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Functional responses to edge effects: Seed dispersal in the southern Atlantic forest, Argentina

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ABSTRACT

Recent studies have advanced our understanding of the mechanisms behind population and community responses to edge effects. However, functional responses remain poorly explored. Seed dispersal is a key process in ecosystem functioning, and edge effects may alter patterns of seed dispersal through changes in dispersers' behavior and environmental conditions. Here, we test predictive models of edge effects and habitat suitability on seed dispersal by considering different scenarios given by differences in the dispersal agent (wind and vertebrate dispersal), and the contrast between habitats of native southern Atlantic forest and tree plantations that occur across the entire area of influence of the edge. We fit our data to non-linear theoretical models to explore the response of seed rain to three general patterns of response to edge effects and differences on habitat suitability: (1) monotonic (sigmoid or exponential) (seed rain is higher in one of the habitats), (2) unimodal (seed rain shows either a maximum or a minimum near the edge, with or without differences on habitat suitability between adjacent habitats) and (3) neutral response (seed rain is constant across the ecotone). We estimated abundance and richness of wind- and vertebrate-dispersed seeds using seed traps, and measured vegetation structure in four different edges between native forest and tree plantations (from recent to mature plantations). Edge effects affected seed rain patterns depending on both the degree of vegetation contrast between habitats and the dispersal agent. Wind-dispersed seeds showed a monotonic response to most edges, whereas responses of vertebrate-dispersed seeds varied among edges (monotonic, unimodal and neutral), consistent with the dispersers' behavior. High contrast edges (forest-recent plantation) showed unimodal edge response, while those created by low contrast edges (forest-mature plantation) exhibited monotonic responses (sigmoid). Differences on habitat suitability on vertebrate-dispersed seeds increased with edge contrast, while richness and abundance of vertebrate-dispersed seeds in the habitat interior showed the opposite pattern. The abundance of wind-dispersed seeds inside the studied habitats increased with edge contrast. The current analytical framework developed to explore responses of populations and communities to edge effects successfully described the response of seed dispersal. Furthermore, edge effects affected seed dispersal patterns differently depending on the dispersal agent and the contrast between habitats. Our findings contribute to the understanding of forest regeneration processes and may help increase the effectiveness of restoration efforts.

1. Introduction

The area of transition between adjacent habitats exhibits particular features that differ from those within each habitat due to the interaction between the two environments (Murcia, 1995). The contact between habitats (or edge) results in alterations of environmental conditions (known as edge effects), which may influence community and population attributes, and ecological processes (Oosterhoorn and Kapelle, 2000). A series of recent studies have provided an integrated theoretical and analytical framework to explore the mechanisms behind population and community responses to edge effects, using a continuous approach from one habitat interior to the other (Ries et al., 2004; Ewers and Didham, 2006; Porensky, 2011; Zurita et al., 2012; Peyras et al., 2013). Ries and Sisk (2004) proposed models to predict population abundance near the habitat edge based on three mechanisms involving resource distribution: (1) spillover or mass effects, (2) edges as enhanced habitat, and (3) complementary resource distribution. Although these models help understand responses

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of populations and communities to edge effects, mechanisms driving functional responses have been poorly explored.

Edge effects have been recognized as a major factor influencing ecological processes such as species invasions (Cadenasso and Pickett, 2001; Honnay et al., 2002), species interactions (Fagan et al., 1999; Harper et al., 2005), nutrient cycling (Sizer et al., 2000), pollination (Chacoff et al., 2008) and herbivory (Cadenasso et al., 2003). Most studies, however, have focused on the effects of edges on abiotic factors (Didham and Lawton, 1999), or population and community structure (Ewers and Didham, 2006), whereas the responses of ecological processes such as seed dispersal remain poorly explored (Willson and Crome, 1989; Ingle, 2003). Moreover, previous studies analyzing edge effects on ecological processes focused exclusively on one side of the edge (Willson and Crome, 1989; Restrepo et al., 1999; Cadenasso et al., 2003), and/or used a binary approach of habitat interior vs edge (Lopes de Melo et al., 2006; Estrada-Villegas et al., 2007).

Seed dispersal is a key process in the maintenance and regeneration of plant communities (Howe and Smallwood, 1982; Chapman, 1995). It is a passive process mediated primarily by dispersal agents, such as wind or vertebrates in terrestrial ecosystems. Edge effects may alter the patterns of seed dispersal through changes in the behavior and abundance of dispersal agents and abiotic conditions (e.g. resistance to wind flow) (Willson and Crome, 1989). Previous studies have showed that mechanisms affecting seed dispersal differ in relation to dispersal agents. Release height of seeds (Thomson et al., 2011), wind speed and wind turbulence (Augsperger and Franson, 1987), are the main factors determining seed rain patterns of wind-dispersed seeds. On the other hand, vertebrate movements across the edge and into the adjacent habitat determine seed dispersal patterns of bird- and bat-dispersed seeds (Ries and Sisk, 2004). Visitation rates and foraging times of frugivorous birds and bats are affected by local food availability, determined by the density and composition of fleshy-fruiting plants (Da Silva et al., 1996; García et al., 2010; Herrera et al., 2011), fruit shape and size (Wheelwright, 1993; Kalko et al., 1996; Wendeln et al., 2000), microhabitat types (Jordano and Schupp, 2000), vegetation height, and predation risks (McDonnell and Stiles, 1983).

In this study we investigate edge effects and differences on habitat suitability on seed dispersal between native forest and tree plantations using the procedure described by Dewers and Didhman (2006), Zurita et al. (2012) and Harper et al. (2005). Our hypothesis is that seed dispersal patterns across the transitional area between adjacent habitats are determined by both the degree of contrast between habitats and the dispersal agent. We expected three patterns of response of seed rain: (1) monotonic (different suitability of contrasting habitats with or without edge effect), (2) unimodal (seed rain has a maximum or minimum near the edge, with or without differences on habitat suitability on each side of the edge) and (3) neutral response (no response to edge, similar suitability of habitats).

Winds in open areas are typically stronger than in forests. Moreover, the shape of wind profiles suggests that seeds dispersed in open habitats are exposed to stronger horizontal winds over a much wider vertical range than seeds released within forests (Nathan et al., 2002). Consequently, we expect that (1) richness and abundance of wind-dispersed seeds will decline from high contrast edges (e.g. forest-recent plantations) to low contrast edges (e.g. forest-mature plantations) (e.g., Figs. 1a,b and (2) the extent of edge effects on wind-dispersed seeds will decrease, and the magnitude will increase, from high to low contrast edges (e.g. Fig. 1a and b) as a consequence of the reduction of physical barriers and the increased wind velocity in the first case (Pazos et al., 2013).

The suitability of tree plantations for native vertebrates (particularly birds) increases with plantation age, associated to the degree of development of the understory (Zurita et al., 2006; Nájera and Simonetti, 2009). Therefore, we predict that the response of vertebrate-dispersed seed rain will adjust to disperser's behavior based on the distribution of resources, and habitat suitability (Ries and Sisk, 2004). Consequently, we expect the extent of edge effects on richness and abundance of vertebrate-dispersed seeds to decrease, and the magnitude to increase, from low to high contrast edges (contrary to the expected pattern for wind-dispersed seeds).

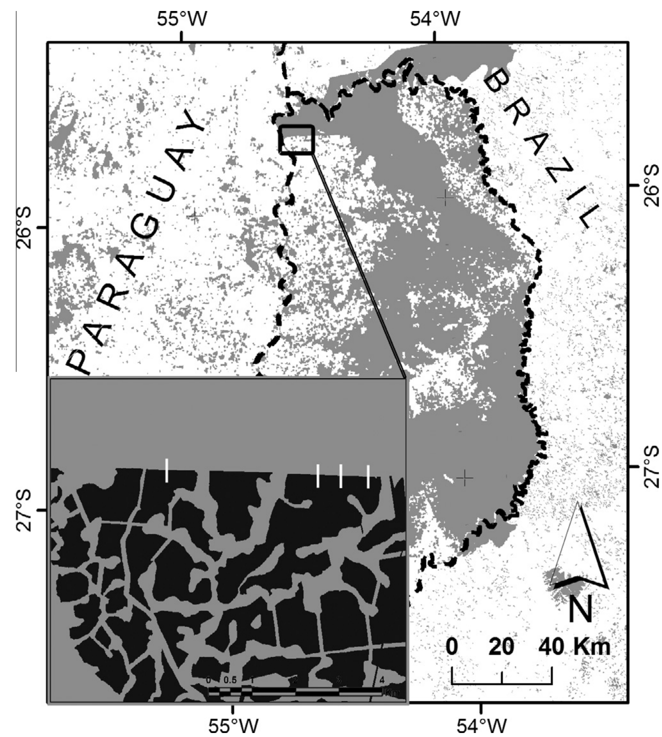

Fig. 1. Study area in northeastern Argentina. Atlantic forest remnants are shaded in grey and tree plantations in black in the detail of the study area (transects are marked on white). Modified from Peyras et al. (2013).

2. Materials and methods

2.1. Study area

The study site is located in the subtropical semideciduous Atlantic forest of northeastern Argentina. The native forest is characterized by three to five arboreal strata, numerous epiphytes, and lianas, and an understory composed mainly by ferns and bamboo (Campanello et al., 2007). The most abundant canopy tree species include *Nectandra megapotamica* (Lauraceae), *Lonchocarpus leucanthus* (Fabaceae), *Balfourodendron riedelianum* (Rutaceae), *Bastardiopsis densiflora* (Malvaceae), *Cedrela fissilis* (Meliaceae) and *Cordia americana* (Boraginaceae). Common species in the low stratum are *Sorocea bonplandii* (Moraceae), *Allophyllus edulis* (Sapindaceae), *Trichilia catigua and Trichilia elegans* (Meliaceae). Climate is subtropical; mean annual precipitation and temperature are 2000 mm and 21 °C, respectively, with a cold season between June and August. Rainfall is evenly distributed throughout the year (Servicio Meteorológico Nacional, 2006).

Commercial tree plantations occupy most of the land used for human activities in the study area (Zurita and Bellocq, 2010). Plantations were mainly composed of pines (*Pinus taeda*); other species such as eucalypt (*Eucalyptus* spp) and the native Araucaria (*Araucaria angustifolia*) are also planted as timber.