

Fruiting phenology as a “triggering attribute” of invasion process: Do invasive species take advantage of seed dispersal service provided by native birds?

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Abstract Mechanisms underlying biological invasion of highly disturbed ecosystems are well known, yet mechanisms responsible for biological invasion of undisturbed or weakly disturbed ecosystems are less understood. The triggering attribute (TA) approach, proposed as a mechanism that explains plant invasion success in undisturbed or weakly disturbed systems, considers that the spread of alien species depends on specific vegetative or regenerative traits in invasive species, discontinuously distributed in comparison to the resident community. In mountain Chaco woodland, fruiting phenology of ornithocorous invasive plants has been proposed as a TA, because it would allow invasive species to benefit from seed dispersal service, which is unused by native plants during a

specific period of the year (winter). Under the seed dispersal ecology framework, we evaluated if fruiting phenology (fructification largely uncoupled with native species) of the fleshy-fruited invasive *Pyra-cantha angustifolia* affects bird fruit consumption, and allows the invasive to take advantage of the unused seed dispersal service during winter. If uncoupled fructification phenology represents a TA, seed disperser, seed predator, and pulp consumer diversity, abundance, and fruit consumption on *P. angustifolia* (which fructifies in winter), will be higher than on its exotic congeneric *P. coccinea* during summer, when fructification overlaps with native *Celtis ehrenbergiana* and many other native species. We found that: (1) disperser bird abundance and fruit consumption did not differ between *P. angustifolia* and *P. coccinea*; (2) the most diverse frugivorous assemblage was observed on *C. ehrenbergiana*, yet it had the lowest proportion of seed dispersers and the highest fruit consumption by seed predators and, (3) we also observed higher proportion of seed predators on *P. angustifolia* (uncoupled fructification scenario) than on *P. coccinea* (coupled fructification scenario). Our results suggest that invasive uncoupled fructification phenology does not represent a true TA which facilitates plant invasion processes in undisturbed or weakly disturbed ecosystem.

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Introduction

Since Elton's publication in (1958), the interest in the study of biological invasions has experienced an important increase (see Kolar and Lodge 2001). Several attempts have been made to generate a complete and general understanding of the invasion processes [e.g. universal invasive plant syndrome (Rejmanek and Richardson 1996), the release from natural enemies (Keane and Crawley 2002), and the diversity of the target community (Levine and D'Antonio 1999)]. Yet, although we have gained some understanding regarding the mechanisms of invasion in highly disturbed ecosystems, our understanding of the mechanisms underlying invasions of either undisturbed or weakly disturbed ecosystems is still limited (e.g. Godfree et al. 2004). For example, it has been proposed that plant invasions are regulated by the same processes that operate on community dynamics (Davis and Pelsor 2001; Shea and Chesson 2002). This idea, framed within community ecology theory, offers a mechanistic explanation involving fluctuation of resources (particularly those produced by a disturbance) as producers of temporal windows in which reduced competition is capitalized by exotic species to increase their densities. However, such explanation only works in scenarios of disturbed ecosystems, but it is not able to explain the success of biological invasions in systems without obvious human-caused disturbances. Another attempt to explain biological invasions success considers the presence of universal plant syndromes (Rejmanek and Richardson 1996). Yet empirical evidence indicates that invasive plants do not share a universal suit of traits (Leffler et al. 2014; Thompson et al. 1995). So far, three factors have been identified to be widely associated with invasion success: the number of alien propagules entering the environment (propagule pressure), the characteristics of the alien species, and invasibility (the susceptibility of the environment to invasion by alien species; Lonsdale 1999). Invasibility may also be affected by the presence (or absence) of herbivores and pathogens (D'Antonio 1993; Lonsdale 1999), facilitative effects of resident plant species (Maron and Connors 1996), and mutualists (Crawley 1987; Marler et al. 1999; Richardson et al. 2000; Traveset and Richardson 2014).

Mutualistic interactions between alien and native species may facilitate the integration of alien species into native communities and further disrupt their function (see Richardson et al. 2000). Positive

interactions such as seed dispersal by animals are recognized worldwide among invasive plants (Cronk and Fuller 1995). In particular, alien fleshy-fruited plants may rapidly establish relationships with native birds that consume their fruit and often disperse their seeds (references in Gosper et al. 2005). In fact, over 40 % of invasive tree species and over 60 % of invasive shrubs are dispersed by birds (Richardson and Rejmanek 2011). From the viewpoint of functional diversity of the frugivorous assemblage, different functional groups may or may not contribute to seed dispersal regarding the way they handle/consume the fruit (i.e. *legitimate seed dispersers*: swallow the whole fruit and defecate or regurgitate intact seeds; *pulp consumers*: peck the fruit to obtain pulp pieces either without detaching it from the peduncle or, after plucking, by tearing off the pulp while the fruit is in the bill or held against a perch (they may damage the embryo); and *seed predators*: feed on the seed contents and always damage the embryo;—Jordano et al. 2007; see Jordano and Schupp 2000 for classification). The prevalence of legitimate dispersers in the frugivorous assemblage, would be a key factor on the spread stage, increasing the invasion success of an alien fleshy-fruited plant. Contrary to the prevalence of dispersers in the assemblage, a greater proportion of seed predators would have detrimental effects on the dispersal process (Jordano 2000).

The success or effectiveness of seed dispersal depends mainly on two components (sensu Schupp 1993; frameworked and reviewed in Schupp et al. 2010). A qualitative component is defined as the quality of the scarification treatment given to a seed in the mouth or gut of the bird, and the quality of the seed deposition site as determined by the probability that a deposited seed will survive and become an adult. On the other hand, a quantitative component depends on the number of visits made to the plant by a disperser and the number of seeds dispersed per visit. For an alien plant, higher scores on any of these variables relative to the score of co-occurring native species may increase its chances of establishing, persisting, and spreading at a new environment (see Aslan 2011; Aslan and Rejmanek 2012). Factors associated with visitation advantage of invasive plants over natives may be related to displaying greater fruit attractiveness to dispersers (i.e. more attractive color, higher nutritious content, etc.; Gleditsch and Carlo 2011;

Kueffer et al. 2009; Mokotjomela et al. 2013), and/or having longer fruiting periods than natives (Cordeiro et al. 2004). On the other hand, the existence of alternate native-invasive fruiting phenologies may reduce competition of species with equally attractive fruit (Gosper 2004), increasing the rate of consumption of invader’s fruit.

Gurvich et al. (2005) proposed a theoretical approach to explain and predict the invasion success of alien plant species in undisturbed areas, providing as example the case of an alien fleshy-fruited species. The approach is based on the idea that some traits that allow the alien species to gain access to resources untapped by native species should be enough to trigger an invasion process. These attributes were defined as *Triggering Attributes* (TA) and represent a trait state that is absent in the native community, which allows the invader to spread by using a resource that is unused or very poorly used by the native community (i.e. niche opportunity). From an analysis of invasive elements in the plant community of mountain Chaco woodland at Sierras Centrales of Argentina, Gurvich et al. (2005) proposed that fleshy-fruited invasive plants bear a TA which is the production and ripening of fruit during autumn–winter, period during which no native plant species offer fleshy fruits. This largely uncoupled fruiting phenology would allow alien species to take advantage of a resource (i.e. bird seed dispersal service) that native species cannot momentarily tap. In addition, Tecco et al. (2013) evidenced that among all alien plants in this system there is a high frequency of species with fruiting phenologies spread between autumn and early spring, contrary to the phenology of native species. The *triggering attribute approach* allows us to generate predictions regarding the invasion success of fleshy-fruited invasive species in mountain Chaco woodland. If fruiting phenology is considered a TA that exploits bird seed dispersion, those alien species that produce fruit seasonally and largely uncoupled with all native fleshy-fruited species (which fruit production occurs in spring-summer; see Table S1 and S2 in supplementary material), will experience higher consumption of their fruits and consequently higher seed dispersion.

We used the conceptual framework provided by seed dispersal ecology to empirically evaluate if the largely uncoupled fruiting phenology of invasive fleshy-fruited plants may represent a TA in mountain Chaco woodland (Gurvich et al. 2005). Therefore, (1) we classified

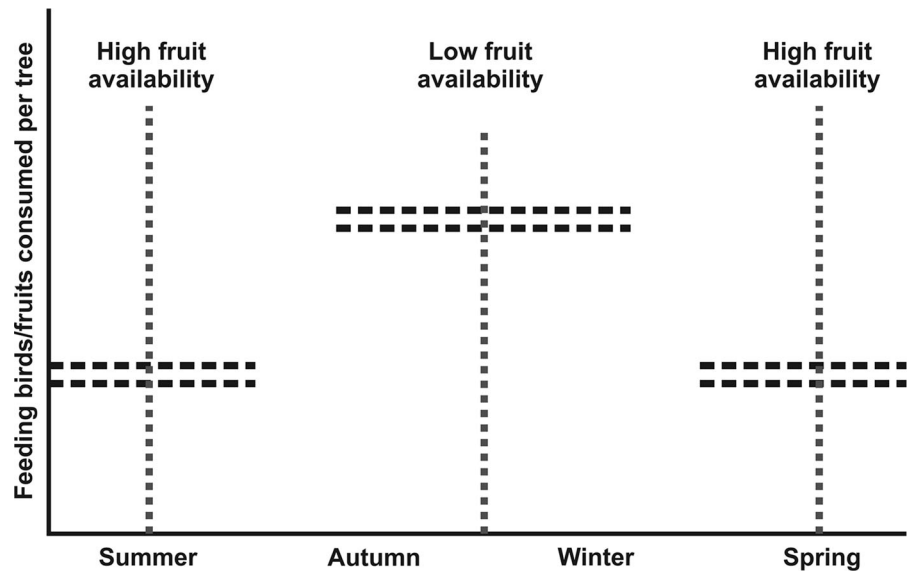
bird species into major functional groups regarding their fruit manipulation/consumption (i.e. seed disperser, pulp consumer, and seed predator); (2) we estimated variables that define the quantitative component of seed dispersal effectiveness to evaluate if invasive and native plants differentially exploit seed dispersal service by birds (variables: number of frugivorous species—including all fruit consumers: seed dispersers and seed predators—feeding on target plant species, number of seed disperser/seed predator birds, number of fruits consumed;—see Schupp 1993; Schupp et al. 2010). Our study system represents a valuable opportunity to compare those parameters in invasive and native plants that overlap their fructification in summer (e.g. *Celtis ehrenbergiana*—native—and *Pyracantha coccinea*—invasive—) with plant species that produce fruit uncoupled with native flora in winter (*Pyracantha angustifolia*—invasive—; see Tables S1, S2). If uncoupled fruiting phenology of invasive fleshy-fruited plants is a TA for *P. angustifolia* in mountain Chaco woodland, we expect to observe greater use of bird dispersal service by *P. angustifolia* in winter (season of lower fruit abundance; see Table S2), than by any other plant species fructifying during spring-summer (season of higher fruit abundance; see Table S2). In other words, we expect to observe higher diversity of frugivorous species, greater abundance of, and higher fruit consumption by disperser species on *P. angustifolia* than on plant species that produce fruit simultaneously (*P. coccinea* and *C. ehrenbergiana*; Fig. 1). Initially we explored the composition of the frugivorous assemblage (i.e. proportion of seed dispersers vs. seed predators) that visits the fruiting plants either when their phenologies are overlapped or uncoupled. Then, we focused on the avian seed dispersers which would be essential components of the seed dispersal service to test the TA hypothesis.

Methods

Study area

The study was conducted in the western slopes of Sierras Grandes (32°54′S, 64°57′W), between 1000 and 1200 m above sea level close to the locality of Los Hornillos, Córdoba, Argentina. The site extends over ca 150 ha and comprises a ravine where runs the Los Hornillos stream. Mean annual precipitation in the

Fig. 1 Predictive scenario that considers uncoupled fruiting of exotics relative to native flora as a triggering attribute. Number of birds and/or number of fruit consumed per plant would be higher on those individuals that produce fruit in opposite periods with respect to the majority of plants, in the case of mountain Chaco woodland that would happen in autumn–winter



area is approximately 700–800 mm (concentrated in summer) and mean annual temperature is 17.5 °C (data taken at the station La Ventana; Acosta et al. 1992). The study area comprises a weakly disturbed system, representative of the mountain Chaco woodland. Its vegetation is dominated by *Lithraea molleoides* (Vell.) Engl., *Celtis ehrenbergiana* (Klotzsch) Liebm., *Acacia caven* (Molina) Molina, and *Bougainvillea stipitata* Griseb (Luti et al. 1979). Additionally, the invasive shrubs *Pyracantha angustifolia* (Franch) C.K. Schneid, and *Pyracantha coccinea* M. Roem. are amply widespread (see Cabido et al. 1998 for vegetal community descriptions).

P. angustifolia and *P. coccinea* (Rosaceae) are fleshy fruited evergreen and thorny shrubs, originated in Asia and widely used in gardening and landscaping around the world (Novara 1993). Their fruits are dispersed by birds and it is believed that such ornithocorous dispersion played a key role in moving propagules from gardens into the wild, with the subsequent naturalization of the species in several sectors of mountain Chaco woodlands (Delucchi 1991; Giorgis and Tecco 2014; Gurvich et al. 2005; Tecco et al. 2010).

Focal plant species characteristics

We selected as focal species two fleshy-fruited invasive shrub species *P. coccinea* and *P. angustifolia*

and the native shrub *C. ehrenbergiana* (“*Celtis*” hereafter) which rarely reaches tree height in our study system. The selection of these focal species is due to the fact that they share morphological and functional traits that may influence bird attractiveness. All three species are thorny, branchy shrubs, with similar sized orange or red fruit (6–13 mm in diameter), highly attractive to birds (Burns and Dalen 2002; Schaefer et al. 2007; Willson and Whelan 1990). The native *Celtis* is the only species in our study site that produces orange fruit similar to *Pyracantha* species; (Sanchez Hümoller 2009; Santos 1990; see Table S1). According to vegetation surveys conducted in the study area, the surface covered by *Celtis*, *P. coccinea* or *P. angustifolia* is similar (Tables S1, S3). Besides these similarities, both *Pyracantha* species differ from *Celtis* on the fruit display. Both *Pyracantha* species produce approximately tenfold more fruit per branch than *Celtis* (Table 1).

Fructification timing of the three species differs partially in our study site. Fruit maturation of *Celtis* runs from January to April, *P. coccinea* fruit ripening occurs between March and late July, whereas *P. angustifolia* fructification runs from May to October (Fig. 2). This results in a complex fruiting phenology scheme, in which the two invasive shrubs differ in time of fruit maturation. Fruit from *P. coccinea* mature during late summer, partially overlapping with *Celtis* fruiting, and persists on plant until early winter

Table 1 We assessed the mean number of fruit per branch for each plant species in 3 branches of 30 cm, randomly selected per individual. Fruit quantification of *Celtis* and *P. coccinea* was conducted in the same time period. The comparison of mean values of *Celtis*, *P. angustifolia* and *P. coccinea* fruit number was performed by ANOVA and LSD Fisher’s test a posteriori for multiple comparisons. The comparison of number of fruits per branch among three vegetal species was significantly different ($F = 256.27$; $P < 0.001$). Different superscript letters indicate significant differences among plant species

Vegetal species	n	Mean	SE
<i>Celtis ehrenbergiana</i>	33	10.64 ^a	10.39
<i>Pyracantha coccinea</i>	42	176.31 ^b	9.20
<i>Pyracantha angustifolia</i>	40	103.25 ^c	9.42

overlapping with the beginning of *P. angustifolia* fructification (see Fig. 2; Table S1).

Having two congeneric invasives compared with an unrelated native may have consequences in the interpretation of the results. Yet, the fact that both *Pyracantha* species are phylogenetically closely related far from being undesirable could be a positive condition, given that the two invasives share most of the traits important for frugivorous birds except the attribute of interest (fruiting phenology). It would have been desirable to include in the study a native closely related to the invasives. However, in the study system there are no native trees or shrubs belonging to rosaceae family that produce fleshy fruits. The selected native species (*Celtis*) is the only one that also shares with the invasives most of the attributes important for frugivorous (see Table S1).

Bird feeding observations

We conducted surveys on each season comprising approximately 45 plant observations. The number of observations was limited by the time required to survey each individual plant, and the need to perform all surveys within 20–25 days (time window during which we registered the overlapping of fruit production in the focus plant species). During late summer and early autumn (March–April, when fruit of both plant species occurs simultaneously) observations were conducted on *Celtis* (30 individuals), and *P. coccinea* (15 individuals), and during winter (July–August; see Fig. 2) on *P. angustifolia* (46 individuals), when its fructification largely does not overlap with other fleshy-fruited plants. All plants observed of the three species were of similar size (2.5–3 m of height), and were separated by at least 50 m. At each plant, observations were conducted during 60 min in the morning between 07:00 and 13:00 in the summer/autumn and 08:00–13:00 in the winter (in these time periods occur the highest bird activity). Variables recorded were: bird species feeding on fruit, number of individuals per species and number of fruit consumed per individual.

To categorize bird species into major functional groups (i.e. seed disperser, pulp consumer, and seed predator; see Table S4 in supplementary material), we documented the behavior of birds while feeding, either during the direct observations or during additional observation periods. For each bird sighted, the following information was recorded: total time spent at the shrub, number of fruit removed, number of fruit

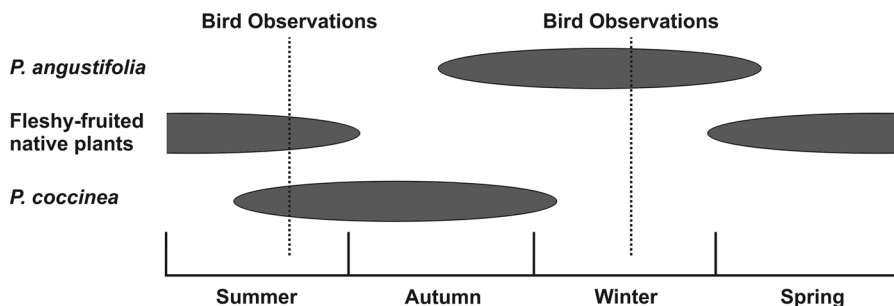


Fig. 2 Fruiting phenology of the invasive *P. angustifolia* and *P. coccinea* and the native species *C. ehrenbergiana* in the mountain Chaco woodland, Córdoba, Argentina. The dashed lines indicate the periods in which we conducted observations

during the summer (observations on *P. coccinea* and *C. ehrenbergiana*: overlapped fructification scenario) and in the winter (observations on *P. angustifolia*: largely uncoupled fructification scenario). Modified from Gurvich et al. (2005)

swallowed, number of fruit touched but not detached from the peduncle, number of fruit carried away from the plant in the bill, and for bird species eating only pulp, we recorded whether the pulp was pecked from the fruit without detaching it from its peduncle or was stripped from the seed while holding it in the bill (and the seed dropped).

Data analysis

Previous to data analysis migrant birds were removed from the data base due to their variable presence in the community.

Significant differences in Shannon Wiener Index (H; for all frugivorous birds associated to each plant species) were assessed using bootstrapping techniques to determine 95 % confidence intervals for each estimate of H, and compared indexes using a randomization test for computing significant differences in diversity between two samples (Solow 1993; using software Species Diversity and Richness 3.02).

We compared the number of seed disperser and seed predator individual birds feeding as well as fruit ingested by both groups among selected plant species. We used a generalized linear model (GLM with a Poisson link) and LSD Fisher's test a posteriori for each of these multiple comparisons (R Core Team 2012). The Poisson distribution is typically used for count data, and its main advantages are that the mean variance relationship allows for heterogeneity (Zuur et al. 2009). Finally, we compared the proportion of major functional groups of frugivorous birds among plant species (i.e. seed dispersers, pulp consumers and seed predators) and the proportion of fruits consumed by these groups using G-test (Agresti 1990) with Infostat software (2002). For all analysis performed we used a significance level of 0.05.

Results

Assemblages of frugivorous birds differed significantly among the plant species, and they were relatively more diverse on *Celtis* ($H = 1.61$) than on *P. coccinea* ($H = 0.88$; $P = 0.004$) and on *P. angustifolia* ($H = 1.28$; $P = 0.018$). Frugivorous birds diversity did not differ between *P. coccinea* and *P. angustifolia* ($P = 0.122$). The lower diversity observed in both *Pyracantha* species coincides with a high proportion of

Chiguanco Thrush in the frugivorous assemblage (over 60 %; Fig. 3). Chiguanco Thrush also represents the highest proportion of dispersers for all plant species (Fig. 3).

The abundances of disperser birds among plant species was significantly different ($\chi^2_2 = 6.56$; $P = 0.037$). On *P. angustifolia* we observed the highest abundance of bird dispersers, on *Celtis* the lowest values, and on *P. coccinea* intermediate abundance, which wasn't significantly different from the abundances observed on either of the other species (Table 2). It is worth mentioning that all but one seed disperser species of *P. coccinea* overlapped with those of *Celtis*. Disperser birds consumed significantly different amounts of fruit among plant species ($\chi^2_2 = 18.06$; $P < 0.001$), which was higher on both *Pyracantha* species than on *Celtis*. On the other hand, the abundance of seed predator birds was higher on *Celtis* and *P. angustifolia* than on *P. coccinea* ($\chi^2_2 = 23.85$; $P < 0.001$). Fruit consumption by seed

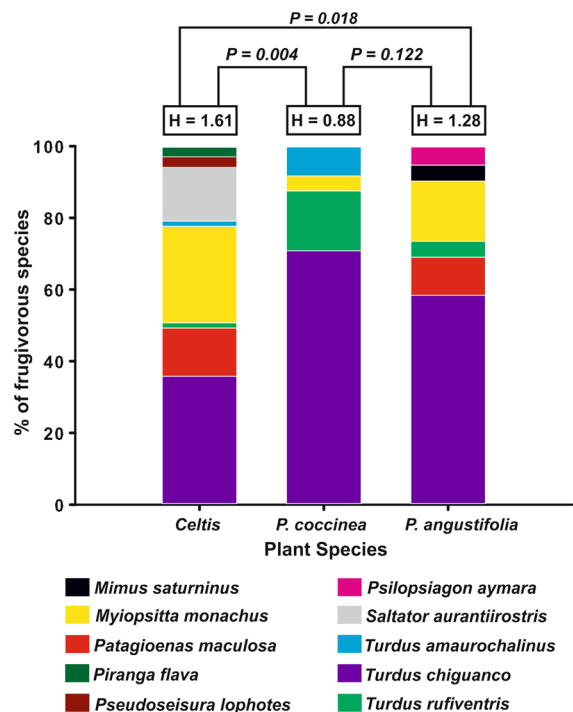


Fig. 3 Frugivorous bird proportions observed consuming fruit of the three plant species (treatments). Each pattern represents a bird species. Superior diagrams in each figure indicate the observed Shannon Wiener Index (H) on each plant species and P values from all comparisons, using a randomization test (Solow 1993)

Table 2 Differences in amount of fruit consumed and abundance (mean ± SE) of seed disperser and seed predator birds observed per hour feeding on individual plants of *Celtis*, *P. coccinea*, and *P. angustifolia* (treatments). Different

superscript letters indicate significant differences in seed disperser and seed predator bird abundance as well as fruit consumed among plant species (GLM and LSD test)

	<i>Celtis ehrenbergiana</i>	<i>Pyracantha coccinea</i>	<i>Pyracantha angustifolia</i>	χ^2	<i>P</i>
Seed disperser birds					
Abundance	0.91 ± 0.21 ^a	1.53 ± 0.24 ^{ab}	1.65 ± 0.19 ^b	6.56	0.037
Consumed fruit	5.43 ± 1.31 ^a	8.87 ± 2.58 ^b	7.76 ± 1.22 ^b	18.06	<0.001
Seed predator birds					
Abundance	1.28 ± 1.56 ^a	0.07 ± 0.26 ^b	0.59 ± 1.24 ^a	23.85	<0.001
Consumed fruit	4.38 ± 5.91 ^a	0.27 ± 1.03 ^b	3.11 ± 6.50 ^c	78.85	<0.001

predators was highest on *Celtis*, intermediate on *P. angustifolia* and lowest on *P. coccinea* ($\chi^2 = 78.85$; $P < 0.001$; Table 2).

Regarding the major functional groups of frugivorous birds, we observed significant differences among plant species ($G^2 = 26.41$; $P < 0.001$). Partitioned comparisons showed that *P. coccinea* had the highest proportion of “seed dispersers” relative to *Celtis*, and *P. angustifolia*; and *P. angustifolia* had a greater proportion of seed dispersers than *Celtis*. Regarding “seed predators”, *Celtis* showed the highest proportion relative to *P. coccinea*, and *P. angustifolia*; whereas *P. angustifolia* had a greater proportion of seed predators than *P. coccinea* (Fig. 4a).

In addition, focusing on the proportion of fruit consumption by each major functional group of frugivorous birds we observed significant differences among plant species ($G^2 = 82.58$; $P < 0.001$); *P. coccinea* showed the highest proportion of fruit consumed by “seed dispersers” relative to *Celtis*, and *P. angustifolia*; and *P. angustifolia* had a greater proportion of fruit consumption by dispersers than *Celtis*. On the other hand, *Celtis* showed higher proportion of consumption by “seed predators” relative to *P. coccinea*; whereas *P. angustifolia* had a greater proportion of consumption by seed predators than *P. coccinea* (Fig. 4b).

Discussion

Our results suggest that the largely uncoupled fruiting phenology of *P. angustifolia* in the mountain Chaco woodland may not be a key factor which determines

dispersion success of this exotic species, and such character would not be one that facilitates the exploitation of an unused service in the system (i.e. seed dispersal service). We found no difference on the number of visits and fruit consumption by seed dispersers between the two invasive species regardless of their fruiting phenology. This observation evidences that the largely uncoupled fruiting phenology of *Pyracantha* species may not serve as a triggering attribute (sensu Gurvich et al. 2005), suggesting that other characteristics of the plants may be more important to make a better use of the dispersal service in the system to be a successful invader, (e.g. fruit display, fruit color and aggregation per branch; discussed below).

In an overlapping fruiting phenology scenario, frugivorous diversity on *Celtis* was higher than on *P. coccinea*. During the summer-autumn, the number of bird species on *Celtis* doubled the number observed on *P. coccinea* (Fig. 3). Some evidence suggests that native birds may prefer native fruit when exposed to a diverse fruit offer from native and exotic plants (Aslan and Rejmanek 2012; Aslan 2011; Buckley et al. 2006; Lichstein et al. 2004). The possible mechanisms proposed to explain such pattern entail selection of food items based on nutritional characteristics (Kueffer et al. 2009; Mokotjomela et al. 2013) and/or the display of neophobia toward novel food items such as fruit from exotics (Greenberg and Mettke-hofmann 2001). In our study, we did not analyze food preference quantitatively. Yet, although densities of *Celtis* and *Pyracantha* individuals were similar (Tables S1, S3), fruit production per branch is greater on *Pyracantha* than on *Celtis* (Table 1). This observation, in addition to the frugivory pattern observed (higher

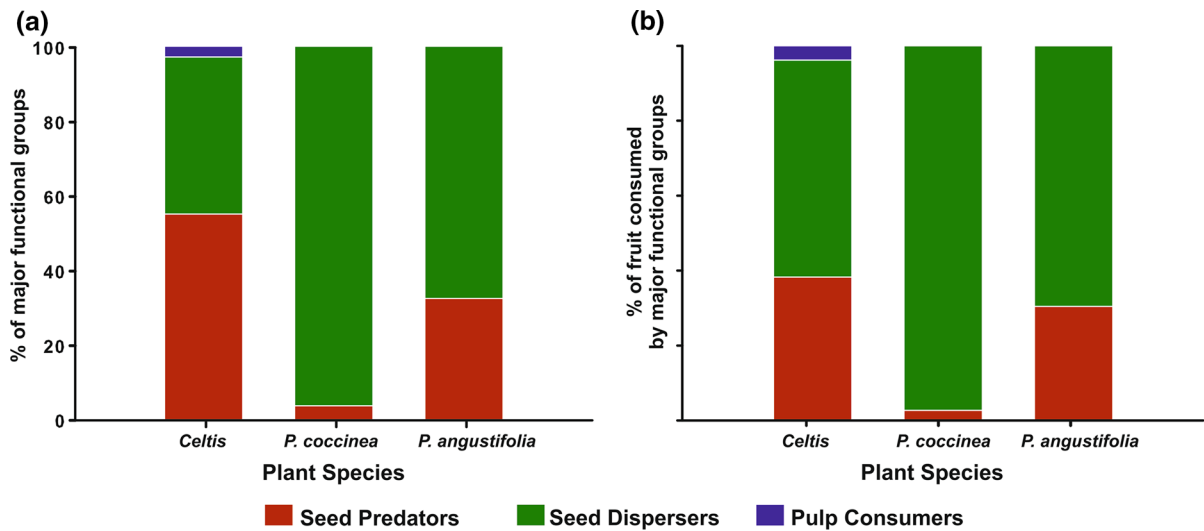


Fig. 4 Proportion of (a) major functional groups (based on Jordano and Schupp 2000) and (b) fruit consumed by each functional group, observed consuming fruit of the three plant species (treatments). Each pattern represents a major functional groups of frugivorous birds

diversity and number of species that visited *Celtis* than *Pyracantha*) suggests a possible preference of *Celtis* over *Pyracantha* by frugivorous birds. However, the proportional visitation and fruit consumption by each major functional group of frugivorous birds (i.e. seed predators and seed dispersers), greatly differed among the plant species (Fig. 4a, b).

The greater diversity of frugivorous assemblage on *Celtis*, was mainly composed by seed predators and the relative proportion of seed predators to seed dispersers was significantly greater than the relative proportion of such groups on *P. coccinea* (Fig. 4a). Indeed, only one of the species that consumes fruit from *P. coccinea* is a seed predator (the Monk parakeet, *Myiopsitta monachus*). Similarly, fruit consumption by seed predators on *Celtis* was higher than on *P. coccinea* (Table 2). Once again, as we suggested earlier, this pattern could be attributed to preference of native fruits by seed predators. In that regard, the coupled phenologies of *P. coccinea* and *Celtis* could benefit the exotic if natives were attracting more seed predator frugivores and preventing them from consuming fruit from the exotics. In the same way, the largely uncoupled fruiting phenology of *P. angustifolia* could result detrimental if seed predators that cannot consume native fruits end up consuming their fruits, decreasing the plant dispersal success. Indeed, our results show that the proportion of seed predators relative to seed dispersers which visit *P. angustifolia*

(largely uncoupled fruiting phenology) is greater than that for *P. coccinea*. Our results also indicate that, given that the presence and abundance of seed predators in the assemblage do not change year round (unpublished data; Ordano 1996), *P. angustifolia* is being consumed in the winter by all seed predators that during the summer-autumn consume *Celtis* (among other natives; Fig. 3; Table 2).

Regarding the other major functional group of frugivorous birds, our results show that in an overlapping fruiting phenology scenario the proportional visitation of seed dispersers relative to seed predators was greater on *P. coccinea* than on *Celtis*. Moreover, in an overlapping (*Celtis* and *P. coccinea*) and largely non-overlapping (*P. angustifolia*) fructification scenario most seed disperser species have been observed visiting the three plant species (Fig. 3). Nevertheless, abundance of seed dispersers and their fruit consumption was higher on *Pyracantha* species than on *Celtis*, and it did not differ between the exotics (Table 2). This suggests that the fruiting phenology scenario of these exotic species may not confer an advantage towards the attraction of frugivorous birds in general and seed dispersers in particular, and may be irrelevant for their ability to exploit the seed dispersion service. Moreover, these results indicate that both *Pyracantha* species are using the dispersal service disproportionately more than *Celtis*. Even more so, when *P. coccinea* and *Celtis* fructify synchronously, the exotic seems to

better exploit the service from disperser birds than the native species with similar type of fruit (fruit consumed by seed dispersers was higher on *Pyracantha* species than on *Celtis*; Table 2). This last observation suggests the existence of some kind of competition for seed dispersers between *P. coccinea* and *Celtis*.

In our study system the seed dispersal service offered by birds is provided mainly by Chiguanco Thrush (*Turdus chiguanco*), Creamy-bellied Thrush (*T. amaurochalinus*) and Rufous-bellied Thrush (*T. rufiventris*; Table S4 in supplementary material). Although all three bird species are common year round residents, Chiguanco Thrush is the most abundant (~2 individuals per 1000 m², unpublished data; see also Bellis et al. 2009; Ordano 1996). Its high density and the proportion of visits in addition to the amount of fruit it consumes, highlights the importance of Chiguanco Thrush in the seed dispersion processes of the fleshy-fruited plant species here studied. Approximately 80 % of the bird abundance in the three plant species corresponded to Chiguanco Thrush (Fig. 3). Thus we infer that the major contribution to seed dispersion in our study system may be provided just by one species. A pattern that has been generally observed regarding seed dispersal service is that only a few species in the assemblage make the most contribution (see Vázquez et al. 2005 for references). For example, Montaldo (2000) observed an asymmetric pattern similar to ours, in which the disperser assemblage was dominated by Rufous-bellied Thrush that made the greatest contribution to seed dispersal service. Our results suggest that Chiguanco Thrush may be the most important seed disperser in our system, and in the context of biological invasions it may be one of the key factors associated to *Pyracantha* spreading along Córdoba highlands.

Gurvich et al. (2005) proposed the existence of triggering attributes, as either discontinuities or extreme values in the range of variation of functional traits in local communities, which may contribute to plant invasion success. Specifically, the cited authors propose that in mountain Chaco woodland, the largely uncoupled fruiting phenology of *P. angustifolia*, behaves as a “triggering attribute”. In the present study we empirically tested such prediction. Our results indicate that this character in *P. angustifolia* is not a true triggering attribute, because its uncoupled fruiting phenology does not seem to improve the use of the seed dispersal service over a closely related species

(*P. coccinea*) which fructification overlaps with natives. Alternatively, we believe that the effectiveness of seed dispersal of this species may not only depend on the fruit consumption but also on other traits which represent extreme values in the resident community. The number of seeds per diaspora and/or the fruit display (number of fruits per branch) may be some of such traits (Table 1, Table S1). Fruit from *Pyracantha* (including all species in the genera) have five-six seeds per fruit, whereas native ornithocorous woody plants in mountain Chaco woodland have one-two seeds (obs. pers.; Demaio et al. 2002). Three factors, the greater number of seeds per fruit, the greater number of fruits per branch (that may contribute on seed disperser bird attractiveness), and the greater fruit consumption by seed disperser birds on *Pyracantha* sp., could synergistically influence the success of this plant invasion. These traits, which may confer higher propagule pressure to *Pyracantha* (Lockwood et al. 2005), would increase the chances of seedling establishment as it is proposed by the seed dispersion ecology theory (Schupp et al. 2010). Our results provide additional support to the current consensus regarding the lack of existence of universal invasive plant syndromes. Once again, the search for general mechanisms underlying invasion processes falls into the unfortunate idiosyncratic explanation (see Pyšek and Richardson 2007; Moles et al. 2012).

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