

# Human-induced vegetation changes did not affect tree progeny performance in a seasonally dry forest of central Argentina



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## ABSTRACT

Regeneration by seed is scarce in seasonally dry mountain forests; in these areas, shrub-grass patches intermingled with remnant trees are widespread due to anthropogenic fires and post-fire livestock grazing. We hypothesized that progeny performance of remnant trees would be reduced due to soil loss, water limitation and damage to tree structures. We assessed the progeny performance of three tree species (70 trees per species) distributed in seven sites in central Argentina; in those sites, forest patches and shrub-grass patches with remnant trees coexist at a relatively close distance. Our main results showed no significant differences between progeny of trees located in forest patches and that of shrub-grass patches regarding seed mass, germination percentage in laboratory, seedling growth in greenhouse and survival and growth of outplanted saplings. Thus, our results do not support a hypothesis of human disturbances causing loss of progeny performance in remnant trees. Trees may be resistant to environmental changes, or there may be compensatory mechanisms, such as reduction of competition from neighbor trees, or increased resource allocation to reproduction at the expense of adult survival. We conclude that remnant trees are valuable resources for forest restoration because the quality of their progeny is still intact.

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## 1. Introduction

In seasonally dry mountain forests, vegetation burning, livestock trampling and browsing, logging and expansion of urban areas are known to simplify the vegetation structure and to alter soil properties; these factors lead to forest conversion into shrublands and grasslands, where remnant adult trees become increasingly sparse (García-Fayos, 2004; Cingolani et al., 2008, 2014). Reproduction of remnant trees could potentially be altered due to exposure to soil erosion, reduced soil water retention capacity or damage to the tree due to partial topkill by fires (Roach and Wulff, 1987; Fenner, 1991; Baskin and Baskin, 2014).

Soil erosion may be intense in mountains with steep slopes, reducing nutrient and water availability to plants and, consequently, plant biomass production (Moreno-de las Heras et al., 2005). These effects of soil erosion may in turn affect progeny

performance, since the lack of mineral and organic nutrients and water reduces seed mass, seed germination and seedling growth (Stromberg and Patten, 1990; Cheplick and Sung, 1998; Shaukat et al., 1999; Cierjacks and Hensen, 2004; Zas et al., 2013). In contrast, human disturbances may also have positive effects on seed quality through a reduction in plant density and competition for resources, which indirectly increase resource availability, seed mass and seed germination (Dyer, 2002; Allison, 2002; Baskin and Baskin, 2014).

The reduction of a tree population because of forest degradation can affect pollination and gene fluxes of remnant trees, with consequences on progeny fitness (Ismail et al., 2014; Nagamitsu et al., 2014). However, in a degraded but contiguous forest, where there is no discrete border between forest and isolated trees, negative genetic consequences on progeny fitness can be negligible in comparison with the effects of changes in the environment. For example, in the mountains of central Argentina, human-induced environmental changes have negative effects on progeny performance of *Polylepis australis* trees, but not on their genetic diversity and structure (Renison et al., 2004; Seltsmann et al., 2009; Peng et al., 2017). Moreover, the progeny of tree species is unlikely to

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be affected by changes in pollination and gene fluxes because the long life span of most tree individuals reduces the number of generations affected by the changes.

We hypothesized that, in the environment where parent trees grow, human-induced changes could negatively affect tree reproductive potential, causing loss of progeny performance. We expected that progeny performance of trees growing in conserved forest patches would be better than that of remnant trees growing in a matrix of shrub-grass patches modified by multiple human disturbances. Specifically, we aimed to compare three native tree species of the Chaco Serrano forest in terms of (1) seed mass and germination under laboratory conditions, (2) seedling growth under greenhouse conditions, and (3) survival and growth of planted saplings in the field. We also compared progeny traits among species (4).

Knowledge about the impact of environmental changes on progeny traits is important to help understand the possible consequences of human impacts on tree species populations and their natural and assisted recovery capacity. Many studies have evaluated the effects of forest fragmentation due to large-scale agriculture. However, very few studies have attempted to the understanding of forest degradation processes, which are more relevant than fragmentation in mountain areas where agriculture is unusual.

## 2. Materials and methods

### 2.1. Study area

In the mountains of central Argentina, mean annual precipitation is about 725 mm, mainly concentrated in the warm season (October to April) and mean annual temperature is about 13.9 °C (Colladon, 2014). The vegetation in the study area (lat. 30° 51' 25.20" S to 32° 7' 15.60" S; long. 65° 6' 54.00" W to 64° 22' 26.40" W) corresponds to the Chaco Serrano forest, one of the largest seasonally dry forests in South America. Fires, combined with 400 years of domestic livestock grazing, have greatly degraded and reduced the forest area, with mature forests being almost non-existent (Cingolani et al., 2008; Renison et al., 2011). In the last century, accelerated changes occurred, such as logging for fuel and charcoal, increased wildfires in deforested areas and an expansion of urbanizations, non-native species invasion and agriculture (Gavier and Bucher, 2004; Zak et al., 2008; Hoyos et al., 2010; Giorgis et al., 2011). Zak et al. (2004) estimated a conversion of 94% of Chaco Serrano mature forest into shrublands and other cover types between 1969 and 1999. Although most native tree species of Chaco Serrano resprout after disturbances such as fires and livestock grazing, seedling regeneration is scarce (Torres et al., 2014).

Environmental gradients such as altitude, slope aspect and topographic position also have an important role in structuring vegetation type. Shrub-grass patches are more frequent at high altitudes and in flat sites that are accessible to livestock, which retard regeneration, whereas forest patches are more frequently found at lower altitudes and in steep ravines that have damper soils and are less accessible to livestock than other topographies (Cingolani et al., 2008; Alinari et al., 2015; Renison et al., 2015).

### 2.2. Study species

The study tree species were *Ruprechtia apetala* Weddell (Polygonaceae), *Lithraea molleoides* (Vell.) Engler (Anacardiaceae) and *Schinopsis lorentzii* (Griseb.) Engler (Anacardiaceae), hereafter referred to by their genus name. *Ruprechtia* is a 2–10 m tall deciduous tree distributed in Bolivia and Argentina. In the mountains of central Argentina, it is a relatively abundant tree in the transition with adjacent lowland forests. Its fruits are achenes of 9 × 3–4 mm.

At maturity, fruits are found inside three thin wings (Demaio et al., 2015). The species has been characterized as of “lower risk/near threatened” by the IUCN due to habitat degradation caused by overgrazing by cattle, sheep and goat (IUCN, 2016a). *Lithraea* is an evergreen tree, up to 14 m tall, distributed in Argentina, Brazil, Bolivia, Uruguay and Paraguay from 500 to 1600 m asl. It often dominates the canopy of mature stands. Its fruit is a drupe of 4–8 mm in diameter (Demaio et al., 2015). *Schinopsis* is a deciduous tree, up to 20 m tall, distributed in Argentina and Bolivia. In central Argentina, it is dominant or co-dominant with *Lithraea* in the boreal part of the Chaco Serrano. The fruits of *Schinopsis* are woody samaras with a membranous wing (Demaio et al., 2015). The species has been characterized as “vulnerable” by the IUCN due to habitat degradation, particularly in the mountains of central Argentina (mentioned with its former name: *Schinopsis haenkeana* IUCN, 2016b).

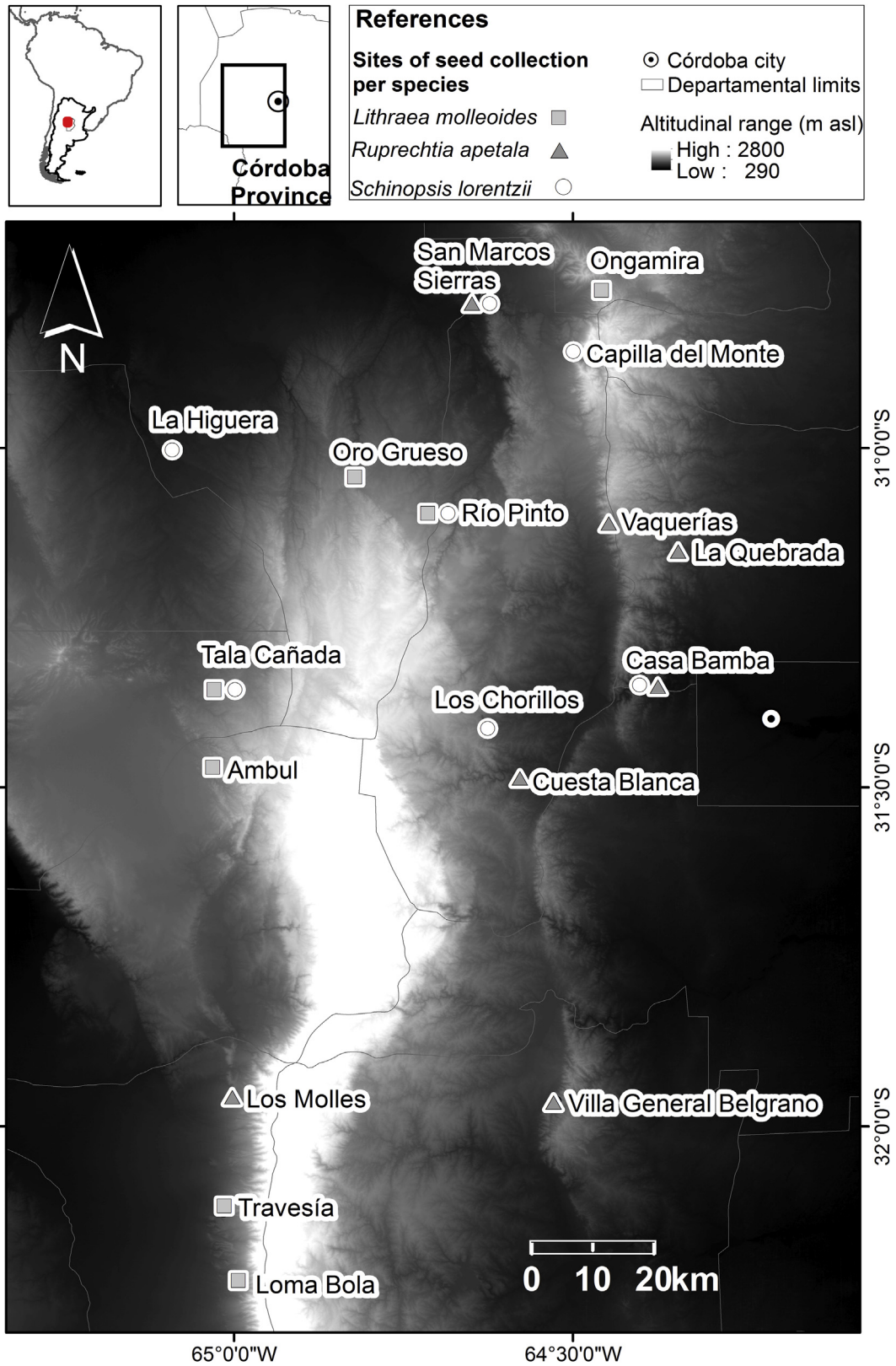
### 2.3. Seed material

From March to October 2008, we collected seeds of each species from seven sites in the mountainous region of Córdoba province, central Argentina (Fig. 1, see Appendix A for coordinates). At each site, we collected more than 800 mature seeds per tree from a sample of five trees in forest patches and five trees in adjacent shrub-grass patches. To maintain independence of samples, all selected parent trees were at a minimum distance of 100 m from the closest sampled tree of the same species. We collected seeds from forest and shrub-grass patches at the same time for each species and site. Collection dates only differed among species due to differences in the timing of fruit maturity. We defined a forest patch as a matrix dominated by woody vegetation taller than 2.5 m and shrub-grass patches as a matrix dominated by grasslands intermingled with sparse woody plants lower than 2.5 m in height. To characterize the vegetation structure of the patches, we estimated (1) height of woody plants and proportion (in %) of (2) woody plants, (3) grassland, (4) rocks and (5) anthropized cover in a 0.78-ha area around each parent tree (plots of 100 m diameter) using Google Earth satellite images. In total, we characterized 105 forest patches and 105 shrub-grass patches for the three species. Some patches were not characterized because Google Earth satellite images with good resolution were not available. Anthropized cover included buildings, roads, gardens and swimming pools.

For each parent tree, we measured (1) height and (2) proportion of aboveground rocks under the crown of each parent tree because rocks may protect trees from fires. We also recorded (3) local slope inclination and (4) slope aspect with a clinometer and compass (RECTA SA, CH-2501). The collected seeds were dried at ambient temperature during two to three days and stored in paper bags at ambient temperature and humidity until assays were performed. Seeds were stored for 1–7 months, depending on the date of collection of each species.

### 2.4. Seed mass and germination experiment

We determined seed mass by weighing three samples of 20 seeds per tree (3 × 20 seeds × 70 trees × 3 species) 1–15 days before initiating germination tests. In the laboratory, we determined germination capacity per parent tree in three Petri dishes/pots of 20 seeds each (3 Petri dishes/pots × 20 seeds × 70 trees × 3 species). For *Ruprechtia* and *Schinopsis* germination, we placed seeds on filter paper in Petri dishes of 5 cm and 10 cm of diameter, respectively. For *Lithraea*, we treated seeds with 10% NaClO for 7 min and then washed the seeds with running water. During this process, we partially removed the exocarp. Then, we used plastic pots of 7 cm of diameter and 5 cm in depth containing sterilized sand as substrate because previous *Lithraea* germination trials in



**Fig. 1.** Elevational map of the study area in the mountains of central Argentina. The sites of seed collection of the three different species are indicated with different symbols followed by the locality. The small maps show the study area within South America, Argentina, and the province of Córdoba (asl = above sea level).

Petri dishes became highly contaminated by fungi. For the three species, we moistened the seeds with distilled water and kept them in a germination chamber at 15–25 °C in a 12 h light: 12 h dark

cycle. We counted germinated seeds once a week until no more seeds germinated and re-moistened the dishes as necessary. For *Lithraea*, we applied a fungicide (Benomil 0.05%) once a week.

## 2.5. Greenhouse experiment

In December 2008, we sowed 700 seeds per tree (to ensure the production of a sufficient number of seedlings for further experiments) in plastic pots of 10 cm depth in a greenhouse. We transplanted seedlings with more than two true leaves to black polyethylene tubes of 5–8 cm in diameter and 20–30 cm in height, using local soil (without sterilizing). We assessed seedling growth of a sample of four seedlings per tree by measuring seedling height after one year. Progeny from 29 of the 70 *Schinopsis* trees were excluded because they did not produce seedlings. We monitored a total of 724 seedlings belonging to 70, 70 and 41 trees of *Ruprechtia*, *Lithraea* and *Schinopsis*, respectively.

## 2.6. Common garden field experiment

In November and December 2010, we established a common garden experiment in a 9-ha enclosure in Cuesta Blanca (31°30'6.53" S, 64°35'24.98" W, at 830 m asl) affected by a wildfire in July 2009. At the moment of planting, vegetation had already covered most of the exposed soil (see Torres et al., 2014 for description in a similar site). We planted 10 to 13 saplings per parent tree, totaling 1675 saplings belonging to 70, 68 and 27 parent trees of *Ruprechtia*, *Lithraea* and *Schinopsis*, respectively. Missing parent trees are due to absence of sapling production from trees that had low or zero viable seeds. Common garden saplings production and greenhouse seedling production were conducted simultaneously. Planting sites had an irregular distribution pattern, with individual saplings separated by at least 2 m. Height at planting was  $16.4 \pm 0.2$ ,  $15.6 \pm 0.2$  and  $15.4 \pm 0.4$  for *Ruprechtia*, *Lithraea* and *Schinopsis*, respectively. We recorded survival and growth in November and December 2011, one year after planting.

## 2.7. Statistical analysis

To compare the progeny performance, we used Linear Mixed Models for each species separately. As response variables we used the mean per tree of (1) seed mass ( $\text{mg}\cdot\text{seed}^{-1}$ ), (2) seed germination evaluated in the laboratory (%), (3) seedling growth in the greenhouse ( $\text{cm}\cdot\text{yr}^{-1}$ ), (4) sapling growth in the field ( $\text{cm}\cdot\text{yr}^{-1}$ ), and (5) sapling survival in the field (%). The predictor variables included vegetation structure (two levels: 1. forest patch and 2. shrub-grass patch) as the fixed factor and site (with seven levels, corresponding to the seven sites of seed collection) as the random factor. When we did not find an effect of vegetation structure on progeny traits, we explored to what extent the height of the parent tree and the rockiness of the microsite (proportion of aboveground rocks under the crown) explained the variance. We then ran the analysis using the same response variables described above, as well as the height of parent tree and the proportion of above ground rocks under the crown as covariables and the site of seed collection as a random factor.

To characterize the forest and shrub-grass patches, we provided mean and SE values for vegetation structure, soil cover, slope and slope aspect. The latter variable was used to calculate two variables: the relative North–South and the relative East–West component of the slope, by multiplying slope (%) by the cosine (for North–South) or sine (for East–West) of aspect. These variables range from highly positive values (North or West aspect with steep slopes) to highly negative values (South or East aspect with steep slopes). We compared patch type characteristics using Wilcoxon test. In addition, we provided mean and SE values of the five response variables related to progeny performance for each species. We compared species using ANOVA and used Bonferroni test for *post-hoc* comparisons. Three statistical tests did not comply with the assumption

of a normal distribution of residuals (germination and survival of *Ruprechtia*, germination of *Lithraea*), but did comply with the assumptions using an assumption of a Poisson distribution, providing similar non-significant p values to those obtained when using an assumption of a normal distribution (see results). As linear models are robust to the normal distribution assumption when samples sizes are large, as is our case, for simplicity and easier comparability, we preferred to report all statistical analyses assuming a normal distribution. For all analyses, we used Infostat statistical package (Di Rienzo et al., 2013).

## 3. Results

### 3.1. Effects of vegetation patch structure on progeny performance

For all species, seed mass did not differ between seeds from patches with different vegetation structure (Table 1). Germination of seeds collected from forest and shrub-grass patches did not differ for *Lithraea* and *Schinopsis*, whereas for *Ruprechtia*, we found a marginally significant difference, with germination being higher in seeds from parent trees in forest patches than from shrub-grass patches ( $p = 0.06$ ; Table 1). Seedling growth under greenhouse conditions and survival and growth of planted saplings in the field did not differ between seeds collected from forest and shrub-grass patches for any of the study species (Table 1).

The woody vegetation surrounding the study seeder trees in forest patches was twice as high as in shrub-grass patches. Woody species cover was slightly greater in forest patches than in shrub-grass patches, whereas grassland and anthropogenic covers were slightly smaller. Rock proportion, slope inclination and slope aspect did not differ between vegetation patch types (Table 2).

For *Ruprechtia*, we found variations in seedling growth in the greenhouse among sites of seed collection ( $p = 0.01$ ). For *Schinopsis*, we found variations in germination ( $p < 0.001$ ) and survival of planted saplings ( $p = 0.03$ ) among sites of seed collection (Appendix B).

Most progeny traits differed significantly among the study species (Table 3). Seed mass was low for *Ruprechtia*, intermediate for *Lithraea* and high for *Schinopsis*, whereas germination followed an opposite pattern (seed germination: ANOVA  $n = 200$ ,  $\chi^2 = 310.1$ ,  $p < 0.001$ ; Table 3). One-year mean seedling growth under greenhouse conditions were higher for *Ruprechtia* and *Lithraea* than for *Schinopsis* (GLM  $n = 181$ ,  $\chi^2 = 26.6$ ,  $p < 0.001$ ; Table 3). One-year mean survival of planted *Ruprechtia* saplings was higher than that of *Lithraea* saplings and had no differences between *Ruprechtia* and *Schinopsis* and between *Lithraea* and *Schinopsis* (GLM  $n = 165$ ,  $\chi^2 = 9.7$ ,  $p = 0.007$ ; Table 3). One-year mean growth of planted saplings was higher for *Ruprechtia* than for *Lithraea* and *Schinopsis*, and had no significant differences between the latter two species (GLM  $n = 165$ ,  $\chi^2 = 108.2$ ,  $p < 0.001$ ; Table 3).

Seed mass of all species was not correlated with germination or other progeny traits (Appendix C). *Ruprechtia* seedling growth in greenhouse was positively and significantly correlated with planted sapling survival (Pearson coefficient = 0.2,  $p = 0.05$ ). Likewise, seedling growth of *Schinopsis* in greenhouse was positively and significantly correlated with germination percentage (Pearson coefficient = 0.4,  $p = 0.02$ ). The height of the parent tree and the rockiness of the microsite did not affect the progeny traits of any of the study species (Appendix D).

## 4. Discussion

Our results show that changes in vegetation structure, which in our study context are mainly induced by human activities, such as fires and livestock, had little or no effects on the studied progeny traits of remnant trees. To our knowledge, few studies have focused

**Table 1**

Progeny traits from trees of the three species and from seven sites in the different vegetation patch types of the Chaco Serrano forest in central Argentina (Mean  $\pm$  SE). A marginally significant p value is shown in bold.

Progeny traits	Vegetation patch type				F	p
	n	Forest patches	Shrub-grass patches			
<i>Ruprechtia</i>						
Seed mass (mg. seed <sup>-1</sup> )	70	26.63 $\pm$ 0.90	25.86 $\pm$ 0.94		0.38	0.54
Germination (%)	70	86.16 $\pm$ 1.72	81.20 $\pm$ 1.93		3.75	<b>0.06</b>
Seedling growth in greenhouse (cm. year <sup>-1</sup> )	70	20.92 $\pm$ 1.19	20.91 $\pm$ 1.10		0.00	0.99
Survival of planted saplings (%)	70	89.97 $\pm$ 1.58	92.10 $\pm$ 1.86		0.72	0.40
Growth of planted saplings (cm. year <sup>-1</sup> )	70	8.04 $\pm$ 0.45	8.73 $\pm$ 0.50		0.99	0.32
<i>Lithraea</i>						
Seed mass (mg. seed <sup>-1</sup> )	70	82.54 $\pm$ 2.52	82.30 $\pm$ 1.78		0.01	0.94
Germination (%)	70	41.05 $\pm$ 2.55	41.98 $\pm$ 2.72		0.06	0.80
Seedling growth in greenhouse (cm)	70	18.53 $\pm$ 0.72	19.05 $\pm$ 0.76		0.26	0.61
Survival of planted saplings (%)	68	86.20 $\pm$ 2.04	85.08 $\pm$ 1.81		0.18	0.67
Growth of planted saplings (cm. year <sup>-1</sup> )	68	3.75 $\pm$ 0.43	3.34 $\pm$ 0.40		0.60	0.44
<i>Schinopsis</i>						
Seed mass (mg. seed <sup>-1</sup> )	70	169.26 $\pm$ 4.97	164.22 $\pm$ 4.17		0.65	0.43
Germination (%)	70	1.39 $\pm$ 3.03	1.39 $\pm$ 2.52		0.22	0.64
Seedling growth in greenhouse (cm)	41	14.85 $\pm$ 1.03	15.72 $\pm$ 0.89		0.22	0.64
Survival of planted saplings (%)	27	85.80 $\pm$ 2.96	86.49 $\pm$ 3.08		0.20	0.66
Growth of planted saplings (cm. year <sup>-1</sup> )	27	3.56 $\pm$ 0.49	3.23 $\pm$ 0.59		0.001	0.98

**Table 2**

Characteristics of 105 forest patches and 105 shrub-grass patches (Mean  $\pm$  SE) of 0.78-ha size around the studied parent trees of the three species. Significant p values are in bold.

Variable	Forest patches n = 105	Shrub-grass patches n = 105	Wilcoxon test	p
Woody plant height (cm)	577.16 $\pm$ 20.83	220.88 $\pm$ 9.40	3403.5	< <b>0.001</b>
Woody plant cover (%)	75.6 $\pm$ 2.1	67.5 $\pm$ 2.1	12434.0	<b>0.002</b>
Grassland cover (%)	17.4 $\pm$ 1.8	22.9 $\pm$ 1.8	9756.5	<b>0.003</b>
Rock cover (%)	2.1 $\pm$ 0.4	2.2 $\pm$ 0.4	10971.0	0.8
Anthropogenic cover (%)	4.1 $\pm$ 0.7	7.1 $\pm$ 1.0	10102.5	<b>0.02</b>
North-south component of the slope aspect	0.1 $\pm$ 0.1	0.2 $\pm$ 0.1	10790.0	0.5
East-west component of the slope aspect	-0.1 $\pm$ 0.1	-0.1 $\pm$ 0.1	11018.0	0.9
Slope inclination (°)	25.0 $\pm$ 1.5	24.1 $\pm$ 2.1	11602.5	0.2

**Table 3**

Progeny traits from trees of the three species and from seven sites of the Chaco Serrano forest in central Argentina (Mean  $\pm$  SE). The numbers between parentheses indicate the number of replicates. Different letters show significant differences at  $p \leq 0.05$  (Bonferroni post-hoc test). Significant p-values are in bold. Germination was checked for 44 days in *Ruprechtia* and *Schinopsis*, and for 56 days in *Lithraea*.

Progeny traits	<i>Ruprechtia</i>	<i>Lithraea</i>	<i>Schinopsis</i>	F	p
Seed mass (mg. seed <sup>-1</sup> )	26.3 $\pm$ 0.6 (70) a	82.4 $\pm$ 1.5 (70) b	166.7 $\pm$ 3.2 (70) c	1135.5	< <b>0.001</b>
Germination (%)	83.7 $\pm$ 1.3 (70) a	41.5 $\pm$ 1.9 (70) b	13.9 $\pm$ 1.7 (70) c	412.9	< <b>0.001</b>
Seedling growth in greenhouse (cm. year <sup>-1</sup> )	20.9 $\pm$ 0.8 (70) a	18.8 $\pm$ 0.5 (70) a	15.3 $\pm$ 0.7 (41) b	14.1	< <b>0.001</b>
Survival of planted saplings (%)	91.0 $\pm$ 1.2 (70) a	85.6 $\pm$ 1.4 (68) b	86.2 $\pm$ 2.1 (27) ab	4.9	<b>0.009</b>
Growth of planted saplings (cm. year <sup>-1</sup> )	8.4 $\pm$ 0.3 (70) a	3.5 $\pm$ 0.3 (68) b	3.4 $\pm$ 0.4 (27) b	75.1	< <b>0.001</b>

on how progeny performance is affected by the effects of degradation due to changes in the surrounding environment (i.e. Renison et al., 2004, 2005; Jiao et al., 2009).

We infer that forest degradation had no effects on the studied progeny traits of remnant trees, partly due to the overall high resistance of Chaco Serrano trees. Accordingly, the few studies performed in our region in the context of forest fragmentation due to agriculture also did not find any effects on progeny traits for trees, with fragmentation effects detected only for shrubs and forbs (Ashworth and Martí, 2011; Ashworth et al., 2015). The reasons for the general resistance of the Chaco Serrano tree species to disturbances could be related to the long evolutionary history of fire and herbivory in the region (Gurvich et al., 2005; Cingolani et al., 2014), with trees having adaptations to tolerate these disturbances, such as a high proportion of storage organs in the roots, high resprouting capacity and several mechanisms to resist drought (Lauenstein et al., 2013; Torres et al., 2014). Moreover, worldwide studies

showing differences due to variation in environmental factors among seed collection sites have focused on herbs, with few studies having considered trees (Baskin and Baskin, 2014). Variation in environmental characteristics, such as water and nutrient availability, soil erosion and light incidence, may have lower effects on trees than on herbs, since the larger size of trees facilitates access to these resources, therefore making them more tolerant than herbs.

The lack of forest degradation effects on the studied progeny traits could also partly be due to the location of remnant trees, since they are situated in microsites protected from disturbances such as fires, domestic herbivores and soil erosion (Alinari et al., 2015; Renison et al., 2015). Furthermore, isolated trees in shrub-grass patches could be subject to lower competition than trees in forest patches (Fraver et al., 2014). A combination of better microsites and lower competition could be offsetting a generalized degradation in soils, and higher exposure to sun and winds often found in degraded sites. Another explanation could involve a mechanism of

higher resource allocation to sexual reproduction with increasing environmental stress (Agrawal, 2000). This higher resource allocation to sexual reproduction could be affecting the persistence of adult trees, which we did not evaluate.

We found differences among seed collection sites independently of forest degradation only for three traits and two species; these differences could be due to local environments or adaptations (Borgman et al., 2014). This result is in contrast to findings of other studies in our region reporting differences in seed germination among seed collection sites (Renison et al., 2005; Valfré-Giordano et al., 2012) as well as to findings in other regions (i.e. *Juniperus procera*, Mamo et al., 2006; *Prosopis flexuosa*, Mantovan, 2002; *Populus trichocarpa*, McKown et al., 2014). Possibly, our study sites were geographically too close to show marked differences between sites.

#### 4.1. Implications for forest management and restoration

We conclude that for the three chosen study species, remnant

trees are valuable resources for forest restoration, with most or all of their reproductive potential being still intact. This has important implications for passive restoration. Given that there are areas available for regeneration and enough adult trees left in the area to produce a continuous seed rain, presumably tree populations may recover without interventions. Furthermore, seriously degraded areas that need seed and seedling introduction could be restored using local seed material, since seed and seedling performance appears to be well preserved.

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#### Appendix A. Sites of seed collection of each species

Species	Site	Coordinantes	Altitude (m asl)
<i>R. apetala</i>	San Marcos Sierras	S 30° 47'; W 64° 37'	700
	Casa Bamba	S 31° 20'; W 64° 24'	600
	Vaquerías	S 31° 06'; W 64° 26'	1050
	Los Molles	S 31° 57'; W 64° 59'	1000
	V Gral Belgrano	S 31° 57'; W 64° 31'	1000
	La Quebrada	S 31° 09'; W 64° 20'	850
	Cuesta Blanca	S 31° 29'; W 64° 34'	850
<i>L. molleoides</i>	Tala Cañada	S 31° 35'; W 65° 02'	1100
	Ongamira	S 30° 45'; W 64° 28'	1100
	Travesía	S 32° 07'; W 65° 0'	950
	Río Pinto	S 31° 05'; W 64° 40'	1050
	Oro Grueso	S 31° 2'; W 64° 49'	1050
	Ambul	S 31° 28'; W 65° 01'	1200
	Las Chacras	S 32° 14'; W 64° 59'	1050
<i>S. marginata</i>	San Marcos Sierras	S 30° 46'; W 64° 37'	700
	Capilla del Monte	S 30° 51'; W 64° 29'	1050
	La Higuera	S 30° 59'; W 65° 04'	650
	Río Pinto	S 31° 05'; W 64° 40'	1050
	Los Chorrillos	S 31° 23'; W 64° 38'	950
	Tala Cañada	S 31° 34'; W 65° 00'	1200
	Casa Bamba	S 31° 20'; W 64° 22'	650

#### Appendix B. Linear mixed models performed for each species as response variable using patch type as fixed factor and the site of seed collection as random factor. Sample size (n), F and p are indicated. p-values are in italic. Significant p-values are in bold.

Predictor variables	Seed mass (mg. seed <sup>-1</sup> )	Germination (%)	Seedling growth in greenhouse (cm. yr <sup>-1</sup> )	Survival of planted saplings (%)	Growth of planted seedlings (cm. yr <sup>-1</sup> )
<i>Ruprechtia</i>	n = 70	n = 70	n = 70	n = 70	n = 70
	F(p)	F(p)	F(p)	F(p)	F(p)
Vegetation structure	0.38 (0.54)	3.75 (0.06)	0.00 (0.99)	0.72 (0.40)	0.99 (0.32)
Site	1.84 (0.11)	1.25 (0.30)	2.95 ( <b>0.01</b> )	0.23 (0.97)	0.45 (0.84)
<i>Lithraea</i>	n = 70	n = 70	n = 70	n = 68	n = 68
	F(p)	F(p)	F(p)	F(p)	F(p)
Vegetation structure	0.01 (0.94)	0.06 (0.80)	0.26 (0.61)	0.18 (0.67)	0.60 (0.44)
Site	0.92 (0.49)	1.05 (0.40)	1.45 (0.21)	0.42 (0.86)	1.30 (0.27)
<i>Schinopsis</i>	n = 70	n = 70	n = 41	n = 27	n = 27
	F(p)	F(p)	F(p)	F(p)	F(p)
Vegetation structure	0.65 (0.43)	0.22 (0.64)	0.22 (0.64)	0.20 (0.66)	0.001 (0.98)
Site	1.76 (0.12)	14.32 (< <b>0.001</b> )	0.69 (0.64)	3.03 ( <b>0.03</b> )	2.31 (0.08)

**Appendix C. Pearson's correlation coefficients for seed mass, germination, survival and growth of the three woody species of the Chaco Serrano forest. *p*-values are in italic. Significant *p*-values are in bold.**

	Pearson coefficient ( <i>p</i> values)			
	Germination (%)	Seedling growth in greenhouse (cm. yr <sup>-1</sup> )	Survival of planted saplings (%)	Growth of planted saplings (cm. yr <sup>-1</sup> )
<i>Ruprechtia</i>				
Seed mass (mg. seed <sup>-1</sup> )	0.2 ( <i>p</i> = 0.09)	-0.2 ( <i>p</i> = 0.1)	0.002 ( <i>p</i> = 0.9)	0.1 ( <i>p</i> = 0.4)
Germination (%)		-0.1 ( <i>p</i> = 0.2)	-0.01 ( <i>p</i> = 0.9)	-0.2 ( <i>p</i> = 0.1)
Seedling growth in greenhouse (cm. yr <sup>-1</sup> )			0.2 ( <b><i>p</i> = 0.05</b> )	0.2 ( <i>p</i> = 0.1)
Survival of planted saplings (%)				0.1 ( <i>p</i> = 0.6)
<i>Lithraea</i>				
Seed mass (mg. seed <sup>-1</sup> )	-0.03 ( <i>p</i> = 0.8)	0.1 ( <i>p</i> = 0.6)	0.1 ( <i>p</i> = 0.4)	-0.1 ( <i>p</i> = 0.5)
Germination (%)		0.2 ( <i>p</i> = 0.1)	0.003 ( <i>p</i> = 0.9)	-0.03 ( <i>p</i> = 0.8)
Seedling growth in greenhouse (cm. yr <sup>-1</sup> )			0.2 ( <i>p</i> = 0.1)	0.03 ( <i>p</i> = 0.8)
Survival of planted saplings (%)				-0.1 ( <i>p</i> = 0.4)
<i>Schinopsis</i>				
Seed mass (mg. seed <sup>-1</sup> )	0.2 ( <i>p</i> = 0.2)	-0.2 ( <i>p</i> = 0.3)	0.2 ( <i>p</i> = 0.4)	-0.2 ( <i>p</i> = 0.3)
Germination (%)		0.4 ( <b><i>p</i> = 0.02</b> )	-0.1 ( <i>p</i> = 0.5)	-0.1 ( <i>p</i> = 0.6)
Seedlings growth in greenhouse (cm. yr <sup>-1</sup> )			0.1 ( <i>p</i> = 0.5)	-0.03 ( <i>p</i> = 0.9)
Survival of planted saplings (%)				0.4 ( <i>p</i> = 0.06)

**Appendix D. Linear mixed models performed for each species as response variable using as predictor the continuous variables height of parental tree and rockiness of the microsite (%). The site was included in the model as a random factor. Sample size (*n*), *F* and *p* are indicated. *p*-values are in italic. Significant *p*-values are in bold.**

Predictor variables	Seed mass (mg. seed <sup>-1</sup> )	Germination (%)	Seedling growth in greenhouse (cm. yr <sup>-1</sup> )	Survival of planted saplings (%)	Growth of planted saplings (cm. yr <sup>-1</sup> )
<i>Ruprechtia</i>					
	<i>n</i> = 70	<i>n</i> = 70	<i>n</i> = 70	<i>n</i> = 70	<i>n</i> = 70
	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )
Height of parental tree	0.33 (0.57)	2.96 (0.91)	0.22 (0.64)	0.75 (0.39)	0.01 (0.93)
Rockiness (%)	0.81 (0.37)	1.09 (0.30)	0.95 (0.33)	1.92 (0.17)	0.01 (0.98)
Site	1.64 (0.15)	1.51 (0.19)	3.15 ( <b>0.01</b> )	0.53 (0.79)	0.37 (0.90)
<i>Lithraea</i>					
	<i>n</i> = 70	<i>n</i> = 70	<i>n</i> = 70	<i>n</i> = 68	<i>n</i> = 68
	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )
Height of parental tree	0.03 (0.87)	1.26 (0.27)	0.32 (0.57)	0.08 (0.77)	1.98 (0.17)
Rockiness (%)	0.23 (0.64)	0.05 (0.83)	1.05 (0.31)	2.74 (0.10)	1.41 (0.24)
Site	0.86 (0.53)	1.03 (0.42)	1.56 (0.18)	0.44 (0.85)	1.24 (0.30)
<i>Schinopsis</i>					
	<i>n</i> = 70	<i>n</i> = 70	<i>n</i> = 41	<i>n</i> = 27	<i>n</i> = 27
	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )	<i>F</i> ( <i>p</i> )
Height of parental tree	1.48 (0.23)	0.03 (0.86)	1.13 (0.30)	0.03 (0.86)	0.24 (0.63)
Rockiness (%)	1.80 (0.18)	0.00 (0.96)	0.16 (0.69)	1.06 (0.32)	0.36 (0.55)
Site	1.21 (0.32)	7.85 (< <b>0.001</b> )	0.41 (0.84)	2.16 (0.10)	1.53 (0.23)

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