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Dispersion of seeds at night and day in sub-Andean forests, Cueva Los Guacharos Park, Colombia

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ABSTRACT

Introduction: Much has been argued about the importance of the role that different types of frugivores play as seed dispersers in plant communities, but few studies have been actually carried out.

Objective: We evaluated and compared diurnal and nocturnal seed dispersal in primary and secondary sub-Andean forests in Southern Colombia.

Methods: We estimated number and biomass (kg/ha) of seeds dispersed over one year (2017) using 60 fruit traps that were checked before sunrise and before sunset for 10 continuous days every two months.

Results: We found that from 1 874 dispersed seeds, 55.8 % (10.9 kg/ha) were collected during the day and 44.2 % (6.39 kg/ha) at night. There were no significant differences between diurnal and nocturnal seed dispersal in number of seeds or biomass. We also found no difference in seed dispersal between primary and secondary forest over time. Within diurnal organisms, primates and fruit-eating birds appear to be primarily responsible for this ecosystem service during the day; while bats, birds (e.g. oilbirds), and probably primates did so during the night.

Conclusions: Diurnal and nocturnal dispersal seem to be equal in terms of number and weight of seeds, but not in the similarity of dispersed plant species. It remains a challenge to recognize the relative importance of different fruit-eating organisms as seed dispersers using fruit trap methods.

Key words: seed dispersal; hanging seed traps; day and night frugivores; phenology; Andean forest.

RESUMEN

Dispersión de semillas nocturna y diurna en un bosque sub-Andino, Parque Cueva Los Guacharos, Colombia

Introducción: Mucho se ha discutido sobre la importancia del papel que juegan diferentes tipos de frugívoros como dispersores de semillas en las comunidades vegetales, pero en realidad se han realizado pocos estudios.

Objetivo: Evaluamos y comparamos la dispersión diurna y nocturna de semillas en bosques subandinos primarios y secundarios en el sur de Colombia.

Métodos: Estimamos el número y la biomasa (kg/ha) de semillas dispersadas durante un año (2017) utilizando 60 trampas de frutos que se revisaron antes del amanecer y antes del atardecer durante 10 días continuos cada dos meses.

Resultados: Se encontró que, de 1 874 semillas dispersas, el 55.8 % (10.9 kg/ha) se recolectaron durante el día y el 44.2 % (6.39 kg/ha) durante la noche. No hubo diferencias significativas entre la dispersión de semillas diurna y nocturna en número de semillas o biomasa. Tampoco encontramos diferencias entre la dispersión de semillas en el bosque primario y el bosque secundario a lo largo del tiempo. Dentro de los organismos diurnos, los primates y las aves frugívoras parecen ser los principales responsables de este servicio ecosistémico durante



el día; mientras que los murciélagos, las aves (por ejemplo, los guácharos) y probablemente los primates lo hicieron durante la noche.

Conclusiones: La dispersión diurna y nocturna parecen ser iguales en número y peso de semillas, pero no en la similitud de especies de plantas dispersadas. Sigue siendo un desafío reconocer la importancia relativa de los diferentes organismos frugívoros como dispersores de semillas utilizando métodos de trampa de frutos.

Palabras clave: dispersión de semillas; trampas colgantes de semillas; frugívoros diurnos y nocturnos; fenología; bosque andino.

INTRODUCTION

Seed dispersal is one of the most important interactions in tropical forests (Howe & Smallwood, 1982; Willson & Traveset, 2000). It is fundamental for the subsistence of plant communities over time (Cain et al., 2000; Chazdon, 2003; Stevenson, 2011), since frugivores can modify demographic processes, population dynamics, potential recruitment area, and density-dependent processes (Connell et al., 1984; Janzen, 1971; Nathan & Muller-Landau, 2000; Willson, 1993). Several organisms perform seed dispersal services in different ecosystems, where birds and mammals have been suggested as the main ones dispersing seeds of many tropical plant species (Howe, 1990).

Bats have been considered the main nocturnal seed dispersers (Fleming & Heithaus, 1981; Mello et al., 2011). Different studies have cataloged bats as efficient seed dispersers from a quantitative point of view, finding that they move a high number of seeds by consuming large amounts of fruit, even more than birds (Brosset et al., 1996; Duncan & Chapman, 1999; Medellín & Gaona, 1999). Bats are also effective seed dispersers, with high germination percentages after seeds pass throughout their digestive system (Fleming, 1988; Vasquez-Yanes & Orozco-Segovia, 1986).

Some authors highlight bats as important seed dispersers because when defecating in flight they are more likely to deposit seeds in forest clearings and open areas than birds and primates, playing a very important role in forest regeneration (Korine & Kalko, 2005;

Thies & Kalko, 2004; Thomas et al., 1988). For other nocturnal mammals such as opossums (Didelphidae), raccoons and mountain dogs (Procyonidae), and rodents (Rodentia) efficient seed dispersal has also been observed (Fleming & Williams, 1990; Howe, 1990; Jansen et al. 2012).

In contrast, diurnal birds have been considered the main dispersers in a variety of habitats (Howe, 1977; Wang & Smith, 2002; Wenny et al., 2016). Birds have been described as efficient seed dispersers due to their wide home ranges, flight capacity, broad frugivorous diet, and the likelihood of recruitment (Herrera & Jordano, 1981; Levey et al., 2005; Stiles, 1980). Due to the great morphological, behavioural, and ecological diversity of frugivorous birds, it has been found that they are also important in the restoration of forests and especially increasing the connectivity of patches isolated as a consequence of forest fragmentation, in addition to promoting plant diversity (Carlo & Morales, 2016; Emer et al., 2018). As a particular case in neotropical forests is a nocturnal frugivorous bird known as oilbird (*Steatornis caripensis*), which presents a diverse diet of fruits and seeds, and a great capacity to disperse a high number of seeds (Stevenson et al., 2017).

On the other hand, in tropical zones, it has been shown that diurnal primates play disproportionate ecological roles as seed dispersers (Link & Di Fiore, 2006). Because of their high abundance and large size relative to other frugivores in many tropical forests (Bravo, 2012; Campbell et al., 2016), their large biomass,

and their ability to ingest large seeds, primates are also considered efficient seed dispersers (Chapman & Dunham, 2018; Stevenson et al., 2005). Additionally, they disperse high amounts of seeds over long distances, are effective seed dispersers, and their seed dispersal pattern shows a high correlation with seedling recruitment (Gelmi-Candusso et al., 2019; Stevenson et al., 2002; Zárate et al., 2019).

The purpose of this study is to compare daytime and nighttime seed dispersal, as an approximation to seed dispersal roles of diurnal and nocturnal arboreal and flying frugivores in a secondary and primary sub-Andean forest of Colombia. We expect to find differences in the amount, biomass and species of seeds dispersed between day and night.

MATERIALS AND METHODS

Study area: The study was conducted in the Cueva de Los Guácharos National Natural Park (PNNCG) located in the department of Huila and the Southwestern part of the department of Caquetá (Colombia). The predominant habitat is a sub-Andean forest, both primary and secondary, the latter being a forest with a growth close to 40 years (Prada & Stevenson, 2016). The study area is on average at 2 000 m.a.s.l. with a mean temperature of 18.8 °C. The annual precipitation is 2 284 mm and the rainy season presents a bimodal pattern with a first peak between March and June, and a second peak between September and October. Species richness of different organism groups has been partially registered for PNNCG. Prada and Stevenson (2016) report 458 species/morphospecies of trees, about 200 bird species (Stevenson et al., 2022), 10 species of medium and large mammals (Gast & Stevenson, 2021), 11 species of small nonflying mammals (Bautista-Plazas et al., 2017), 5 species of primates (Vargas et al., 2014) and 25 species of bats (Walteros-Vergara, 2018).

Seed dispersal: Hanging traps of 0.56 m² were used to capture the dispersed seeds, the porosity of the traps was < 1 mm to ensure

that small seed species were represented in the study. The material was cloth and they were tied to four nearby trees, following the recommendations of Stevenson & Vargas (2008). A total of 60 traps were arranged in four 1 km long linear transects, two of these transects were placed in the secondary forest and two in the primary forest, each with 15 hanging traps. The location of each trap within the transect was determined by three random numbers: 1. The space between adjacent traps (between 15 and 20 m), 2. The side of the trails (right or left), and 3. The distance to the trails (between 1 and 10 m).

Traps of each transect were checked before sunrise (5:00) and before sunset (17:00) for 10 continuous days every two months (February, April, June, August, October, December) throughout 2017. Once the contents were collected, the seeds were identified at the species level when possible. This material was dried in a portable oven at an average temperature of 60 °C to achieve constant dry weight. Then, we counted the number of dispersed seeds and estimated the biomass of dispersed seeds (kg/ha) (Stevenson, 2004). Seeds were classified as dispersed when they were associated with dung and all the adult trees, lianas, and shrubs within a 10 m radius of each hanging trap were identified to discern whether the seeds deposited in the trap were dispersed or came from nearby parents (Stevenson, 2007). Besides, it was corroborated that they were dispersed seeds since there were no immature fruits, whole fruits, or flowers of the same species in each trap.

Statistical analysis: A linear mixed model was used to evaluate the fixed effects as time (day/night) and forest type (primary/secondary), and month as a random effect (February, April, June, August, October, December), on the logarithm of the number of dispersed seeds and the logarithm of dispersed seeds biomass (kg/ha). The linear mixed model was carried out using “lme4” and “lmerTest” packages from software R 4.2.3 (R Core Team, 2023). We also estimated random effects for each month and their interval estimate using

“merTools” package. We calculate similarity between seed species dispersed in the day and seeds dispersed in the night with the Jaccard similarity index using “Vegan” package.

RESULTS

A total of 93 species of seeds were identified, 65 species were dispersed during the day and 56 during the night. We found that around half of the species dispersed in the day were not shared with the species dispersed in the night (Jaccard similarity index = 0.54). Twenty-eight species were exclusively dispersed during the night and 37 during the day.

The plant species with the highest seed biomass dispersed during the day were *Alchornea grandis*, *Tapirira guianensis subandina*, *Chamaedorea linearis*, *Guettarda crispiflora*, and *Rollinia dolichopetala*. On the other hand,

the plant species with the highest seed biomass dispersed at night were *Tapirira g. subandina*, *Sapium stylare*, *Hieronima huilensis*, *Rollinia dolichopetala* and *Anthurium multinervium*.

The plant species with the highest number of seeds dispersed during the day were *Ficus* sp.1, *Cecropia telenitida*, *Solanum* sp.1, *Morus insignis*, and *Cecropia angustifolia*. In contrast, at night the highest number of dispersed seeds were recorded for *Ficus* sp.1, *Cecropia telenitida*, *Anthurium multinervium*, *Solanum* sp.1, and *Hieronima andina*.

We recorded a total of 1874 effectively dispersed seeds, of which 1046 (55.8 %) were collected during the day and 828 (44.2 %) at night. The total dispersed seed biomass was higher in the day with 10.96 kg/ha, while for night it was 6.39 kg/ha; however, the variation was large and no significant differences were found ($T = -1.25$, $P = 0.22$, Fig. 1A). Similarly, no significant differences were found between

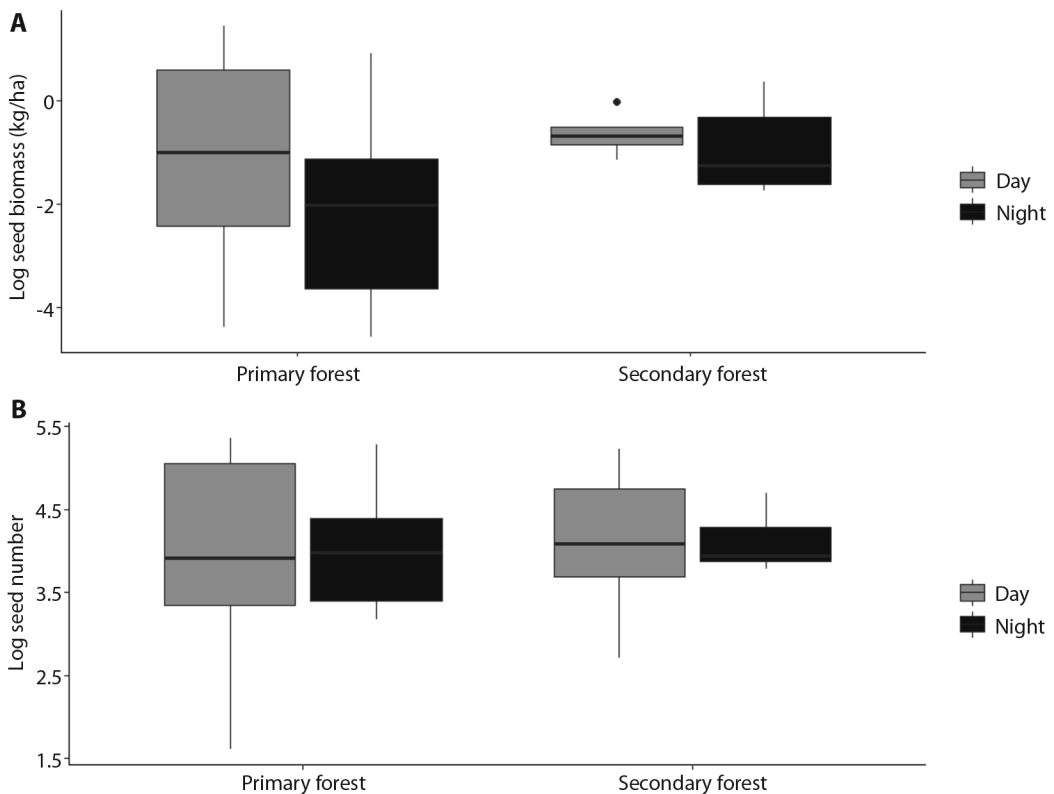


Fig. 1. A. Biomass of seeds dispersed (kg/ha) day and night at secondary and primary forest in PNNCG. **B.** The number of seeds dispersed day and night at secondary and primary forest in PNNCG.

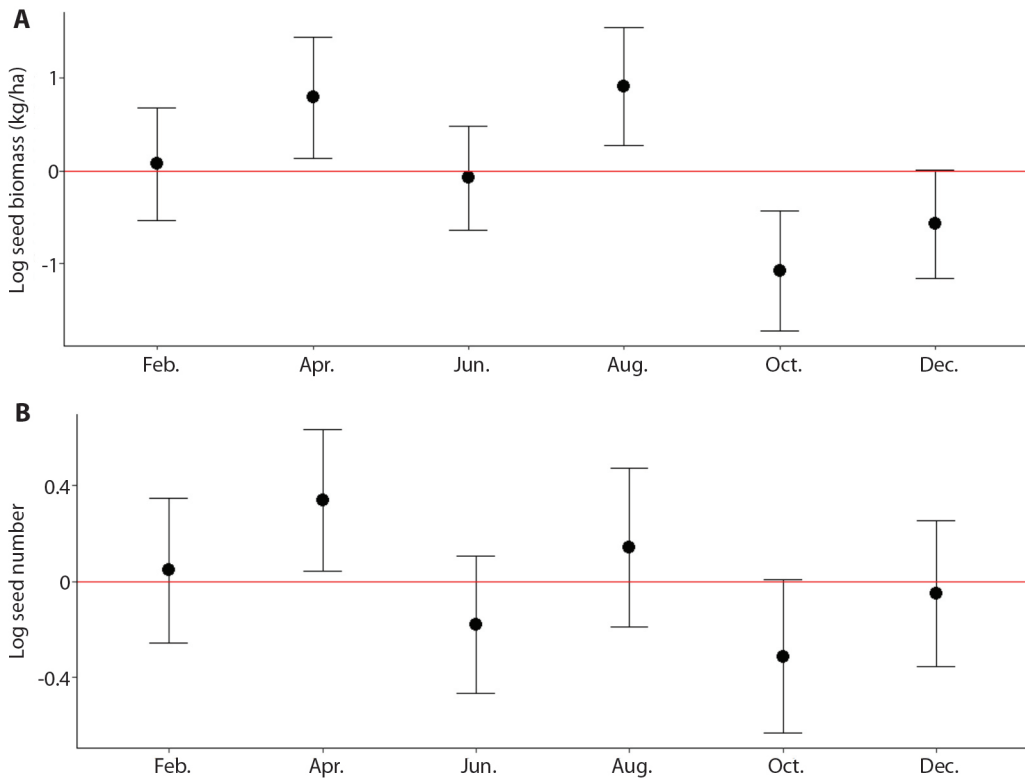


Fig. 2. A. Biomass of seeds dispersed (kg/ha) through the year at PNNCG. **B.** The number of seeds dispersed through the year at PNNCG.

the number of seeds dispersed during the day and night ($T = 0.18$, $P = 0.85$, Fig. 1B).

In the primary forest, a total of 995 seeds were dispersed (551 during the day and 444 at night) and 879 (495 during the day and 384 at night) in the secondary forest, no significant differences were found in the number of seeds between forest types ($T = 0.41$, $P = 0.68$, Fig. 1B). Additionally, we did not observe a significant difference between the primary and secondary forests in the biomass of dispersed seeds ($T = 1.58$, $P = 0.13$, Fig. 1A), a total of 10.79 kg/ha of seeds was dispersed in the primary forest and 6.57 kg/ha in the secondary forest. No significant differences were found in the number or biomass (kg/ha) of seeds dispersed between the months sampled. However, April and August recorded the highest number and biomass of dispersed seeds, while

in October and December the lowest seed dispersion (Fig. 2).

DISCUSSION

Both, birds and bats, have been widely regarded as the main seed dispersers of day and night seeds respectively, in terms of the number of seeds transported (Fleming & Heithaus, 1981; Janson, 1983; Levey et al., 2002; Mello et al., 2015; Wenny & Levey, 1998). In this study, we did not observe marked differences in the number of seeds dispersed during the day and night, nor in the number of plant species dispersed in these two periods. Our results agree with what was found for trees isolated within grasslands by Galindo-González et al. (2000), however, for other tropical forests, a greater dispersion of seeds by one of the two



large groups (birds or bats) has been reported (Gonzales et al., 2009; Ingle, 2003; Jacomassa & Pizo, 2010;).

We did not find a greater nocturnal seed dispersal for any of the studied forests (primary and secondary), although we observed a slightly higher seed biomass at night in secondary forests than in primary forests. This contrasts with what was found by other authors where bats are more important in successional forest states where they disperse significantly more seeds and are important for the natural regeneration of ecosystems (Duncan & Chapman, 1999; Medellín & Gaona, 1999). This can be explained by the fact that secondary forests in the study area are relatively old (ca. 40 years in recovery).

Similarly, it has been suggested that birds have greater importance in terms of seed dispersal within mature forests than in disturbed forest in recovery and with fragmentation (Ingle, 2003; Whittaker & Jones, 1994). However other studies support that seed dispersal by birds is crucial in forest regeneration for disturbed habitats (Carlo & Morales, 2016; Saavedra et al., 2014). In our case, although there are no notable differences in diurnal seed dispersal between primary and secondary forests, our results show a greater value in both the number of seeds and the biomass of seeds dispersed by diurnal animals for the secondary forest.

For our study forest, there was high variability in the dispersion of seeds at day and night, being slightly higher during the day both in biomass and number of dispersed seeds. The slightly higher biomass and seed count during the day is expected since not only bird droppings but also primate droppings were found in seed traps collected at day-time. In the PNNCG study site, it has been reported that the most abundant primates in the area are the woolly monkeys (*Lagothrix lagothricha*) who disperse a large number of seeds, with an average of 11 000 seeds km² day⁻¹ (Ramírez et al., 2014). This explains the high dispersion of large seeds such as *Tapirira g. subandina*, *Sapium stylare*, and *Rollinia dolichopetala* which are known to be heavily consumed and dispersed by woolly

monkeys (Ramírez et al., 2014). Additionally, in the area there are other species of primates such as *Sapajus apella*, *Alouatta seniculus* and *Saimiri sciurus*, which could also disperse large seeds (Chapman, 1995), but occur at very low density (Vargas et al., 2014).

Within the seeds dispersed at night, we found a high number of seeds from *Tapirira g. subandina* which is the most important plant for the population of woolly monkeys and has not been reported in the diet of bats. Therefore, we believe that this species and other plants preferred by monkeys (e.g. *Rollinia dolichopetala*) are dispersed during nighttime by primates in their sleeping trees. These nocturnal depositions by primates are important and should be considered for nocturnal dispersal as they can comprise up to 19 % of the total seeds dispersed during the day by primates (Stevenson, 2007). We cannot rule out that these seeds were dispersed by other nocturnal organisms such as nocturnal monkeys (*Aotus* sp), *Potos flavus*, or marsupials, but presumably, the effect of the woolly monkeys could be greater, given their high abundance (ca. 20 individuals/km²) (Vargas et al. 2014). It is also important to bear in mind that the study area has a large oilbird colony (*Steatornis caripensis*). This species could also be responsible for nocturnal seed dispersal of species such as *Chamaedorea linearis*, *Hedyosmum cuatrecasanzum* and *Nectandra* sp. which are part of the diet of this nocturnal bird (Stevenson et al., 2017). Nevertheless, nocturnal seeds dispersal from species such as *Tapirira g. subandina*, *Rollinia dolichopetala* and *Hieronyma huilensis*, probably come from diurnal frugivores, because of their size and not being registered in the oilbird's diet.

Our observations indicated that the trends in both the number and amount of biomass of seeds dispersed at night and daytime generally kept the same trend overtime with April being the month of greatest dispersal and October the one with the least dispersal. Seed dispersal at this location seems to be affected mainly by changes in fruit production throughout the year. In fact, the months with higher fruit

production also showed a peak in the number of dispersed seeds (Bautista, unpublished). Additionally, when there is greater production of fruits, more visits of fruit eaters are expected. So, it seems that it could be important in future studies to evaluate productivity as predictor of the amount of seed dispersion, as has been observed in other studies (Albrecht et al. 2012; Hampe, 2008).

Knowing the dispersion of seeds in forests with different degrees of disturbance is of vital importance to understand the processes of natural regeneration (Gorchov et al., 1993; Uriarte & Chazdon, 2016). It is also essential to estimate the contribution of different organisms to the seed rain of particular species within the plant community (Howe, 1990). From the results found in this study, we can say that for the primary and the old secondary sub-Andean forests of the PNNCG, share many frugivores such as primates and birds (Vargas et al., 2014), which may explain the lack of differences in diurnal and nocturnal dispersal.

Our main conclusion was diurnal and nocturnal dispersal but that is not saying much about seed dispersal by birds and primates vs. bats, and that in natural tropical forests the role of primates and nocturnal birds might be substantial, where they reach high densities and are not subject to hunting (Howe, 1990; Stevenson, 2011; Stevenson et al., 2017; Wright et al., 2000). For this reason, it is imperative to generate conservation strategies to protect the different species of seed-dispersing organisms, since the persistence of multiple species and ecosystems depends on them (Chazdon & Guariguata, 2016; Kozłowski, 2002). By preserving these organisms, damages to the plant community such as deforestation, fragmentation, and loss of species can be ameliorated and remedied (Bacles et al., 2006; Cramer et al., 2007; McConkey et al., 2012; Ozinga et al., 2009), because frugivores help in the processes of regeneration and restoration of degraded forests (Parrotta et al., 1997).

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REFERENCES

- Albrecht, J., Neuschulz, E. L., & Farwig, N. (2012). Impact of habitat structure and fruit abundance on avian seed dispersal and fruit predation. *Basic and Applied Ecology*, 13(4), 347–354.
- Bacles, C. F., Lowe, A. J., & Ennos, R. A. (2006). Effective seed dispersal across a fragmented landscape. *Science*, 311(5761), 628–628.
- Bautista-Plazas, S., Rodríguez-Bolaños, A., Castellanos, R., & Stevenson, P. R. (2017). First inventory of small non-flying mammals of the Cueva de los Guacharos National Natural Park (Huila, Colombia). *Mammalogy Notes*, 4(2), 18–21.
- Bravo, S. P. (2012). The impact of seed dispersal by black and gold howler monkeys on forest regeneration. *Ecological Research*, 27(2), 311–321.
- Brosset, A., Charles-Dominique, P., Cockle, A., Cosson, J. F., & Masson, D. (1996). Bat communities and deforestation in French Guiana. *Canadian Journal of Zoology*, 74(11), 1974–1982.
- Cain, M. L., Milligan, B. G., & Strand, A. E. (2000). Long distance seed dispersal in plant populations. *American Journal of Botany*, 87(9), 1217–1227.
- Campbell, G., Head, J., Junker, J., & Nekaris, K. A. I. (2016). Primate abundance and distribution: background concepts and methods. In S. A. Wich & A. J. Marshall (Eds.), *An introduction to primate conservation* (pp. 79-104). Oxford Academic.



- Carlo, T. A., & Morales, J. M. (2016). Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. *Ecology*, 97(7), 1819–1831.
- Chapman, C. A. (1995). Primate seed dispersal: coevolution and conservation implications. *Evolutionary Anthropology: Issues, News, and Reviews*, 4(3), 74–82.
- Chapman, C. A., & Dunham, A. E. (2018). Primate seed dispersal and forest restoration: an African perspective for a brighter future. *International Journal of Primatology*, 39(3), 427–442.
- Chazdon, R. L. (2003). Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, 6(1–2), 51–71.
- Chazdon, R. L., & Guariguata, M. R. (2016). Natural regeneration as a tool for large scale forest restoration in the tropics: prospects and challenges. *Biotropica*, 48(6), 716–730.
- Connell, J. H., Tracey, J. G., & Webb, L. J. (1984). Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. *Ecological Monographs*, 54(2), 141–164.
- Cramer, J. M., Mesquita, R. C., & Williamson, G. B. (2007). Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. *Biological Conservation*, 137(3), 415–423.
- Duncan, S. R., & Chapman, C. A. (1999). Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications*, 9(3), 998–1008.
- Emer, C., Galetti, M., Pizo, M. A., Guimaraes-Jr, P. R., Moraes, S., Piratelli, A., & Jordano, P. (2018). Seed-dispersal interactions in fragmented landscapes—a metanetwork approach. *Ecology Letters*, 21(4), 484–493.
- Fleming, T. H. (1988). *The short-tailed fruit bat: a study in plant-animal interactions*. University of Chicago Press.
- Fleming, T. H., & Heithaus, E. R. (1981). Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica*, 13(2), 45–53.
- Fleming, T. H., & Williams, C. F. (1990). Phenology, seed dispersal, and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical dry forest. *Journal of Tropical Ecology*, 6(2), 163–178.
- Galindo-González, J., Guevara, S., & Sosa, V. J. (2000). Bat-and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conservation Biology*, 14(6), 1693–1703.
- Gast, F., & Stevenson, P. R. (2021). Relative abundances of medium and large mammals in the Cueva de Los Guácharos National Park (Huila, Colombia). *Biota Neotropica*, 20(3), e20160305.
- Gelmi-Candusso, T. A., Bialozyt, R., Slana, D., Zarate-Gomez, R., Heymann, E. W., & Heer, K. (2019). Estimating seed dispersal distance: a comparison of methods using animal movement and plant genetic data on two primate-dispersed Neotropical plant species. *Ecology and Evolution*, 9(16), 8965–8977.
- Gonzales, R. S., Ingle, N. R., Lagunzad, D. A., & Nakas-hizuka, T. (2009). Seed dispersal by birds and bats in lowland Philippine forest successional area. *Biotropica*, 41(4), 452–458.
- Gorchov, D. L., Cornejo, F., Ascorra, C., & Jaramillo, M. (1993). The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. *Vegetatio*, 107(1), 339–349.
- Hampe, A. (2008). Fruit tracking, frugivore satiation, and their consequences for seed dispersal. *Oecologia*, 156(1), 137–145.
- Herrera, C. M., & Jordano, P. (1981). Prunus mahaleb and birds: the high efficiency seed dispersal system of a temperate fruiting tree. *Ecological Monographs*, 51(2), 203–218.
- Howe, H. F. (1977). Bird activity and seed dispersal of a tropical wet forest tree. *Ecology*, 58(3), 539–550.
- Howe, H. F. (1990). Seed dispersal by birds and mammals: implications for seedling demography. In K. S. Bawa & M. Hadley (Eds.), *Reproductive Ecology of Tropical Forest Plants*, (pp. 191–218). UNESCO.
- Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13(1), 201–228.
- Ingle, N. R. (2003). Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. *Oecologia*, 134(2), 251–261.
- Jacomassa, F. A. F., & Pizo, M. A. (2010). Birds and bats diverge in the qualitative and quantitative components of seed dispersal of a pioneer tree. *Acta Oecologica*, 36(5), 493–496.
- Jansen, P. A., Hirsch, B. T., Emsens, W. J., Zamora-Gutierrez, V., Wikelski, M., & Kays, R. (2012). Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences*, 109(31), 12610–12615.
- Janson, C. H. (1983). Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science*, 219(4581), 187–189.
- Janzen, D. H. (1971). Seed predation by animals. *Annual Review of Ecology and Systematics*, 2(1), 465–492.

- Korine, C., & Kalko, E. K. (2005). Fruit detection and discrimination by small fruit-eating bats (Phyllostomidae): echolocation call design and olfaction. *Behavioral Ecology and Sociobiology*, 59(1), 12–23.
- Kozłowski, T. T. (2002). Physiological ecology of natural regeneration of harvested and disturbed forest stands: implications for forest management. *Forest Ecology and Management*, 158(1-3), 195–221.
- Levey, D. J., Bolker, B. M., Tewksbury, J. J., Sargent, S., & Haddad, N. M. (2005). Effects of landscape corridors on seed dispersal by birds. *Science*, 309(5731), 146–148.
- Levey, D. J., Silva, W. R., & Galetti, M. (2002). *Seed dispersal and frugivory: ecology, evolution, and conservation*. CABI Publishing.
- Link, A., & Di Fiore, A. (2006). Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity. *Journal of Tropical Ecology*, 22(3), 235–246.
- McConkey, K. R., Prasad, S., Corlett, R. T., Campos-Arceiz, A., Brodie, J. F., Rogers, H., & Santamaria, L. (2012). Seed dispersal in changing landscapes. *Biological Conservation*, 146(1), 1–13.
- Medellin, R. A., & Gaona, O. (1999). Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica*, 31(3), 478–485.
- Mello, M. A. R., Marquitti, F. M. D., Guimaraes-Jr, P. R., Kalko, E. K. V., Jordano, P., & de Aguiar, M. A. M. (2011). The missing part of seed dispersal networks: structure and robustness of bat-fruit interactions. *PLoS One*, 6(2), e17395.
- Mello, M. A. R., Rodrigues, F. A., Costa, L. D. F., Kissling, W. D., Şekercioğlu, Ç. H., Marquitti, F. M. D., & Kalko, E. K. V. (2015). Keystone species in seed dispersal networks are mainly determined by dietary specialization. *Oikos*, 124(8), 1031–1039.
- Nathan, R., & Muller-Landau, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, 15(7), 278–285.
- Ozinga, W. A., Römermann, C., Bekker, R. M., Prinzing, A., Tamis, W. L., Schaminée, J. H., Henneken, S. M., Thompson, K., Poschlod, P., Kleyer, M., Bakker, J. P., & van Groenendael, J. M. (2009). Dispersal failure contributes to plant losses in NW Europe. *Ecology Letters*, 12(1), 66–74.
- Parrotta, J. A., Turnbull, J. W., & Jones, N. (1997). Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology and Management*, 99(1-2), 1–7.
- Prada, C. M., & Stevenson, P. R. (2016). Plant composition associated with environmental gradients in tropical montane forests (Cueva de Los Guacharos National Park, Huila, Colombia). *Biotropica*, 48(5), 568–576.
- R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Ramírez, M. A., Galvis, N. F., Vargas, S. A., León, J. J., Cifuentes, E. F., & Stevenson, P. R. (2014). Seed dispersal by woolly monkeys in Cueva de los Guacharos National Park (Colombia): An amazonian primate dispersing montane plants. In N. B. Grow, S. Gursky-Doyen & A. Krzton (Eds.), *High altitude primates* (pp. 103–114). Springer.
- Saavedra, F., Hensen, I., Beck, S. G., Böhning-Gaese, K., Lippok, D., Töpfer, T., & Schleuning, M. (2014). Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. *Oecologia*, 176(2014), 837–848.
- Stevenson, P. R. (2004). Phenological patterns of woody vegetation at Tinigua Park, Colombia: Methodological comparisons with emphasis on fruit production. *Caldasia*, 26(1), 125–150.
- Stevenson, P. R. (2007). Estimates of the number of seeds dispersed by a population of primates in a lowland forest in western Amazonia. In A. J. Dennis, E. W. Schupp, R. J. Green & D. A. Westcott (Eds.), *Seed dispersal: Theory and its application in a changing world* (pp. 340–362). CABI Publishing.
- Stevenson, P. R. (2011). The abundance of large Ateline monkeys is positively associated with the diversity of plants regenerating in Neotropical forests. *Biotropica*, 43(4), 512–519.
- Stevenson, P. R., Castellanos, M. C., Pizarro, J. C., & Garavito, M. (2002). Effects of seed dispersal by three ateline monkey species on seed germination at Tinigua National Park, Colombia. *International Journal of Primatology*, 23(6), 1187–1204.
- Stevenson, P. R., Cardona, L. M., Acosta-Rojas, D. C., Henao-Díaz, F., & Cárdenas, S. (2017). Diet of oilbirds (*Steatornis caripensis*) in Cueva de los Guácharos National Park (Colombia): Temporal variation in fruit consumption, dispersal, and seed morphology. *Ornitología Neotropical*, 28(2017), 295–307.
- Stevenson, P. R., Cortés, C., Reyes, R., Paramero, R., Uni, J. F., Peña-Núñez, J. L., & Henao-Díaz, L. F. (2022). Avifauna asociada a bosques primarios y secundarios del Parque Nacional Natural Cueva de Los Guácharos, Colombia. *Actualidades Biológicas*, 44(116), 1–18.
- Stevenson, P. R., Link, A., & Ramírez, B. H. (2005). Frugivory and seed fate in *Bursera inversa* (Burseraceae) at Tinigua Park, Colombia: Implications for primate



- conservation. *Biotropica: The Journal of Biology and Conservation*, 37(3), 431–438.
- Stevenson, P. R., & Vargas, I. N. (2008). Sample size and appropriate design of fruit and seed traps in tropical forests. *Journal of Tropical Ecology*, 24(1), 95–105.
- Stiles, E. W. (1980). Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. *The American Naturalist*, 116(5), 670–688.
- Thies, W., & Kalko, E. K. (2004). Phenology of neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). *Oikos*, 104(2), 362–376.
- Thomas, D. W., Cloutier, D., Provencher, M., & Houle, C. (1988). The shape of bird-and bat-generated seed shadows around a tropical fruiting tree. *Biotropica*, 20(1988), 347–348.
- Uriarte, M., & Chazdon, R. L. (2016). Incorporating natural regeneration in forest landscape restoration in tropical regions: synthesis and key research gaps. *Biotropica*, 48(6), 915–924.
- Vargas, S. A., León, J., Ramírez, M., Galvis, N., Cifuentes, E., & Stevenson, P. R. (2014). Population density and ecological traits of highland woolly monkeys at Cueva de los Guácharos National Park, Colombia. In N. Grow, S. Gursky-Doyen & A. Krzton, (Eds.), *High altitude primates* (pp. 85–102). Springer.
- Vasquez-Yanes, C., & Orozco-Segovia, A. (1986). Effect of light controlled dormancy in *Cecropia obtusifolia*. In A. Estrada & T. H. Fleming (Eds.), *Frugivores and seed dispersal* (pp. 71–77). Springer Dordrecht.
- Walteros-Vergara, A. (2018). *Lista comentada de las especies de murciélagos presentes en el parque Nacional Natural Cueva de los Guácharos. Ubicado en el municipio de Acevedo-Huila* (Tesis de grado). Universidad Distrital Francisco José de Caldas, Colombia.
- Wang, B. C., & Smith, T. B. (2002). Closing the seed dispersal loop. *Trends in Ecology & Evolution*, 17(8), 379–386.
- Wenny, D. G., & Levey, D. J. (1998). Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences*, 95(11), 6204–6207.
- Wenny, D. G., Sekercioglu, C., Cordeiro, N. J., Rogers, H. S., & Kelly, D. (2016). Seed dispersal by fruit-eating birds. In C. H. Sekercioglu, D. G. Wenny & C. J. Whelan (Eds.), *Why birds matter: avian ecological function and ecosystem services* (pp. 107–145). University of Chicago Press.
- Whittaker, R. J., & Jones, S. H. (1994). The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. *Journal of Biogeography*, 21(3), 245–258.
- Willson, M. F. (1993). Dispersal mode, seed shadows, and colonization patterns. In T. H. Fleming & A. Estrada (Eds.), *Frugivory and seed dispersal: ecological and evolutionary aspects* (pp. 261–280). Springer Dordrecht.
- Willson, M. F., & Traveset, A. (2000). The ecology of seed dispersal. In M. Fenner (Ed.), *Seeds: the ecology of regeneration in plant communities* (pp. 85–110). CABI International.
- Wright, S. J., Zeballos, H., Domínguez, I., Gallardo, M. M., Moreno, M. C., & Ibáñez, R. (2000). Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology*, 14(1), 227–239.
- Zárate, D. A., Andresen, E., & Santos-Heredia, C. (2019). Seed fate and seedling recruitment in monkey latrines in rustic cocoa plantations and rain forest in southern Mexico. *Journal of Tropical Ecology*, 35(1), 18–25.