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Seed movement between the native forest and monoculture tree plantations in the southern Atlantic forest: A functional approach

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ABSTRACT

The native vegetation within tree plantations increases the suitability for native biodiversity; however, the regeneration of this vegetation depends on the movement of seeds from the native forest by vertebrates and wind. In the present study, we examined functional patterns of seed dispersal between the native forest and tree plantations with different degrees of contrast. We expected that the movement of seeds between the native forest and plantations would depend on the degree of edge contrast, the dispersal syndrome, and the size/weight of seeds. We sampled the seed rain by using seed traps, and measured vegetation structure in the ecotone between four different plantations and the native forest (300 m inside both the native forest and the plantations) in the Atlantic forest of Argentina during a 12-month period. We weighed wind-dispersed seeds and measured vertebrate-dispersed seeds. Edge effects acted as a filter for seed size/weight of both vertebrate- and wind-dispersed seeds. The abundance and functional diversity of seeds arriving at tree plantations increased with plantation age; large seeds were more sensitive to habitat disturbance than small seeds, independently of the dispersal syndrome. Our results highlight that seed movements between the native forest and human-created habitats largely depend on the interaction between dispersal syndrome, seed size, distance to the edge and habitat contrast. Our results also showed that long-term plantation cycles will increase the functional diversity of seeds in the seed bank and facilitate the regeneration of the native vegetation, and that small mature stands close to the native forest will largely facilitate the arrival of seeds and increase the suitability for native fauna.

1. Introduction

Tree plantations are one of the primary land uses in the southern Atlantic forest, occupying more than 4000 km^2 in the northeast of Argentina. The replacement of the originally continuous forest by tree plantations (and other land uses) increases the surface of habitat influenced by edge effects (Ribeiro et al., 2009). Edge effects have been recognized as a key ecological process influencing population abundance, community structure and ecological interactions in fragmented landscapes (Aizen and Feisinger, 1994; Santos and Tellería, 1994; Ries and Sisk, 2004), and are among the main factors causing population decline and species extinction in highly fragmented ecosystems (Banks-Leite et al., 2010). Previous studies in the Atlantic forest dealing with edge effects between the native forest and tree plantations have focused on changes in the diversity and abundance of animal populations and communities (Zurita et al., 2012; Peyras et al., 2013); however, this is the first study assessing functional processes such as seed dispersal.

Changes in biotic and abiotic environmental conditions associated with edge effects have also functional consequences on ecosystem processes (Didham et al., 1998; Restrepo and Gómez, 1998; Oliveira et al., 2004; Pardini, 2004; Laurance, 2008). Seed dispersal is a key ecological process in the dynamics and regeneration of natural ecosystems and the recovery of the structure and composition of native vegetation in anthropogenic habitats (Jordano et al., 2011). Particularly, the use of tree plantations by native animals increases with the regeneration of vegetation in the understory (Nájera and Simonetti, 2010), a process that depends on the movement of seeds from the native forest to plantations, and by the type of vegetation surrounding plantations (Zamora et al., 2010).

Habitat disturbance affects natural patterns of seed dispersal mainly

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through changes in the behavior (edge avoidance) and/or abundance (or extinction) of dispersers (e.g. birds and mammals), and the alteration of abiotic conditions (e.g. wind direction and speed) (Willson and Crome, 1989; Galetti et al., 2003; Vespa et al., 2014). The relative influence of habitat disturbance on seed rain patterns depends not only on changes in biotic and abiotic conditions but also on the functional traits of the dispersed seeds, such as dispersal syndromes and seed size and weight (Tabarelli and Peres, 2002; Galetti et al., 2013).

Seed size and weight have a strong influence on the dispersal pattern of both wind- and vertebrate-dispersed seeds (Howe and Smallwood, 1982). The dispersal distance of wind-dispersed seeds is determined by the height of release, vegetation structure, and horizontal wind speed (Soons et al., 2004); furthermore, larger seeds disperse shorter distances than smaller seeds (Greene and Johnsons, 1996). The size and weight of vertebrate-dispersed seeds depend largely on the assemblage composition of frugivorous vertebrates (Christian, 2001). In general, the dispersal of larger seeds depends on a few large frugivorous species, which are usually more sensitive to human disturbances and tend to avoid edges (Hamann and Curio, 1999; Christian, 2001; Markl et al., 2012). In contrast, smaller seeds are dispersed by many small and medium-sized frugivores (ecological redundancy), which are less sensitive to human disturbance and then have low impact on the seed dispersal network in case of population decline or local extinctions (Corlett, 1998).

The dispersal of large seeds (both wind- and vertebrate-dispersed) is particularly affected by human disturbances (McConkey et al., 2012). Since seed size and weight are positively correlated with the amount of reserves (Dalling and Harms, 1999; Green and Juniper, 2004), the resistance to herbivory (Hammond et al., 1999; Green and Juniper, 2004), seedling size (Moles and Westoby, 2004) and reproductive success (Leishman et al., 2000), changes in patterns of seed dispersal may have strong mid- and long-term consequences on the ecosystem (Galetti et al., 2013; Bello et al., 2015). Recent studies have evaluated the response of the seed rain composition and abundance to edge effects; however, only a few contributions have focused on seed functional traits (Ingle, 2003; Lopes de Melo et al., 2006). Besides, seed size reflects plant life strategies because most pioneer species have smaller seeds than late successional species (Westoby, 1998). Consequently, changes in functional traits of dispersed seeds strongly influence the seed rain composition, habitat regeneration and succession.

The replacement of native forests by tree plantations has modified the environmental conditions, the structural complexity of the vegetation, and the composition of animal assemblages and, consequently, the patterns of seed dispersal (Zurita et al., 2006; Carnus et al., 2006; Zamora et al., 2007, Gardner et al., 2009; Nájera and Simonetti, 2010). However, those changes depend on the plantation age, because the structural complexity of the vegetation and the composition of animal assemblages become more similar to those of the native forest through plantation development (Brockerhoff et al., 2003; Bremer and Farley, 2010; Zurita and Bellocq, 2012). In a previous study, we found higher abundance and richness of dispersed seeds in older plantations than in recent plantations, associated with the recovery of the richness and abundance of frugivorous birds and bats (Vespa et al., 2014).

In this study, we aimed to explore patterns of seed movement between the native forest and tree plantations by using a functional approach (dispersal syndrome and seed size and/or weight) in the southern Atlantic forest of Argentina. We selected the ecotone between the native forest and tree plantations of different ages to provide a range of edge contrasts. We expected that the movement of seed functional types between the native forest and plantations would depend on the environmental contrast between both habitat types (low in mature plantations and high in recent plantations), the dispersal

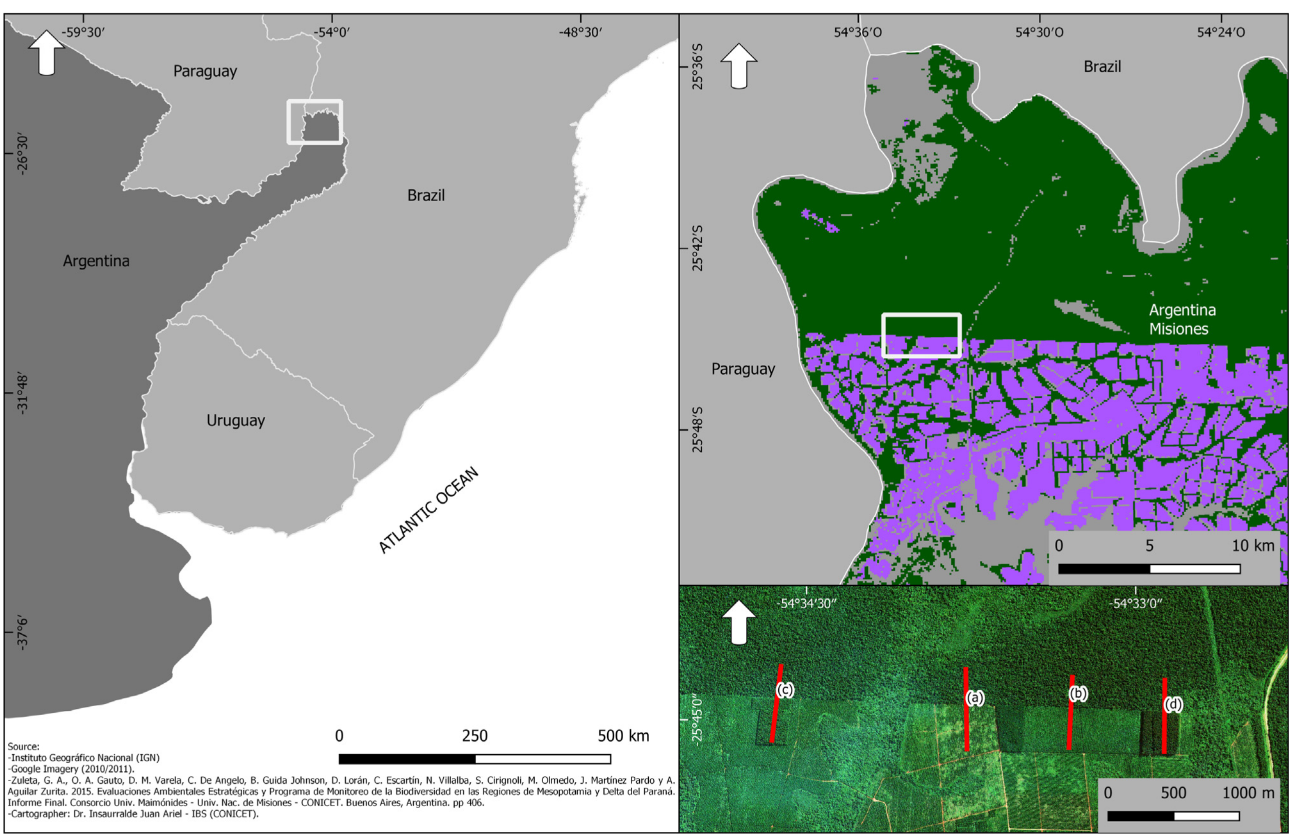

Fig. 1. Study area in the Atlantic forest of northeastern Argentina. In the detail of the study area, Atlantic forest remnants are shaded in green and tree plantations in violet. Transects in the sampling sites are drawn in red. (a) Recent pine plantation, (b) intermediate pine plantation, (c) mature pine plantation and (d) eucalyptus plantation.