RESEARCH ARTICLE

Small mammal abundance and seed predation across boundaries in a restored-grazed woodland interface

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Passive restoration is an effective tool for the maintenance and conservation of biodiversity. Often areas in recovery are immersed in a matrix of land uses, in which the expansion and intensification of human activities exert new visible pressures at their boundaries. The degree of connectivity between these areas and their peripheral lands can be analyzed by mobile link species, organisms that actively move in the landscape by connecting areas to one another through their functional roles. We focus our design on the interface generated by the long-term restoration area and surrounding grazing lands. We analyze the changes on boundary structure, small mammal abundance, and on the function of native seed dispersal by these vertebrate species. We captured small mammals and determined seed removal of *Prosopis flexuosa* at three distances inside and outside a fence that delineates passively restored and currently grazed areas. Our results indicate that small rodents find more suitable habitats at the site under restoration than in grazing lands. The restored-grazing interface shows a decrease in small mammal abundance from the protected area to the grazed lands. From a functional perspective, an increase in small mammal abundance results in an increase in their seed removal activity with implications for seed fate, because the long-term recovery of vegetation could enhance seed predation on a native tree species.

Key words: grazing, passive restoration, *Prosopis flexuosa*, rodents, woodland

Implications for Practice

- Examining changes in small mammal diversity, knowing the roles of species as seed predators or dispersers, can help to understand restoration success better than monitoring vegetation changes alone.
- The occurrence and flow of small mammals can be limited by the contrast of habitats generated by jurisdictional boundaries between restored areas and grazed fields.
- The functional group of animals favored by long-term recovery policies can impact ecosystem dynamics in unexpected ways, and their consequences should be monitored next to the trajectories of vegetation communities.

Introduction

Promoting ecological connectivity across the landscape has become an emerging challenge for the conservation of species and processes in terrestrial ecosystems fragmented by land uses (Mayer et al. 2016). An issue of concern is the growing loss of connection between passive restoration areas (PRAs) devoted to biodiversity conservation and the surrounding private lands (Palomo et al. 2014).

Passive ecosystem restoration is a strategy implemented to promote the natural development of communities with a minimal human intervention. This strategy is emerging as the most appropriate for restoring native communities (Hobbs & Cramer 2008). Thus, the rewilding of abandoned farmland in Europe has shown an increase in biodiversity and ecosystem services achieved through an unassisted restoration process (Navarro & Pereira 2015). Protected areas are the clearest examples of recovery of plant biomass achieved at post-disturbance sites following passive strategies; thereby, this practice has been interpreted as a successful indicator of the system's potential for resilience (Aronson et al. 1993).

However, the manner in which communities under restoration interact with the surrounding landscape, influencing plant−animal interactions and key ecological processes across their borders, remains little explored. There is evidence that the advancement of land use promotes the isolation of protected areas and the occurrence of biological invasions across their boundaries (Wilson et al. 2015). But, on the other hand, several ecosystem services and processes can occur in these peripheral areas, contributing to the permanence of habitats for wildlife species (Mitchell et al. 2013). For example, lands outside of protected areas may contain unique habitats that are required by mammals and birds, playing a complementary role in their conservation (Pino et al. 2000; Hansen & Defries 2007; Tabeni

et al. 2013). Furthermore, it has been noted that the spatial continuity of processes and ecosystem services performed by animals can require habitats spatially connected across different land uses (Kremen et al. 2007).

In drylands, landscape connectivity is an essential property of many ecosystem processes that shape habitat structure and whose modification can lead to desertification (Okin et al. 2015). Usually, landscape connection between PRAs and their surrounding lands is molded by uses and demands of local people living in the adjacencies (Newmark 2008). The boundaries between adjacent management practices aim to avoid any interaction with agents of disturbance. In particular, fenced boundaries can prevent the entry of livestock in neighboring protected areas, providing different levels of restriction to the spatial continuity of biotic interactions and of ecosystem functions across managed lands (Durant et al. 2015). Permeability of habitat structure, which facilitates or prevents the flow of organisms, is dependent on scale and on species concerned (Cadenasso et al. 2003). Mostly, fenced boundaries are considered to be an effective barrier to inhibit the movement of native wildlife of medium and large body size (Wisdom et al. 2013). However, this barrier would not constitute an obstacle to the movement of small vertebrates, but would rather represent a change in habitat conditions and in the species' use of resources (Spirito & Tabeni 2016).

Some animal groups act as *mobile linkers*, sustaining essential ecosystem processes by connecting different or similar types of habitats through the transporting of resources such as genetic information, organic material, nutrients, pollen, and seeds (Polis et al. 1997; Lundberg & Moberg 2003). They can also promote the flow of resources from high to low productivity areas, fulfilling an important role against disturbances as they contribute to sustaining ecosystem resilience (Lindenmayer et al. 2008). In other words, although the importance of including the role of animals in restoration is well known (Majer 2009), monitoring the functions mediated by mobile organisms has been recently highlighted (Kennedy et al. 2013; Kollmann et al. 2016). Desert small mammals have been widely recognized to be mobile link species, with significant effect on ecosystem processes across the landscape. From local to a large scale, they have several functional roles, such as pollination, spread of mycorrhizal fungi, soil nutrient distribution, and seed dispersal (Wilcox & Murphy 1985; Lindenmayer et al. 2008; Giannoni et al. 2013; Zoeller et al. 2016). Seed dispersal of keystone trees, such as *Prosopis* species in dry woodlands, is carried out by a diversity of mammal species (Campos et al. 2016). This process can be influenced by the presence and abundance of natural dispersers, as well as by the distinctive strategies of seed consumption and seed hoarding they display in response to the fluctuating availability of seeds (Vander Wall et al. 2005; Zhibin Zhang 2007; Ratiarison & Forget 2011; Campos & Velez 2015).

We analyzed the habitat changes imposed by the boundaries between a long-term restoration area and the surrounding grazing fields on small mammal abundance and seed removal activity. The land use pressures exerted on dry ecosystems around the world, and their consequent loss of native wildlife and functional diversity (Chillo & Ojeda 2012), are demanding to know how the restoration and protection of habitats adjacent to grazed

ecosystems shape the occurrence of specific animal groups and the resources they vectorize (native seeds in this study). *Prosopis* seed removal could be considered the net outcome of animal activity, which may result in successful seed dispersal if done by seed dispersers (e.g. frugivores and scatter-hoarders), or seed loss if done by seed predators, depending largely on animal feeding behavior, fruit processing, and post-feeding movements (Giannoni et al. 2013; Campos & Velez 2015). We applied an unusual animal-based approach in a restoration context, from a recommended two-sided perspective (sensu Fonseca & Joner 2007), to address the following questions:

1 Can the abundance of mobile organisms change through adjacent land uses and to what extent does the resulting habitat structure predict this pattern?
2 Do the abundance and identity of small mammals across land uses influence seed removal from a key tree species?
3 Is it possible to interpret the functional status of the restored-grazing lands and their connectivity through mobile indicators and their functional roles?

Our objectives were to: (1) compare the occurrence of small mammal species and their abundances from set distances inside and outside a fence that excludes grazing; (2) quantify *Prosopis* seed removal by small mammal species along these distances; and (3) test the influence of local habitat structure on the presence and abundance of small mammals across the fence boundary and how seed removal is affected.

Methods

Study Area

We conducted our study in the boundaries between a PRA corresponding to the Man and Biosphere Reserve of Ñacuñán (34°02′S, 67°58′W; 12,300 ha) and the peripheral areas under continuous cattle grazing. The study area is located in the Monte Desert biome of Argentina. The climate is semiarid, with warm rainy summers (mean temperature > 20°C) and cold dry winters (mean temperature <10°C). Average annual rainfall is 329 mm (Estrella et al. 2001). The reserve was created in 1961 to protect native *Prosopis* woodlands by implementing a fencing policy aimed to exclude the grazing activities conducted on the surroundings fields and promote passive restoration of the ecosystem. In 1986, it was included into the UNESCO Man and Biosphere Reserve Network and is currently a key site for monitoring post-disturbance processes in the Monte Desert. The main plant communities are open woodland of *Prosopis flexuosa* interspersed by shrubland dominated by *Larrea* spp. The open woodland is structured with a layer of tree species (*P. flexuosa* and *Geoffroea decorticans*), a shrub layer dominated by *Larrea divaricata*, *Larrea cuneifolia*, and *Condalia microphylla*, and a grass layer of *Pappophorum* spp. *Trichloris crinita* and *Digitaria californica*, among others (Roig 1971). *Prosopis flexuosa* is a key tree species because it provides important ecosystem services to local communities, such as shade and forage for livestock, food, firewood, and materials for house building (Álvarez & Villagra 2009). It also
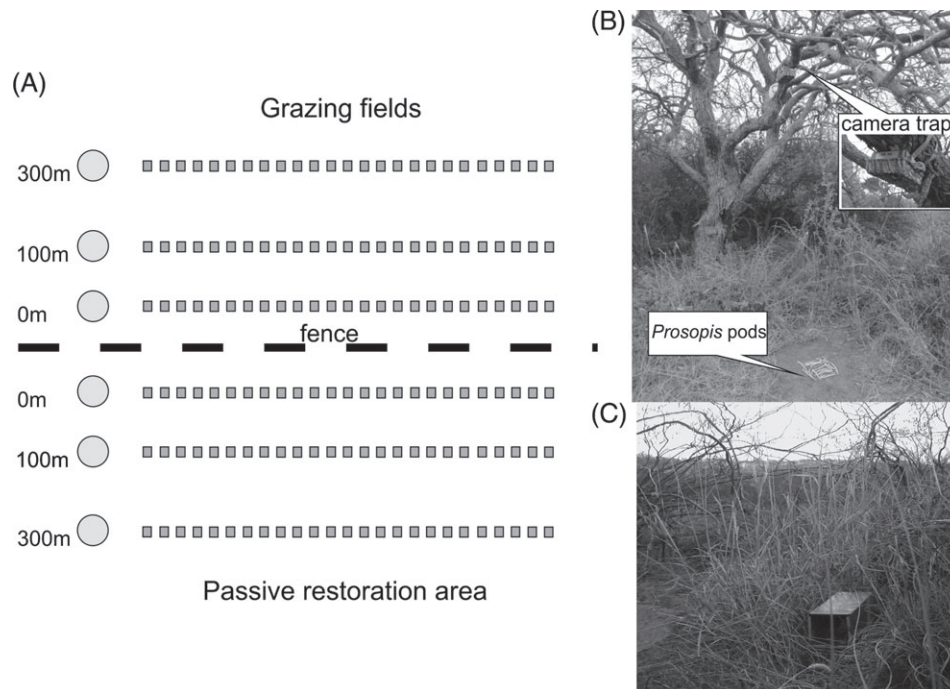
Figure 1. (A) Diagram of station placement for camera traps (gray circles) and live traps (gray squares) at every distance considered (0, 100, and 300 m) from the fenced boundary to the inside of the PRA and adjacent grazing fields. (B) Camera trap on an adult *Prosopis* tree oriented toward *Prosopis* fruits on the ground. (C) Live trap for small mammal captures.

acts as a nurse plant for shrubs and grasses, favored by shaded and humid microhabitat formed under their canopy (Rossi & Villagra 2003) and maintains multiple interactions with local wildlife (Aschero & Vázquez 2009; Campos et al. 2016, 2017). The small mammal species (<100 g) inhabiting this woodland comprise rodents such as the silky mouse (*Eligmodontia typus*), the gray leaf-eared mouse (*Graomys griseoflavus*), the grass mouse (*Akodon dolores*), the vesper mouse (*Calomys musculinus*) (Rodentia, Cricetidae), and a small opossum (*Thylamys pallidior*) (Marsupialia, Didelphidae).

Sampling Design

The sampling sites were established in the area of adjacency between the PRA and surrounding grazing fields, corresponding to *Prosopis* woodland communities. The areas delimiting the passive restoration site correspond to fenced, unpaved roads (mean width 9 m) maintained by vegetation clearing, which act as firebreaks.

Along this area, we randomly distributed six transects arranged perpendicular to the boundary fence. On each transect we established three sampling sites at three distances (0, 100, and 300 m) from the boundary fence to the inside of the PRA (18 sites) and of the grazing fields (18 sites) (Fig. 1). The distances considered in the sampling design were built on significant spatial scales for the species studied here, for which we considered previous studies on spatial use, movement patterns, and home range of small mammal species in this study area (Corbalán 2006; Tabeni et al. 2007; Spirito 2015).

Small mammal trapping sessions and seed removal experiments were conducted during April 2015 and 2016 by implementing a paired design using live-trap and camera-trap methodologies. At every distance we placed one camera-trap and a trap-line comprising 25 trapping stations at 10-m intervals. A 250-m long trap line was consistent with the home range of some small mammals in the area (30 m in diameter, Spirito 2015). Abundance of small mammals was measured by a total of 900 live capture traps along boundaries. Sherman live traps were baited with rolled oats and vegetable oil and remained open at night for four consecutive days, totaling 3,600 trap-nights in both years. Traps were checked in the morning, captured animals were marked, and their weight, sex, and reproductive condition recorded before being released in the same place where they had been captured.

For the *Prosopis* seed removal experiment, at every distance we placed a camera trap (Moultrie m-990i) paired with a live trap line (Fig. 1). Each camera trap was located on an adult *P. flexuosa* tree, and during five consecutive days and nights it recorded animals removing the offered seeds. The cameras took three consecutive pictures every 30 seconds whenever movement was detected. The total number of camera stations was 36 (18 camera stations on either side of the fence). We placed a bait station on the ground, immediately below the canopy of each *Prosopis* tree, which consisted of 20 entire *Prosopis* pods with 15 seeds each (300 seeds per tree). Bait stations were checked every day, and replenished when animals had removed all of the fruits. As animals removed entire *Prosopis* fruits from the field of vision of camera traps, we converted the number of removed

Table 1. Total captures for each species between passive restoration area and grazing fields at three distances and number of captures of the same individual in both land managements.

Small Mammal Species	Total Captures	Passive Restoration Area			Grazing Fields			Number of Captures on Both Sides
		300 m	100 m	0 m	0 m	100 m	300 m	
Graomys griseoflavus	136	20	46	25	22	14	9	1
Akodon dolores	41	10	6	3	3	3	16	0
Eligmodontia typus	33	7	3	8	9	1	5	3
Calomys musculinus	17	7	3	3	1	3	0	0
Thylamys pallidior	17	2	1	0	5	4	3	0

fruits into number of removed seeds per animal species at every distance. We obtained this variable by multiplying the number of fruits removed by every small mammal species on each visit to the trees by the number of seeds contained in each fruit. Offered fruits consisted of ripe ones collected in the study area from multiple *Prosopis* trees. For small mammal identification from each individual image obtained by camera traps, we visually compared tail and body length, fur color and other physical aspects, following species descriptions (Ojeda 1989; Braun et al. 2000).

We measured the local habitat variables on a 2-by-2 m plot centered in each live trap station. We recorded the percent cover of grasses, forbs, shrubs, subshrubs, trees, bare ground, and litter. A total of 450 plots were established on both sides of the boundary fence. Then we estimated the proportion of each cover type dividing it by the sum of the total cover recorded on each plot.

Statistical Analyses

We built generalized linear mixed models fitted with a Poisson error distribution because abundance of small mammals as well as number of seed removed were count data variables (McCulloch & Searle 2001). As we detected a higher amount of zeros than expected for a Poisson distribution, we fitted zero-inflated mixed models with a Poisson error structure (Zeileis et al. 2008; Zuur et al. 2009). The sign of parameters having significant effects was used to interpret the results (McCulloch & Searle 2001; Bolker et al. 2008).

We examined whether mammal total abundance varied with distance along the zone of interaction and with different local habitat variables. We performed a full model, considering land uses (with two levels: restored and grazing lands), distances (with three levels: 0, 100, and 300 m), and all habitat variables (bare ground, litter, herb, tree, shrub, subshrub, and grass cover) as explanatory variables. We constructed models with different combinations of habitat variables and selected the model with the lowest Akaike's information criterion value (AIC) (Table S3, Supporting Information). Before fitting the models, we tested for collinearity among local habitat variables; as none of the correlation pairs obtained had a magnitude greater than ±0.5 (Booth et al. 1994; Zar 1996), we included all of them in the full model. Based on the hierarchical structure of our design, we constructed mixed models and nested line-transects within distances and traps within line-transects (McCulloch & Searle 2001). For the generalist and most abundant small mammal,

G. griseoflavus, we evaluated the effects of distance and habitat characteristics on its abundance. We followed the same steps explained above regarding model building and selected the best zero-inflation mixed models with a Poisson error structure for that species.

We also analyzed whether the number of seeds removed by small mammals varied with distance along the restored-grazed boundary fence and whether species abundance at each distance affected the number of seeds removed. The hierarchical structure of this design was considered by nesting camera trap replicates within distances and fruit replenishment events within camera trap replicates (McCulloch & Searle 2001). We constructed separate specific models for *G. griseoflavus*, which was the rodent species that removed the majority of *Prosopis* seeds in our study (see Table 1 for species details). Owing to a low sample size we did not build separate models for the other species recorded removing *Prosopis* seeds. For both the abundance and the seed removal models we included habitat covariates only in the positive count model, while we modeled the probability of the false zeros with a constant (intercept; Zuur et al. 2009).

All analyses and graphs were performed using program R 3.3.1 (R Development Core Team 2016). We used the function *zeroinlf* in the package "pscl" for building zero-inflated models (Zeileis et al. 2008) and the *cor* function in the "stats" package for testing collinearity of habitat variables using a Spearman correlation method (Becker et al. 1988). For representing the number of independent detections of each small mammal species captured by the camera traps we used the function *detectionMaps* in the package camtrapR (Niedballa et al. 2016). By plotting maps of species records, this function allows a clear visualization of species detections by different camera stations. Considering the spatial location of each station and the number of independent detections per species we constructed detection maps.

Results

We captured a total of 242 individuals over 3,600 trap-nights belonging to five small mammal species (Table 1). Only 0.02% of the total number of individuals was captured on both sides of the boundary fence, indicating a very low frequency of animals crossing between areas under different land uses (Table 1). The number of individuals recaptured between distances was
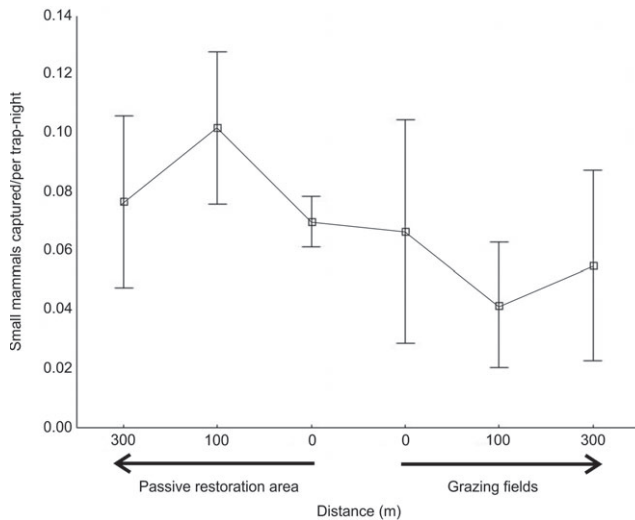
Figure 2. Small mammal captures per trap-night along distances (0, 100, and 300 m) from the fenced boundary to the inside of the PRA and adjacent grazing fields. Data are means ± SE of 150 live traps for each distance considered (*n* traps = 900).

also remarkably low, with only one recapture, of *Graomys griseoflavus*, between 100 and 300 m inside the PRA. Overall, each species has a different response to distance and land management. Thus, for *G. griseoflavus*, the most abundant species of the assemblage, its greater abundance was recorded at 100 m within the PRA, while *Akodon dolores* was more abundant far from the edge and inside the grazing fields. *Eligmodontia typus*, on the other hand, showed similar abundances on both sides of the boundary, although slightly higher at distances nearer the fence. *Calomys musculinus* was more abundant at 300 m within the PRA and *Thylamys pallidior* showed greater abundance within grazing fields, although homogeneously distributed across distances (Table 1).

Small mammal captures decreased with distance along the zone of interaction from the PRA to the grazing fields ($z = -1.98$; $p = 0.04$; Fig. 2). At 100 m distance, inside the PRA, we recorded the highest number of mammal captures (PRA 100 m; Table S1). The models revealed that bare ground and litter cover were the local habitat variables that best explained the total abundance of small mammals across boundaries ($z = -5.49$, $p < 0.0001$; $z = -2.6$, $p = 0.009$, respectively; Table S1), showing that a decrease in vegetation cover toward the interior of the fields affects this species negatively. Model building at the species level indicated that abundance of *G. griseoflavus* decreased with distance along the zone of interaction toward the interior of the fields, with bare ground cover being the variable that best explained this response ($z = -3.6$, $p = 0.0003$; Table S1).

Three of the species captured with live traps were detected removing *Prosopis* seeds by camera traps (Fig. 3). About a total of 36 camera stations, *G. griseoflavus* was detected removing seeds at 23 camera stations, *A. dolores* at 8, and *C. musculinus* at only 1 station (Fig. 3). *Prosopis* seed removal by small mammals showed a tendency to decrease across boundaries

from the PRA to the grazing fields (Table S2). Models indicate that the seed removal function is strongly positively affected by abundance of small mammal species ($z = 4.74$, $p < 0.0001$; Table S2).

Of the three rodent species recorded by camera traps, *G. griseoflavus* was the species that removed the highest number of seeds, which was positively associated with its abundances on both sides ($z = 5.27$, $p < 0.0001$). The distances nearer the junction of the two adjacent areas (G0 m and G100 m) showed a decrease in the number of *Prosopis* seeds removed by *G. griseoflavus* (Table S2; Fig. S1). The smallest species of the assemblage, *E. typus*, was not recorded in our camera trap study, either visiting trees or removing fruits. However, this species was present at the sites since we captured *E. typus* individuals in the live traps.

Discussion

Influence of Restored-Grazing Area on Desert Small Mammals

Mobile organisms offer a nonstatic vision to interpret how changes in landscape features limit their movement among habitats and their functional roles as biotic vectors (Lundberg & Moberg 2003). Here we focus on a restored-grazed interface to explore current ecological connectivity using small native mammals. Putting our results into a classic restoration context, that is setting the focus on restoring the natural conditions after disturbances, the overall abundance of these native organisms shows an effective increase within the restored area with respect to the surrounding fields, which could be interpreted as an indicator of restoration success. This is because it is known that long-term fencing policies have traditionally focused on the development of vegetation in the first instance, and then assumed the recovery of animal populations with a passive approach (Corlett 2016). Furthermore, more remarkable is that this success was considered in comparison with an ideal habitat structure and ecosystem functioning, based on reference sites often considered as static states (Ruiz-Jaén & Aide 2005). However, recent perspectives have emphasized the notion that restoring biota composition must involve more than plant restoration. Furthermore, it requires inclusion of functional aspects necessarily linked with appropriate methodological approaches and scaled at the species level (Perring et al. 2015; Kollmann et al. 2016). Along these lines, we tried to explore the interface using combined animal sampling methodologies with a two-sided approach. We detected changes in small mammal abundance in function of the distance across the interface, decreasing toward the inside of the grazing field. For instance, animals must make a series of decisions when crossing a boundary between habitat types and this is highly influenced by the local structural variables (Fahrig 2007). Our findings are consistent with boundary studies of mammals, which suggest that local-scale management of habitats exerts a significant influence on mammal populations and their response across natural and urban landscapes (Villaseñor et al. 2015).

In addition, a key factor knows how these local variables contribute to build the permeability perceived by each species, because this is what determines the rate of ecological flows
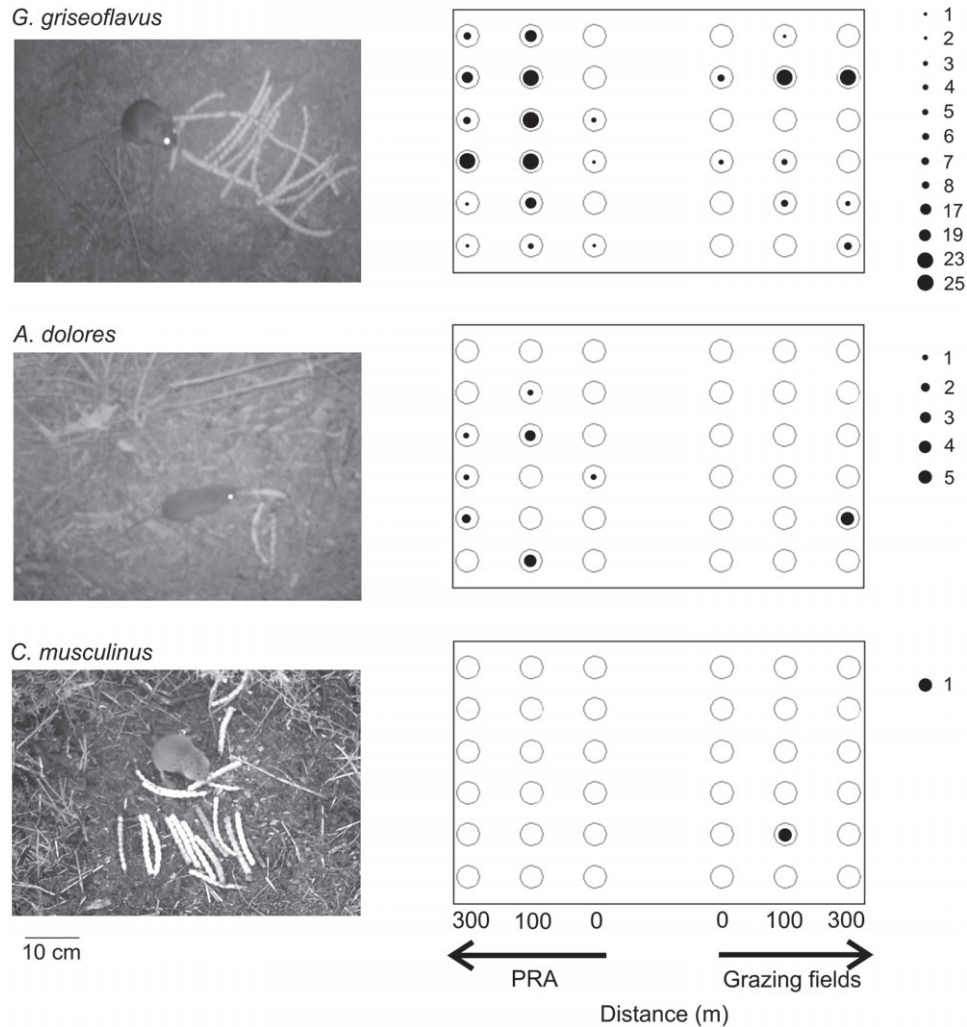
Figure 3. Number of independent detections (using the *detectionMaps* function) of rodent species in camera traps. Species are *Graomys griseoflavus*, *Akodon dolores*, and *Calomys musculinus*. Each white circle corresponds to a camera-trap station at every distance considered (0, 100, and 300 m) from the fenced boundary to the inside of the PRA and adjacent grazing fields.

between patches and the resulting connectivity (Ries et al. 2004). In desert rangelands, this is especially important because a decrease in plant cover due to grazing management affects the dispersal ability of animals and increases their predation risk (Ojeda & Tabeni 2009). In fact, we found that small mammals are negatively affected by the increasing expansion of bare ground cover crossing the boundaries (Fig. S2), although, surprisingly, some species dependent on high cover, such as *Thylamys pallidior* and *Akodon dolores,* were slightly more abundant within the grazing field. It is likely that the heterogeneous distribution of local variables along the boundaries may lead individuals to cluster in remnant patches (Driscoll et al. 2013), where even those species that tend to avoid grazing areas find in them suitable ungrazed patches that would act as a refuge (Tabeni et al. 2007). As other authors have noted, the dispersal of species within modified habitats, seemingly hostile, must be carefully interpreted, since while the movement across boundaries is possible, it should not necessarily be interpreted as a sign of functional connectivity (Cooney et al. 2015).

The abundance patterns reported on boundaries are, in short, the result of different mechanisms, such as the flow of species to one side or another (i.e. spillover effect), boundaries as enhanced habitats, or resource distribution (Ries & Sisk 2004). In the latter, organisms occurring near a lower-quality habitat, where offered resources are supplementary, are predicted to decrease in abundance within higher-quality habitats near boundaries. Our findings would be closely related to this response, showing how disruption of the structural similarity between management practices can have an impact on specific species and their needs, leading to increased functional isolation (Prevedello & Vieira 2010). Therefore, the few recaptures of animals that crossed from one side to the other, together with the negative impact of increased bare ground on their abundance, would suggest a low permeability toward the surrounding grazing areas, reinforcing the notion of a disconnected interface.

Functional Response across the Restored-Grazing Interface

Small mammals are one of the main groups removing seeds in deserts (Marone et al. 2000; Kelt et al. 2004). While handling fruits, seeds can be consumed, lost, and cached by rodent species (Vander Wall & Beck 2012). Seed caching involves two main strategies, caching of seeds in multiple places on the ground within the home range of the animal species (i.e. scatter-hoarder; Vander Wall & Beck 2012) or in a single place inside animal burrows (i.e. larder–hoarder; Longland et al. 2001). According to these strategies, a larder-hoarding species contributes less than a scatter–hoarder to the effectiveness of a plant's seed dispersal (Schupp et al. 2010). All rodent species studied here include *Prosopis* fruits in their diets (Giannoni et al. 2005) and are recognized to have different hoarding strategies (Giannoni et al. 2013). Considering the effects on *Prosopis* seeds, *Graomys griseoflavus* behaves as a *Prosopis* seed predator (Giannoni et al. 2013). Previous studies in the Monte Desert showed that this species is the main *Prosopis* seed remover, whereas other functional groups prevail on grazed sites (Miguel et al. 2017). The present results are consistent with previous studies, showing that seed removal by *G. griseoflavus* is high inside the PRA and decreases in grazing fields. In addition, we found that seed removal by species was positively influenced by population abundance. In other words, the pattern of seed removal along restored-grazing interfaces was similar to the pattern of small mammal abundance. Local abundance of seed removers is a demographic parameter that affects the number of seeds removed and dispersed by an animal population (Schupp et al. 2010). We clearly found that the more locally abundant rodent (*G. griseoflavus*) was the species making a greater number of visits to *Prosopis* trees, whereas one of the least locally abundant rodents (*Calomys musculinus*) made the lowest number of visits. Through the combined use of two field methodologies, live trapping and camera traps, we were able to bear out the presence and abundance of rodent species in the areas and to establish the functional importance of species actually removing *Prosopis* seeds. In fact, and different from previous results of laboratory studies (Giannoni et al. 2005, 2013) we found that *Eligmodontia typus* did not contribute to *Prosopis* seed removal in our field study.

Seed predation by rodents generally increases on sites with shrub and herb cover, mainly due to their predator avoidance behavior (Hulme 1998; Taraborelli et al. 2009; Spencer et al. 2014). Previous studies that considered highly vegetated boundaries, which maintain native flora and serve as refuge for small mammals (Hodara & Busch 2006; Gómez et al. 2011), showed a decrease in seed predation from boundaries to interiors (Kollmann & Buschor 2003). However, boundaries of grazing fields in drylands are generally maintained by vegetation clearing (Guevara et al. 2009; Durant et al. 2015). To the best of our knowledge, our results are the first to provide an insight into seed predation by small mammals in a dry restored-grazing interface. We clearly found that rodent species removed more *Prosopis* seeds at distances inside the area under passive restoration. Seemingly, the more open interfaces and grazing habitats studied here negatively affect the number of *Prosopis* seeds removed by seed predating species. Our results are consistent with the statement that seed predation is high on sites with high vegetation cover (Hulme 1998).

The seed predation exerted by small rodents in the PRA would contrast with the surrounding grazing sites if we considered the fact that other mammal species such as *Microcavia australis* and *Dolichotis patagonum*, regarded as more efficient *Prosopis* seed dispersers (Campos & Ojeda 1997; Campos et al. 2017), could find more suitable habitats in areas under grazing (Tabeni & Ojeda 2005). Contrary to small mammal preferences, these medium-sized mammals prefer more open habitats (Tognelli et al. 1995; Corbalán & Ojeda 2004). Therefore, the seed removal activity of these species along the interfaces could be rather different from seed removal by small rodents, which could imply different fates for native tree seeds. Further research considering the whole animal assemblage removing *Prosopis* fruits along interfaces would give us a better comprehension of functional processes in drylands.

The functional connectivity of the restored-anthropogenic interface can be evaluated through mobile indicators and their functional roles. Although conservation of species is valuable in itself, analyzing their functional aspects can reveal another perspective for rethinking changes in their abundance or local extinctions in order to achieve restoration goals. In this study, we showed that changes in the local habitat characteristics across boundaries can restrict the flow of native species and model their abundance. Decrease in the abundance of native small rodents in the surrounding grazing areas is reflected in an ecological process, thus increasing the activity of seed predators in the restoration area. We stress that long-term recovery of vegetation involves restructuring of animal–plant interactions and their specific functional roles, promoting more seed predators than dispersers in the restored area. Looking ahead toward a balance between seed-dispersing and seed-predating mammals across management practices would add a new dimension to assess the recruitment of key plant species and their impact on the woodland, which still remains unelucidated.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Number of seeds removed by (A) small mammal species and (B) *Graomys griseoflavus* along distances (0, 100, and 300 m) from the fenced boundary to the inside of the PRA and adjacent grazing fields.

Figure S2. Mean proportion and standard error of vegetation cover along distances (0, 100, and 300 m) from the fenced boundary to the inside of the PRA and adjacent grazing fields.

Table S1. Results of the selected zero-inflated Poisson mixed models of total rodent's abundance and *Graomys griseoflavus* abundance along restored-grazing interface at 0, 100, and 300 m distances.

Table S2. Results of the selected zero-inflated Poisson mixed models of total seed removal by rodents and *Graomys griseoflavus* seed removal along restored-grazing interface at 0, 100, and 300 m distances.

Table S3. List of zero-inflated Poisson mixed models for (a) total abundance of small rodents (response variable) and (b) *Graomys griseoflavus* abundance (response variable), at different distances across restored-grazed boundaries.