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 re-generation 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 verte-brate-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 syn-drome. 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 in-fluenced by edge effects (Ribeiro et al., 2009). Edge effects have been recognized as a key ecological process influencing population abun-dance, 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 eco-systems and the recovery of the structure and composition of native vegetation in anthropogenic habitats (Jordano et al., 2011). Particu-larly, 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 plan-tations (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
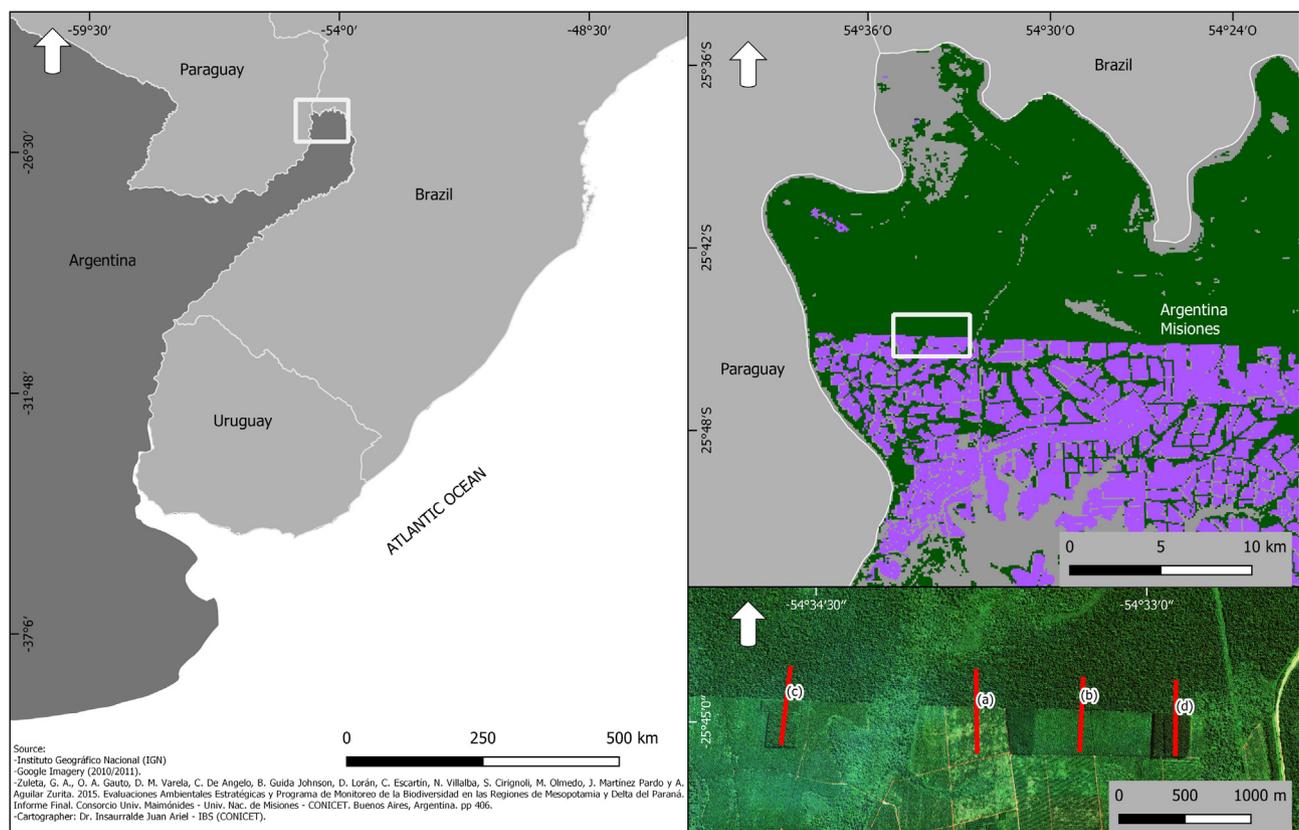

Fig. 1. Study area in the Atlantic forest of northeastern Argentina. In the detail of the study area, Atlantic forest remnants are shaded in green and tree plantations in violet. Transects in the sampling sites are drawn in red. (a) Recent pine plantation, (b) intermediate pine plantation, (c) mature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

syndrome (wind- and vertebrate-dispersed seeds), and the seed size and/or weight. Trough the use of seed traps, we focused on seeds dispersed by volant vertebrates (birds and bats) and excluded seeds dispersed by terrestrial mammals.

2. Methods

2.1. Study area

The study was conducted in the subtropical semideciduous Atlantic forest of northeastern Argentina, one of the largest forest remnants of the Atlantic forest eco-region. The area has a humid subtropical climate with marked seasonality regarding photoperiod and temperature (Di Bitetti and Janson, 2001). The mean annual precipitation varies between 1700 and 2200 mm, the mean annual temperature ranges between 16 and 22 °C, and there is no dry season (Di Bitetti et al., 2003). The native forest has three to five arboreal strata and numerous epiphytes and lianas; the understory is composed mainly of ferns and bamboo (Campanello et al., 2007). The landscape in the study area consists primarily of large fragments of continuous native forest in protected areas, native forest fragments of various sizes, and commercial tree plantations (especially *Pinus taeda*) used for pulp production (Zurita and Bellocq, 2010).

2.2. Study design

Within the study area, we selected four edges of native forest contiguous to tree plantations to represent a gradient of contrast between habitats: three pine plantations of 2-, 6- and 19-year-old pines (*Pinus taeda*), hereafter, recent, intermediate and mature plantations, respectively, and a 23-year-old eucalyptus plantation (*Eucalyptus dunnii*). Through the plantation cycle, plantations become similar to the native forest in vegetation structure and bird community (Zurita and Bellocq, 2012). In our gradient, mature plantations (of both pines and eucalyptus) were considered low-contrast edges, whereas the recent plantation reflected a high-contrast edge (Peyras et al., 2013, Vespa et al., 2014). The intermediate plantation showed moderate contrast between habitats.

On each edge, we outlined a 600-m transect across the habitats, which started 300 m inside the native forest and ended 300 m inside the plantation. On each transect, we set 46 sampling points at the following distances from the edge and towards the interior of each habitat: 0, 5, 15, 30, 50, 75, 100, 150, 200, 250 and 300 m. Distances of 15, 75 and 150 m had five sampling points each, separated by 50 m between them, while the others distances only had one sampling point. We therefore concentrated the sampling effort near the edge, where we expected the highest rate of seed rain change (Zurita et al., 2012; Peyras et al., 2013). Transects were located at least 500 m apart from each other (Fig. 1) and in the same direction (north-south) to avoid biases associated with wind direction.

At each sampling point, we sampled the seed rain by using seed traps that operated continuously over one year (January 2010 to January 2011). Each seed trap consisted of a 2 m² (2 × 1 m) fine nylon fabric net, with a 0.5 mm mesh, supported on an iron frame of about 1 m high. This methods is widely used to capture seed rain from birds and bats but exclude seeds dispersed by terrestrial mammls (peccaries, tapirs, etc). The material collected on seed traps (seeds, leaves, woody debris, etc.) was gathered every 10 days to avoid seed decomposition. Then, woody plant seeds were separated from the debris for further examination. Additionally, we identified all trees with a diameter at breast height (DBH) equal or higher than 5 cm within a 25 m² plot around each seed trap, and seeds from those trees were excluded from the analysis to avoid analyzing seed species that may have been collected by gravity. Around each seed trap, we defined a 5 × 20 m plot, where we identified and measured the DBH of trees and palms > 5 cm DBH, their basal area and stem density, and estimated arboreal and

understory cover.

2.3. Seed processing

We identified collected seeds to the lowest possible taxonomic level by using both a reference collection and morphological descriptions. Based on both external morphology and bibliography, we classified seeds as wind- or vertebrate-dispersed seeds (Lorenzi, 2002; Lopez et al., 2002). To estimate seed weight and size, we randomly selected three to twenty seeds per species (depending on the number of seeds collected), weighed them with a digital balance (accurate to 1 mg) and measured the largest diameter of vertebrate-dispersed seeds by using a caliper with a 1 mm precision. We did not measure wind-dispersed seeds because of the high morphological variability. Finally, we calculated the average weight or length of each dispersed species. Because the weight and length of vertebrate-dispersed seeds were highly correlated ($R_{Spearman}$ = 0.9, p < 0.001), we excluded seed weight from the statistical analysis for this type of seeds. Finally, we assigned vertebrate-dispersed seeds to one of the following four size categories as defined by Tabarelli and Peres (2002) for the Atlantic forest: very small (1–3 mm), small (3.1–6 mm), medium (6.1–15 mm) and large (15.1–30 mm). Size categories were not used for wind-dispersed seeds because of the wide variety of morphologies; instead, we estimated the average weight and its coefficient of variation within each distance. We used the coefficient of variation as a measure of variability in seed morphology.

2.4. Data analyses

In a previous study, we tested the assumption that the contrast in vegetation structure (i.e. basal area, stem density, canopy and understory cover and canopy height) between habitats (native forest and plantations) decreases from recent to mature plantations (Vespa et al., 2014). In this study, we used the Euclidean distance in a Multidimensional Scaling Analysis (MDS) calculated in Vespa et al. (2014) between the forest interior centroid and the plantation interior centroid as a measure of vegetation contrast (Banks-Leite et al., 2010), with lower distances indicating similar vegetation structure. We used this estimation to relate changes in the functional composition of the seed rain and the habitat contrast.

To explore the response of functional traits of dispersed seeds (dispersal syndrome and size and weight of seeds) to edge effects (extent and magnitude), we followed a procedure similar to that used in Harper et al. (2005), Ewers and Didham (2006), Porensky (2011), Zurita et al. (2012) and Vespa et al. (2014). For wind-dispersed seeds, we considered seed average weight and coefficient of variation as dependent variables, whereas for vertebrate-dispersed seeds, we included the proportion of each size category (very small, small, medium, large) across the ecotone. In all the regression analyses, the distance from the forest or plantation to the edge was the independent variable. We first fitted each dependent variable for each transect to four statistical models to represent theoretical responses to edge effects (i.e. monotonic-edge avoidance, unimodal-edge preference, exponential-edge avoidance and neutral response). Then, we compared the ability of each of these models to explain patterns of seed rain using the Akaike's information criterion with a correction for small sample size (AICc) (Burnham and Anderson, 2003). A detailed description of the procedure can be found in Vespa et al. (2014).

The extent of edge effects was calculated from the two inflection points of the second derivative of the model fit (Ewers and Didham, 2006). The extent represents the distance of the influence of edge effects in both directions (plantations and forest). To calculate the magnitude of edge effects on each habitat, we used the MEI index (MEI = (e − i)/(e + i)) suggested by Harper et al. (2005), using the value of the response variable inside each habitat (asymptotes, i) and on the edge (e). The magnitude of edge effects denotes changes in the

response variables (e.g. number of species) between each habitat and the edge.

To explore the difference in habitat suitability (Ymax and Ymin) between habitats and the influence of the edge contrast between habitats on the extent of edge effects on the functional attributes of the seed rain on plantations, we performed simple correlation analyses between those response variables and the degree of contrast between habitats (Euclidian distance on the MDS). We also correlated the interior-edge contrast in each habitat with the MEI calculated for the same habitat.

3. Results

A total of 20,607 vertebrate-dispersed seeds and 5837 wind-dispersed seeds were collected in the 184 seed traps during the 12-month sampling period. Among vertebrate-dispersed seeds, very small seeds were the most abundant (92.5% of the total seeds collected), whereas large seeds were the least abundant (0.07% of the total seeds collected and of only one species, *Syagrus romanzoffiana*). In the native forest and mature plantations (both of pines and eucalyptus), the four size categories of vertebrate-dispersed seeds were present (from very small to large seeds), whereas in recent and intermediate pine plantations, the large seed category was absent (Fig. 2). Because of the scarcity of large
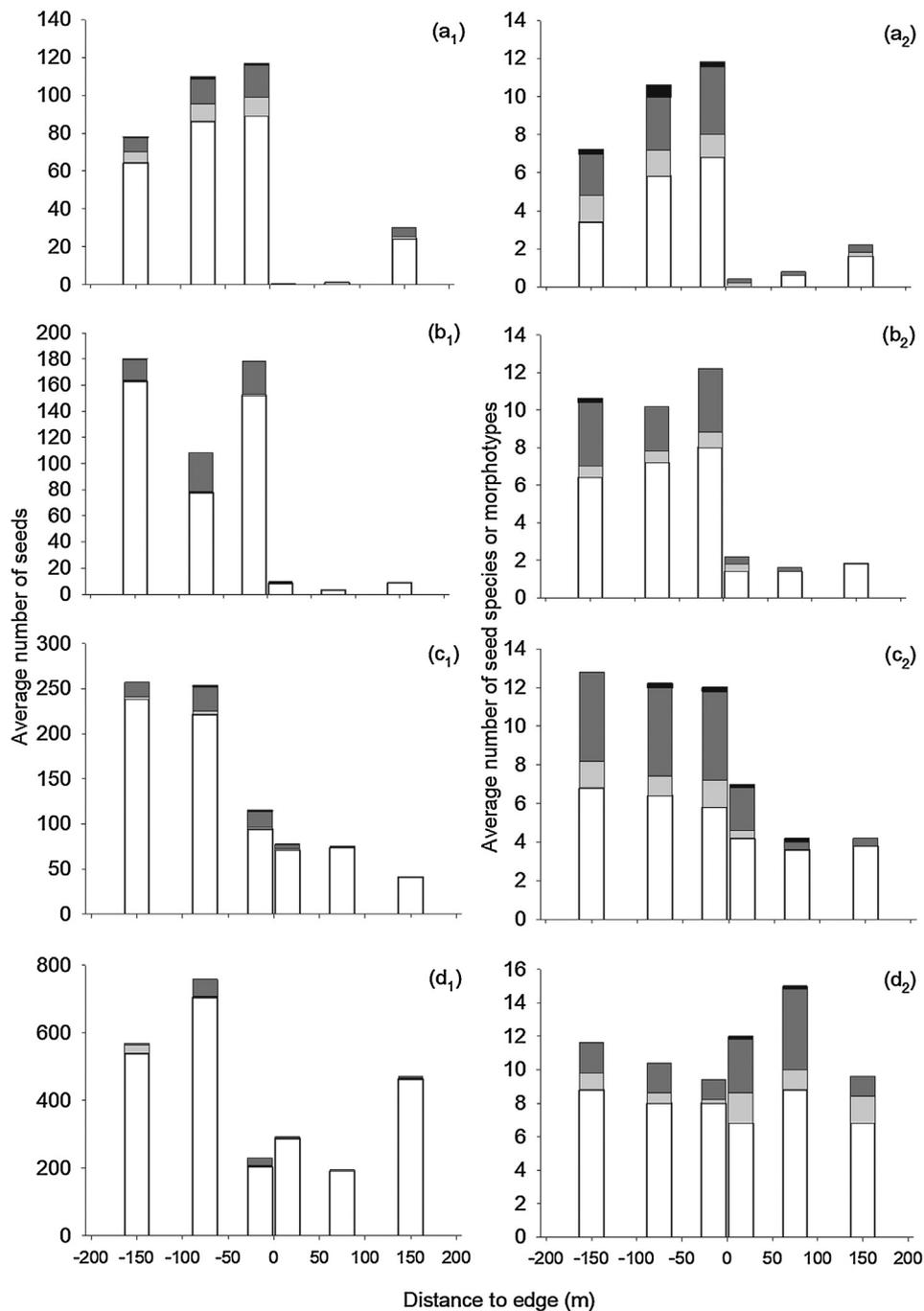

Fig. 2. Abundance (left figure) and richness (right figure) of vertebrate-dispersed seeds in the ecotone between native forest and tree plantations in the Atlantic forest of northeastern Argentina. (a) Recent pine plantation, (b) intermediate pine plantation, (c) mature pine plantation and (d) eucalyptus plantation. Seed size categories: very small (white), small (gray), medium (dark gray) and large (black). Negative values indicate distances inside the native forest whereas positive values indicate distances inside the plantations.
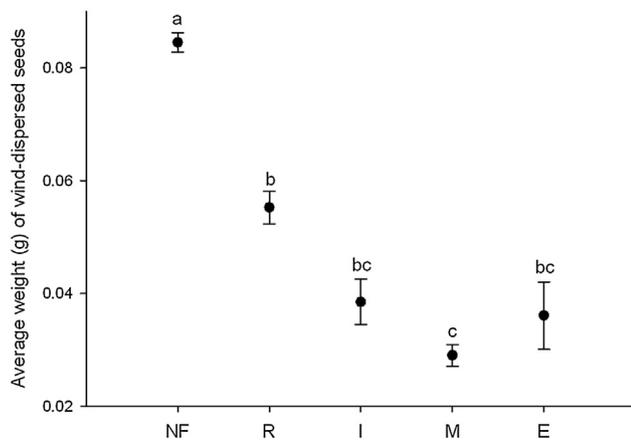
Fig. 3. Average weight of wind-dispersed seeds in the native forest and four different tree plantations in the Atlantic forest of northeastern Argentina (H = 66.97; p < 0.001). NF: native forest, R: recent pine plantation, I: intermediate pine plantation, M: mature pine plantation, E: eucalyptus plantation. Bars indicate the standard error. Equal letters indicate no significant differences.

vertebrate-dispersed seed species, the group was excluded from the regression analysis.

The average number of seeds dispersed (from the interior of the native forest to the interior of the plantation) increased from recent plantations (higher contrast) to mature plantations (lower contrast) (Fig. 2), mainly because of the increase in the number of very small seeds. Similarly, seed richness increased from recent to mature plantations for all seed sizes, but only inside plantations.

For wind-dispersed seeds, the average weight of seeds was higher in the native forest than in the tree plantations (Fig. 3). Among tree plantations, recent plantations showed the highest seed weight, whereas mature plantations showed the lowest seed weight (Fig. 3). For vertebrate-dispersed seeds, the proportion of dispersed seed size categories showed three different response patterns to edge effects: unimodal, sigmoid and neutral (Fig. 4; Table 1). The unimodal pattern was the most frequently found (42%) and was concentrated in the most abrupt edges (recent and intermediate pine plantations). The sigmoid (or exponential) and neutral patterns represented 50% of the responses, in equal parts, and were concentrated in the softest edges (mature pine and eucalyptus plantations).

In the native forest, the habitat suitability (Ymax) for the proportion of very small seeds in the seed rain correlated negatively with the contrast of vegetation between habitats (Euclidean distance of the MDS analysis) ($R_{Spearman}$ = −0.99; p = 0.03) (Fig. 5a; Table 1). In forest plantations, the habitat suitability (Ymin) for the proportion of small seeds in the seed rain correlated negatively with the contrast of vegetation between habitats ($R_{Spearman}$ = −0.95; p = 0.04) (Fig. 5b; Table 1). In contrast, for the proportion of medium-sized seeds, we found a marginally and negatively relationship with the extent of edge effects ($R_{Spearman}$ = −0.91; p = 0.08) (Fig. 5c; Table 1), and for the rest of the variables, we found no relationship with the contrast of vegetation between habitats ($R_{Spearman}$ < 0.5; p > 0.1). The average weight of wind-dispersed seeds decreased exponentially from the edge to the interior of plantations (Fig. 6). The extent of edge effects into the native forest decreased with habitat contrast: 222 m alongside the recent pine plantation, 95 m alongside the intermediate pine plantation and 2 m alongside the eucalyptus plantation. The edge between the native forest and the mature pine plantation showed no significant regression (Fig. 6). The weight coefficient of variation for wind-dispersed seeds had a sigmoid response in all cases (Fig. 7); the maximum value was reached in the native forest, whereas the minimum was reached in tree plantations.

Supplementary data associated with this article can be found, in the

online version, at https://doi.org/10.1016/j.foreco.2018.07.051.

4. Discussion

As expected, the edge effects and the replacement of the native forest by tree plantations strongly influenced the functional composition of the seed rain. However, the shape and magnitude of the response of the functional composition of the seed rain to edge effects depended on the degree of contrast between habitats, the seed size/weight and the dispersal syndrome. Our results support the hypothesis that the dispersal of large seeds from birds and bats, independently of the dispersal syndrome, is more sensitive to habitat disturbance (edge effects in our study) (Da Silva and Tabarelli, 2000; Galetti et al., 2013).

The vertical complexity of the vegetation limits wind speed and, consequently, represents a barrier for wind-dispersed seeds (Pazos et al., 2013), particularly for heavier seeds. The increase in the vegetation vertical complexity through the plantation cycle may explain the increase in the average weight of seeds from mature to recent plantations and the decrease in the extent of the edge effect in the opposite sense; this means that heavier seeds disperse larger distances in recent plantations than in older ones. Besides, in older plantations differences in the architecture of pines and eucalypts could influence the permeability for wind-dispersed seeds; mature eucalyptus have, in general, less branches improving the movement of wind into the plantation. Although the weight of dispersed seeds may explain the pattern of seed size distribution observed along the ecotone, the morphology of wind-dispersed seeds (winged, plumose, pilose, etc.), which was not recorded in this study, is a very influential factor in the mechanisms of seed transport (Augspurger, 1986). We found that heavier wind-dispersed seeds moved larger distances in recent plantations than in mature plantations. However, those seeds are typical of late successional species, intolerant to light and high temperature, typical of recent plantations. In contrast, heavier wind-dispersed seeds may find more suitable conditions to germinate and establish in older plantations under shader conditions (Zurita and Bellocq, 2012).

The movement of very small vertebrate-dispersed seeds between the native forest and tree plantations was, by far, larger than that of the other seed sizes (small, medium and large seeds). This pattern can be explained by two mechanisms: (i) that very small seeds belong to pioneer woody species, which normally produce large numbers of seeds as a reproductive strategy (Fenner and Thompson, 2005), or (ii) that the scarcity of the larger seeds could be a consequence of a defaunation process in the study area over time (Escobar, 2010). Large frugivorous birds, such as Dusky-legged guans and Toucans, are more sensitive to changes in the natural habitats and illegal hunting (Da Silva and Tabarelli, 2000; Galetti et al., 2001; Uezu and Metzger, 2011), and are also dispersers of plant species with large seeds such as *Syagrus romanzoffiana*. Although *S. romanzoffiana* individuals are abundant in the native forest of the study area, only 14 seeds were collected during the sampling period, suggesting a possible effect of defaunation. However, the sampling methods used in this study (seed traps one meter above ground) exclude terrestrial mammals moving large seeds (tapirs, peccaries, etc.); in consequence the richness and abundance of this type of seeds are probably underestimated.

The recovery of the native bird community (primary dispersers) through the plantation cycle is probably the mechanism underlying the increase in the functional diversity of vertebrate-dispersed seeds. In turn, the regeneration of native plants in tree plantations may increase the suitability for native dispersers and, consequently, the movement of seeds from the native forest, creating a positive feedback (Kissling et al., 2008, Clough et al., 2009). Our study supports this idea since we observed that although the arrival of seeds was dominated by very small seeds, medium and large seeds were found only in mature plantations.

The environmental conditions in the ecotone between the native forest and tree plantations change through the plantation cycle (Peyras et al., 2013). Seed size is directly related to the germination conditions
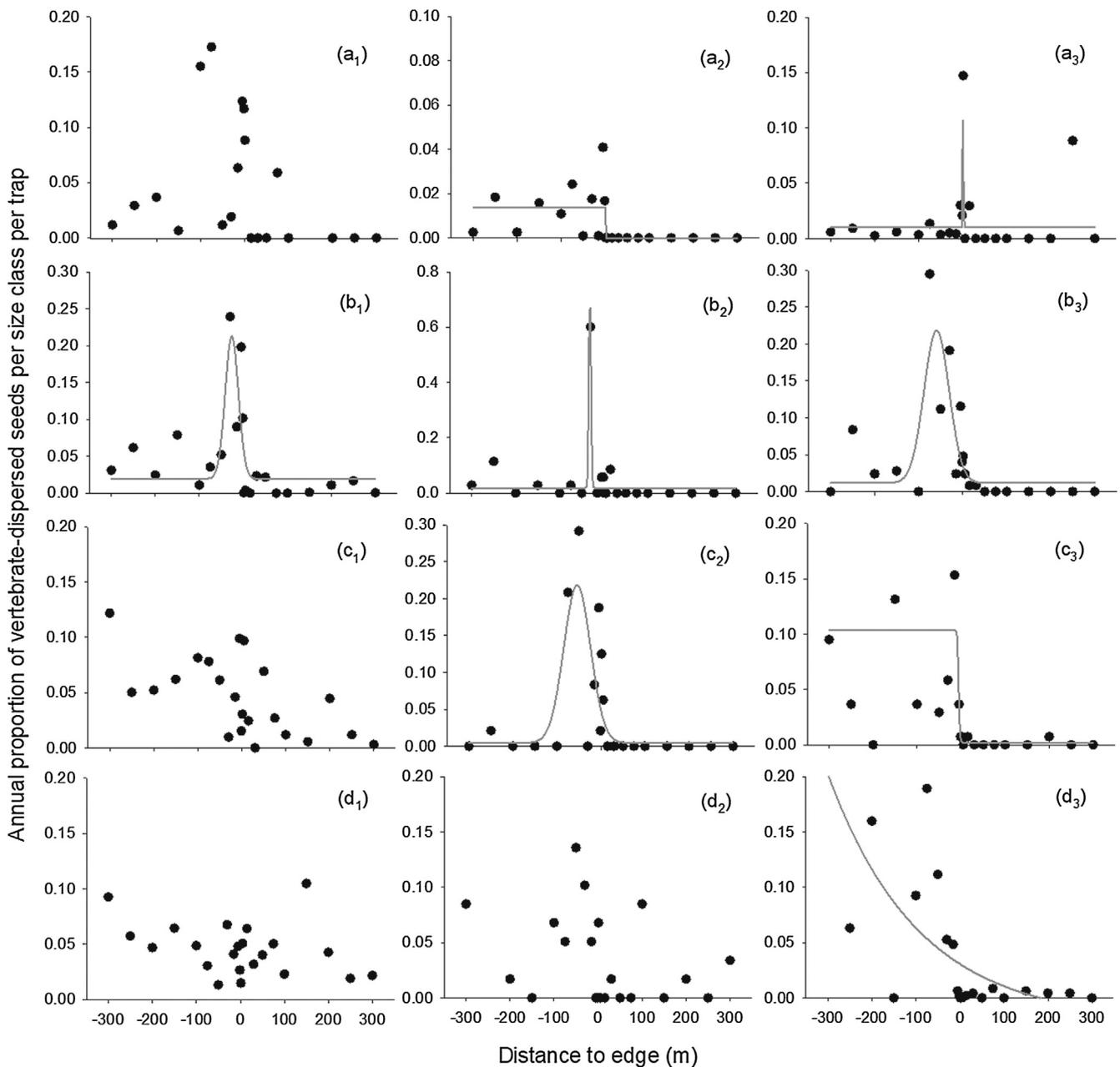
Fig. 4. Proportion of vertebrate-dispersed seeds per size category in the Atlantic forest of northeastern Argentina. (a) Recent pine plantation, (b) intermediate pine plantation, (c) mature pine plantation and (d) eucalyptus plantation. Subscript numbers from one to three indicate very small, small and medium-sized seeds respectively. Lines show the best fit regression. Negative values indicate distances inside the native forest, whereas positive values indicate distances inside the plantations.

and plant establishment (Moles and Westoby, 2004): smaller seeds germinate fast and seedlings grow better under high light conditions (Salisbury, 1942; Foster and Janson, 1985; Hewitt, 1998; Rose and Poorter, 2003; Baraloto et al., 2005), whereas larger seeds generally present dormancy and their seedlings are shade tolerant (Foster and Janson, 1985). In concordance with Tabarelli et al. (2010), if the seed rain in the ecotone area consists mostly of small seeds, all the edge area will remain in early successional stages, with dominance of pioneers and loss of some late successional species and their associated fauna. From an evolutionary perspective, the reduction in the size of dispersed seeds has significant adverse effects on the dynamics of plant populations and communities. In deciduous forests and defaunated forest areas, Galetti et al. (2013) demonstrated that defaunation influences the size reduction of *Euterpe edulis* seeds, which in turn increases the vulnerability of seeds to desiccation and makes seedling populations

more sensitive to damage by herbivory.

Our results showed an increase in the diversity of seed dispersal syundrome on the seed rain through the plantation cycle, associated with an increase in the permeability for native dispersers. They also showed that long-term plantation cycles will increase the abundance and functional diversity of seeds arriving from the native forest, improving the seed bank and facilitating the regeneration of native vegetation after the plantation cycle. The seed rain into tree plantations tends to concentrate in short distances (< 200 m) from the native forest; consequently, large continuous stands will be less suitable for the regeneration of native vegetation and will not be used by the native fauna.

Table 1

Response and influence (magnitude and extent) of edge effects on the seed rain of the proportion of vertebrate-dispersed seeds per size category in the Atlantic forest of northeastern Argentina. NF: Native Forest, R: Recent pine plantation, I: intermediate pine plantation, M: mature pine plantation, E: eucalyptus plantation, NS: No significant, Exp.: Exponential, Mon.: Monotonic, Uni.:unimodal, Neu.: Neutral, Ymax: Upper asymptote of the best fit regression, Ymin: Lower asymptote of the best fit regression.

Edge Contrast	Size	Model	R^2	P	Ymax	Ymin	Magnitude		Extent (m)
							Native Forest	Plantation	
NF-R	very small	NS	NS	NS	NS	NS	NS	NS	NS
	small	Mon.	0.31	0.02	0.01	0.00	0.00	1.00	0
	medium	Uni.	0.69	< 0.0001	0.01	0.01	0.82	0.87	2
NF-I	very small	Uni.	0.62	0.00	0.02	0.02	0.83	0.51	92
	small	Uni.	0.94	< 0.0001	0.02	0.02	0.95	0.00	17
	medium	Uni.	0.61	0.00	0.01	0.01	0.84	0.30	184
NF-M	very small	Neu.	–	< 0.0001	0.04	0.04	0.00	0.00	0
	small	Uni.	0.50	0.00	0.01	0.01	0.96	0.83	214
	medium	Mon.	0.20	0.07	0.10	0.00	− 0.94	0.15	31
NF-E	very small	Neu.	–	< 0.0001	0.04	0.04	0.00	0.00	0
	small	Neu.	–	0.003	0.04	0.04	0.00	0.00	0
	medium	Exp.	0.50	0.00	–	0.00	− 0.74	1.00	482

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