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Seed predation and removal from faeces in a dry ecosystem

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Abstract

The fate of dispersed seeds from mammal faeces depends both on the animal that finds the seeds and environmental conditions. We explored the simultaneous influence of microhabitat and food availability on seed predation and removal from faeces by different animals in a protected *Prosopis flexuosa* open woodland site of the central Monte desert (Argentina). Using exclusion trials on simulated cattle faeces, we quantified seed predation *in situ* (within cages) and seed removal from faeces by rodents and ants in two different microhabitats (under shrub cover and on bare soil). This was done for two levels of availability of *P. flexuosa* fruits (during the fruiting season of *P. flexuosa* and when there are no fruits on the ground). We found that 67.9% of seeds remained in faeces, 28.9% were removed, and 3.2% were depredated *in situ*. Rodents removed more seeds under shrub cover than on bare soil, and during the non-fruiting period than during the fruiting period, whereas ants removed similar proportions of seeds in different microhabitats but almost exclusively during the fruiting season. This work acknowledges the complexity of dispersal processes and identifies the relative importance of some environmental factors for seed fate.

Zusammenfassung

Das Schicksal von aus Säugetierkot verbrachten Samen ist abhängig von der Art des Tieres, das die Samen findet und von den Umgebungsbedingungen. In den lichten *Prosopis flexuosa*-Wäldern der zentralen Monte-Wüste Argentiniens wurden der Samenfraß und die Samenentfernung aus dem Kot durch verschiedene Tiere sowie der Einfluss von Mikrohabitat und Nahrungsverfügbarkeit auf die Samenentfernung untersucht. In Ausschlussversuchen mit simuliertem Rinderkot quantifizierten wir die Samenprädation *in situ* (innerhalb von Käfigen) und die Samenentfernung aus dem Kot durch Nagetiere und Ameisen in zwei unterschiedlichen Mikrohabitaten (unter Sträuchern und auf nackter Erde) sowie bei unterschiedlicher Verfügbarkeit von *P. flexuosa*-Früchten (während des Fruchtens und zu einer Jahreszeit als keine Früchte mehr zur Verfügung standen). Wir fanden, dass 67.5% der Samen im Kot verblieben, 28.9% aus ihm entfernt wurden und 3.2% *in situ* gefressen wurden. Nagetiere entfernten mehr Samen aus dem Kot, der sich unter Sträuchern befand und in der Zeit nach dem Fruchten von *P. flexuosa*,

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wohingegen Ameisen in beiden Mikrohabitaten etwa gleich viele Samen entfernten, dies aber fast ausschließlich während des Fruchtens von *P. flexuosa*. Diese Untersuchung verdeutlicht die Komplexität der Ausbreitungsprozesse und die Bedeutung von Umwelteinflüssen auf das Schicksal von Samen.

Keywords: Rodents; Ants; Seeds in faeces; Microhabitat; Fruit availability; Seed fate

Introduction

Seed dispersal can be a complex multi-stage process (Vander Wall & Longland 2004, 2005; Vander Wall, Forget, Lambert, & Hulme 2005; Vander Wall, Khun, & Beck 2005) where the initial dispersal movement is usually obvious (*e.g.* wind, frugivorous animals), but subsequent movements are often not so evident. The potential fate of seeds deposited in faeces is immediate germination, dormancy, mixing into the litter by the action of trampling and faeces decomposition (Malo & Suárez 1995a, 1995b; Dai 2000; Campos, Mangeaud, Borghi, de los Rios, & Giannoni 2011), or removal by animals (Brown & Heske 1990; Price & Joyner 1997; Hulme & Benkman 2002). In arid and semiarid ecosystems, faecal material can be an unfavourable environment for seed survival and seedling establishment for three reasons. First, faeces can be exposed to harsh environmental conditions, such as extreme temperatures and radiation, which produce seed desiccation (Borchert & Tyler 2010). Second, seed aggregation in faeces may attract seed predators (Janzen 1982; Chapman 1989; LoGiudice & Ostfeld 2002). Third, if germination occurs, seedling competition can be strong (*e.g.* Loiselle 1990). Survival of seeds in faeces and seedling establishment has been associated with a second movement away from the point of deposition after primary dispersal (Vander Wall, Khun, & Gworek 2005). Therefore, seed removal from faeces appears as a relevant stage in the seed dispersal process which is worth assessing to understand the dynamics of seedling establishment and plant recruitment.

Nearly all existing studies that address secondary movement of seeds from faeces come from temperate and tropical systems (Vander Wall, Khun, & Beck 2005; Vander Wall, Khun, & Gworek 2005; D'hondt, Bossuyt, Hoffmann, & Bonte 2008; Manzano, Azcárate, Peco, & Malo 2010 and references therein), while in dry ecosystems we know almost nothing about this process. Studies from the tropics point out that dung beetles, ants and rodents are the major secondary seed dispersers (Vander Wall, Khun, & Beck 2005). Rodents have been historically considered seed predators, but certain species with scatter-hoarding behaviour (Wenny 1999; Feer & Forget 2002; Giannoni et al. 2013) play roles as both predators and dispersers (Theimer 2005). Ants also play a dual role because, although they consume many seeds, they may also disperse some of them (in trails and refuse dumps), thus influencing seed-bank dynamics and promoting seedling establishment of some plant species in tropical forests (Levey & Byrne 1993; Passos & Oliveira 2002). In the Monte desert, some studies have studied the removal of *Prosopis flexuosa* fruits from under the trees' cover by small rodents, but there is no information on removal of seeds from faeces. We know that the sigmodontine rodent *Graomys griseoflavus* transports an important number of propagules, but they are left mainly in larders and later depredated, whereas *Eligmodontia typus* scatter-hoards propagules and leaves intact seeds removed from the fruits (Giannoni et al. 2013). Both species move fruits and store seeds at short distances (200 cm; Campos, Giannoni, Taraborelli, & Borghi 2007). Regarding ants, eleven species have been recorded exploiting *P. flexuosa* fruits, most of them remove the mesocarp *in situ*, and only *Acromyrmex* and *Pheidole* species were capable of carrying fruit segments (Milesi & Lopez de Casenave 2004).

Abiotic factors and ecological interactions can affect the fate of seeds in faeces. Attraction to high density of seeds clumped in faeces (Traveset 1990; Hulme 1994) and granivore satiation (Janzen 1971) influence the choices of secondary seed removers. Additionally, abiotic characteristics of the sites where faeces are deposited, such as vegetation structure (Christianini & Galetti 2007) and local availability of alternative food (Bermejo, Traveset, & Wilson 1998; LoGiudice 2001), affect animal foraging and the probability of a second dispersal event of seeds from faeces.

P. flexuosa is a keystone tree species in the Monte desert. It produces abundant fruits that accumulate on the ground, representing a source of food for a wide variety of organisms. Cattle may transport, disperse, and redistribute a large number of *Prosopis* seeds. However, survival of seedlings in dung is virtually negligible (Campos et al. 2008, 2011), and therefore a second movement may represent another chance for seeds to survive. Our main goal is to investigate the fate of seeds in faeces and to identify the particular ecological conditions that promote a second movement of seeds. To achieve this goal, we evaluate the magnitude of seed predation and removal from faeces by rodents and ants. Moreover, we assess the simultaneous influence that different microhabitats and availability of *P. flexuosa* fruits have on seed removal and predation. Using a field experiment with simulated cattle faeces, we aimed at answering the following questions: (1) Do rodents and ants differentially remove and depredate seeds found in faeces? (2) Does the microhabitat where the faeces are deposited affect removal and predation of seeds? (3) Does availability of *P. flexuosa* fruits influence removal and predation of seeds found in faeces? Regarding the last two questions, we expect to find: (a) lower seed removal and *in situ* predation on seeds located in faeces lying on bare soil,