



## Original article

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

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## 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.

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## 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).

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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

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