379

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Secondary seed dispersal by mammals between protected and grazed semiarid woodland

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ABSTRACT

The spatial continuity of habitats contributes to maintaining ecological processes across human-modified landscapes. Boundaries between differently managed lands may affect species interactions, such as seed dispersal, which is a key ecological process contributing to plant recruitment. We proposed a study of plant-frugivore interactions based on an experimental design of offering fruits at distance from a boundary to interior areas between protected and grazed drylands. We found that the number of visits and fruits removed differed among distance classes and among mammalian frugivores. Also, habitat cover differed across distance classes. Interactions by seed disperser species were more frequent at distances nearer boundary and from boundary toward grazed fields. Conversely, interactions by seed predator species were more frequent at distances further from boundary to both land uses. We suggest that seed dispersers may be connecting lands at different spatial scales according to species-specific differences in body size and movement capacity. Studying boundaries with a functional approach contributes to assessing the sensitivity of species to boundaries and its effect on key ecological functions between protected areas and human-managed surrounding lands.

1. Introduction

Land-use changes have become one of the most challenge issues in the face of global environmental change (Mayer et al., 2016). Currently, due to land use expansion and intensification, protected areas are left embedded within human-modified landscapes (Hansen and DeFries, 2007). Dry woodlands around the world have undergone human modifications mainly related to intensive agriculture, grazing by livestock and tree felling (Fischer and Lindenmayer, 2007; Solé, 2007). In this context, establishing nature reserves has been an effective approach for the conservation of woodland resources (Hobbs and Cramer, 2008), though boundaries typically have not been designed to accommodate flows of nutrients, resources and organisms across the landscape (DeFries et al., 2007). In particular, fencing has been the most used intervention in drylands for protecting natural populations and to avoid any interactions with agents of disturbance outside the limits of protected areas (Durant et al., 2015). As boundaries impose changes in habitat structure, the transition of ecological variables from one to the other side of the boundary may be gradual or abrupt depending on the contrast of that characteristics between the areas (e.g. plant architecture; Cadenasso et al., 2003; López-Barrera et al., 2007). However,

the consequences of such spatial discontinuity (due to boundaries delimitation) on conservation of species and ecosystem functions remain poorly explored (Hansen and DeFries, 2007).

Boundaries (i.e. the zones of contact between spatially heterogeneous areas; Cadenasso et al., 2003) between different land use practices may affect species interactions such as seed dispersal and predation (Cadenasso et al., 2003; López-Barrera et al., 2007). Seed dispersal is an important ecological process as it is the only way for plant species to move in response to land-use changes (Howe, 2016). During their movement from one habitat to another, animals may connect different patches by transporting seeds (Lundberg and Moberg, 2003). In particular, seed dispersal by animals is a mutualistic interaction likely to suffer disruption by fragmentation and landscape disturbances, ultimately affecting plant recruitment (Cordeiro and Howe, 2003; Galetti et al., 2006). It has been proposed that anthropogenic activities may impact on seed dispersal by altering the number of visits to the fruiting plants, the number of fruits or seeds removed and the seed-dispersal distance (Markl et al., 2012).

Visitations to the fruiting plants and fruit removal by animals are components of the dispersal or interaction stage of the seed dispersal process (Jordano and Schupp, 2000; Schupp et al., 2017). Different

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ecological factors influence plant-frugivore interactions, such us habitat structure, surrounding neighborhood and fruit crop size (Jordano and Schupp, 2000; Carlo 2005; Blendinger and Villegas, 2011). Specifically, habitat boundaries can facilitate the occupancy of seed-dispersing animals (e.g. foxes and birds) which may select and disseminate seeds on these sites promoting plant dispersal (López-Bao and González-Varo, 2011; Suárez-Esteban et al., 2013). In other cases, boundaries characterized by high vegetation cover may contain a higher abundance of small rodents compared to interior lands (Hodara and Busch, 2006; Gómez et al., 2011) and consequently, register a higher seed predator activity (Kollmann and Buschor, 2002; Jacob et al., 2006; Baraibar et al., 2009).

We focused on studying the dispersal or interaction stage (Jordano and Schupp, 2000; Schupp et al., 2017) of the *Prosopis flexuosa*- frugivorous mammal interaction from a boundary between a protected area and surrounding grazed fields. *Prosopis flexuosa* is the dominant tree species in the dry woodland community (Roig et al., 2009). Previous studies have described the functional roles of native and domestic mammals in *Prosopis* seed dispersal, with species acting as endozoochorous dispersers such as the gray fox (*Lycalopex griseus)*, the Patagonian hare (*Dolichotis patagonum*) and domestic cattle (Campos and Ojeda, 1997; Campos et al., 2008, 2011); seed dispersers by scatter-hoarding such us the small cavy (*Microcavia australis)* and the silky mouse (*Eligmodontia typus;* Giannoni et al., 2013; Campos et al., 2017), and finally seed predator species such as the grass mouse (*Akodon dolores*) and the gray leaf-eared mouse (*Graomys griseoflavus;* Giannoni et al., 2013), which may eventually act as seed dispersers (Giannoni et al., 2001; Giannoni et al., 2013). By using a repeated experimental design of fruit stations and combining different distance classes from the boundary between protected and grazed fields, we analyzed variation in fruit removal and animal visitation (the first interaction stage of seed dispersal; Schupp et al., 2017) regarding distances from boundary to both sides. We addressed the following questions: Are boundary between the protected area and grazed fields characterized by changes in habitat cover? Do changes in habitat cover influence plant-frugivore interactions? and, is there any clear pattern of fruit removal and visits by seed dispersers or predators from boundary to land interiors? Our objectives were to: characterize the vegetation cover at different distances from boundary, analyze the number of fruits removed and visits to focal trees by mammal species, and, finally, identify frugivorous species that contribute to the highest number of fruits removed and visits as seed dispersers or predators. We expected that the contrasting habitat cover from the boundary influence the presence of frugivorous mammals in function of their habitat requirements and, consequently, the seed dispersal process regarding the functional role of species in the *Prosopis* seed dispersal (i.e. seed dispersers or predators).

2. Material and methods

2.1. Study area

The study was conducted in the central part of the Monte Desert, Argentina. The climate is semiarid and markedly seasonal, with cold dry winters (mean temperature lower than 10 °C) and warm rainy summers (mean temperature above 20 °C). Average annual rainfall is 326 mm. (Estrella et al., 2001). A gently undulating plain is the dominant landscape in the region, with sandy-silt soils mainly of aeolian origin. These deep soils support open woodland characterized by a tree layer dominated by *P. flexuosa* and *Geoffroea decorticans*, a shrub layer of *Larrea divaricata*, *L. cuneifolia* and *Condalia microphylla,* and a layer of grass and herbs.

Boundary where this study was conducted is located in the Ñacuñán Forest Reserve and surrounding grazed fields. The Ñacuñán Reserve (34°02′S, 67°58′W; Fig. 1) was created in 1961 for the purpose of recovering the natural vegetation and protecting *P. flexuosa* woodland. In

1986, the Reserve was incorporated into the UNESCO Man and Biosphere Reserve Network. The long-term grazing exclusion over 40 years resulted in a remarkable natural recovery of native plant species, and this is the most important reference site in Argentina for monitoring the ecological health of the Monte Desert (Ojeda et al., 1998). In the surrounding areas, grazing by domestic animals, predominantly cattle, is intensive, with an average stocking density of 27 ha per animal unit (Guevara et al., 2009).

2.2. Study tree species

Prosopis flexuosa (Fabaceae, Mimosoideae) is a key tree species that forms extensive woodlands across the Monte biome (Roig et al., 2009) and provides to humans with services such as shade and goods like wood, flour and food (Ladio and Lozada, 2009). Moreover, *P. flexuosa* maintains multiple ecological interactions with other plant species acting as a nurse plant for shrubs and grasses (Rossi and Villagra, 2003), and with pollinators and seed dispersers (Aschero and Vázquez, 2009; Campos et al., 2016).

This tree species blooms in spring (October to December) and fruits start to ripen in summer (February). Fruits are indehiscent pods, composed of a relatively soft exocarp (Burkart, 1976) and a thick mesocarp that contains the major portion of sugars and protein (Kingsolver et al., 1977). Seeds are covered by a bony endocarp and a coat that acts as barrier inhibiting germination (Warrag, 1994). Germination is accelerated by the passage of seeds through the digestive tracts of animals, with some costs to seed viability (Campos and Ojeda, 1997; Campos et al., 2008).

2.3. Experimental design

Boundary between the protected area and surrounding grazed fields is delimited by an open unpaved road subject to vegetation clearing that act as firebreaks (mean total cleared width of 9 m). Along this area, we sampled six different boundary locations separated by a minimum distance of 1 km. At each location, we established a linear transect, perpendicular to the boundary, consisting on six different distances from boundary to interior fields. Three distances were inside the protected area and three inside grazed fields (at 0 m, 100 m and 300 m; total replicates per land use = 6; total stations = 36; Fig. 1). The experiment was conducted at two times overall, during April 2015 and April 2016, after *Prosopis* fruits had reached the ground.

At every distance interval we randomly selected a focal adult *P. flexuosa* tree. We removed all other ripe fruits on the ground before camera trap installation, and under the crown of each tree, we placed a group of 20 *Prosopis* fruits. Fruits consisted of ripe pods collected from different adult trees and mixed together. We placed one camera trap (Moultrie M-990i, Alabaster, AL, USA) on every tree to identify animal species removing pods and visiting trees. The total number of camera traps used was 36, and the camera-night's effort was 144 (36 camera traps by 4 nights per camera). Cameras were active during four consecutive nights and days over the two sampling periods, totaling 3456 h of operation (36 camera traps by 96 h per camera). Stations were checked every day, and when we detected that animals had removed all the offered fruits (in order to be able to identify some trees and distances from boundaries in which the fruit removal may occur at different rates), we offered a new group of 20 pods (fruit replenishment event hereafter). The sequence of three consecutive photographs by a frugivore species was defined as a visitation event, and to determine the number of removed fruits by each frugivore species per visit we subtracted the number of final fruits (number of fruits left after each frugivore visit) from the number of initial fruits.

All camera traps were set in "motion detect mode", taking three consecutive photos once movement was detected. We set the delay between three shots at 30 s and at high sensitivity to detect small mammal species (< 100 g). Cameras were placed approximately 1.8 m
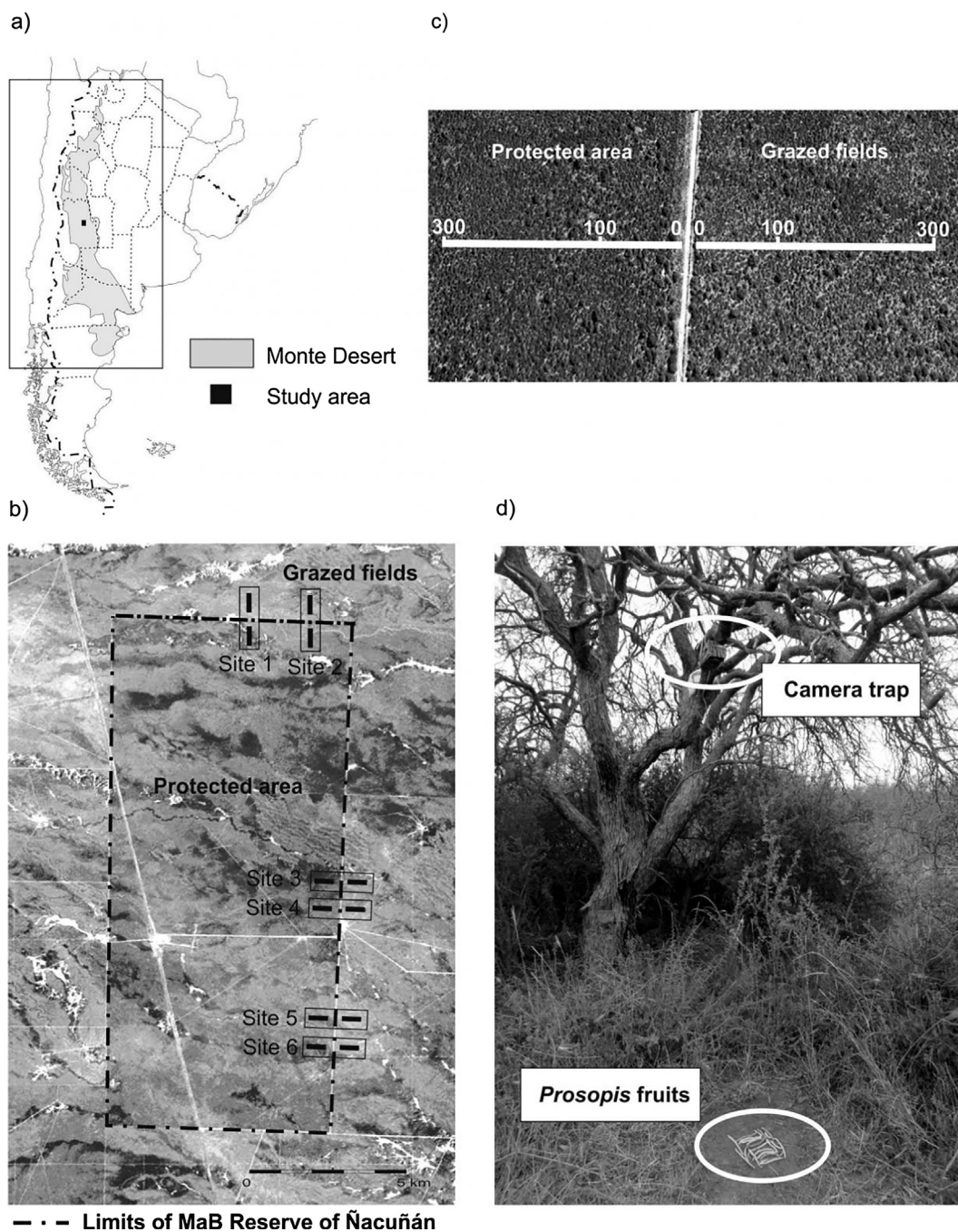
Fig. 1. Study area and sampling design from boundary to protected and grazed fields; (a) geographical location of the study sites showing the Monte Desert distribution and the study area; (b) location of the six sampling sites, from boundary to inside the protected area and grazed fields; (c) scheme representing distances from boundary (open unpaved road) to interior land use (0 m, 100 m and 300 m) in areas with different protection status; (d) picture showing a camera trap on an adult *P. flexuosa* tree focused on a group of *Prosopis* fruits placed on a cleared location on the ground (no. of replicates = 36).

above ground. Animal species were identified by fur color, tail and body length and other species-specific physical traits (Ojeda, 1989; Braun and Ojeda, 2000; Giannoni et al., 2001; Tognelli et al., 2001).

2.4. Habitat structure

To precisely describe the habitat structure at each distance from boundary to protected and grazed fields, we used 25 plots of $4 m^2$ (total plots = 900). Plots were located every 10 m, starting from every focal *Prosopis* tree trunk, along a linear transect 250 m long perpendicular to distance gradient (total number of transects = 36). Within each quadrat, we quantified the percent cover of trees, shrubs, grasses and

bare ground. We estimated the proportion of each cover type by dividing it by the sum of the total cover recorded at each plot.

2.5. Data analyses

To make a clear description of the vegetation structure from boundary to protected and grazed fields (Cadenasso and Pickett, 2000; Kollmann and Buschor, 2002), we used the non-parametric Mann-Whitney test to compare the cover of habitat variables between the protected and grazed fields and the Kruskal-Wallis test, with the post-hoc pairwise Wilcox test with Holm correction ($p < 0.05$), to compare the cover of habitat variables (cover of trees, shrubs, grasses and bare

ground) among distance classes within each land use and among all the distance classes from boundary (Zar, 1996).

We analyzed the number of animal visits and the number of fruits removed by frugivorous species at different distances as quantitative components of the Interaction Stage of seed dispersal (Schupp et al., 2017). We performed zero-inflated mixed models with Poisson error structure (Zeileis et al., 2008; Zuur et al., 2009) to compare both the number of *Prosopis* fruits removed and the number of visits to *Prosopis* trees by mammal species (response variables) among distances from boundary. The explanatory variables used in models were: distance from boundary and mammal species (with four levels, *M. australis*, *L. griseus*, *G. griseoflavus* and *A. dolores*). We also analyzed the interaction between distance and mammal species. To account for the hierarchical structure of our design, we constructed mixed models by nesting camera trap station within distance and fruit replenishment events within camera trap station (McCulloch and Searle, 2001). As a measure of model fit, we calculated the R^2 for zero-inflated Poisson models (Martin and Hall, 2016).

We fitted separate zero-inflated mixed models with Poisson error structure to each of the four species removing the highest number of fruits and with the highest number of visits to trees (see Fig. A.1). Due to a low sample size we did not build separate models for the other species recorded removing *Prosopis* fruits (see Table 2 for species detail). In order to compare the number of fruits removed by the four mammal species from boundary we constructed statistical models considering as explanatory variables: distances from boundary and habitat variables (cover of trees, shrubs, grasses and bare ground expressed as proportions). Before fitting the models, we tested for collinearity among local habitat variables, and we did not include in models those correlation pairs with a magnitude greater than ± 0.5 (Booth et al., 1994; Zar, 1996).

All analyses and graphs were performed using the R package, v. 3.2.5 (R Core Team, 2016). We used the *kruskal.test* function in package stats for habitat structure analyses, and the *zeroinlf* function in package pscl for zero-inflated model building (Zeileis et al., 2008).

3. Results

The extent of grass and tree cover differed between the protected and grazed fields (U = 21.16, n = 450, p = 0.02; U = 19.1, n = 450, p = 0.0002), showing a contrasting pattern between both land practices. Grass cover decreased from boundary to interior in protected area and increased from boundary to interior in grazed fields. Tree cover showed an opposite trend to grass cover, increasing in the protected area from boundary to interior and decreasing from boundary to interior in grazed fields, although the significant differences were among distance classes within the protected area (see below). Cover of bare ground increased in the grazed fields compared to the protected area (Table 1). Cover of all habitat variables differed among distance classes from boundary. Bare ground cover was different among distances within both land uses (H = 13.24, p = 0.0013; H = 62.29, p < 0.0001), while tree cover differed among distance classes only within the protected area (H = 6.22; p = 0.003; H = 3.92; p = 0.06; Table 1).

Table 2

List of species recorded by camera traps. Some species removed *Prosopis* fruits (R.f.) while others only visited trees (V.t.). Data are means ± SE of total fruits removed and visits to trees and the total number of trees visited by mammals (sampled trees = 36).

|	Mammal species	Fruits removed	Visits	Number of trees visited
	Microcavia australis	29.64 ± 4.84	58.78 ± 11.87	26
	Lycalopex griseus	18.06 ± 3.82	18.83 ± 4.10	19
	Graomys griseoflavus	13.94 ± 2.60	34.53 ± 4.40	35
R.f.	*Akodon dolores*	4.78 ± 1.59	6.50 ± 1.83	17
	Conepatus chinga	0.47 ± 0.37	0.78 ± 0.45	6
	Chaetophractus vellerosus	0.33 ± 0.31	0.31 ± 0.20	5
	Calomys musculinus	0.03 ± 0.03	0.06 ± 0.06	1
V.t.	*Galictis cuja*	0	0.03 ± 0.03	1
	Leopardus geoffroyi	0	0.08 ± 0.06	2
	Thylamys pallidior	0	0.14 ± 0.07	4
	Dolichotis patagonum	0	0.03 ± 0.03	1

The number of fruit replenishment events did not differ between land uses (U = 349, n = 18, p = 0.56) or among distances from boundary (H = 1.30, n = 6, p = 0.45; H = 3.03, n = 6, p = 0.13). We obtained a total of 21,045 images, in which we recorded 11 terrestrial native mammal species, four species only visited *Prosopis* trees but did not remove fruits, whereas seven species removed *Prosopis* fruits (Table 2).

The number of fruits removed by mammals differed among distances (z = −4.57, p < 0.0001; R^2 = 0.61). Moreover, models showed that the number of fruits removed was different among species (Table 3), with *M. australis* and *L. griseus* removing the highest number of fruits (Table 2). The interaction between distance and mammal species was also significant. *Microcavia australis* removed the highest number of *Prosopis* fruits at 0 m distances from protected and grazed lands, *L. griseus* removed the highest number of fruits at 100 m from the grazed lands, *G. griseoflavus* at 100 m from the protected and 300 m from the grazed lands, and *A. dolores* removed the highest number of fruits at 300 m from grazed lands (Fig. 2). The number of fruits removed by *M. australis* was positively explained by the cover of bare ground, shrub and grass (z = 2.80, p = 0.005; z = 2.27, p = 0.02; z = 2.29, p = 0.02, respectively). For *L. griseus* was negatively explained by the cover of bare ground, shrub and grass (z = −6.97, p < 0.0001; z = −4.94, p < 0.0001; z = −4.86, p < 0.0001, respectively). The number of *Prosopis* fruits removed by *G. griseoflavus*, was explained by the cover of trees and grass (z = 3.28, p = 0.001; z = 2.08, p = 0.04, respectively). Finally, the number of fruits removed by *A. dolores* was negatively explained by the cover of bare ground (z = −2.04, p = 0.04; Table A.1). The number of visits by mammal species to *Prosopis* trees also varied with distance (z = −8.47, p < 0.0001; R^2 = 0.55) and with frugivorous species. *Microcavia australis*, followed by *G. griseoflavus*, were the species with the highest number of visits recorded (Table 3).

Table 1

Vegetation cover and comparisons by Kruskal- Wallis test from boundary to protected area and grazed fields at different distances (0 m, 100 m and 300 m). Data are means ± 1 standard error (SE), given as percentages.

Habitat variable	Protected			Grazed			Kruskal test	
	0 m	100 m	300 m	0 m	100 m	300 m	Chi-squared	p value
Trees	3 ± 1	4 ± 1	8 ± 1	11 ± 1	9 ± 1	5 ± 1	29.89	< 0.0001
Shrubs	37 ± 2	39 ± 1	36 ± 1	35 ± 2	42 ± 2	35 ± 1	19.40	0.002
Grasses	16 ± 1	13 ± 1	12 ± 1	8 ± 1	12 ± 1	19 ± 1	51.44	< 0.0001
Bare ground	18 ± 1	13 ± 1	18 ± 1	24 ± 2	9 ± 1	20 ± 2	82.54	< 0.0001

Table 3

Results of zero-inflated mixed models with a Poisson error structure testing whether the number of *Prosopis* fruits removed and the number of visits to trees differ among distance and mammal species (with four levels, *M. australis*, *L. griseus*, *G. griseoflavus* and *A. dolores*).

Adjusted model	Effect	Estimate	Std. error	z value	p value
No. fruits removed ~ distance * species	Intercept	4.49	0.1	36.8	< 0.0001
	Distance	−0.0014	0.0003	−4.57	< 0.0001
	Microcavia australis	0.52	0.1	4.9	< 0.0001
	Lycalopex griseus	−0.177	0.105	−1.68	0.09
	Graomys griseoflavus	−3.372	0.470	−7.16	< 0.0001
	Akodon dolores	−3.998	0.821	−4.86	< 0.0001
	Distance * *Microcavia australis*	−0.0009	0.0002	−3.87	0.0001
	Distance * *Lycalopex griseus*	0.0006	0.0002	2.31	0.02
	Distance * *Graomys griseoflavus*	−0.0006	0.0002	−2.31	0.02
	Distance * *Akodon dolores*	0.0009	0.0003	2.48	0.01
No. visits ~ distance * species	Intercept	5.38	0.09	58.9	< 0.0001
	Distance	−0.002	0.0002	−8.47	< 0.0001
	Microcavia australis	0.99	0.07	14.3	< 0.0001
	Lycalopex griseus	−1.44	0.11	−13.6	< 0.0001
	Graomys griseoflavus	−0.95	0.07	−13.72	< 0.0001
	Akodon dolores	−2.18	0.12	−18	< 0.0001
	Distance * *Microcavia australis*	−0.0004	0.0002	−2.39	0.01
	Distance * *Lycalopex griseus*	0.001	0.0002	5.82	< 0.0001
	Distance * *Graomys griseoflavus*	0.0002	0.0002	0.80	0.42
	Distance * *Akodon dolores*	0.002	0.0003	5.76	< 0.0001
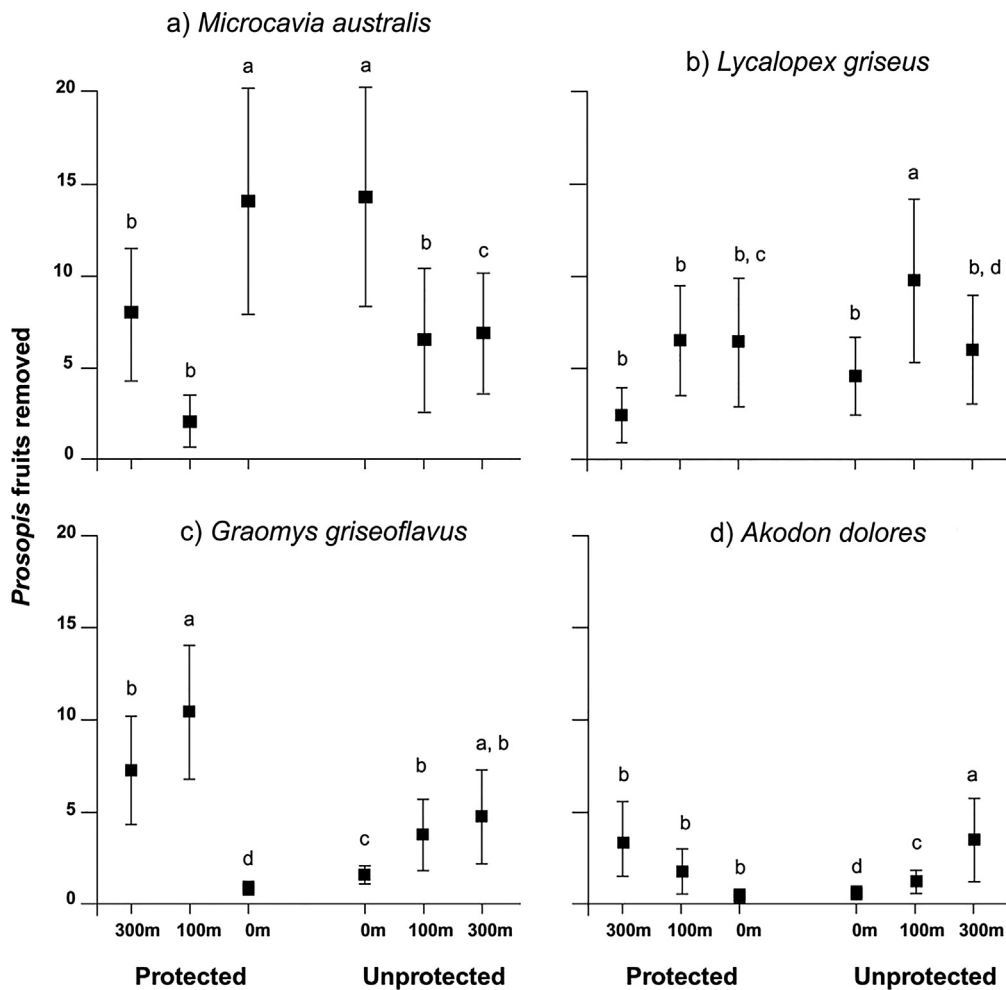
Fig. 2. *Prosopis* fruits removed between protected and grazed fields at 0 m, 100 m and 300 m from boundary toward both sides. Different panels represent fruits removed by (a and b) seed disperser species and (c and d) seed predator species. Data are means ± S.E. Differences in number of fruits removed by species across distances (results of GLMM) are shown by different letters.

4. Discussion

The quantitative components of seed dispersal, i.e. the number of *Prosopis* fruits removed and the number of visits by mammals, varied with distance from boundary to protected area and grazed fields and also with frugivorous species. Moreover, we registered habitat cover changes among distance classes from the boundary that explained frugivore interactions with focal trees. Enhancing the spatial continuity among differently managed areas and particularly between protected areas and adjacent modified lands is essential for maintaining wildlife populations and ecosystem functions in the context of land-use change (DeFries et al., 2010). Furthermore, it is crucial to consider seed dispersal in this context because it is a process that affects plant persistence and migration in response to global change (Howe, 2016). Although more studies are needed to assess plant recruitment, only a minor subset of *Prosopis* frugivores appears to potentially contribute to seed dispersal events suggesting its importance in the connection of landscapes.

Changes in some biotic or abiotic attributes near boundaries may affect species interactions and ecological processes (Fagan et al., 1999; Kollmann and Buschor, 2002). Here, we described changes in habitat covers at different distances from boundary and we found that these habitat modifications influence interaction among focal trees and mammal species. Specifically, these functional responses are in accordance with the habitat preferences of different functional groups. Thus, seed dispersers, which are associated with high bare ground cover and an arboreal structure, were related with distances near boundary and from boundary to grazed fields. However, seed predators were closely associated with densely vegetated patches in distances further from boundary. This habitat pattern may entail functional implications to the *Prosopis* seed dispersal dynamics, regarding plant recruitment and seed dispersal distances. Furthermore, some other ecological factors of boundaries not evaluated here, such us the fruit crop size (Jordano and Schupp, 2000), may also be influencing the pattern of plant-frugivore interaction.

Boundaries between land uses may be differently perceived by mammal species, depending on species traits, kind of land uses that boundaries separate, and habitat attributes of boundaries themselves (Lidicker and Peterson, 1999; Lidicker, 1999; Fahrig, 2007). The assemblage of frugivores in our study varies from small rodents to medium-sized carnivores, which implies species with a different landscape-scale perception (Tabeni et al., 2007). We found an effect of distance from the boundary on the number of fruits removed and visits to trees by each mammal and, therefore, by different functional groups. Thus, medium-sized mammals, such as *M. australis* and *L. griseus,* removed a higher number of fruits at distances nearer the junction of protected-grazed fields, while the small mammals *A. dolores* and *G. griseoflavus,* did so at distances furthest from boundary to both land uses (Fig. A.2). *Microcavia australis* was the species responsible for the highest number of fruits removed and also was the most frequent visitor of *Prosopis* trees. Considering that removal of fruits generally leads to seed dispersal if done by legitimate seed disperser (Jordano and Schupp, 2000), our results suggest an increase in the frequency of interactions by a hoarder species (Campos et al., 2017) at distances nearer boundary.

The assemblage of *Prosopis* frugivores is also composed of species that can act as seed predators, implying that their interactions are often non-mutualistic. For example, *G. griseoflavus* and *A. dolores* mainly predate on *Prosopis* seeds (Giannoni et al., 2013), but can sporadically act as seed dispersers. There is ample evidence that seed predation by small mammals increase at sites with high vegetation cover because of the high abundance of rodents (Kollmann, 1995; Hulme, 1997; Kollmann and Buschor, 2002). We showed that habitat structure close to boundary seems to be not favorable for occupation by small rodents who prefer sites with dense grass cover (Tabeni and Ojeda, 2003, 2005; Corbalán, 2006; Campos et al., 2016). In accordance with this, we

clearly recorded that these species removed a lower number of *Prosopis* fruits at distances nearer boundary. The increase in fruits removed by small rodents to grazed interior lands may be due to the increased grass cover in some remnant ungrazed patches. Besides, a previous study in the area found that small rodents removed a higher number of *Prosopis* seeds inside the protected area than from the adjacent grazed fields (Miguel et al., 2017). Our results support the idea that there is an increased probability for *Prosopis* seeds to be predated in more covered interior habitats than in open boundaries.

Conversely, open boundaries may have a positive effect on seed dispersal processes mediated by large mammals (Suárez-Esteban et al., 2013), because these animals may select for and disseminate viable seeds along unpaved roads, especially at the margins. As regards seed dispersers, we found an increased number of *Prosopis* fruits removed by *M. australis* at distances nearer open unpaved boundary. Additionally, the number of fruits removed by *L. griseus* increased from boundary to grazed interior fields. Both mammals disperse *Prosopis* seeds by different strategies. On the one hand, *M. australis* is recognized as a scatter-hoarder that stores seeds in small caches in the ground for future consumption (Campos et al., 2017). On the other hand, *L. griseus* disperses *Prosopis* seeds by endozoochory (Campos and Ojeda, 1997), ingests entire fruits to then defecate viable seeds (Jordano, 2000; Forget and Cuijpers, 2008). Our results are supported by the known variation in habitat preferences among species. Thus, for *M. australis*, we found a positively association with bare ground confirmed by previous studies that described a preference of this species for open spaces to build its colonies, beneath an umbrella-like tree structure (Tognelli et al., 1995). Regarding *L. griseus*, it is recognized that carnivores are generalist species and may select open roads to move between sites and to search for food (López- Bao and González-Varo, 2011; Rost et al., 2012; Suárez-Esteban et al., 2013).

Seed fluxes across the landscape are of crucial importance for the functional connectivity of areas (Lundberg and Moberg, 2003). This ecological process maintains plant population and allows for colonization of new habitats and migration in response to global change (Nathan, 2006; Howe, 2016). According to our results, we suggest that seed disperser mammals may be acting as important connectors between the protected area and the surrounding human modified landscape. However, the contribution of both species to the functional connectivity of sites may be occurring at different scales, because of species-specific differences in body size and movement capacity (Correa Cortes and Uriarte, 2013). Thus, because of the smaller body size of *M. australis* in comparison with *L. griseus*, the first species might be acting at small spatial scale (Campos et al., 2017) and maintaining *P. flexuosa* populations. Instead, *L. griseus* might be acting at a larger spatial scale, moving *Prosopis* seeds throughout the landscape, considering its greater movement capacity (Jiménez et al., 2008). Nonetheless, further research on the seed shadow (Nathan and Muller-Landau, 2000) among protected areas and grazed fields is needed to completely explain the functional connectivity mediated by these mammals through seed gene flow (Cadenasso and Pickett, 2000, Correa Cortes and Uriarte, 2013).

5. Conclusion

We provide evidences of different habitat structure and functional activity of frugivorous mammals imposed by the boundary between a protected area and surrounding grazed fields. As we focused on a boundary between gradual woodland transitions (Cadenasso et al., 2003; Fahrig, 2007), the different responses of each species to the physiognomic vegetation gradient changes were explained by their habitat preferences. Mammalian seed dispersers could in turn assist the functional connectivity of differently managed sites by moving seed across boundaries at different spatial scales, effectively contributing to plant recruitment. Moreover the demographic effects of seed predators on *P. flexuosa* populations remain to be investigated. Therefore, studying boundaries between protected areas and surrounding

agricultural landscapes with a functional approach may help in determining how effectively connected protected areas are, and consequently help assessing their role as sites for biodiversity and ecosystem function maintenance.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.03.056.

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