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Facilitation and interference underlying the association between the woody invaders *Pyracantha angustifolia* and *Ligustrum lucidum*

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Abstract

Questions: 1. Is there any post-dispersal positive effect of the exotic shrub *Pyracantha angustifolia* on the success of *Ligustrum lucidum* seedlings, as compared to the effect of the native *Condalia montana* or the open herbaceous patches between shrubs? 2. Is the possible facilitation by *Pyracantha* and/or *Condalia* related to differential emergence, growth, or survival of *Ligustrum* seedlings under their canopies?

Location: Córdoba, central Argentina.

Methods: We designed three treatments, in which ten mature individuals of *Pyracantha*, ten of the dominant native shrub *Condalia montana,* and ten patches without shrub cover were involved. In each treatment we planted seeds and saplings of *Ligustrum* collected from nearby natural populations. Seedlings emerging from the planted seeds were harvested after one year to measure growth. Survival of the transplanted saplings was recorded every two month during a year. Half of the planted seeds and transplanted saplings were cage-protected from rodents.

Results: *Ligustrum* seedling emergence did not differ among treatments while growth was significantly higher in the absence of shrub cover. Sapling survival was significantly higher under the canopy of *Pyracantha,* intermediate under *Condalia,* and lowest in the absence of shrub cover. Caging did not affect growth but enhanced seedling emergence and sapling survival.

Conclusion: The differential sapling survival in the shrub canopy treatments is consistent with natural sapling distribution. *Pyracantha* and, less so, *Condalia*, has a nurse-plant effect on *Ligustrum*. This results from contrasting effects of the shrubs on different stages of the life cycle of *Ligustrum*: no effect on seedling emergence, negative on seedling growth, and positive on sapling survival. This suggests that efforts to control the expansion of *Ligustrum* over the landscape should tackle *Pyracantha* as well.

Keywords: Argentina; *Condalia montana*; Experiment; Invasional meltdown; Nurse effect; Positive interaction; Rodent predation; Seedling survival.

Nomenclature: Zuloaga & Morrone (1996, 1999).

Introduction

There are many observational and experimental studies on competitive interactions between exotic and native plant species (Woods 1993; Dunbar & Facelli 1999; Callaway & Aschehough 2000; Levine et al. 2003; Fargione et al. 2003) and on community resistance to invasion (Burke & Grime 1996; Davis et al. 2000; Symstad 2000; Cleland et al. 2004; Levine et al. 2004). Far less attention has been paid to positive interactions among invaders, despite the fact that positive interactions (or the lack thereof) have been involved in the success (or failure) of many exotic species to become established in new habitats (Simberloff & Von Holle 1999; Richardson et al. 2000).

Seedling recruitment represents a major filter to the spread of a species in a new habitat and is often limited by seed rain and microsite availability (Fuentes 2000). Because of this, dispersal by animals and microhabitat modification by resident or exotic plants can play an essential role in the success of invasive species (Simberloff & Von Holle 1999). Both mechanisms are known to be involved in the invasion of some ecosystems by fleshy-fruited trees and shrubs, aided by generalist native or exotic frugivores (Sallabanks 1993; Richardson et al. 2000).

Co-existence between species engaged in facilitative associations often involves both positive and inhibitory effects (Kollmann & Grubb 1999; Riginos et al. 2005; Lloret et al. 2005). On one hand, the protection from environmental stress by shrubs (Holmgren et al. 1997; Callaway & Davis 1998; Stachowicz 2001; Castro et al. 2002) together with the refuge from predation (García & Obeso 2003), enhanced nutrient conditions (Vieira et al. 1994; Pugnaire et al. 1996; Gómez- Aparicio et al. 2005), and/or reduced herbaceous competition (Vieira et al. 1994; Feyera et al. 2002; Holl 2002), have been often described as nurse-plant effects that reduce the mortality of the seedlings established under the canopy of shrubs and trees. On the other hand, nurse plants can also have negative effects on other factors; for example, they can impede seedling emergence by litter accumulation or limit growth of newly established plants by reducing the availability of light and soil water (Holmgren et al. 1997). However, strong benefits, such as increased survival rate, often override negative competitive effects on growth, resulting in a net positive interaction even when the costs of co-existence are high (Stachowicz 2001).

In central Argentinian mountains, the invasive exotic shrub *Pyracantha angustifolia* (*Rosaceae*) provides recruitment foci for both native and exotic bird-dispersed woody species. Among the recruiting species, *Ligustrum lucidum* (*Oleaceae*), an exotic bird-dispersed shade-tolerant tree, is the most abundant. Tecco et al. (2006) reported densities of *Ligustrum* more than four times higher under the canopy of *Pyracantha* than under the canopy of the dominant native shrub *Condalia montana* (*Rhamnaceae*) and 67 times higher than in the absence of shrub cover. These authors suggested that the simultaneous fruit ripening and bird-assisted dispersal of the exotic species (with the resulting higher seed input under the shrubs used as perches by frugivorous birds) and the shadier, cooler and moister micro-habitat conditions under *Pyracantha* were likely factors explaining the higher density of exotic species under its canopy. With our experiments we wish to gain further insight into the facilitative interaction between these two invasive species, and whether the observed positive association between both invaders is a response to a nurse effect by *Pyracantha* on *Ligustrum* during the germination and establishment stages. Two specific questions are: 1. Is there any positive post-dispersal effect of *Pyracantha* on the success of *Ligustrum* seedlings, as compared to the effect of the native *Condalia* or the open herbaceous patches between shrubs? 2. Is the possible facilitation by *Pyracantha* and/or *Condalia* related to differential seedling emergence, growth, or survival under their canopies?

Methods

Study area and background information

The study area was a 4-ha site close to Salsipuedes (31º07'18" S; 64º19'13" W), in the Córdoba mountains, Central Argentina. The altitude is 878 m and the mean annual temperature is 14 ºC, with common frosts from May to September. The mean annual rainfall is ca. 800 mm, mainly concentrated in the warm season (October to April) (De Fina 1992). The dominant vegetation is Chaco montane woodland (Luti et al. 1979). The primary woodland has been modified by livestock grazing, logging and frequent burning into a mosaic of grassland, shrubland and open woodland (Zak & Cabido 2002). Our study site was an open shrubland, which is the most representative community in the area. The dominant shrubs are the exotic *Pyracantha* and the native *Condalia*, naturally interspersed within an herbaceous matrix *with Leonurus sibiricus, Conium maculatum, Eupatorium argentinum, Hyptis mutabilis, Baccharis cordifolia, Bidens pilosa, Carduus acanthoides,* and *Senecio pampeanus*.

Pyracantha and *Condalia* have functional and morphological similarities (they are fleshy-fruited, thorny and branchy, which allows us to use *Condalia* as a 'native shrub control treatment' in the examination of the effect of the invasive *Pyracantha*. Regardless these functional similarities, Tecco et al. (2006) found earlier that the canopies of *Pyracantha* and *Condalia*, and the patches with no shrub cover, offered different micro-habitat conditions in terms of photosynthetically active radiation and soil temperature and moisture. *Pyracantha* offers a significantly shadier microhabitat than *Condalia*, both in summer and in winter, cooler topsoil layer in summer, and moister soil in winter. Additionally, soil under *Pyracantha* and *Condalia* has significantly more organic matter than that in plots with no shrub cover, but no significant differences in mineral nutrient availability ($N\text{-}NO_3$ and P) (Tecco et al. 2006). Finally, both shrubs also differ in their reproductive phenology, fruit dispersal of *Pyracantha* occurs during the cold season while that of *Condalia* takes place during the warm season.

Experimental design

Three canopy treatments were considered to assess *Ligustrum* emergence, growth and survival: *Pyracantha* understorey, *Condalia* understorey, and no-shrub canopy (patches of herbaceous vegetation). Ten mature individuals of *Pyracantha* and ten of *Condalia* were randomly chosen as replicates of both canopy treatments. Ten 16-m^2 plots of herbaceous vegetation intermingled with the shrubs were also randomly chosen as replicates of the no-shrub treatment. All shrub/plots were interspersed within the study site at a minimum distance of five meters from the nearest neighbours' shrub/plots. Since shrubs often provide refuge for seed-predating rodents that may reduce shoot emergence and/or seedling survival and growth; each replicate was split in two, and half of the measures were performed on plants protected by cages and the other half on unprotected plants. The 17 × 20 × 30 cm cages were built of 1 cm-mesh plastic net, which it is appropriate to exclude most rodents present in this ecosystem, such as *Microcavia australis, Galea musteloides, Calomys* spp.*, Mus musculus* and *Rattus* spp. (Orlog & Lucero 1980). The field experiment was carried out between July 2001 and July 2002. The first date was chosen to coincide with the peak of *Ligustrum* fruit production and dispersal (Aragón & Groom 2003).

Seedling emergence and growth

Seeds were collected directly from 13 *Ligustrum* individuals growing near the study site. Fruit collection was done immediately prior to the beginning of the experiment and the fleshy mesocarp was removed to simulate the effect of the passage through the digestive tract of a bird, since endozoochory by perching birds is the most common dispersal mechanisms of the species (Aragón & Groom 2003). To measure seedling emergence, 100 *Ligustrum* seeds were placed on the soil surface within each replicate. Half of these seeds were protected from seed removal with a cage staked to the ground. Trying to simulate the natural process as much as possible, seeds were not buried, but they naturally buried themselves at a depth of ca. 1 cm after being sown. A total of 3000 seeds were planted in the study site (100 seeds × 10 shrub/plot replicates × 3 canopy treatments). Seeds were monitored monthly. Seedling emergence started three months after sowing. Seedlings were harvested one year later, in order to record growth performance. The growth variables considered were: plant height, stem diameter at the base (DAB), total above-ground biomass, leaf biomass, and number of leaves and buds.

Sapling survival

Naturally-growing saplings of *Ligustrum* were carefully removed from the field and immediately transplanted into the experimental plots. All saplings were approximately one year old, on the basis of the fruiting time of the previous year. Saplings ranged from 4 to 7 cm in height and had 2-4 true leaves when transplanted. Twenty saplings were transplanted within each replicate of each treatment; half of them were protected with a cage and the other half remained unprotected. A total of 600 saplings were transplanted in the study site (20 saplings × 10 shrub/plot replicates × 3 canopy treatments). All saplings were watered immediately after transplant, but no additional treatment was applied afterwards. Survival percentage was monitored every two months during a year. Seedling emergence and sapling survival were thus measured in different individuals. This was because otherwise the often low and variable survival in the seedling stage would have resulted in an insufficient sample size at the sapling stage. However, at the end of the experiment, the emerging seedlings that were harvested to measure growth attained the equivalent age to those that had been transplanted at the beginning of the experiment. Moreover, although studying survival on planted saplings within the canopy treatments could be considered a more realistic experimental setting, the use of 1 year old transplanted sapling allows investigating the effect of the shrubs on older saplings. The use of transplanted saplings has already been reported in the examination of nurse effects by shrubs on tree sapling survival in abandoned tropical pastures (Holl 2002). Some replicates were lost during the course of the experiment causing the design to be unbalanced.

Canopy size

We estimated the projected canopy surfaces of shrubs in order to assess the existence of a ‘benefactor size effect’ (i.e. a positive relation between sapling survival and seedling growth with canopy size of the benefactor shrub; *sensu* Tewksbury & Lloyd 2001). This was done by measuring crown diameter and calculating the area as $p \times r^2$.

Data analysis

To perform all data analyses, two values for each response variable were calculated for each replicate, one for the caged treatment, and other for the unprotected treatment. Response variables were: seedling emergence (% of seedlings present 1 year after seed planting), seedling growth (average of all seedlings growing within each plot, for all growth variables measured one year after planted) and sapling survival (% of saplings present 1 year after transplanting). Raw data on total above-ground biomass and leaf biomass were ln-transformed prior to the analyses to meet the assumption of normality.

To evaluate the effect of the three canopy treatments and discriminate the effect of the caging treatments, repeated measures ANOVAs were performed for all response variables, where each replicate (plot/shrub) was the subject variable, the canopy treatment was the only between factor, and the cage treatment was the only within factor (Underwood 1997). To evaluate the effect of canopy treatment and cage protection on sapling survival, another ANOVA for repeated measures was performed in a similar way as in the previous analyses, but including a second within factor: the different dates after each two-month interval. Differences among treatment means were tested using Tukey test (Sokal & Rholf 1995).

Linear-mixed model was used in order to asses the effect of the shrub canopy sizes on each response variable. Shrub sizes were considered as the continuous variable while the canopy treatments (*Pyracantha* and

Condalia) were considered as the factor. This analysis was preformed twice for each response variable (with and without cages).

Results

Seedling emergence and growth

The percentage of seedling emergence did not statistically differ among canopy treatments but it was significantly higher within cages (Fig. 1; $F_{(2,26)} = 0.28$, $P = 0.76$ for the canopy treatment and $F_{(1,26)} = 6.13$, $P = 0.02$ for the caging treatment). We found no interaction between the effects of canopy and caging treatments on seedling emergence ($F_{(2,156)} = 0.51$, $P = 0.61$).

Seedling growth differed among canopy treatments (Table 1). Seedlings grown in the absence of shrub cover showed enhanced growth according to most variables measured: height, total above-ground and leaf biomass, and number of leaves. Seedlings growing under *Pyracantha* and *Condalia* canopies did not differ in their growth, with the exception of the number of leaves, which was higher on seedlings growing under the canopy of *Pyracantha*. The protection with cages had no significant effect on seedling growth and there was no interaction between the effects of canopy and caging treatments ($P > 0.1$ for all growth variables)

Sapling survival

Ligustrum saplings survived differentially under different canopy treatments through time (canopy treatment × time, $F_{(10,468)} = 2.38$, $P < 0.01$). Sapling survival was significantly higher under *Pyracantha,* as compared to the no-shrub treatments, while saplings under *Condalia* showed an intermediate percentage of survival (Fig. 2a). Caging also enhanced sapling survival (Fig. 2b; $F_{(1,26)} = 55.57$, $P < 0.001$). We found no interaction between the effects of canopy and caging treatments on sapling survival ($F_{(2,156)} = 1.19$, $P = 0.15$).

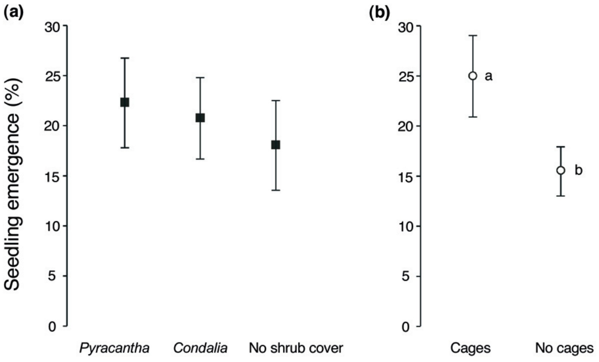

Fig. 1. Differences in *Ligustrum* seedling emergence under the (**a**) canopy and (**b**) caging treatments one year after sowing. Different letters indicate significant differences in seedling emergence among caging treatments ($P = 0.05$).

Canopy size

Pyracantha individual shrubs tended to have larger canopies (27.79 ± 1.87 m^2) than *Condalia* shrubs (8.64 ± 0.7 m^2). However this difference in shrub size had no detectable effect on seedling emergence, growth or sapling survival when analysed as covariate of the canopy treatments ($P > 0.1$ in all cases).

Discussion

Our experimental results suggest a facilitation effect exerted on *Ligustrum* by the exotic *Pyracantha*, as compared with the no-shrub treatment and, to a lesser

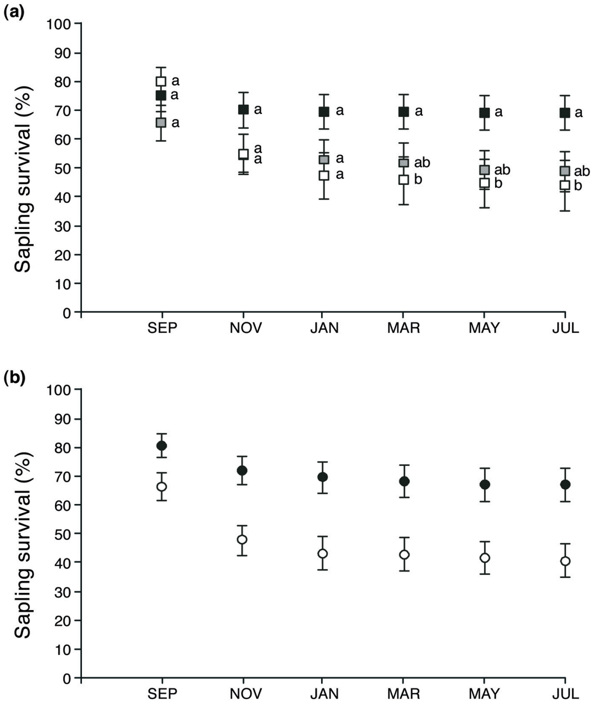

Fig. 2. Differences in *Ligustrum* sapling survival considering the (**a**) canopy treatment: *Pyracantha* understorey (black squares), *Condalia* understorey (gray squares) and plots without shrub cover (white squares); and considering the (**b**) caging treatments: saplings protected with cages (black circles) and unprotected saplings (white circles). Different letters indicate significant differences in seedling survival among canopy treatments every two-month after transplantation ($P = 0.05$), caging enhanced sapling survival throughout the experiment.

Table 1. Effects of canopy and caging treatments on the growth of *Ligustrum* seedlings (estimated by six different variables). Different letters indicate differences in growth variables between canopy treatments. *N* = number of replicates for each canopy treatment (without cages; with cages, respectively). Degrees of freedom are indicated in parentheses for each source of variance. Significant differences are indicated as * = $P< 0.05$ and ** = $P< 0.01$.

	Canopy treatment			Source of variance	
Growth variables	*Pyracantha* *N*= (7; 9)	*Condalia* *N*= (10; 7)	No shrub cover *N*= (7; 9)	Canopy $F_{(2,26)}$	Caging $F_{(1,26)}$
Height (cm)	6.10 ^{a}	5.86 ^{a}	7.96 ^{b}	7.34**	2.36
DAB (mm)	0.86	0.84	0.97	0.84	0.04
Total above-ground biomass (g dry weight)	0.05 ^{a}	0.05 ^{a}	0.20 ^{b}	5.84**	0.19
Leaf biomass (g dry weight)	0.03 ^{a}	0.03 ^{a}	0.16 ^{b}	5.27*	0.21
Number of leaves	3.98 ^{ab}	3.34 ^{a}	5.81 ^{b}	4.40*	0.01
Number of buds	3.01	2.98	3.68	1.35	0.57

degree, with the native shrub *Condalia*. This is consistent with observations of natural *Ligustrum* sapling distribution at this study site (Tecco et al. 2006). This effect would be in addition to the higher seed input under the canopy of *Pyracantha*, which was not measured but seems likely in view of the simultaneous fruit ripening and dispersal of *Ligustrum* and *Pyracantha* (Tecco et al. 2006). Therefore, our study provides a new example of synergistic links between invading species (Simberloff & Von Holle 1999). The facilitative association found in the present study appears to be the result of a balance between null (emergence), negative (growth), and positive (survival) effects of both shrubs, but particularly of *Pyracantha* individuals on *Ligustrum* seedlings and saplings, as summarized below. The results we found for this Chaco montane woodland from central Argentina are therefore in accordance with examples from other ecosystems and regions, in which facilitation, tolerance and competition have been shown not to be mutually exclusive (Holmgren et al. 1997; Holzapfel & Mahall 1999; Callaway & Walker 1997; Holl 2002; Bruno et al. 2003).

Contrasting effects on seedling emergence, growth and survival

1. Emergence of *Ligustrum* seedlings did not differ between canopy treatments, suggesting that the positive effect of *Pyracantha* or *Condalia* on *Ligustrum* was not based on improved germination of seeds under their canopies. Rather, the nurse association occurred after seedling emergence. Additionally, although shrubs often provide refuge for rodent seed predators (Kollmann & Buschor 2002), this did not appear to directly reduce germination or seedling emergence in our case study, as shown by the lack of interactive effects between caging and canopy treatment on these variables. Other studies comparing seed predation below grass and shrubs in temperate old fields have shown higher seed predation below shrubs and small trees compared with areas with dense herbaceous cover (Webb & Willson 1985; Myster & Pickett 1993). This difference in predation was related to the reduced grass cover below shrub patches, which increased the probability of animals encountering seeds (Holl 2002). In this study, although herbaceous cover was low under the shrubs, *Ligustrum* seeds became naturally buried within the litter layer. As a consequence, the probability of finding seeds may not have been higher under the shrubs. In fact, considering the differences in seedling emergence between caged and uncaged seeds, post-dispersal predation of seeds seemed to be high throughout the study site.

2. *Pyracantha* and *Condalia* reduced the growth of *Ligustrum* seedlings established under their canopies. This was not associated to predation by rodents, since caging, did not modify seedling growth. Rather, it is likely associated to the lower availability of photosynthetically-active radiation under the shrubs (Tecco et al. 2006). The possible beneficial effects of shrubs on the water balance of *Ligustrum* seedlings (moister and cooler conditions) seemed not to be enough to compensate for the negative effect of their shady understorey on growth, as observed in other nurse-associations (Holmgren et al. 1997). Similar findings have been reported by other authors (Berkowitz et al. 1995; Schenk & Mahall 2002; Yamashita et al. 2003). For example, the seedlings of the invasive trees *Sapium sebiferum* (in southeastern US) and *Bischofia javanica* (on Bonin Island) recruit preferentially under the dense canopy of the invaded forests, but grow more rapidly in full sunlight (Yamashita et al. 2003).

3. Finally, the enhanced sapling survival under the canopies of *Pyracantha* and *Condalia* supports the existence of nurse-plant associations between *Ligustrum* and both shrubs, despite their negative effect on *Ligustrum* seedling growth. While both shrubs influence *Ligustrum* recruitment in the study site, *Pyracantha* appears to have a more reliable effect on sapling survival. This is

consistent with the natural sapling distribution in the study area where *Ligustrum* are positively associated to both shrubs although with remarkably lower density under *Condalia* as compared to *Pyracantha* (Tecco et al. 2006). The higher sapling survival under cages might be attributed to an intense rodent activity, that resulted in the removal of soil and litter that covered the saplings, and even uprooting of whole plants not protected by cages. However, it does not explain differential survival among canopy treatments since rodent activity seemed to enhance sapling mortality throughout the study site.

Although we did not investigate the mechanisms underlying the enhanced survival of *Ligustrum* saplings under *Pyracantha*, the amelioration of environmental stress has been widely described as a typical nurse-plant facilitative mechanism (Kitzberger et al. 2000; Tewksbury & Lloyd 2001; Castro et al. 2002; Bruno et al. 2003). Since *Pyracantha* offered a significantly cooler micro-environment in summer and a moister soil in the dry season as compared to the *Condalia* canopy (Tecco et al. 2006), the differential survival of *Ligustrum* saplings under *Pyracantha* could partly be related to environmental amelioration. Another factor proposed to explain nurse effects is a large benefactor size of the nurse plant (Callaway & Walker 1997; Tewksbury & Lloyd 2001).

This approach assumes that larger nurse plants accumulate more nutrients and a larger seed bank both by collecting leaves, soil and wind-dispersed seeds, and by accumulating seeds through the foraging behaviour of birds that use them as roosts and nesting substrate and disperse seeds beneath the canopy (Tewksbury & Lloyd 2001). While an enhanced seed accumulation may occur (Tecco et al. 2006), our results do not support the existence of a post-dispersal benefactor size by *Pyracantha*, since seedling emergence, growth and survival were unaffected by shrub size. Moreover, although *Pyracantha* showed larger canopies than *Condalia*, the soil under the shrubs and that in the plots without shrub cover did not show different mineral nutrient content (Tecco et al. 2006). Shrub facilitation of seedling survival might have also resulted from more indirect mechanisms. For example, herbaceous competition amelioration by shady canopies has been reported as a facilitative mechanism improving seedling success of woody species in degraded woodlands and forest plantations (Parrotta 1995; Archer et al. 1998; Callaway 1992; Callaway & Davis 1998; Li & Wilson 1998; Stachowicz 2001; Holl 2002). In relict Pampean grasslands the recruitment of *Ligustrum* is strongly limited by the availability of favourable microsites and by the interference from herbaceous vegetation (Mazia et al. 2001). Considering that in our study site the herbaceous vegetation in the open was dominated by a dense matrix of tall annual herbs that were absent under the shrubs (e.g., *Leonurus sibiricus, Conium maculatum, Carduus acanthoides*), this mechanism appears as a good candidate for explaining the facilitation pattern observed, and thus merits testing in future studies.

Conservation implications

Overall, our work illustrates the importance of considering positive, synergistic interactions among invaders ('invasional meltdown' *sensu* Von Holle & Simberloff 1999) in designing conservation and management policies. There is no published evidence suggesting a negative ecosystem impact of *Pyracantha*, other than a decrease in aesthetic value of the landscape. However, through its invasional meltdown with *Ligustrum*, *Pyracantha* may indirectly alter community structure and successional pathways in the invaded region. The negative ecosystem- and community-level effects of *Ligustrum* and some of its close relatives have been documented in a number of cases, including the formation of dense, impenetrable thickets, a strong reduction of understorey diversity and the suppression of tree regeneration (Montaldo 1993, 2000; Ribichich & Protomastro 1998; Lavergne et al. 1999; Richardson et al. 2000; Merriam & Feil 2002; Gavier 2003; Aragón & Morales 2003; Gavier & Bucher 2004; Lichstein et al. 2004).

Plant interactions can be viewed as complex combinations of positive and negative components (Callaway & Walker 1997). These complex interactions are also at play on the invasional meltdown between *Pyracantha* and *Ligustrum* in our study. In view of these interactions we suggest that an early control of *Pyracantha* would still be more effective as a long-term control of *Ligustrum* expansion than only controlling the fewer fast-growing *Ligustrum* saplings in the herbaceous matrix.

It has been observed that *Ligustrum* recruitment is limited by cattle browsing and positively associated to the mechanical shelter provided by spiny shrubs (Malizia & Greslebin 2000). In contrast, *Pyracantha* successfully invades logged and livestock-grazed areas in the secondary woodlands around our study site (P. A. Tecco unpubl. data). Therefore, while ungulates may control *Ligustrum* populations in the herbaceous patches, *Pyracantha* may shelter its seedlings against livestock and favour its recruitment in the community. In addition, regardless of their slower growths, *Ligustrum* saplings that have naturally established under *Pyracantha* often overtop the shrub. This suggests that *Ligustrum* saplings may eventually replace the shrub under which they establish with the potential to dominate the invaded community.

This study does not suggest that *Pyracantha* is essential for *Ligustrum* successful establishment in the region. It rather highlights that even aggressive invaders like *Ligustrum* may establish positive interactions with other species triggering its spread. It also warns that interactions among invaders should be seriously taken into account since their joint impact can be more severe than that of the different species acting separately.

Finally, we suggest that land-management practices aimed to prevent further expansion of *Ligustrum* over the landscape are likely to be more effective if they tackle its synergistic partner *Pyracantha* as well.

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