

# Do Wildfires Promote Woody Species Invasion in a Fire-Adapted Ecosystem? Post-fire Resprouting of Native and Non-native Woody Plants in Central Argentina

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**Abstract** We asked whether prescribed fire could be a useful management tool to reduce invasion by non-native plants in an ecosystem where native plants are supposed to be adapted to fires. Specifically, we compare the post-fire resprouting response of native and non-native woody species in Chaco Serrano forest of central Argentina. The measurements were carried out in five burnt areas where we selected ten native and seven non-native species. Our response variables were (1) post-fire survival, (2) types of resprouts, and (3) the growth of the resprouts. Our main results show that one year after the fire, survivals of native and non-native species were 0.84 and 0.89, respectively, with variances in survival seven times smaller in the native species group. Type of resprout was also less variable in native species, while growth of the resprouts was similar in native and non-native groups. We interpret that in most cases, the burning a forest with mixed native and non-native plants through prescribed fires will not differentially stop the invasion by non-native woody species even in ecosystems which are presumed to be relatively resistant to fires such as our study area.

**Keywords** Burning · Invasive · Alien · Exotic · South America · Fire management

## Introduction

Fire-prone ecosystems comprise a significant portion of the world (Krawchuk et al. 2009). In these fire-prone regions the physiognomy and composition of plant communities is highly dependent on the fire regime and many plant species have adapted to fire by resprouting or by evolving mechanisms for recolonizing burnt areas by seed dispersion (Pyke et al. 2010). Species better adapted to fires will prevail over non-adapted species in environments with high fire recurrence. Moreover, many studies have shown that when non-native fire-adapted species are introduced to regions without an extended fire history, fires in the new environment can increase non-native plant abundance, sometimes creating new, self-sustaining, invasive plant/fire cycles (Mandle et al. 2011; Brooks et al. 2004). In these situations manager decisions to maintain fire regimes through prescribed fires or letting fires burn could further favor non-native plant invasion over native plant communities (i.e., Keeley 2006).

Conversely, non-native invasive species might proliferate in sites less affected by fires while relatively frequently burnt sites may maintain native biodiversity in regions with fire-adapted native plants. This scenario has been described in Australia (i.e., Watson et al. 2009), where both native community composition and fire regimes may be restored with no management conflicts. However, so far it is difficult to predict successional trajectories and response to different fire regimes due to the possible combinations of post-fire responses of native and non-native woody plants (Zouhar et al. 2008; Pyke et al. 2010; Keeley and Brennan 2012). In particular, if non-native plants are also pre-adapted to fire, they might outperform the native communities even under high fire frequencies due to their new range having less or no specific predators, less competition,

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or having a climate better suited to the species than the climate at the native range (Mack et al. 2000).

The study of plant resprouting ability is important to understand the community plant response after fire in fire-prone regions, because here resprouting is the main adaptation to fire in woody species (Wells 1969; Bellingham and Sparrow 2000; Bond and Midgley 2001). Post-fire resprouting often occurs from protected meristems and allows plants to reduce mortality and obtain a fast biomass recovery (Lamont and Downes 2011; Lawes and Clarke 2011). Under these conditions fires produce few changes in floristic composition and the dependence on seeds for population maintenance is low (Bond and Midgley 2001). Different resprouting types can be present in plants after fires. Bellingham and Sparrow (2000) suggest that basal resprouting should be most common in areas with severe and frequent disturbances, whereas resprouting from aerial stems should be more abundant in areas with relatively fewer disturbances.

Studies on fire effects should also take into account plant size and the effect of topographic features such as rocks on fire behavior. Plant size can affect post-fire survival and the type of resprouting because tall plants can keep their buds far from flames and therefore may resprout from above ground organs. Conversely, small plants can be completely scorched during the fire thus increasing mortality or basal resprouting from stem collar or below-ground organs. Moreover, larger plants usually have more roots where carbohydrates are stored to help in the growth of resprouts while smaller plants have less storage capacity and resprouts grow slower (Gurvich et al. 2005). In mountain regions the high topographic heterogeneity may influence fire behavior through slope, boulders, herbivore preferences, and fine fuel availability. This could originate different plant responses because trees may be differentially affected at different sites (Alinari et al. 2015; Moreira et al. 2009). In particular, fire severity can diminish in rocky microsites where plants are less exposed to fire and buds may remain unburnt.

The effect of fire on plant communities invaded by non-native invasive plants has gone almost unstudied in the South American Gran Chaco, the second largest biome of South America, where fires are frequent and resprouter woody plants dominate the system (Gurvich et al. 2005; Verzino et al. 2005; Torres et al. 2014; Bravo et al. 2014). Here, we study the post-fire resprouting response of native and non-native species in Chaco Serrano forest of central Argentina. Specifically, we compare between native and non-native plant groups and among species (1) post-fire survival, (2) types of resprouts after fire and (3) the growth of resprouts; and determine (4) the effect of plant size and microsite rockiness on survival and growth of resprouts. Finally, we discuss the results in relation to fire regime, to

which non-native species are adapted, focusing in management implications of fires and plant invasions.

In this work, we assumed a long fire history in our study region according some antecedents within other mountain ecosystems of Argentine North region with a dry season (Grau and Veblen 2000; Aráoz and Grau 2010) and because in our study region all woody plants resprout after fires albeit resprouting is not necessarily an adaptation to fires (Gurvich et al. 2005; Torres et al. 2014). Considering the diverse geographical origins of non-native species, our hypothesis is that native woody species would respond to fires relatively better as compared to non-native woody species which should present a greater diversity of responses to fire. We predicted: (1) Post-fire survival of native species will be higher and more homogeneous than of non-native species. (2) Most native species will present basal resprouts while non-native species will be more variable in the types of resprouts. (3) Post-fire growth of resprouts will follow a similar pattern as survivals with higher and more homogeneous growth in native than in non-native species.

## Methods

### Study Area

The Córdoba mountains of central Argentina have a warm temperate to subtropical climate, with a mean annual temperature of 13.9° C and a mean annual precipitation of around 725 mm, concentrated during the warm season from September to March (Capitanelli 1979). The original vegetation corresponds to the Chaco Serrano district which extended approximately from 500 to 1300 m asl (Cabrera 1994). Twenty five native and 19 non-native tree species have been described for the Chaco Serrano of the Córdoba Mountains. The common native trees in mature forests are *Lithraea molleoides* and *Schinopsis lorentzii* which are co-dominant along altitudinal, latitudinal, and longitudinal gradients with other woody species as *Celtis ehrenbergiana*, *Ruprechtia apetala*, *Acacia caven*, *Aspidosperma quebracho-blanco*, *Condalia microphylla*, *Kageneckia lanceolata*, *Prosopis chilensis*, and *Schinus fasciculatus*. The most abundant non-native trees include *Cotoneaster glaucophyllus*, *Cotoneaster franchetii*, *Ligustrum lucidum*, *Gleditsia triacanthos*, *Melia azedarach*, *Morus alba*, *Pyracantha angustifolia*, and *Ulmus pumila* (Giorgis and Tecco 2014). Fires are most frequent during the long dry season extending from June to November (Miglietta 1994). Fires, in combination with livestock grazing, urbanization and agriculture have greatly reduced native forest extension and its original structure, and mature forests are almost non-existent (Gavier and Bucher 2004; Renison et al. 2011; Zak et al. 2004).

The long-term evolutionary history of fire regimes are unknown in the Chaco Serrano but a long history of disturbances such as fire and herbivory is presumed on the basis that most trees survive these disturbances very well by resprouting (Bellingham and Sparrow 2000; Bond and Midgley 2001; Gurvich et al. 2005; Torres et al. 2014). However, debate exist to the extent that resprouting is an adaptation to fire and not to other disturbances because a low proportion of Chaco species have seeds whose germination is enhanced by heat, albeit most species tolerate heat (Jaureguiberry and Díaz 2015).

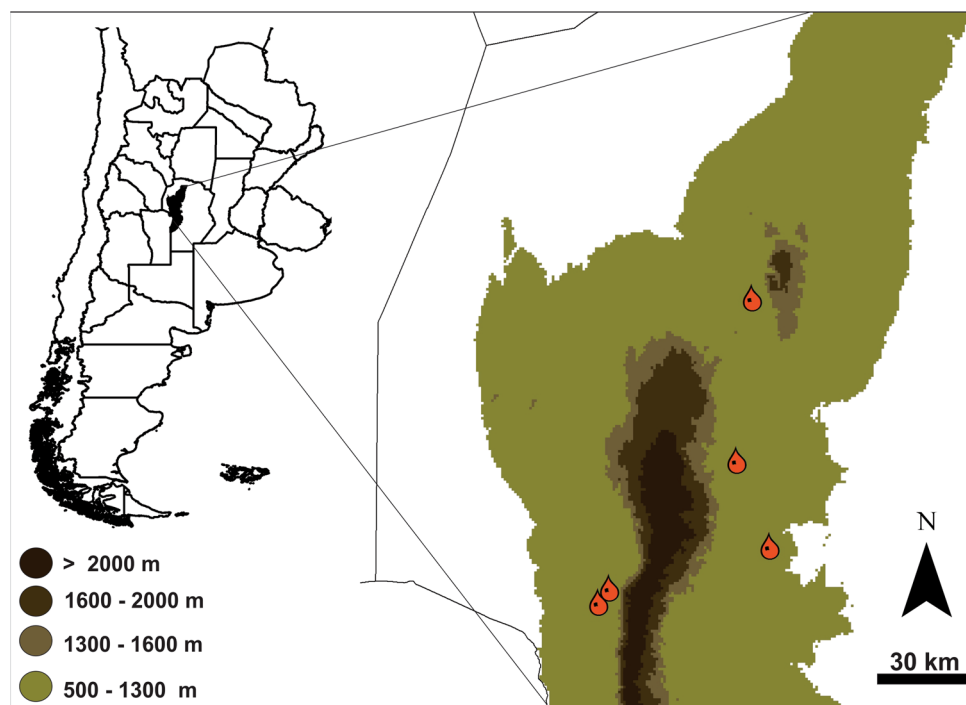
At the beginning of the XVI century intense forest logging took place which stimulated an increase of fine fuel availability thus predisposing fire occurrence, followed by an intensification of the European type livestock production system which transformed Chaco mountain forests into shrublands (Gavier and Bucher 2004). Then since the XVII century the use of fire is associated to livestock production in Jesuit ranches along the Córdoba Mountains (Kunst et al. 2003). Additionally, in the last decades large extents of remaining Chaco Serrano forests have been invaded by several non-native species (Giorgis et al. 2010), which in some sectors represents more than 90 % of the plant cover (Hoyos et al. 2010). For the present study, we selected five areas affected by fires occurring from June to November of 2009 (Fig. 1). These areas represented the heterogeneity of fire behavior with the size of the burnt patches being (La Cumbre 1000 ha, Cuesta Blanca 276 ha, Villa Ciudad de

América 985 ha, Los Hornillos 109 ha, and Villa de las Rosas 354 ha).

### Species and Measurements

The measurements were carried out at the end of first growing season after fires (autumn 2010). For each studied burnt area, we selected the native and non-native woody species available on the burned area. Because the non-native species were more restricted to particular burnt sites than the natives who were more widespread, the native and non-native species totaled 10 and 7, respectively (Table 1). The number of native and non-native burnt species per burnt area ranged between 1 and 3. For each species and site, we located between 15 and 30 individuals taking into account a minimum distance of 50 m from each other and representing a wide range of tree sizes. For each individual, we registered if it was dead or alive. We recognized the species identity of dead individuals by analyzing the bark and the plant architecture. We estimated pre-fire height as judged by the remaining tree stems (as in Renison et al. 2002). The use of remaining tree stems may underestimate pre-fire tree size, but in our region only small branches and twigs are completely burnt, representing an insignificant proportion of the total pre-fire woody biomass (Gurvich et al. 2005). For surviving individuals, we recorded the height of the new shoots and the type of resprouts (aerial, basal, and below-ground, see Clarke et al. 2013).

**Fig. 1** Location of the five study areas in the Chaco Serrano district (500–1300 m asl), Córdoba, Argentina. From North to South: La Cumbre (30° 57'S, 64° 29'W), Cuesta Blanca (31° 29'S, 64° 34'W), Villa Ciudad de América (31° 46'S, 64° 34'W), Los Hornillos (31° 54'S, 65° 00'W), and Villa de las Rosas (31° 57'S, 65° 02'W)



**Table 1** Native and non-native woody species selected for the study

Species	$N_i$	$N_a$	Family	Origin	Pre-fire height (m)	
					Mean $\pm$ SE	Min and max
<i>Acacia caven</i> (Molina) Molina	60	2	Fabaceae	Native	2.57 $\pm$ 0.17	0.84–9.80
<i>Aspidosperma quebracho-blanco</i> Schlttdl.	20	1	Apocynaceae	Native	3.78 $\pm$ 0.56	0.40–8.00
<i>Celtis ehrenbergiana</i> (Klotzsch) Liebm.	80	4	Celtidaceae	Native	3.26 $\pm$ 0.21	0.60–11.20
<i>Condalia microphylla</i> Cav.	20	1	Rhamnaceae	Native	2.42 $\pm$ 0.16	1.17–3.40
<i>Kageneckia lanceolata</i> Ruiz & Pav.	20	1	Rosaceae	Native	2.57 $\pm$ 0.28	0.80–4.70
<i>Lithraea molleoides</i> (Vell.) Engl.	120	4	Anacardiaceae	Native	3.58 $\pm$ 0.19	0.46–10.00
<i>Prosopis chilensis</i> (Molina) Stuntz emend. Burkart	40	2	Fabaceae	Native	3.43 $\pm$ 0.27	0.46–8.00
<i>Ruprechtia apetala</i> Wedd.	103	4	Polygonaceae	Native	2.90 $\pm$ 0.16	0.30–7.50
<i>Schinopsis lorentzii</i> (Griseb.) Engl.	30	1	Anacardiaceae	Native	4.24 $\pm$ 0.63	0.90–12.00
<i>Schinus fasciculatus</i> (Griseb.) I. M. Johnst.	60	2	Anacardiaceae	Native	2.50 $\pm$ 0.14	0.60–4.90
<i>Cotoneaster</i> spp. <sup>a</sup>	30	1	Rosaceae	Southwest of China	2.71 $\pm$ 0.18	1.00–4.39
<i>Gleditsia triacanthos</i> L.	50	2	Fabaceae	South of USA	3.60 $\pm$ 0.29	0.50–8.10
<i>Ligustrum lucidum</i> W.T. Aiton	41	2	Oleaceae	China, Korea and Japan	3.52 $\pm$ 0.24	0.81–6.70
<i>Melia azedarach</i> L.	40	2	Meliaceae	Southeast of Asia	3.21 $\pm$ 0.27	0.67–8.00
<i>Morus alba</i> L.	42	2	Moraceae	China	4.66 $\pm$ 0.43	0.76–12.00
<i>Pyracantha angustifolia</i> (Franch.) C.K. Schneid.	50	2	Rosaceae	Southwest of China	2.79 $\pm$ 0.14	1.30–5.30
<i>Ulmus pumila</i> L.	45	2	Ulmaceae	Temperate regions of East Asia	3.86 $\pm$ 0.32	0.42–9.40

Number of individuals ( $N_i$ ), Number of burned areas where it was measured ( $N_a$ ), family, region of origin of non-native species and pre-fire height is detailed

<sup>a</sup> Two species of *Cotoneaster* spp. are invading the study sites and which we were unable to distinguish under post-fire conditions: *Cotoneaster glaucophyllus* Franch and *C. franchetii* Bois

Additionally, as an indicator of fuel availability in the area under the tree crown, we visually estimated the proportion occupied by rocks.

### Statistical Analyses

Our response variables were post-fire survival, type, and height of resprouts. Every response variable was analyzed at two levels of detail: (1) A comparison between native and non-native plant groups where the species averages were used as individual data points ( $N = 17$ , comprising 10 native and 7 non-native species), and; (2) an among species comparison independently of their origin where the measurements of each plant were used as data points ( $N = 851$ , varying the number of individuals from 20 to 120 according to species, see Table 1).

To compare post-fire survival between native and non-native woody plants species, we used as response variable the mean post-fire survival of each species. We used the Wilcoxon matched pairs test to compare between native and non-native groups and a Fisher's  $F$  test to assess whether the variances were significantly different. We used non-parametric tests because the normality of the residuals of parametric tests was doubtful upon visual inspection.

Among species post-fire survival was assessed using binary logistic regression, the response variable was survival (alive or dead) and the explanatory variables were species (categorical with 17 levels or species), pre-fire height, and proportion of rock under the projection of the tree crowns (continuous variables).

To compare the variability in the proportion of each type of resprouts between native and non-native groups, we carried out a Fisher's  $F$  test to assess whether the variances were significantly different. The response variables were the proportion of aerial, basal, and below-ground resprouts.

To compare the height of resprouts, we only used basal and below-ground resprouts which corresponded to trees completely top-killed. We excluded aerial resprouts because they were present in trees with portions of above ground tissues not completely killed and individuals with aerial resprouts represented a small proportion of post-fire survivors. We compare mean height one year after fire in native and non-native woody plants groups through Student's  $t$  test for independent samples. To compare the growth of resprouting among species, we run an ANCOVA. We used as response variable the height of resprouts and as predictors: the categorical variable species, and pre-fire height and proportion of rocks under

crown as covariates. To achieve homogeneity of variances, height of resprouts and pre-fire height were square root transformed prior to analysis. We used R statistical package for all analysis (R Core Team 2014).

## Results

### Post-fire Survival

We registered a total of 851 individuals belonging to both native and non-native species. The average post-fire survivals for the native and non-native groups of species were similar, with values of  $0.89 \pm 0.03$  and  $0.84 \pm 0.10$ , respectively (Wilcoxon  $W = 31$ ,  $P < 0.73$ ). Instead, the variance in the post-fire survival was seven times smaller for the native species group as compared to the non-native species group (Fig. 2a; variance for native species = 0.01,  $df = 9$ ; variance for non-native species = 0.07,  $df = 6$ ; Fisher's  $F$  test,  $F = 0.1423$ ,  $P = 0.01$ ).

The post-fire survival of the natives *Lithraea molleoides* and *Aspidosperma quebracho-blanco* was slightly lower than the other eight native species, and the survival of the non-native *Ligustrum lucidum* was specially low as compared to other six non-natives (Fig. 2b; Logistic regression: *L. molleoides*,  $n = 120$ , Wald = 6.05,  $P < 0.01$ ; *A. quebracho-blanco*,  $n = 20$ , Wald = 3.19,  $P = 0.06$ ; *Ligustrum lucidum*,  $n = 41$ , Wald = 28.5,  $P < 0.001$ ). Survival was not significantly affected by pre-fire height ( $P = 0.45$ ) nor by the proportion of rocks under the crown ( $P = 0.08$ ).

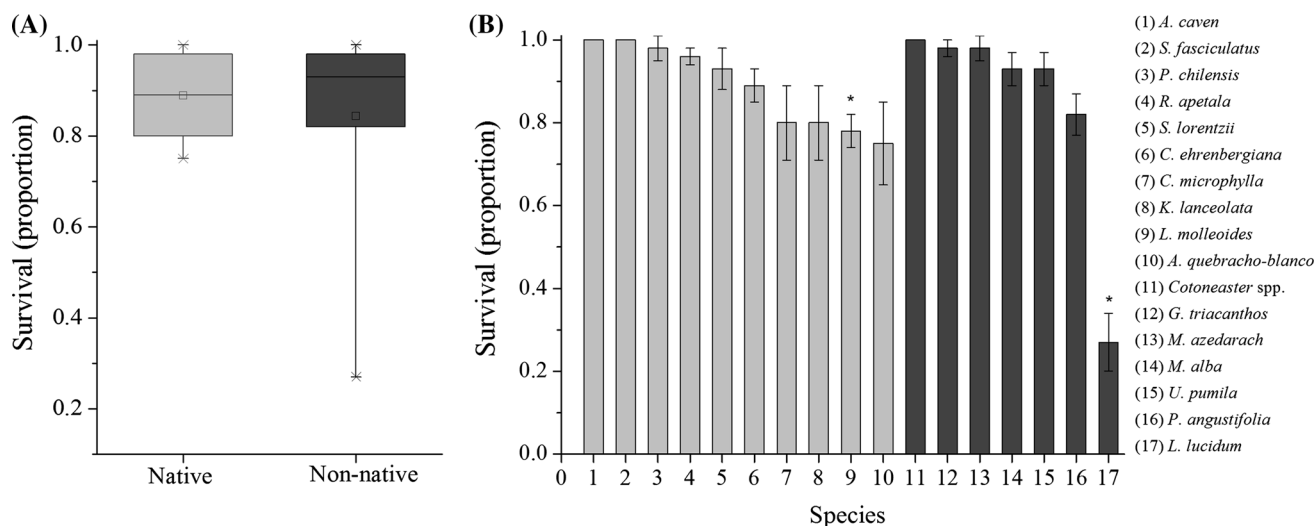
### Type of Resprouts

The averages in the proportions of basal, aerial, and below-ground resprouts for the native species were 0.90, 0.06, and 0.03, respectively, while the respective proportions for the non-native species were 0.6, 0.23, and 0.16. The variance in the proportion of basal, aerial, and below-ground resprouts was, respectively, 11, 19, and 9 times smaller for the native species than for non-native species (Fig. 3a; Fisher's  $F$  test: for basal resprouts, variance = 0.006 and 0.076,  $df = 9$  and 6  $F = 11.15$ ,  $P < 0.001$ ; for aerial resprouts, variance = 0.004 and 0.077,  $df = 9$  and 6,  $F = 18.81$ ,  $P < 0.001$ ; for below-ground resprouts variance = 0.007 and 0.06,  $df = 9$  and 6,  $F = 8.9$ ,  $P = 0.004$ ).

### Growth of Resprouts

The height of basal and below-ground resprouts one year after the fire did not differ significantly among the native and non-native groups in average and variance values (Fig. 4a; Student's  $t$  test for means,  $t = -1.82$ ,  $df = 10.244$ ,  $P = 0.098$ ; Fisher's  $F$  test for variances,  $F = 0.51$ ,  $P = 0.36$ ).

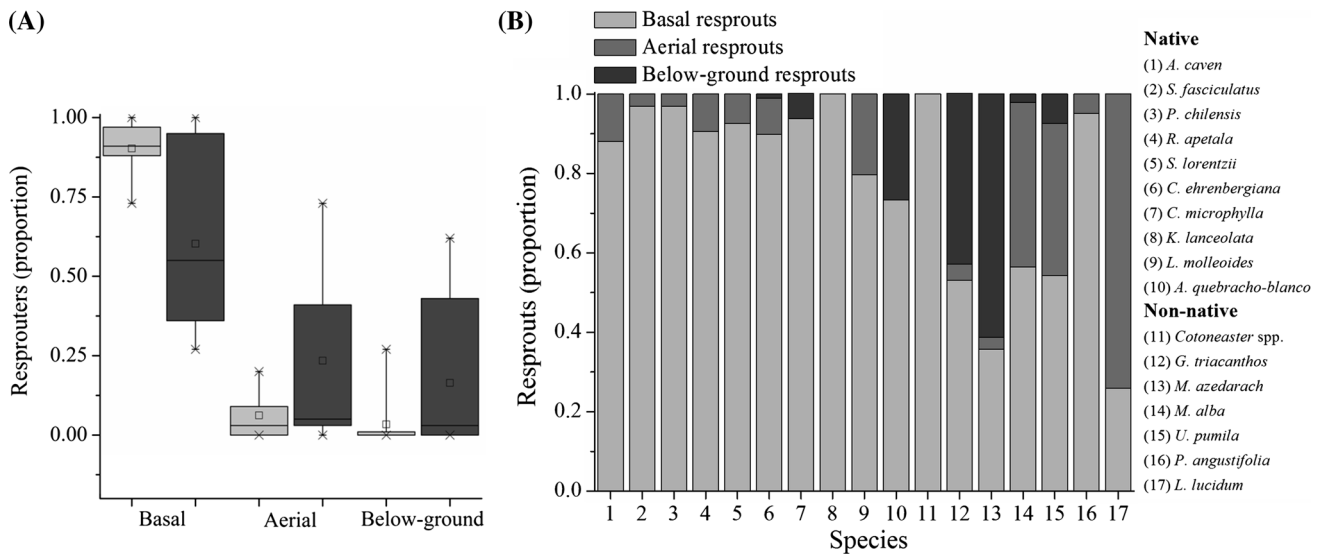
The height of resprouts differed among species (ANCOVA:  $n = 622$ ,  $F = 10.57$ ,  $P < 0.001$ ). Additionally, the height of the resprouts was positively related with the pre-fire height ( $P < 0.001$ ) and the proportion of rocks under the crown ( $P = 0.02$ ), though these relations were significant for some of the species. The height of resprouts



**Fig. 2** Post-fire survival (expressed as a proportion) for **a** Average and variability of native and non-native tree species groups. **b** Detail showing average and SE per species. *Light gray* represent native tree

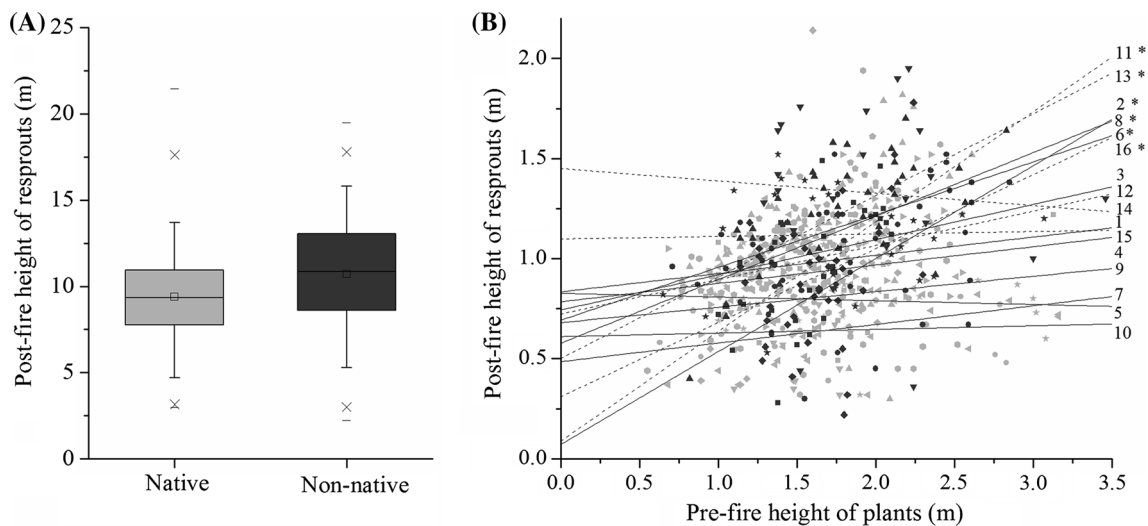
species and *dark gray* represent non-native tree species. *Asterisks* indicate significant differences among species with a survival lower than expected, at  $P < 0.05$





**Fig. 3** Types of resprout for **a** Native and non-native tree species groups. Light gray boxes represent native tree species and dark gray boxes represent non-native tree species. Wider boxes indicate greater variability in the data. **b** Proportion of basal, aerial, and below-ground

resprouts of native and non-native species. Different colors inside bars show the three different types of resprouts (light gray bars, basal resprouts; dark gray bars, aerial resprouts; and black bars, below-ground resprouts)



**Fig. 4** Post-fire height of basal resprouts for **a** Average and variability of native and non-native tree species groups. **b** One year post-fire height of resprouts in relation to pre-fire height of individuals (square root transformed). The light gray circles represent native species and dark gray circles represent non-native species. Numbers indicate the species: (1) *A. caven*, (2) *S. fasciculatus*, (3) *P. chilensis*, (4) *R. apetala*, (5) *S. lorentzii*, (6) *C. ehrenbergiana*, (7) *C.*

*microphylla*, (8) *K. lanceolata*, (9) *L. molleoides*, (10) *A. quebracho-blanco*, (11) *Cotoneaster* spp., (12) *G. triacanthos*, (13) *M. azedarach*, (14) *M. alba*, (15) *U. pumila*, and (16) *P. angustifolia*. Continuous lines represent the adjusted functions for native species and dashed lines represent the adjusted functions for non-native species. Asterisks indicate species with a significant relationship between the pre-fire and the post-fire height, at  $P < 0.05$

increased with pre-fire height for the native species *Celtis ehrenbergiana* ( $P = 0.01$ ), *Kageneckia lanceolata* ( $P = 0.008$ ), *Schinus fasciculatus* ( $P = 0.01$ ) and the non-native species *Cotoneaster* spp. ( $P < 0.001$ ), *Melia azedarach* ( $P = 0.001$ ), and *Pyracantha angustifolia* ( $P = 0.01$ ), while for other seven native and three non-

native species, we did not find a significant effect of pre-fire height in the growth of resprouts (interaction of species \* pre-fire height,  $P < 0.001$ ; Fig. 4b). We excluded the non-native species *Ligustrum lucidum* from the analysis because the number of individuals with basal and adventitious resprouts was low ( $n = 3$ ).

## Discussion

Our main results did not support our hypothesis that native woody species would respond to fires relatively better as compared to non-native woody species. As predicted, responses were more homogenous in the native than in the non-native species in terms of survival and type of resprout, but not in growth. However, average post-fire survival and growth of the native species were not higher than in the non-native group of species even though not all the non-native species originated from areas with high fire recurrence. We interpret that in most cases the burning of mixed native and non-native forests through prescribed fires will not differentially stop the invasion by non-native woody species even in ecosystems which are presumed to be relatively well adapted to fires such as our study area.

### Post-fire Survival

Post-fire survival of native species was high and in accordance with previous studies in our region (Miglietta 1994; Renison et al. 2002; Verzino et al. 2005; Gurvich et al. 2005; Torres et al. 2014) and other fire-prone ecosystems (Brown et al. 2000; Vallejo et al. 2012). Contrary to our predictions, the post-fire survival of non-native species present in the study area showed similarly high average performance with a higher variability mainly due to low survival of *Ligustrum lucidum*. The values we determined for the post-fire survivals of the non-natives *L. lucidum*, *Gleditsia triacanthos*, and *Pyracantha angustifolia* coincide fairly well with those reported by Torres et al. (2014) in our study area. The high mortality of *L. lucidum* may be due to its thin bark which is easily damaged by fire. This high mortality is in agreement with the fact that in the native range of *L. lucidum* in Southeast China, Korea, and Japan fires are limited by moisture and presumably have not been a major selective factor (Myers 2006; Peláez 2010). Except for *L. lucidum* the other six studied non-native species had high post-fire survivals which could be due to high fire incidence in their native range or due to a long history of other disturbances such as browsing which could have selected for resprouting.

### Type of Resprouts

Basal resprouts was the main type of resprout present in native species, as was found in other studies in the region, probably due the high frequency and intensity of fires (Gurvich et al. 2005; Verzino et al. 2005; Torres et al. 2014). Basal resprouts are common in communities where fires destroy all aboveground parts of the plants due to their

high intensity or due to plants having a thin bark or unprotected meristems (Bond and Midgley 2001).

Among native woody species only a small proportion of individuals resprouted from below-ground or from aerial meristems like stem (epicormic), indicating that the meristems responsible of this types of resprouting might be located in axillary buds or in swollen lignotubers (Gurvich et al. 2005; Torres et al. 2014). In fire-prone environments species with basal resprouting are highly resilient to frequent and intense disturbances. However, resprouting under repeated disturbances depends not only on the availability of buds but also below-ground reserves. Schutz et al. (2011) showed that initial growth of resprouts depended of reserve mobilization from roots and that such process could be depleted under chronic defoliation, compromising resprouting ability.

In this study non-native species resprouted more of stem (aerial) and below-ground as compared to native species. The non-natives *Morus alba* and *Ulmus pumila* resprouted from aerial meristems, it may be that these species have protected aerial meristems or because the individuals of these species reach great heights (Max height: 12 and 9.5 m, respectively) and in consequence were less affected by fire (Bond and Midgley 2001). *Melia azedarach* and *Gleditsia triacanthos* resprouted from below-ground tissues such as roots often several meters away from the bunt crown, which is in accordance with Waggy (2009) who point out the ability of these species for invading open sites (Fig. 3b).

### Post-fire Growth of Resprouts

In contrast with our expectations, the variability of resprout height did not differ between native and non-native groups. Also, we did not find higher growth rates in the native species. Possibly, the presumed advantage of native species due to their adaptations for resprouting after fires was compensated by the equally good advantage of non-native species gained at their new range by having less or no specific predators, less competition, or having a climate better suited to the species than the climate at the native range (Mack et al. 2000; Seastedt 2014). Supporting this explanation studies in the Chaco Serrano of the functional traits of non-native tree species have shown higher growth rates than native tree species (Tecco et al. 2010; Zeballos et al. 2014).

We found differences among species in the mean height of resprouts and for some native and non-native species the growth was positively related with the pre-fire height, which was also reported in previous studies (Gurvich et al. 2005). The positive relationship between post-fire growth and pre-fire height of individuals could be due to a positive relationship between the size of individuals and the ability

to supply plant nutrients as carbohydrates and water to the meristem that remained active after fire (Hodgkinson 1998; Cruz et al. 2003). The native species with the highest vigor of resprouting were *Schinus fasciculatus*, *Celtis ehrenbergiana* and *Kageneckia lanceolata*, the first two species also reported in Gurvich et al. (2005) as with high post-fire growth rate (*C. ehrenbergiana*, Synonym: *Celtis pallida* Torr. var. *pallida*). Non-native species with the highest vigor of resprouting growth were *Cotoneaster* spp., *Melia azedarach* and *Pyracantha angustifolia* (Fig. 4b), probably because of their high overall growth rates (Sarry and Abedini 2001; Tecco et al. 2006).

Even though we did not find an effect of rocks on survival, we found a positive effect of rockiness in post-fire height of resprouts. Similar results were reported by Renison et al. (2002) for *Polylepis australis* in a mountain region, where high rockiness favored the growth of resprouts probably due to sites with rocks have low fine fuel availability and low fire severity.

### Implications for Chaco Serrano Management

Our results highly suggest that the use of prescribed burns cannot be a generalized management tool to reduce plant invasion in our study system. Fires damage native and non-native species and generate variable responses in non-native species which make it difficult to give general recommendations for all invaded communities. Thus, fire management should be decided on the basis of the non-native species present in the considered area (Keeley 2006). In our study region, it can be presumed that populations of the invasive *Ligustrum lucidum* could be reduced through application of prescribed burns in areas with a high proportion of this species. Also in favor of burns would be the fact that Torres et al. (2014) reported a low post-fire seedling establishment of *L. lucidum* in a site with high abundance of individuals and presumably a high propagule pressure. Accordingly, the use of fire has been suggested for other *Ligustrum* species invading in the USA (Batcher 2000; DiTomaso et al. 2006). Before developing this practice it would be important to determine with further studies that *L. lucidum* does not compensate its low post-fire survival with other persistence mechanisms as post-fire dispersal through seed from non-burnt adjacent areas, or by their high growth rates in the intervals between fires. It would also be important to determine the effects of prescribed burns on soil erosion as the only related study in our region reported very high soil erosion rates after a wildfire (Cingolani et al. 2013). For areas invaded by *Cotoneaster* spp., *Gleditsia triacanthos*, *Melia azedarach*, *Morus alba*, *Pyracantha angustifolia*, and *Ulmus pumila*, we do not recommend the use of fire and suggest more

targeted methods such as the eradication of individual plants. The mechanical control of individual plants could be achieved through programs for extracting wood as use for fuel, which might limit the expansion of the targeted invasive plants. To reduce reinvasion these strategies must be accompanied with education programs for promoting the use of native plants in urbanizations, roadsides and other human modified sites (Brooks 2008; Stone 2009). Finally, the prevention of invasion is always the best strategy, since control and eradication are costly and may never be complete (Klinger et al. 2000).

We studied post-fire survival and growth of resprouts but omitted to study post-fire reproduction by seeds. However, we believe that incorporating a study of the reproduction by seeds would not change the management implications against prescribed fires as a measure to reduce non-native invasion. The reason for our belief is that the long dry season prevailing in the Chaco Serrano precludes massive establishment of native species by seed and post-fire recovery occurs overwhelmingly by resprouting as shown by Torres et al. (2014) who reported a ratio of post-fire crown recovery because of resprouts and seedlings of 1562 to 1. Thus, the study of resprouting patterns should contribute to a better understanding of post-fire vegetation succession than the study of regeneration by seed as also postulated by Bond & Midgley (2001).

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