

Spatial Pattern of Pindó Palm (*Syagrus romanzoffiana*) Recruitment in Argentinian Atlantic Forest: The Importance of Tapir and Effects of Defaunation

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ABSTRACT

Hunting pressure, fragmentation and deforestation have caused global declines in animal abundance, and the consequences for plant communities are poorly understood. Many large-seeded plants, for instance, depend on large and endangered vertebrates for seed dispersal. In some Semi-deciduous Atlantic Forests, endangered tapirs (*Tapirus terrestris*) are major dispersers of pindó palms (*Syagrus romanzoffiana*). Here, we compare recruitment patterns of pindó palms between protected and disturbed (defaunated) Atlantic Forest areas in Argentina and evaluate the potential consequences of the lack of the main disperser for pindó palm regeneration. We analyzed the number and spatial pattern of pindó adults, offspring, and tapir dung piles within ten plots established in an area spanning tapir latrines inside Iguazú National Park and in a fragmented forest area outside the park where tapir is locally extinct. In both areas, we evaluated recruitment levels beneath 24 adult palms in circular plots centered on adult stems. We found lower pindó palm recruitment outside the park where offspring tended to be aggregated around adult palms. In contrast, in Iguazú National Park offspring were spatially associated with tapir dung-piles, in which most offspring were registered. Recruitment under adults was higher outside the park suggesting a lower rate of seed removal in disturbed areas. Our results show that tapir dispersal promotes higher recruitment levels of pindó offspring and shapes their spatial pattern, breaking the spatial association with adult (presumably maternal) palms. These results are useful for predicting the impact of local tapir extinction on this palm.

Abstract in Spanish is available in the online version of this article.

Key words: Iguazú National Park; seed dispersal; spatial analysis; *Tapirus terrestris*.

THE SEED DISPERSAL CYCLE INVOLVES SEVERAL PROCESSES: fruit production, movement of seeds away from the parent plant via primary and secondary seed dispersal, germination of seedlings, and recruitment to adults (Wang & Smith 2002). Seed dispersal links the end of the reproductive cycle of an adult plant with the establishment of its seedlings, and influences plant fitness by determining where seeds and subsequently offspring live or die (Hammond & Brown 1998, Wenny 2001). For instance, the dispersal pattern of an agent that transports a large amount of seeds to suitable sites for germination (*i.e.*, directed dispersal) will be reflected in the distribution of adult plants (Wenny 2001). Therefore, seed dispersal plays an important role in the spatial structure, composition and demographic pattern of plant species in a community (Nathan & Muller-Landau 2000, Wang & Smith 2002).

Birds and mammals disperse up to 90 percent of tree species in Neotropical rain forests (Howe & Smallwood 1982). The spatial arrangement of the dispersed seeds and offspring can be affected by intrinsic characteristics of the disperser such as body size, home range, initial handling of seeds, digestive strategy and defecation pattern (Stoner *et al.* 2007). Many large and medium-

sized vertebrates produce a spatially aggregated pattern of seed deposition (Pinazo *et al.* 2009), which could generate conditions similar to those found in the surroundings of the parental plant. However, in places of high probability of seed arrival, such as latrines or sleeping sites, recruitment is often very high (Fragoso 1997, Giombini *et al.* 2009, Bravo 2012).

Hunting pressure, fragmentation and deforestation have caused global decline in animal abundance with unknown consequences for the plant communities with which these animals interact (Wright & Duber 2001, Wright 2005). Large vertebrates are particularly vulnerable to extinction due to their large territorial requirements, small population size and high prey value (Bodmer *et al.* 1997). A key piece of information to understand the effect of such vertebrate declines in the regeneration of plant species is the degree to which animal-dispersed trees depend on their dispersers (Howe 1977). For instance, is seed dispersal reduced by the loss of large mammals or can the redundant roles among frugivores compensate for such loss conferring functional resilience to the plant community (Walker *et al.* 1999, Lyons *et al.* 2005)? There is evidence for functional redundancy in the literature (Alves-Costa & Eterovick 2007, Moore & Swihart 2007). However, some authors have shown that such compensation does not exist (Christian 2001, Bueno *et al.* 2013, Galetti *et al.*

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2013). Evaluation of the specificity and ecological redundancy of dispersers is very important to maintain the proper functioning of tropical forests, as it can lead to the design of management strategies that mitigate possible changes in forest composition and structure (Sethi & Howe 2009).

Many studies indicate that the defaunation of mammal or bird communities reduces recruitment of animal-dispersed species (Chapman & Chapman 1995, Cordeiro & Howe 2001, Beckman & Muller-Landau 2007, Wang *et al.* 2007, Sethi & Howe 2009). This reduction may be due to a decline in seed dispersal increasing seed or seedling mortality by predators and/or pathogens. The Janzen-Connell hypothesis posits that the main benefit of seed dispersal is the reduction of the density-dependent mortality (Janzen 1970, Connell 1971). Hence, it is important to study the effects of defaunation on plant regeneration. Galetti *et al.* (2006) found that survival probability of *Astrocaryum aculeatissimum* (Arecaceae) seeds declined as defaunation levels increased, in which more defaunated sites had higher seed predation by insects. Wang *et al.* (2007) found higher accumulation of *Antrocaryon klaineianum* (Anacardiaceae) seeds below adult trees in defaunated areas, indicating a lower rate of seed removal. Moreover, 42 percent of seeds in protected areas were not the offspring of the closest adult, while this value declined to two percent in areas impacted by hunters. These findings suggest that the disappearance of primary dispersers can generate an early break in the dispersal cycle by altering recruitment patterns of the dispersed species.

Ungulates, particularly tapirs (*Tapirus* sp.) are one of the most important dispersers of large seeded plants (Fragoso 1997, Stoner *et al.* 2007, Giombini *et al.* 2009, Tobler *et al.* 2010). In the Atlantic Forest, they are also among the most affected by hunting, habitat fragmentation and habitat unsuitability (Paviolo *et al.* 2009, Jorge *et al.* 2013). Tapirs are able to disperse numerous seeds and defecate them in suitable sites for germination (Fragoso & Huffman 2000, Fragoso *et al.* 2003, Tobler 2008, Giombini *et al.* 2009, Tobler *et al.* 2010). Seeds dispersed by tapirs experience higher survival rates than those remaining beneath conspecific adult trees (Fragoso 1997, Fragoso *et al.* 2003). This seed transport over long distances and repeated defecation of large amounts of seeds in circumscribed sites (*i.e.*, latrines) creates a clustered dispersal pattern (Giombini *et al.* 2009).

Syagrus romanzoffiana (Arecaceae), locally known as pindó, is the most commonly consumed fruit by lowland tapirs (*T. terrestris*) in the Semi-deciduous Atlantic Forest (Olmos *et al.* 1999, Galetti *et al.* 2001, Giombini *et al.* 2009). Giombini *et al.* (2009) determined that tapirs are effectively the main dispersers of pindó seeds in Iguazú National Park. Pindó seedlings were 21 times more abundant in tapir dung piles than under adult palm trees and, either seeds, seedlings or both, were present in 98 percent of all recorded tapir dung piles. These findings point out the importance of tapir dispersal in the establishment of this palm, suggesting a strong plant-animal interaction. However, dispersal patterns generated by other dispersal agents (*e.g.*, coatis, monkeys, agoutis, foxes, cracid birds) have not been evaluated yet.

In this study we assessed the effects of habitat disturbance and the local extinction of the main disperser on pindó recruitment in the Semi-deciduous Atlantic Forest of Argentina. By comparing protected and disturbed areas, we tested the hypothesis that pindó offspring recruitment is negatively affected in fragmented and partially defaunated sites. In defaunated forest fragments, our two main predictions were: (1) the recruitment of pindó palms will be reduced; and (2) offspring will tend to aggregate around conspecific adult trees.

METHODS

STUDY AREAS.—The study was conducted in a continuous and protected Atlantic Forest area in Iguazú National Park (PNI) and a nearby area outside the park called Comandante Andresito (12 km east PNI border), where partially defaunated forest fragments remain embedded in crop fields. Both areas are located in the province of Misiones, northeast Argentina. The climate is warm and humid, with average temperatures of 15°C in winter and 25°C in summer and average rainfall reaching 2000 mm/yr.

PNI (25°40' S, 54°24' W) is a 58,600-ha protected area that represents the southern limit of the Semi-deciduous Atlantic Forest. The park limits are: (1) the eastern boundary located at the town of C. Andresito; (2) the northern and western boundaries are the Iguazú River, which separates PNI from Parque Nacional do Iguazú (Brazil); (3) the southwestern boundary borders the Iguazú Natural Reserve; and (4) the southeastern boundary borders the Urugua-í Provincial Park. Even though the Semi-deciduous Atlantic Forest ecosystem has been subjected to strong hunting pressure and degradation during the past 80 years, PNI still preserves a significant richness of medium to large mammals (Di Bitetti *et al.* 2003). Tree flora in the park comprise more than 90 species, with black laurel (*Nectandra megapotamica*) and guatambú (*Balfourodendron riedelianum*) being the most abundant. In some areas there is a distinct forest community, locally called palmital, dominated by palmito (*Euterpe edulis*) and palo rosa (*Aspidosperma polyneuron*).

Comandante Andresito (25°40' S, 54°02' W) is located in a fragmented Atlantic Forest area in the Department of General Manuel Belgrano. Until the 1970s, it was mainly primary forest with some local inhabitants living on public land. In the 1990s C. Andresito became the most populated town in the department ($N = 14,286$ inhabitants; INDEC 2001). The main economic activities are 'yerba mate' crops, livestock and forestry. Forest fragments remain among fields, roughly preserving the basic vegetation structure and composition. Small-to-medium size vertebrates, which may feed on and disperse pindó fruits (coatis, brocket deer, capuchin monkeys, toucans and cracids), are still present in these fragments, although in lower abundances than within PNI (Paviolo *et al.* 2009, pers. obs.). However, these fragments are not large enough to allow the persistence of large vertebrates (jaguars, pumas, ocelots, tapirs, peccaries) and they are frequently subject to illegal hunting activity. For instance, tapir is locally extinct, as its presence is usually limited to fragments larger than 10,000-ha, which do not exist in this area (Paviolo *et al.* 2009).

STUDY SPECIES.—*Syagrus romanzoffiana* is a medium size palm (8–25 m in height) with a grayish stem of up to 60 cm in basal diameter and alternate 2–3 m palms with a feathery appearance. Its geographical distribution ranges from eastern and southern Brazil to northern Argentina (Bernacci *et al.* 2008) and is one of the most abundant species in Semi-deciduous Atlantic Forest. Each palm produces one or two infructescences that can contain up to one thousand fruits 1–3 cm in diameter. The mature pericarp is orange, fleshy, fibrous, sweet, and sticky which makes it attractive to many birds and mammals (Guimarães *et al.* 2005). The assemblage of vertebrates that feed upon these drupes include several small rodents, squirrels, agoutis, pacas, coatis, foxes, peccaries, monkeys, tapirs and birds such as cracids and ramphastids (Di Bitetti *et al.* 2003, Guimarães *et al.* 2005, Giombini *et al.* 2009). The peak of pindó seed production occurs from February to August, coinciding with a shortage of fruit of other species (Olmos *et al.* 1999). Hence, the frugivore community strongly depends on this resource (Galetti *et al.* 2001, Keuroghlian & Eaton 2008).

DATA COLLECTION.—We set up five 100 m × 10 m plots inside PNI and other five plots outside the park. Within PNI, we worked in sites under special protection (*i.e.*, well-preserved sites, not accessible by tourists) with an active presence of tapir. Three plots, separated by 170–340 m, were placed on laurel and guatambú forest and the other two plots, separated by 210 m, were located in palmital forest at about 20 km away from laurel and guatambú plots. These sampling plots were chosen from larger ones (500 m × 50 m) previously established by Giombini *et al.* (2009) so that they included tapir latrines. Likewise, outside PNI, three plots were placed in three laurel and guatambú forest fragments and the others in two palmital forest fragments. These forest fragments were 3.5–10 km distant from each other and 2.5–5.5 km away from C. Andresito village center. Sizes ranged from 15 and 150 ha, and they did not contain any dung piles or signs of tapir presence.

All offspring recorded in this study were either seedlings with leaves of less than 2 cm width (presumably younger than a year old and still depending on seed resources) or saplings more than a year old with wider but still not pinnated leaves (categorized as first-stage juveniles by Bernacci *et al.* 2008). All pindó offspring were counted in the plots by registering their spatial location using a xy coordinate system. In PNI plots, we registered whether each individual was clearly associated with tapir dung piles as inferred from remains of feces at the base of the offspring. Tapir dung piles were also counted by registering the coordinates of a central point in the middle of the pile. As the number of offspring found within the 100 m × 10 m plots might simply reflect the local density of nearby adult trees (putative mothers), we also registered the location of adult palms. Given that the density of adult palms is much lower than the density of seedlings and 100 m × 10 m plots are expected to contain very few adults, we extended the plot size to 140 m × 40 m (20 m the plot length and 10 m the plot width to each side) to estimate the number of nearby adult palms.

To quantify recruitment under adult palms, we randomly chose 24 focal adults outside the plots, 12 inside PNI, and other 12 in the study's forest fragments outside the park. A 3 m-radius circular plot, centered on each adult stem, was delimited and we counted all offspring recruited within this plot. All adults were separated by a minimum distance of 350 m.

DATA ANALYSIS.—We compared the number of pindó offspring inside and outside PNI, taking into account the type of forest (laurel and guatambú or palmital), through a two-way ANOVA. Each plot was a replica ($N = 5$). We applied log₁₀ transformation to meet the assumptions of ANOVA.

To assess the local contribution of tapirs to pindó recruitment, we compared the average density of offspring associated with tapir dung piles (visible fecal remains) against 'background density' (*i.e.*, the density of those offspring not clearly associated with tapir dung piles). This background density may include offspring coming from non-dispersed seeds, seeds dispersed by other agents, seeds dispersed secondarily from tapir dung piles, or even tapir dispersed seeds in which no recognizable fecal remains were found. To estimate the density of seedlings and saplings associated with tapir dung piles, we gridded the plots *a posteriori* in 1000 1 m × 1 m cells and calculated the ratio of the total number of offspring in cells containing tapir dung piles to the total number of cells containing dung piles. Analogously, background density was calculated from an equal number of randomly chosen cells that did not contain any dung piles. The statistical comparison between tapir-associated and background densities was carried out inside PNI using a nonparametric Wilcoxon matched pairs test ($N = 5$).

Because the assumptions of normality and homocedasticity were not met, offspring recruitment under adult palms was assessed by comparing the number of offspring under palms located inside and outside the park with a nonparametric Mann-Whitney *U*-test (one-sided). Each adult palm provided a replicate ($N = 12$).

The spatial pattern of seedlings and saplings in all plots was analyzed using Point Pattern Analysis. This analysis aims to test if the location of points in space follows a non-random statistical distribution (repulsion or aggregation) by comparing the observed pattern against a null model of the variable distribution. In most cases, the null model is given by a Poisson process (uniformity and independence of the points) that generates a pattern of complete spatial randomness (CSR) (Wiegand & Moloney 2004).

Some methods of spatial analysis consider the intensity of the spatial dependency in the entire sampling area and summarize it in a single global statistic, whereas other methods (local statistics) aim to detect the precise location of the aggregation (Getis & Ord 1995, Fortin & Dale, 2005). To compare the spatial patterns of recruitment in and outside PNI, we applied the standardized Ripley's *K* function $L(r)$ as a global statistic (Ripley 1981). It compares the observed point pattern against a CSR pattern, where r corresponds to the radius being evaluated. An excess of spatial aggregation or regularity up to distance r is indicated by $L(r) > 0$ or $L(r) < 0$, respectively. As the observed pat-

terns in each plot inside the park are strict replicates of an underlying process, we calculated an overall estimate (Diggle 2003). This resulting average function is a weighted average of the individual estimates, where the weight is the number of points in each plot divided by the total number of points in all replicate plots (Wiegand & Moloney 2004). The same process was used for the five plots outside the park for the comparison. We used the free software *Programita* (Wiegand & Moloney 2004) to compare the observed values of $L(r)$ against the most extreme values obtained after 99 Monte Carlo simulations under CSR. The spatial pattern was analyzed up to a distance of $r = 5$ m (half of the smaller dimension of the plot).

The association between the spatial pattern of offspring and the location of adult palms occurring within the plots was evaluated by applying the local statistic Getis $G_i(d)$ to the offspring dataset. Local $G_i(d)$ allows the identification of offspring aggregation in particular locations (for instance, adult palm locations) when used as focal analysis (Getis & Ord 1995). The null hypothesis of this test is that there is no association between the observed density of points in a certain location and its neighbors at a specific distance d . When using $G_i(d)$ as a focal statistic, we considered more than one location as a potential source of offspring aggregation and corrected for multiple comparisons by adopting the significance levels listed by Ord and Getis (1995). As $G_i(d)$ was calculated for all the cells in the plot (1000 cells), significant clustering ($\alpha = 0.05$) occurs when $G_i(d) > 3.88$. We calculated $G_i(d)$ using *PPA* free software (Chen & Getis 1998). The spatial pattern was analyzed up to a distance of $d = 5$ m (half of the smaller dimension of the plot).

The relationship between offspring and dung-pile spatial patterns inside PNI was evaluated using a bivariate extension of Ripley's K function (Wiegand & Moloney 2004), as there were enough dung piles (pattern one) and offspring (pattern two) to perform this analysis. Bivariate Ripley's function ($L_{12}(r)$) is defined as the expected number of points of pattern two to a distance r of an arbitrary point of pattern one, divided by the average intensity of points of pattern two (Wiegand & Moloney 2004). Values of the standardized bivariate Ripley's function ($L_{12}(r)$) greater than 0 indicate that there are more points of pattern two within a radius r to points of pattern one than expected by chance, indicating an attraction between the two patterns at distance r (Wiegand & Moloney 2004).

We used a null model of Antecedent Condition (AC) because the pattern of dung pile locations (pattern one) is presumably generated regardless of the locations of the offspring (pattern two), whereas the creation of pattern two might be influenced by pattern one (Wiegand & Moloney 2004). Hence, tapir dung pile locations were held fixed and offspring locations were changed randomly. To determine the statistical significance of the association between both patterns, confidence envelopes for $L_{12}(r)$ were obtained after 99 Monte Carlo simulations based on CSR distribution of saplings and seedlings (pattern two). We performed all statistics and simulations with the free software *Programita* (Wiegand & Moloney 2004) which allowed us to combine the data from the five plots inside PNI.

RESULTS

The number of seedlings and saplings in both forest types within PNI (483 ± 38 SE and 96 ± 20 SE, for laurel and guatambú forest and palmital respectively) were significantly higher than outside the park (142 ± 24 SE and 56 ± 19 SE) (PNI vs. outside PNI $df = 1$, $F = 22.99$, $P = 0.003$; Fig. 1). The mean num-

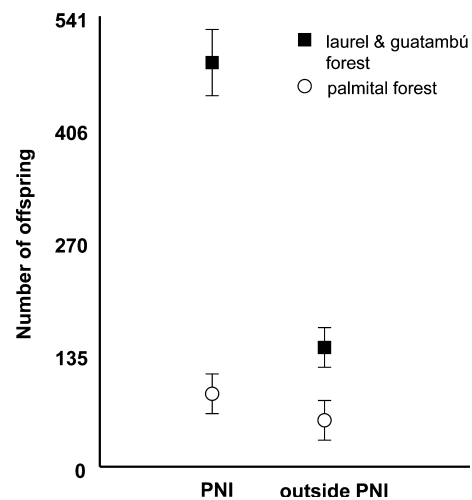


FIGURE 1. Number of seedlings and saplings in and outside PNI. Bars represent standard error. Black squares indicate mean number of offspring from laurel and guatambú forest sites; white circles indicate values from palmital forest sites.

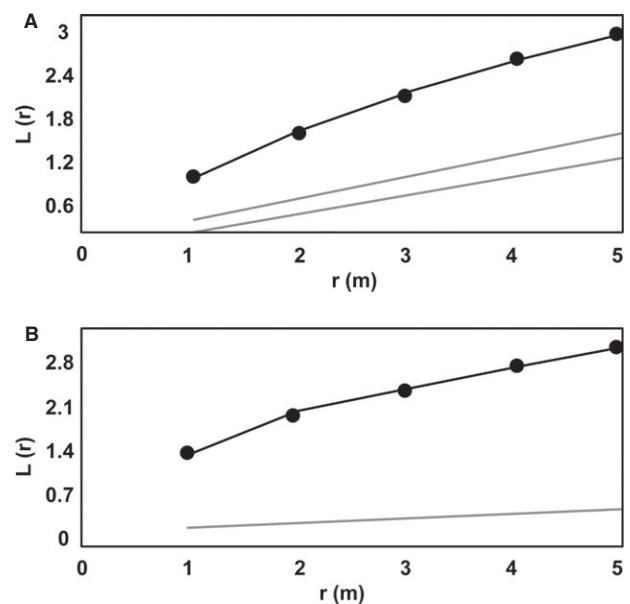


FIGURE 2. Weighted standardized Ripley's function ($L(r)$) for seedlings and saplings plotted against radius distances (r) for (A) PNI, and (B) outside PNI. Lines with circles indicate observed $L(r)$ and grey lines represent upper and lower confidence envelope limits expected under CSR.

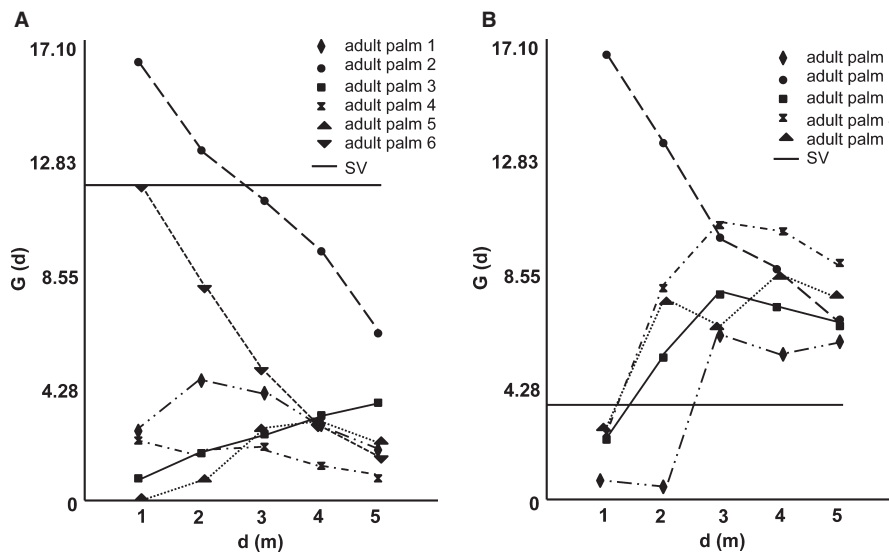


FIGURE 3. $G(d)$ Getis Statistic for each adult palm in (A) PNI and (B) outside the park (one plot is missing because of lack of adult palms). The black line represents the Significance Value (SV) of $G(d)$ for 1000 events ($SV = 3.88$).

ber of adult palms was very similar within extended plots inside and outside the park (5.4 ± 1.5 SE and 5.8 ± 0.8 SE adults, respectively) suggesting a higher survival rate of seeds or seedlings within PNI. Interestingly, palmatal forest exhibited lower levels of recruitment than laurel and guatambú forest both inside and outside PNI (Type of forest $df = 1$, $F = 46.28$, $P = 0.0005$; Fig. 1). No significant interaction was observed between disturbance level and type of forest ($df = 1$, $F = 3.02$, $P = 0.13$).

A total of 1653 pindó seedlings and saplings were counted inside PNI. 54 percent were associated with tapir dung piles (range among plots: 34 to 84 percent). Offspring density associated with tapir dung piles (15.2 individuals/ m^2) was significantly higher than background density (0.16 individuals/ m^2) ($Z = 2.023$, $P = 0.043$). Censusing of offspring recruited directly underneath adult palms showed that they were more abundant outside the park (Median [lower–upper quartiles] = 56.5 [32–70.5] vs. 14 [9.5–18.5]; $U = 16.0$, $P = 0.0003$).

At the spatial scale of our study, pindó seedlings and saplings showed an aggregated pattern as indicated by significant positive values of $L(r)$ inside PNI (Fig. 2A) and outside the park (Fig. 2B). The Getis statistic indicated offspring were significantly grouped around adult palms outside the park (Fig. 3B), whereas such a spatial association was not observed inside PNI (Fig. 3A). In contrast, the aggregation of seedlings and saplings in PNI was spatially associated with tapir dung pile locations, as indicated by positive $L_{12}(r)$ values (Fig. 4). Up to the maximum radius analyzed ($r = 5$), there were more seedlings and saplings in the neighborhood of tapir dung piles than expected by chance.

DISCUSSION

We found that seed dispersal by tapirs shapes the amount and spatial pattern of the seedlings and saplings of pindó. In areas

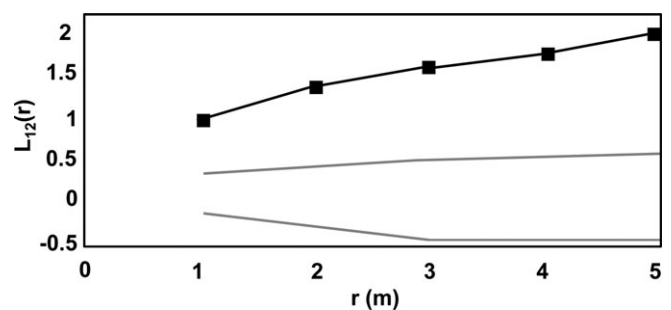


FIGURE 4. Weighted standardized bivariate Ripley's function ($L_{12}(r)$) plotted against radius distances (r) in PNI. The line with black squares represents observed $L_{12}(r)$ and grey lines are the upper and lower confidence envelope limits expected under the Antecedent Condition null model.

including tapir latrines a substantial proportion of offspring are associated with tapir feces, indicating that pindó's spatial pattern of recruitment is heavily affected by tapir defecation. Though our design does not allow us to extrapolate either the observed spatial pattern of pindó recruitment or the relative contribution of tapirs to larger spatial scales, our results suggest this key component for recruitment will be lost if tapirs become locally extinct. For instance, the plots inside PNI spanning latrines contained 48 percent more offspring than plots outside the park. These results support the conclusions of Cordeiro and Howe (2001), Beckman and Muller-Landau (2007), Wang *et al.* (2007) and Sethi and Howe (2009), who proposed that the elimination of large frugivores limits recruitment of animal-dispersed plants. Galetti *et al.* (2006) went so far as to suggest that the combined effect of defaunation and fragmentation could greatly decrease the removal and successful recruitment of palms in small and medium-sized forest fragments. Evidence supporting this assertion was found

by Fleury and Galetti (2006), who concluded that Atlantic Forest fragments in southern Brazil smaller than 1000-ha are not safe sites for pindó recruitment. However, our results do not support this conclusion – in the tapir-free forest fragments smaller than 150-ha we sampled, many offspring were still recruited beyond adult crowns.

On average, 35 percent of the offspring outside PNI were located more than 10 m from the nearest adult. In the disturbed areas lacking tapirs, smaller frugivores may have contributed to reducing the aggregation of recruitment around adult palms. Birds such as cracids (*Penelope* spp.) and toucans (*Ramphastos* spp.), as well as medium-sized mammals such as capuchin monkeys (*Cebus apella* [*Sapajus* *nigrinus*]), brocket deer (*Mazama* spp.) and coatis (*Nasua nasua*) remain in the fragments (Giraud *et al.* 2008, Paviolo *et al.* 2009, pers. obs.), and most likely accounted for those seedlings recorded relatively far from adults outside PNI. Nevertheless, their potential contribution to dispersal remained insufficient to preclude a significant aggregation of seedlings around adults. Thus, the magnitude and quality of tapir dispersal (*i.e.*, transport of great amount of viable seeds and putative long distance movements) is unlikely to be compensated for by other vertebrates. Instead, these dispersers might have complementary roles, as recently shown for co-occurring tapirs and primates (Bueno *et al.* 2013). A comparison within PNI of recruitment in areas with and without tapir activity is necessary to obtain insights on the specific effect of tapirs with respect to other potential dispersers of pindó seeds.

The greater recruitment of pindó under adult palms outside PNI is consistent with the results of Sethi and Howe (2009), who found 93 percent fewer *Chisobeton paniculatus* (Meliaceae) seedlings beyond parental crowns and a high accumulation of seedlings under reproductive adults in disturbed Indian forests. This accumulation of seedlings and saplings directly under reproductive adults could have important effects on plant population and genetic structure. Dispersers that move seeds away from the parents tend to reduce genetic structuring (Hamrick *et al.* 1993). In Bolivia, for example, Pacheco and Simonetti (2000) found that seedlings of *Inga ingoides* (Mimosoideae) that recruited under reproductive adults had fewer alleles in common (reflecting less genetic relatedness) in areas where its main disperser (*Ateles paniscus*) was present than in areas lacking *A. paniscus*. In this sense, tapirs may play a key role in maintaining gene flow within and among pindó populations, and the genetic structure of this species could be altered by defaunation.

We found higher levels of pindó recruitment inside PNI, where the continuous and protected Atlantic Forest allows the persistence of higher abundances of medium and large frugivores (Paviolo *et al.* 2009). This pattern is probably not due to differences in the number of nearby adults – which was actually very similar inside and outside PNI – although higher fruit productivity of neighboring adults inside the park cannot be ruled out as a potential mechanism. Inside the park the lower aggregation of offspring around adults suggests that the difference in the amount and spatial patterns of recruitment is more likely due to a higher rate of seed removal after fruits fall and subsequent deposition in safer sites, as the Janzen-Connell model proposes.

Laurel and guatambú forests and palmitals are the most predominant vegetation types in Semi-deciduous Atlantic Forest. Although precise estimates of their abundance in these habitats are lacking, pindó adults are quite abundant in both (though not exceeding 20 adults/ha). Interestingly, we found lower recruitment of early-stage pindó individuals in palmital forest. This forest type is characterized by a high density of *E. edulis* (up to 500 adults/ha; Reis *et al.* 2000) and an understory carpeted by their offspring. *Enterpe edulis* is a shade tolerant species that does not grow in gap openings and does not resist frost (Gatti *et al.* 2008). Because the lowest winter temperatures are often registered in the lower elevations of the PNI, palmital forests grow in high elevation sites (Gatti *et al.* 2008, 2011). These sites usually contain well drained soils and may also differ in the availability of specific nutrients or other physical properties. These conditions, suitable for *E. edulis*, may inhibit the recruitment of pindó.

Lowland tapir was previously identified as a prominent disperser of pindó palm in Argentina's Semi-deciduous Atlantic Forest (Giombini *et al.* 2009). Our results support this view, as pindó are often associated with dung piles. Indeed, our results may even be conservative, as our methods could have led us to underestimate tapir contribution to pindó recruitment. This is because seedlings may have been misclassified as background density for two main reasons. First, some may have been secondarily dispersed from dung piles (Fragoso 1997). Second, we may not have been able to identify older defecations. More generally, our findings also support the conclusion that tapirs play a key role in the dispersal of palm seeds (Bodmer 1990, Fragoso & Huffman 2000, Rios & Pacheco 2006, Tobler *et al.* 2010, O'Farrill *et al.* 2012).

The aggregation of saplings in latrine areas has been observed in other dispersal systems (Stoner *et al.* 2007). In a Peruvian Neotropical forest, the largest proportion of saplings of *Virola calophylla* (Myristicaceae) was found in the latrines of *Ateles paniscus*, its main disperser (Russo & Augspurger 2004). Similarly, saplings of several species in Argentinian flooded forest recruit in latrines of *Alouatta caraya*, the most abundant frugivore in this forest type (Bravo 2012). Fragoso (1997) proposed that animals using latrines generate a pattern of punctuated large-scale seed deposition, and this may be the case with pindó palms in PNI. The evaluation of such a hypothetical spatial pattern, however, would require a quantitative assessment of the spatial distribution of adults and tapir latrines at greater scales.

Tapirs have been driven to local extinction in much of their historical range, primarily because of habitat loss and hunting (Brooks *et al.* 1997). Our results add to the increasing body of evidence that they are critical seed dispersers, and that their loss could have major effects on plant population distribution and abundance.

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