



Secondary seed dispersal by mammals between protected and grazed semiarid woodland



M. Florencia Miguel, Solana Tabeni*, Mónica I. Cona, Claudia M. Campos

Instituto Argentino de Investigaciones de las Zonas Áridas (UNCuyo- Gobierno de Mendoza-CONICET), Av. A. Ruiz Leal s/n, Parque General San Martín, CC 507, Mendoza CP 5500, Argentina

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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

* Corresponding author.

E-mail addresses: fmiguel@mendoza-conicet.gob.ar (M.F. Miguel), stabeni@mendoza-conicet.gob.ar (S. Tabeni), mcona@mendoza-conicet.gob.ar (M.I. Cona), c campos@mendoza-conicet.gob.ar (C.M. Campos).

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ecological factors influence plant-frugivore interactions, such as 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 scatterhoarding such as 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

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