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NATIVE MAMMALS ACROSS GRAZING AND RESTORED WOODLANDS: AN OVERVIEW OF ECOLOGICAL CONNECTIVITY IN THE CENTRAL MONTE DESERT

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ABSTRACT. The semi-arid regions of Argentina have been subject to numerous human activities such as grazing by domestic animals. These activities bring about changes in the spatial pattern of the landscape by altering a variety of ecological processes due to loss of natural habitats and reduction of native species diversity. In the central Monte Desert, the establishment of protected areas has been implemented as a strategy for the recovery of native woodland communities. In addition, to ensure woodland perpetuity and the maintenance of ecological functions it is required to incorporate new approaches that include woodland connectivity with the surrounding landscape. The response of small and medium-sized mammals to boundaries highlights the need to consider the species-specific response in the selection of resources, the use of space and scales of observation fitted for the species. We focused on the socio-political boundaries between land uses to illustrate the changes in structural connectivity and their impact on functional connectivity through seed dispersal by mammals. Overall, understanding how differently managed lands are structurally and functionally connected may help us to design better management strategies aimed at biodiversity conservation, with focus both on species and the ecological processes they are involved in.

RESUMEN. **Mamíferos nativos a través de bosques restaurados y pastoreados: una perspectiva de la conectividad ecológica en el desierto del Monte central.** Las tierras secas de Argentina han sido objeto de numerosas actividades humanas como el pastoreo por herbívoros domésticos. Estas actividades provocan cambios en los patrones espaciales del paisaje alterando una variedad de procesos ecológicos debido a la pérdida de los hábitats naturales y a la reducción de la diversidad de especies nativas. El establecimiento de áreas protegidas en el desierto del Monte central constituye una estrategia para la recuperación de las comunidades de bosques nativos. Adicionalmente, asegurar la perpetuidad del bosque, de sus funciones y procesos, requiere incorporar nuevos enfoques que contemplen acciones tendientes a incrementar la conectividad con el paisaje circundante. La respuesta de mamíferos pequeños y medianos a los bordes pone de relieve la necesidad de considerar sus requerimientos específicos en la selección de los recursos, el uso del espacio, así como también el uso de escalas de observación ajustadas a las mismas. Nos centramos en los límites sociopolíticos entre usos de la tierra para ilustrar los cambios en la conectividad estructural y su impacto en la conectividad funcional a través de la dispersión de semillas por mamíferos. En general, la comprensión de cómo las áreas bajo diferente manejo

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están conectadas puede ayudarnos a diseñar mejores estrategias de manejo orientadas a la conservación de la biodiversidad.

Key words: Boundaries. *Prosopis flexuosa.* Protected areas. Rodents. Seed dispersal.

Palabras clave: Áreas protegidas. Bordes. Dispersión de semillas. *Prosopis flexuosa.* Roedores.

INTRODUCTION

Grazing by domestic herbivores is considered one of the land uses that most contribute to global degradation of drylands (Peters et al. 2015). Particularly, dry woodland ecosystems are subject to incessant biomass extraction processes linked not only to grazing but also to deforestation (Grau & Aide 2008; Guevara et al. 2009; Vilela et al. 2009). The native woodlands of *Prosopis flexuosa* in the desert plains of central-western Argentina (Monte Desert) underwent the greatest deforestation during the first decades of the twentieth century, mainly associated to the expansion of the railway (Villagra et al. 2009). Intensive logging was intended for firewood, charcoal and gas production for urban lighting (Roig 1971). The gradual decline in forest products and the changes in ecosystem structure, mediated by the emergence of heliophilous species, favored the beginning of a new scenario characterized by expansion of livestock production systems. These practices affect multiple biotic and abiotic interactions mainly through loss of habitat, increasing landscape fragmentation, changing plant cover and biodiversity, and the provision of ecosystems services (Alvarez et al. 2006; Rojas et al. 2009).

In the context of land degradation, the establishing of natural reserves has been an effective tool for the maintenance and conservation of woodland resources (Hobbs & Cramer 2008). Conservation efforts in the central region of the Monte Desert have increased the number of protected areas and experimental stations (as Ñacuñán Reserve and Telteca Reserve), promoting the passive recovery of the native communities. Furthermore, the exclusion of livestock activities demarcated the so-called socio-political boundaries as barriers defined by legal, institutional, and social processes (Dallimer & Strange 2015).

As in many dryland landscapes, the limits to the protection areas have not been designed to encompass the flows of water, energy, nutrients, and organisms across the landscape (Defries et al. 2007). On the contrary, protected areas are usually embedded in a matrix of land uses where expansion and intensification of human activities exert new visible pressures at the level of their boundaries. Moreover, the consequences of such fragmentation on preservation of species, ecosystem functions and provision of goods and services demanded by local communities are scarcely explored (Hansen & Defries 2007).

Global initiatives guided by the Strategic Plan for Biodiversity 2011-2020 (see www.cbd.int) and the UNCCD (United Nations Convention to Combat Desertification, see www.unccd.int) identified that one of the biggest challenges ahead for biodiversity conservation is to enhance habitat connectivity, enabling the movement of organisms and resources. Desert mammals have been widely recognized to be mobile link species, with significant effect on ecosystem processes across the landscape. From local to regional scale, they have a role in the distribution of soil nutrients and seed dispersal (Lindenmayer et al. 2008; Giannoni et al. 2013), also having a scarcely explored role in the pollination of desert plants and dissemination of mycorrhizal fungi essential for the survival of many higher plants (Wilcox & Murphy 1985; Zoeller et al. 2016).

Overall several questions of growing interest arise: How the conservation practices and land uses can affect landscape connectivity for mammals? How the ecological functions performed by these organisms are influenced by changes in land use? In this paper we offer a synthesis based on regional studies to illustrate the effect of grazing on mammals and conservation measures on native woodland. We will focus on how changes in landscape structure influence resources selection and movement of mammals. We will consider studies carried out in the Ñacuñán region in the Monte Desert, where the impact on native communities has been widely studied. Finally we will point out how changes in structural connectivity impact on functional connectivity through seed dispersal mediated by mammals.

PASSIVE RESTORATION AND CONSERVATION OF MAMMAL ASSEMBLAGES IN NATIVE WOODLANDS

Since the pioneering initiatives began, in the 60's, aimed at the preservation of native woodland and wildlife in the Monte Desert, the concept of protected area has evolved. Initial efforts setted the focus in restoring the natural conditions prior to disturbances, thus rigidly delimitating protected landscapes in isolation from their adjacent social-ecological context, often considered hostile. This deterministic perspective, based on the Clementsian successional paradigm (Briske et al. 2003) guided the design of protected areas around the world (Suding et al. 2004) as well as in the Monte woodlands. But the resources over-exploitation in the surrounding of protected areas, principally by agricultural land uses, resulted in isolation and lack of connectivity among protected areas due to landscape fragmentation (Palomo et al. 2014). The emerging criteria for conservation in the 70's focused on the interrelationships between natural ecosystems and socio-economic processes (such as UNESCO's Man and the Biosphere Programme). These efforts were focused on the integration of local communities, through the creation of buffer zones, and on the conservation strategy supported by outstanding environmental values (Rubio et al. 2014).

Passive ecosystem restoration for the management of wildlife, after eliminating a stressor, such as livestock, seems to be a common approach for restoring degraded lands. While degraded land restoration depends on disturbance history and intrinsic ecological potential of lands. The unassisted regeneration of ecosystems is considered to be the most efficient way in terms of cost-effectiveness to recover many components of their original biodiversity (Chazdon 2008; Hobbs & Cramer 2008).

The removal of livestock and subsequent development of plant biomass trigger a response that is inherently linked to disturbance intensity, site-specific properties, and time of cessation of disturbance. As a general pattern, it has been noted, within the first 10-20 years of grazing abandonment, the physiognomy of the fields is characterized by a phase of lower cover of therophyte plants and little recovery of the perennial grass layer. At least 20 years are required to observe a significant increase in the cover of perennial grasses, and 20-30 years to reach a state characterized by dominance of shrubs. After 30-40 years, long-term exclusion results in increased plant biomass, in turn leads to a significant spatial rearrangement of plant patches and modifications of certain functions, such as soil stability and nutrient cycling (Ruecker et al. 1998; Valone & Sauter 2005; Cramer et al. 2008; Arnaez et al. 2010).

The increasing appraisal of these areas with long-term exclusion grazing stock rests on the possibility of exploring the regeneration of ecological systems by autogenic processes. Specifically in the central Monte, after 50 years of grazing exclusion, natural habitats showed an increase in species diversity and richness compared to a previous state in which grazing was permitted (Rossi 2004). For instance, the abundance-dominance or frequency of the main palatable grasses such as *Digitaria californica*, *Trichloris crinita*, *Pappophorum caespitosum*, as well as some species of shrubs (*Lycium tenuispinosum, Capparis atamisquea* and *Condalia microphylla*) have increased considerably since then (Rossi 2004). Moreover, the increased of plant cover over time also restored the spatial arrangement of vegetation patches and consequently reestablished landscape connectivity (Tabeni et al. 2016). It seems that these changes in vegetation patterns induced spatial homogenization. Inside the protected areas, the strong contrast among pre-exclusion habitats tended to diminish, mainly due to colonization, distribution and expansion of some species through time (Roig 1971; Tabeni & Ojeda 2005).

By contrast, under the dominant production system, peripheral areas are mainly subjected to continuous grazing, by cows or goats, and to a lesser extent to rest-rotational grazing systems (Guevara et al. 2009). These areas showed several signs of degradation, such as a total plant cover and grass strata reduction, and an increase in unpalatable species and bare ground cover (Villagra et al. 2009). Irrespective of these widely reported landscape indicators, habitat structure is important to the occurrence and persistence of native mammals. The continuous livestock grazing produced a landscape pattern with a high number of gaps in plant distribution and higher spatial heterogeneity (Spirito 2015; **Fig. 1**). This heterogeneity is also observed at a regional scale, showing variable spatial patterns of grazing management hotspots (e.g., ranch settlements, water sources) and a regional mosaic of highly aggregated vegetation clusters (Asner et al. 2003).

Specific responses of species according to their ecological requirements suggest that protected and peripheral areas can play different and supplementary roles. Some studies have found in peripheral areas a decrease in species richness, diminished abundance and diversity of small and medium-sized mammals in response to reduction of the herbaceous-grass layers, increased bare ground and simplification of habitat structure (Wada et al. 1995; Keesing 1998; Eccar et al. 2000; Mathis et al. 2006). Thus, animals requiring densely vegetated patches, such as the gray leaf-eared mouse (*Graomys griseoflavus*), the grass mouse (*Akodon dolores*) or the yellow-toothed cavy (*Galea leucoblephara*), thrive in recovered habitats.

Otherwise, species with biological and morphological attributes to detect predators and exploit open habitats, such as *Eligmodontia typus* and *Dolichotis patagonum*, are more frequent in the surrounding grazed areas (Kufner & Chambouleyron 1991; Tabeni et al. 2013).

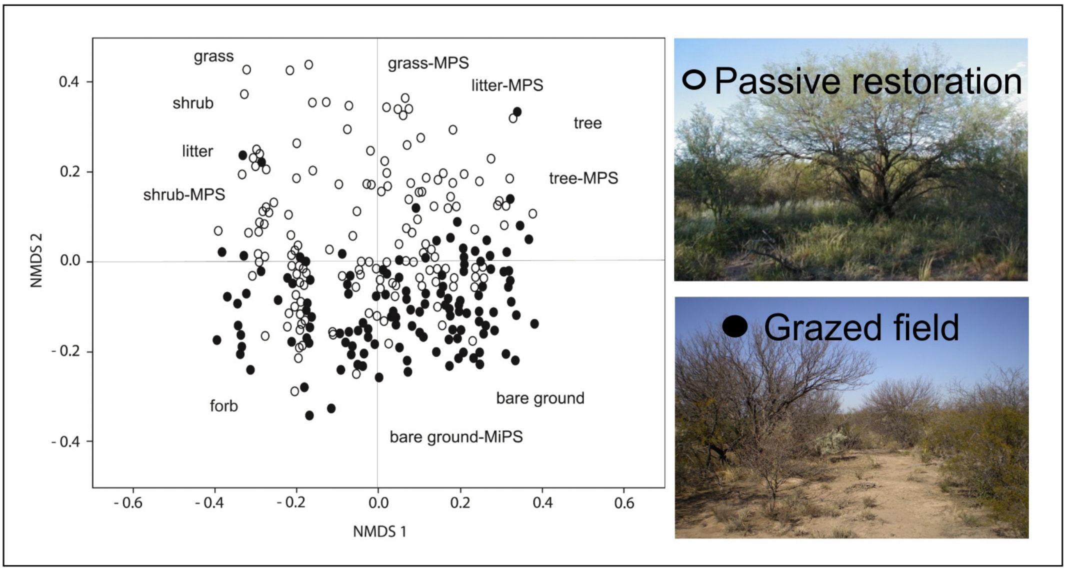

Fig. 1. Nonmetric multidimensional scaling ordination showing differences in habitat variables: grass, shrub, litter, tree, forb and bare ground; and structural variables: mean patch size of shrub (shrub-MPS), grass (grass-MPS), litter (litter-MPS), tree (tree-MPS) and mean inter-patch size of bare ground (bare ground-MiPS) in the passive restoration and grazed areas of the central Monte Desert (from Spirito 2015).

For example, the woody clusters of *P. flexuosa* that occur in higher densities around settlements outside of the Ñacuñán Reserve (Asner et al. 2003), are food and shelter providers for cattle and native mammals like *Microcavia australis*. Considering that *M. australis* is an effective seed dispersal agent for *P. flexuosa*, it could play a key role for the native woodland regeneration under anthropogenic disturbance (Campos et al. 2017; Miguel et al. 2017). The spatial proximity of these seed sources to protected areas highlights many still unexplored aspects, such as seed dispersal across boundaries by native mammals, spillover processes across fences and improvement of functional connectivity between management conditions (Gray et al. 2016).

It is well known that resource selection depends on the spatial scales at which organisms perceive changes in the landscape (Wiens 2002). From small to coarse scale, small mammals inside and outside of protected areas, follow a non-random distribution, forming clumps associated with habitat patches and plant cover types (Tabeni et al. 2007). Spatially explicit analyses point out how even species that avoid grazed lands around protected areas, can find suitable habitats within the available patches. For example, inside of grazing areas, *A. dolores* was more abundant in ungrazed vegetation patches where the high density of grasses, acting as a refuge, could reduce its vulnerability to predation (Tabeni et al. 2007).

The role of these refuge patches, proved to be of importance for the conservation of desert mammals (Pavey et al. 2015). Therefore, land management can play a crucial role in sustaining animal populations in a disturbed matrix through the provision of refuges, food composition and distribution of diverse types of covers (Shenbrot et al. 1999).

SMALL MAMMALS RESPONSE TO BOUNDARIES

Boundaries between protected areas and their surrounding grazing lands are usually physical barriers, such as fences, which may influence the movement of wildlife across these areas (Durant et al. 2015). This infrastructure is in itself seen as a disturbance for wildlife given its effect in habitat fragmentation. In other words, it provides perches for raptor species, thereby increasing the risk of predation, and especially it acts as a barrier to the movement and dispersal of animals (Wisdom et al. 2013).

This boundary conforms one of the first filters for organism dispersal across a fragmented landscape, thus affecting many processes and functions performed by mobile organisms (Cousins 2013). Boundary permeability depends on both its physical features and each species' perception of habitat features (Cadenasso et al. 2003). Usually, socio-political boundaries are considered to be an effective barrier to inhibit the movement of livestock and native wildlife of a considerable size (Wisdom et al. 2013). These boundaries represent a change between two habitat conditions, therefore it raises the question on whether they can constitute an obstacle to the movement of small mammals in the Monte Desert. Previous studies in agricultural matrices revealed that boundary habitats are less disturbed than adjacent patches of agricultural fields. Consequently, they maintain high plant cover throughout the year and provide good habitat conditions for mobile organisms such as small rodent species (Hodara & Busch 2006; Bilenca et al. 2007; Sommaro et al. 2010). However, habitat conditions across boundaries and their consequences on mobile organisms in drylands, under extensive cattle grazing, have been almost unexplored (see Wilson et al. 2010). The distinction between ecological boundaries (i.e., the natural boundaries between habitats and ecosystems) of those imposed by ecosystem management, has allowed us to observe that the habitat structure of socio-political boundaries impacted on the abundance of small mammals (**Fig. 2**). These boundaries were more contrasting in habitat variables than the ecological ones and a strong contrast was perceived by small mammals as quality changes across managements units, leading to lower richness in the mammal assemblage (Spirito & Tabeni 2016).

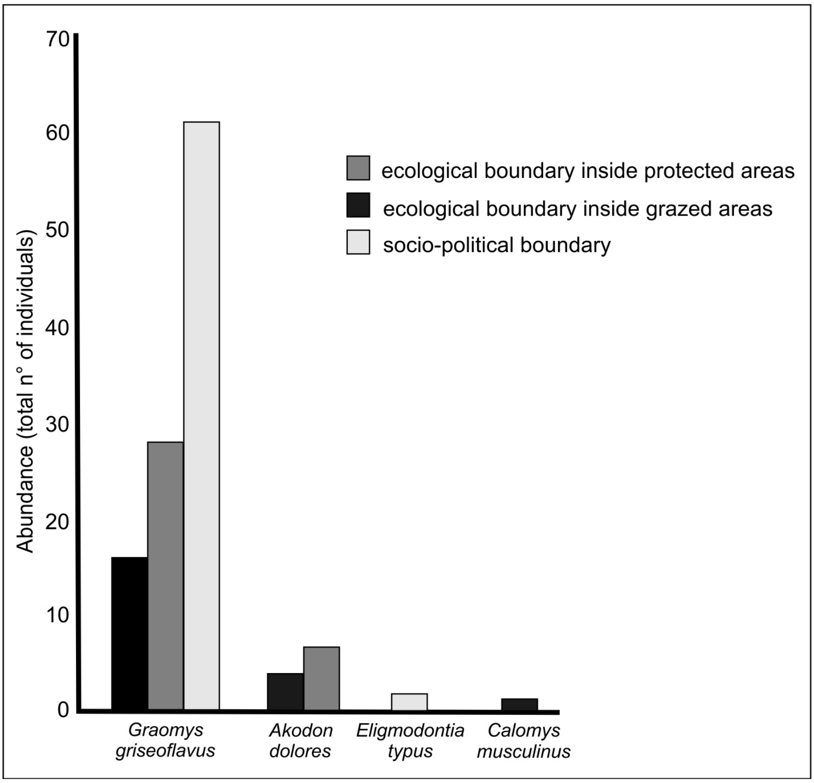

Fig. 2. Total abundance of small mammal species along ecological and socio-political boundaries. Ecological boundaries are *Larrea* shrubland – *Prosopis* woodland under continuous grazing conditions and under passive restoration. The socio-political boundary in *Prosopis* woodland between continuous grazing and passive restoration (from Spirito & Tabeni 2016).

RESOURCE SELECTION AND MOVEMENT PATTERN UNDER MANAGEMENT CONDITIONS: FUNCTIONAL CONNECTIVITY FOCUS ON *G. griseoflavus*

Connectivity is an important component of dryland ecosystem given its relation to the flow of soil resources and seeds across the landscape (primarily by wind and water, but also by animals; Okin et al. 2015). If we focus on a mobile organism, many factors intrinsic to the species influence decisions to leave a habitat patch and move to another, namely antipredatory behavior, acquisition of resources, competition and social interactions, among others (Nams 2005; Fahrig 2007). Changes in the movement of animal also induce modifications in their home-range sizes (Spencer 2012). Many space-use models assume home-range existence a priori rather than treating it as an emergent property of animal movements (Powell & Mitchell 2012). Knowledge of how landscape features affect the movement of organisms and home-range size, is critical for addressing the impacts of degradation (Fischer & Lindenmayer 2007) and potential landscape-level conservation initiatives (Minor & Lookingbill 2010).

Spirito (2015) studied functional connectivity in the central Monte Desert using *G. griseoflavus*, the most abundant small mammal in the Ñacuñán region, as an example of a mobile organism, and analyzed its response to grazing-induced changes in landscape structure. When analyzing landscape structure, Spirito (2015) found a clear differentiation in vegetation communities in the Ñacuñán Reserve. Specifically, there was greater connectivity among plant patches and higher litter and forage cover (i.e., species consumed by *G. griseoflavus*) than the area under grazing. The most structurally connected sites were associated with increased movement and space used by this species. Movement patterns, studied through the step-length and home-range size, denoted a lower movement in grazed areas (step-length 9.91 ± 3.17 m; home-range 992.45 m^2), than in areas under passive restoration (step-length 25.43 ± 3.71 m; home-range 3099.69 m^2).

Most resource selection studies show that small mammals select resources to take refuge from predators and ensure food access by avoiding open spaces (Turcotte & Desrochers 2003; Corbalán et al. 2006). As a main outcome, *G. griseoflavus* seems to display a different strategy depending on the management used. Under passive restoration, this species selected grass patches, while outside of the restoration area it chose patches with high species richness avoiding the open space (**Fig. 3**). This highlights how fine-scale changes in the landscape are perceived by small mammals pointing to them as significant constraints on their movement and ecological requirements (Spirito 2015).

A FUNCTIONAL INTERACTION ACROSS SOCIO-POLITICAL BOUNDARIES: *Prosopis flexuosa* FRUIT REMOVAL BY TERRESTRIAL MAMMALS

In socio-political boundaries, some ecological functions can be affected, with consequences for biodiversity (Cadenasso & Pickett 2001; Cadenasso et al. 2003). The activity of animals along boundaries can be affected by their responses to these habitats, and therefore some ecological processes, such as seed dispersal, may be modified (Chauvet & Forget 2005).

Seed dispersal is one of the most important ecological functions in the life cycle of plants (Nathan et al. 2009). Considering the increased use of lands by humans, the number of studies evaluating the effects of anthropogenic activities on seed dispersal has increased over the last years. Specifically, they have assessed the effects of habitat fragmentation (Markl et al. 2012; Aliyu et al. 2014), defaunation (Galetti & Dirzo 2013; Dirzo et al. 2014; Galetti et al. 2015) and selective logging (Ochoa 2000; Forget & Cuijpers 2008; Markl et al. 2012). Previous studies have found a higher probability of a seed being predated than dispersed in fragmented habitats, mainly due to a higher seed availability on less disturbed sites (i.e., high seed abundance may satiate seed-predating rodents; Forget et al. 2002; Aliyu et al. 2014). Furthermore, an increase in seed predation by small mammals on defaunated sites, explained by direct and indirect impacts of large herbivores on small mammal communities has been reported (Galetti et al. 2015).

In the Monte Desert, fruits of *P. flexuosa* are consumed by a variety of native and domestic mammals. Some species disperse *Prosopis* seeds by endozoochory (*Bos taurus*, *D. patagonum, Lycalopex griseus;* Campos et al. 2008; Campos & Velez 2015), others by hoarding the seeds in small caches on the ground (scatter-hoarders, *E. typus*, *M. australis*; Giannoni et al. 2013; Campos et al. 2017), and small rodents mainly prey upon *Prosopis* seeds (*A. dolores*, *G. griseoflavus*; Giannoni et al. 2013). Considering seed dispersal is a crucial ecological function for woodland recruitment, seed removal by different animal species may involve different seed fates and consequently affect plant population dynamics (Jordano & Herrera 1995). Therefore, it is essential to understand how seed removal can be affected by changes in the habitat due to different types of land management. Yet this aspect remains poorly explored in the Monte. However, recent studies have evaluated the effect of different land uses on *Prosopis* dispersal, with focus on the removal of its propagules by animals. In this sense, fenced and unfenced reserves varied in the main animal seed removers. Thus, in fenced reserves the main *Prosopis* seed removers were medium and large-sized mammals, while in the fenced ones were small- sized rodents (Campos et al. 2017). Because mutualistic interactions may be altered by anthropogenic activities (Dirzo et al. 2014), the effect of grazing on *Prosopis* seed dispersal showed seed predators removed a high number of seeds at an ungrazed site while animals that mainly disperse seeds removed a high number of *Prosopis* seeds at site under grazing (Miguel et al. 2017). These results suggest that animal species from the *Prosopis* frugivore assemblage remove seeds at different intensities according to the land use.

Future studies on ecological interactions in boundaries between different land uses may contribute to a better comprehension of the functional connectivity between land managements. Animals with different functional roles in the seed dispersal process may respond differently to socio-political boundaries, with

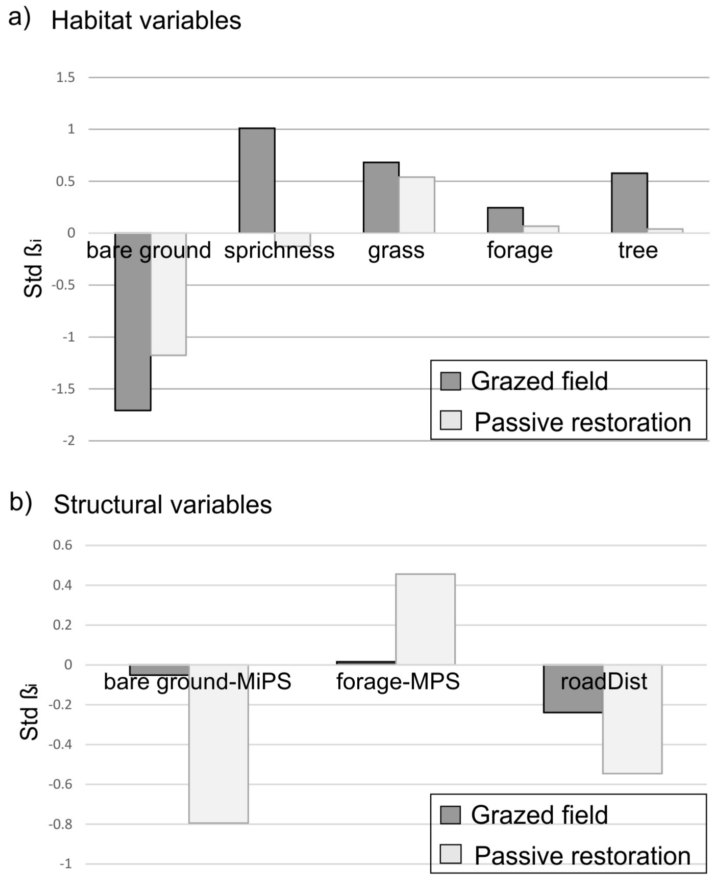

Fig. 3. Environmental variables estimates from Resource selection functions (RSF) models for *G. griseoflavus* in the Monte Desert of central Argentina. Standardized parameter estimates (Std β_i) are reported so that the effect size of model variables can be compared. Std β_i denoted the selection (positive values) or avoidance (negative values) for environmental variables under the two management conditions (grazed vs passive restoration). The models were divided into (a) habitat variables (forage represents the species consumed by *G. griseoflavus*) and (b) structural variables (MiPS = mean interpatch size; forage-MPS = mean patch size of forage species and roadDist = distance to roads).

different implications for seed survival and native tree recruitment.

DISCUSSION AND CONCLUSIONS

The demarcation of protected areas and the exclusion of persistent disturbance, such as grazing by domestic herbivores, are necessary but not sufficient strategies to ensure the conservation of biodiversity (Hobbs & Cramer 2008). The growing land use demands in the peripheries, and how these affect the native wildlife, highlight the extent to which management areas influence each other beyond the physical or legal barriers imposed.

We note that, over time, disturbance exclusion and increasing improvement in the Monte woodlands have molded a singular form of connectivity between mammals and their surroundings, whose future consequences are still unknown.The long-term passive restoration promoted the expansion of shrubland and woodland patches and the increase in plant density, favoring rodent species requiring densely vegetated patches (e.g., *G. griseoflavus*, *A. dolores* or *G. leucoblephara*). On the other hand, the extensive livestock grazing resulted in more contrasting landscape with a high number of open spaces interspersed with vegetation patches that allow the occupation of a greater diversity of species, from small to medium-sized mammals, as some endangered species, such as the endemic Patagonian hares (*D. patagonum*). This contrasting heterogeneity plays a major role in understanding species responses to landscape changes caused by grazing impact. We stress the importance of assessing the response of mammal species considering spatial scales fitted for the species under study. At fine scale, the spatially explicit analysis showed that both grazing impact and the long processes of vegetation recovery imply high intra-habitat variability in the spatial organization of resources for mammals such as the cover of trees, shrubs and grasses. These signals in the habitat are perceived by the animals, impacting not only in their abundances, but also in their spatial distributions while searching for optimal patches.

As mammal assemblages change in consonance with the varying landscape it is necessary to incorporate a functional approach. Thus interpreting connectivity as a species-based attribute, the landscape will have many possible forms of connectivity based on the habitat requirements and dispersal capacity of each species (Watts & Handley 2010). The movement of animals between socio-political boundaries and their decision to move between patches are influenced by many features of boundaries and the intrinsic characteristics of the species (Fahrig 2007). In studies of movement and home-range size of a native small mammal in the Monte (*G. griseoflavus*) we found that its step length and home range were larger on a site subject to passive restoration than in grazed areas (Spirito 2015). Therefore, to highlight how landscape features affect the movement of organisms and the home-range size can be critical for addressing the impacts of degradation and future landscape-level conservation initiatives.

The most current approaches have begun to inquire whether mammal species play an essential role as promoters of the restoration of degraded ecosystems by connecting different or similar habitat patches through the distribution of resources (Martin 2003; Yoshihara et al. 2009). Even more important is that key processes, such as nutrient distribution and seed dispersal, can be affected when faunal assemblages of degraded sites loose mammal species performing these functions (Chillo & Ojeda 2012; Dirzo et al. 2014). To study the occurrence of mammals across boundaries, and their different roles in the seed dispersal process are ways to know how restored and connected different managed units are. In our study area, the different functional activities of mammals along boundaries (i.e. seed predators, endozoochorous dispersers and scatter-hoarders) may imply different probabilities for a seed to be predated or dispersed and therefore constitute indicators of processes under threat, essential for woodland recruitment.

In light of the rapid changes taking place in land use and socio-economic dynamics it may be predicted that many protected areas around the world will be under the influence of increasing pressures (Defries et al. 2007). The dry woodland of central Argentina is not out of this scenario; on the contrary, the region is also expected to face strong processes of restructuring production and changes in land use with environmental and social consequences (Torres et al. 2014) that will expose wildlife to new vulnerabilities.

Overall, the implementation of reserves is a very useful strategy to conserve biodiversity, but we should consider the connectivity of the entire landscape. Protected areas should be structurally and functionally connected with their surroundings, allowing that species find their requirements in several habitat patches (Soulé & Terborgh 1999; Fuller et al. 2006). Decision making for conservation, facing increasing degradation, must be prioritized, under a framework that considers the structural and functional diversity of the landscape, and the preservation of key elements for the viability of mammal populations, such as connectivity between habitats.

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LITERATURE CITED

Aliyu, B., H. Adamu, E. Moltchanova, P. M. Forget, & H. Chapman. 2014. The interplay of habitat and seed type on scatter hoarding behavior in a fragmented afromontane forest landscape. Biotropica 46:264-267.

Alvarez, J. A., P. E. Villagra, M. A. Cony, E. Cesca, & J. A. Boninsegna. 2006. Estructura y estado de conservación de los bosques de *Prosopis flexuosa* D.C. en el Noreste de Mendoza, Argentina. Revista Chilena de Historia Natural 79:75-87.

Armesto, J. J. et al. 2007. Towards an ecological restoration network: reversing land degradation in

Latin America. Frontiers in Ecology and Environment 5:1-4.

Arnaez, J., T. Lasanta, M. P. Errea, & L. Ortigosa. 2010. Land abandonment, landscape evolution, and soil erosion in a Spanish Mediterranean mountain region: the case of Camero Viejo. Land Degradation and Development 22:537-550.

Asner, G. P., C. E. Borghi, & R. A. Ojeda. 2003. Desertification in central Argentina: changes in ecosystem carbon and nitrogen from imaging spectroscopy. Ecological Applications 13:629-648.

Bilenca, D. N., C. M. Gonzalez-Fischer, P. Teta, & M. Zamero. 2007. Agricultural intensification and small mammal assemblages in agroecosystems of the Rolling Pampas, central Argentina. Agriculture, Ecosystems & Environment 121:371-375.

Briske, D. D., S. D. Fuhlendorf, & F. E. Smeins. 2003. Vegetation dynamics on rangelands: a critique of the current paradigms. Journal of Applied Ecology 40:601-614.

Cadenasso, M. L., & S. T. A. Pickett. 2001. Linking forest edge structure to edge function: mediation of herbivore damage. Journal of Ecology 88:31-44.

Cadenasso, M. L., S. T. A. Pickett, K. C. Weathers, & C. G. Jones. 2003. A framework for a theory of ecological boundaries. BioScience 53:750-758.

Chazdon, R. L. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320:1458-1460.

Campos, C. M., V. E. Campos, S. M. Giannoni, D. Rodriguez, S. Albanese, & M. I. Cona. 2017. Role of small rodents in the seed dispersal process: *Microcavia australis* consuming *Prosopis flexuosa* fruits. Austral Ecology 42:113-119.

Campos, C. M., B. Peco, V. E. Campos, J. E. Malo, S. M. Giannoni, & F. Suarez. 2008. Endozoochory by native and exotic herbivores in dry areas: consequences for germination and survival of *Prosopis* seeds. Seed Science Research 18:91-100.

Campos, C. M., & S. Velez. 2015. Almacenadores y frugívoros oportunistas: el papel de los mamíferos en la dispersión del algarrobo (*Prosopis flexuosa* DC) en el desierto del Monte, Argentina. Revista Ecosistemas 24:28-34.

Chauvet, S., & P. M. Forget. 2005. Edge effects on post-dispersal seed removal in a fragmented rain forest in French Guiana. Journal of Tropical Ecology 21:113-116.

Chillo, V., & R. A. Ojeda. 2012. Mammal functional diversity loss under human-induced disturbances in arid lands. Journal of Arid Environments 87:95-102.

Cousins, W. B. 2013. Boundary conditions and uncertainty quantification for hemodynamics. PhD dissertation. North Carolina State University. North Carolina, USA.

Cramer, V. A., R. J. Hobbs, & R. J. Standish. 2008. What's new about old fields? Land abandonment and ecosystem assembly. Trends in Ecology and Evolution 23:104-112.

Corbalán, V., S. Tabeni, & R. A. Ojeda. 2006. Assessment of habitat quality for four small mammal species of the Monte Desert, Argentina. Mammalian Biology 71:227-237.

Dallimer, M., & N. Strange. 2015. Why socio-political borders and boundaries matter in conservation. Trends in Ecology and Evolution 30:132-139.

Defries, R., A. Hansen, B. L. Turner, R. Reid, & J. Liu. 2007. Land use change around protected areas: management to balance human needs and ecological function. Ecological Applications 17:1031-1038.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, & B. Collen. 2014. Defaunation in the Anthropocene. Science 345:401-406.

Durant, S. M. 2015. Developing fencing policies for dryland ecosystems. Journal of Applied Ecology 52:544-551.

Durant, S. M., M. S. Becker, S. Creel, S. Bashir, A. J. Dickman, R. C. Beudels-Jamar, & L. Badamjav. 2015. Developing fencing policies for dryland ecosystems. Journal of Applied Ecology 52:544-551.

Eccar, J. A., R. B. Walther, & S. J. Milton. 2000. How livestock grazing affects vegetation structures and small mammal distribution in the semi-arid Karoo. Journal of Arid Environments 46:103-106.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21:1003-1015.

Fischer, J., & D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16:265-280.

Fitzgibbon, S., D. Putland, & A.W. Goldizen. 2007. The importance of functional connectivity in the conservation of a ground-dwelling mammal in an urban Australian landscape. Landscape Ecology 22:1513-1525.

Forget, P. M., & L. Cuijpers. 2008. Survival and scatter hoarding of frugivores-dispersed seeds as a function of forest disturbance. Biotropica 40:380-385.

Forget, P. M., D. Hammond, T. Milleron, & R. Thomas. 2002. Seasonality of fruiting and food hoarding by rodents in Neotropical forests: consequences for seed dispersal and seedling recruitment. Seed dispersal and frugivory. Ecology, Evolution and Conservation (D.J. Levey, W.R. Silva & M. Galetti, eds.). CABI Publishing, Wallingford, Oxfordshire, UK.

Fuller, T., M. Munguia, M. Mayfield, V. Sanchez Cordero, & S. Sarkar. 2006. Incorporating connectivity into conservation planning: a multi-criteria case study from central Mexico. Biological Conservation 133:131-142.

Galetti, M., & R. Dirzo. 2013. Ecological and evolutionary consequences of living in a defaunated world. Biological Conservation 163:1-6.

Galetti, M., R. S. Bovendorp, & R. Guevara. 2015. Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. Global Ecology and Conservation 3:824-830.

Giannoni, S. M. et al. 2013. Hoarding patterns of sigmodontine rodent species in the Central Monte Desert (Argentina). Austral Ecology 38:485-492.

Grau, R. H., & M. Aide. 2008. Globalization and land-use transitions in Latin America. Ecology and Society 13:16.

Gray, C. L, B. I. Simmons, T. M. Fayle, D. J. Mann, & E. M. Slade. 2016. Are riparian forest reserves sources of invertebrate biodiversity spillover and associated

ecosystem functions in oil palm landscapes? Biological Conservation 194:176-183.
Guevara, J. C. et al. 2009. Range and livestock production in the Monte Desert, Argentina. Journal of Arid Environments 73:228-237.
Hansen, A. J., & R. Defries. 2007. Ecological mechanisms linking protected areas to surrounding lands. Ecological Applications 17:974-988.
Hobbs, R. J., & V. A. Cramer. 2008. Restoration ecology: interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. The Annual Review of Environment and Resources 33:39-61.
Hodara, K., & M. Busch. 2006. Return to preferred habitats (edges) as a function of distance in *Akodon azarae* (Rodentia, Muridae) in cropfield-edge systems of central Argentina. Journal of Ethology 24:141-145.
Jordano, P., & C. M. Herrera. 1995. Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. Ecoscience 2:230-237.
Keesing, F. 1998. Impacts of ungulates on the demography and diversity of small mammals in central Kenya. Oecologia 116:381-389.
Kufner, M. B., & M. Chambouleyron. 1991. Actividad espacial de *Dolichotis patagonum* en relación a la estructura de la vegetación en el Monte Argentino. Studies in Neotropical Fauna and Environment 26:249-255.
Lindenmayer, D. B. et al. 2008. Contrasting mammal responses to vegetation type and fire. Wildlife Research 35:395-408.
Markl, J. S. et al. 2012. Meta-analysis of the effects of human disturbance on seed dispersal by animals. Conservation Biology 26:1072-1081.
Martin, G. 2003. The role of small ground-foraging mammals in topsoil health and biodiversity: implications to management and restoration. Ecological Management and Restoration 4:114-119.
Mathis, V. L., W. G. Whitford, F. R. Kay, & P. U. Alkon. 2006. Effects of grazing and shrub removal on small mammal populations in southern New Mexico, USA. Journal of Arid Environments 66:76-86.
Miguel, F., M. I. Cona, & C. M. Campos. 2017. Seed removal by different functional mammal groups in a protected and grazed landscape of the Monte, Argentina. Seed Science Research 27:174-182.
Minor, E. S., & T. R. Lookingbill. 2010. A multiscale network analysis of protected-area connectivity for mammals in the United States. Conservation Biology 24:1549-1558.
Nams, V. O. 2005. Using animal movement paths to measure response to spatial scale. Oecologia 143:179-188.
Nathan, R., J. M. Bullock, O. Ronce, & F. M. Schurr. 2009. Seed Dispersal. Encyclopedia of Life Sciences (ELS). John Wiley & Sons, Ltd: Chichester.
Ochoa, J. G. 2000. Efectos de la extracción de maderas sobre la diversidad de mamíferos pequeños en bosques de tierras bajas de la Guayana Venezolana. Biotropica 32:146-164.
Okin, G. S. et al. 2015. Connectivity in dryland landscapes: shifting concepts of spatial interactions. Frontiers in Ecology and the Environment 13:20-27.
Palomo, I. et al. 2014. Incorporating the social-ecological approach in protected areas in the Anthropocene. BioScience 64:181-191.
Pavey, C. R. et al. 2015. The role of refuges in the persistence of Australian dryland mammals. Biological Reviews 92:647-664.
Peters, D. P. C., K. M. Havstad, S. R. Archer, & O. E. Sala. 2015. Beyond desertification: new paradigms for dryland landscapes. Frontiers in Ecology and the Environment 13:4-12.
Powell, R. A., & M. S. Mitchell. 2012. What is a home range? Journal of Mammalogy 93:948-958.
Roig, F. A. 1971. Aportes al inventario de los recursos naturales renovables de la provincia de Mendoza. 1. La reserva forestal de Ñacuñán. Deserta 1:25-232.
Rojas, J. F., M. R. Prieto, J. Alvarez, & E. Cesca. 2009. Procesos socioeconómicos y territoriales en el uso de los recursos forestales en Mendoza desde fines de siglo XIX hasta mediados del XX. Proyección 7(5):1-33.
Rossi, B. E. 2004. Flora y vegetación de la Reserva de Biosfera de Ñacuñán después de 25 años de clausura. Heterogeneidad espacial a distintas escalas. Tesis de doctorado. Universidad Nacional de Cuyo, Mendoza, Argentina.
Rubio, M. C., S. Fermani, & V. Parera. 2014. Evolución de la conservación en la provincia de Mendoza. Desafíos en el proceso de ordenamiento territorial en tierras secas. Zonas Áridas 15:195-210.
Rudnick, D. et al. 2012. The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in Ecology. Report No. 16. Ecological Society of America. Washington, DC.
Ruecker, G., P. Schad, M. M. Alcubill, & C. Ferrer. 1998. Natural regeneration of degraded soils and site changes on abandoned agricultural terraces in Mediterranean Spain. Land Degradation and Development 9:179-188.
Shenbrot, G. I., B. R. Krasnov, & K. A. Rogovin. 1999. Spatial ecology of desert rodent communities. Springer, Berlin.
Sommaro, L., D. Gomez, F. Bonatto, A. Steinmann, M. Chiappero, & J. Priotto. 2010. Corn mice (*Calomys musculinus*) movement in linear habitats of agricultural ecosystems. Journal of Mammalogy 91:668-673.
Soulé, M. J., & J. Terborgh. 1999. Continental conservation: scientific foundations of regional reserve networks. Washington, DC. Island Press.
Spencer, W. D. 2012. Home ranges and the value of spatial information. Journal of Mammalogy 93:929-947.
Spirito, F. 2015. La desertificación en el Monte central: pequeños mamíferos como indicadores ecológicos de cambio en la estructura y funcionalidad del paisaje. Tesis de doctorado. Universidad Nacional de Cuyo, Mendoza, Argentina.
Spirito, F., & S. Tabeni. 2016. Impacts of socio-political boundaries on small desert mammals of west-central Argentina. Journal of Arid Environments 131:6-14.

Suding, K. N., K. L. Gross, & G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology and Evolution 19:46-53.

Tabeni, S., & R. A. Ojeda. 2005. Ecology of the Monte Desert small mammals in disturbed and undisturbed habitats. Journal of Arid Environment 63:244-255.

Tabeni, S., L. Mastrantonio, & R. A. Ojeda. 2007. Linking small desert mammal distribution to habitat structure in a protected and grazed landscape of the Monte, Argentina. Acta Oecologica 31:259-269.

Tabeni, S., F. Spirito, & R. A. Ojeda. 2013. Conservation of small and medium-sized mammals following native woodland regrowth: a case study in a long-term UNESCO biosphere reserve, Argentina. Journal of Arid Environment 88:250-253.

Tabeni, S., F. A. Yannelli, N. Vezzani, & L. E. Mastrantonio. 2016. Indicators of landscape organization and functionality in semi-arid former agricultural lands under a passive restoration management over two periods of abandonment. Ecological Indicators 66:488-496.

Tischendorf, L., & L. Fahrig. 2000. On the usage and measurement of landscape connectivity. Oikos 90:7-19.

Torres, L. M., D. Pessolano, & R. G. Sales. 2014. Procesos de avance territorial del capitalismo en Mendoza (Argentina): transformaciones en la ganadería al quiebre del siglo XXI. Territorios 30:39-67.

Turcotte, Y., & A. Desrochers. 2003. Landscape-dependent response to predation risk by forest birds. Oikos 100:614-618.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates Sunderland, MA, USA.

Valone, T. J., & P. Sauter. 2005. Effects of long-term cattle exclosure on vegetation and rodents at a desertified arid grassland site. Journal of Arid Environments 61:161-170.

Vilela, A, M. L. Bolkovic, P. Carmanchahi, M. Cony, D. De Lamo, & D. Wassner. 2009. Past, present and potential uses of native flora and wildlife of the Monte Desert. Journal of Arid Environments 73:238-243.

Villagra, P. E. et al. 2009. Land use and disturbance effects on the dynamics of natural ecosystems of the Monte Desert: implications for their management. Journal of Arid Environment 73:202-211.

Wada, N., K. Narita, S. Kumar, & A. Furukawa. 1995. Impact of overgrazing on seed predation by rodents in the Thar desert northwestern India. Ecological Research 10:217-221.

Watts, K., & P. Handley. 2010. Developing a functional connectivity indicator to detect change in fragmented landscapes. Ecological Indicators 10:552-557.

Wiens, J. A. 2002. Central concepts and issues of landscape ecology. Applying landscape ecology in biological conservation (K. J. Gutzwiller, ed.). Springer.

Wilcox, B. A., & D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist 125:879-887.

Wilson, J. W., R. L. Stirnemann, Z. S. Shaikh, & M. Scantlebury. 2010. The response of small mammals to natural and human-altered edges associated with Afromontane forests of South Africa. Forest Ecology and Management 259:926-931.

Wisdom, M. J., M. M. Rowland, C. D. Vojta, & M. I. Goldstein. 2013. Chapter 7. Monitoring human disturbances for management of wildlife species and their habitats. A technical guide for monitoring wildlife habitat (M. M. Rowland & C. D. Vojta, eds.). United States Department of Agriculture.

Yoshihara, Y., T. Okuro, J. Undarmaa, T. Sasaki, & K. Takeuchi. 2009. Are small rodents key promoters of ecosystem restoration in harsh environments? A case study of abandoned croplands on Mongolian grasslands. Journal of Arid Environments 73:364-368.

Zoeller, K. C., S. L. Steenhuisen, S. D. Johnson, & J. J. Midgley. 2016. New evidence for mammal pollination of *Protea* species (Proteaceae) based on remote-camera analysis. Australian Journal of Botany 64:1-7.

GLOSSARY

Passive restoration: ecological systems are likely to recover unaided through ecological succession rather than through active restoration strategies (Armesto et al. 2007).

Boundary permeability: the probability of crossing a boundary between two landscape components (Wiens 2002).

Structural connectivity: defined by the spatial structure and composition of the landscape, independent of any attributes of the organism(s) of interest (Rudnick et al. 2012).

Functional connectivity: relative to the requirements of the organisms that live landscape and move through the landscape structure, and describes the extent to which landscape fragments facilitate or prevent the movement of an individual among resource patches (Tischendorf & Fahrig 2000; FitzGibbon et al. 2007).

Step-length: straight line connecting two successive locations of the same individual at regular time intervals (Turchin 1998).