

Differences in phenology and fruit characteristic between invasive and native woody species favor exotic species invasiveness

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Abstract This study evaluates the idea that differences in reproductive phenology and traits between coexisting exotic and native species may promote exotic invasiveness. Reproductive phenology, proportions of flowers setting unripe fruits and ripe fruits (fruit set), abundance and morphology of fruits, and seed viability were compared between two invasive (*Crataegus monogyna* and *Sorbus aucuparia*) and six native woody fleshy-fruited species at three sites in temperate forests of northwestern Patagonia, Argentina. Flowering and the onset of fruit ripening occurred later in the exotic species than in most of the native species. The exotic species differed between them in some aspects of the reproductive process: *C. monogyna* had a higher fruit set, whereas *S. aucuparia* produced more flowers which offset its low values of

fruit set. In both the exotic species and one simultaneously fruiting native species (*Schinus patagonicus*), high numbers of ripe fruits with a high proportion of viable seeds remained on the plants at a time when fruits of other native species were either scarce or absent (autumn–winter period). Compared to the fruits of *S. patagonicus*, those of both the exotic species are larger and fleshier. Therefore, the fruits of both the exotic species offer the dispersers, especially birds which were the most important frugivores in these studied temperate forests, a resource that would not be provided by the native plants. The success of these exotic species in Patagonian forests appears to be attributable in part to differences in their reproductive attributes such as fruit phenology and fruit traits such as size and fleshiness.

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Introduction

Understanding functional traits of exotic species improves predictions of invasiveness by enabling the detection of potentially invasive species before they impact upon ecosystems (Rejmánek and Richardson 1996; Sakai et al. 2001; Pyšek and Richardson 2007). The comparison between exotic and coexisting native species is particularly important in this regard by providing hints about those traits that give invasive species an advantage over native species and enhance the potential of invaders to outnumber natives (Daehler 2003; Hamilton et al. 2005; Van Kleunen et al. 2010b). Some traits associated with plant growth, such as photosynthetic rate and biomass production, can have higher values in exotic invasive than in coexisting native species (Pattison et al. 1998; Lake and Leishman 2004; McAlpine et al. 2008; van Kleunen et al. 2010a; Dickson et al. 2012). Among reproductive traits, large seed crop, high seed dispersal rate, and vegetative propagation are relevant for the establishment and spread of exotic species and may determine their invasion success in new areas (Lodge 1993; Rejmánek and Richardson 1996; Gibson et al. 2011). The timing of reproduction is also critical for the reproductive success of exotic plants (Wolkovich and Cleland 2011).

The comparison of fruit and flower phenology between exotic invasive species and coexisting native species enables the identification of possible changes at community level that may favor exotics. Overlapping of the reproductive phenology of exotic and native species can result in competition for pollination and dispersing services, and reduce the reproductive success of native species (Gosper et al. 2005; Morales and Traveset 2009). This effect was observed in the invasive species *Lythrum salicaria* and *Taraxacum officinale* and co-occurring native species which suffered both reduced pollinator visits and seed production (Brown et al. 2002; Muñoz and Cavieres 2008); furthermore, the higher production and quality of fruits developed by exotic species may cause native seed dispersers to switch their preferences to the fruits of exotic species (Vila and D'Antonio 1998; Sallabanks 1993a). On the other hand, when flowering or fruiting phenology of exotic and native species does not overlap, the lack of competition may enhance the seed dispersal, by mutualists, of exotic species, thus favoring their spread (Richardson et al. 2000; Gosper 2004; Gosper et al. 2005; Lloret et al. 2005; Godoy et al. 2009a, b). Among introduced species, fleshy-fruited plants with the

potential for dispersal by efficient local vertebrates (particularly birds) are very likely to become invasive (Richardson et al. 2000; Rejmánek et al. 2005). Invasive species can offer, for the native community, a resource that was previously unavailable or scarce, such as fruits that ripen during a time of the year when no other fleshy fruits are ripe or when fleshy fruits of native species are scarce. The newly available food resource for the local community results in more dispersal and faster invasion by exotic species (Richardson et al. 2000; Gosper 2004; Gosper et al. 2005; Greenberg and Scott 2010). Fruit abundances and fruit traits such as morphology, color, and composition could change dispersers' preferences and the success of invasive species (Gosper et al. 2005; Gosper and Vivian-Smith 2010; Aslan and Rejmánek 2012).

In this work, we compare the reproductive traits of two recently invasive exotic woody species, *Crataegus monogyna* Jacq. and *Sorbus aucuparia* L. (Rosaceae), with those of six coexisting native woody species in temperate Patagonian forests of Argentina. All studied species develop fleshy fruits which are dispersed by birds, the most important frugivores in temperate South American forests (Armesto et al. 1987). We focused on flowering and fruiting onset and duration, proportion of flowers setting unripe and ripe fruits (fruit set), production of fruits and seeds, and seed viability. The aims of this study are to determine whether the introduction of these exotic species represents a change in the timing of events related to seed production in the invaded area and to evaluate the qualitative and quantitative differences between each of the two exotic species and the native species regarding the resources offered to seed dispersers. We hypothesized that the lack of reproductive phenological overlapping between exotic and native species would play a key role in the invasion success of exotic species. In addition, we would expect these exotic species to have, compared to native coexisting species, larger fruits, fruit sets (proportion of flower setting ripe fruits), and seed viability.

Materials and methods

Study species

Crataegus monogyna is a small tree or shrub up to 10 m in height native to Europe, West Asia, and North Africa, while *S. aucuparia* is a tree up to 15–20 m in

height native to Europe and Asia. Both species are invasive in New Zealand (Webb et al. 1988); *C. monogyna* is also cited as invasive in Australia and North America (Sallabanks 1993a, b; Cronk and Fuller 1995; Bass et al. 2006). In the Andean area of Argentina, *C. monogyna* is more widely spread than *S. aucuparia* (Fernández 2007; Lediuk, unpublished data). Both the species were introduced as ornamentals and are used for hedging (Rovere et al. 2013). In 1940, they were planted in nurseries located in some areas of the Andean National Parks of Argentina (Simberloff et al. 2002).

Both the species are deciduous and produce hermaphroditic white flowers in inflorescences and fleshy red pomes. Fruits of *C. monogyna* are single-seeded (the seed being enclosed by a woody carpel wall), and those of *S. aucuparia* contain 1–6 seeds. In their native ranges, flowers of both the species are pollinated by a wide variety of insects (García and Chacoff 2007; Pías et al. 2007). Although they are partially self-compatible, their fruit sets increase by insect visits and cross-pollination (Raspé et al. 2000; García and Chacoff 2007). Fruits ripen in summer and are dispersed during autumn–winter (Raspé et al. 2000; Sobral et al. 2010) by birds, especially by the *Turdus* genus (Guitián and Fuentes 1992; Guitián et al. 2000).

Six native woody species of the areas invaded by *C. monogyna* and *S. aucuparia* in the Patagonian forests were also studied: *Aristotelia chilensis* (Molina) Stuntz, *Azara microphylla* Hook. f., *Berberis serrato-dentata* Lechl., *Maytenus boaria* Molina, *Ribes magellanicum* Poir., and *Schinus patagonicus* (Phil.) I. M. Johnst. (Table 1). All of them develop small flowers (<1 cm in diameter) gathered in inflorescences. Native species selection was based on growth form (woody: trees and shrubs), production of fleshy fruits, seed dispersal by birds, and abundance of reproductive individuals in the study plots. The range of canopy openness under which flower production takes place is widely variable in the cases of *C. monogyna*, *R. magellanicum*, and *S. patagonicus*, intermediate to high in *S. aucuparia* and *M. boaria*, and low to intermediate in *A. chilensis*, *A. microphylla*, and *B. serrato-dentata* (Table 1).

Study area

The study took place in three sites of the North Andean-Patagonian forests of Argentina. Study sites

were disturbed forests located at the surroundings of San Martín de los Andes city (hereafter named Sma site: 41°08.737'S, 71°21.849'W, 830 m a.s.l.) in Lanín National Park and Bariloche city (termed Otto site: 41°08.758'S, 71°21.977'W, 1,285 m a.s.l., and Crub site: 41°08.654'S, 71°18.889'W, 871 m a.s.l.) near Nahuel Huapi National Park. The regional climate is temperate cold with a mean temperature of 5–8 °C (Ezcurra and Brion 2005) and annual precipitations between 1,100 and 1,400 mm in Bariloche (Pereyra 2007) and about 1,500 mm in San Martín de los Andes (Funes et al. 2006). In the study region, the period of plant growth coincides with the dry season (spring and summer, see Online Resource 1).

The Sma site is characterized by a deciduous *Nothofagus obliqua* (Mirb.) Oerst. (Nothofagaceae) forest, the Crub site is occupied by a mixed conifer forest of *Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizarri (Cupressaceae) and the exotic *Pinus contorta* Douglas & Loudon (Pinaceae), and the Otto site is characterized by a deciduous *Nothofagus pumilio* (Poepp. & Endl.) Krasser forest. Site disturbance is mainly due to the presence of roads and trails and trampling by visitors.

Sampling

Sampling was carried out in 50 × 50 m randomly selected plots within an area where reproductive individuals of native and exotic studied species were frequent: two plots at each of the Otto and Sma sites and one at Crub site. *Ribes magellanicum* was studied at two plots in Sma and Otto sites and *B. serrato-dentata* at two plots in Otto site. The other native species were studied in one plot per site because reproductive individuals were not found in all plots (Table 1). Plot differences in plant height, stem diameter at soil level, cover, and the range of canopy openness under which the plants of each species are able to develop flowers are shown in Table 1. Plant cover was estimated by the line intercept method (Muller-Dombois and Elleberg 1974) using five 50-m parallel transects by plot (Crub) or site (Sma and Otto). Each transect began from a random point determined at the border of each plot. Canopy openness was estimated with hemispherical photographs (Nikon Coolpix 950 fitted with a fish-eye lens) taken next to each selected plant. The photographs were analyzed with the Gap Light Analyzer software,

Table 1 Latin name (abbreviation), family, growth form, leaf and fruit types, fruit size, and mean (\pm SD) values of plant height, basal diameter (BD), cover (%), and canopy openness (%) for the exotic species and coexisting native species studied at each site

Species	Family	Growth form	Leaf type	Fruit type	Fruit size (mm)	Site	Height (m)	BD (cm)	Cover (%)	Canopy openness (%)
<i>Crataegus monogyna</i> (Cm)	Rosaceae	Tree or shrub	Deciduous	Red pome	10 × 9	1	4.4 ± 1.2	11.3 ± 4.8	20.5 ± 12.9 (a)	19.1–73.6
						2	4.0 ± 0.6	11.9 ± 3.1	11.8 ± 10.7	40.7–64.7
<i>Sorbus aucuparia</i> (Sa)	Rosaceae	Tree	Deciduous	Red pome	8	2	8.6 ± 2.3	9.8 ± 1.8	6.3 ± 8.7	26.0–50.6
						3	6.8 ± 1.2	11.3 ± 4.8	9.9 ± 7.3	38.2–78.3
<i>Aristotelia chilensis</i> (Ac)*	Elaeocarpaceae	Shrub or tree	Semideciduous	Black berry	5–6	1	4.1 ± 0.6	5.9 ± 1.9	5.6 ± 6.2 (bc)	19.3–55.8
<i>Azara microphylla</i> (Am)*	Salicaceae	Shrub or small tree	Evergreen	Brown berry	2.5–3	1	3.9 ± 0.7	5.9 ± 1.0	4.8 ± 3.0 (bc)	16.1–33.8
<i>Berberis serrato-dentata</i> (Bs)	Berberidaceae	Shrub	Evergreen	Black-blue berry	7	3	0.9 ± 0.2	1.7 ± 0.4	8.5 ± 5.9	7.7–45.7
<i>Maytenus boaria</i> (Mb)*	Celastraceae	Tree	Evergreen	Capsule with red fleshy arils	5–6 × 5.5–6	2	5.2 ± 1.4	18.9 ± 6.3	4.9 ± 6.7	33.3–70.9
						1	2.0 ± 0.3	8.9 ± 7.9	1.3 ± 2.9 (b)	19.2–39.5
<i>Ribes magellanicum</i> (Rm)*	Grossulariaceae	Shrub	Deciduous	Black berry	5–8	3	1.3 ± 0.2	1.8 ± 0.5	18.0 ± 6.7	9.9–76.8
						1	1.9 ± 0.3	4.8 ± 0.6	17.3 ± 9.2 (ac)	16.9–35.2
<i>Schinus molle</i> (Sp)*	Anacardiaceae	Shrub or small tree	Evergreen	Purple drupe	5–7	2	2.6 ± 0.5	5.5 ± 0.9	7.8 ± 5.5	34.3–75.5
						3	1.9 ± 0.6	4.1 ± 1.2	18.3 ± 17.1	31.0–82.9

Numbers in the site column correspond to each study site (1 Sma, 2 Crub, and 3 Otto)

Bold letters in parenthesis indicate statistically significant differences (Tukey test $P < 0.05$) in plant cover (%) between species at Sma (site 1)

Fruit size of native species was obtained from Correa (1984)

* Dioecious species

version 2.0. The selection of plants within each plot was made by setting random points on the plots; the plants of the selected species located nearest to these points were marked. During the late winter–spring period of 2011, ten reproductive plants of each species were randomly selected and labeled at each plot (Table 1). Five selected plants per species were considered for the reproductive phenological study, and the other five plants of each species were used in biomass estimation. For dioecious species, reproductive phenology was followed only in female individuals; observations on unlabeled male individuals were made during the flowering period.

For the phenological study, as all studied species produced flowers at the distal end of their peripheral branches, three 10-cm-long distal portions of reproductive branches present in opposite points of the crown were labeled in each plant before flower bud opening. For tall plants, labeled branches were located from the middle of the crown downward. Phenological observations were made at 10–15-day intervals from flower bud opening to fruit ripening (determined by color indicated in botanical descriptions, see Table 1) and monthly until all fruits fell or were dispersed. The numbers of closed and open flowers, unripe and ripe fruits per branch were recorded at each sampling date.

For shoot biomass estimation, three 20-cm-long distal portions of reproductive branches per individual were collected after fruit ripening. Fruit dry mass per branch was measured after oven-drying at 70 °C until constant weight. The number of seeds and the dry masses of pulp and seeds per fruit were determined in 25 fruits for each species and site. For each labeled plant, the number of ripe fruits in 10 distal branch ends was counted in order to estimate the number of seeds for the same branch length, using the mean numbers of seeds per fruit and fruits per branch.

Seed viability was evaluated in 25 seeds per plant for five plants of each species and site using the flotation method (Tierney and Fahey 1998; Pairon et al. 2006). Seeds that sank after remaining in water for ten minutes were considered viable. To verify whether this method was appropriate; subsamples of sunken and floating seeds of the target species were dissected to verify the presence or absence of an embryo and subjected to viability tests using a 1 % solution of 2,3,5-triphenyl tetrazolium chloride (Delouche et al. 1971).

Statistical analyses

The following variables were compared among species: (a) proportion of flowers setting unripe fruits and (b) setting ripe fruits (fruit set), (c) number of ripe fruits, (d) number of seeds, and (e) seed viability (all variables except seed viability were analyzed at branch level). Generalized linear mixed models (GLMMs) were fitted using the lme4 (Bates et al. 2009) package in Rv.2.12.0 (R Development Core Team 2010) and by assuming either a Poisson or a Binomial error distribution, according to the dependent variable, and a log or a logit link function, respectively. Species was included as a fixed factor and site as a random factor. For each variable, one GLMMs analysis was run for *C. monogyna* and its native coexisting species and one for *S. aucuparia* and its native coexisting species. Pairwise multiple comparisons between species were made by Tukey tests in the package multcomp (in R). Differences were considered significant whenever error probabilities were <0.05.

Results

Reproductive phenology

Except for *M. boaria*, whose male flowers opened one month earlier than female flowers, all other dioecious species (Table 1) showed synchronic flowering in both the sexes (data not shown). All studied species flowered and fructified in the period of the year when precipitation was low and temperatures were high (Fig. 1 and Online Resource 1). However, there was inter-species and inter-site variability in flowering time (Figs. 1, 2). The flower opening of species growing in more than two sites (*S. aucuparia* and the native species *R. magellanicum* and *S. patagonicus*) was delayed with altitude: plants at the Otto site (1,285 m a.s.l.) flowered later than those at the other sites (830–871 m a.s.l.; Fig. 1). For each species, flowering occurred within a period of two weeks or less (data not shown). Flower opening was later in both exotics and the native species *A. chilensis* and *S. patagonicus* than in the other native species (Fig. 1). When flower opening overlapped between exotic and native species, the percentage of open flowers was higher in exotic than native species, except *S. patagonicus* at Sma, where this species was similar to *C. monogyna* in this regard (Online Resource 2). The

Native species

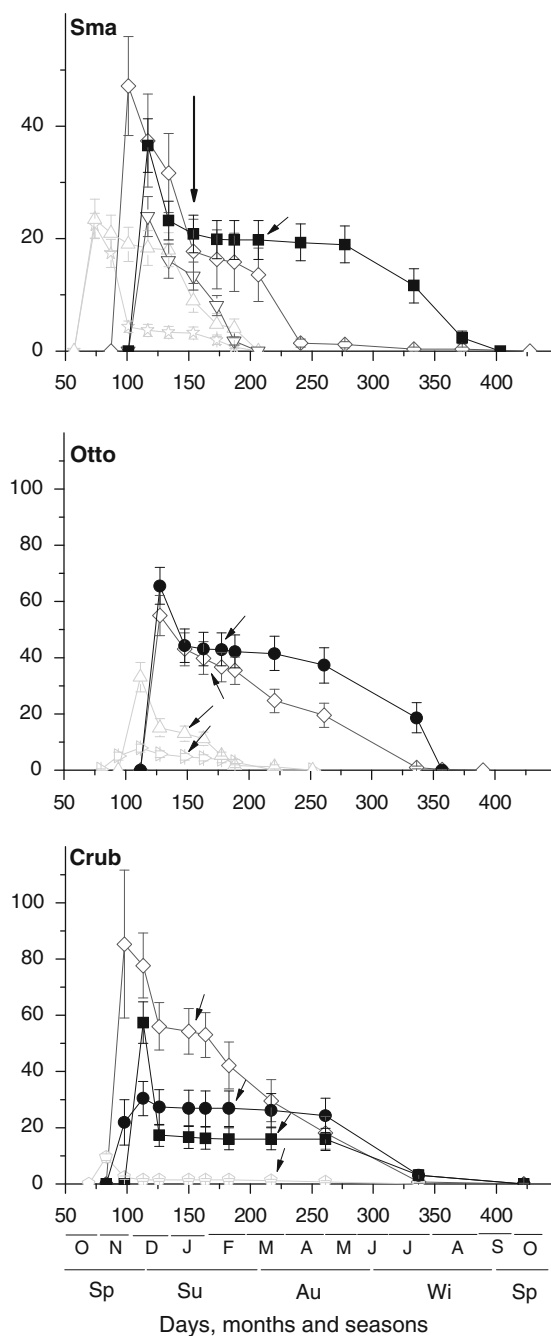
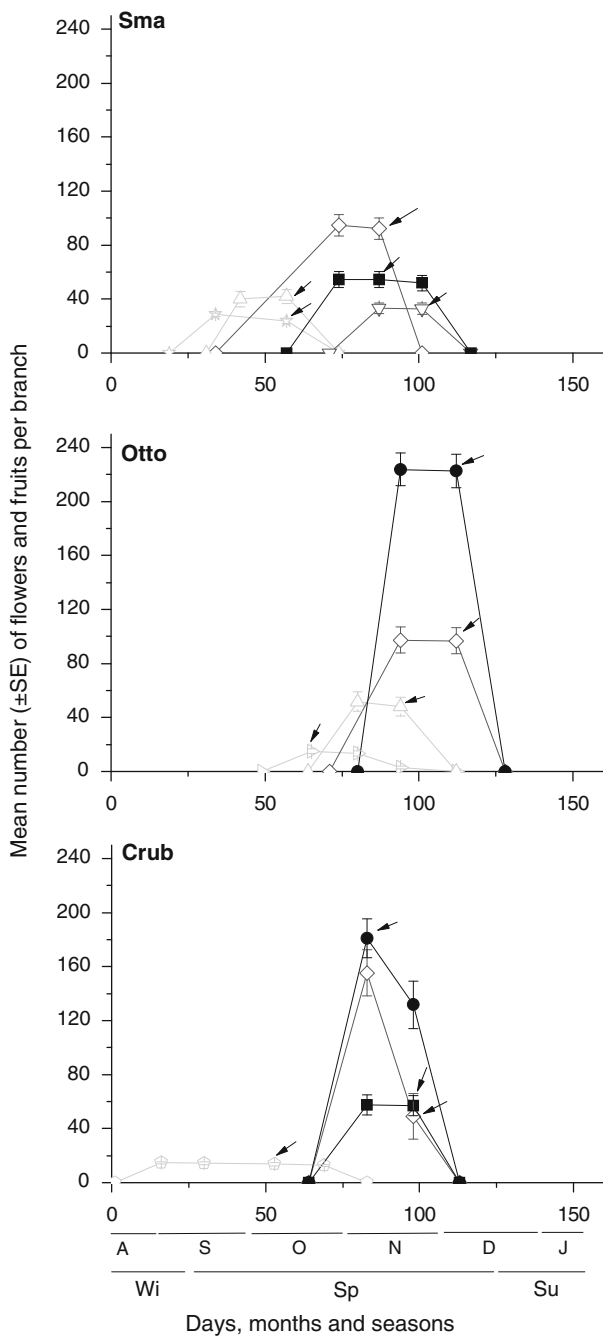


Exotic species



Flowering period

Fruiting period



◀ **Fig. 1** Mean (\pm SE) numbers of flowers and fruits per branch in exotic and native species at the study sites Sma, Otto, and Crub. Graphs on the *left* correspond to flowering periods and graphs on the *right* to fruiting periods. *Arrows* on lines point either at the moments when closed and open flowers coexist or at the moments of fruit ripening onset (the latter was the same for all native species at the Sma site and is indicated with a larger arrow). *Empty symbols* and *gray lines* correspond to native species and *filled symbols* and *black lines* to exotic species. Note that the Y and X axis scales differ between graphs

length of the open-flower period (in days) of both the exotic species and that of the majority of native species was similar (Online Resource 3), except for *S. aucuparia* at Crub site which had a period of intermediate length in comparison to the native species.

Unripe fruits were evident in the exotic species and in the native species *A. chilensis* and *S. patagonicus* two weeks or more later than in the other native species

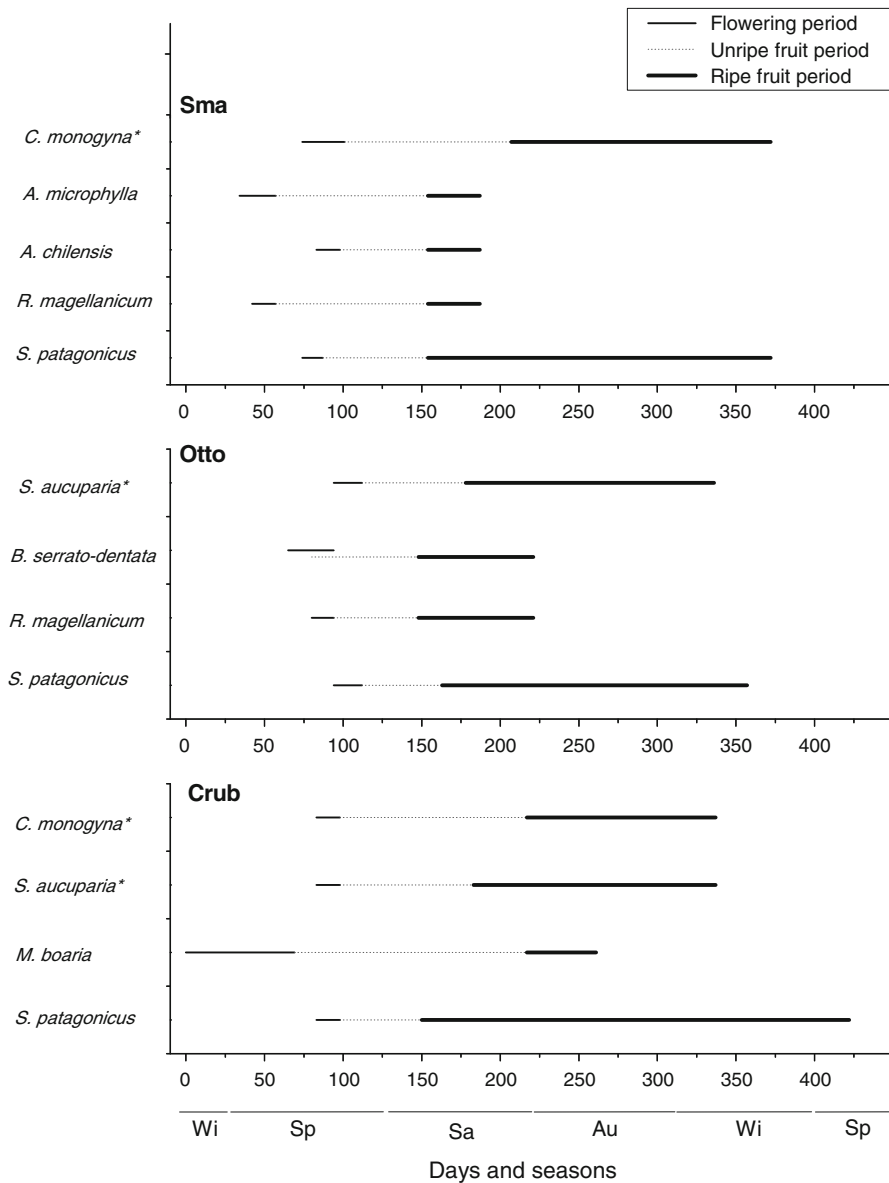


Fig. 2 Flowering (*thin lines*), unripe fruit (*dashed lines*), and ripe fruit (*thick lines*) periods of exotic and coexisting native species at the sites Sma, Otto, and Crub during seasons (*Sp* spring, *Su* summer, *Au* autumn and *Wi* winter) of the study period

(Fig. 2). The length of time for unripe fruits to ripen varied among species (Fig. 2 and Online Resource 3); it was longer in *C. monogyna* than in most native species and *S. aucuparia* and shortest in *S. patagonicus* and *A. chilensis* (Fig. 2 and Online Resource 3).

Fruit ripening in both the exotic species and *M. boaria* occurred later (at the end of summer) than in the other native species (in midsummer; Figs. 1, 2). At the time when ripe fruits were found on the labeled branch for all species (onset of ripening indicated with arrows in Fig. 1), both exotic trees and the native species *M. boaria* and *R. magellanicum* had all of their fruits per branch ripening; in the other species, the proportion of ripe fruits at that time varied from above 50 % in *S. patagonicus* and *B. serrato-dentata* to below 20 % in *A. chilensis* and *A. microphylla* (data not shown). All fruits per branch were ripe 15–20 days after the onset of ripening (data not shown). Except for the native *S. patagonicus*, at the time when the exotic species had fully ripened all of their fruits, the native species possessed either low numbers or the absence of ripe fruits on the labeled branches (Figs. 1, 2). Ripe fruits of both the exotic species remained on their branches for a longer period (autumn and early winter) than those of all native species except *S. patagonicus* and *M. boaria* (Online Resource 3). However, the latter two species had few fruits standing by early winter (Fig. 1). The number of ripe fruits on the branches tended to decline faster in the native species than in both the exotic species (Fig. 1).

Flower and fruit production

The proportion of flowers setting unripe fruits and fruit set differed among species (Online Resource 4). The proportion of flowers that set unripe fruits was higher in *C. monogyna* than in most native species, whereas *S. aucuparia* had the lowest values (Table 2). *Crataegus monogyna* exhibited the highest fruit sets, and *S. aucuparia* reached intermediate values (Table 2). *Schinus patagonicus* had the highest fruit set in areas invaded by *S. aucuparia* and, together with *R. magellanicum* and *A. chilensis*, had a higher fruit set than the other native species at the site invaded by *C. monogyna*. The number of ripe fruits per branch varied among species (Online Resource 4). Both the exotic species had more fruits per branch than the native species except *S. patagonicus*, which had the highest number of ripe fruits per branch (Table 2).

Seed production and viability

The number of seeds per fruit was low and similar for all species (1–3 seeds/fruit) except *R. magellanicum*, which had, on average, 13 seeds/fruit (Table 3). Significant differences between species were found regarding the estimated number of seeds per branch (Table 2 and Online Resource 4). The number of seeds per branch was highest in *R. magellanicum* followed by *S. aucuparia* and lowest in *M. boaria* preceded by *C. monogyna* (Table 2).

Seeds of *C. monogyna* had a higher level of viability than those of all native species studied (Table 2 and Online Resource 4). *Sorbus aucuparia* showed a slightly lower seed viability than *C. monogyna* and higher values than all native species except *S. patagonicus*.

Fruit and seed mass

The mass of ripe fruits per branch was significantly higher in exotic than in native species (Fig. 3 and Online Resource 4). Both the exotic species had higher pulp content per fruit than the native species (Table 3). Seed mass proportion per fruit was similar between *C. monogyna* and those native species with more than one seed per fruit (*A. chilensis* and *R. magellanicum*); *S. aucuparia* exhibited the lowest seed mass proportion, about 20–80 and 40 % lower compared to the native species and *C. monogyna*, respectively (Table 3).

Discussion

Our results indicate that neither *C. monogyna* nor *S. aucuparia* introduce a new flowering phenology at the invaded sites, since both of them overlap, in this regard, with at least one of the studied native species. This overlap may indicate a period of high competition for pollinators (Wolkovich and Cleland 2014). In spite of this overlap, both the exotic species produced large numbers of ripe fruits. They achieved high fruit productions through different pathways. *Crataegus monogyna* produced a high number of flowers that developed into unripe fruits, which may be attributed to a combination of high levels of flower production and a generalist relationship with pollinators (Guitián and Fuentes 1992; Aizen et al. 2008). On the other hand, *S. aucuparia* showed low fruit set values like

Table 2 Mean (\pm SE) percentages of flowers setting unripe fruits and ripe fruits (fruit set) and seed viability, and mean (\pm SE) numbers of ripe fruits and seeds per branch in exotic and coexisting native species

Species	Percentage (\pm SE)			Mean number (\pm SE) per branch	
	Flowers to unripe fruits	Fruit set	Seed viability	Ripe fruits	Seeds
<i>Crataegus monogyna</i> *	76.7 \pm 3.5 ^b	34.8 \pm 3.4 ^a	99.7 \pm 0.3 ^a	18.5 \pm 2.6 ^b	17.7 \pm 1.6 ^d
<i>Aristotelia chilensis</i>	70.7 \pm 8.7 ^b	22.9 \pm 5.5 ^b	86.4 \pm 10.8 ^c	8.0 \pm 1.8 ^c	29.9 \pm 4.9 ^b
<i>Azara microphylla</i>	82.7 \pm 5.8 ^a	6.7 \pm 2.6 ^c	54.4 \pm 7.8 ^d	1.9 \pm 0.7 ^d	24.5 \pm 8.5 ^c
<i>Maytenus boaria</i>	67.3 \pm 7.1 ^c	7.9 \pm 3.0 ^c	26.7 \pm 9.3 ^d	1.2 \pm 0.4 ^e	2.5 \pm 0.4 ^e
<i>Ribes magellanicum</i>	55.4 \pm 5.2 ^e	24.4 \pm 4.9 ^b	64.0 \pm 4.4 ^d	8.9 \pm 2.0 ^c	159.9 \pm 21.3 ^a
<i>Schinus patagonicus</i>	60.2 \pm 4.8 ^d	25.4 \pm 3.4 ^b	92.4 \pm 2.0 ^b	35.6 \pm 5.9 ^a	43.2 \pm 3.8 ^b
<i>Sorbus aucuparia</i> *	25.7 \pm 2.1 ^D	17.4 \pm 1.8 ^C	80.5 \pm 2.9 ^A	37.6 \pm 4.5 ^B	130.6 \pm 12.5 ^B
<i>Berberis serrato-dentata</i>	47.9 \pm 6.1 ^C	26.6 \pm 5.3 ^B	56.9 \pm 11.0 ^B	4.5 \pm 1.2 ^D	18.2 \pm 3.6 ^D
<i>Maytenus boaria</i>	67.3 \pm 7.1 ^{AB}	7.9 \pm 3.0 ^D	26.7 \pm 9.3 ^C	1.2 \pm 0.4 ^E	2.5 \pm 0.4 ^E
<i>Ribes magellanicum</i>	60.6 \pm 4.8 ^B	17.8 \pm 3.4 ^C	54.0 \pm 7.7 ^B	9.9 \pm 2.3 ^C	265.6 \pm 39.8 ^A
<i>Schinus patagonicus</i>	65.1 \pm 4.5 ^A	37.4 \pm 3.4 ^A	85.2 \pm 2.2 ^A	45.3 \pm 4.9 ^A	44.8 \pm 3.4 ^C

Lowercase and uppercase bold letters show differences between species in areas invaded by *C. monogyna* and *S. aucuparia*, respectively (GLMM, Tukey contrast test, $P < 0.05$)

* Exotic species

some of the coexisting native species but, in contrast to them and to *C. monogyna*, *S. aucuparia* exhibited low numbers of pollinated flowers. However, because of its high flower production, *S. aucuparia* developed high numbers of ripe fruits. Low fruit sets have also been found for *S. aucuparia* in its native range and for other invasive species of Rosaceae (Gutián 1993; Pairon et al. 2006). The delay in flower opening observed for the *S. aucuparia* population at higher altitude is likely to be related to a plastic response to altitudinally decreasing mean temperatures. Plasticity in flowering time could increase the invasive success of *S. aucuparia* and could mean a benefit for this species in the future, considering the rising temperatures predicted for the next decades (Wolkovich and Cleland 2014).

At the community level, and because of the fruiting phenology and/or fruit quality differences between *C. monogyna* and *S. aucuparia* and their coexisting native species, both the exotic species provide a resource for dispersers that would not be available from the native plants. Fruits of *C. monogyna* and *S. aucuparia* start to be dispersed from the plants (by gravity or frugivory) later than those of all native species except *M. boaria*, which produces few ripe fruits. Therefore, as suggested by Cavallero and Raffaele (2010) in a study on the invasive shrub *Rosa*

rubiginosa (in a study site close to that of the present study), successful exotic species could occupy an empty space free of competition regarding reproductive phenology. The same has been reported for the invasive exotic shrub *Chrysanthemoides monilifera* in Australia, which has a fructification peak unmatched by those of coexisting native species (Gosper 2004). In the present study, we found that *C. monogyna* and *S. aucuparia* shared the autumn–winter period of ripe fruit dispersal with only two of the six native species, *S. patagonicus* and *M. boaria*. However, these coexisting native species had the low fruit pulp contents and developed low numbers of ripe fruits as compared to the exotics for the same period. For a *C. monogyna* invasive population in North America, Sallabanks (1993a) found that fruit consumption by frugivorous dispersers was highly positively correlated with fruit size, number of fruits, and fruit pulp proportion. The same author showed that *C. monogyna* fruits are more attractive to frugivores than fruits of the native *Crataegus douglasii* var. *suksdorfii* (Sallabanks 1993b). In temperate South American forests, birds are the most important frugivores (Armesto et al. 1987); among these, *Turdus falcklandii* prefers grouped and large fruits and is a key dispersal agent for fleshy-fruited plants during spring and autumn (Amico and Aizen 2005). Species of the same genus

Table 3 Number of seeds (mean \pm SE), dry mass of entire fruit, dry mass of pulp and seed per fruit ($n = 25$ fruits), and proportion of fruit mass in the seed/s (%) for reproductive individuals of each species at each invaded site (1 Sma, 2 Crub, and 3 Otto)

Species	Site	Values per fruit				
		Number of seeds	Fruit dry mass (mg)	Pulp dry mass (mg)	Seed dry mass (mg)	Seed proportion (%)
<i>Crataegus monogyna</i> *	1	1.0 \pm 0.0	148.8	68.8	80.0	53.8
	2	1.0 \pm 0.0	196.1	94.4	101.7	51.9
<i>Sorbus aucuparia</i> *	2	2.4 \pm 1.5	111.4	105.0	6.4	5.7
	3	3.5 \pm 1.6	81.5	72.1	9.4	11.5
<i>Azara microphylla</i>	1	2.3 \pm 1.7	21.1	15.3	5.8	27.5
<i>Aristotelia chilensis</i>	1	2.0 \pm 1.1	50.2	21.4	28.8	57.4
<i>Berberis serrato-dentata</i>	3	2.6 \pm 1.1	41.6	27.0	14.6	35.1
<i>Maytenus boaria</i>	2	1.3 \pm 0.5	20.9	3.6	17.3	82.8
<i>Ribes magellanicum</i>	1	13.2 \pm 4.6	48.9	19.8	29.1	59.5
<i>Ribes magellanicum</i>	3	13.1 \pm 5.5	51.0	29.2	21.8	42.7
<i>Schinus patagonicus</i>	1	1.0 \pm 0.0	32.9	3.1	29.8	90.6
<i>Schinus patagonicus</i>	2	1.0 \pm 0.0	34.5	3.5	31.0	89.9
<i>Schinus patagonicus</i>	3	1.0 \pm 0.0	38.8	3.8	35.0	90.2

* Exotic species

are the main dispersers of *C. monogyna* and *S. aucuparia* in other areas invaded by these species (Williams 2006) as well as in their native ranges (Gutián and Fuentes 1992; Gutián et al. 2000). In the present study we observed individuals of *T. falcklandii* feeding on fruits of both the exotic species (Lediuk, personal observation). Therefore, at the sites of the present study, this bird species, like other native dispersers, could have started to prefer the high fruit crop, pulp mass per fruit, and fruit size of both the exotic trees, in detriment of the native species with similar fruit dispersal period. Exotic frugivores also facilitate plant invasions (Richardson et al. 2000; Mandon-Dalger et al. 2004), so dispersion and invasion of these exotic plants could increase in case alien birds (such as *Lophura nycthemera* “silver pheasant” in northern Patagonia) preferred the exotics rather than the native fruits. A better knowledge about the suites of frugivorous seed dispersers, and the distances and directions of seed spread they are able to achieve, would be necessary for an appropriate and effective management of the exotic species studied here (Buckley et al. 2006).

Another important dispersal characteristic is fruit color (Gosper et al. 2005). *Crataegus monogyna* and *S. aucuparia* present red fruits, while *S. patagonicus* (the most important studied native species in terms of number of ripe fruits during the same period) has dark violet fruits (Table 1). Armesto et al. (1987) indicated

that black fruits reflect UV radiation and are more striking for birds in shaded evergreen forests, while red fruits are preferred in open deciduous forest. Thereby, under the relatively open canopies of disturbed Patagonian forests, where *C. monogyna* and *S. aucuparia* have established, their fruits may have high visibility for dispersers. The continued disturbance in these forests could promote the attractiveness of these red fruits and promote invasion. Fruits of *S. patagonicus* are also dispersed by *T. falcklandii* (Amico and Aizen 2005) and, according to our results, have fast release rates, i.e., the number of ripe fruits per branch decreases rapidly, possibly as a consequence of the adaptation of native frugivores to the fruit characteristics of native plants, such as fruit color and type (Aslan and Rejmánek 2012). In the long term, however, the more fleshy nature and the progressively higher abundance of the exotic fruits during the cold season, the time when the food resource is scarce for the native frugivorous, could reverse this choice.

Seed viability was, in broad terms, higher in the exotic than in coexisting native species (Table 2). Seeds of both *C. monogyna* and *S. aucuparia* in an invaded site of Patagonia showed high germination potential in early spring (64 and 34 %, respectively; Lediuk unpublished data). The combination of high seed viability and high germination potential would confer a high potential for these exotic species to

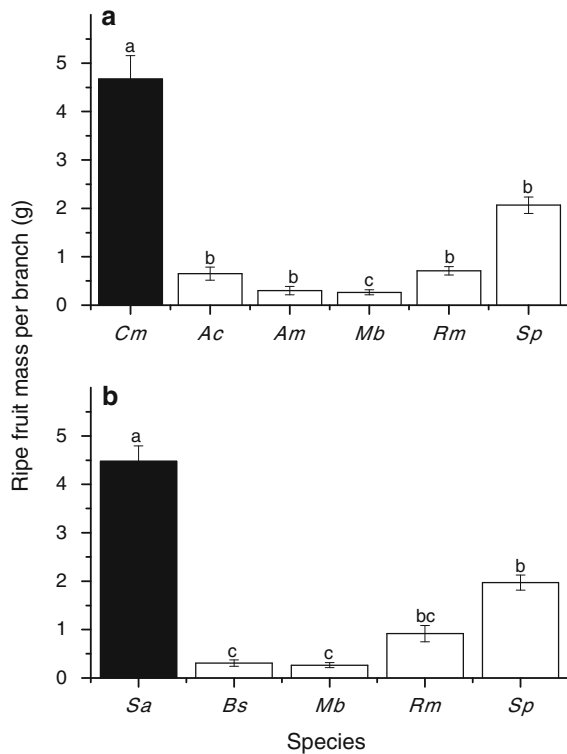


Fig. 3 Mean (\pm SE) mass (g) of ripe fruits per branch for *C. monogyna* (a, *Cm*) and *S. aucuparia* (b, *Sa*) and their respective coexisting native species (empty bars). For species names, see Table 1. Statistical differences between species are indicated with letters on top of the bars (GLMM, Tukey contrast test, $P < 0.05$)

successfully colonize different environments. The establishment of exotic species has been found to be positively correlated with propagule pressure (Kolar and Lodge 2001). In the present case, propagule pressure of both of the exotic species would be increased by a combination of large size of the seed set (i.e. high number of fruits per branch), high capacity to produce several dispersal events (long period of ripe fruits on branches), and high seed viability.

It is important to note that the reproductive phenology and traits exhibited by both the exotic species are quite similar to those of the coexisting native species of highest frequency, *S. patagonicus*, which behaves as a generalist species with high cover in both disturbed and undisturbed forests (Damascos 2005). This species had late flowering, high values of fruit set, fruit and seed production and seed viability, and longer ripe fruit presence on the branches than all other native species. The reproductive phenology and

the production of ripe fruits were similar among *C. monogyna*, *S. aucuparia*, and *S. patagonicus*, so that the differences in fructification peak and fruit structure appear to be the main traits that benefit the exotic species. Consequently, it would be important for subsequent work to focus on the similarity in phenology and functional traits between exotic invasive species and abundant and successfully reproducing native species.

Conclusions

Crataegus monogyna and *S. aucuparia* overlap in their reproductive phenologies with some coexisting native species. However, both the exotic species were able to develop higher numbers of fruits with viable seeds than most of the native species in the invaded communities of the Patagonian forests. Fruits of *C. monogyna* and *S. aucuparia* start to be dispersed later than those of native species and remain on the plants for a long period (autumn–winter), unlike those of all coexisting native species except *S. patagonicus*. Compared to this native species, the fruits of *C. monogyna* and *S. aucuparia* were larger and more fleshy, thus providing frugivorous birds with a resource not offered by the native species. Since birds are the most important frugivorous seed dispersers in these temperate forests, differences in fruit phenology and fruit structure between exotic and native species would be key factors to drive invasiveness by boosting dispersal and therefore the potential spread of exotic species.

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