

Positive interaction between invasive plants: The influence of *Pyracantha angustifolia* on the recruitment of native and exotic woody species

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Abstract: Positive interactions between species are known to play an important role in the dynamics of plant communities, including the enhancement of invasions by exotics. We studied the influence of the invasive shrub *Pyracantha angustifolia* (Rosaceae) on the recruitment of native and exotic woody species in a secondary shrubland in central Argentina mountains. We recorded woody sapling recruitment and micro-environmental conditions under the canopies of *Pyracantha* and the dominant native shrub *Condalia montana* (Rhamnaceae), and in the absence of shrub cover, considering these situations as three treatments. We found that native and exotic species richness were higher under *Pyracantha* than under the other treatments. *Ligustrum lucidum* (Oleaceae), an exotic bird-dispersed shade-tolerant tree, was the most abundant species recruiting in the area, and its density was four times higher under the canopy of *Pyracantha*. This positive interaction may be related to *Pyracantha*'s denser shading, to the mechanical protection of its canopy against ungulates, and/or to the simultaneous fruit ripening of both woody invaders.

Key words: bird-dispersed fruit, facilitation, *Ligustrum lucidum*, plant invasion, recruitment foci.

INTRODUCTION

Plant invasions represent a major threat to native biodiversity worldwide (Vitousek *et al.* 1997). Introduced species sometimes establish facilitative interactions among themselves (Simberloff & Von Holle 1999), and with native species (Richardson *et al.* 2000; Stachowicz 2001; Lenz & Facelli 2003). Although invasive plants and their facilitative interactions are not confined to any particular growth form, bird-dispersed perennial woody species have been reported as the most successful invasive species of natural and semi-natural systems (Cronk & Fuller 1995). This is not surprising, since fleshy-fruited species are known to have a strong influence in determining successional patterns and hence community structure in many ecosystems (Debussche & Isenmann 1994; Herrera *et al.* 1994; Kollman 1995; Cabral *et al.* 2003). The attractiveness of fruiting plants to frugivorous birds plays an essential role in their effective dispersal and thus in their success as invaders (Rejmánek & Richardson 1996). As well as these positive interactions with native or exotic birds, invasive plants can also influence recruitment of other exotic plants by affecting bird movement and subsequent seed dispersal patterns (Parrota 1995). Other important factors through

which shrubs are likely to influence seedling distribution are microhabitat modification (Lenz & Facelli 2003), herbaceous competition amelioration (Stachowicz 2001) and shelter against livestock grazing and trampling (Bruno *et al.* 2003; García & Obeso 2003). In fact, the protection against environmental stress, predation and competition (Holmgren *et al.* 1997; Stachowicz 2001; García & Obeso 2003) provided by shrubs appears to affect strongly spatial and temporal patterns in plant communities (Callaway 1992).

Pyracantha angustifolia (Rosaceae), hereafter *Pyracantha*, is a woody naturalized species, widely spread in shrublands and to a lesser extent in grasslands of central Argentina (Delucchi 1991; Zuloaga & Morrone 1996a). The aim of the present work was to study the influence of *Pyracantha* on the recruitment of native and exotic woody species, and to relate the observed patterns to the phenological and micro-environmental attributes of this invasive shrub.

METHODS

Study area

The study was carried out in 2001 in a 4-ha site close to Salsipuedes (31°07'18"W; 64°19'13"S), in

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Córdoba mountains, central Argentina. The altitude is 878 m a.s.l and the mean annual temperature in the region is 14°C, with frosts being common from May to September. The mean annual rainfall is around 800 mm, mainly concentrated in the warm season (October to April). The dominant vegetation of the area corresponds to the woodland belt of the Chaco Serrano biogeographical district (Luti *et al.* 1979). Due to human activities such as livestock grazing, logging and frequent fires, the original woodland has been almost completely transformed into a mosaic of grassland, shrubland and open woodland (Zak & Cabido 2002). In particular, our study site was restricted to an open shrubland, which is the most widespread community in the Córdoba mountains. The dominant shrubs are the exotic *Pyracantha* and the native *Condalia montana* (Rhamnaceae). The open space among these shrubs is dominated by the herbaceous species *Leonurus sibiricus*, *Conium maculatum*, *Eupatorium argentinum*, *Hyptis mutabilis*, *Baccharis cordifolia*, *Bidens pilosa*, *Carduus acanthoides* and *Senecio pampeanus*.

Pyracantha is an evergreen, thorny and fleshy-fruited shrub, native to Asia, and widely used in gardening and landscaping (Novarra 1993). This invader has abundant horizontal branches and twigs, which are likely to be attractive for perching birds (Kollman & Grubb 1999). The native *C. montana* (hereafter *Condalia*) is of similar size and is also a thorny, branchy shrub with fleshy bird-dispersed fruits (Escalante *et al.* 1971). These functional and morphological similarities allow the use of *Condalia* as a 'native shrub control treatment' in the examination of the effect of the invasive *Pyracantha*. In this context, and in order to assess whether *Pyracantha* affects the community assemblage in a different way than the dominant native shrub, we analysed (i) the richness and abundance of the woody saplings recruiting under *Pyracantha* and *Condalia*; and (ii) the fruit-dispersal phenology of both shrub species, and the micro-environmental conditions under their canopies.

Experimental design

We considered three 'treatments': under *Pyracantha* canopy, under *Condalia* canopy and no shrub cover (patches of herbaceous vegetation between shrubs). Sixteen mature individuals of *Pyracantha*, 16 of *Condalia* and 16 plots of 16 m² of herbaceous vegetation were chosen at random to be used as replicates. We recorded the presence of saplings of all woody species in each experimental plot (including all individuals from 10-cm up to 200-cm height). In addition, for each fleshy-fruited woody species (14 species in total), we counted all the individuals present in each plot, and then calculated their densities as individuals per

square meter. In order to assess the relationship between the observed sapling richness and the size of the shrub canopies, we estimated the surfaces of projected canopy cover by measuring the crown diameter and calculating the area as $\pi \times r^2$, whereas r represents the radius of the crown. Nomenclature of plants followed Zuloaga and Morrone (1996a,b) and Boelcke (1992).

Phenological patterns of dispersal

Since fleshy-fruited shrubs influence the recruitment of new species by affecting bird movements (Fuentes 2000), simultaneous fruit ripening of different species may enhance their dispersal and subsequent establishment. Consequently, we analysed the fruiting phenology of *Pyracantha*, *Condalia* and all bird-dispersed woody species recruiting under their canopy and in open plots. We obtained the information from the literature (Boelcke 1992) and our own observations (repeated visits to the field sites during each season).

Micro-environmental variables

Since invasive species can alter micro-environmental conditions (Holmes & Cowling 1997), they can affect either directly or indirectly the recruitment success under their canopies (Holl 2002). Consequently, we used the same sampling plots and measured the following micro-environmental variables under *Pyracantha* and *Condalia* canopies and in plots with no shrub cover: percentage of photosynthetic active radiation (PAR) reaching ground level, soil and air temperature, and soil gravimetric water content, texture, pH, organic matter and nitrogen and phosphorus content. The soil properties were measured on eight compound samples per treatment on only one occasion, while all the other measurements were carried out over the 16 replicates of each treatment both in summer and in winter.

Photosynthetic active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured with a LICOR sensor (LI-COR Environmental, Lincoln, NE, USA) (Stoutjesdijk & Barkman 1992). PAR reaching the ground in each treatment was calculated as PAR at ground level \times 100/PAR above the canopy. Soil temperature was measured at 5-cm depth and at ground level with a digital thermometer both in winter (in the early morning) and in summer (at midday) in order to record minimum and maximum diurnal temperatures. Soil temperature was measured in all plots over 30 min to minimize differences due to normal diurnal fluctuations. To measure soil gravimetric water content, three compound samples were taken at each plot, and stored in sealed polyethylene bags until measurement. After measuring soil fresh weight (FW), the samples were oven-dried

at 70°C for 48 h in order to measure dry weight (DW). Percentage of gravimetric water content was calculated as $[(FW - DW)/DW] \times 100$ (Ratto 2000). Soil organic matter content was obtained by means of the Walkley-Black method (Nelson & Sommers 1996). Nitrogen and phosphorus analyses followed Setaro and Jones (1989). Soil subsamples were placed in a block digester and subsequently analysed for total nitrogen with a modified indophenol method and for total phosphorous with a modified molybdenum blue assay. Soil nitrate was measured using a copperized cadmium reduction method (Page *et al.* 1982). Available ammonium was extracted with potassium chloride and measured with a modified indophenol method. Soil pH was determined with a potentiometer (Jackson 1982). Carbon was measured through acid digestion following the Walkley-Black method (Nelson & Sommers 1996).

Data analysis

When the data were normally distributed we used ANCOVA and LSD to test for differences in woody vegetation richness among treatments, considering the plot size as covariable (InfoStat 2002). Data for species abundance and micro-environmental variables were not normally distributed (Sokal & Rohlf 1995), and we used the Kruskal-Wallis test and the multiple comparison method (Marasculio & McSweeney 1977). We used the Spearman correlation test to analyse the relation of density between bird-dispersed saplings and shrub size.

RESULTS

Species richness

The woody species richness significantly differed among treatments (Table 1). The species richness of woody saplings was significantly higher under *Pyracantha* canopy than under *Condalia* or in the absence of shrub cover. This pattern remained unchanged when considering the richness of native, exotic, or bird-dispersed species separately (Table 1). In comparisons between the non-shrub treatment and under *Condalia*, only bird-dispersed richness was significantly higher under the native shrub canopy than in the absence of shrub cover. In all cases, the differences in richness between treatments were independent of differences in shrub size. Shrub size was not significantly related to total, native or exotic richness ($P = 0.3$, 0.76 and 0.23 , respectively, ANCOVA) or to total, native or exotic bird-dispersed species richness ($P = 0.85$, 0.57 and 0.62 , respectively).

Table 1. Differences in woody species richness established under the canopies of *Pyracantha*, *Condalia*, and in plots with no shrub cover

	<i>Pyracantha</i>	<i>Condalia</i>	No shrub cover
Mean richness			
All woody species	6.06 ± 0.38^a	3.50 ± 0.34^b	2.63 ± 0.24^b
Native	3.63 ± 0.30^a	2.38 ± 0.33^b	2.06 ± 0.21^b
Exotic	2.44 ± 0.26^a	1.13 ± 0.22^b	0.56 ± 0.13^b
Bird-dispersed species	4.31 ± 0.35^a	2.44 ± 0.33^b	0.81 ± 0.14^c
Native	2.13 ± 0.29^a	1.38 ± 0.27^b	0.75 ± 0.14^b
Exotic	2.19 ± 0.21^a	1.06 ± 0.19^b	0.06 ± 0.06^c
Total richness (all plots)	19	15	10

Richness is expressed as the mean number of species per plot ± 1 SE. Different superscript letters indicate significant differences in richness among treatments (in all cases $P < 0.01$; ANOVA and LSD test).

Almost half of all woody species surveyed under the different treatments were exotic (12 native *vs.* nine exotic). Out of a total of 19 species, 14 were fleshy-fruited and bird-dispersed (six of them exotic and eight native; Fig. 1). Bird-dispersed species were found mostly under *Pyracantha* canopies. In the absence of shrub cover we found less than half of the total recorded species (full list of species available from the corresponding author upon request).

Density of bird-dispersed species

The densities of native bird-dispersed saplings did not differ between treatments ($P = 0.293$; Kruskal-Wallis test; Fig. 2). However, the density of exotic species growing under *Pyracantha* was higher than those under *Condalia* and in the non-shrub treatment ($P < 0.001$; Fig. 2). Moreover, under *Pyracantha* the recruitment of bird-dispersed exotic species was eight times higher than that of native species (0.8 and 0.08 individuals per square metre, respectively; $P < 0.0001$). In contrast, the densities of native and exotic species established under *Condalia* canopy did not differ significantly ($P = 0.67$). The density of bird-dispersed species recruiting in absence of shrub cover was, in general, very low. However, the recruitment of native species in this treatment was higher than that of exotic (0.15 and 0.03 individuals per square metre, respectively; $P < 0.016$).

Under the canopy of *Pyracantha* we found saplings of almost all the woody species sampled in the study area. Among them, the Asiatic tree *Ligustrum lucidum*

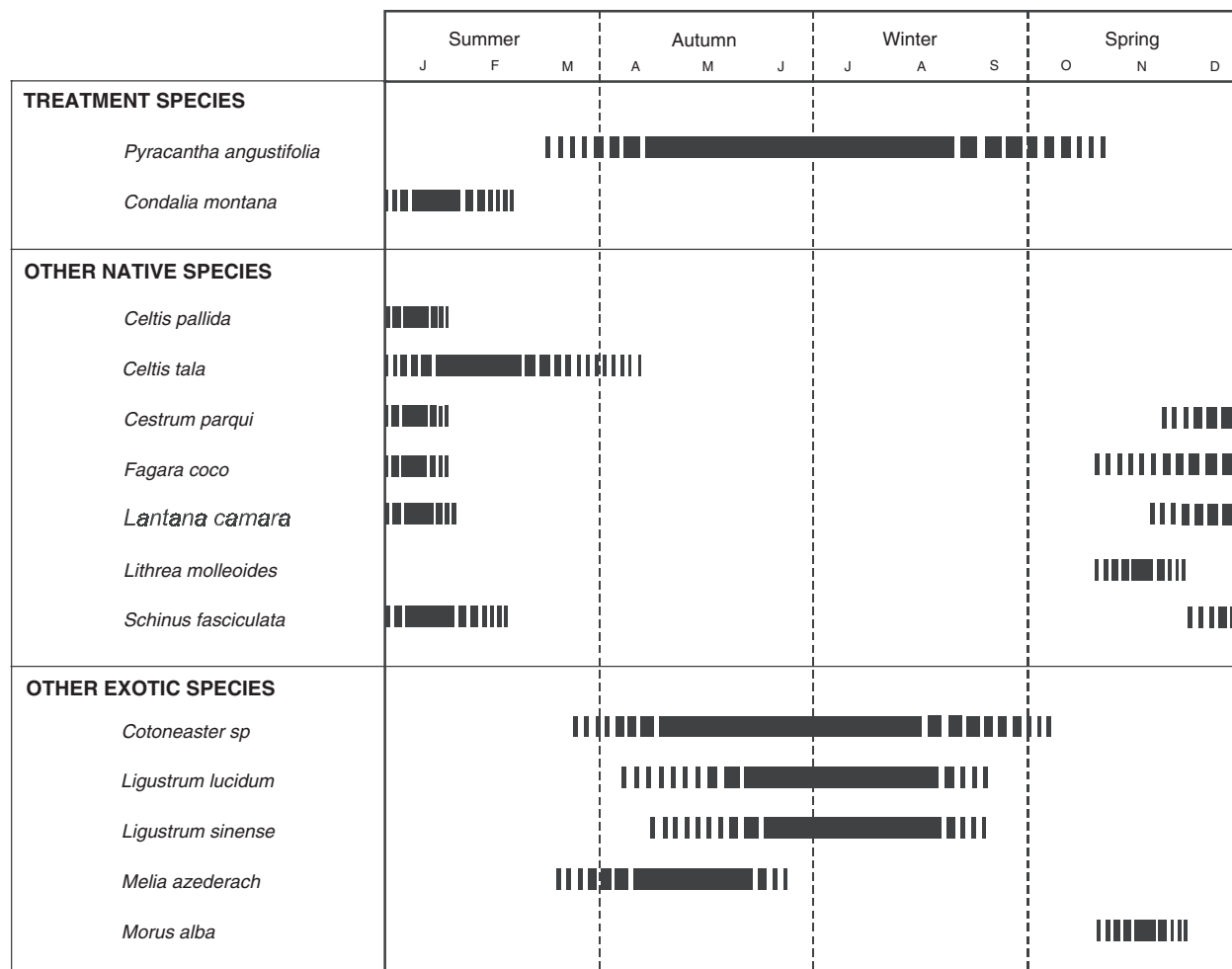


Fig. 1. Dispersal phenology of all bird-dispersed species recruiting in the study area. Horizontal bars indicate the period in which each species was dispersing and illustrate which species are simultaneously dispersing at any given time.

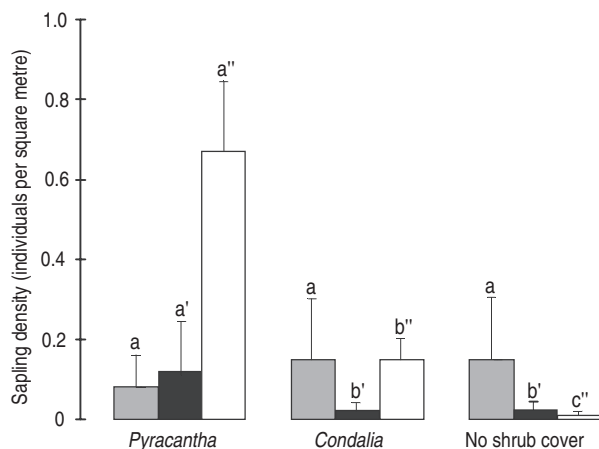


Fig. 2. Sapling density of bird-dispersed species under the canopies of *Pyracantha*, *Condalia* and in plots with no shrub cover. Different letters indicate significant differences ($P < 0.001$) between treatments in the density of saplings of (■) native species (a), (■) exotic species other than *Ligustrum* (a'-b') and (□) *Ligustrum* (a''-c'').

('glossy privet') was by far the most abundant. *Ligustrum* accounted for 56% of the total bird-dispersed exotic density in the study site, and the 84% of the exotic sapling density under *Pyracantha*. *Ligustrum* had significantly higher density under *Pyracantha* than under *Condalia* and in absence of shrub cover (Fig. 2).

Dispersal phenology of bird-dispersed species

The bird-dispersed species recruiting in the study area fell into two clear groups according to their fruit dispersal phenology (Fig. 1). One group consisted of species dispersing during the warm season. This group included all native species and only one of the exotic species recorded. The second group consisted of species dispersing in autumn and winter. These included all the exotic species except *Morus* and no native species.

Shrub canopy size and micro-environmental conditions

The canopy size of the *Pyracantha* individuals used in the samples was significantly larger than that of the *Condalia* individuals (Table 2). However, the higher sapling recruitment recorded under *Pyracantha* would not be necessarily related to this higher projected canopy surface since, as already mentioned, the size of shrubs did not explain the differences in richness between treatments (ANCOVA). Moreover, the density of bird-dispersed saplings was not significantly related to the sizes of either shrub species ($P > 0.1$ for all the recorded species; Spearman correlation coefficient).

Soils under both shrub canopies presented more organic matter and provided a cooler microclimate in summer compared with the non-shrub treatment. On the other hand, there were few significant differences in micro-environmental conditions or in soil chemical properties under the *Pyracantha* and *Condalia* canopies (Table 2). Indeed, the main difference between the two shrub treatments was that *Pyracantha* offered a significantly shadier microhabitat than *Condalia* both in summer and in winter, and a cooler environment in the topsoil layer in summer (Table 2). There was also a tendency of the soil under *Pyracantha* to be moister in winter, and to show slightly lower nitrate and sig-

nificantly higher ammonium availability than under *Condalia*.

DISCUSSION

In our study, the richness of native woody species was higher under the canopy of the exotic shrub *Pyracantha* than under the native shrub *Condalia* or at sites without shrub cover. At first inspection, this may suggest that *Pyracantha* can potentially enhance the recruitment of forest species rather than reducing it. However, a considerable number of exotic woody species, and especially *Ligustrum*, also tended to recruit preferentially under this shrub. *Condalia* also favoured exotic bird-dispersed woody species recruitment over sites with no shrub cover, but the richness and density of species found under its canopy were much lower than those under *Pyracantha*. The presence of *Ligustrum* under *Condalia* suggests that the region would be exposed to the spread of this invasive species even in the absence of *Pyracantha*. However, the density of *Ligustrum* was four times higher under *Pyracantha* than under *Condalia*, representing a higher invasion pressure. This clearly indicates a positive interaction between these two invaders, at least at this early stage of *Ligustrum*'s life cycle. The differential sapling distri-

Table 2. Microhabitat conditions (mean \pm 1 SE) under the canopies of *Pyracantha* and *Condalia*, and in plots with no shrub cover

	<i>Pyracantha</i>	<i>Condalia</i>	No shrub cover
<i>Physical variables</i>			
Canopy size (m ²)	27.79 \pm 1.87 ^a	8.64 \pm 0.7 ^b	—
PAR (%)			
Summer	2.89 \pm 0.39 ^a	6.14 \pm 0.98 ^b	18.15 \pm 1.97 ^c
Winter	12.37 \pm 0.98 ^a	20.88 \pm 1.44 ^b	64.48 \pm 2.25 ^c
Temperature (°C)			
Summer			
Surface	25.15 \pm 0.34 ^a	30.41 \pm 0.87 ^b	37.73 \pm 1.50 ^c
5-cm depth	19.49 \pm 0.11 ^a	21.43 \pm 0.41 ^b	24.29 \pm 0.32 ^c
Winter			
Surface	6.33 \pm 0.14	6.19 \pm 0.11	6.27 \pm 0.08
5-cm depth	9.95 \pm 0.21	10.04 \pm 0.14	10.01 \pm 0.12
Soil moisture (%)			
Summer	35.18 \pm 1.94	35.75 \pm 3.44	33.09 \pm 2.40
Winter	21.76 \pm 1.68 ^a	16.82 \pm 0.93 ^b	21.3 \pm 2.03 ^a
<i>Soil chemical variables</i>			
Organic matter (%)	21.99 \pm 1.25 ^a	20.40 \pm 1.63 ^a	13.31 \pm 1.31 ^b
Total N (%)	0.33 \pm 0.02	0.36 \pm 0.04	0.27 \pm 0.02
Total P (%)	0.0016 \pm 0.0002	0.0025 \pm 0.0005	0.0016 \pm 0.0002
C/N	38.47 \pm 1.90 ^a	34.59 \pm 3.03 ^{ab}	28.42 \pm 0.57 ^b
N/P	221.89 \pm 19.38	167.99 \pm 18.33	180.63 \pm 14.17
Nitrate (p.p.m.)	98.35 \pm 7.01	120.40 \pm 14.29	104.76 \pm 10.12
Ammonium (p.p.m.)	73.85 \pm 7.46 ^a	53.56 \pm 2.88 ^b	65.83 \pm 2.67 ^a
pH	6.37 \pm 0.09 ^a	6.62 \pm 0.07 ^a	6.04 \pm 0.07 ^b

Different superscript letters represent significant differences among treatments ($P < 0.05$; Kruskal–Wallis and multiple comparison test).

bution observed under *Pyracantha* may subsequently influence successional patterns and community structure in the invaded system (Herrera *et al.* 1994; Cabral *et al.* 2003). In tropical and temperate forests, the abundance of various species of saplings established beneath an adult tree reflects the probability of the subsequent replacement of the adult tree by each of those species (Horn 1975). If this assumption of equal survivorship of the established seedlings is also true in secondary shrublands of Córdoba, *Ligustrum* saplings may eventually replace the shrub under which they establish and replace *Pyracantha* and *Condalia* as the community dominant.

Why do *Pyracantha* shrubs offer more favourable recruitment foci for exotics in general and *Ligustrum* in particular? The canopies of *Pyracantha* and *Condalia* may differ in many ways. Chief among them are micro-environmental conditions (Callaway 1992; Holmes & Cowling 1997; Kitzeberger *et al.* 2000), external seed input (Reichard & Hamilton 1997) and mechanical protection against browsing by large mammals (Tewksbury & Lloyd 2001; Bruno *et al.* 2003; García & Obeso 2003). Although not directly measured in this study, these factors, alone or in combination, may affect seedling germination, growth and/or sapling survival and have all been reported as facilitative mechanisms for seedling recruitment in other systems. The difference between *Pyracantha* and *Condalia* as recruitment foci can be only partially explained by differences in microhabitat conditions. Other studies of woody invasions have reported changes in the nutrient and water supply promoted by the invader (Vitousek & Walker 1989; Zavaleta *et al.* 2001). In our study, differences in mineral nutrient availability did not appear large enough to explain the recruitment differences found between treatments. In fact, the main significant and consistent differences in micro-environmental variables between the *Pyracantha* and *Condalia* treatments were canopy light interception and summer topsoil temperature. The higher light interception by the dense *Pyracantha* canopy would allow the survival of shade-tolerant species but appears to be detrimental to species with high light requirements. *Ligustrum*, the most abundant species under the shadier *Pyracantha*, is indeed a shade-tolerant species (Panetta 2000; Aragón & Groom 2003). Similarly, Lenz and Facelli (2003) found that a shadier and cooler microhabitat, but not increased nutrient levels or water availability, were the main factors explaining the facilitation effect of shrubs on the invasive stem succulent *Orbea variegata* in South Australia. Unfortunately, we lack information about the light requirements of the other native and exotic species recruiting under *Pyracantha*, although personal observations by the authors suggest that most of the other exotics except *Ligustrum sinense* are shade-intolerant. The negative influence of

exotic dense-canopied trees or shrubs on shade-intolerant native species has been reported in other areas of the world (e.g. the invasive *Acacia saligna* in African shrublands; Holmes & Cowling 1997; the invasive *L. sinense* in western North Carolina hardwood forests; Merriam & Feil 2002).

The higher recruitment of exotic species under *Pyracantha* might also be accounted for by differences in dispersal phenology. The fruiting peak of most bird-dispersed exotic species included in this study, including *Pyracantha* and *Ligustrum*, occurred in autumn–winter. All recorded bird-dispersed native species, in contrast, produced and dispersed fruits in spring–summer. Therefore, the fleshy fruits of exotic species appeared to be the only source of food for fruit-eating birds during autumn and winter. This could probably enhance the seed input of exotics under the *Pyracantha* canopy, which is used by birds to perch and feed, and thus is where most previously eaten seeds are dispersed by defecation. In fact, differences in seed production and in the length of flowering and fruiting periods between invasive and non-invasive species are known to be determining factors of invasiveness in other regions of the world (Rejmánek & Richardson 1996; Reichard & Hamilton 1997). Although dispersing phenology could partly explain the higher density of exotics beneath *Pyracantha*, it does not explain the dominance of *Ligustrum* over other winter bird-dispersed exotics.

Finally, recruitment differences under *Pyracantha* and *Condalia* canopies could be related to their architecture. As shown in the results, the larger canopy of *Pyracantha* is not enough to explain the higher woody recruitment under this shrub. However, a partial explanation may relate to differences in the canopy structure of *Pyracantha* and *Condalia*. In anthropogenic pastures, those originated after woodland clear-cutting, of mountain forest in NW Argentina, *Pyracantha coccinea* and *Crataegus oxiacantha* have been reported to facilitate the replacement of pastures by forest tree species since the branches and thorns of these two exotic shrubs protect saplings growing underneath them from cattle browsing (Malizia & Greslebin 2000). Although we have not measured canopy structure or ungulate activity in this study, the canopy of *Pyracantha* is comparable to that of *P. coccinea* and *C. oxiacantha*. Thus, its mechanical shelter effect could also be expected to be similar. The canopy of *Condalia*, although branchy and thorny like *Pyracantha*, is not as dense near the ground. Thus, the native shrub would probably not provide the same protection against ungulates as *Pyracantha*. Again, there is no reason to expect that this factor would favour *Ligustrum* more than other species.

In total, although all exotic species recruiting under *Pyracantha* may benefit with the enhanced external seed input and mechanical protection against brows-

ing provided by the shrub, *Ligustrum* may get additional benefits from the differential micro-environmental conditions. In this sense, the best candidate factor appears to be the lower availability of photosynthetically active radiation, since *Ligustrum* can germinate and establish in very-low-light conditions (Panetta 2000). In conclusion, our findings show a clear positive association between *Pyracantha* and *Ligustrum*, with the latter recruiting in much higher numbers under the canopy of the former than under the canopy of the native *Condalia* or in sites with no shrub cover. The non-experimental nature of our work only allows speculation on the underlying mechanisms. Yet, one may speculate that a combination of a shadier micro-environment and higher protection from ungulates under *Pyracantha*, and the simultaneous fruit ripening and bird dispersal of exotic species, are plausible mechanisms underlying the higher density of exotic species under the *Pyracantha* canopy. However, the dominance of *Ligustrum* over other exotics and its apparently higher invasiveness are more difficult to explain, and merit further experimental investigation. Of particular interest would be the transition from germination to establishment, since seedling recruitment represents a major filter to the spread of invasive species and is often limited by the interaction of seed and microsite availability (Mazia *et al.* 2001).

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