



Original article

Genetic consequences of seed dispersal to sleeping trees by white-bellied spider monkeys

Jordan Karubian ^{a,*}, Kym Ottewell ^{a,b}, Andres Link ^c, Anthony Di Fiore ^d^a Department of Ecology and Evolutionary Biology, Tulane University, 400 Lindy Boggs Building, New Orleans, LA, 70118, USA^b Department of Environment and Conservation, 17 Dick Perry Avenue, Kensington, Western Australia, 6158, Australia^c Department of Biological Sciences and School of Management, Universidad de los Andes, Carrera 1 No. 18^a-12, Bogotá, Colombia^d Department of Anthropology, University of Texas, Speedway Stop C3200, Austin, TX, 78712, USA

ARTICLE INFO

Article history:

Received 14 February 2015

Received in revised form

26 June 2015

Accepted 31 July 2015

Available online 15 August 2015

Keywords:

Alpha diversity

Animal behavior

Arecaceae

Ateles belzebuth

Destination-based seed dispersal

Frugivory

Genetic structure

Maternal seed source diversity

Palm

Primate

Oenocarpus bataua

ABSTRACT

Frugivorous animals frequently generate clumped distributions of seeds away from source trees via 'destination-based' dispersal processes. For example, use of traditional sleeping trees by white-bellied spider monkeys *Ateles belzebuth* generates high densities of seeds of a preferred food source, the palm *Oenocarpus bataua*, at these sites. Little is known about the maternal seed source diversity and population genetic metrics of seed pools encountered at these sites. Given the repeated use of sleeping trees over time, and the fluid social organization and wide ranging movements exhibited by spider monkeys, we predicted that *O. bataua* seed pools beneath sleeping trees would be characterized by relatively high values of maternal seed source diversity and standard metrics of genetic diversity. Contrary to these expectations, we found relatively low average maternal seed source diversity beneath each of 6 sleeping trees we studied (weighted mean $\alpha = 3.74$), but considerable variation in diversity of maternal seed sources between sleeping trees (range = 1.75–10.1) and high heterogeneity in standard genetic diversity measures between sleeping trees. There was no evidence for overlap in maternal seed sources between sleeping tree sites ($\delta = 1.0$), resulting in significant genetic differentiation ($F_{st} = 0.055\text{--}0.319$) between these sites. Observed variation between sleeping trees could not be explained by the number of individual spider monkeys whose core home ranges included a given tree, nor by distance to a central mineral lick, a focal point of spider monkey activity. These findings suggest that spider monkey seed dispersal to sleeping trees is spatially restricted, perhaps because the animals visit sleeping trees at the end of the day and therefore only disperse *O. bataua* fruits that they ingest late in the day. These results add to our growing appreciation of the ways frugivore behavior mechanistically shapes seed dispersal outcomes.

© 2015 Elsevier Masson SAS. All rights reserved.

1. Introduction

Seed dispersal is a widespread ecological process known to influence plant population dynamics and plant community structure and dynamics (Schupp et al., 2010; Wang and Smith, 2002). Seed dispersal determines the deposition site of plant propagules and sets the initial template for the recruitment of seedlings and saplings. Thus, seed dispersal largely determines the spatial distribution of seeds and influences the probability of seeds reaching the seedling stage while being exposed to density dependent processes and other stochastic effects (Howe and Miriti, 2004; Russo et al.,

2006). Seed dispersal also plays a crucial role in shaping patterns of genetic structure and diversity within and among plant populations because it moves both male and female gametic genomes from the source tree to the seed's final location and influences which seeds will reach the seedling stage (Garcia and Grivet, 2011). In many habitats, particularly tropical rainforest, vertebrate animals are prominent seed dispersal vectors (Herrera, 2002). The behavior and movement of frugivorous animals therefore has important ecological and evolutionary consequences for the plant species that they disperse (Russo et al., 2006; Galetti et al., 2013). For these reasons, a better understanding of plant-animal dispersal mutualisms is a long-standing goal among evolutionary ecologists and conservation biologists (e.g., Dirzo et al., 2014; Sica et al., 2014; Caughlin et al., 2015).

* Corresponding author.

E-mail address: jk@tulane.edu (J. Karubian).

Vertebrate dispersal agents often engage in 'destination-based' dispersal by repeatedly using specific locations for behaviors like rest, sleep, caching, or display, which over time leads to high densities of dispersed seeds in these areas (Schupp et al., 2010). The demographic and ecological consequences of destination-based dispersal have received extensive attention (e.g., Wenny and Levey, 1998; Russo and Augspurger, 2004), but the genetic consequences remain poorly understood (Karubian and Durães, 2009). Destination-based seed dispersal by vertebrates might be expected to impact genetic characteristics of plant populations at both local and landscape scales (Herrera, 2002; Sork and Smouse, 2006). At the local scale, the diversity of maternal source trees that contribute to these clumped patches of seeds, as well as cumulative metrics of genetic diversity at these sites, are both likely to have important consequences for localized patterns of genetic structure of recruiting individuals (Bialozyt et al., 2014). At larger spatial scales, long-distance seed dispersal by vertebrates may increase degree of overlap in maternal seed sources between distinct pools of seedlings (Sork and Smouse, 2006). Resolving the degree of maternal seed source sharing within and between destination-based dispersal sites and exploring how this relates to standard population genetic metrics represents an important step toward understanding the genetic consequences of vertebrate seed dispersal.

One fruitful approach to resolving this issue is to use molecular markers to assess seed source diversity and genetic diversity among pools of dispersed seeds that can be linked to specific a dispersal vector or behavior (Jordano et al., 2007). While few in number, such studies suggest that destination-based dispersal may yield dramatically different outcomes across systems. For example, lekking behavior by frugivorous long-wattled umbrellabirds *Cephalopterus penduliger* results in high maternal seed source diversity and reduced fine-scale genetic structure for a preferred food source, the palm *Oenocarpus bataua*, at lek sites (Karubian et al., 2010; Scofield et al., 2012). In contrast, defense of exclusive foraging territories by small groups of acorn woodpeckers *Melanerpes formicivorus* results in much lower maternal seed source diversity for acorns of the valley oak *Quercus lobata* and coast live oak *Quercus agrifolia* in granaries where the acorns are cached (Grivet et al., 2005; Scofield et al., 2010, 2012). There is little overlap among seed sources represented in granaries of different acorn woodpecker groups, despite the fact that some long distance seed dispersal occurs (Thompson et al., 2014), whereas extensive movement by 'floater' umbrellabird males (Karubian et al., 2012; Karubian and Durães, 2014) contributes to moderate seed source overlap between umbrellabird leks (J. Karubian & K. Ottewell, unpublished data). These variable outcomes raise the question of how seed source diversity and genetic structure might be affected by foraging or social behaviors in other plant-animal seed dispersal mutualisms.

Like the aforementioned bird species, white-bellied spider monkeys *Ateles belzebuth* are capable of long-distance seed dispersal (Link and Di Fiore, 2006), and they engage in destination-based dispersal, in this case to sleeping trees (below). Like umbrellabirds, spider monkeys are a dominant dispersal agent of *O. bataua* (Link and de Luna, 2004). However, spider monkey social organization and ranging behaviors are distinctive, as are their usage patterns of sleeping trees. Spider monkeys live in multi-male multi-female groups (15–30 individuals) that defend large (ca. 400 ha) territories from neighboring groups and exhibit a high degree of fission fusion dynamics (Aureli et al., 2008). Sleeping trees are distributed throughout the group's territory, and individual spider monkeys often begin and end their activities in one of a set of repeatedly used sleeping trees, thus behaving as Multiple Central Place Foragers (Chapman et al., 1989). Unlike umbrellabird dispersal into lek sites, which occurs through out the day, dispersal

to sleeping trees occurs only between the end of the day, when the animals arrive at these sites to sleep, and the following morning, when they move off to begin the day's foraging.

In this study, we explore how repeated use of specific sleeping trees by white-bellied spider monkeys may impact seed source diversity, genetic diversity, and genetic structure of *O. bataua*, both within and among sleeping trees. Given the repeated use of multiple sleeping trees over time, and the fluid social organization and wide ranging movements exhibited by spider monkeys, we predicted that *O. bataua* seed pools at sleeping trees would be characterized by relatively high maternal seed source diversity and standard metrics of genetic diversity, equivalent to those recorded at umbrellabird leks and considerably higher than those found at acorn woodpecker granaries. These same factors also led us to predict that there would be moderate to high levels of overlap in maternal seed sources of *O. bataua* between different sleeping trees, resulting in low genetic structure for *O. bataua* at the landscape level. We also expected that sleeping trees located close to a mineral lick used regularly by all group members, and in other areas where the core home ranges of many group members also overlap, would exhibit the highest levels of seed source diversity and overlap. An alternative, post-hoc hypothesis is that dispersal to sleeping trees may be dominated by seeds ingested late in the day, yielding relatively low maternal seed source diversity beneath sleeping trees, little or no overlap of maternal seed sources between sleeping trees, and limited impact of variation in the number of group members using the trees.

2. Methods

2.1. Study location and species description

2.1.1. Study location

Fieldwork was conducted at the Tiputini Biodiversity Station (hereafter TBS; 76°10' W, 0°37' S; 190–270 m elevation; 2.74 m rain/yr; Karubian et al., 2005), located on the border of the 999,000 ha Yasuní Biosphere Reserve, eastern Ecuador. TBS covers ~650 ha of primary terra firme rain forest dissected by several permanent streams.

2.1.2. *O. bataua*

The canopy palm *O. bataua* is common at TBS and is widely distributed throughout Neotropical rain forest on both sides of the Andes in South America (Henderson et al., 1995; ter Steege et al., 2013). It is a long-lived, slow-growing monoecious species that produces inflorescences of thousands of small flowers, and is effectively outcrossed (Ottewell et al., 2012). Fertilized flowers develop large-seeded, lipid-rich fruits (up to 2000 fruits per infructescence) available for 4–8 weeks that are consumed by a range of large-bodied vertebrates, including birds, primates and humans (Goulding and Smith, 2007; Rojas-Robles and Stiles, 2009).

2.1.3. Spider monkeys

The white-bellied spider monkey *A. belzebuth* is an important seed dispersal agent for *O. bataua* at TBS in western Amazonia (Link and Di Fiore, 2006; Link and de Luna, 2004). *A. belzebuth* (approximately 9 kg) is the largest of 10 primate species found in the study area. Strier (1992) proposed that *Ateles* optimize foraging by visiting large fruiting trees and feeding on large quantities of fruits at these trees. Given that they swallow the seeds of more than 95% of the fruits they consume, these feeding bouts are typically followed by long resting periods. Defecation rates (and thus the liberation of weight) increase significantly a few minutes before beginning to travel towards the next large feeding resource (Link and Di Fiore, 2006). White-bellied spider monkeys eat fruits from

a large number of plant species, but consume *O. bataua* fruits in large quantities whenever ripe fruits of that species are available. At a different study site, a single individual white-bellied spider monkey was observed eating 90 fruits in a single foraging bout (>15% of their mass; Link and de Luna, 2004), and spider monkeys can remove the majority of available ripe *O. bataua* fruits from any given tree (A. Di Fiore and A. Link, pers. obs.). Other potential dispersal agents for *O. bataua* at this site include toucans (Ramphastidae), oilbirds (*Steatornis caripensis*), and terrestrial mammals. Long-wattled umbrellabirds are absent from TBS.

Spider monkeys have relatively fast gut retention times relative to body size, averaging $4.5 \text{ h} \pm 1.5 \text{ h}$ (SD), and are capable of providing long-distance dispersal to seeds, with maximum estimated dispersal distances of 1250 m (Link and Di Fiore, 2006). Link and Di Fiore (2006) also showed that spider monkeys deposit at least 12% of the seeds they ingest beneath sleeping trees where they spend the night, a value that is likely to be an under-estimate because observers could not fully account for seeds deposited during the night and twilight hours. Individual sleeping trees are used repeatedly by spider monkeys (but not by other primates), leading to high concentrations of dispersed seeds beneath them that are likely to be the direct result of spider monkey sleeping behavior (Russo and Augspurger, 2004). This allows us to link spider monkey use of sleeping trees with the seed dispersal outcomes that this behavior generates. In their fission-fusion social system, females maintain relatively small but overlapping core home ranges that occupy different portions of the entire group's territory, while adult males move freely across the entire territory (Spehar et al., 2010). Use of a given sleeping tree is typically dominated by 2–3 females whose core home range it falls within, with less frequent usage by males and other females whose core home ranges are further away (A. Di Fiore & A. Link unpublished data).

2.2. Sample collection, laboratory methods, & genetic analysis

We collected samples of pericarp tissue from seeds attached to established *O. bataua* seedlings in a single sampling bout in June–August 2010. Samples were collected from beneath the canopies of each of 6 sleeping trees actively used by spider monkeys (Fig. 1). The average pairwise distance between sleeping trees we sampled was 1157 m (range = 507–2289 m), and each was located at least 15 m away from the nearest *O. bataua* tree (the locations of *O. bataua* adults, i.e., source trees, are not yet mapped at the study site). It is worth emphasizing that, as was the case in Karubian et al.'s (2010) study of umbrellabird dispersal, these analyses were conducted on seeds that were attached to established seedlings that had already passed through the transition from seed to seedling, as opposed to primary seed rain. For this reason, the present study assesses consequences of 'effective' seed dispersal (i.e., seedlings that have successfully recruited into the population), not primary seed rain. Viable *O. bataua* seeds germinate within 1–2 months of dispersal, and the seed remains attached to the growing seedling for up to 24 months (Karubian et al., 2010; J. Karubian, unpublished data). We can therefore infer that the seeds we collected had been dispersed some time between mid-2008 and sample collection. Seeds were sampled by removing a portion of the fibrous outer covering (pericarp), which was then silica-dried and stored for subsequent use in DNA extractions.

2.2.1. Laboratory methods

Genomic DNA was extracted from pericarp material by grinding samples with tungsten beads and using the Qiagen 96 Plant kit (Qiagen, California USA) following the manufacturer's instructions. We amplified samples for 10 microsatellite loci (excluding Ob 04) using PCR and genotyping conditions described in Ottewell et al.

(2012). The combined probability of identity using this 10-locus dataset was 3.49×10^{-12} and the probability of two unrelated individuals having the same multilocus genotype was 6.06×10^{-10} , demonstrating a high level of discrimination between individual genotypes.

2.2.2. Seed source diversity

We were able to unambiguously differentiate source trees for each of the *O. bataua* seeds because the pericarp is derived solely from maternal tissue, as opposed to the diploid embryo genotype. This fact allows us to identify the genotype of the maternal source tree for each seedling, without directly sampling the maternal source tree (Godoy and Jordano, 2001). We estimated maternal seed source diversity within and between sleeping trees using a newly developed analytical method that extends Grivet et al.'s (2005) probability of maternal identity (PMI) framework for seed source diversity by making it directly comparable to classic estimators of ecological diversity (Scofield et al., 2012). Scofield et al.'s (2012) approach presents alpha, omega, and gamma diversity estimators that are equivalent to these familiar estimators of species diversity (Whittaker, 1960, 1972), except in this case they estimate the diversity of maternal seed sources represented within and between seedling pools. A benefit of this approach is that it allows insights into seed movement and seed source diversity without the need to explicitly identify or genotype maternal source trees. Another benefit is that this method was also applied to studies on umbrellabirds and acorn woodpeckers (Scofield et al., 2012), facilitating comparison between spider monkeys and these systems.

We estimated maternal seed source alpha (α) diversity (the effective number of maternal seed sources represented under each sleeping tree; raw and sample-size weighted), omega (δ) diversity (the degree of divergence between seed pools beneath different trees, a measure qualitatively similar to beta (β) diversity; see Scofield et al., 2012) and gamma (γ) diversity (the effective number of maternal seed sources contributing to the entire collection of seeds across sleeping tree sites) using the formulas in Scofield et al., 2012 and implemented in the R routine pmiDiversity.R available at <https://github.com/douglasgscfield/dispersal>. We tested for homogeneity in the number of seed sources (α diversity) between individual sleeping trees using Bartlett's test for heteroscedasticity in intra-group variances (see Scofield et al., 2012). We also tested for significant variation in total seed source diversity (γ diversity) to understand the landscape scale outcomes of dispersal. In each case we calculated the test statistic T , which has a chi-square distribution. To test for significance we compared observed T against a null distribution calculated from 10000 randomizations. Tests were also performed using diversityTests.R (<https://github.com/douglasgscfield/dispersal>).

2.2.3. Population genetic summary statistics

We calculated standard population genetic parameters in GENALEX v6.501 (Peakall and Smouse, 2006, 2012), including the number of alleles (N_a), number of effective alleles (N_e), observed heterozygosity (H_o), expected heterozygosity (H_e) and Wright's inbreeding coefficient (F_{is}). We used rarefaction to estimate allelic richness (A_R) standardized for sample size using HP-RARE (Kalinowski, 2005). We standardized A_R to the smallest sample size among the set of sleeping trees (Guacamayo 1375, $n = 14$). We tested for significant differences in genetic diversity parameters using ANOVA and Tukey's HSD post-hoc tests in R v3.0.2 (R Core Team, 2014).

2.2.4. Genetic differentiation between sleeping trees

We estimated all pairwise genetic differentiation between sleeping tree sites using two descriptors, F_{ST} and D_{est} , in GENALEX.

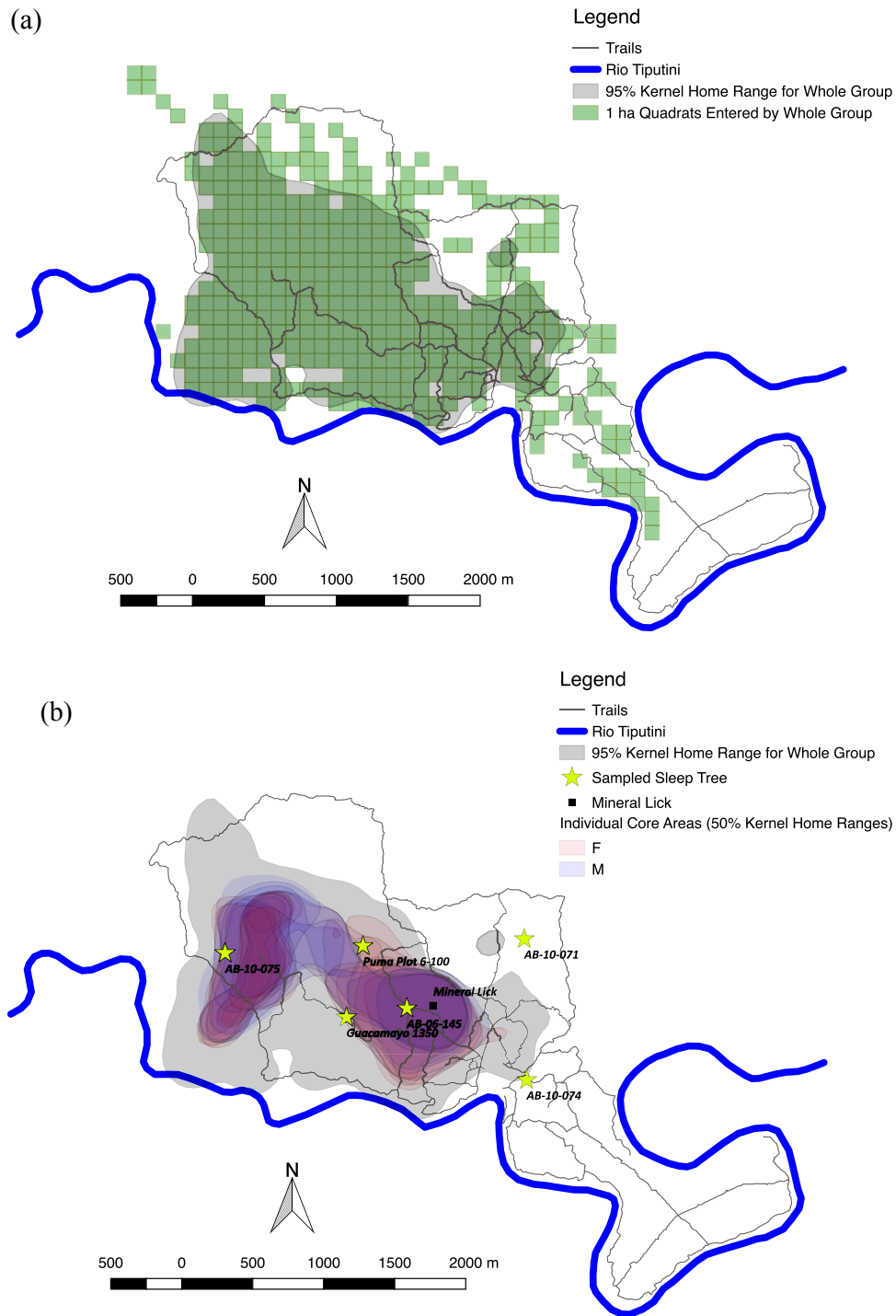


Fig. 1. Map of the study area, Tiputini Biodiversity Station in eastern Ecuador. In both maps, location of each of the 6 sampled sleeping trees is denoted by a star, and the cumulative 95% home range kernel for the entire focal study group of white-bellied spider monkeys (MQ-1) is shaded gray. Panel (a) depicts each 1 ha quadrat in which the group was recorded, and panel (b) depicts the core areas (50% kernel density ranges) for each of the 16 adults in the group.

The significance of the observed F_{ST} and D_{est} values was assessed using permutation testing (999 permutations). As trends in genetic differentiation between sleeping trees were consistent between our two estimators, we performed the following two analyses using F_{ST} as this statistic tends to be more commonly reported. First, we used F_{ST} to derive the average number of migrants per generation (N_m) in GENALEX. Second, we used F_{ST} to test for an isolation by distance effect using Mantel tests of linearized genetic distance (1-

F_{ST}/F_{ST}) and geographic distance between sites (in kilometers) in GENALEX. Spatial autocorrelation analysis was performed on individual seed maternal genotypes using geographic coordinates of each individual seedling in the program SPAGED1 v1.2 (Hardy and Vekemans, 2002). The analysis was performed using the kinship coefficient (F_{ij}) of Loiselle et al. (1995) and distance classes with equal numbers of pairwise comparisons. Spatial locations were permuted 10,000 times to obtain error estimates of the null

hypothesis ($F_{ij} = 0$), and error estimates of the observed kinship values amongst adult trees were calculated by jackknifing over loci 1000 times. The strength of spatial genetic structure was assessed using the S_p statistic of [Vekemans and Hardy \(2004\)](#), calculated as $-b_{F_{log}}/(1-F_1)$ where $b_{F_{log}}$ is the mean slope of the regression of kinship coefficients on \log_{10} distance and F_1 is the mean kinship coefficient of the first distance class.

2.3. Spider monkey home range estimates

The two principal spider monkey study groups at TBS (MQ-1 & MQ-2) comprise roughly 15–20 adult individuals each and utilize adjacent but minimally overlapping home ranges of approximately 400 ha each. All sleeping trees included in the current study fall within the habitual home range of group MQ-1, which consisted of 16 adult individuals (6 males, 10 females) for the bulk of the four-year period preceding sample collection from the field (i.e., 2006–2010). Spider monkeys exhibit a high-degree of fission-fusion dynamics ([Aureli et al., 2008](#)) in which subgroups frequently change their size and composition. Females tend to use more intensively smaller areas within the group's home range, while males use the total home range more evenly while monitoring the reproductive status of the group's females and patrolling the borders of the group's range (A. Link & A. Di Fiore unpublished data). From 2006 to 2010, researchers conducted dawn to dusk behavioral follows using focal animal sampling ([Altmann, 1974](#)) on all adult group members of group MQ-1 and obtained georeferenced location data at 15 min intervals throughout the day. Home ranges were calculated for each individual using locations collected either during focal behavioral sampling on that individual, or when that individual was in a subgroup traveling together with different individual that was being sampled. These locations were visualized in QGIS ([QGIS Development Team, 2015](#)), and home ranges for each individual member of group MQ-1 were estimated as 95% and 50% kernels ([Worton, 1989](#)) using the *kernelUD* function from the R package *adehabitatHR* version 0.4.13 (<http://cran.r-project.org/web/packages/adehabitatHR/index.html>) on a grid size of 200 m, assuming a bivariate normal utilization distribution, with the smoothing parameter, h , estimated by the default *ad hoc* method. We used this information to determine the number of individual 50% kernel density ranges (i.e., “core area”) and 95% kernel density ranges (i.e., “individual home ranges”) that included each sleeping tree. We also calculated the distance from each sleeping tree to a single mineral lick, which is a ‘hotspot’ of spider monkey activity that we predicted might be associated with higher levels of seed source diversity at nearby sleeping trees because it attracts individuals from through out the group's home range ([Link et al., 2011](#)).

3. Results

3.1. Diversity within sleeping tree sites

We detected a sample-size weighted average of 3.74 maternal seed sources (α_r) represented in *O. bataua* seedlings beneath each spider monkey sleeping tree, with considerable variation in this metric between individual sleeping trees (unweighted $\alpha_r \approx N_{em} = 1.8–10.1$; [Table 1](#)). A non-parametric test for homogeneity of variance showed there was highly significant variation in observed alpha diversity of maternal seed sources among sleeping trees ($T_\alpha = 6.628$, $P = 0.0001$). Low diversity sleeping trees (e.g., AB-06-145, AB-10-075) were dominated by seeds from a single source *O. bataua* tree, whereas other trees had more even representation of seed sources ([Fig. 2a](#)).

Similarly, there was significant variability in traditional

measures of genetic diversity among seed pools beneath sleeping trees, with expected heterozygosity (H_e) ranging from 0.53 to 0.74 and mean allelic richness (AR) from 3.5 to 6.2 alleles per locus ([Table 2](#)). As with α diversity of maternal genotypes, both H_e and AR were significantly differentiated between sleeping trees ($H_e F_{5,54} = 6.37$, $p < 0.001$; $AR F_{5,54} = 5.98$, $p < 0.001$). Allelic richness was highly correlated with α diversity of maternal genotypes detected beneath sleeping trees ($r^2 = 0.93$), with the most diverse sleeping tree sites (Guacamayo 1375, Puma Plot 6) having the highest number of effective maternal sources ($N_{em} = 10.1$ each). Expected heterozygosity displayed a similar, but less consistent trend ($r^2 = 0.73$).

3.2. Genetic differentiation amongst sleeping trees

We found complete divergence (i.e., no overlap) of *O. bataua* maternal genotypes between sleeping tree sites ($\delta_r = 1.0$), indicating that pools of dispersed *O. bataua* seeds encountered beneath different sleeping trees are sourced wholly from distinct suites of adult *O. bataua* fruiting adults, with no sharing of seeds from the same source trees among different sleeping trees. This pattern leads to a linear increase in gamma diversity (γ_r) with the inclusion of each new sleeping tree ([Fig. 2b](#)), yielding a cumulative gamma diversity value of 20.9 maternal seed sources at the site scale.

Congruent with this limited overlap in maternal seed sources, we found significant genetic structuring amongst pools of seeds found beneath sleeping trees. We detected significant genetic differentiation (F_{ST}) between seed deposition sites, ranging from 0.055 to 0.319 (mean $F_{ST} = 0.167$, $P = 0.010$; equivalent to $N_m = 1.25$; [Table 3](#)); D_{est} exhibited a qualitatively similar pattern (mean $D_{est} = 0.410$, range = 0.192–0.611). However, there was no apparent isolation by distance effect between sleeping trees ($r = 0.179$, slope = 0.00004, $P = 0.280$) and spatial autocorrelation analysis showed no relationship of genetic relatedness amongst individuals at larger spatial distances (e.g. 500 m–2.2 km; results not shown). Overall, spatial genetic structure at the landscape level was high ($S_p = 0.403$).

3.3. Spider monkey home ranges

Among females, the average core area size was 64.87 ha (50% kernels) and the average home range size was 294.28 ha (95% kernels); equivalent measures for males were 96.84 ha and 416.4 ha, respectively ([Fig. 1](#)). The average number of individual spider monkeys whose 50% kernel core areas included a given sleeping tree was $4.0 \pm SE 2.0$ (range: 0–12), while the equivalent measure for 95% kernel home ranges was $11.0 \pm SE 5.6$ (range: 0–16) ([Table 1](#)). There was no relationship between either the number of core areas or individual home ranges that included a given sleeping tree and the maternal seed source diversity at that tree (core areas: $r^2 = 0.51$, $P = 0.10$; individual home ranges: $r^2 = 0.05$, $P = 0.33$). Indeed, the non-significant trend for the core areas (50% kernels) was negative (i.e., highest levels of maternal seed source diversity were associated with lowest number of overlapping home ranges), rather than the positive relationship we had predicted. Qualitatively similar results were obtained for analyses repeated with males and females separately (results not shown). The average distance from the sleeping trees to the mineral lick was $766 \pm SE 177$ m (range 186–1509 m), and there was no relationship between distance to mineral lick and maternal seed source diversity ($r^2 = 0.04$, $P = 0.70$).

4. Discussion

This study focused on a tight mutualism between the large-

Table 1

The maternal seed source diversity represented among pools of *Oenocarpus bataua* seeds (attached to established seedlings) beneath each of six white-bellied spider monkey sleeping trees in Tiputini Biodiversity Station, western Amazonia. Also shown is the number of individual spider monkey home ranges that include each sleeping tree. The table's first three rows summarize *O. bataua* maternal seed source diversity beneath each of the six focal sleeping trees (n_{seeds} = number of seeds per pool, n_{sources} = total number of individual source maternal trees identified per seed pool, α_r = number of effective mothers per seed pool). The bottom four rows show the number of individual spider monkeys whose 95% kernel and 50% kernel (in parentheses) home ranges include each sleeping tree, and the distance of each sleeping tree to a highly visited mineral lick. There is no relationship between number of home ranges including a given sleeping tree or distance of a tree to mineral lick with maternal seed source diversity.

	AB-06-145	AB-10-071	AB-10-074	AB-10-075	Guacamayo-1375	Puma plot-6-100	Site
n_{seeds}	33	32	41	24	14	30	174
n_{sources}	8	13	14	8	8	18	69
α_r (Ne_m)	1.75	6.99	5.00	2.03	10.11	10.12	3.74
Males # overlap 95% (50%) kernel	6 (6)	4 (0)	2 (0)	6 (4)	6 (0)	6 (0)	
Females # overlap 95% (50%) kernel	10 (6)	0 (0)	2 (0)	10 (4)	8 (1)	6 (3)	
Total # overlap 95% (50%) kernel	16 (12)	4 (0)	4 (0)	16 (8)	14 (1)	12 (3)	
Dist. mineral lick (m)	186	796	842	1509	615	649	

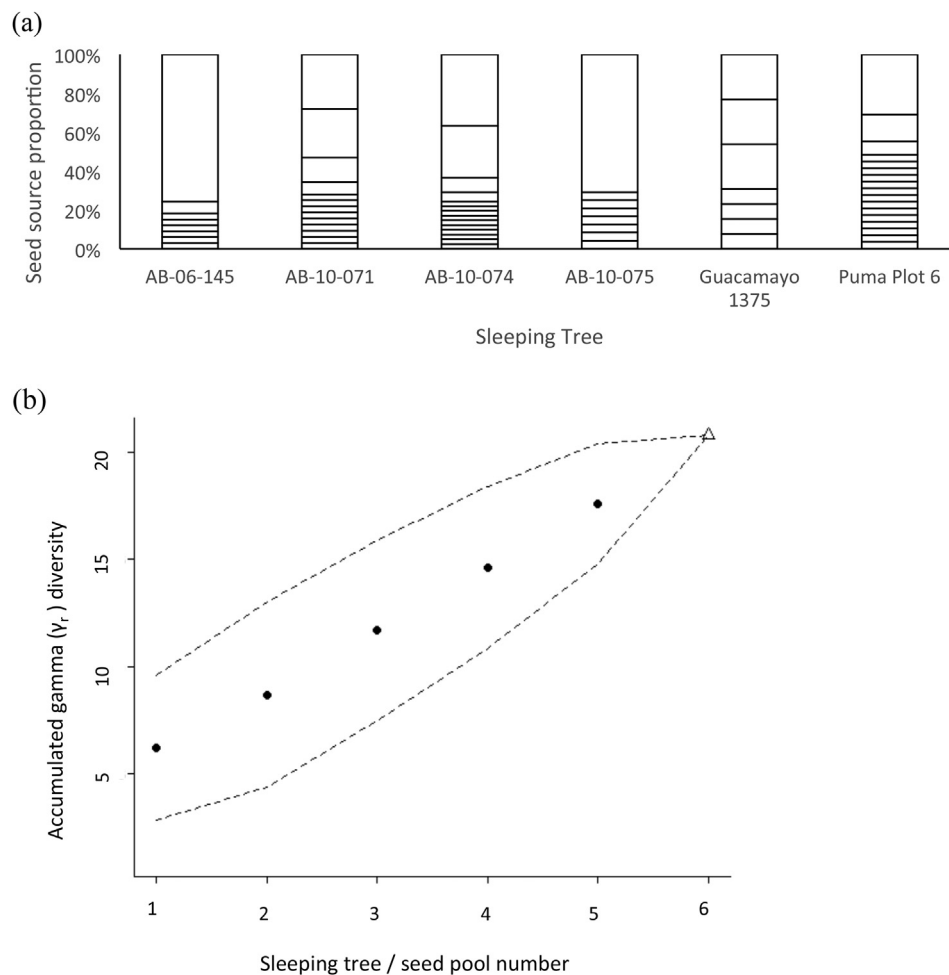


Fig. 2. White bellied spider monkeys *Ateles belzebuth* disperse seeds beneath repeatedly used sleeping trees. For seeds of the palm *Oenocarpus bataua*, this behavior generates varying, but relatively low, levels of maternal seed source diversity beneath individual sleeping trees and no evidence of seed source sharing between different sleeping trees. Panel (a) shows the relative representation of different *O. bataua* maternal seed sources encountered beneath the canopies of 6 individual sleeping trees. Each white bar represents the relative frequency of a seed source unique to that plot/sleeping tree because there was no overlap in seed sources between sleeping trees. Panel (b) shows linear accumulation of gamma diversity at the site level with the addition of each new sleeping tree.

seeded canopy palm *O. bataua* and its principal seed dispersal agent at our western Amazonian study site, the white-bellied spider monkey *A. belzebuth*. Spider monkeys are characterized by the capacity for long-distance seed dispersal, fission-fusion social organization that leads to distinctive home ranges among members of the same group, and destination-based seed dispersal to repeatedly used sleeping trees (Link and Di Fiore, 2006; Aureli et al., 2008).

These factors led us to predict that spider monkey sleeping trees would have highly diverse seed pools with moderate overlap in seed sources among sleeping trees. Instead, we found low to moderate amounts of seed source diversity among *O. bataua* seedlings encountered beneath sleeping trees, and no evidence for overlap of maternal seed sources between sleeping trees separated by approximately 1 km, resulting in significant genetic structure at

Table 2
Genetic diversity summary statistics for *Oenocarpus bataua* seeds (attached to established seedlings) collected beneath White-bellied Spider Monkey sleeping trees in Tiputini Biodiversity Station. N_a = number of alleles, N_e = number of effective alleles, H_o = observed heterozygosity, H_e = expected heterozygosity, F_{is} = inbreeding coefficient, A_R = allelic richness rarefied to $n = 14$ (smallest sample size). Superscripts refer to significantly different groups determined by Tukey's HSD post-hoc test ($p < 0.05$) following ANOVA (i.e., trees denoted by an 'a' or 'b' are statistically different from each other for a given measure).

Location/Site	N	N_a	N_e	H_o	H_e	F_{is}	A_R
AB-06-145	33	5.7 ± 0.40 ^{a,b}	2.3 ± 0.22 ^a	0.64 ± 0.12	0.53 ± 0.06 ^a	-0.10 ± 0.17 ^{a,b}	4.2 ± 0.26 ^a
AB-10-071	32	6.6 ± 0.76 ^a	3.8 ± 0.46 ^b	0.51 ± 0.05	0.68 ± 0.06 ^b	0.25 ± 0.04 ^{a,b}	5.5 ± 0.62 ^b
AB-10-074	41	5.9 ± 0.43 ^{a,b}	3.7 ± 0.16 ^b	0.65 ± 0.06	0.73 ± 0.01 ^b	0.11 ± 0.08 ^{a,b}	5.0 ± 0.23 ^b
AB-10-075	24	3.9 ± 0.31 ^b	2.3 ± 0.17 ^a	0.72 ± 0.11	0.53 ± 0.05 ^a	-0.24 ± 0.17 ^a	3.5 ± 0.22 ^a
Guacamayo 1375	14	6.0 ± 0.58 ^{a,b}	4.3 ± 0.49 ^b	0.68 ± 0.07	0.74 ± 0.03 ^b	0.06 ± 0.11 ^{a,b}	6.0 ± 0.58 ^b
Puma Plot 6	30	7.2 ± 0.61 ^a	3.7 ± 0.29 ^b	0.48 ± 0.06	0.71 ± 0.03 ^b	0.33 ± 0.08 ^b	6.2 ± 0.47 ^b
Mean across sleep trees		5.9 ± 0.25	3.4 ± 0.16	0.61 ± 0.03	0.65 ± 0.02	0.07 ± 0.05	5.1 ± 0.47
Total (cumulative)	174	9.9 ± 0.64	4.9 ± 0.44	0.61 ± 0.04	0.78 ± 0.02	0.23 ± 0.05	–

Table 3
Pairwise F_{ST} and D_{est} (in italics) (below diagonal) and geographic distance in meters (above diagonal) between sampled spider monkey sleeping trees at the Tiputini Biodiversity Station. All pairwise F_{ST} comparisons were significant at $P < 0.01$ determined by permutation testing; D_{est} showed qualitatively similar results.

	AB-06-145	AB-10-071	AB-10-074	AB-10-075	Guacamayo 1375	Puma plot 6
AB-06-145	–	959	989	1317	421	549
AB-10-071	0.231 <i>0.518</i>	–	980	2094	1358	1156
AB-10-074	0.212 <i>0.522</i>	0.087 <i>0.272</i>	–	2290	1346	1508
AB-10-075	0.319 <i>0.611</i>	0.221 <i>0.541</i>	0.211 <i>0.554</i>	–	950	939
Guacamayo 1375	0.194 <i>0.461</i>	0.066 <i>0.223</i>	0.089 <i>0.307</i>	0.175 <i>0.392</i>	–	507
Puma Plot 6	0.175 <i>0.392</i>	0.101 <i>0.308</i>	0.080 <i>0.271</i>	0.226 <i>0.583</i>	0.055 <i>0.192</i>	–

this scale. Also, there was no association between the number of spider monkeys whose home ranges encompassed a given sleeping tree and maternal source diversity of the seeds dispersed beneath that tree. These findings contradict our initial predictions, and indicate that the spatial scale of seed dispersal by spider monkeys to sleeping trees may be spatially restricted, leading to relatively homogenous seed pools at these sites that may end up increasing fine-scale and landscape genetic structure over the long term.

An alternative, post-hoc hypothesis proposes that these results may be attributable to the behavior and ranging patterns of spider monkeys, and in particular to their daily patterns of sleeping tree usage. As is the case with many primate species, spider monkeys repeatedly return to specific sites for the purposes of sleeping, resting, or other behaviors (e.g., Julliot, 1997; Muñoz Lazo et al., 2011; Rogers et al., 1998) and as a consequence of this and other behaviors, dispersal services may vary in relation to the time of day that the seed was ingested (e.g., Stevenson et al., 2014). This Multiple Central Place Foraging (Chapman et al., 1989) system may cause spider monkeys to concentrate a significant proportion of dispersed seeds into discrete areas throughout their territory. Gut retention time for spider monkeys is relatively fast relative to body size (Link and Di Fiore, 2006), and they have long feeding bouts at *O. bataua*, with one individual ingesting as many as 98 fruits during a single foraging episode on a single fruiting adult (Link and de Luna, 2004). This foraging behavior leads to a significant addition of seed mass that might impede movement, and also requires substantial retention times in order to break apart the outer surface of the seed and digest the nutrient-rich pulp. In fact, a substantial proportion of ingested *O. bataua* seeds is dispersed whole (seed, pulp and husk) suggesting that digestion may represent a substantial energetic cost (A. Link unpub. data).

These observations lead us to propose that spider monkeys may be feeding on multiple fruits from *O. bataua* palms located relatively close to sleeping trees at the end of the day and then

dispersing those seeds beneath sleeping trees during the night. Spider monkeys may bias consumption of *O. bataua* fruits to the late hours of the day in order to increase nutrient assimilation (Chapman and Chapman, 1991), or simply because the mass and volume of several large *O. bataua* seeds may impede movement or increase predation risk during the day. The wide variation in α diversity we observed between sleeping trees might be due to the number of adult *O. bataua* trees in close proximity to each sleeping tree, leading to a higher diversity of seed sources beneath sleeping trees with many *O. bataua* trees nearby relative to those sleeping trees with fewer *O. bataua* trees nearby. Similarly, the temporal usage pattern of nearby *O. bataua* trees described above may swamp any effects associated with differing numbers of animals using the trees, though it is also possible that the home range estimates we used are poor indicators of the actual usage patterns at each sleeping tree. These ideas remain speculative at present because adult *O. bataua* are not mapped in our study area at TBS, but they do provide a clear set of predictions to be addressed in future studies.

The current study is one of the few to simultaneously present results on diversity of seed sources and more traditional population genetic indices in a single study. We found that the two indices corroborate each other reasonably well at both local and landscape levels. Both α diversity and standard population genetic measures like allelic richness and heterozygosity revealed qualitatively similar patterns beneath sleeping trees, though variation among sleeping trees was greater for α diversity than for standard population genetic measures. Among sleeping trees, δ diversity and F_{ST} also followed qualitatively similar patterns, both indicating very low levels of overlap. The value for genetic structure that we obtained ($Sp = 0.43$) is at the high end among adult trees of 10 tropical species reported by Hardy et al. (2006), especially among those that are primate-dispersed. However, it is important to note that our study was conducted on *O. bataua* seedlings, and that structure

among subsequent life stages up to and including adults is likely to be considerably lower (Ottewell et al., 2012; Berens et al., 2013).

The core analytical approach used here adapts classic indices of ecological diversity to characterize maternal seed source diversity in pools of seeds. Scofield et al. (2012) recently developed and deployed this approach to examine destination-based seed dispersal by long-wattled umbrellabirds in western Ecuador and acorn woodpeckers in California, facilitating comparison with the spider monkey system. We had predicted that levels of seed source mixing due to spider monkey dispersal would be equivalent to that of *O. bataua* seedlings dispersed by umbrellabirds, and well above that of *Quercus* acorns cached by acorn woodpeckers. We reasoned that active defense of territories that usually contain <3 source trees by acorn woodpeckers would lead to lower levels of seed source diversity in granaries, while the wide ranging movements and central place foraging behaviors exhibited by both spider monkeys and male umbrellabirds would lead to equivalent levels of seed source diversity at sleeping trees and leks. In reality, however, sample-size weighted α diversity of seedlings under spider monkey sleeping trees (3.74) was similar to that of acorn woodpecker granaries (2.57 ± 0.4) and well below that of umbrellabird leks (25.9 ± 6.9) (Scofield et al., 2012). We did not measure seed source diversity at 'random' plots away from sleeping trees in the current study – an acknowledged shortcoming – but at the umbrellabird study site in western Ecuador, α diversity at random plots away from lek sites was 21.3 ± 6.4 , also considerably higher than the values obtained beneath spider monkey sleeping trees. Also, the zero overlap in seed sources between pairs of spider monkey sleeping trees more closely resembles the very low overlap values observed among acorn woodpecker granaries (Grivet et al., 2005) than the moderate levels observed among umbrellabird leks (J. Karubian & K. Ottewell, unpublished data).

Although on the surface, our results indicate that spider monkeys may be 'underperforming' as seed dispersal agents in the specific context of destination-based dispersal, it would be misleading to judge the overall efficacy of spider monkey dispersal services by the seed pools encountered beneath sleeping trees alone. Indeed, other behaviors by spider monkeys might be expected to generate markedly different outcomes in terms of the distances that seeds are dispersed and patterns of seed source diversity in other areas that they visit (i.e., along transit routes, beneath trees where they forage, underneath resting trees used in the day). Additional work to characterize dispersal outcomes in these different contexts is needed to obtain a full appreciation of the seed dispersal services provided by spider monkeys.

In conclusion, the use of sleeping trees by spider monkeys provides a well-known example of destination-based seed dispersal that, contrary to initial expectations, leads to low diversity seed pools indicative of spatially restricted dispersal to these sites. This finding extends our understanding of the mechanistic linkages between seed disperser behaviors and the patterns of seed source diversity and spatial genetic structure that they generate. It also provides information needed to assess how anthropogenic perturbation to seed dispersal mutualisms might be expected to impact seed movement and genetic structure of tropical tree populations. Similar inquiries into other representative seed dispersal mutualisms will further enhance our basic ecological understanding of seed dispersal while providing information needed to address mounting perturbations to across tropical landscapes and beyond.

Acknowledgments

We thank D. Scofield, V. Sork and P. Smouse for diversity analysis advice and access to R code, M. Newman and T. Roorda for

assistance in the laboratory, and two anonymous reviewers, C. Addis, S. Alvarez, D. Cabrera, R. Tennyson, and the Karubian Lab for assistance in the field, feedback on the manuscript, or both. Funding was provided by the National Science Foundation DEB1548548 and BCS1025675, the Harry Frank Guggenheim Foundation, and the National Geographic Society. This research was conducted with all applicable permits from the Ecuadorian Ministry of the Environment. We thank C. Romo, D. Romo, K. Swing, D. Mosquera and the staff at Tiputini Biodiversity Station for all their support within our long-term study of the primate community at their research station.

References

- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–267.
- Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Di Fiore, A., Dunbar, R.I.M., Henzi, P.S., Helekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J.H., Ramos-Fernandez, G., Strier, K., van Schaik, C.P., 2008. Fission-fusion dynamics: new research frameworks. *Curr. Anthropol.* 49 (4), 627–654. <http://doi.org/10.1086/586708>.
- Berens, D.G., Griebeler, E.M., Braun, C., Chituyi, B.B., Nathan, R., Boehning-Gaese, K., 2013. Changes of effective gene dispersal distances by pollen and seeds across successive life stages in a tropical tree. *Oikos* 122 (11), 1616–1625. <http://dx.doi.org/10.1111/j.1600-0706.2013.00515.x>.
- Bialozyt, R., Luettmann, K., Michalczyk, I.M., Saboya, P.P.P., Ziegenhagen, B., Heymann, E.W., 2014. Primate seed dispersal leaves spatial genetic imprint throughout subsequent life stages of the Neotropical tree *Parkia panurensis*. *Trees*. <http://dx.doi.org/10.1007/s00468-014-1061-7>.
- Chapman, C.A., Chapman, L.J., 1991. The foraging itinerary of spider monkeys: when to eat leaves? *Folia Primatol.* 56 (3), 162–166.
- Chapman, C.A., Chapman, L.J., McLaughlin, R.L., 1989. Multiple central place foraging by spider monkeys: travel consequences of using many sleeping sites. *Oecologia* 79 (4), 506–511.
- Caughlin, T.T., Ferguson, J.M., Lichstein, J.W., Zuidema, P.A., Bunyavechewin, S., Levey, D.J., 2015. Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proc. Biol. Sci.* 282 (1798), 20142095. <http://dx.doi.org/10.1098/rspb.2014.2095>.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. *Science* 345 (6195), 401–406. <http://dx.doi.org/10.1126/science.1251817>.
- Galetti, M., Guevara, R., Cortes, M.C., Fadini, R., Matter, Von, S., Leite, A.B., Labacca, F., Ribeiro, T., Carvalho, C., Collevatti, R.G., Pires, M.M., Guimaraes, P.R., Brancalion, P.H., Ribeiro, M.C., Jordano, P., 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340 (6136), 1086–1090. <http://doi.org/10.1126/science.1233774>.
- Garcia, C., Grivet, D., 2011. Molecular insights into seed dispersal mutualisms driving plant population recruitment. *Acta Oecol. Int. J. Ecol.* 37 (6), 632–640. <http://dx.doi.org/10.1016/j.actao.2011.04.009>.
- Godoy, J.A., Jordano, P., 2001. Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. *Mol. Ecol.* 10 (9), 2275–2283.
- Goulding, M., Smith, N., 2007. Palms: Sentinels for Amazon Conservation. Amazon Conservation Association, Missouri Botanical Garden Press, Saint Louis, Missouri.
- Grivet, D., Smouse, P.E., Sork, V.L., 2005. A novel approach to an old problem: tracking dispersed seeds. *Mol. Ecol.* 14 (11), 3585–3595. <http://dx.doi.org/10.1111/j.1365-294X.2005.02680.x>.
- Hardy, O.J., Vekemans, X., 2002. SPAGEDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Mol. Ecol. Notes* 2 (4), 618–620.
- Hardy, O.J., Maggia, L., Bandou, E., Breyne, P., Caron, H., Chevallier, M.H., Doligez, A., Dutech, C., Kremer, A., Latouche-Hallé, C., Troispoux, V., Veron, V., Degen, B., 2006. Fine-scale genetic structure and gene dispersal inferences in 10 Neotropical tree species. *Mol. Ecol.* 15 (2), 559–571. <http://dx.doi.org/10.1111/j.1365-294X.2005.02785.x>.
- Henderson, A., Galeano, G., Bernal, R., 1995. *Field Guide to the Palms of America*. Princeton University Press, Princeton, New Jersey.
- Herrera, C.M., 2002. Seed Dispersal by Vertebrates. In: *Plant–animal Interactions: an Evolutionary Approach*, pp. 185–208.
- Howe, H.F., Miriti, M.N., 2004. When seed dispersal matters. *BioScience* 54 (7), 651–660.
- Jordano, P., Garcia, C., Godoy, J.A., Garcia-Castano, J.L., 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proc. Natl. Acad. Sci. U. S. A.* 104 (9), 3278–3282. <http://dx.doi.org/10.1073/pnas.0606793104>.
- Julliot, C., 1997. Impact of seed dispersal of red howler monkeys *Alouatta seniculus* on the seedling population in the understorey of tropical rain forest. *J. Ecol.* 85 (4), 431–440. <http://doi.org/10.2307/2960567>.
- Kalinowski, Steven T., 2005. hp-rare 1.0: a computer program for performing rarefaction on measures of allelic richness. *Mol. Ecol. Notes* 5 (1), 187–189.

- Karubian, J., Fabarra, J., Yunes, D., Jorgenson, J., Romo, D., Smith, T.B., 2005. Temporal and spatial patterns of macaw abundance in the Ecuadorian Amazon. *Condor* 107, 617–626.
- Karubian, J., Durães, R., 2009. Effects of seed disperser social behavior on patterns of seed movement and deposition. *Oecologia Brasiliensis* 13, 45–57.
- Karubian, J., Durães, R., 2014. Impacts of mating behavior on plant-animal seed dispersal mutualisms: a case study from a Neotropical lek-breeding bird. In: Macedo, R., Machado, G. (Eds.), *Sexual Selection: Insights from the Neotropics*. Elsevier Press, pp. 365–390.
- Karubian, J., Sork, V.L., Roorda, T., Durães, R., Smith, T.B., 2010. Destination-based seed dispersal homogenizes genetic structure of a tropical palm. *Mol. Ecol.* 19 (8), 1745–1753. <http://dx.doi.org/10.1111/j.1365-294X.2010.04600.x>.
- Karubian, J., Durães, R., Storey, J.L., Smith, T.B., 2012. Mating behavior drives seed dispersal by the long-wattled umbrellabird *Cephalopterus penduliger*. *Biotropica* 44 (5), 689–698. <http://dx.doi.org/10.1111/j.1744-7429.2012.00859.x>.
- Link, A., de Luna, G., 2004. The importance of *Oenocarpus bataua* (Arecaceae) in the diet of spider monkeys at Tinigua National Park, Colombia. *Folia Primatol.* 75 (Suppl. 1), 391.
- Link, A., Di Fiore, A., 2006. Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity. *J. Trop. Ecol.* 22, 235–246. <http://dx.doi.org/10.1017/S0266467405003081>.
- Link, A., Galvis, N., Fleming, E., Di Fiore, A., 2011. Patterns of mineral lick visitation by spider monkeys and howler monkeys in Amazonia: are licks perceived as risky areas? *Am. J. Primatol.* 73 (4), 386–396. <http://doi.org/10.1002/ajp.20910>.
- Loiselle, B.A., Sork, V.L., Nason, J., Graham, C., 1995. Spatial genetic-structure of a tropical understory shrub, *Psychotria Officinalis* (Rubiaceae). *Am. J. Bot.* 82 (11), 1420–1425. <http://dx.doi.org/10.2307/2445869>.
- Muñoz Lazo, F.J.J., Culot, L., Huynen, M.-C., Heymann, E.W., 2011. Effect of resting patterns of tamarins (*Saguinus fuscicollis* and *Saguinus mystax*) on the spatial distribution of seeds and seedling recruitment. *Int. J. Primatol.* 32 (1), 223–237. <http://doi.org/10.1007/s10764-010-9463-x>.
- Ottewell, K., Grey, E., Castillo, F., Karubian, J., 2012. The pollen dispersal kernel and mating system of an insect-pollinated tropical palm, *Oenocarpus bataua*. *Hereditas* 109 (6), 332–339. <http://dx.doi.org/10.1038/hdy.2012.40>.
- Peakall, R., Smouse, P.E., 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Mol. Ecol. Notes* 6 (1), 288–295. <http://dx.doi.org/10.1111/j.1471-8286.2005.01155.x>.
- Peakall, R., Smouse, P.E., 2012. GenALEX 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics* 28 (19), 2537–2539. <http://dx.doi.org/10.1093/bioinformatics/bts460>.
- QGIS Development Team, 2015. QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>.
- R Development Core Team, 2008. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: <http://www.R-project.org>.
- Rogers, M.E., Voysey, B.C., McDonald, K.E., Parnell, R.J., Tutin, C.E.G., 1998. Lowland gorillas and seed dispersal: the importance of nest sites. *Am. J. Primatol.* 45 (1), 45–68. [http://doi.org/10.1002/\(SICI\)1098-2345\(1998\)45:1<45::AID-AJP5>3.0.CO;2-W](http://doi.org/10.1002/(SICI)1098-2345(1998)45:1<45::AID-AJP5>3.0.CO;2-W).
- Rojas-Robles, R., Stiles, F.G., 2009. Analysis of a supra-annual cycle: reproductive phenology of the palm *Oenocarpus bataua* in a forest of the Colombian Andes. *J. Trop. Ecol.* 25, 41–51.
- Russo, S.E., Augspurger, C.K., 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Viola calophylla*. *Ecol. Lett.* 7 (11), 1058–1067. <http://dx.doi.org/10.1111/j.1461-0248.2004.00668.x>.
- Russo, S.E., Portnoy, S., Augspurger, C.K., 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology* 87 (12), 3160–3174.
- Schupp, E.W., Jordano, P., Gómez, J.M., 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytol.* 188 (2), 333–353. <http://doi.org/10.1111/j.1469-8137.2010.03402.x>.
- Scofield, D.G., Smouse, P.E., Karubian, J., Sork, V.L., 2012. Use of alpha, beta, and gamma diversity measures to characterize seed dispersal by animals. *Am. Nat.* 180 (6), 719–732. <http://dx.doi.org/10.1086/668202>.
- Scofield, D.G., Sork, V.L., Smouse, P.E., 2010. Influence of acorn woodpecker social behaviour on transport of coast live oak (*Quercus agrifolia*) acorns in a southern California oak savanna. *J. Ecol.* 98 (3), 561–572. <http://dx.doi.org/10.1111/j.1365-2745.2010.01649.x>.
- Sica, Y.V., Bravo, S.P., Giombini, M.I., 2014. Spatial pattern of Pindó Palm (*Syagrus romanzoffiana*) recruitment in Argentinian Atlantic forest: the importance of tapir and effects of defaunation. *Biotropica* 46 (6), 696–703. <http://dx.doi.org/10.1111/btp.12152>.
- Sork, V.L., Smouse, P.E., 2006. Genetic analysis of landscape connectivity in tree populations. *Landsc. Ecol.* 21 (6), 821–836. <http://dx.doi.org/10.1007/s10980-005-5415-9>.
- Spehar, S.N., Link, A., Di Fiore, A., 2010. Male and female range use in a group of white-bellied spider monkeys (*Ateles belzebuth*) in Yasuni National Park, Ecuador. *Am. J. Primatol.* 72 (2), 129–141. <http://dx.doi.org/10.1002/ajp.20763>.
- Stevenson, P.R., Link, A., Onshuus, A., Quiroz, A.J., Velasco, M., 2014. Estimation of seed shadows generated by Andean woolly monkeys (*Lagothrix lagothricha lugens*). *Int. J. Primatol.* 1–16. <http://dx.doi.org/10.1007/s10764-014-9795-z>.
- Strier, K.B., 1992. Atelinae adaptations: behavioral strategies and ecological constraints. *Am. J. Phys. Anthropol.* 88 (4), 515–524.
- ter Steege, H., Pitman, N.C., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., et al. Silman, M.R., 2013. Hyperdominance in the Amazonian tree flora. *Science* 342 (6156), 1243092.
- Thompson, P.G., Smouse, P.E., Scofield, D.G., Sork, V.L., 2014. What seeds tell us about birds: a multi-year analysis of acorn woodpecker foraging movements. *Mov. Ecol.* 2 (1), 1–10. <http://dx.doi.org/10.1186/2051-3933-2-12>.
- Vekemans, X., Hardy, O.J., 2004. New insights from fine-scale spatial genetic structure analyses in plant populations. *Mol. Ecol.* 13 (4), 921–935. <http://dx.doi.org/10.1046/j.1365-294X.2004.02076.x>.
- Wang, B.C., Smith, T.B., 2002. Closing the seed dispersal loop. *Trends Ecol. Evol.* 17 (8), 379–385. [http://dx.doi.org/10.1016/S0169-5347\(02\)02541-7](http://dx.doi.org/10.1016/S0169-5347(02)02541-7).
- Wenny, D.G., Levey, D.J., 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proc. Natl. Acad. Sci. U. S. A.* 95 (11), 6204–6207. <http://dx.doi.org/10.1073/pnas.95.11.6204>.
- Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30, 279–338.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon* 21, 213–251.
- Worton, B.J., 1989. Kernel methods for estimating the utilization distribution of home range studies. *Ecology* 70, 164–168.