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.

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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

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
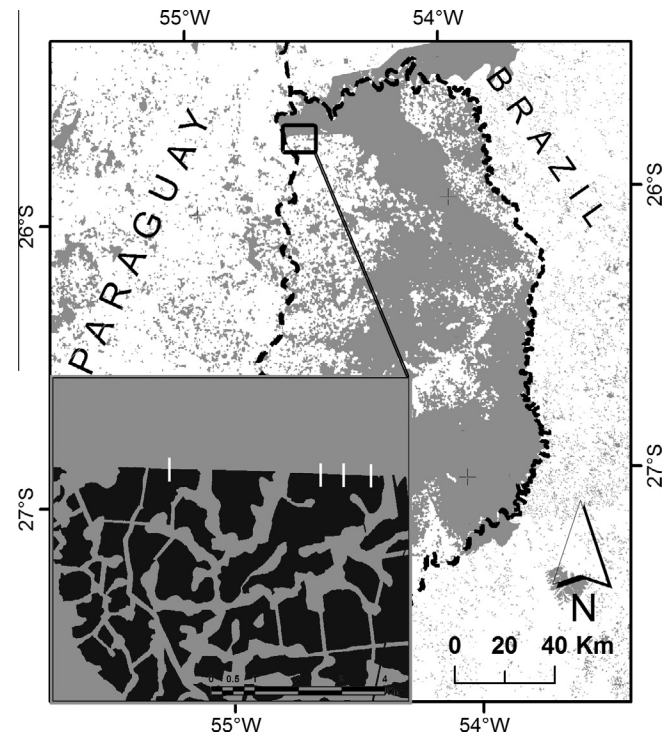

Fig. 1. Study area in northeastern Argentina. Atlantic forest remnants are shaded in grey and tree plantations in black in the detail of the study area (transects are marked on white). Modified from Peyras et al. (2013).

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).

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.

We focused our study in the Atlantic forest, where both edge effects and seed dispersal are critical ecological processes in the natural regeneration and conservation of native forests. The native Atlantic forest habitat has been converted and fragmented over the last decades, associated with the expansion of agriculture, livestock and commercial tree plantations. Currently, most forest remnants are smaller than 50 ha, and over 75% of the area is already affected by edge effects (Ribeiro et al., 2009). Edge effects are considered one of the primary factors determining the observed changes in populations and communities (Banks-Leite et al., 2010; Zurita et al., 2012; Hanski et al., 2013).

2.2. Study design

To study the influence of edge effects and habitat contrast on patterns of seed dispersal (wind, birds and bats), we analyzed seed rain richness and abundance across four contrasting adjacent habitats (from one habitat interior to the other) between the native forest and tree plantations. Selected edges were part of the same continuous protected area (Puerto Península Provincial Park, 25° 44′ S 54° 33′ W) to minimize biases related to abundance and distribution of seed sources, and were oriented in the same direction (the native forest located north of the plantations) to minimize potential biases related to differences in wind direction. We selected three pine plantations of 2-yrs-old (recent), 6-yrs-old (intermediate) and 19-yrs-old (mature) pine (*Pinus taeda*), and one 23-yrs-old eucalypt plantation (*Eucaliptus dunnii*). As plantations grow vegetation structure becomes more similar to native forest and the contrast between habitats decreases (Zurita and Bellocq 2012; Peyras et al., 2013).

In each edge, we established a 600 m transect, starting 300 m inside the native forest and ending 300 m inside the plantation. On each transect, we set 22 sampling points at the following distances from the edge between habitats, in both directions: 0, 5, 15, 30, 50, 75, 100, 150, 200, 250 and 300 m. We concentrated sampling effort near the edge where we expected a high rate of change based on previous studies in the area (Zurita et al., 2012; Peyras et al., 2013). Transects were located at least 500-m apart from each other (Fig. 1).

At each sampling point, we sampled seed rain continuously over 1 year using seed traps. A seed trap was 2 m² in area (2 × 1 m), and consisted of a fine nylon fabric (0.5 mm) supported
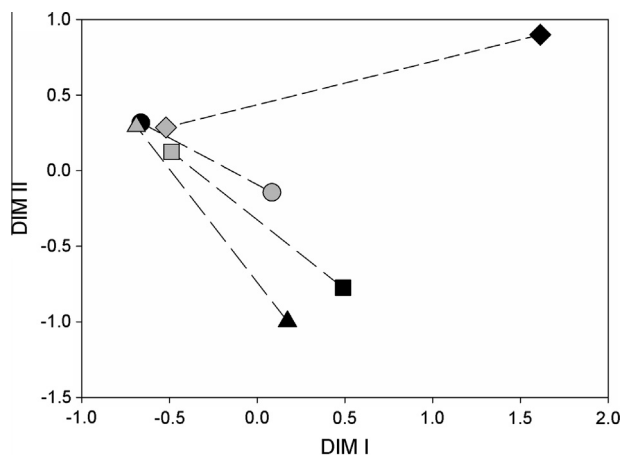
Fig. 3. Abundance (a) and richness (b) of wind- (black bars) and vertebrate-dispersed seeds (grey bars) in native forest and four different tree plantations in the Atlantic forest of northeastern Argentina. Numbers above bars are the total seed species or morphotypes collected in habitat interiors (>100 m from the edge). NF: native forest, E: eucalypt plantation, M: mature pine plantation, I: intermediate pine plantation, R: recent pine plantation.

to an iron frame about 1 m above the ground. Materials captured by the seed traps (seeds, leaves and woody debris) were collected every 10 days to avoid decomposition, and brought to the laboratory for later analysis. We classified collected seeds as wind- or vertebrate-dispersed seeds based on their morphology, and we identified them to the lowest possible taxonomic level using a reference collection and morphological descriptions (Lorenzi, 2002; Lopez et al., 2002). Additionally, we surveyed and identified all trees with DBH ⩾ 5 cm in a 25 m² plot located around each seed trap, and then excluded from the analysis those seed species that may have been collected by gravity.

At each sampling site we also established 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. To estimate arboreal and understory cover, we used digital photos taken from 1.5 m above the ground toward the canopy (tree cover) and to the ground (understory cover) (Peyras et al., 2013). The percent canopy and understory cover on each photo was analyzed with Scion-Image Alpha 4.0.3.2.

2.3. Data analyses

To test for the assumption that contrast between habitats (forest-plantations) decreases from recent to mature plantations we first performed a multidimensional scaling analysis (MDS) including all sampling sites (R Development Core Team, 2010). We used the basal area, stem density, tree cover, understory cover,

Fig. 2. Vegetation structure dissimilarity (Euclidian distance on a MDS analysis) between native forest (grey) and tree plantations (black). Circles: eucalypt plantation; Squares: mature pine plantation; Triangles: intermediate pine plantation; Diamonds: recent pine plantation. The points represent the centroid of each group (native forest and plantations) and the line represents the Euclidian distance between centroids.
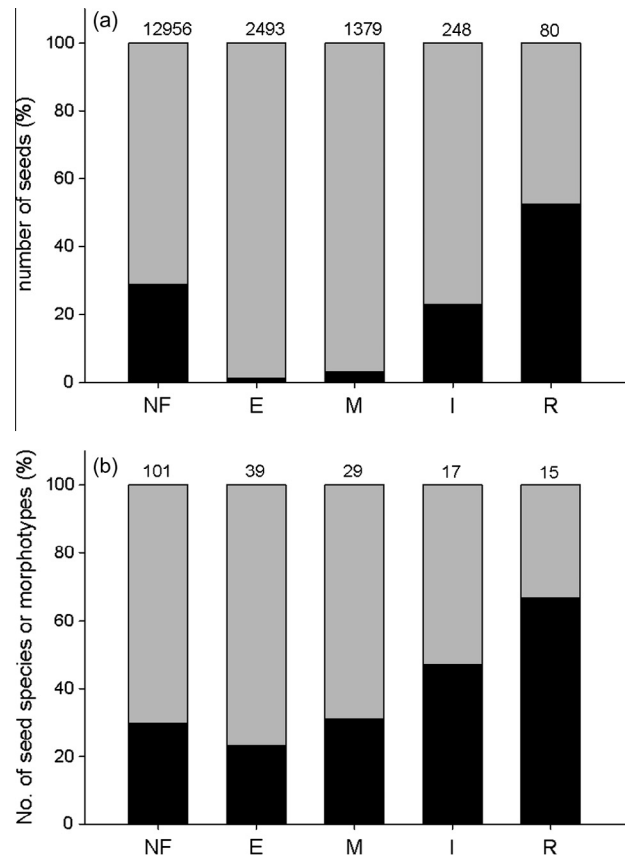
and canopy height as grouping variables. Then, we estimated the Euclidian distance between the centroids of the forest-interior and the plantation-interior sampling sites as a measure of the environmental contrast (Banks-Leite et al., 2010); lower distances indicate similar vegetation structure. We included only interior sampling sites on the MDS to represent habitats beyond edge effects. In a separate analysis, we performed the MDS but including only edge sampling sites (0–15 m). Results were very similar (correlation between ordinations 0.99) to the previous analysis; therefore, we include only interior sites in the estimation of environmental contrasts. To examine the role of contrast between the edge and the interior of each habitat (forest or plantation) on the magnitude of edge effects (MEI), we performed two separate MDS analysis: one to compare edge (0–15 m)–interior (100–300 m) native forest sites and the other to compare edge–interior plantation sites. We used the Euclidian distance between edge and interior sampling sites as a measure of contrast.

To study the response of seed rain to edge effects and differences on habitat suitability we analyzed the abundance and richness of wind- and vertebrate-dispersed seeds using the
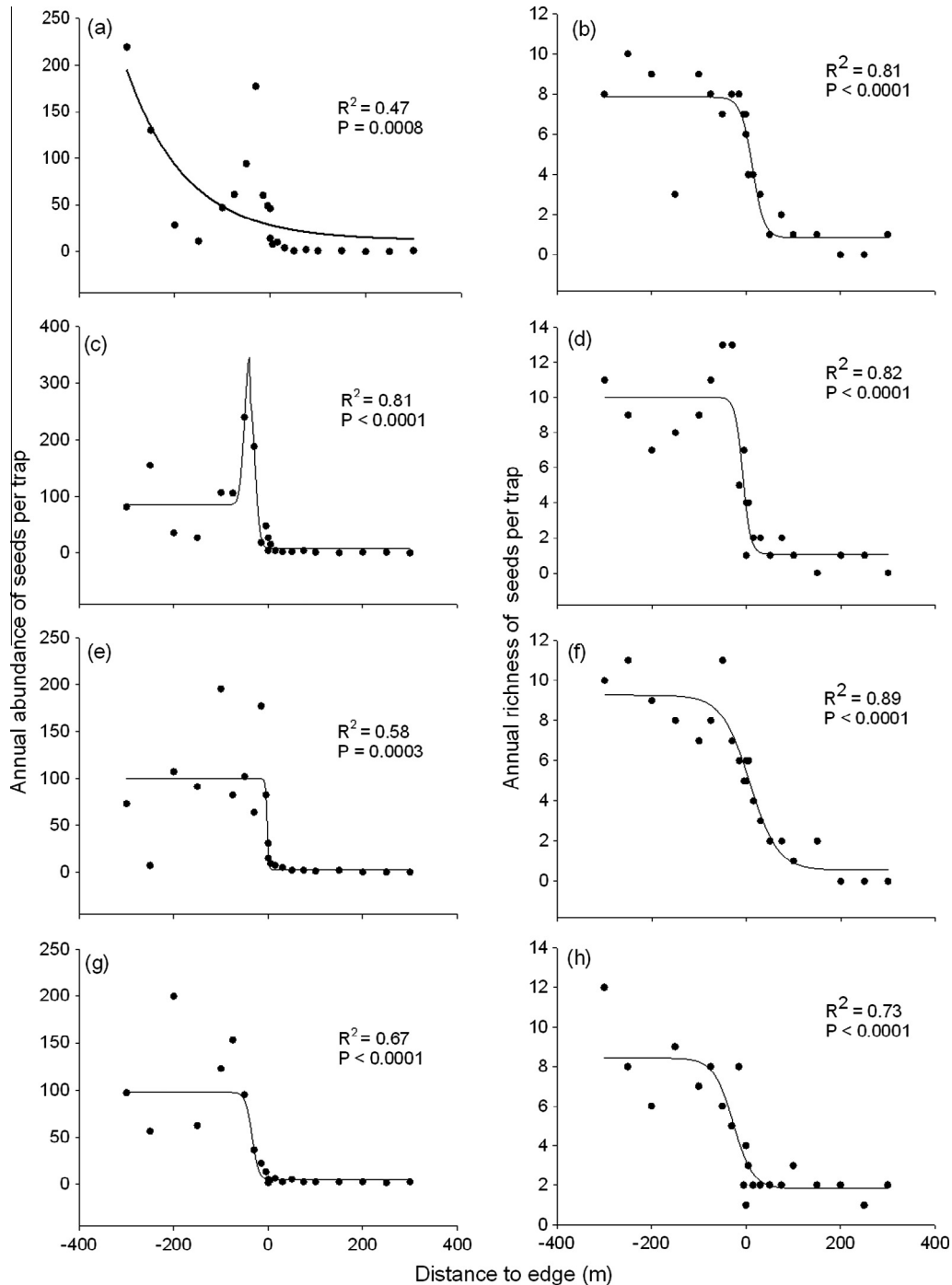

Fig. 4. Annual richness (left) and abundance (right) of wind-dispersed seeds per trap in the Atlantic forest of northeastern Argentina. Negative values indicate distances into the native forest whereas positive values indicate distances into the plantations. (a,b) Recent pine plantation, (c,d) intermediate pine plantation, (e,f) mature pine plantation and (g,h) eucalypt plantation. Lines correspond to the best fit regression.

procedure proposed by Ewers and Didham (2006), Porensky (2011), Zurita et al. (2012) and Harper et al. (2005) for continuous variables. We first fitted each dependent variable (abundance and richness of wind- or vertebrate-dispersed seeds) to four statistical models representing the three possible patterns of responses (monotonic, unimodal and neutral), and then 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 2002). Three statistical regression models are necessary to represent all theoretical responses to edge effects and to calculate differences on habitat suitability.

However, we also included an exponential regression model to account for potential incomplete edge responses where edge effects extend beyond sampled distances (Ewers and Didham, 2006).

We fitted seed rain to the following statistical regression models: (1) *sigmoid model*: describe the complete monotonic response where habitat suitability changes from one habitat to the other ($Y = Y_0 + a/(1 + e(-(d-x_0)/b))$), (2) *exponential model:* represents an incomplete monotonic response where edge response extends beyond the sampled area (only in one side of the edge) ($Y = Y_0 + a*e(d*x_0)$), (3) *unimodal model*: implies an increase or decrease
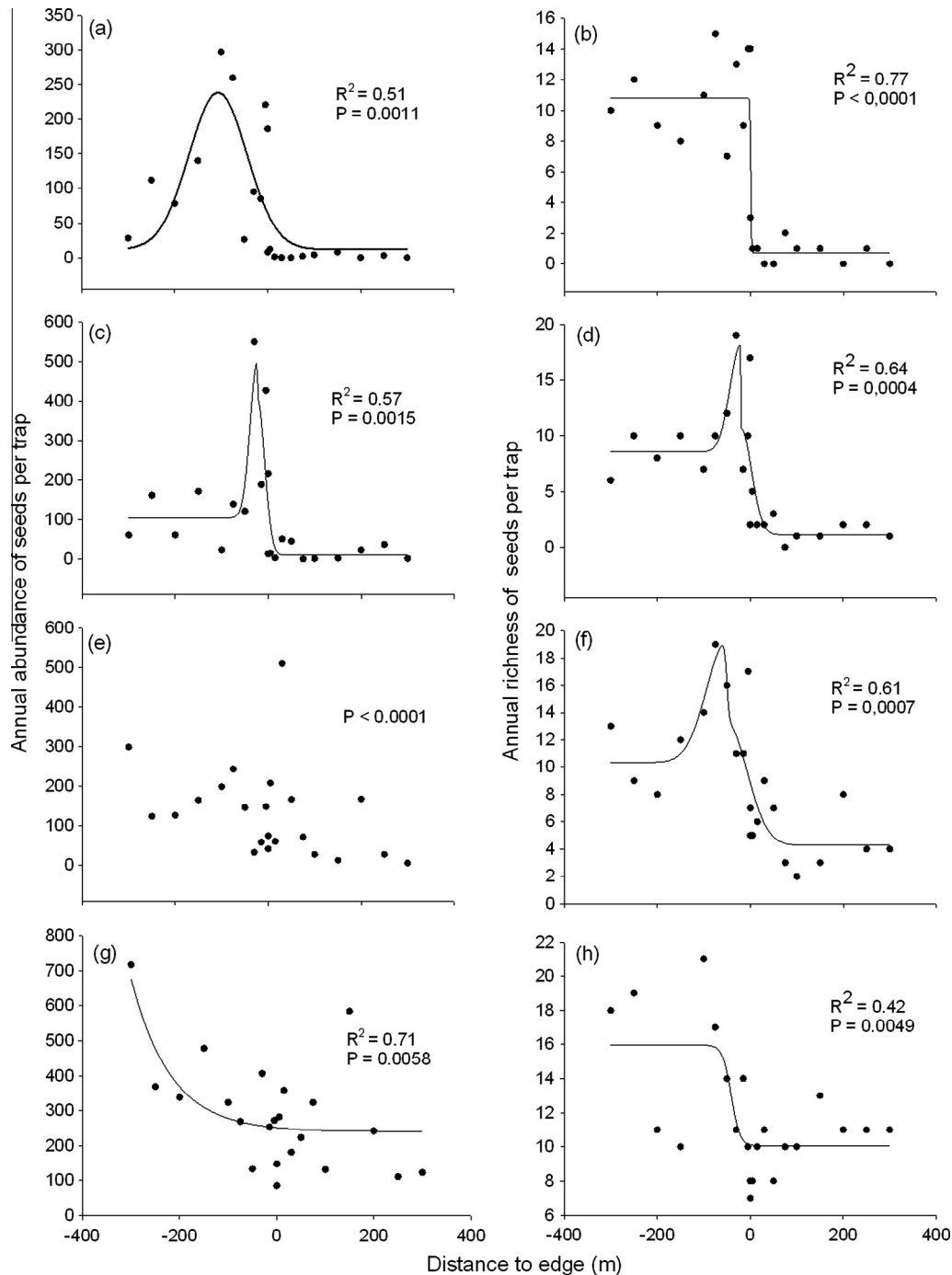

Fig. 5. Annual richness (left) and abundance (right) of vertebrate-dispersed seeds per trap in the Atlantic forest of northeastern Argentina. Negative values indicate distances into the native forest while positive values indicate distances into the plantation. (a,b) Recent pine plantation, (c,d) intermediate pine plantation, (e,f) mature pine plantation and (g,h) eucalypt plantation. Lines correspond to the best fit regression.

on the response variable near the edge where habitat suitability can change or not from one habitat to the other ($Y = Y_0 + a/(1 + e(−(d−x_0)/b)+a*e(−.5*((d−x_0)/b)^2))$) and (4) *neutral model*: in this case the dependent variable is constant across the forest-plantation ecotone (there are no edge response and similar suitability of both habitats) ($Y = Y_0$).

To quantify the extent of edge effects on seed dispersal (the distance in both directions of the influence of the edge) we calculated the distance between the two inflection points of the second derivative for all models (Ewers and Didham, 2006). To quantify the difference on habitat suitability between adjacent habitats we calculated the percent difference between the lower and upper asymptotes of the curve ($(Y_{max}−Y_{min})/Y_{max}*100$). In the sigmoidal model, Y_{max} and Y_{min} (Y_0) correspond to the upper and lower asymptote, respectively. Y_{max} was calculated from the inflection point of the first derivative in the unimodal and combined models. Finally, to calculate the magnitude of edge effects on each habitat we used the MEI index proposed by Harper et al. (2005). We calculated the MEI using the asymptotes on each habitat (i) and the value of the response variable at the edge (e); MEI = (e−i)/(e+i).

To explore the influence of edge contrast between habitats on the difference on habitat suitability and the extent of edge effects and on the richness and abundance of dispersed seeds on plantations (Y_{min}), we performed simple correlation analyses between the response variables (difference on habitat suitability, extent and Y_{min}) and the degree of contrast between habitats (Euclidian distance on the MDS, representing dissimilarity on vegetation structure between native forest and tree plantation). We also correlated the interior–edge contrast on each habitat with the MEI calculated for the same habitat.

3. Results

A total of 17156 seeds were collected in the 88 seed traps during the 12 months sampling period. Seeds represented 102 species and morphotypes, of which 68 were vertebrate-dispersed seeds and 34 were wind-dispersed seeds. Most of the trapped seeds belonged to the Fabaceae, Lauraceae, Cecropiaceae, Solanaceae and Piperaceae families (Appendix A).

In all forest-plantation sites, the MDS showed two distinct groups based on vegetation structure: forest sampling sites grouped on one side of the bi-plot, whereas plantation sampling sites grouped on the opposite side (with the exception of the eucalypt plantation) (Fig. 2 and Appendix B). As expected, the Euclidian distance between centroids (native forest and plantations) increased from mature (pine and eucalypt) to intermediate, and recent pine plantations. This result validates the assumption that the contrast between edges increases from mature to recent plantations. The MDS on vegetation structure between edge and interior for each habitat (forest and plantations) sampling sites showed no clear pattern of aggregation (Appendix C).

Total richness and abundance of seeds decreased from low (eucalypt plantation) to high contrast edges (recent pine plantation) (Fig. 3). When considered separately, by dispersal agent, however, the proportion of vertebrate-dispersed seeds (both abundance and richness) in the plantation decreased from the low to the high contrast edge, but the proportion of wind-dispersed seeds followed the opposite pattern (Fig. 3).

As expected, wind-dispersed seeds showed similar patterns of edge effects in all studied forest-plantation transects, but responses of vertebrate-dispersed seeds varied among edges (Appendix D). Abundance and richness of wind-dispersed seeds showed a monotonic response to edge effects (Fig. 4a–h) with the exception of seed abundance in the native forest-intermediate pine edge (Fig. 4c). Seed rain of vertebrate-dispersed seeds showed

a unimodal response to edge effects in high contrast edges (recent and intermediate pine plantations) (Fig. 5a–d), except for seed richness in the native forest-recent pine edge (Fig. 5a and b); and a variety of responses in low contrast edges (mature plantations), including neutral (seed abundance in mature pine plantation, Fig. 6e), monotonic (seed abundance and richness in the eucalypt plantation, Fig. 5g and h), and unimodal (seed richness in the mature pine plantation, Fig. 5e) responses.
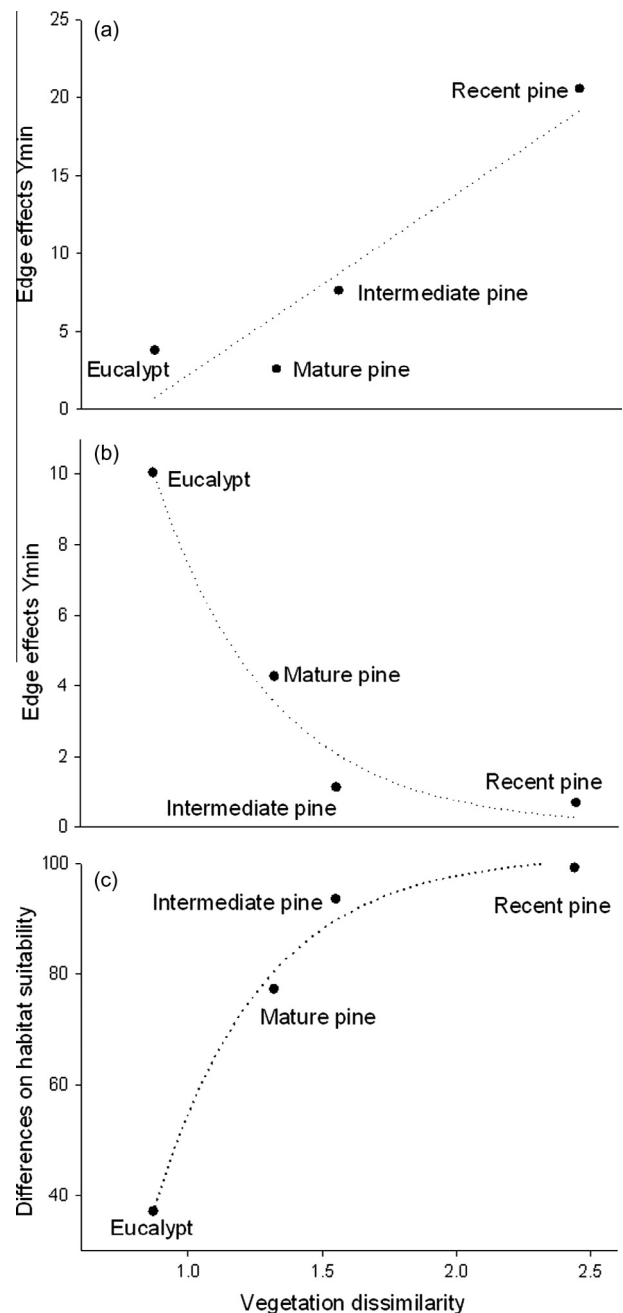

Fig. 6. Relationship between habitat contrast in vegetation structure (Euclidian distance on a MDS analysis) on the Y_{min} (lower asymptote) and differences on habitat suitability (the percent difference between the lower and upper asymptotes), between native forest and tree plantations in the Atlantic forest of northeastern Argentina. Y_{min} (a) of edge effects on the abundance of wind-dispersed seeds, Y_{min} (b) of edge effects on the richness of vertebrate-dispersed seeds and differences on habitat suitability (c) on the richness of vertebrate-dispersed seeds.

The suitability of tree plantations to favor vertebrate-dispersed seeds (lower asymptote, Y_{min}) was negatively correlated to vegetation dissimilarity between the native forest and tree plantations ($r = -0.9$, $P = 0.05$) (Fig. 6a, Table 1). Also, the suitability difference between habitats on richness of vertebrate-dispersed seeds was marginally and positively correlated to vegetation dissimilarity (Euclidian distance) between the native forest and plantations ($r = 0.95$, $P = 0.07$) (Fig. 6b, Table 1). For wind-dispersed seeds, there was a marginal and positive correlation between habitat contrast and the suitability of tree plantations with respect to abundance of wind-dispersed seeds ($r = 0.9$, $P = 0.06$) (Fig. 6c, Table 1). For the rest of the edges there was no correlation between habitat contrast and the difference on habitat suitability, the extent of edge effects or the lower asymptote (Y_{min}) ($r < 0.5$, $P > 0.1$ in all cases). That means that high contrast edges produced greater differences on habitat suitability and edge effects on vertebrate-dispersed seeds, and were less suitable for bird- and bat-dispersed seeds than low contrast edges. For wind-dispersed seeds we observed the opposite pattern: high contrast edges were more suitable than low contrast edges.

The magnitude of edge effects (MEI) between native forest and tree plantations showed no correlation to vegetation contrast between edge and habitat interior on both richness and abundance of vertebrate- and wind-dispersed seeds ($r < 0.8$, $P > 0.1$ in all cases).

4. Discussion

The results of our study are consistent with our predictions that edge effects can affect differently seed rain patterns, depending on both the degree of contrast between habitats and the dispersal agent. The current analytical framework developed to explore population and community responses to edge effects (Ewers and Didham, 2006; Porensky, 2011; Zurita et al., 2012), successfully described the response of seed dispersal; however, we showed that mechanisms behind the observed patterns differed depending on the dispersal agent.

The observed response of richness and abundance of wind-dispersed seeds was transitional in most of the studied edges, as expected for patterns of seed rain determined by abiotic factors (Davies-Colley et al., 2000). However, contrary to our predictions, we found a larger edge influence in high contrast edges compared to that in low contrast edges. We had expected that the absence of physical barriers would facilitate movements of seeds from the native forest into recent plantations resulting in greater extent and lower magnitude of edge effects in the abundance and richness of wind-dispersed seeds compared to mature tree plantations. A possible explanation for this pattern may be that the predominant wind direction in the study area is from the south, and transects were located with plantation habitat at the south, and native forest at the north side of the edge; therefore, the main wind direction tended to blow seeds back to the source habitat. Also, an endogenous contribution of seeds from inside mature plantations could contribute to the decline in the magnitude of edge effects on seed rain dispersed by wind. Moreover, in two cases (Fig 5a and d) the visual interpretation of patterns and the statistical comparison of models leaded to different interpretations, emphasizing the relevance of a critical examination of the patterns after analysis to achieve a coherent biological interpretation of edge effects.

Ries and Sisk (2004) proposed a model based on the spatial distribution of resources in the edge to predict the response of animal species to edge effects. The model may provide an explanation for the patterns of vertebrate-dispersed seeds that we observed. According to Ries and Sisk (2004), positive responses to edges are expected when resources are concentrated near the edge or when the distribution of resources on both sides of the edge is complementary (different). While transitional and neutral responses are expected in cases of supplementary distribution of resources. Lopez de Casenave et al. (1995) showed, in a Chaco semi-arid Forest, that abundance and basal area of understory tree species with fleshy fruit are higher in the edge than in forest interiors. In the southern Atlantic forest, bird density/activity is higher in high (forest-open habitats) than in low contrast edges (forest-mature plantations) edges (Zurita et al., 2012), which is associated to resource concentration (arthropods, flowers and fruits) (Oosterhoorn and Kapelle, 2000). Seed rain of vertebrate-dispersed seeds measured in our study had the same pattern of response to edge effects as expected for the dispersal agent: positive in high contrast edges (complementary resources) and transitional in low contrast edges (supplementary resources).

We found that the proportion of vertebrate-dispersed seeds increased with forest age, with recent plantations showing the lowest proportion of vertebrate-dispersed seeds. A similar pattern was observed by Tabarelli and Peres (2002) in plots of varying regeneration stages or ages in the Atlantic forest of southeastern

Table 1

Edge response and differences on habitat suitability of wind- and vertebrate-dispersed seeds across four edges between native forest and tree plantations in the Atlantic forest of northeastern Argentina. UM: modified unimodal, Y_{max}: upper asymptote of the best fit regression, Y_{min}: lower asymptote of the best fit regression.

Habitat	Dispersal agent	Model	AICs	Y_{max}	Y_{min}	Differences on habitat suitability (%)	Magnitude		Extension (m)
							Native forest	Plantation	
Abundance									
R	Wind	Exp.	170.97	205.36	21.64	89.46	−0.75	0.35	–
	Vertebrates	UM	188.23	238.80	12.91	94.59	0.89	0.69	50
I	Wind	UM	155.93	346.50	7.64	97.80	0.96	0.02	–
	Vertebrates	UM	207.57	495.29	9.78	98.03	0.65	0.87	–
M	Wind	Sig.	165.89	99.70	2.62	97.37	−0.62	0.8	5
	Vertebrates	Mean	212.28	–	–	–	0	0	–
E	Wind	Sig.	153.99	97.64	3.80	96.11	−0.91	0.08	10
	Vertebrates	Exp.	214.18	1038.45	216.50	79.15	−0.46	0.02	–
Richness									
R	Wind	Sig.	22.47	7.85	0.84	89.30	−0.12	0.76	32
	Vertebrates	Sig.	48.77	10.79	0.07	99.35	−0.12	0.85	2
I	Wind	Sig.	32.87	7.85	1.07	86.38	−0.47	0.55	20
	Vertebrates	UM	54.16	17.89	1.14	93.66	0.36	0.74	20
M	Wind	Sig.	11.67	9.26	0.55	94.06	−0.26	0.82	76
	Vertebrates	UM	55.21	18.90	4.28	77.35	0.29	0.35	270
E	Wind	Sig.	26.41	8.43	1.83	78.35	−0.44	0.28	55
	Vertebrates	Sig.	52.07	15.98	10.06	37.07	−0.22	0	80

Brazil. Our results are also consistent with previous evidence indicating that the suitability of plantations for native bird species increases with plantation age in the Atlantic forest (Zurita and Bellocq 2012). The contribution of arboreal and terrestrial mammals to seed rain is also important for the natural regeneration of subtropical forests; however, birds and bats are much more abundant than other vertebrate dispersers in tree plantations.

The objective of this study was to compare seed rain among edges differing in habitat contrast (high and low contrast), rather than studying a particular edge situation. Thus, differences among transects that are attributed to different levels of contrast between adjacent habitats could alternatively be due to other unmeasured differences, such as relative abundance of different tree species. To minimize this effect and any difference related to the origin of native forest species, all transects started in the same continuous protected area. The similarity among native forest sites is evident from the MDS biplot (Fig. 2).

The inclusion of functional responses on the study of edge effects increases our understanding of mid- and long-term effects of habitat fragmentation on ecosystem functioning. Natural regeneration of the native forest in tree plantations is highly dependent on seed arrival. Our results indicate the relevance of considering the contrast between habitats and the dispersal agent when planning passive or active restoration techniques in areas influenced by edge effects. This is particularly important in highly fragmented landscapes such as the Atlantic forest. Last, understanding the effects of human disturbances on seed dispersal must be a priority to be able to accurately predict potential mid- and long- term effects on forest structure and functioning, and to develop low cost restoration techniques.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.05.054.

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