Offspring performance and recruitment of the pioneer tree *Acacia caven* (Fabaceae) in a fragmented subtropical dry forest

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Abstract   The process of habitat fragmentation results in the breaking apart of originally continuous habitats, causing multiple changes in biotic and abiotic interactions. Alterations in resource availability and in mutualistic and antagonistic plant–animal interactions may impact plant offspring quantity and quality. Currently, several old fragmented systems evidence a process of flora homogenization, where shade-tolerant species are replaced by pioneer light-demanding species. Notably, the relationship between quantity and quality parameters of plant offspring production and the successful recruitment of pioneer species in fragmented forests has been poorly explored. Here, we assess population size, sapling recruitment and offspring performance of one of the most widespread tree species of subtropical South America, the native pioneer *Acacia caven* (Fabaceae). Population size of adults and saplings increased from small to continuous forests, whereas the sapling recruitment per adult tree (sapling/adult ratio) showed no significant differences among forests of different size. Seedling performance was negatively related to forest area and population size, implying potential superior competitive ability of seedlings produced in smaller populations compared to larger ones. Our results show that *A. caven* is resilient to habitat fragmentation effects, which may be ascribed to a set of advantageous ecological traits such as outcrossing, massive flowering, generalist pollination, drought resistance, rapid growth and re-sprouting. Thus, this pioneer tree benefits from the availability of vacant sites and resources released by declining plant populations of other species, eventually becoming the dominant species in fragmented habitats. Pioneer native plant species with ecological traits such as *A. caven* may represent the silent successful survivors and new colonizers of fragmented habitats, the ubiquitous landscapes of the future.

Key words: Argentina, Chaco Serrano forest, habitat fragmentation, progeny vigor, seedling fitness.

INTRODUCTION

Habitat loss and fragmentation are widespread drivers of global biodiversity decrease (Sala *et al.* 2000; Krauss *et al.* 2010). The process of habitat fragmentation implies the breaking apart of originally continuous habitats causing irreversible changes. After the land is cleared, remnant vegetation patches embedded in anthropogenic matrices are subjected to changes in the physical environment due to edge effects, resulting in increased solar radiation and exposure to winds, which affect nutrient cycling processes, soil microorganisms and soil moisture retention, as well as increased evapotranspiration and desiccation of plants growing in forest patches (Saunders *et al.* 1991; Didham & Lawton 1999; Mix *et al.* 2006). Simultaneously, reductions of population sizes and increased isolation among remaining populations can alter key ecological interactions that affect the viability of plant populations (McGarigal & Cushman 2002; Fahrig 2003). Habitat fragmentation often modifies mutualistic and antagonistic plant–animal interactions (Aguilar *et al.* 2009; Cagnolo *et al.* 2009) changing pollination dynamics and plant mating patterns, herbivory levels and plant offspring quantity and quality (e.g. Aguilar *et al.* 2006, 2008, 2012; Ruiz-Guerra *et al.* 2010; Ashworth & Martí 2011). In the long term, such changes may modify the taxonomic, genetic and functional diversity of plant communities in fragmented forests (e.g. Tabarelli *et al.* 2004; Cagnolo *et al.* 2006; Laurance *et al.* 2006; Girao *et al.* 2007; Aguilar *et al.* 2008; Lobo *et al.* 2011), decreasing resilience capacity and ecosystem services provision of remaining forests (Díaz *et al.* 2006).

Today, several old fragmented systems show a 'fragmentation-driven' process of flora homogenization where certain species such as shade-tolerant trees, typical of old-growth forests, are replaced by a subgroup of pioneer light-demanding tree species that can take advantage of some micro-environmental changes associated with edge effects triggered by habitat fragmentation (e.g. Laurance *et al.* 2006; Lobo *et al.* 2011;

Tabarelli *et al.* 2012). Particularly, pioneers, small-seeded, pollination-generalist and soft-wooded native species tend to proliferate in fragmented landscapes around the world, replacing shade-tolerant, large-seeded and pollination-specialist species (Zhu *et al.* 2004; Laurance *et al.* 2006; Girao *et al.* 2007; Melo *et al.* 2010; Lobo *et al.* 2011). In fact, the few studies evaluating fragmentation effects on certain demographic parameters and community composition discriminating pioneer and non-pioneer plant species have found prevalence of pioneer species in the seed rain, seedling assemblage and recruitment rate in forest fragments compared to continuous forests (e.g. Laurance *et al.* 1998; Knorr & Gottsberger 2012). Pioneer species might be favoured by increased light incidence generated by edge effects following fragmentation (Laurance *et al.* 1998; Zhu *et al.* 2004; Girao *et al.* 2007), optimizing recruitment and eventually dominating forest remnants. Moreover, higher outcrossing rates in fragmented populations of pioneer animal-pollinated tree species, can impact positively on offspring fitness (Mathiasen *et al.* 2007; Broadhurst *et al.* 2008; Davies *et al.* 2013; Correia *et al.* 2014) and its probability of successful recruitment.

The amount of offspring produced in a reproductive event by plant individuals growing in fragmented forests is an important demographic parameter, as it determines the maximum population recruitment potential for the next generation (Wilcock & Neiland 2002). Likewise, the quality or biological performance of offspring is another important feature determining the recruitment success of populations (Cascante *et al.* 2002; Mathiasen *et al.* 2007; González-Varo *et al.* 2010). Notably, the relationship between these quantity and quality parameters of plant offspring and the successful recruitment of pioneer species in fragmented forests has been poorly explored (but see Cordeiro *et al.* 2009; González-Varo *et al.* 2010, 2012). Indeed, studies evaluating recruitment did not assess offspring quality and quantity (e.g. Laurance *et al.* 1998; Melo *et al.* 2010; Knorr & Gottsberger 2012), and those evaluating offspring quality did not consider recruitment (e.g. Cascante *et al.* 2002; Mathiasen *et al.* 2007; Simonetti *et al.* 2007; Broadhurst *et al.* 2008; Ashworth & Martí 2011; Breed *et al.* 2012).

Here, we assess population size, sapling recruitment and offspring performance of *Acacia caven* in a fragmented landscape. *Acacia caven* is a common, native, pioneer tree that is dominant in disturbed sites of the Gran Chaco forest, the most extensive dry forest of South America (Argentina, Bolivia, Brasil and Paraguay; Moglia & Giménez 1998; Giorgis *et al.* 2011), and it is also present in Chile and Uruguay (Aronson & Ovalle 1989; Van de Wouw *et al.* 2011). In central Argentina, *A. caven* is the most abundant tree species within the community of the Chaco Serrano Forest

(Giorgis *et al.* 2011). In contrast to other pioneer species, which dominate fragmented habitats (e.g. Girao *et al.* 2007), *A. caven* is self-incompatible and highly outcrossing (Peralta *et al.* 1992; Baranelli *et al.* 1995; Pometti *et al.* 2011). It flowers massively at the onset of the growing season (dry season), being the most important floral resource in the community at that time (Baranelli *et al.* 1995), attracting a wide array of native pollinators and honeybees (Ashworth 2004; Aguilar 2005). Pollination of *A. caven* is not reduced in fragmented populations as observed in previous studies in the area, where fruit production was similar to that of continuous forests (Ashworth 2004; Aguilar 2005). Here, we hypothesize that population of adult individuals of *A. caven* increase with increasing forest area. Nevertheless, maternal trees in fragmented habitats may exploit their advantageous pioneer ecological traits, increasing outcrossing matings and benefiting from increased sunlight exposure and niche availability triggered by habitat fragmentation. As a result, we expect that maternal trees from smaller fragments will produce offspring with higher performance and more chances to be successfully recruited than offspring of maternal trees from continuous forests. Accordingly, we expect to find a negative relationship between forest area and offspring performance.

METHODS

Study system and species

The Chaco Serrano District (within the Gran Chaco region) is a xerophytic and subxerophytic forest growing in the slopes of the hills between 500 and 1300 m above sea level (Giorgis *et al.* 2011). The typical vegetation is a low and open woodland (Cabido *et al.* 1991) of high floristic diversity, with floral elements from different lineages such as Andean, Patagonian and cosmopolitan plant species (Cabido & Zak 1999; Giorgis *et al.* 2011). Rainfall (944 mm annual) is concentrated in the warm season (October–April), and minimum and maximum mean temperatures range between −10°C and 26°C, respectively. The original area of Chaco Serrano forest has suffered a dramatic decrease as a result of the expansion of agricultural frontiers over the last 45 years (Zak *et al.* 2004). In central Argentina, this forest holds one of the highest estimates of deforestation worldwide with only 6% of the original Chaco Serrano forest cover remaining as a fragmented mosaic of forest of different sizes with only six fragments larger than 400 ha (Zak *et al.* 2004).

Acacia caven (Molina) Molina (Fabaceae;) grows between 18° and 36° latitudes S, from the Atlantic Ocean to the Pacific Ocean (Ovalle *et al.* 1999) and between 360 m to 1700 m above sea level (Giorgis *et al.* 2011). It is a small (2–5 m) thorny phreatophyte tree (Aljaro 1984) that flowers massively during August–September. It is andromonoecious, its flowers are small, nectarless, very fragrant and clustered in inflorescences (Peralta *et al.* 1992; Baranelli *et al.* 1995; Calviño *et al.* 2014). The flowers are pollinated by a wide

assemblage of insects including bees, flies and wasps, with the exotic bee *Apis mellifera* as the most frequent pollinator (Ashworth 2004; Aguilar 2005). *Acacia caven* can only reproduce by seeds, which are dispersed by goats, guanacos and cattle (Fuentes *et al.* 1989; Ashworth 2004). Pods ripen in autumn (March–April), and the majority of them fall to the ground, while some of them remain on the tree for a year (Ashworth 2004).

Sampling design

Nine study sites were selected using Landsat ETM satellite images (Landsat ETM, CONAE, Córdoba, Argentina), and are located between 31°09′–31°35′ S and 64°13′–64°27′ W. All the studied sites are within private properties with similar loads of livestock thus are non-protected areas. Forests were classified into three forest-size categories based on their area. We used area as the main site selection criterion because it has been shown to have the highest explanatory value for plant species richness within the studied system (Cagnolo *et al.* 2006), thus forest area is an important factor involved in species recruitment. Three sites were continuous forests (>500 ha), three were medium-sized fragments (10–29 ha), and three were small-sized fragments (1–3 ha). Sites were selected with the criteria of covering a wide range of areas while maintaining comparable isolation levels (75–200 m to the nearest largest forest fragment), matrix characteristics, altitudinal position (500–800 masl) and general climatic conditions. However, as small forest fragments have higher edge/area ratios and thus higher edge exposure, they experience more micro-environmental disturbances associated with edge effects (e.g. increased solar radiation, higher soil temperatures and wind exposure, decreased soil moisture retention, etc.) compared to larger forest fragments and continuous forests (Saunders *et al.* 1991; Didham & Lawton 1999). All forest fragments are immersed in intensively managed matrices, dominated by wheat in winter and soybean or maize in summer. For a map with the spatial distribution of studied sites see Ashworth and Martí (2011). In each site, we marked five maternal trees of similar size separated by at least 7 m (range 7–30 m). In March 2005, seven ripe fruits were collected randomly from three different branches of similar size per maternal tree (a total of 20–21 fruits per tree).

Population size

For small and medium-sized forest fragments, we counted all adult reproductive individuals (>1 m height) and saplings (0.7–1 m height) of *A. caven*. For continuous forests, we estimated population size using conventional distance sampling (CDS) analysis (Buckland *et al.* 1993, 2001). In the CDS analysis, a detection probability function is modelled based on the perpendicular distance of all objects at a point or a line (Thomas *et al.* 2010). To do so, we made six 350 m transects in each continuous forest and measured the perpendicular distance to each *A. caven* sapling and adult individuals. Owing to reduced visibility within the forest, the maximum detection distance was fixed at 10m and 6m for adults and saplings, respectively.

Offspring performance

We randomly selected three healthy seeds (non-predated, non-aborted) from each of the 20 fruits per tree ($n = 60$ seeds per maternal tree). Seeds were placed in Petri dishes on filter paper and moistened with distilled water every five days. Dishes were placed in a chamber at $25 \pm 5°C$ with a 12/12 h daily photoperiod for 30 days (Funes & Venier 2006). Three germinated seeds per maternal tree (totalling 135 seedlings) were sowed individually in tubular plastic pots of 60 cm depth and 20 cm diameter filled with a mixture of 60% soil and 40% sand. Pots were tabulated by site and maternal tree and maintained in a greenhouse and watered once a week. Pots were randomly interchanged around the greenhouse every two weeks. Performance was measured as seedling growth and survivorship after 60 days. Seedling height was measured with a digital caliper from the cotyledon scars to the base of the newest leaf in the apical meristem. The number of completely expanded leaves was counted, and their lengths (main rachis length) were measured with a digital caliper. These three seedling performance parameters (height, number and length of leaves) were significantly correlated among themselves ($r_s \geq 0.70$, $P \leq 0.03$). Thus, in order to obtain a synthetic measure of offspring performance and to avoid inflating type I error by repeating statistical tests on related response variables, we calculated a per seedling multiplicative performance function (seedling height × number of leaves × mean leaf length × mean proportion of germinated seeds, Willi *et al.* 2013). Data for seed germination and mean seed mass (used as covariate) per maternal tree were obtained from Ashworth and Martí (2011).

Data analysis

Population size in continuous forests was estimated using a detection probability function with the software Distance 6.0 (Thomas *et al.* 2010). This method is more precise when plants are either clumped or sparsely distributed and allows covering more area in a given time than quadrat or strip sampling designs (Buckland *et al.* 2007). Therefore, modeling detectability provides an accurate way to estimate population size with better spatial coverage (Buckland *et al.* 2007). Here, half-normal and uniform key functions with cosine adjustment were used to model detectability for adults and saplings, respectively (Thomas *et al.* 2010).

Statistical analyses were performed using R environment (R Development Core Team 2009). We used Spearman's rank correlation test for small sample sizes with pre-computed null distribution and exact approximation (pspearman package; Savicky 2014) to evaluate the relationship between log-area and log-population size of adults, saplings, sapling/adult ratios and seedling multiplicative performance ($n = 9$). To evaluate forest size category effects on seedling multiplicative performance controlling for maternal effects, we used linear mixed effects models (*lme* function of the nlme package, Pinheiro *et al.* 2009). For this analysis, the spatial structure of the data was: forest size category ($n = 3$) as the fixed main effect, site ($n = 9$) as random effect nested within forest size category and maternal plant ($n = 45$) as random effect nested within site and forest size category. After checking assumptions for the inclusion of a covariate, we included seed mass as

a covariate in the model. The three categorical levels of forest size were established by the area of the fragments: small, medium and continuous forest. The significance of the fixed effect was determined by comparing two models, one with the fixed effect and the other without it, but both sharing the same structure of random effects using a likelihood ratio test (L ratio). Random effects and covariate effects were tested by comparing two nested models, one with and one without the random and covariate effect using a likelihood ratio test. Model parameters were estimated with restricted maximum likelihood methods.

RESULTS

Forest fragments ranged from 1.14 to 29.53 ha, whereas continuous forests were larger than 500 ha (Table 1). Within this gradient of forest area, population size of adults ranged from 16 to 45 178 and saplings from 0 to 4532 (Table 1). Population size of adults and saplings significantly increased with forest area (Fig. 1a,b). However, the sapling/adult ratio showed a non-significant relationship with forest area (Fig. 1c). However, it is interesting that when dropping the only zero value of sapling/adult ratio observed in site S3 (Table 1) the relationship becomes significant ($r_s = -0.739$, $P = 0.021$), implying potential higher sapling recruitment per adult tree in fragmented forests compared to continuous forests.

The performance parameters used to calculate the multiplicative seedling performance are detailed in Table 2. When running the categorical linear mixed effects model, which included maternal identity and sites as random effects and seed mass as a covariate, we found no significant fragmentation effects on the multiplicative seedling performance (L ratio = 1.69, $P = 0.43$; Table 2). Moreover, the use of seed mass as a covariate did not influence the multiplicative seedling performance (L ratio = 0.20, $P = 0.65$), and neither site nor maternal tree (random effects) had significant effects on multiplicative seedling performance (L ratio ≤ 0.66; $P \geq 0.41$). Finally, survivorship of seedlings was 100% after 60 days independent of the landscape condition and population size they belonged to.

Because of the lack of significant effects of the random factors and the covariate, we assessed the relationship of the multiplicative seedling performance parameter with the forest area gradient. We found a significant negative correlation between forest area and seedling performance (Fig. 2), indicating a decrease in overall performance of seedlings generated in larger forests. As expected, due to the highly significant and positive relationship between adult population size and forest area, the multiplicative seedling performance was also significantly negatively correlated with adult population size ($r_s = -0.76$; $P = 0.036$).

DISCUSSION

Pioneer species usually present ecological traits that make them successful in disturbed habitats (e.g. Swaine & Whitmore 1988, Girao *et al.* 2007, Lobo *et al.* 2011). Here, we observed that fragment area mirrors the population size of adults and saplings of *A. caven*. However, the negative and significant relationships found between forest area and seedling performance suggest superior competitive ability of seedlings produced in smaller populations compared to larger ones (Houssard & Escarré 1991; Biere 1996). While seedling performance may also be influenced by maternal effects, our results indicate it would not be the case here. Firstly, seed mass, which was under significant maternal influence (Ashworth & Martí 2011), had no effect on offspring performance after 60 days of growth. Second, maternal identity included in the model as a random factor showed no effects on seedling performance. These results suggest that maternal resources are unlikely to influence *A. caven* offspring performance, and the differences observed across the forest fragmentation gradient may be a response to ecological and genetic factors.

Because *A. caven* is self-incompatible and highly outcrossing (Peralta *et al.* 1992; Baranelli *et al.* 1995;

Table 1. Area of forests, number of adults, saplings and sapling/adult ratios of *Acacia caven* in small, medium and continuous forests

Forest size category	Sites	Area (ha)	Number of adults	Number of saplings	Sapling/Adult ratio
Small	S1	1.14	104	12	0.12
Small	S2	2.89	22	4	0.18
Small	S3	3.58	16	0	0.00
Medium	S4	10.70	455	96	0.21
Medium	S5	13.77	267	31	0.12
Medium	S6	29.53	511	52	0.10
Continuous	S7	>500	35 205	2089	0.06
Continuous	S8	>500	27 677	1956	0.07
Continuous	S9	>500	45 178	4532	0.10

Sites correspond to references given in Ashworth and Martí (2011).
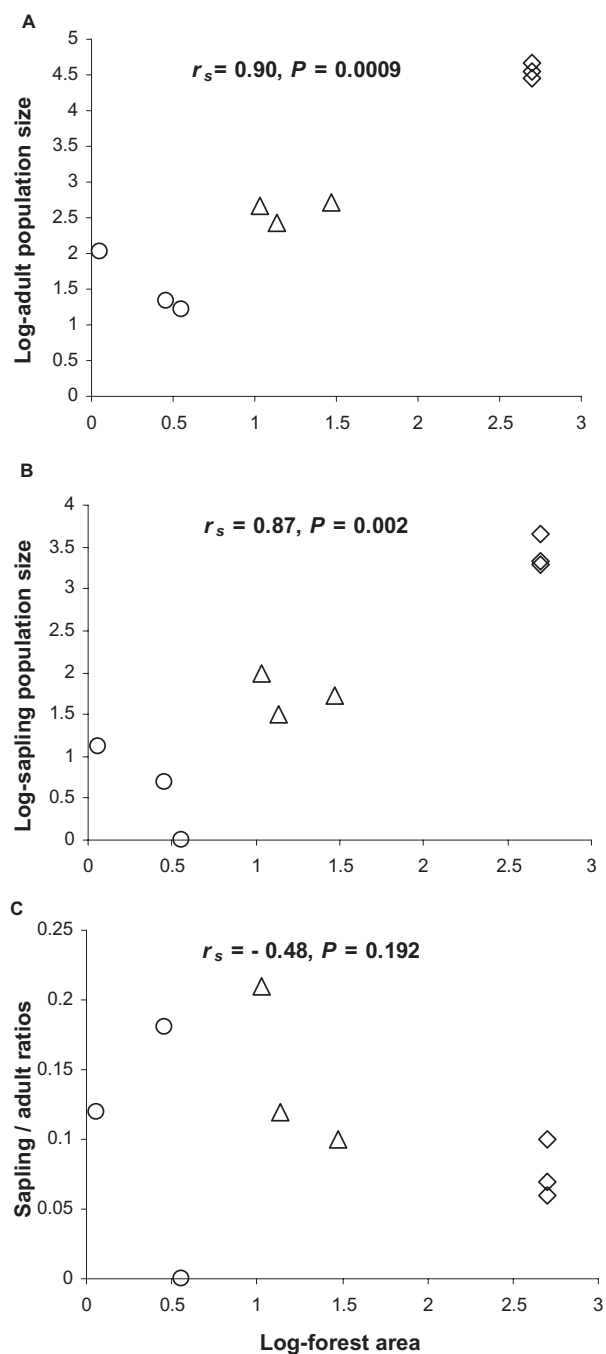
Fig. 1. Relationships between log-forest area and (a) log-adult population size, (b) log-sapling population size and (c) sapling/adult ratio of *Acacia caven*. Symbols: circle, triangle and diamonds correspond to small, medium and continuous forests, respectively.

Pometti *et al.* 2011), higher offspring performance in smaller populations may be the result of higher outcrossing rates. Previous research has observed such changes in outcrossing rates in other self-incompatible, animal pollinated and highly outcrossing pioneer tree species such as *Embothrium coccineun* and *Acacia*

dealbata: as their population size decreased in fragmented landscapes, their outcrossing rates significantly increased (Mathiasen *et al.* 2007; Broadhurst *et al.* 2008; Correia *et al.* 2014). The massive flowering of *A. caven* individuals in a period of the year where other floral resources in the community are almost non-existent (Baranelli *et al.* 1995, L.A., pers. obs.) may force pollinators to move among forest fragments. Comparatively, smaller populations have less flower resources than larger ones, thus the ratio of pollinator exchange may be higher in smaller populations, promoting pollen immigration and increasing offspring performance. Should this be the case, our results contradict previous findings from literature reviews showing that habitat fragmentation tends to decrease outcrossing rates and to increase inbreeding coefficients in plant offspring (Aguilar *et al.* 2008). However, little research has focused on plant mating patterns of pioneer species in fragmented systems (e.g. Mathiasen *et al.* 2007; Broadhurst *et al.* 2008; Davies *et al.* 2013) to allow the comparison with non-pioneer species.

The relative efficiency in sapling recruitment per adult tree (sapling/adult ratio), however, was independent of the forest area, suggesting that offspring of higher fitness produced in smaller populations would not necessarily result in a more successful recruitment. In this regard, it is important to highlight that the seedling performance parameters were taken in greenhouse conditions, so our results show the potential fitness of the species and not necessarily the real fitness in natural conditions. Therefore, strong environmental filtering imposed by natural conditions would be equalizing *A. caven* recruitment per adult tree, regardless of forest area. However, similar recruitment rates per adult trees imply that smaller forest fragments will be dominated in a shorter time due to their reduced and limited area, increasing future plant density of *A. caven*. Similarly, in a Mediterranean fragmented system, the seedling establishment of the shrub *Myrtus communis* depended more on abiotic factors than on offspring fitness (González-Varo *et al.* 2012). Taken together, the results found here and those from previous studies on fruit and seed set, seed abortion, predation and germination of *A. caven* in the same studied sites (Aguilar 2005; Ashworth & Martí 2011) reveal the overall resilience of *A. caven* to habitat fragmentation effects.

Like several other *Acacia* species (Fagg & Stewart 1994), *A. caven* is very resistant to drought (Kraiser *et al.* 2008) and can resprout successfully after cutting, grazing and burning (Fuentes *et al.* 1989; Torres *et al.* 2014). This set of ecological traits together with its particular mass flowering phenology are part of a successful strategy of *A. caven* to face landscape changes imposed by habitat loss and fragmentation. The success of *A. caven* to offset the consequences derived from isolation and reduced population size may

Table 2.   Mean ± SD of offspring performance parameters of *Acacia caven* from maternal trees growing in small and medium-sized forest fragments and continuous forests

Offspring performance parameters	Small	Medium	Continuous
Height (mm)	71.57 ± 18	57.07 ± 10	59.13 ± 20
Number of leaves	13.40 ± 2.70	12.20 ± 2.50	12.19 ± 3.40
Leaf length (mm)	21.80 ± 3.30	20 ± 3.21	19.70 ± 4.81
Multiplicative performance	344 ± 60	242 ± 41	211 ± 61

Seedling height, number of leaves, leaf length and multiplicative performance (height × number of leaves × leaf length × proportion of seed germination).
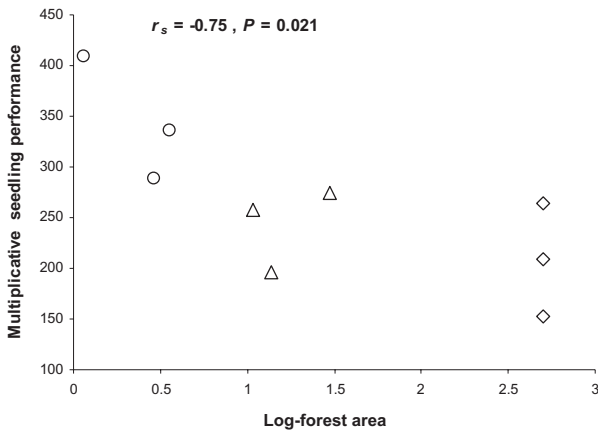
Fig. 2.   Relationship between log-forest area and multiplicative seedling performance of *Acacia caven*. Symbols: circle, triangle and diamonds correspond to small, medium and continuous forests, respectively.

explain its widespread distribution in disturbed and fragmented landscapes. In a recent exhaustive study covering almost the entire longitudinal, latitudinal and altitudinal floristic diversity of the Subtropical Chaco Serrano forest in the province of Cordoba, Giorgis *et al.* (2011) found that *A. caven* is the most frequent species regardless of the life form and the functional group (pioneer, non-pioneer). Its widespread prevalence would reveal the overall deteriorated status of the remnant vegetation in the region, where more than 94% of the original area of the Chaco Serrano forest has been lost in the last 45 years (Zak *et al.* 2004).

In neotropical forests, anthropogenic disturbance caused by habitat fragmentation is promoting the proliferation of native pioneer species to the detriment of non-pioneer ones (e.g. Tabarelli *et al.* 2012). The proliferation of pioneer species is a phenomenon associated with natural forest regeneration and succession dynamics. However, in fragmented forests, pioneer proliferation may be indicative of forest degeneration (Santos *et al.* 2008). Degeneration of forest fragments imply a retrogressive succession at the habitat patch scale in which plant communities will retain gradually fewer species and lower biomass over time (Santos *et al.* 2008). Forest degeneration at the habitat patch

scale has been studied particularly in tropical forests of Brazil (e.g. Laurance *et al.* 2006; Lobo *et al.* 2011; Tabarelli *et al.* 2012; but see Zhu *et al.* 2004). Although our study was not aimed at testing a degeneration process in the subtropical dry Chaco Serrano forest, our findings suggest it may be a potentially ongoing process. Results of a previous study within the same studied sites found negative effects of habitat fragmentation on overall plant species richness (Cagnolo *et al.* 2006). Our findings on the sapling/adult ratio show no effects on *A. caven* regeneration. Therefore, this pioneer species could take advantage of the availability of vacant sites and resources released by declining plant populations of other species and eventually become the dominant species. While there is widespread evidence of reduced native plant diversity in fragmented habitats, mainly due to decreased plant population performance, as a result of both ecological and genetic factors (e.g. Aguilar *et al.* 2006, 2008, 2009), there is still a lack of information about the identity and demographic characteristics of successful plant species thriving in remaining fragmented habitats. From our findings, we argue here that pioneer native plant species with ecological traits such as *A. caven*, may represent the silent successful survivors and new colonizers of fragmented habitats, the ubiquitous landscapes of the future.

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