure if mates arrive later in the invasion process (Barrett 2010). It may be common in woody invaders to be highly outcrossing and strongly dependent on local pollinating mutualists (Parker 1997). However, there are some cases in which pollination mutualistic relationships might not be the key for the establishment success of non-native plants in the introduced area (Montero-Castaño et al. 2014). Understanding how plants succeed despite being decoupled from their native pollinators is critical if we are to understand and predict biological invasions (Harmon-Threatt et al. 2009).

Sexual reproduction may have genetic benefits for plants. Yet, many angiosperm species have evolved predominant autogamous reproductive strategies, which releases individuals from the need of having mating partners, allowing rapid colonization of unoccupied space. However, autogamy is associated with diverse costs, such as inbreeding depression, pollen discounting and genetically uniform populations (Barrett 2002). Thus, a fundamental dichotomy is whether offspring arises from uniparental or biparental reproduction. This distinction is particularly important for invasive species. Mates or pollinators may be limiting during the establishment and subsequent colonizing episodes, which may favor uniparental over biparental reproduction (Barrett 2010).

Baker (1955) posited that species capable of uniparental reproduction should be more likely to establish after long-distance dispersal than species that rely on suitable mates and pollinators. This hypothesis, known as Baker's Law or Baker's Rule, is likely to apply to both the initial establishment of alien plants after a long-distance dispersal event and their subsequent spread into a new range (Pannell et al. 2015).

Extending Baker's Rule to invasive plant species, it is reasonable to expect that uniparental reproduction alleviates mate shortages experienced by introduced plant species in new habitats when conspecific plants are scarce or absent (Hao et al. 2011; Ward et al. 2012; Torres et al. 2013). Although outcrossing might be beneficial for the evolution of invasive plants, the ability for autonomous seed production, which does not necessarily preclude outcrossing, is likely to be important during several stages of the invasion process. For example, autonomous seed production is likely to allow further spread of the naturalized plants by increasing propagule pressure, thus facilitating invasion (Van Kleunen and Johnson 2007). However, when populations become larger and mates or pollinators are less limiting, outcrossing should become more beneficial, promoting recombination and adaptive evolution. Therefore it becomes important to analyze if invasive species have flexible mating systems and if patterns of mating are context dependent (Barrett 2015).

A mechanism for autonomous seed production is apomixis: the asexual, clonal production of seeds, which helps avoiding the processes of meiosis and fertilization. This reproduction mode has been documented in over 300 species, in 30 out of 460 angiosperm families (Kandemir and Saygili 2015), and combines the advantages of seed propagation (high multiplication rate, long distance dispersal) with those of clonal propagation (maintaining genetic structure and hence fixing superior genotypes after crossing, alleviating mate shortage; van Dijk and Vijverberg 2005; Dellinger et al. 2015; Kandemir and Saygili 2015). Traits related with clonal propagation are typical in invasive species (Kolar and Lodge 2001). More specifically, apomixis is found in several invasive species (Rambuda and Johnson 2004). However, little information exists about the contribution of asexual reproduction to the invasion process (Budde et al. 2010).

We studied the breeding system of two exotic invasive species, *Rosa rubiginosa* and *R. canina*, in a natural reserve in Argentina. Although these exotic species have been cited as problematic invaders in several parts of Argentina (Aguirre et al. 2009; Cavallero and Raffaele 2010; Giorgis et al. 2011; Zimmermann et al. 2012) and the world (Hunter 1983; Hatton 1989), little information exists about their breeding system in the invaded area. Roses are an

important horticultural crop, receiving much attention from rose breeders, but comparatively little is known about the reproduction biology of wild roses (MacPhail and Kevan 2009). Pollination in *Rosa* species has not been well studied experimentally (MacPhail and Kevan 2007).

The most common type of sexual breeding system in wild species of *Rosa* is xenogamy or cross-pollination (Wissemann and Hellwig 1997; MacPhail and Kevan 2009). These species bear flowers with entomophilous traits, such as odor and bright coloured petals, which suggests that pollination and sexual reproduction could play a role in fruit production. Both species are, however, presumably able to reproduce without pollination, as several *Rosa* species are known to be apomictic, including *R. canina* and *R. rubiginosa* (Wissemann and Hellwig 1997; Werlemark 2000; van Dijk and Vijverberg 2005; MacPhail and Kevan 2009). Previous studies have found low genetic diversity in invasive populations of *R. rubiginosa* in Argentina and suggested that this might be a result of mainly asexual reproduction (Zimmermann et al. 2010). In addition, in previous visits to the study site we had observed few or no floral visitors for these species in spite of a profuse production of fruits (B. Padron; H. J. Marrero and A. C. Mazzolari, pers. obs.), which further suggests uniparental reproduction.

Given that reproduction imposes an important barrier for an exotic species during the invasion process (Barrett 2010; Torres et al. 2013; Correia et al. 2014; Moodley et al. 2015), our aim was to assess the reproductive strategies of two invasive species, *R. rubiginosa* and *R. canina* in a natural reserve in Argentina. Specifically, we asked how the different reproductive modes of these species affect the quantity and quality of the fruits and seeds produced. Based on the existing evidence that many successful invasive plant species present uniparental reproduction (Petanidou et al. 2012), we expected that both study species were capable of producing seeds and fruits through self-pollination and apomixis. However, taking into account the possible effects of inbreeding depression, we expected that seeds and fruits produced by self-pollination and apomixis were of lower quality and quantity than in strategies involving cross-pollination. We assumed that heavier seeds and fruits are of a better quality because larger, better provisioned seeds are expected to be at an advantage in situations with limited access to water or light, in which

seedlings are forced to rely on stored reserves (Leishman 2001; Moles and Westoby 2006). Understanding the mating system of invasive species can contribute to predict species invasiveness, which is one of the long-term goals of invasion biology. Such understanding will not be accomplished by a single study, but is likely to benefit greatly from further case studies examining modes of reproduction in invasive species (Ward et al. 2012).

Methods

Study area

We conducted this study at Villavicencio Natural Reserve, located 30 km northwest from Mendoza city, Department of Las Heras, Argentina. The reserve has an area of 72,000 ha and an altitudinal range of 700–3000 m above sea level, in which the Monte, Cardonal and Puna phytogeographical provinces are represented (Dalmaso et al. 1999). In this area, *R. rubiginosa* and *R. canina* have invaded and coexist in several valleys of the reserve.

Study species

Rosa rubiginosa and *R. canina* are erect, scrambling, deciduous shrubs of variable height (up to 3 m). They are native to Europe and Asia, and they were introduced to Argentina at the beginning of the twentieth century (Damascos and Bran 2006). The stems have numerous curved thorns and bristles and the leaves are bright green with 5–7 ovate or obovate leaflets, 10–25 mm long, 10–15 mm wide, with toothed margins. In *R. rubiginosa* the lower surface usually presents simple hairs mixed with glandular hairs; the foliage has an apple-like fragrance, a distinctive character for *R. rubiginosa*. In contrast, *R. canina* has no glandular hairs in the leaf surface, and lacks the apple-like fragrance. Both species present small clusters of flowers. Flowers are pink in *R. rubiginosa* and white in *R. canina*. One seed is produced per pistil. In both species the rose hips (infrutescences) are made up of the fleshy or pulpy receptacle surrounding the actual fruits (achenes). The rose hips are orange-red, ovoid to globose, 15–20 mm long, and contain numerous achenes, where the seed is enclosed in a

hard pericarp (Damascos and Bran 2006; Aguirre et al. 2009; MacPhail and Kevan 2009).

Description of breeding system

To study the breeding system of both *Rosa* species we performed pollination experiments at ten sites, separated 200 m from each other, located along one valley (Quebrada de Hornillos; 32°30'33.71"S, 69°1'4.08"W). At each site, we randomly selected flower buds in at least 10 different ramets of each species. On each experimental flower we applied one of the following six treatments: (a) emasculation ($n = 48$ and 50 flowers for *R. canina* and *R. rubiginosa*, respectively): we cut anthers in flower buds and bagged them with nonwoven fabric bags to exclude wind-borne pollen and flower visitors and to study apomixis; (b) hand self-pollination ($n = 45$ and 36): we bagged flower buds with nonwoven fabric bags, and when the flower developed, we hand-pollinated them with pollen from flowers of the same shrub to assess the effects of self-pollination; (c) bagged control ($n = 79$ and 45): we bagged flowers with nonwoven fabric bags and left them unmanipulated to assess a possible effect of bagging on fruit production; (d) pollinator exclusion ($n = 33$ and 35): we bagged flowers with a coarser mesh cloth that did not exclude wind-borne pollen, but excluded flower visitors, in order to assess the role of flower visitors in rose hips and fruit production; (e) hand cross-pollination ($n = 48$ and 45): we hand-pollinated unbagged flowers with pollen from another ramet separated at least 400 m to study the effects of cross-pollination; and (f) natural pollination ($n = 65$ and 73): we left unbagged flowers unmanipulated.

We recorded the number of marked flowers that developed a rose hip. Once the rose hips ripened, we collected them and counted the number of formed and aborted fruits. To assess fruit quality, in each treatment we randomly selected three fruits in each rose hip and recorded the fresh weight. To assess seed viability we pooled all the fruits of each treatment, randomly selected 20 fruits per treatment, and performed the Tetrazolium seed viability test (Miller 2004).

Data analysis

We estimated the following variables for each treatment: (a) proportion of fruits formed per rose hip (i.e. number of formed fruits/[number of aborted

fruits + number of formed fruits]), (b) proportion of formed rose hips (i.e. proportion of marked flowers that developed into rose hip), (c) fruit weight and (d) proportion of viable seeds. For the variable proportion of formed rose hips we decided not to include data from the natural pollination treatment, as several marked flowers were lost at the end of the experiment, and we were unable to determine if the flower developed into a rose hip and was removed afterwards (e.g. by the wind or animals), or if it did not develop at all. To estimate the proportion of fruits formed per rose hip, fruit weight and the proportion of viable seeds in the natural pollination treatment, we collected rose hips randomly in the study area to obtain the fruits and seeds.

The effect of each treatment on quantity (i.e. proportion of fruits per rose hip and proportion of rose hips) and quality (i.e. fruit weight and proportion of viable seeds) of fruits and seeds produced was analyzed with generalized mixed models, which included "site" as a random factor. We fitted generalized linear mixed models (GLMMs) using the lme4 package (Bates et al. 2015) in R statistical software version 3.2.0 (R Core Team 2015).

We evaluated the differences between treatments using pairwise multiple comparisons with Tukey tests with the multcomp R package (Hothorn et al. 2008). We considered differences between treatments to be statistically significant whenever error probabilities were <0.05 . We evaluated the significance of model coefficients using the Anova function in car package (Fox and Weisberg 2011).

Results

For both *Rosa* species, the proportion of fruits per rose hip were significantly lower where the flowers were emasculated compared to other treatments (Fig. 1; Table 1). Regarding the proportion of formed rose hips, in *R. canina*, emasculated flowers formed fewer rose hips than in the other treatments. Only 6.5% of the emasculated flowers developed into a rosehip, 76% in the bagged control, and 100% in all other treatments (Fig. 2; Table 1). In *R. rubiginosa*, there were no differences between treatments regarding the proportion of formed rose hips (Fig. 2; Table 1).

For fruit weight, *R. canina* fruits from self-pollination were significantly smaller than other treatments (Fig. 3; Table 1). In *R. rubiginosa*, fruits from self-

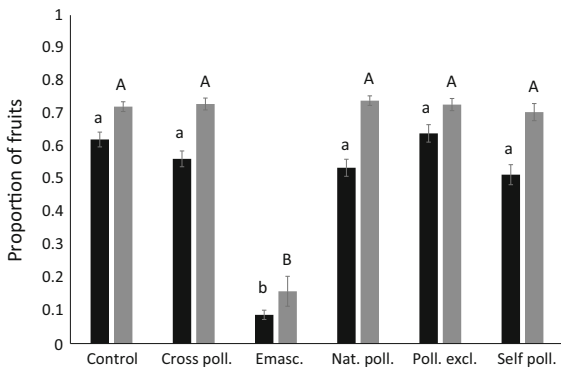


Fig. 1 Mean (\pm SE) proportion of formed fruits per rose hip for *Rosa canina* (black) and *Rosa rubiginosa* (grey). Small letters for *R. canina* and capital letters for *R. rubiginosa* show differences between treatments (GLM, Tukey contrast test $p < 0.05$)

pollination and control were smaller than in other treatments, and emasculated flowers produced the biggest fruits (Fig. 3; Table 1). Seed viability was high in both species and did not differ significantly among treatments for both species (Fig. 4; Table 1). The percentage of viable seeds in *R. canina* was 70 and 85% for emasculated and self-pollinated flowers, respectively, and 95% for all other treatments. *R. rubiginosa* produced more than 90% viable seeds in all treatments, reaching 100% in pollinator exclusion and cross-pollination treatments.

Discussion

This is the first study that analyses the effects of apomixis, self-pollination, and cross-pollination on

seed and fruit production of *R. canina* and *R. rubiginosa* in Argentina. We found that both species are capable of reproducing by apomixis in the invaded area. We found, however, that both species produce fewer fruits by apomixis when compared to the other reproductive modes. This is because no rose hips are formed, or when they are, few fruits are formed within them. Our results are in agreement with previous studies that show that both *R. canina* and *R. rubiginosa* are able to reproduce by apomixis (Wissemann and Hellwig 1997; Werlemark 2000; van Dijk and Vijverberg 2005; MacPhail and Kevan 2009). However, Weissmann and Hellwig (1997) reported a lower percentage of viable seeds produced by apomixis in both rose species, while we observed no differences in viable seeds between the different strategies. Furthermore, in our study fruits produced by apomixis were heavier, suggesting improved quality (Leishman 2001; Moles and Westoby 2006; Pérez-Harguindeguy et al. 2013) and the seeds were as viable as seeds produced by the other strategies. This is in line with the evidence of a trade-off between propagule size and number. As resources are finite, plants must choose to allocate these resources between producing few large propagules versus many smaller ones (Leishman 2001). As larger propagules are better able to withstand the hazards of establishment (Leishman 2001; Moles and Westoby 2006), the fact that both *Rosa* species produce fewer, but larger fruits by apomixis and considering that both species are successful invaders in the study area, our results suggest that apomixis could play an important role in the process of invasion. Although the proportion of formed rose hips and fruits in the emasculated flowers

Table 1 Parameters of the models used to evaluate the effects of different treatments on the variables “proportion of formed fruits”, “proportion of formed rose hips”, “fruit weight” and “proportion of viable seeds” of *Rosa canina* and *R. rubiginosa*

	Model	Likelihood ratio Chi-square	Degrees of freedom	<i>p</i> value
<i>Rosa canina</i>	Prop. fruits ~ (1 site) + treatment	55.684	6	$\ll 0.001$
	Prop. rose hips ~ (1 site) + treatment	17.448	4	0.00015
	Fruit weight ~ (1 site) + treatment	80.027	6	$\ll 0.001$
	Viable seeds ~ (1 site) + treatment	0.5285	5	0.991
<i>Rosa rubiginosa</i>	Prop. fruits ~ (1 site) + treatment	123.25	5	$\ll 0.001$
	Prop. rose hips ~ t(1 site) + treatment	6.0753	4	0.1936
	Fruit weight ~ (1 site) + treatment	92.643	5	$\ll 0.001$
	Viable seeds ~ (1 site) + treatment	0.0858	5	0.9999

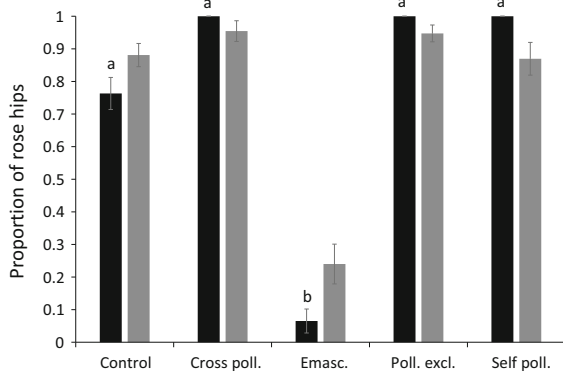


Fig. 2 Mean (\pm SE) proportion of formed rose hips for *Rosa canina* (black) and *Rosa rubiginosa* (grey). Letters show differences between treatments in *R. canina*. In *Rosa rubiginosa* there are no differences between treatments (GLM, Tukey contrast test $p < 0.05$). We decided not to include data from the natural pollination treatment because of methodological problems (see [Materials and Methods](#))

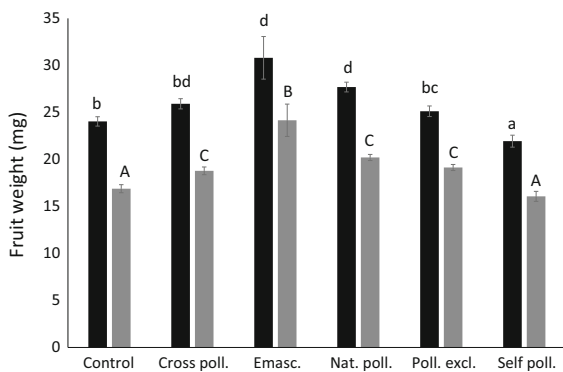


Fig. 3 Mean (\pm SE) of fruit weight for *Rosa canina* (black) and *Rosa rubiginosa* (grey). Small letters for *R. canina* and capital letters for *R. rubiginosa* indicate significant differences between treatments (GLM, Tukey contrast test $p < 0.05$)

is rather low, given the high density of plants and the large number of flowers produced by the rose population, the seeds produced by apomixis may still represent an important propagule source. Several studies have shown that autonomous seed production is associated with naturalized and invasive plant species (Rambuda and Johnson 2004; Van Kleunen and Johnson 2007). This association highlights the importance of considering apomixis as an important plant attribute that deserves further research, using approaches that allow the assessment of the occurrence of natural apomixis in the population, such as the analysis of chromosomes in seed endosperm.

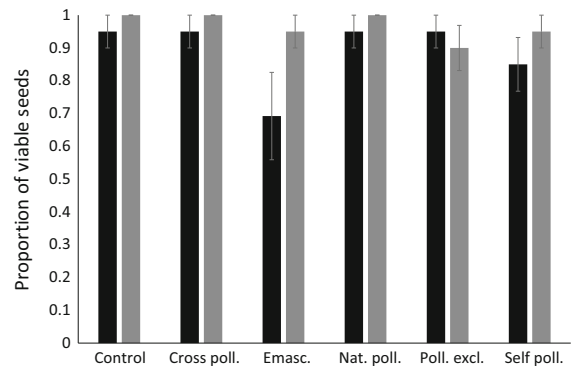


Fig. 4 Mean (\pm SE) proportion of viable seeds for *Rosa canina* (black) and *Rosa rubiginosa* (grey). There are no differences between treatments (GLM, Tukey contrast test $p < 0.05$)

We expected that cross-pollination produced a greater amount of fruits per rose hip than other reproductive strategies. Instead, we found differences in the number of rose hips and fruits produced only with emasculated flowers. This result suggests that both species can reproduce equally successfully with self- and cross-pollination. Proportion of formed fruits and rose hips from natural pollination were similar to those from self-pollination, suggesting a mixed mating system with relatively high rate of selfing. Previous results regarding the effects of self and cross pollination on rose hips and seed production are variable. MacPhail and Kevan (2009) reported lack of differences regarding production of rose hips between self and cross pollination for *R. canina*, but not for *R. rubiginosa*. On the other hand, Ueda and Akimoto (2001) reported higher percentage of seed set under self-pollination for *R. rubiginosa*. This result differed from Wissemann and Hellwig (1997), who concluded that the main form of reproduction in both *R. canina* and *R. rubiginosa* is cross-pollination, because they found that these rose species produce less seeds with self-pollination than with cross-pollination.

We did not perform germination experiments or any other technique that allow us to follow the development and fitness of the progeny, but as there are no differences in quality and quantity of fruits and seed viability produced via self- and cross-pollination, we can conclude that there are no evident effects of inbreeding depression in the populations we studied, at least at the stage of seed and fruit development. Considering that both species are successful invaders in the region, these results are in line with Baker's rule,

which posits that self-compatible plants, particularly those capable of autonomous self-pollination, are more likely to invade (Baker 1955; Harmon-Threatt et al. 2009; Barrett 2010).

We found no differences in the number of rose hips and fruits produced between the pollinator exclusion and cross-pollination treatments. This result indicates that for these species, biotic pollination does not represent a barrier for invasion. Several authors have found in previous studies that pollination is an important process for woody invasive species and that introduced plants can successfully attract resident generalist pollinators (Richardson et al. 2000; Brown et al. 2002; Memmott and Waser 2002; Morales and Aizen 2006; Olesen et al. 2008). The fact that *R. canina* and *R. rubiginosa* do not depend on biotic pollination is of particular importance as mates or pollinators will not limit establishment and subsequent colonization. This is in line with the results obtained by Montero Castaño et al. (2014), who found that pollination mutualistic relationship may not be the key for non-native plant establishment success in the introduced area.

In this study we found that both species are capable of reproduce successfully with uniparental reproduction, and this could lead to low genetic variability. This is in line with results obtained in previous studies, in which populations of *R. rubiginosa* have very low genetic variability (Zimmermann et al. 2010). Nevertheless, both species are successful invaders, supporting the idea that genetic diversity is not always an important factor for the invasion process. Genetic diversity has been demonstrated to be positively correlated with invasion success (Crawford and Whitney 2010), and standing genetic variation is believed to be important to invasive species' ability to adapt to novel environments (Barrett and Schluter 2008). For these reasons, biological invasions of asexual species are perplexing evolutionary phenomena. Such invasions often consist of a few genotypes or clones, suggesting a limited contribution of natural selection in the exotic range to invasion success (Clark et al. 2012). Many introduced populations with very low neutral genetic diversity become successful invaders (Ren et al. 2005; Zimmermann et al. 2010) and have the ability to adapt to their new environments (Roman and Darling 2007; Rollins et al. 2013).

Research on invasive species has increased exponentially throughout the last century (Richardson and Pysek 2008). However, the biology and ecology of

most invasive species is not well understood, which limits our ability of devising knowledge-based decisions and management protocols (Simberloff 2003; Esler et al. 2010) for which knowledge of the biology of the target organism is essential (Hoffmann 2014). Determining the reproductive system of a species is crucial for understanding the demography and genetics and for predicting how invasive species will respond to future environmental challenges, and hence to establish viable management strategies (Barrett 2010; Hao et al. 2011). In addition to the reproductive strategies described in this paper, both species are able to reproduce clonally via roots, and the relative contribution of each mode of reproduction to their spread still needs to be assessed. Another relevant topic to consider in further studies is the probable hybridization between both rose species, which has been suggested by Wissemann and Hellwig (1997). Given broad range of reproductive strategies to produce fruits and seeds in our two study species, they are likely to colonize new areas through dispersal vectors, such as birds or large mammals. This is why management of these species requires, besides reducing the number of plants in the invaded area, an intensive monitoring to prevent new invasion foci.

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