

Patch size, shape and edge distance influence seed predation on a palm species in the Atlantic forest

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Seed predation is an important ecological process that affects the abundance, diversity and distribution of plant species, and it is known to be influenced by defaunation and forest fragmentation. Most studies on seed predation in human-modified landscapes do not take into account the different spatial scales in which this process operates. In this study, we evaluated how variables at three distinct spatial scales affected the seed predation of a palm that provides a keystone resource to the frugivore community, the queen palm *Syagrus romanzoffiana*. Thirteen landscapes that vary in forest cover, number of fragments and patch sizes were sampled in the Brazilian Atlantic forest. We also evaluated the contribution of the three main groups of seed predators: squirrels, terrestrial rodents and invertebrates. Our results indicate that seed predation is more affected by fragment and local variables than by landscape influences. In addition, the size of the fragment, its shape and the distance from the nearest forest edge were the main predictors of the proportion of predated seeds. Moreover, the two main seed predators (squirrels and invertebrates) responded to the same fragment and local variables. Because most of the Atlantic forest consists of small fragments, we expect that the seed predation of this keystone palm should be high in most of its distribution, with potential consequences for the frugivore community.

Habitat loss and fragmentation are considered dominant threats to biodiversity (Fahrig 2003, Laurance et al. 2006). Due to its severe effects on species populations, several studies were developed to evaluate how patch size and isolation affects community composition, species abundance and density (Laurance et al. 2006, 2011). Beyond the effects on populations, the landscape structure also influences several key ecological aspects, such as connectivity (Martensen et al. 2008, 2012), gene flow (Robinson et al. 2012), microclimate (Murcia 1995, Laurance et al. 2002), landscape resilience (Tamboosi et al. 2014) and carbon stock (Pütz et al. 2014). Nevertheless, much less attention has focused on the effects of landscape structure on important ecological processes, such as seed dispersal (Levey et al. 2005), herbivory (Kruess 2003) and seed predation (Orrock et al. 2003).

The amount of habitat within a landscape (i.e. habitat amount) and its spatial configuration strongly influences species interactions (Tewksbury et al. 2002, Pardini et al. 2005, 2009, Mortelliti et al. 2011). For example, habitat loss, when reaching critical amounts (i.e. around 70%), has severe effects on the persistence of several species, and therefore impacts the composition of the local community (Terborgh et al. 2001, Pardini 2004, Dirzo and Mendoza 2007, Pardini et al. 2009), creating landscapes with impoverished communities and simpler interaction networks (Terborgh et al. 2001, Fahrig 2003, Tylianakis et al. 2010). These ecological interactions losses can occur due to the extinction of the involved species (Fleury and Galetti 2006, Valiente-Banuet

et al. 2015), by reductions in the species abundances to a level where ecologically functional interactions between species are no longer possible (i.e. ecological extinction) (McConkey and Drake 2006, Galetti et al. 2013) or as a response to changes in the behavior of the involved species (Brinkerhoff et al. 2005, McConkey and Drake 2006). The loss of important mutualistic interactions, such as seed dispersal and pollination, can influence species recruitment, composition and even the evolution of species (Dirzo and Mendoza 2007, Muller-Landau 2007, Galetti et al. 2013).

Seed predation is an important type of ecological interaction because it has direct consequences for plant recruitment (Orrock et al. 2006), regeneration (Wright et al. 2007), species abundance (Smith III 1987), spatial distribution (Smith III 1987), and evolution (Talluto and Benkman 2013). To understand the effects of habitat loss and fragmentation on seed predation, it is paramount to evaluate the influences of landscape, habitat and microhabitat characteristics on the abundance and behavior of seed predators. This is particularly important for plants that provide keystone resources to the animal community, because even though tropical forests hold a high diversity of plant species, few species are able to maintain the population of resident frugivores (Terborgh 1986, Peres 2000).

In this study, we investigated how variations in the landscape habitat amount, fragment size, shape, palm fruit productivity and distance from the forest edge affect the seed predation of the queen palm *Syagrus romanzoffiana*,

an important resource for the frugivore community in the Atlantic rainforest (Peres 1994, Genini et al. 2009). We also estimated the relative contribution of the three main groups of seed predators (squirrels, invertebrates, and terrestrial rodents) and tested five hypotheses regarding how the seed predation should respond to changes in the landscape structure.

We chose the queen palm *S. romanzoffiana* as the model species because of its importance to the frugivore fauna. It is also an abundant species in the semi-deciduous Atlantic forest (Henderson et al. 1995) and is present even in the smaller fragments. This is what enabled us to collect data in extremely degraded landscapes. This palm has a large distribution in South America (Henderson et al. 1995) and produces abundant fruits throughout the entire year, which are consumed by at least 60 vertebrate species, including primates, ungulates, rodents, birds (Supplementary material Appendix 1, Table A1), and by several invertebrates (Silva et al. 2008). However, few species can prey upon the seeds that are protected by a thick endocarp. The few seed predators of *S. romanzoffiana* can be divided into three main groups: a) squirrels (represented in the study region only by *Sciurus ingrami*; Supplementary material Appendix 1, Fig. A1), which prey upon seeds of ripe and unripe fruits, collecting them both on the ground and directly from the tree (Galetti et al. 1992, Paschoal and Galetti 1995, Bordignon et al. 1996); b) agoutis (*Dasyprocta* spp.) and other small rodents (hereafter terrestrial rodents) that prey only upon seeds on the ground (Guimarães et al. 2005); and c) specialized invertebrates (hereafter invertebrates), mainly the curculionid *Revena rubiginosa* and the bruchid *Pachymerus cardo*, which oviposit on the fruit so that the larvae can grow, eat the endosperm and kill the seed (Alves-Costa and Knogge 2005, Silva et al. 2008). Although squirrels and terrestrial rodents are mainly seed predators, they also prey upon some amount of invertebrate larvae that grow inside the seeds (Visser et al. 2011). Peccaries were not considered a fourth group of seed predators because they usually spit or swallow the endocarp of the *S. romanzoffiana* fruits, acting more as pulp eaters and seed dispersers than seed predators (Keuroghlian and Eaton 2008, 2009). Moreover, due to hunting, the peccaries only occur in one landscape of the study area.

Material and methods

Hypotheses

Based on the literature, we developed five hypotheses regarding how the seed predation should respond to changes in the landscape structure. In the Rodentation hypothesis (Fig. 1; Dirzo et al. 2014), we propose that highly degraded landscapes (defined as landscapes with less than 20% of forest cover, with small fragments, and with a relatively higher amount of areas under edge effect; Tambosi et al. 2014) the density of rodents should be higher than in more preserved landscapes, due to the absence of more sensible predators or competitors (Terborgh 1986) and/or due to the higher productivity of the edges (Murcia 1995). In this way, the palms in these degraded landscapes should suffer a higher seed predation than palms in more preserved ones.

In the Intermediate hypothesis, we propose that in landscapes with intermediate levels of degradation (with forest cover between 20 and 60%, and with fragments between 50 and 500 ha) seed predation should be more intense because these landscapes should have enough habitat to maintain the seed predator populations, which should benefit from the higher productivity of the areas under the edge effect (Murcia 1995, Bayne and Hobson 2000, Koprowski 2005, Fleury and Galetti 2006). On the contrary, the seed predation should be low in more degraded landscapes, due to the lack of habitat to maintain healthy seed predator populations (Koprowski 2005, Freire et al. 2013). The seed predation in well preserved landscapes should be lower, due to the healthy community of mesopredators that control the population of rodents (Bayne and Hobson 2000, Solórzano-Filho 2006).

In the Invertebrate control hypothesis, we propose that seed predation by invertebrates should be higher in areas with lower seed predation by rodents. It should happen because the rodents prey upon invertebrate larvae (Visser et al. 2011), a negative interaction which tend to have strong effects on invertebrate populations (Peguero and Espelta 2013). Moreover, the rodents compete for the fruits with the adult invertebrates, destroying and reducing the availability of reproduction sites. Some rodent species also burry and cache fruits, making then unavailable for the invertebrates (Andreazzi et al. 2009, Visser et al. 2011).

In the Predator turnover hypothesis, we propose that all the three hypotheses above (i.e. Rodentation, Intermediate and Invertebrate control) are correct, but the Rodentation hypothesis is applied mainly to seed predation by terrestrial rodents due to their opportunistic behavior, which allow them to exploit both degraded habitat and non-habitat areas such crops (Andreazzi et al. 2009), while the Intermediate hypothesis is applied mainly to seed predation by squirrels, which require a minimal amount of forest to live (Freire et al. 2013). This way palms in very preserved landscapes (with more than 60% of forest cover, fragments with more than 500 ha, and a relative lower amount of area under the edge effect) should suffer an intense seed predation by invertebrates as described in the Invertebrate control hypothesis. Finally, there is also the Null hypothesis, where we propose that habitat degradation would have no effect on the overall seed predation, nor on the seed predators.

Study area and landscape selection

We performed our study in one of the most fragmented regions of the interior of São Paulo State, Brazil. The region is part of the Atlantic forest domain, originally with 150 million ha and now reduced to only 12% of forest cover, where approximately 83% of the remaining fragments are small in size (< 50 ha; Ribeiro et al. 2009). We chose 13 landscapes with a 1500 m radius around a midpoint position (~700 ha), in a gradient of forest cover amount ranging from 2 to 70% (Fig. 2 and Supplemental material Appendix 1, Table A2). The predominant matrix is sugar cane, and the size of our chosen landscapes were based on the literature, which showed that both small vertebrates and beetles from the family Curculionidae usually respond to landscape variables in

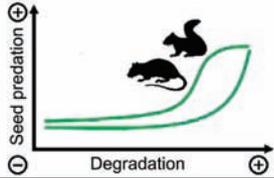
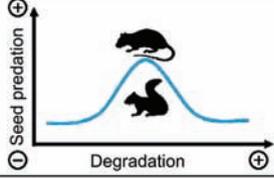
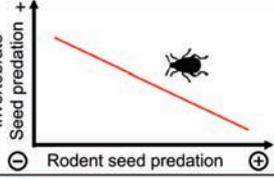
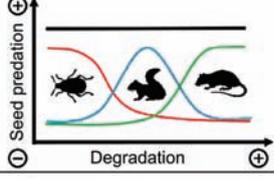
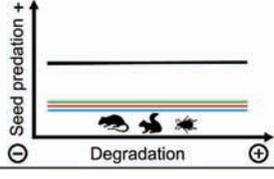
Hypothesis	Description of the expected responses	Sketch of expected responses
H1: Rodentation hypothesis	A positive relationship exists between degradation and seed predation, due to the high presence of rodents in more degraded areas	
H2: Intermediate hypothesis	Seed predation is high in areas with intermediate levels of degradation, because rodents thrive in these areas	
H3: Invertebrate control hypothesis	Areas with high seed predation by rodents should have low seed predation by invertebrate, because rodents prey upon invertebrate larvae and destroy their reproduction sites	
H4: Predator turnover hypothesis	The overall seed predation is not affected by any of the tested variables, but there is a turnover between the groups of seed predators	
H0: Null hypothesis	Neither the overall seed predation nor the main groups of seed predators are affected by habitat degradation	

Figure 1. Hypotheses, with their respective description and a sketch of the expected results. Note that not all hypotheses are mutually exclusive and some of them can be true at the same time to different seed predators (e.g. hypotheses H1 to terrestrial rodents and H2 to squirrels).

scales below 2 km (St Pierre and Hendrix 2003, Boscolo and Metzger 2009, Lyra-Jorge et al. 2010).

To minimize the spatial autocorrelation between our sampling landscapes, the margins of each landscape buffer zone were located with a minimal distance of 3 km from the margin of another landscape (Fortin and Dale 2005). We used a set of CBERS 2B (spatial resolution of 20 and 3 m) and Landsat 7 (spatial resolution of 30 m) imagery to aid in the process of landscape selection. Forest and non-forest (i.e. matrix) classes were used in our analyses. All of the images were obtained freely from the Brazilian National Inst. for Space Research (INPE) website.

Metrics and explanatory variables

In each landscape, we chose a focal fragment and randomly selected and sampled between one to nine palms, according to the fragment size and to the palm availability (Supplementary material Appendix 1, Table A4). When possible, a second fragment in the landscape was also sampled. For each palm, we estimated the amount of fruits on the ground under the palm canopy and the proportion of predated seeds. The geographic (UTM, South America

Datum) coordinates of the palms were also taken, which were used to calculate the palm distance from the nearest forest edge. Because these three variables had different values for each palm, they were called ‘local level variables’.

For each fragment, we calculated its area and a shape variable by dividing the fragment in a grid with cells of 5×5 m and calculating the average Euclidean distance of the grid cells to the nearest forest edge (average edge distance). Then, to extract the effect of the fragment area from the fragment shape, we created a generalized additive model (GAM), with the average edge distances as a function of the fragment area. We used the model residuals as our fragment shape variable (Supplementary material Appendix 1, Fig. A2A). The fragment area and the shape were both called ‘fragment level variables’.

The percentage of forest cover was calculated for each landscape using three different scales (buffers of 500, 1000 and 1500 m radius). These metrics were considered as ‘landscape level variables’. The buffers were created from the geographic centroid of the sampled trees in the landscape (Supplementary material Appendix 1, Fig. A2B). We chose these scale sizes because the response of small vertebrates to landscape variables usually occur in scales below 2 km (Boscolo and Metzger 2009, Lyra-Jorge et al. 2010).

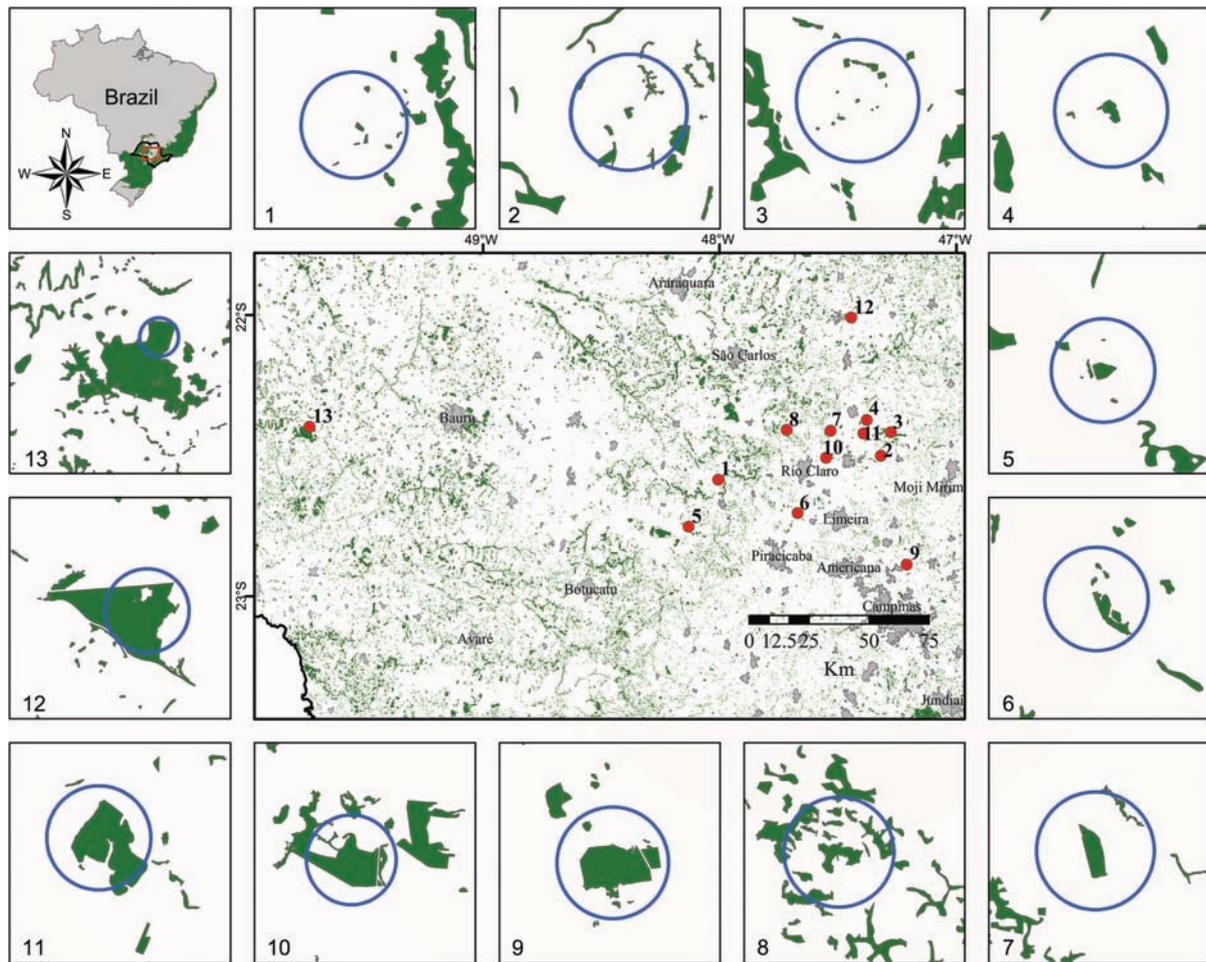


Figure 2. Location of landscapes (red dots) in Atlantic forest remnants, São Paulo, Brazil. Around, in clockwise, the landscapes are shown in ascending order of habitat amount. The blue circles have 1500 m radius and show the biggest scale tested in the forest cover variable.

We did not calculate any connectivity variable because the connectivity can also be expressed as the inverse of the amount of habitat in a landscape (Bender et al. 2003, Fahrig 2003, 2013). The list of explanatory variables is shown in the Table 1.

Seed predation

We delineated four squares of 1 m² each beneath each sampled palm. The squares were placed 30 cm apart from the plant trunk in each cardinal direction. All of the fruits on the leaf-litter within the squares were collected, washed and peeled to expose the endocarp. The endocarps were separated and counted according to seed fate, and we used this data to calculate the proportion of predated seeds by each seed predator. We excluded the endocarps that were decomposed enough to be crushed by hand, because they could obscure the predator's marks.

The identification of the seed predator of each seed was possible due to the patterns left in the fruit endocarp (Supplementary material Appendix 1, Fig. A3). The squirrels leave thin and deep cuts, usually with a triangular shape or, less frequently, using other patterns (Bordignon et al. 1996). Terrestrial rodents gnaw the fruit endocarp in

a way that all of the teeth marks have the same direction, making a concave mark. The invertebrates create a small and perfectly round hole when the larvae bore the endocarps. The

Table 1. List of explanatory variables, with the respective descriptions, used to explain the seed predation of *Syagrus romanzoffiana* by squirrels, invertebrates and terrestrial rodents within the Brazilian Atlantic forest. For more details about the fragment shape and forest cover variables, see Supplementary material Appendix 1, Fig. A1.

Variable	Level	Description and unit
Edge distance	Local	Euclidean distance in meters of the palm tree to the edge of fragment
Fruit amount	Local	Mean of the number of fruits collected using four 1 × 1 m squares under the palm tree
Fragment area	Fragment	Area in ha of the fragment where the palm is located
Fragment shape	Fragment	Residual of the mean Euclidean distance of the fragment area to the nearest edge as a function of fragment area. Unitless variable
Local forest cover	Landscape	Percentage of habitat inside a buffer around the geographic centroid of the palms. Calculated in 3 scales: 500, 1000 and 1500 m

endocarps with no marks were opened to confirm whether there was a larva inside, because the larvae only bored out of the seed in the final stages of larvae development (Brancalion et al. 2011). Then, the endocarps with larvae were counted as predated by invertebrates, while the ones without larvae were counted as non-predated.

The rare endocarps with both marks of invertebrates and squirrels were counted as preyed upon by invertebrates. If there was a hole bored by the larva, it meant that the larva killed the seed and left the endocarp before the squirrel gnawed on it. Moreover, when a squirrel preys upon an invertebrate larva, it gnaws the endocarp and creates a different pattern, with a single short and deep cut resembling the invertebrate hole. Because it is difficult to differentiate the larva predation marks created by the squirrels from the usual invertebrate hole, the seeds with these marks were also counted as predated by invertebrates. Since the marks of terrestrial rodents were very uniform, it was not possible to know if the rodent preyed upon a larva or a healthy seed, moreover, endocarps with marks of both invertebrate and terrestrial rodents were not found in the present study.

Data analyses

We used a multiple competing hypothesis approach (Burnham and Anderson 2010), using generalized additive models (GAM) to fit the relationship between the proportion of predated seeds and the explanatory variables. The Akaike information criteria values were corrected for the small sample sizes (AICc) so we could compare them. For each model, we calculated the Akaike's weights (wAICc), the AIC difference of a given model and the best model (Δ AICc). The wAICc and Δ AICc are parameters of the relative likelihood and relative difference between the models, respectively. The model with a higher wAICc have a higher weight of evidence in its favor and was considered the best model of the set, and models with Δ AICc < 2 were considered equally plausible (Burnham and Anderson 2010). We also calculated a bootstrap model selection frequency (π_i), which was the frequency that each model i received the lowest AICc value in 10 000 random resamples of the data (Burnham and Anderson 2010).

Before we ran the analyses, we compared the three different scales of the forest cover variable using the same method described above (i.e. using model selection approach), and only the best scale was used in the final analyses. This process was applied both to the analysis of the overall seed predation and to each one of the three groups of seed predators. Because squirrels and terrestrial rodents can prey upon invertebrate larvae (Visser et al. 2011), we added five models in the analysis of the seed predation by invertebrates which consider the seed predation by these rodents as a predictor variable (Supplementary material Appendix 1, Table A3). We used the seed predation by squirrels and terrestrial rodents as a proxy of larvae predation, because it was not possible to safely quantify the larvae predation by the marks in the endocarps. We did a model validation by plotting the model predictions against the residuals of the independent variables and visually looking for patterns in the scatterplots (Burnham

and Anderson 2010). We also ran the Moran's I spatial autocorrelation test with 10 000 permutations and found no spatial autocorrelation. The analyses were performed using the statistical software SAM ver. 4.0 and R (R Development Core Team), using the *bbmle* and *gam* packages. The list of competing models is shown in the Supplementary material Appendix 1, Table A3.

Results

We sampled 76 palms from 15 fragments, totaling 107 869 fruit endocarps (Supplementary material Appendix 1, Table A4). Due to difficulties with permissions and access to several fragments, only two landscapes had a second fragment sampled. We collected an average of 1449.3 ± 1441.9 endocarps per palm (minimum of 21, maximum of 8170), and an average of 7191.2 ± 5915.3 (minimum of 692, maximum of 25 139) endocarps per sampled fragment. We found that 50% of the seeds were preyed upon by invertebrates (*Pachymerus cardo*, *Revena rubiginosa* and *Coccytrypes* sp.), 15.37% by squirrels and only 5.38% by terrestrial rodents. We also observed a negative correlation between the seed predation by squirrels and invertebrates ($r = -0.72$, $DF = 72$, $p < 0.01$), and a negative correlation between the seed predation by squirrels and terrestrial rodents ($r = -0.25$, $DF = 72$, $p = 0.03$), but not between the invertebrates and terrestrial rodents ($r = 0.03$, $DF = 72$, $p = 0.77$).

The seed predation by squirrels was best explained by the combined effect of fragment area and shape (model GAM08), with a wAICc = 1 and a π_i value = 0.954 (Table 2). The model prediction described a higher seed predation by squirrels in fragments between 150 and 400 ha than in smaller or larger fragments, and a higher seed predation in fragments with a more irregular shape (which was prone to be more influenced by the edges) than in more circular ones (Fig. 3A). The intensity of the fragment shape effect on squirrel seed predation was also stronger in fragments between 150 and 400 ha. The observed seed predation by squirrels strongly agreed with our Intermediate hypothesis, as it was higher in moderately degraded areas than in very degraded and very preserved ones. No other model was plausible to explain the seed predation by squirrels, because the second best model obtained a Δ AICc = 16, and both the π_i value and the wAICc were 0.036.

The seed predation by invertebrates was best explained by the summation effect of seed predation by squirrels, terrestrial rodents and the distance from the nearest edge (GAM11), with a wAICc = 0.894 and a π_i value = 0.633. As predicted by the Invertebrate control hypothesis, the model described a higher proportion of seed predation by invertebrates in areas where the seed predation by the rodents was lower. Anyway, the seed predation by invertebrates was also lower in areas between 100 m and 400 m from the forest edge (Fig. 3B). No other model was plausible to explain the seed predation by invertebrates. The second best model obtained a Δ AICc = 5.4, a wAICc = 0.059 and a low π_i value = 0.223.

The seed predation by terrestrial rodents was best explained by the amount of forest cover at the 500 m scale (GAM05), with a wAICc = 0.946 and a π_i value = 0.757. As predicted by the Rodentation hypothesis, the model

Table 2. Results of the model selection for seed predation (SP) of *Syagrus romanzoffiana* by all seed predators (overall) and by each group of seed predators in Brazilian Atlantic forest. We fitted generalized additive models and calculated the parameters of relative difference ($\Delta AICc$), relative likelihood (wAICc) and a bootstrap model selection frequency (π_i) to all models. The best models for each seed predator group are highlighted in bold. Models with $\Delta AICc < 2$ or wAICc > 0.1 were considered as equally plausible. Selection frequency (π_i) were calculated using 10 000 bootstraps.

Models	Overall seed predation				Squirrel				Invertebrate				Terrestrial rodents			
	$\Delta AICc$	wAICc	π_i	$\Delta AICc$	wAICc	π_i	$\Delta AICc$	wAICc	π_i	$\Delta AICc$	wAICc	π_i	$\Delta AICc$	wAICc	π_i	
GAM0: SP ~ Mean (Null model)	29.2	<0.01	<0.01	41.1	<0.01	<0.01	67	<0.01	0	20.5	<0.01	<0.01	20.5	<0.01	<0.01	
GAM01: SP ~ Edge distance (m)	5.6	0.026	<0.01	35.8	<0.01	0	64	<0.01	0	21.7	<0.01	<0.01	21.7	<0.01	<0.01	
GAM02: SP ~ Fruit amount	16.8	<0.01	<0.01	40	<0.01	<0.01	68.8	<0.01	0	21.2	<0.01	0.067	21.2	<0.01	0.067	
GAM03: SP ~ Fragment area (ha)	7	0.013	<0.01	17.9	<0.01	<0.01	54.2	<0.01	0	18.9	<0.01	<0.01	18.9	<0.01	<0.01	
GAM04: SP ~ Fragment shape (index)	4.4	0.048	0.024	23.1	<0.01	<0.01	59.8	<0.01	0	22.5	<0.01	0.047	22.5	<0.01	0.047	
GAM05: SP ~ Forest cover (only the best scale)	4.8*	0.039*	0.124*	24.2*	<0.01*	<0.01*	56.8*	<0.01*	0*	0*	0.946*	0.757*	0*	0.946*	0.757*	
GAM06: SP ~ Fruit amount + Edge distance	9.8	<0.01	0.019	40.5	<0.01	<0.01	68	<0.01	0	22.8	<0.01	0.025	22.8	<0.01	0.025	
GAM07: SP ~ Fragment area + Edge distance	0.1	0.413	0.321	16	<0.01	0.036	50.5	<0.01	0	24	<0.01	<0.01	24	<0.01	<0.01	
GAM08: SP ~ Fragment area + Fragment shape	0	0.434	0.484	0	1	0.954	57.2	<0.01	<0.01	19.2	<0.01	0.087	19.2	<0.01	0.087	
GAM09: SP ~ Forest cover + Edge distance	6.8*	0.014*	0.021*	21.1*	<0.01*	<0.01*	58*	<0.01*	0*	5.7*	0.054*	<0.01*	5.7*	0.054*	<0.01*	
GAM10: SP ~ Rodent activity (proxy)							9.8	0.006	<0.01							
GAM11: SP ~ Edge distance + Rodent activity							0	0.894	0.633							
GAM12: SP ~ Fragment area + Rodent activity							6.3	0.037	0.070							
GAM13: SP ~ Forest cover + Rodent activity							5.4*	0.059*	0.223*							
GAM14: SP ~ Fruit amount + Rodent activity							11.9	0.002	0.070							

Best scale of forest cover for each group of seed predators: *1500 m, +500 m.

prediction described a higher intensity of seed predation by rodents in areas with less than 20% of habitat (Fig. 3C). None of the other models were plausible to explain the seed predation by terrestrial rodents. The second best model obtained a $\Delta AICc = 5.7$, a wAICc = 0.054 and a very low π_i value = <0.01.

Two models were equally plausible in describing the overall seed predation of *S. romanzoffiana*. The first model considered the combined effect of fragment area and the shape (GAM08), with a wAICc = 0.434 and a π_i value = 0.484. This model had a very similar response to the model that better explained the seed predation by squirrels. The prediction of the first model described a higher intensity of seed predation in fragments between 150 and 400 ha than in smaller or bigger ones, and in fragments with a more irregular shape, where the effect of the fragment shape was also stronger in fragments between 150 and 400 ha (Fig. 4A). The second model considered the combined effect of the fragment area and the palm distance from the nearest edge (GAM07), with a $\Delta AICc = 0.1$, a wAICc = 0.413 and a π_i value = 0.321. The prediction of the second model described a higher proportion of predated seeds in fragments between 150 and 400 ha, as predicted for squirrels, and a lower seed predation in areas between 100 and 400 m from the forest edge, as predicted for invertebrates (Fig. 4B).

Finally, since all Rodentation, Intermediate and Invertebrate control hypotheses were supported by our results to terrestrial rodents, squirrels and invertebrates respectively, the Predator turnover hypothesis is also supported. However, the overall proportion of predated seeds was not constant as predicted by the Predator turnover hypothesis, and we found an unexpected response of the invertebrate seed predation to the edge distance. This way, although we found a predator turnover, we prefer to consider the hypothesis as partially supported.

Discussion

Our results indicated that the overall seed predation of queen palm seeds was mainly affected by the fragment size, shape and the distance from the edge, which is a reflection of the response of the two main groups of seed predators. The seed predation by squirrels was affected by the fragment size and shape, whereas the invertebrates were affected by the edge distance and by the seed predation by rodents, mainly the squirrels and secondarily by terrestrial rodents. In general, terrestrial rodents have only a small effect on the invertebrates and overall seed predation, preferring areas with low forest cover. Therefore, although there was a turnover between the seed predators, it was not as complete as predicted by the Predator turnover hypothesis. The overall seed predation fluctuated according to these three variables that affected squirrels and invertebrates.

Fragment level response

The overall predation of seeds responded mainly at a fragment level and a local level, rather than at a landscape level, because predation by the two main groups of seed predators also responded at a local level and a fragment level.

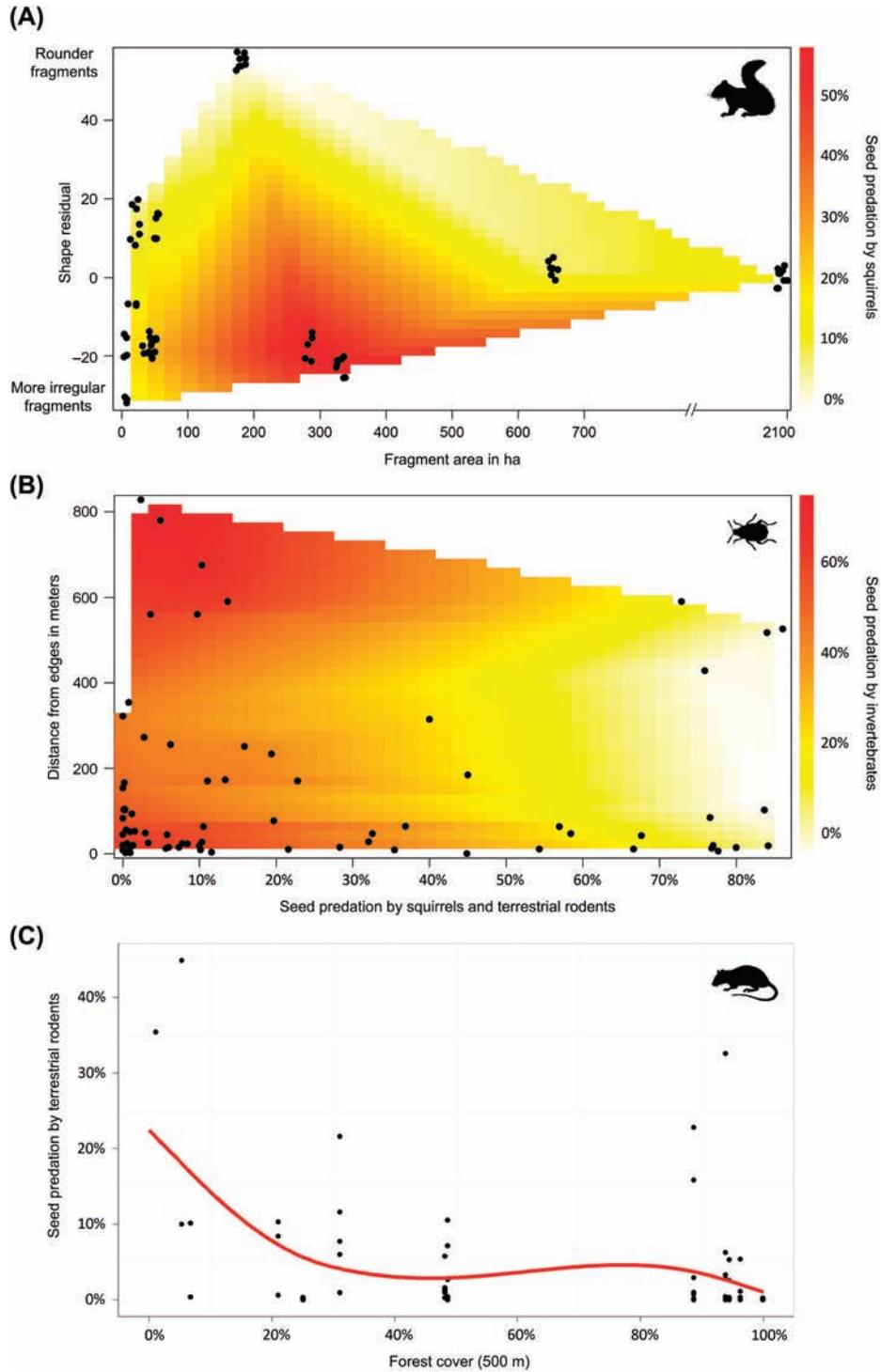


Figure 3. Predicted distribution of the predation of *Syagrus romanzoffiana* seeds by each predator group: (A) squirrels; (B) invertebrates; (C) terrestrial rodents. Study developed within Brazilian Atlantic forest fragments along a gradient of patch size, habitat amount and edge distances. The black points represent sampled palms and reddest colors represent areas with a higher seed predation.

A possible explanation for why the seed predation by squirrels responded both at a fragment level and a local level, but not at the landscape level, lies in their arboreal life-style (Reis et al. 2014) with small home ranges (Bordignon and Monteiro-Filho 2000). Due to the low use of matrix areas, *S. ingrami* may not be significantly affected by changes out of the limits of the fragment in which the animal lives, such

as the reduction in the landscape forest cover by the destruction of other fragments. The same response was observed in forest-dwelling bird species with low mobility (Graham and Blake 2001). Moreover, the presence of croplands, such as sugar cane, which was present in all of the sample landscapes, reduces the capacity of small forest mammals to move in the matrix by blocking the vision and reducing

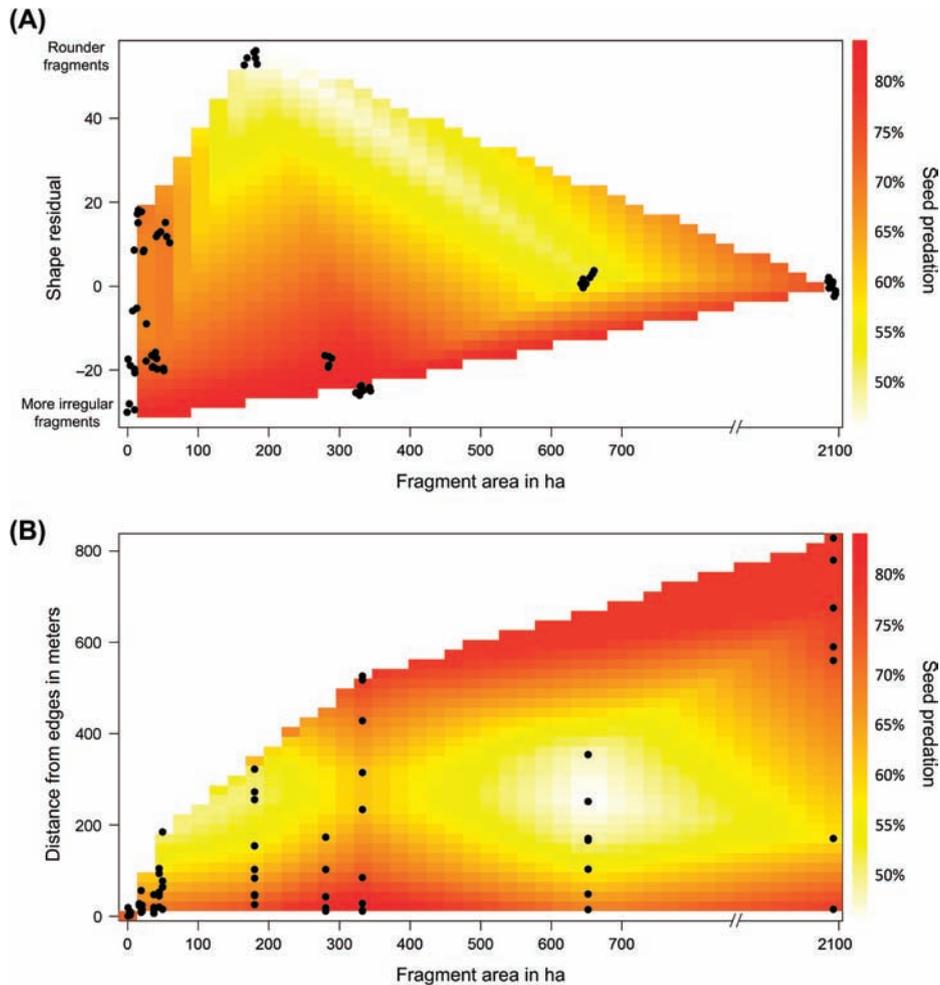


Figure 4. Predicted distribution of the overall predation of *Syagrus romanzoffiana* seeds in the Brazilian Atlantic forest along a gradient of: (A) fragment area and fragment shape (index, where the smaller numbers represent shapes that are more irregular); (B) fragment area and distance from the nearest edge. The black points represent sampled palms and reddest colors represent areas with a higher seed predation.

the animals' perceptual range and navigation capacity. These impacts raise the mortality of the animals that use these areas (Zollner and Lima 1997, Prevedello et al. 2010).

The invertebrates' response to the rodent activity, in turn, should have happened mainly due to their negative relationship with the squirrels. Although the squirrels ate mainly uninfested fruits, they can be important predators of bruchid larvae, and in some situations, they can even prefer infested fruits over uninfested ones (Visser et al. 2011), probably due to the higher nitrogen content (Sallabanks and Courtney 1992). In addition, larvae predation by vertebrates is a significant mortality factor that affects the abundance of several invertebrate species (Sallabanks and Courtney 1992, Delobel et al. 1995, Visser et al. 2011, Peguero and Espelta 2013) and has indirect effects on the species that are predated by these invertebrates (Visser et al. 2011).

Fragment size, shape and edge distance

The effect of fragment size and shape on the overall seed predation occurred mainly due to the squirrels, which were the only seed predators that responded to these variables. It is possible that fragments with a size between 150 and 400 ha could have ideal conditions to maintain a high

density of squirrels, because they may have an area large enough to reduce the threat of extinction by stochastic events (Laurance et al. 2002, 2011) and to hold a squirrel population large enough to avoid genetic complications (Keller and Waller 2002). At the same time, these fragments may not have enough area to maintain a healthy community of mesopredators, such as ocelots and margays (Koprowski 2005, Fleury and Galetti 2006, Solórzano-Filho 2006). Some squirrel species of the north hemisphere are also more abundant in fragments than in continuous areas (Bayne and Hobson 2000, Koprowski 2005, Walpole and Bowman 2011).

The effect of fragment shape on a biological process is usually related to its influence in the edge amount (Harper et al. 1993, Davis 2004). Due to geometrical reasons, fragments with more irregular shapes have a higher perimeter-area ratio, and they have relatively more area affected by the edge effect (Benitez-Malvido 2008). Because the areas under the edge effect have a higher productivity (Murcia 1995), and given that the seed predation of *S. romanzoffiana* is correlated with squirrel density (Fleury and Galetti 2006), it is possible that fragments with a more irregular shape could keep a higher density of squirrels due to the relatively higher amount of highly productive edge areas. The shape of the

fragment should not be as important if the fragment is too small to keep a squirrel population, or too big, because large fragments have a relatively smaller amount of area under the edge effect and can maintain a healthy community of mesopredators. This possibility explained why the effect of shape was stronger in fragments between 150 and 400 ha. This explanation also agreed with the literature, which show that fragment area and shape together are better predictors of vertebrate species richness, abundance and the probability of occurrence than fragment area alone (Helzer and Jelinski 1999, Davis 2004).

Another possible explanation of the effect of fragment shape in the seed predation of *S. romanzoffiana* is that the amount of edge did not affect the density of squirrels, but it affected their behavior, such as food preference and foraging time, due to changes in food items availability, predation risk and vigilance behavior. There are examples in the literature where the amount of edges affected the rodent's behavior, with consequences on the proportion of predated seeds (Orrock and Damschen 2005, Orrock and Danielson 2005).

The effect of the palm distance from the fragment edge in the overall seed predation occurred mainly due to the invertebrates, which were the only seed predators that responded to this variable. However, the way in which the distance from the edge affects the invertebrate seed predation remains unclear. It is known that lower humidity, higher temperature and light incidence of the areas near the fragment edges have direct effects on the invertebrate community (Laurance et al. 2002) and that the response of curculionids to the edge effect can be highly variable and species specific (Didham et al. 1998). Therefore, it is important to highlight that each of the three registered species of invertebrates in this study may have its own response to the edge distance and that the pattern of seed predation by invertebrates that we observed can be, in fact, the sum of these different responses.

Conservation implications

Our findings showed that the overall seed predation of *S. romanzoffiana* can be extremely high near the mother tree, with peaks of seed predation up to 96% in some palms. Because seed predation is an important factor that affects the recruitment of plant species (Smith III 1987, Orrock et al. 2006), we can predict that these levels of seed predation have some negative impact on the palm populations.

Assuming that the observed pattern of seed predation can occur along the entire Atlantic forest, the predation of the non-dispersed seeds of *S. romanzoffiana* should be intense in most of its distribution. It should occur because 83% of the remaining Atlantic forest fragments have less than 50 ha (Ribeiro et al. 2009), and in these fragments, the predicted average seed predation is between 55 and 75%. Furthermore, nearly 50% of the remaining Atlantic forest area is < 100 m from an edge (Ribeiro et al. 2009, Pütz et al. 2014), and in these areas, the predicted average seed predation is between 65 and 85%. The consequences of these high proportions of seed predation to the *S. romanzoffiana* population are still not clear (Andreazzi et al. 2009), but similar seed predation proportions registered in other species were enough

to deeply affect the species recruitment, abundance and distribution (Smith III 1987, Orrock et al. 2006). Although seed dispersal may play an important role in reducing seed mortality, depending on the fate of the dispersed seeds, it is an ecological process that has been reduced in degraded areas due to the severe defaunation of the Atlantic forest remnants (Galetti et al. 2006, Donatti et al. 2009, Sica et al. 2014).

In other hand, if *S. romanzoffiana* is adapted to endure this high seed predation levels and able to prone even in the most degraded areas, it can be a crucial and indispensable resource to the maintenance of the local fauna. Future studies should help to evaluate the effect of seed predation in the *S. romanzoffiana* demography, the importance of this palm to the maintenance of the local biodiversity, and if similar results are observed in other palm species with similar ecology, such as *Attalea tessmannii*, *A. phalerata* and *Astrocaryum aculeatissimum*, in which the seed predation can be above 80% in forest fragments (Delobel et al. 1995, Galetti et al. 2006, de Almeida and Galetti 2007, Andreazzi et al. 2009, Dracxler et al. 2011).

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Supplementary material (Appendix ECOG-01592 at <www.ecography.org/readers/appendix>). Appendix 1.