Forest Fragmentation and Seed Germination of Native Species from the Chaco Serrano Forest

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ABSTRACT

Habitat fragmentation is a widespread phenomenon that alters pollination and plant reproductive processes. These effects have demographic and genetic implications that determine offspring fitness and the long-term viability of plant populations in fragmented systems. We evaluated fragmentation effects on early plant offspring fitness traits, individual seed mass, and percentage of seed germination in five native plant species (*Acacia caven, Celtis ehrenbergiana, Croton lachnostachyus, Rivina humilis, Schinus fasciculatus*) from the Chaco Serrano forest, a subtropical highly fragmented ecosystem. We found evidence of strong negative fragmentation effects on germination in the shrub *C. lachnostachyus* and the perennial herb *R. humilis*, after 30 d of controlled tests. No fragmentation effects were found in the studied traits on the remaining three tree species. We found significant maternal effects in offspring fitness traits in all five species. We discuss the relative magnitude of maternal vs. fragmentation effects taking into account both plant species' lifespan and the time elapsed in fragmentation conditions. We emphasize the need to increase the study of early and late plant offspring fitness produced in fragmented habitats coupled with analyses of genetic parameters and the pollination process in order to evaluate the conservation value of remnant forest fragments.

Key words: Argentina; habitat fragmentation; maternal effect; plant lifespan; plant offspring performance; plant progeny fitness; seed size.

HABITAT FRAGMENTATION IS A WIDESPREAD PHENOMENON ACROSS TERRESTRIAL ECOSYSTEMS and the main current driver of biodiversity loss (Sala *et al*. 2000). The most immediate consequences of fragmentation involve the loss of habitat and the formation of remnant fragments embedded in an anthropogenic matrix. Forest fragmentation often implies a reduction of population sizes and an increase in the degree of isolation among remaining populations (McGarigal & Cushman 2002, Fahrig 2003). These changes at the landscape level affect environmental abiotic conditions such as air and soil temperature, soil ph, relative humidity and light incidence (Didham & Lawton 1999, Mix *et al*. 2006), as well as biotic factors such as mutualistic and antagonistic plant–animal interactions (*e.g.*, Aizen & Feinsinger 1994, Tscharntke & Brandl 2004, Valladares *et al*. 2006). Therefore, remnant plant populations surviving in habitat fragments are confronted with a highly modified biotic and abiotic scenario with novel ecological boundaries (Ewers & Didham 2006). Such rapidly modified environments are unlikely to provide the conditions for the long-term persistence of many native plant species.

Much research has been conducted globally on how habitat fragmentation affects either plant sexual reproduction or genetic diversity, and the overall response patterns obtained through quantitative reviews reveal strong and negative effects of fragmentation on these parameters (Aguilar *et al*. 2006, 2008). Currently we know that plants in fragmented habitats produce, on average, significantly fewer offspring (*i.e.*, reduced fruit and seed set) than in continuous

forests (Aguilar *et al*. 2006). Much less is known about the performance of offspring produced in fragmented habitats. The magnitude of negative fragmentation effects on plant reproduction may be underestimated if habitat fragmentation also negatively affects aspects of offspring performance, such as seed mass, germination capacity, and seedling vigor (Benítez-Malvido 1998, Bruna 2003, Seltmann *et al*. 2007, but see Cascante *et al*. 2002, Mathiasen *et al*. 2007, Kolb 2008). Thus, it is important to assess variability in such offspring traits in fragmented habitats, as they can affect plant population viability of future generations (Menges 1991, Ellstrand & Elam 1993, Oostermeijer *et al*. 1995, Young *et al*. 1996; reviewed by Keller & Waller 2002).

Recently, Aguilar *et al*. (2008) found that the overall mean outcrossing rate of adult plants growing in fragmented habitats significantly decreased while the overall mean inbreeding coefficient of offspring significantly increased. These results suggest changes in the mating patterns of fragmented plant populations toward increased selfing and/or mating among relatives (Aguilar *et al*. 2008). Offspring with higher inbreeding coefficients might have higher chances of expressing negative effects of inbreeding (*i.e.*, inbreeding depression), which may negatively affect one or some of their fitness parameters. Moreover, early offspring fitness traits in particular (*i.e.*, seed mass or seed germination) might also be negatively affected as a consequence of adverse abiotic conditions that often prevail in forest fragments (*e.g.*, lower relative humidity, higher temperatures, lower nutrient cycling rates; Didham 1998, Didham & Lawton 1999, Laurance *et al*. 2002, Vergeer *et al*. 2003). Such conditions may result in fewer resources available for maternal plants to invest in offspring provisioning (Stephenson 1992).

Finally, biotic conditions such as lower availability of conspecific mates, and/or altered mutualistic and antagonistic animal–plant interactions in forest fragments may also affect offspring fitness (*e.g.*, Glémin *et al.* 2008, Aguilar *et al.* 2009).

Most studies to date have analyzed how population size affects plant offspring fitness (*e.g.*, Reed 2005 and citations therein; Leimu *et al.* 2006, Le Cadre *et al.* 2008). Nevertheless, habitat fragmentation is a complex, widespread, and ubiquitous process involving several co-occurring factors, where population size is only one factor. Other factors, such as population isolation, matrix characteristics, or nonrandom species loss are also inherent to the fragmentation process and can affect plant offspring fitness by yielding changes in mating patterns (*i.e.*, pollen flow) among populations (Steffan-Dewenter & Tscharntke 2000, McGarigal & Cushman 2002, Fahrig 2003, Larsen *et al.* 2005, Laurance 2008). In fragmented systems, the pervasive structural pattern of current landscapes, remaining habitat fragments are the common available sources of plant offspring production to be dispersed throughout the landscape. It seems crucial to assess, therefore, whether offspring fitness is negatively affected in real fragmented habitats.

The original area of the Chaco Serrano forest has suffered a dramatic decrease as a result of intensive agricultural activities over the last 30 yr (Zak *et al.* 2004). Within the province of Córdoba, only 6 percent of the original forest cover remains mainly as forest fragments (Zak *et al.* 2004) immersed in intensively managed agricultural matrices. As a consequence of habitat fragmentation, the Chaco Serrano forest is experiencing profound ecological modifications, which can severely alter ecosystem functioning. This fragmented system has suffered loss of native species, exotic species invasions, and changes in plant–animal interaction dynamics (Aguilar & Galetto 2004, Dardanelli *et al.* 2006, Ferreras *et al.* 2008, Cagnolo *et al.* 2009).

Here, we examined whether the high levels of fragmentation in the Chaco Serrano forest affect early offspring fitness of native plant species originated in forest fragments of different sizes. Our predictions are based on the previously stated evidence of increased inbreeding coefficients in plant offspring (Aguilar *et al.* 2008) and of more adverse abiotic conditions in fragments than in continuous forest (Didham 1998, Didham & Lawton 1999, Vergeer *et al.* 2003). Thus, we expected to find lower mean seed mass and seed germination percentage in small forest fragments compared with continuous forest.

METHODS

STUDY AREA.—The Chaco Serrano is a subtropical dry forest of a high floristic diversity (Luti 1982). This forest is characterized by a low and open tree stratum (8–15 m high), a shrub (1–3 m high), and a herbaceous stratum and many epiphytes and vines species (Cabido *et al.* 1991). In Argentina, the Chaco Serrano forest covers an area between 29° and 33°30′ S ranging in elevation from 400 to 1300 m asl. Rainfall (750 mm annual) is concentrated in the warm season (October–April), and average maximum and minimum temperatures range between 26°C and $-10°$C, respectively (Luti *et al.* 1979, Moglia & Giménez 1998). These forests grow on

hillslopes, thus providing key ecosystem services such as the protection of river basins and soil erosion. Moreover, the Chaco Serrano forest is also interesting from a scientific, touristic, and conservational point of view (Luti *et al.* 1979, Gavier & Bucher 2004, Zak *et al.* 2004).

Nine study sites were selected using Landsat ETM satellite images (Landsat ETM, CONAE, Córdoba, Argentina). Three of the sites are small size fragments (1–3 ha, S1–S3 in Fig. 1), three are medium size fragments (10–29 ha, S4–S6 in Fig. 1), and three are continuous forests (> 500 ha, S7–S9 in Fig. 1). These forest fragments were created in the 1970s, as a result of agricultural land clearing. Currently, the study sites are immersed in intensively managed matrices, dominated by wheat in winter and glyphosate-resistant soybean or maize in summer. Pesticide and herbicide applications are frequent practices in these matrices. All the sites are comparable in altitudinal position (500–800 m asl), degree of isolation (75–200 m to the nearest higher forest fragment), and belong to the same biogeographic region (Chaco Serrano forest), sharing similar climatic conditions (Fig. 1). Thus, we are mainly evaluating decreases in forest fragment size, which in this system is not necessarily linked to decreases in population size (Aguilar & Galetto 2004).

PLANT SPECIES.—We selected species that are characteristic of the Chaco Serrano and are relatively well-known biologically and ecologically. Adult reproductive individuals of these species are also commonly found in sufficient numbers in the studied forest fragments. Some important ecological and reproductive traits of the studied species are listed in Table 1. In each study site we marked four to five focal plants (hereafter maternal plants) per species (40–45 plants per species throughout all sites). For each species, maternal plants were similar in size and at least 7 m apart. All fruits collected from maternal plants were taken randomly from three different branches of similar size in January–March 2005. Information on the number of collected fruits and seeds used, per maternal plant, per species is given in Table 2.

MEAN SEED NUMBER PER FRUIT.—In the two species with multiseeded fruits (*Acacia caven* and *Croton lachnostachyus*) we calculated the mean seed number produced per fruit. This enabled us to account for possible trade-offs between seed mass and seed number that may involve differential resource allocation per individual seed, depending on the number of seeds produced. That is, should fragmentation negatively affect the quantity of seeds per fruit, we may expect resources for seed production to be allocated among fewer seeds. As a result, we may find larger seeds in smaller fragments. If this is the case, by accounting for the differences in seed number we can claim that this trade-off explains how fragmentation positively affects seed mass at the expense of seed number. The mean seed number per fruit was obtained by averaging seed number from fruits obtained from each of the three branches per maternal plant ($N = 7$ per branch; 21 per maternal plant; Table 2). In *A. caven* we also quantified aborted seeds per fruit, which ranged from 2.8 ± 1.5 in small fragments to 4 ± 1.6 in medium fragments. Mean aborted seeds per fruit did not significantly differ among fragment sizes ($F_{[2, 80]} = 0.02$; $P = 0.98$), but they did significantly vary among
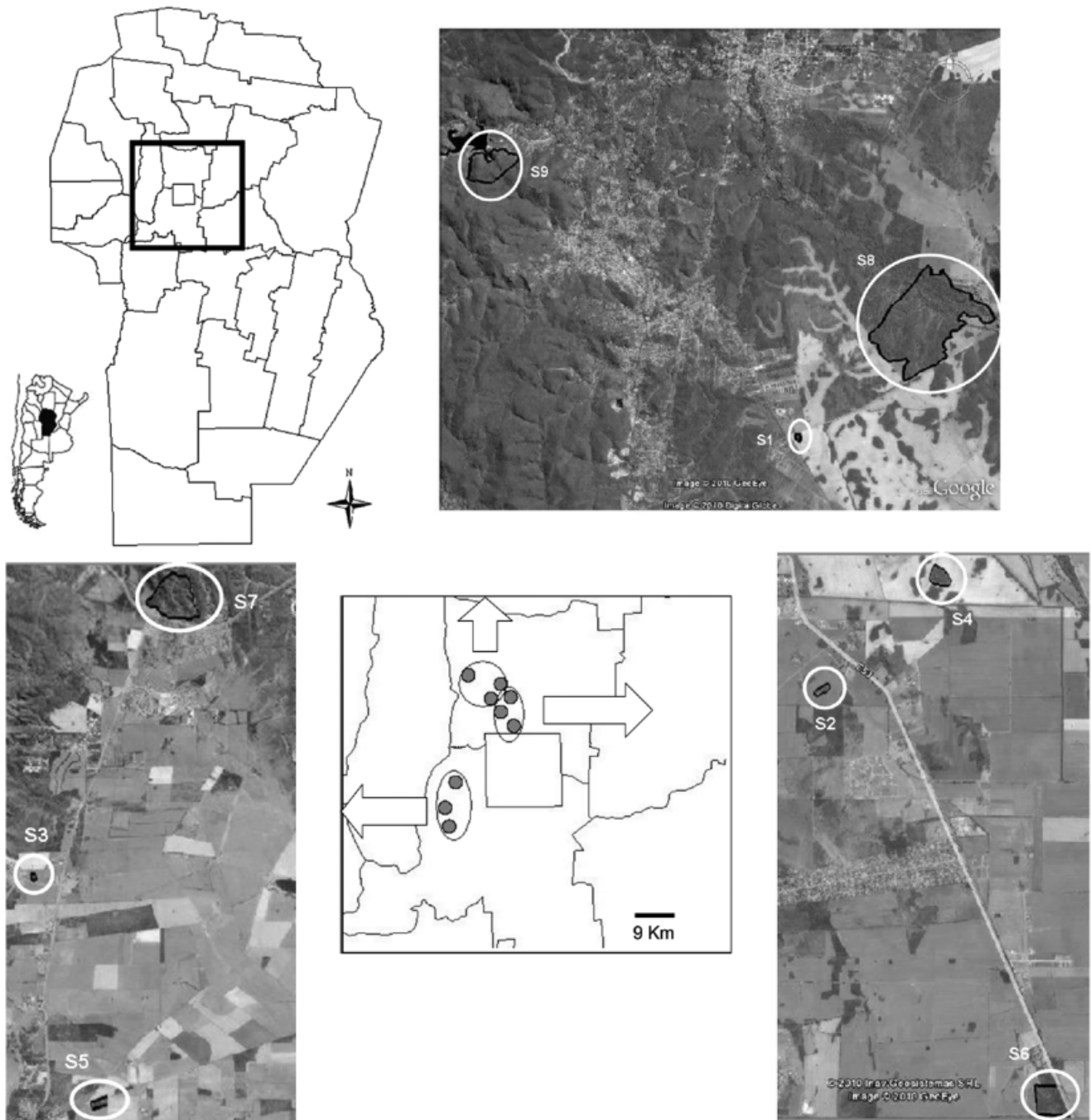
FIGURE 1. Spatial location of the studied sites in the Chaco Serrano forest. Small (S1, S2, S3), medium fragments (S3, S4, S5), and continuous forests (S7, S8, S9). In the Quickbird Google Earth images, more irregular-shaped and darker areas correspond to remaining forests.

maternal plants ($\chi_1^2 = 6.43$; $P = 0.01$). Seeds of *A. caven* also show some levels of predation by bruchids (Di-lorio 2005). These insects only consume the inner content of seeds, leaving the seed coat almost intact, so predated seeds were easily identified for inclusion in seed set calculation per fruit. Predation was low and not significantly different among fragment sizes and maternal plants ($z = 0.35$; $P = 0.73$; $\chi_1^2 = 0.62$; $P = 0.54$, respectively), so this selective pressure was similar for all seeds. This result concurs with current studies on

seed predation of this species along the same fragmentation size gradient (M. Jausoro, pers. comm.). Similar levels of bruchid predation across all sites, and the high number of nonpredated healthy seeds left in each fruit, imply that selected seeds for the germination trials can be taken as a random sample.

OFFSPRING FITNESS TRAITS: SEED GERMINATION AND INDIVIDUAL SEED MASS.—We used 30–60 seeds per maternal plant (depending on the

Table 1. *Life history and ecological traits of five native plant species from the Chaco Serrano forest. A, andromonoecious; H, hermaphrodite; D, doiecious; Dc, diclinous-monoeciuos; SI, self-incompatible; SC, self-compatible.*

Plant species	Life form	Mean height (m)	Ecological status	Sexual system	Compatibility system	Pollination vector
Acacia caven (Fabaceae)	Tree	4	Pioneer[a]	A[b]	SI[b]	Insect[b]
Celtis ehrenbergiana (Celtidaceae)	Tree	8	Shade tolerant[c]	A[d]	SC[d]	Wind[d]
Croton lachnostachyus (Euphorbiaceae)	Shrub	0.80	Shade tolerant[c]	Dc[e]	SC[e]	Insect[e]
Rivina humilis (Phytolaccaceae)	Perennial herb	0.30	Shade tolerant[c]	H[c]	SC[c]	Insect visited[c]
Schinus fasciculatus (Anacardiaceae)	Tree	4	Shade tolerant[c]	D[f]		Insect visited[c]

[a]Peralta *et al.* (1992).
[b]Baranelli *et al.* (1995).
[c]L. Ashworth (pers. obs).
[d]Torretta and Basilio (2009), sub *Celtis tala*.
[e]Freitas *et al.* (2001), sub *Croton sarcopetalus*.
[f]De Dios Muñoz (2000).

species, see Table 2) to conduct the germination trials. For *A. caven*, we randomly selected three nonpredated, nonaborted seeds per fruit from 20 fruits per maternal plant ($N = 60$). Seeds were placed on filter paper in Petri dishes and moistened with distilled water every 5 d. For each maternal plant, seeds were grouped in three different Petri dishes (10–20 seeds each) according to the branches from which fruits were originally obtained (Table 2). Dishes were placed in a chamber at $25 \pm 5°C$ with a 12/12 h daily photoperiod for 30 d. Germination percentage for each maternal plant was registered at the end of the experiment on each Petri dish. In fleshy-fruited species (*Celtis ehrenbergiana*, *Rivina humilis*, and *Schinus fasciculatus*) the pulp of fruits was manually removed before the germination trials and seed mass measurements. Seed mass was measured in a Mettler Toledo PB153 balance (accuracy 2 mg, Ohaus Corporation, Pine Brook, NJ, U.S.A.). For multi-seeded fruit species, we estimated individual seed mass per fruit by weighing all seeds in a fruit and then dividing the total weight by the number of weighed seeds. In *A. caven*, seed mass was obtained by weighing only healthy seeds (nonpredated–nonaborted). For single-seeded fruit species, we weighed together five seeds per collecting branch, and then divided the total weight by five.

Table 2. *Number of fruits collected per maternal plant per species to evaluate seed number per fruit and percentage of seed germination.*

Plant species	Number of fruits collected per branch per maternal plant	Total number of seeds used per maternal plant	Number of seeds per Petri dishes for germination trials
Acacia caven	7	60	20
Celtis ehrenbergiana	10	30	10
Croton lachnostachyus	7	51	17
Rivina humilis	10	30	10
Schinus fasciculatus	10	30	10

DATA ANALYSIS.—Statistical analyses were performed using R environment (R Development Core Team 2009). We used linear mixed effects models (*lme* function of the *nlme* package, Pinheiro *et al.* 2009) to evaluate fragment size effects on mean seed number per fruit and seed mass, and generalized linear mixed effect models (*lmer* function of the *lme4* package, Bates & Maechler 2009) to evaluate seed germination percentage using binomial distribution. The spatial structure of the data was the following: fragment size ($N = 3$) as the fixed main effect, site ($N = 9$) as random effect nested within fragment size, and maternal plant ($N = 40–45$) as random effect nested within site and fragment size. The three categorical levels of fragment size were established by the area of the fragments: small, medium, and continuous forest. The significance of fixed effect was determined with *F*-test in linear mixed models and by Wald-*z* test in generalized linear mixed models. Each random effect was tested by comparing two nested models, one with- and one without the random effect using a χ^2 test. Model parameters were estimated with restricted maximum likelihood methods and Laplace approximation for *lme* and *lmer* models, respectively.

RESULTS

MEAN SEED NUMBER PER FRUIT.—The mean number of seeds per fruit in *A. caven* and *C. lachnostachyus* did not differ significantly among small, medium, and continuous forests (Table 3). Site (random factor) did not have a significant effect on mean number of seeds per fruit in any of the two species ($\chi^2_1 < 3 \times 10^{-8}$; $P > 0.89$). Maternal plant, the other random factor, had a significant effect on mean number of seeds in *A. caven* (Table 3), with 62 percent of the model variance attributable to differences among plants from the same site. Maternal plant did not have any effects on mean seed number in *C. lachnostachyus* (Table 3).

SEED GERMINATION AND SEED MASS.—The percentage of seed germination was significantly affected by fragment size in two of the five studied species (Table 4). In *C. lachnostachyus*, the percentage of

Table 3. *Fragment size effect on mean seed number per fruit in two native plants species from the Chaco Serrano forest. Statistics and* P-*values of maternal plant effect are given in parentheses. Linear mixed models with sites nested within fragment size, and maternal plants within sites and fragment size.*

| Plant species | Mean ± SD | | | Statistical analysis |
	Small	Medium	Continuous	
Acacia caven	27.18 ± 1.45	26.77 ± 3.07	26.85 ± 4.66	$F_{[2, 80]} = 0.07; P = 0.83 (\chi^2_1 = 39.74; P < 0.0001)$
Croton lachnostachyus	2.02 ± 0.02	2.30 ± 0.01	2.64 ± 0.03	$F_{[2, 84]} = 0.90; P = 0.52 (\chi^2_1 = 0.001; P = 0.98)$

seed germination was nearly sixfold lower in small fragments than in continuous forests, whereas in *R. humilis*, seed germination was nearly two times lower in small fragments compared with mid-sized and continuous forests (Table 4). There were no statistically significant effects of fragment size on seed germination in *A. caven*, *C. ehrenbergiana*, and *S. fasciculatus* (Table 4). Site did not have significant effects on seed germination percentage ($\chi^2_1 < 3.37; P > 0.08$), nor on individual mean seed mass ($\chi^2_1 < 3.42; P > 0.08$) in any of the five studied species. An important effect of maternal plant, however, was observed on seed germination (Table 4) and individual seed mass (Table 5) in all five species; with 30–90 percent (depending on the species) of the model variance attributable to differences in germination (Table 4) or seed mass (Table 5) among conspecific maternal plants from the same site.

DISCUSSION

Contrary to our initial hypothesis, and despite previous findings from literature reviews showing that habitat fragmentation reduces offspring production, decreases outcrossing rates and increases inbreeding coefficients in plant offspring, we only found evidence of fragmentation effects on early offspring fitness traits in two of the five studied native plant species from the Chaco Serrano forest.

A more consistent pattern, however, was determined by maternal plant effect, which was considered as a random factor in the models. We observed a significant maternal effect on seed mass and germination percentage in all five species and also for seed number per fruit in *A. caven*. Thus, all species show a high variability in seed mass and germination due mostly to the identity of maternal plants growing within the same site, independently of the fragment size. It

is well known that maternal effects in plants can have important influences on early offspring fitness traits (*e.g.*, Roach & Wulff 1987, Stephenson 1992, Wolfe 1993). Maternal effects are the result of complex interactions involving maternal genetic properties and of the environment where maternal plants grow (Roach & Wulff 1987). For example, severe abiotic conditions suffered by maternal plants during seed development may be translated into decreased early offspring fitness traits (Stephenson 1992). Although we did not evaluate abiotic conditions in the studied sites, no significant site effect was observed in any of the parameters evaluated. This may indicate that in our study system, either the abiotic conditions are rather homogeneous among sites within a fragment size, or that maternal effects due mostly to their intrinsic genetic properties are more important than maternal effects influenced by environmental conditions.

The relative magnitude of inbreeding depression effects due to fragmentation vs. maternal effects on early offspring fitness traits may be difficult to assess, especially in observational studies. We know, however, that in relatively recently fragmented systems (< 50 yr), genetic erosion processes are less evident compared with older (> 100 yr) fragmented systems (Aguilar *et al.* 2008). The fragmented system we studied, generated some 40 yr ago, is relatively recent, thus we may expect maternal effects to prevail over potential genetic erosion effects caused by habitat fragmentation on offspring fitness.

The degree to which genetic erosion will affect the fitness of plant populations depends on the number of generations elapsed in fragmented and isolated conditions, which will vary depending on the lifespan of plant species. In this regard, there are some patterns of lifetime among different plant life forms (Ehrlen & Lehtila

Table 4. *Fragment size effect on percentage of seed germination in five native plant species from the Chaco Serrano forest. Statistics and* P-*values of maternal plant effects, and the percentage of the model variance attributable to variability among maternal plants within sites are given within parentheses. Generalized linear mixed models with sites nested within fragment size and maternal plants within sites and fragment size. Different superscript indicates statistically significant differences.*

Plant species	Small Mean ± SD	Medium Mean ± SD	Continuous Mean ± SD	Statistical analysis
Acacia caven	15.68 ± 9.77	18.46 ± 11	15.85 ± 8.08	$z < 0.61; P > 0.54 (\chi^2_1 = 319; P < 0.0001; 30\%)$
Celtis ehrenbergiana	17.45 ± 16	20.41 ± 16	12.92 ± 9.60	$z < 1,61; P > 0.10 (\chi^2_1 = 2245; P < 0.0001; 90\%)$
Croton lachnostachyus	3.10 ± 6.42[a]	15 ± 23[b]	18 ± 18[b]	$z = 1.98; P = 0.04 (\chi^2_1 = 1612; P < 0.0001; 64\%)$
Rivina humilis	27.70 ± 20[a]	48 ± 21[b]	53 ± 16[b]	$z > 2.33; P < 0.02 (\chi^2_1 = 1636; P < 0.0001; 76\%)$
Schinus fasciculatus	1.50 ± 3.74	5 ± 9.20	3.64 ± 5	$z < 0.23; P > 0.82 (\chi^2_1 = 396; P < 0.0001; 89\%)$

Table 5. *Fragment size effect on individual mean seed mass (mg) in five native plant species from the Chaco Serrano forest. Statistics and P-values of maternal plant effects, and the percentage of the model variance attributable to variability among maternal plants within sites are given within parentheses. Linear mixed effects models with sites nested within fragment size and maternal plants within sites and fragment size.*

Plant species	Mean ± SD			Statistical analysis
	Small	Medium	Continuous	
Acacia caven	96 ± 13	86 ± 13	85 ± 11	$F_{[2, 80]} = 4.41$; $P = 0.28$ ($\chi^2_1 = 68$; $P < 0.0001$; 76%)
Celtis ehrenbergiana	36 ± 11	30 ± 12	35 ± 8.80	$F_{[2, 84]} = -0.03$; $P = 0.88$ ($\chi^2_1 = 376$; $P < 0.0001$; 84%)
Croton lachnostachyus	4 ± 1	4.61 ± 1.61	5.40 ± 1.62	$F_{[2, 84]} = 2.23$; $P = 0.37$ ($\chi^2_1 = 133$; $P < 0.0001$; 45%)
Rivina humilis	3.70 ± 1.07	4.47 ± 0.90	4.94 ± 0.80	$F_{[2, 90]} = 6.48$; $P = 0.24$ ($\chi^2_1 = 466$; $P < 0.0001$; 90%)
Schinus fasciculatus	16 ± 1.33	15.13 ± 3.70	16.80 ± 2.60	$F_{[2, 80]} = 0.32$; $P = 0.67$ ($\chi^2_1 = 376$; $P < 0.0001$; 65%)

2002): trees usually live longer than shrubs and shrubs longer than herbs. From local knowledge and nonsystematic observations of the species, we can roughly estimate the lifespan of the studied species. By the size and structure of maternal plants of the three tree species, it is highly probable that these individuals precede fragmentation events. On the contrary, maternal plants of *C. lachnostachyus* and *R. humilis* are likely to be second or third generation residents in the studied fragments. Decreased seed germination observed in the animal-pollinated, self-compatible *C. lachnostachyus* and *R. humilis* species may be the result of restricted gene flow among their fragmented populations, and/or of changes in mating patterns due to changes in pollinator behavior, richness, and/or abundance, which may have increased inbreeding between parental plants through generations.

In addition to longer generation times, tree species usually have spatially larger breeding neighborhoods compared with shrubs and herbs, which influences the distribution of genetic variability within and between the remaining populations in the landscape (Nason *et al*. 1997, Hamrick 2004). Pollen and seed dispersal vectors of plants shape the degree of genetic connectivity among plant populations growing in forest fragments (Sork *et al*. 1999, Hamrick 2004). If pollen and seed dispersal vectors are able to move across fragmented landscapes, they will ameliorate the loss of genetic diversity by preventing the effects of genetic drift and inbreeding (Sork *et al*. 1999). In particular, the extent to which pollen flow can connect the fragmented populations will affect the genetic and biological characteristics of offspring generated in fragmented habitats. In this regard, extensive pollen flow among fragmented populations has been consistently observed in several insect-pollinated tropical trees and several wind-pollinated temperate trees (reviewed by Hamrick 2004). The three tree species we studied may also be maintaining sufficient levels of pollen flow to prevent genetic erosion. *Celtis ehrenbergiana* is a wind-pollinated tree, which may be benefited by the increased open areas to move pollen through the matrix into the forest fragments, as has been previously observed in several other wind-pollinated trees (Hamrick 2004). The abundance and composition of the wide pollinator assemblage of *A. caven* did not change along these forest fragments, which resulted in similar pollination and reproductive success (Aguilar 2005), suggesting no changes in mating patterns. Finally, the dioecious tree *S. fasciculatus*, is also visited by a wide array of insects, some of which are shared with *A. caven*. More studies on the pollination biology of this species are, however, required to understand its pollination and reproductive dynamics. Using different mechanisms, these tree species may still be able to achieve substantial connectivity among their populations via pollen flow through the fragmented landscape, resulting in an ability to generate similarly fit offspring.

The evaluation of offspring fitness generated by maternal individuals growing in highly fragmented systems provides important information about the potential long-term viability of remnant populations in forest fragments. Such information seems particularly important for conservation biology given the prevalent fragmented characteristics of current landscapes across the earth. For example, by assessing the fitness of plant offspring generated in fragmented and continuous habitats, we may assist with management decisions in selecting progenies for *in situ* conservation as well as for reforestation and restoration programs. Our results show that early offspring fitness traits in two native plant species, a shrub and a herb, declined significantly in small forest fragments, while no such differences were detected among the tree species across the forest fragments. No previous studies have evaluated fragmentation effects on early offspring fitness traits in plant species with different life forms simultaneously in the same environment. The handful of studies evaluating fragmentation effects on offspring fitness have focused either on perennial herbs (*e.g.*, Hooftman *et al*. 2003, Winter *et al*. 2008) or long-lived trees (*e.g.*, Krauss *et al*. 2007). We emphasize the need to increase research on early and late plant offspring fitness traits produced in forest fragments and to incorporate species with contrasting life history and ecological characteristics. Ideally, these fitness traits should be simultaneously assessed with measures of genetic parameters and pollination ecology to fully account for the genetic and ecological mechanisms involved in decreased offspring fitness due to habitat fragmentation.

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