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Parent-parent and parent-offspring distances in *Spondias radlkoferi* seeds suggest long-distance pollen and seed dispersal: evidence from latrines of the spider monkey

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Abstract: Pollen and seed dispersal are key ecological processes, directly impacting the spatial distribution, abundance and genetic structure of plant populations; yet, pollen- and seed-dispersal distances are poorly known. We used molecular markers to identify the parental origin (n = 152 adult trees) of 177 *Spondias radlkoferi* (Anacardiaceae) seeds deposited by the spider monkey (*Ateles geoffroyi*) in latrines located beneath 17 sleeping-trees in two continuous forest sites (CF) and two forest fragments (FF) in the Lacandona rain forest, Mexico. We estimated mean parent-offspring (PO) distances per latrine and, for those seeds (54% of seeds) with more than one candidate parent (i.e. the potential maternal and parental parents), we also estimated parent-parent (PP) distances per latrine, and tested if PO and PP distances differed between forest types. Global PO and PP distances per latrine averaged 682 m (range = 83–1741 m) and 610 m (range = 74–2339 m), respectively, and did not differ significantly between CF and FF. This suggests that pollen dispersal is extensive in both forest types and that long seed dispersal distances (>100 m) are common, thus supporting the hypothesis that the spider monkey is an effective seed disperser of *S. radlkoferi* in continuous and fragmented forests.

Key Words: *Ateles*, forest fragmentation, Lacandona, parental analysis, pollen dispersal, seed dispersal effectiveness

INTRODUCTION

Pollen and seed dispersal influence the spatial distribution, abundance and genetic structure of plant populations (Dick *et al.* 2008, Jordano *et al.* 2011, Wheelwright & Orians 1982). In tropical forests, dioecy and self-incompatibility mechanisms are very common (Ibarra-Manríquez & Oyama 1992), and insects, particularly bees, are the primary pollinators of most tropical tree species (Bawa 1990). Regarding seed dispersal, most tropical woody plant species produce fruits that are primarily dispersed by birds, bats and primates (Arroyo-Rodríguez *et al.* 2015, Bufalo *et al.* 2016). Therefore, pollen- and seed-dispersal patterns can be altered in fragmented forests, where defaunation can lead to pollination and seed-dispersal limitation (Cordeiro *et al.* 2009, Cunningham 2000, Robertson *et al.* 1999). Unfortunately, pollen- and seed-dispersal distances are difficult to quantify in the field, and are therefore largely unknown for most tropical trees.

Pollen- and seed-dispersal distance are frequently estimated from indirect methods, such as feeding and ranging behaviours of animals, controlled pollination treatments, and seed passage time through the animal gut (Russo *et al.* 2006, Sazan *et al.* 2014). Other studies use different kinds of markers to track pollen and seed movements (Reiter *et al.* 2006, Webb & Bawa 1983). Yet, the development of molecular techniques during the last two decades has facilitated the identification of pollen and seed origins in the field (Dick *et al.* 2003, Godoy & Jordano 2001, Grivet *et al.* 2005, Hoban *et al.* 2012), enabling accurate quantifications of the pollen- and seed-dispersal distances. However, only one study of primates has used genetic methods to identify the maternal origin of *Myrica rubra* seeds found in the faeces of the Yakushima macaque (Terakawa *et al.* 2009).

Here, we used molecular markers to identify the parental origin of 177 *Spondias radlkoferi* (Anacardiaceae)

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seeds dispersed by the spider monkey (*Ateles geoffroyi*) in two continuous forest sites and two forest fragments in the Lacandona rain forest, Mexico. As an important proportion of dispersed seeds are defecated by this primate in latrines located beneath sleeping-trees (González-Zamora *et al.* 2014, 2015; Velázquez-Vázquez *et al.* 2015), we assessed the parental origin of seeds located in 17 spider monkey latrines to infer potential pollination and seed-dispersal limitation in fragmented forests. Such information is useful to better understand the role of latrines in forest regeneration (Russo & Chapman 2011), as seedling recruitment can be enhanced if seeds come from different parents and have diverse genotypes (Jordano 2007, Terakawa *et al.* 2009). We therefore used nuclear microsatellite markers, which provide a wealth of information about pollen- and seed-mediated gene flow in plants. We identified all candidate parental trees of each seed, to then quantify mean parent-offspring (PO) distances per latrine as a proxy of seed-dispersal distance. When more than one candidate parent emerged for a given seed, we calculated the parent-parent (PP) distance and estimated the mean PP distance per latrine as a proxy of pollen-dispersal distance, and tested if PO and PP distances differed between forest types. We hypothesized that the scarcity of adult trees in fragmented rain forests (Arroyo-Rodríguez & Mandujano 2006) may 'force' bees to travel longer distances than in continuous forests, thus increasing PP distances (Dick *et al.* 2003, 2008; Stacy *et al.* 1996). In contrast, because the home range size of spider monkeys is smaller in fragments than in continuous forest areas (Chaves *et al.* 2012), we can expect that PO distances are lower in fragmented than in continuous forests.

METHODS

Study area

The Lacandona rain forest constitutes the south-western sector of the Mayan forest in Mexico. The area was originally covered by over 1.4 million ha of rain forest, but deforestation during the last four decades has resulted in the loss of ~70% of the original forest cover. We conducted the study in two adjacent areas separated by the Lacantún river: the Marqués de Comillas region (MCR) and the Montes Azules Biosphere Reserve (MABR) (Figure 1). MCR encompasses *c.* 176,000 ha of fragmented forest, human settlements and agricultural lands. The study fragments were isolated 25–29 y ago and are located within an anthropogenic matrix of cattle pastures and agricultural lands (González-Zamora *et al.* 2012, 2014). In contrast, MARB comprises *c.* 331,000 ha of continuous and undisturbed old-growth forest. Further details on the study landscape are given in González-Zamora *et al.* (2012, 2014, 2015).

Study primate species

Geoffroy's spider monkey (*Ateles geoffroyi* Kuhl) is the largest Mesoamerican primate species, and is distributed from the state of Veracruz (Mexico), throughout most Mesoamerica, to northern Colombia. This species is considered a fruit specialist, as ripe fruits account for more than 70% of its feeding time (González-Zamora *et al.* 2009). It has large home range requirements, rapid speed of travel, and a fission-fusion dynamics (Aureli *et al.* 2008, Di Fiore & Campbell 2007). Published records of *Ateles* home range sizes are highly variable (95–900 ha; Wallace 2008). *Ateles geoffroyi* is probably the primary dispersal agent of *S. radlkoferi* (Chaves *et al.* 2011, González-Zamora *et al.* 2014) as: (1) this tree species is a top food species for spider monkeys throughout its distribution range (González-Zamora *et al.* 2009); and (2) has large diaspores (3–4 cm in length) that are difficult for smaller frugivorous animals to swallow and disperse (Benítez-Malvido *et al.* 2014, Cramer *et al.* 2007).

Seeds and adult trees of *Spondias radlkoferi*

The tropical tree *Spondias radlkoferi* (Anacardiaceae) is self-incompatible and dependent on pollinators (mainly small bees from tribes Meliponini and Exomalopsini) to set its fruit (Carneiro & Martins 2012, Nadia *et al.* 2007). The ranging behaviour of these bees is poorly known, but it has been proposed that when visiting several plants, bees tend to visit first the closest neighbour, or the second nearest neighbour (Collevatti *et al.* 2000, Stacy *et al.* 1996); yet, the nearest-neighbour rule can be violated in fragmented forests (Dick *et al.* 2008). It is andromonoecious, i.e. it produces both bisexual and male flowers on the same plant. Although there is no available information on the reproductive phenology of *Spondias radlkoferi*, *S. mombin* (a sister and sympatric species) has a synchronous reproductive activity (considering both flowering and fruiting) among populations, being sexually mature at the height of 5–30 m and at an approximate age of 5 y (Adler & Kielpinski 2000). This species (as *S. tuberosa*) produces many small and white flowers in large inflorescences (Carneiro & Martins 2012, Nadia *et al.* 2007). Anthesis of flowers is sequential within the inflorescence, beginning early morning (*c.* 05h00), and lasting approximately 2 d to hermaphrodite flowers and only one day to male flowers (Carneiro & Martins 2012, Nadia *et al.* 2007).

Based on recent research on the density and spatial distribution of sleeping trees and latrines of *A. geoffroyi* in continuous and fragmented forests in the Lacandona region, Mexico (González-Zamora *et al.* 2012, 2014, 2015), we selected 17 latrines from two forest fragments in MCR (FF1: 1125 ha, 16°15′10.83″N,

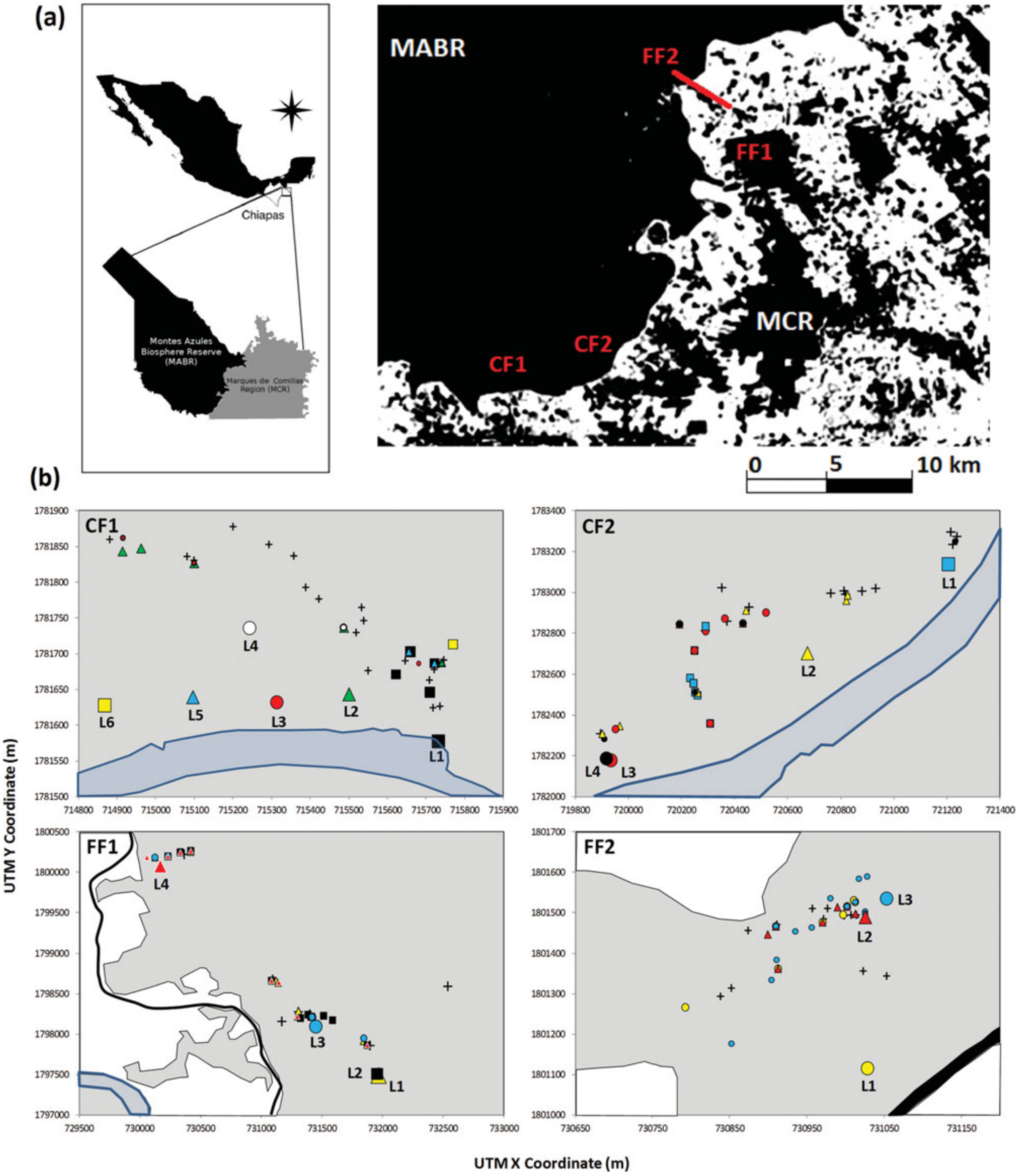

Figure 1. Location of study areas in the Lacandona rain forest, Mexico: the Marqués de Comillas region (MCR) and the Montes Azules Biosphere Reserve (MABR) (a). The location of the spider monkey latrines (L) and all adult trees of *Spondias radlkoferi* sampled in two continuous forest sites (CF1 and CF2) and two forest fragments (FF1 and FF2) is also indicated (b). The candidate parental trees of the seeds collected within a given latrine show the same icon and colour as the latrine (e.g. black squares in CF1 represent candidate parental trees of seeds recorded in latrine L1, and red circles in CF2 are candidate parental trees of seeds collected in latrine L3). Black plus (+) symbols in all forest sites represent adults trees for which we did not identified parent-offspring relationships. The remaining forest in (b) is indicated with light grey polygons, the anthropogenic matrix with white, the Lacantún River with light blue, and roads with black lines.

Table 1. Mean parent-parent (PPD, m) and parent-offspring distances (POD, m) of *Spondias raldkoferi* seeds dispersed by *Ateles geoffroyi* in latrines located in two continuous forest sites (CF1 and CF2) and two forest fragments (FF1 and FF2) in the Lacandona rain forest, Mexico. The total number of seeds/seedlings, latrines and candidate parent trees included in the analyses are also included, as is the percentage of seeds for which we identified the parental origin. The inter-latrine distance (ILD, m) within each forest site is also indicated.

Sites	PPD (mean ± SD)	POD (mean ± SD)	No. seeds/seedlings (no. latrines)	No. adult trees	Parental origin (%)	ILD (mean ± SD)
CF1	197 ± 114	422 ± 288	63 (6)	38	15.9	378 ± 242
CF2	460 ± 186	570 ± 217	39 (4)	42	66.7	788 ± 471
FF1	1458 ± 737	1436 ± 368	39 (4)	35	69.2	612 ± 247
FF2	92 ± 26	204 ± 135	36 (3)	37	50.0	208 ± 110

90°49′53.82″W; and FF2: 33 ha, 16°16′54.15″N, 90°50′19.91″W) and two continuous forest sites within MABR (CF1: 16°06′25.01″N, 90°59′16.61″W; and CF2: 16°06′08.62″N, 90°58′05.29″W) (Table 1; Figure 1). As latrines we refer to sites beneath sleeping trees where spider monkeys deposit copious amounts of dung (and seeds), and that are repeatedly used (1–12 mo) (González-Zamora *et al.* 2012, 2015). In particular, we selected latrines with at least 25 seeds of *S. radlkoferi* each (mean = 99 seeds per latrine, range = 25–287 seeds). The average distance among latrines within each forest site varied from 208 to 788 m (Table 1).

In the context of a 13-mo study (1 February 2011–28 February 2012) of the seed rain produced by spider monkeys in these latrines, we collected 2880 seeds of *S. radlkoferi* (see details in González-Zamora *et al.* 2014, 2015). The seeds were washed and stored in plastic bags with SilicaGel to avoid the proliferation of fungus and other pathogens. We then randomly selected 1250 undamaged seeds for germination in a greenhouse of the Laboratorio de Ecología Genética y Molecular located at the Universidad Nacional Autónoma de México, Morelia, Mexico. After an average germination period of 120 to 180 d, we collected the leaves of 15 randomly selected seedlings per latrine (total = 255 seedlings) for the genetic analyses that are described below. In the genetic analyses we also included mature leaves of all *S. radlkoferi* adult trees found within a *c.* 300-m radius from each latrine. The spatial location of all latrines and adult trees was recorded with a GPS unit (Figure 1).

Microsatellite genotyping

After discarding the individuals for which DNA isolation was not possible, we extracted genomic DNA from 329 plants (152 adult trees and 177 seedlings; Table 1). DNA was isolated from 100 mg of frozen leaf tissue as described in Aguilar-Barajas *et al.* (2014). We employed eight nuclear microsatellites (SPO3, SPO4, SPO8, SPO10, SPO14, SPO15, SPO18, SPO31) loci previously designed for *S. radlkoferi* (Aguilar-Barajas *et al.* 2014). As described in Aguilar-Barajas *et al.* (2014), PCR amplification was performed in a final reaction volume of 5 μl containing 2× QIAGEN multiplex Kit PCR mix (containing HotStar taq DNA polymerase, Multiplex PCR buffer, 3 mM $MgCl_2$ and dNTPs), 0.4 μM of each primer, and ~ 10 ng of DNA template. PCR amplification was performed in Eppendorf Mastercycler (Hamburg, Germany) using the multiplex protocol for amplification of microsatellite loci (QIAGEN Multiplex PCR kit; QIAGEN): first denaturing step 94°C, 15 min; 35 cycles of denaturing 94°C, 30 s; primer annealing at 58°C or 60°C, 1 min 30 s; extension 72°C, 1 min, and finale extension at 72°C for 10 min. Loci that were successfully amplified were then tested with a fluorescent forward primer. Amplified fragments were electrophoresed in an ABI PRISM 3130 XL Genetic Analyzer (Applied Biosystems, Inc., Foster City, CA) with the GeneScan 500 LIZ size standard included (Applied Biosystems, Inc.). We used the PeakScanner software v 1.0 (Applied Biosystems, Inc.) for fragment analysis and final sizing. To detect scoring errors resulting from the presence of null alleles, stuttering or large allele dropout, we tested microsatellite data using the Micro-Checker software (Van Oosterhout *et al.* 2004).

Genetic diversity

We computed the number of alleles (A) and private alleles (PA) following a rarefaction method that compensates uneven population sizes, as implemented by the HP-Rare software (Kalinowski 2005). Both the observed (Ho) and expected heterozygosity (He) were determined with the GenAlEx software, version 6.5 (Peakall & Smouse 2006).

Parental analysis and potential pollen- and seed-dispersal distance

Each forest site was analysed separately, i.e. to assess the parental origin of a given seed we considered all adult trees sampled in the forest site where the seed was collected. The genealogical relationship between seeds and adult trees was represented mathematically as probabilities. In particular, we used the ML-RELATE software for parental tests, which uses maximum likelihood to independently identify the most likely relationship category for each pair of individuals in the dataset (i.e. parent-offspring, full sibling, half-sibling, unrelated). The program was designed to accommodate microsatellite loci with null alleles (Kalinowski *et al.* 2006). For each locus, we tested for the presence of null alleles, as indicated by a deficiency of heterozygotes relative to Hardy–Weinberg expectations. We then applied a correction for the presence of null alleles (Wagner *et al.* 2006) in the calculations of relatedness (r) and the probability of relationships. Because we have alleles from adult trees and from seedlings, we only evaluated parent–offspring (PO) relationships. We used the specific hypothesis test to determine the parent–offspring pair when the values of likelihood among pedigree relationship were close to each other. In total, we were able to identify the parental origin of 16% and 67% of seedlings tested in CF1 and CF2, and 69% and 50% of seedlings tested in FF1 and FF2, respectively (Table 1). Based on these results, we quantified the PO distances by simply calculating the Euclidian distance between the latrine where the seeds were collected and all candidate parent trees of each seed. For 44 out of 81 seeds (54%) we were able to identify more than one candidate parent tree, which can be considered the maternal and paternal parents of those seeds (Appendix 1). Therefore, we calculated the mean parent-parent (PP) distance per seed, and then the mean PP distance per latrine as a proxy of pollen-dispersal distance. As we cannot distinguish the maternal and paternal parents, we estimated the mean PO distance per seed to have a conservative estimate of potential seed dispersal distances. Although the minimum PO distance would have been an even more conservative estimate of seed dispersal distance than mean PO distance, we selected the latter to avoid underestimations (note that the mean day range of the spider monkey is > 2000 m, and this primate can travel up to 4500 m in a day; Wallace 2008).

Statistical analyses

To be conservative in our assessment of potential pollen- and seed-dispersal distances in both forest types (CF and FF), our response variable was a mean of means, i.e. we first calculated the mean PP and PO distance per seed, and then calculated the mean PP and PO distance per latrine (Appendix 1). Although there was no spatial autocorrelation of datasets within the continuous forest sites, nor within the forest fragments (see results of Mantel tests in González-Zamora *et al.* 2015), we used general linear mixed models to test whether mean PP and PO distances differed between forest types. The fixed effect was forest type, and latrines were nested within each forest site and added as a random effect in the model. The residual maximum likelihood method was used to separate variances of fixed from random effects in the models (Grafen & Hails 2002). All analyses were done with the JMP 8.0 software.

RESULTS

The loci tested were polymorphic in both parent trees and seedlings (Table 2). Merging the data for CF and FF, parent trees and seedlings showed similar parameters of genetic diversity (Table 2). The mean allelic richness ranged from 5 to 15 in parent trees, and from 7.5 to 22.5 in seedlings. Private alleles were present in both ontogenetic classes, and mean observed and expected heterozygosity was similar in parent trees and seedlings (Table 2). The genetic differentiation between parent trees ($F_{ST} = 0.05$) and seedlings ($F_{ST} = 0.04$) was low.

Global PP and PO distances per latrine averaged 610 m (range = 74–2339 m) and 682 m (range = 83–1741 m), respectively (Appendix 1). Mean PP distance per latrine averaged (± SD) 197 ± 114 m in CF1, 460 ± 186 m in CF2, 1458 ± 737 m in FF1, and 92 ± 26 m in FF2 (Table 1; Figure 1). Mean PO distance averaged 422 ± 288 m in CF1, 570 ± 217 m in CF2, 1436 ± 368 m in FF1, and 204 ± 135 m in FF2 (Table 1; Figure 1). Mean PP distance per latrine did not differ between CF (348 ± 203 m) and FF (872 ± 897 m) ($F_{1,15} = 2.28$, $P = 0.16$; Figure 2a). Similarly, mean PO distance per latrine was statistically similar in CF (524 ± 281 m) and FF (908 ± 714 m) ($F_{1,15} = 2.42$, $P = 0.14$; Figure 2b).

DISCUSSION

The ecology of spider monkeys has been investigated for more than five decades (reviewed by Campbell 2008). However, this study is the first to assess the parental origin of seeds dispersed by the spider monkey in a fragmented rain forest using molecular methods. Our findings suggest that *Spondias radlkoferi* seeds deposited by spider monkeys in latrines came from distantly located parents, as PO distances per latrine averaged 908 m in forest fragments and 524 m in continuous forests. Although we cannot distinguish between maternal and paternal parents, our results suggest that long-dispersal distances (>100 m) are common in both forest types, as 87–93% of estimate values of mean PO distance per seed were higher than 100 m in forest fragments and continuous forest sites, respectively (Appendix 1). In agreement with previous reports for other tropical trees (reviewed by Dick *et al.* 2008), our findings also suggest that pollen dispersal is extensive in both forest types as mean PP distances per latrine averaged 347 m in continuous forest sites and 872 m in forest fragments.

Table 2. Genetic diversity of the microsatellite loci in adult trees and seedlings of *Spondias radlkoferi* in the Lacandona region, Mexico. A, allelic richness; PA, private allelic richness; Ho, observed heterozygosity; He, expected heterozygosity.

	Adult trees (n = 152)				Seedlings (n = 177)			
Locus	A	PA	Ho	He	A	PA	Ho	He
SPO3	6.80	0.02	0.64	0.53	7.97	1.19	0.64	0.68
SPO4	8.47	0.31	0.76	0.70	8.69	0.53	0.62	0.78
SPO8	5.97	0.00	0.79	0.62	6.70	0.73	0.97	0.71
SPO10	5.00	0.00	0.81	0.61	7.60	2.60	0.97	0.69
SPO14	12.6	1.60	0.69	0.73	13.2	2.23	0.61	0.81
SPO15	15.0	3.00	0.62	0.75	22.5	10.50	0.71	0.83
SPO18	13.3	2.11	0.67	0.71	16.8	5.63	0.72	0.76
SPO31	7.97	0.08	0.86	0.76	7.92	0.03	0.81	0.75
Mean	9.38	0.89	0.73	0.68	11.4	2.93	0.76	0.75
SE			0.03	0.03			0.05	0.02

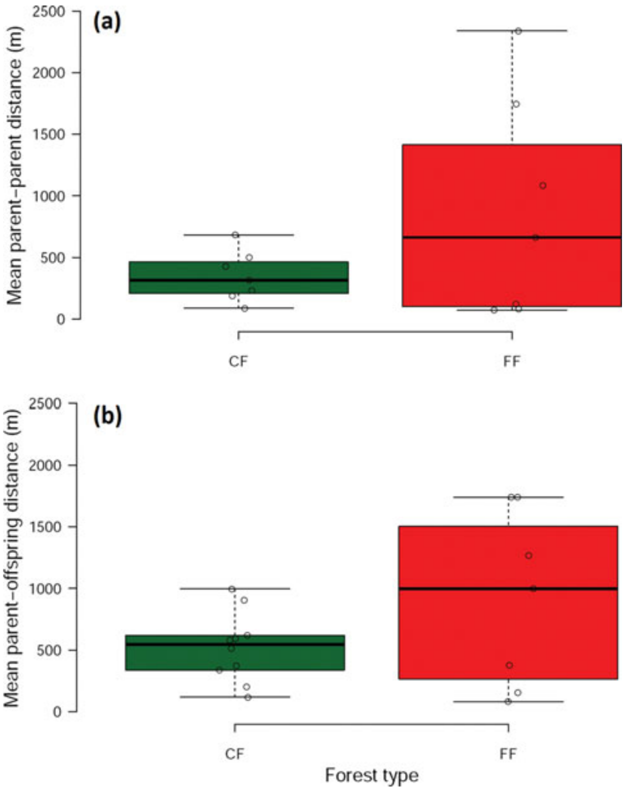

Figure 2. Mean parent-parent (a) and parent-offspring (b) distances in *Spondias radlkoferi* seeds collected within latrines of spider monkeys located in continuous (CF) and fragmented (FF) forests in the Lacandona rain forest, Mexico. The boxplots indicate the median (thick lines), 1st and 3rd quartiles (box), and the range (whiskers).

Our results support the idea that spider monkeys (*Ateles* spp.) are effective seed dispersers (Chaves *et al.* 2011, Dew 2008, González-Zamora *et al.* 2014, Link & Di Fiore 2006). *Ateles geoffroyi*, in particular, has a very high dietetic diversity throughout its geographic range (364 species, 76 families), and fruits are the most common food item in their diet (González-Zamora *et al.* 2009). In fact, they are considered ripe fruit specialists (Di Fiore & Campbell 2007). In the Lacandona rain forest, *A. geoffroyi* feeds on 73 fruit species and swallow seeds of most of them, thus promoting that most spider monkey faeces contain seeds (Chaves *et al.* 2011). In fact, González-Zamora *et al.* (2014) demonstrate that spider monkeys deposited > 45 000 seeds (> 5 mm in length) from 68 plant species in 60 latrines during a 13-mo period. Thus, considering the quantitative component of seed dispersal effectiveness (sensu Schupp 1993), which depends on the number of seeds that are dispersed, there is no doubt that the spider monkey is an effective seed disperser.

Regarding the quality component of seed dispersal effectiveness, which depends on the quality of treatment given to the seed in the animal's mouth and gut, and on the quality of seed deposition (Schupp 1993), there is also evidence that spider monkeys are effective seed dispersers. For example, although there is evidence of positive, negative and neutral net effects of primate gut passage on seed germination, positive effects are more frequent (reviewed by Chaves *et al.* 2011). The number of *S. radlkoferi* seeds that successfully germinate is actually higher for defecated seeds than for control (i.e. from mature fruits) seeds (Chaves *et al.* 2011). Also, seed deposition patterns produced by spider monkeys are mixed, i.e. a fraction clumped in latrines and another one scattered across the forest (Chaves *et al.* 2011, González-Zamora *et al.* 2014, 2015; Russo & Augspurger 2004). This contributes to creating heterogeneous seed deposition patterns, which can favour the colonization of suitable sites for seedling recruitment (Howe & Smallwood 1982).

The present study adds further evidence on the effectiveness of *A. geoffroyi* as a seed disperser, as we demonstrate that mean PO distance per latrine was highly variable (83–1741 m), but most figures were far above 100 m – a typical threshold for long dispersal distances (sensu Cain *et al.* 2000) (Figure 1, 2; Appendix 1). The fact that we identified putative parental trees for only 16–69% of seeds sampled in each forest site can actually be interpreted as a potential underestimation of PO distances (i.e. the parents of 31–84% of seeds would be located outside of the sampled area). In any case, our numbers in both continuous and fragmented forests were within the range values reported for *A. belzebuth* in the Yasuni National Park, Ecuador (up to 1000 m; Dew 2008, Link & Di Fiore 2006). Therefore, seed dispersal by spider monkeys can be of key relevance for seedling recruitment and survival, as long dispersal distance allows seeds and seedlings escaping from areas of high mortality close to parental trees (Howe & Smallwood 1982).

Although we cannot directly measure seed dispersal distances, we are confident that our estimations of mean PO distances can be considered a conservative proxy of seed dispersal distances. First, our figures were within the range reported for other *Ateles* species. Second, they are consistent with our knowledge about the ranging behaviour and gut passage times in spider monkeys. In particular, records of mean day journey length (i.e. day range) are variable, but most mean estimates fall between 2000 and 2300 m (reviewed by Wallace 2008). Thus, because gut passage times range from *c.* 2.5 to 18 h (Milton 1981, Russo *et al.* 2006), we can expect that seed dispersal distances rarely exceed 2000 m, if they do. Finally, as our estimations included all PO relationships (including both maternal and paternal parents) per seed, and we averaged PO distances per latrine (i.e. considering all seeds recorded within each latrine), it is reasonable to suppose that the PO distances reported in this study represent conservative estimation of potential seed dispersal distances per latrine.

Regarding our estimations of parent-parent distances, our findings support the idea that pollinators usually violate the nearest-neighbour rule (Dick *et al.* 2008). Although the ranging behaviour of the primary pollinators of *S. radlkoferi* (e.g. Meliponini and Exomalopsini bees) is largely unknown, our findings support the idea that they travel long distances (> 2 km) in search of flowers. This figure is not surprising, as there is increasing evidence of long pollen-dispersal distances in temperate and tropical trees, including trees pollinated by very small insects, such as figs (*Ficus* spp.), which can show pollen-dispersal distances of > 5 km (reviewed by Dick *et al.* 2008). This suggests that, as in other highly outcrossed mating systems, extensive long-distance pollen dispersal probably plays a key role in maintaining the genetic diversity of *S. radlkoferi*, thereby limiting potential negative genetic effects of inbreeding and drift in fragmented populations (Millar *et al.* 2014). Yet, additional studies with precise paternity assignments (i.e. paternal parent), and those capable of tying dispersed seeds back to the particular tree that bore the fruit consumed by the monkeys (i.e. maternal parent) are needed to accurately quantify pollen- and seed-dispersal distances (Dick *et al.* 2008, Godoy & Jordano 2001, Grivet *et al.* 2005).

Ecological implications

Although contagious seed dispersal (e.g. in primate latrines) can reduce the quality of dispersal because it leads to dispersal and recruitment limitation (Schupp *et al.* 2002), an increasing number of studies suggest that primate latrines can be of key relevance for forest regeneration (Arroyo-Rodríguez *et al.* 2015, González-Zamora *et al.* 2012, 2014, 2015; Russo & Chapman 2011). Considering spider monkey latrines, for instance, evidence indicates that they are relatively abundant in the forests: up to 0.16 latrines ha^{-1} in the Calakmul region, south-eastern Mexico (Velázquez-Vázquez *et al.* 2015), and 0.53 latrines ha^{-1} in the Lacandona rain forest (González-Zamora *et al.* 2012). The spatial distribution of spider monkey latrines is highly variable across the forest (González-Zamora *et al.* 2012), thus increasing the probability that some latrines are located in suitable sites for seed germination and seedling recruitment. The accumulation of copious amounts of faeces in latrines results in soil nutrient enrichment, which further favour the establishment, growth and survival of seedlings (reviewed by Arroyo-Rodríguez *et al.* 2015). Seedling recruitment can also be favoured by the fact that the very high seed arrival rate and high seed germination rates in primate latrines can lead to the saturation of biotic mortality agents (e.g. seed/seedling predators) (González-Zamora *et al.* 2014, Russo & Augspurger 2004), particularly in latrines that are more frequently used by the monkeys, which receive more seeds and from a higher number of plant species (González-Zamora *et al.* 2015).

Here we present additional evidence on the importance of latrines for seedling recruitment and forest regeneration, as we found that seeds deposited in spider monkey latrines came from different distant places. This pattern can be related to the fruiting pattern of *S. radlkoferi*, and the fission-fusion dynamics of spider monkeys (Aureli *et al.* 2008), and their complex feeding and ranging behaviours (Ramos-Fernández *et al.* 2013). In particular, fruiting is spatially and temporally aggregated, thus allowing monkeys to visit several adult trees near their sleeping trees (Russo *et al.* 2006). In fact, the probability of visiting different *S. radlkoferi* adult trees can be promoted by the fact that spider monkeys use home ranges and core areas of variable sizes through time and space (Ramos-Fernández *et al.* 2013), and also, by the fact that groups are split in subgroups of different sizes and composition during the day to feed on several plants located near sleeping trees, and return to the same or different sleeping trees after foraging excursions (Aureli *et al.* 2008). As argued by Terakawa *et al.* (2009) for the Yakushima macaque, the fact that monkey faeces contain seeds from different distantly located parent trees increases the fitness of parental trees by limiting intra-sibship competition and inbreeding depression. Also, and perhaps more importantly, seed germination and seedling recruitment in latrines may be favoured by the fact that seeds from different parents have different genotypes, and hence, different abilities to cope with the heterogeneous environmental conditions that are present in latrines (Jordano 2007, Terakawa *et al.* 2009). Nevertheless, additional studies will be required to accurately assess seed germination and seedling recruitment in spider monkey latrines, as there exist very few studies on this topic, and hence, our understanding on the role that primate latrines may have on forest regeneration is still limited (Arroyo-Rodríguez *et al.* 2015, González-Zamora *et al.* 2014, 2015; Russo & Chapman 2011).

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Appendix 1. Parent-parent and parent-offspring relationships in *Spondias radlkoferi* trees in two continuous and two fragmented forest sites in the Lacandona rain forest, Mexico. We indicate the log-likelihood and relatedness coefficient of each parent (adult tree)-offspring (seed) relationship, the Euclidian distance between each seed (collected in latrines of spider monkeys) and each candidate parental tree (i.e. parent-offspring distance, POD, m), and for those cases in which we found more than one candidate parent for a given seed, we also show parent-parent distances (PPD, m).

Forest site/Latrine	Seed	Adult tree	LnL(R)	Relatedness (r)	POD	PPD
Continuous forest (CF1)						
L1	L1-1	CF1-A1	– 30.67	0.443	110	101
		CF1-A2	– 31.12	0.500	144	
	L1-2	CF1-A3	– 29.98	0.500	72	76
		CF1-A4	– 34.4	0.500	145	
L2	L2-1	CF1-A5	– 20.19	0.574	245	
	L2-2	CF1-A6	– 26.89	0.500	94	315
		CF1-A7	– 29.83	0.500	441	
		CF1-A8	– 26.23	0.595	620	
		CF1-A9	– 31.77	0.500	576	
L3	L3-1	CF1-A7	– 33.33	0.393	289	187
		CF1-A10	– 37.19	0.437	459	
	L3-2	CF1-A11	– 29.35	0.500	371	
L4	L4-1	CF1-A6	– 26.03	0.500	203	
L5	L5-1	CF1-A1	– 28.99	0.500	627	
	L5-2	CF1-A12	– 31.68	0.500	563	
L6	L6-1	CF1-A13	– 28.74	0.505	906	
Continuous forest (CF2)						
L1	L1-1	CF2-A1	– 37.26	0.460	963	
	L1-2	CF2-A2	– 32.88	0.500	1121	
	L1-3	CF2-A3	– 34.15	0.500	1123	161
		CF2-A4	– 24.32	0.381	1045	
	L1-4	CF2-A5	– 35.59	0.513	1188	109
		CF2-A6	– 38.7	0.543	1142	
		CF2-A7	– 28.82	0.507	1141	
	L1-5	CF2-A3	– 36.04	0.442	1123	283
		CF2-A1	– 35.89	0.392	963	
	L1-6	CF2-A8	– 41.73	0.472	424	381
		CF2-A9	– 29.66	0.429	795	
L2	L2-1	CF2-A10	– 31.55	0.500	503	547
		CF2-A11	– 31.03	0.500	792	
	L2-2	CF2-A12	– 32.52	0.472	284	418
		CF2-A13	– 36.75	0.436	322	
	L2-3	CF2-A14	– 40.05	0.520	455	
	L2-4	CF2-A4	– 27.2	0.500	426	535
		CF2-A15	– 27.97	0.573	867	

Appendix 1. Continued.

Forest site/Latrine	Seed	Adult tree	LnL(R)	Relatedness (r)	POD	PPD
L3	L3-1	CF2-A3	– 33.47	0.450	453	
	L3-2	CF2-A1	– 30.9	0.523	747	
	L3-3	CF2-A5	– 35.64	0.213	415	505
		CF2-A12	– 37.77	0.500	835	
	L3-4	CF2-A4	– 29.65	0.521	623	
	L3-5	CF2-A4	– 30.03	0.408	623	
	L3-6	CF2-A16	– 21.58	0.501	816	729
		CF2-A15	– 20.31	0.499	134	
	L3-7	CF2-A17	– 30.85	0.442	929	245
		CF2-A18	– 29.3	0.500	726	
	L3-8	CF2-A4	– 25.56	0.440	623	
	L3-9	CF2-A3	– 31.16	0.537	489	225
		CF2-A1	– 30.15	0.500	747	
		CF2-A10	-24.06	0.533	714	
	L3-10	CF2-A19	– 36.46	0.500	154	
L4	L4-1	CF2-A1	– 23.1	0.560	747	
	L4-2	CF2-A20	– 20.06	0.500	1691	894
		CF2-A7	– 18.04	0.500	465	
		CF2-A10	– 17.71	0.500	713	
	L4-3	CF2-A3	– 33.52	0.500	493	294
		CF2-A10	– 26.64	0.500	713	
	L4-4	CF2-A7	– 30.04	0.500	465	
	L4-5	CF2-A12	– 26.78	0.500	838	770
		CF2-A21	– 26.5	0.500	96	
	L4-6	CF2-A12	– 28.92	0.560	838	770
		CF2-A21	– 28.64	0.550	96	
Forest fragment (FF1)						
L1	L1-1	FF1-A1	– 23.89	0.500	3215	
	L1-2	FF1-A2	– 30.19	0.514	989	
	L1-3	FF1-A3	– 34.8	0.489	441	
	L1-4	FF1-A1	– 25.56	0.444	3215	
	L1-5	FF1-A4	– 33.41	0.500	1035	
	L1-6	FF1-A5	– 27.52	0.457	3264	1818
		FF1-A6	– 35.14	0.500	1447	
	L1-7	FF1-A3	– 29.9	0.500	441	1467
		FF1-A7	– 29.67	0.500	3177	
		FF1-A4	– 31.03	0.463	1035	
		FF1-A8	– 27.89	0.500	1467	
	L1-8	FF1-A9	– 33.97	0.500	3164	
	L1-9	FF1-A10	– 24.41	0.513	865	
	L1-10	FF1-A11	– 30.4	0.500	781	644
		FF1-A12	– 27.7	0.386	1413	
	L1-11	FF1-A10	– 20.35	0.500	865	408
		FF1-A13	– 29.15	0.500	1411	
		FF1-A8	– 26.14	0.500	1466	
L2	L2-1	FF1-A14	– 29.29	0.500	927	
	L2-2	FF1-A10	– 30.06	0.500	843	
	L2-3	FF1-A11	– 28.63	0.500	759	2424
		FF1-A15	– 30.92	0.392	3183	
	L2-4	FF1-A1	– 21.99	0.500	3193	134
		FF1-A15	– 28.83	0.500	3183	
		FF1-A7	– 28.75	0.500	3155	
	L2-5	FF1-A16	– 30.73	0.509	934	98
		FF1-A17	– 33.97	0.500	894	
		FF1-A10	– 23.34	0.500	843	
	L2-6	FF1-A18	– 28.77	0.500	884	
		FF1-A1	– 22.09	0.500	3193	
		FF1-A8	– 27.91	0.500	1444	
	L2-7	FF1-A18	– 30.61	0.400	884	575
		FF1-A19	– 26.47	0.412	362	
	L2-8	FF1-A15	– 33.24	0.446	3183	87
		FF1-A7	– 31.65	0.500	3155	

Appendix 1. Continued.

Forest site/Latrine	Seed	Adult tree	LnL(R)	Relatedness (r)	POD	PPD
L3	L3-1	FF1-A20	– 39	0.411	421	
	L3-2	FF1-A21	– 28.65	0.546	117	2365
		FF1-A5	– 27.35	0.458	2475	
	L3-3	FF1-A18	– 37.33	0.443	121	2313
		FF1-A1	– 26.74	0.500	2430	
L4	L4-1	FF1-A19	– 26.27	0.500	2796	1731
		FF1-A15	– 30.33	0.500	238	
		FF1-A7	– 25.13	0.577	313	
		FF1-A22	– 29.5	0.500	1739	
		FF1-A8	– 27.5	0.500	1686	
	L4-2	FF1-A2	– 40.32	0.470	2175	
	L4-3	FF1-A1	– 27.65	0.500	135	1757
		FF1-A8	– 32.06	0.500	1686	
	L4-4	FF1-A22	– 31.36	0.500	1739	
	L4-5	FF1-A23	– 40.45	0.410	154	
Forest fragment (FF2)						
L1	L1-1	FF2-A1	– 23.95	0.500	381	38
		FF2-A2	– 29.46	0.520	416	
	L1-2	FF2-A3	– 29.57	0.518	401	
	L1-3	FF2-A4	– 26.31	0.410	412	4
		FF2-A2	– 23.48	0.500	416	
	L1-4	FF2-A3	– 29.89	0.529	401	178
		FF2-A5	– 33.32	0.500	272	
	L1-5	FF2-A3	– 24.13	0.454	401	326
		FF2-A6	– 28.62	0.500	280	
	L1-6	FF2-A7	– 25.49	0.500	371	61
		FF2-A8	– 23.34	0.500	366	
L2	L2-1	FF2-A9	– 31.21	0.500	15	
	L2-2	FF2-A3	– 34.14	0.500	36	
	L2-3	FF2-A7	– 27.29	0.445	118	
	L2-4	FF2-A5	– 30.51	0.560	171	105
		FF2-A7	– 24.63	0.551	118	
	L2-5	FF2-A10	– 34.8	0.500	133	
	L2-6	FF2-A11	– 35.25	0.573	44	42
		FF2-A8	– 27.15	0.501	57	
L3	L3-1	FF2-A4	– 26.88	0.500	41	27
		FF2-A12	– 32.8	0.500	43	
	L3-2	FF2-A13	– 33.83	0.500	411	
	L3-3	FF2-A7	– 25.55	0.500	159	28
		FF2-A14	– 41.76	0.501	143	
	L3-4	FF2-A15	– 30.2	0.500	121	78
		FF2-A3	– 27.17	0.589	55	
		FF2-A16	– 33.09	0.500	47	
		FF2-A17	– 30.35	0.528	61	
	L3-5	FF2-A18	– 38.76	0.500	73	
	L3-6	FF2-A19	– 34.03	0.500	60	191
		FF2-A20	– 30.63	0.500	208	
		FF2-A21	– 33.21	0.500	250	