

## Lianas influence fruit and seed use by rodents in a tropical forest

ANTHONY KILGORE<sup>1</sup>, THOMAS D. LAMBERT<sup>1\*</sup> & GREGORY H. ADLER<sup>2</sup>

<sup>1</sup>*Department of Natural Sciences, University of Virginia's College at Wise, Wise, VA 24293, USA*

<sup>2</sup>*Department of Biology and Microbiology, University of Wisconsin-Oshkosh, Oshkosh WI 54901, USA*

**Abstract:** We examined how rodent activity influenced the fates of seeds of two palm species (*Astrocaryum standleyanum* L.H. Bailey and *Attalea butyracea* (Mutis ex L.f.) Wess. Boer). Intact fruits were placed in exclosures at three heights (ground, understory and canopy), and removed seeds were tracked with attached sewing bobbins. We recorded 50 handling events. Most seeds were discarded after removal and the fruit eaten, and only one seed was cached in the ground. Fruit and seed handling activity showed strong associations with lianas, indicating that changes in liana abundance, resulting from human activity, could greatly influence seed fate, and therefore, affect forest regeneration and potentially impact local biodiversity.

**Resumen:** Examinamos la manera en que la actividad de los roedores influyó sobre los destinos de las semillas de dos especies de palmas (*Astrocaryum standleyanum* L.H. Bailey y *Attalea butyracea* (Mutis ex L.f.) Wess. Boer). Se colocaron frutos intactos en áreas excluidas a tres alturas (piso, sotobosque y dosel) y las semillas removidas fueron rastreadas por medio de bobinas de costura fijadas a ellas. Registramos 50 eventos de manipulación. La mayoría de las semillas fueron desechadas después de su remoción y de que el fruto fue comido, y sólo una semilla fue escondida en el suelo. La actividad de manipulación de frutos y semillas mostró asociaciones fuertes con las lianas, lo que indica que los cambios en la abundancia de lianas, resultado de la actividad humana, podrían influir en gran medida en el destino de las semillas y por lo tanto afectar la regeneración del bosque y tener un impacto potencial sobre la biodiversidad local.

**Resumo:** Examinámos como a actividade dos roedores influenciou o destino das sementes de duas espécies de palmeira (*Astrocaryum standleyanum* LH Bailey e *Attalea butyracea* (Mutis ex L.f.) Wess. Boer). Frutos intactos foram colocados em áreas protegidas aos animais em três níveis (solo, no sub-bosque e na copa) e as sementes removidas foram monitorizadas com bobinas de costura anexadas. Registámos 50 eventos de manipulação. A maioria das sementes foram descartados após a retirada do fruto e da sua deglutição, e apenas uma semente foi recolhida no chão. Encontrou-se uma forte associação entre a actividade de manipulação dos frutos e das sementes com as lianas, indicando que as mudanças na abundância de lianas, resultantes da actividade humana, podem influenciar bastante o destino da semente e, portanto, afectar a regeneração da floresta e potencial impacto na biodiversidade local.

**Key words:** *Astrocaryum standleyanum*, *Attalea butyracea*, Panamá, *Proechimys semispinosus*, *Sciurus granatensis*, seed fate.

---

\* *Corresponding Author*; e-mail: tdlambert@frostburg.edu., Present address: Department of Biology, Frostburg State University, Frostburg, MD 21532, USA.

## Introduction

Tropical forests are under increasing pressure from human activities such as farming, logging, hunting, tourism and climate change. While large parks and strictly protected areas are the surest way to preserve this diversity, they are not always practical or feasible. Thus, conservation efforts must manage and mitigate damage in such a way as to minimize ecological damage while simultaneously providing economic and social benefits. These efforts to manage human encroachments into tropical forests and lessen their impacts on biodiversity are often hampered by a lack of knowledge concerning the complex ecological relationships among species that drive the maintenance of tropical diversity (Leigh & Rubinoff 2005). Disturbances such as fragmentation and logging often result in changes to the seed disperser and seed predator communities, which in turn influence seed fate and ultimately forest regeneration (Struhsaker 1997; Terborgh *et al.* 2001). Thus, to develop effective conservation and management schemes, a greater understanding of the factors that influence seed fate is needed.

The reproductive success of many trees is tied to the actions of seed dispersers and seed predators (Connell 1971; Janzen 1970). Small mammal activity can greatly influence seed success. Caching and dispersal increase the distance to conspecifics and may therefore reduce the seed's and seedling's exposure to species-specific pathogens; however, seed predation by those same small mammals also increases seed mortality. Thus, small mammals, especially granivorous rodents, influence forest regeneration and biodiversity (Terborgh *et al.* 2001). Human activity often leads to changes in forest structure such as denser understories, lower and more broken canopies, and increased liana abundance. Such changes in forest structure lead to changes in the small mammal community and to apparent changes in seed predation rates (Adler & Kestell 1998; Asquith *et al.* 1997; Hoch & Adler 1997; Struhsaker 1997; Terborgh *et al.* 2001). This increase in seed predation may lead to an outright suppression of forest regeneration (Struhsaker 1997; Terborgh *et al.* 2001). Despite the perceived importance of small mammals to the maintenance of tropical biodiversity, they remain an understudied group.

This lack of knowledge is especially prominent with respect to the roles played by arboreal small mammals. Considerable research has been con-

ducted in central Panamá on both forest dynamics and the ecological roles of terrestrial small mammals. This work has shown that terrestrial small mammals play important roles in seed and mycorrhizal fungi dispersal and in seed predation (Adler & Kestell 1998; Carvajal & Adler 2008; Hoch & Adler 1997; Mangan & Adler 1999). It is clear from these studies that terrestrial rodents play especially important roles in forest dynamics and regeneration. However, studies have largely ignored arboreal species, which may represent up to 60 % of the small mammal species found in Neotropical forests (Voss & Emmons 1996). Because many arboreal species have diets similar to their terrestrial counterparts (frugivory and granivory), they likely also play a major role in forest dynamics through seed dispersal and predation. Indeed, recent work has demonstrated that arboreal species do in fact remove seeds both from the ground and the canopy and often cache or disperse those seeds (Carvajal & Adler 2008; Flagel *et al.* 2009). Understanding the roles played by arboreal species may be of special importance to conservation and management efforts because arboreal species are often greatly affected by disturbance. Some arboreal species are among the few species known to decline in abundance after disturbance, and the remaining individuals often shift their activities nearer the ground with the corresponding shift in the euphotic zone (Malcolm 1995).

Many arboreal species also show strong habitat associations with lianas (Lambert *et al.* 2006), and recent work has suggested that lianas may be increasing in abundance due to climate change because they hold a competitive advantage in elevated CO<sub>2</sub> environments and under drought conditions (Phillips *et al.* 2002; Schnitzer 2005; Wright *et al.* 2004). An increase in liana abundance combined with continual human disturbance might increase the importance of arboreal small mammals to forest regeneration. In this study, we examined the roles played by arboreal and terrestrial small mammals in relation to habitat structure to better understand how disturbance and climate change may affect forest regeneration.

## Materials and methods

The study was conducted along Pipeline Road in Soberania National Park (9° 10' N, 79° 45' W), a 22,000 ha tract of tropical moist forest in central Panamá. Pipeline Road runs from southeast to northwest and provides access to second-growth

forest that is in various stages of regeneration. Elevation along the road ranges from ca. 40 - 200 m (Karr 1990), and the annual rainfall ranges from a mean of 2188 mm at the southern end of the road to 2685 mm at the northern end (Windsor 1990). Our study was conducted along the first 2 km of Pipeline Road, at the southern end. Forests in this area are young second-growth forest, with canopy heights ranging from ca. 5 - 20 m. The area is highly seasonal and experiences a pronounced four-month dry season from January through April, during which < 10 % of the annual precipitation occurs.

From the beginning of Pipeline Road, we placed two seed-removal stations on either side of the road at ca. 100 m intervals, for a total of ten stations. Each station contained three Tomahawk live traps (40.5 x 12.6 x 13 cm, Tomahawk Live Trap Co., Tomahawk WI, USA) wired open to create semi-permeable enclosures that excluded mammals > 700 g (Flagel *et al.* 2009). Thus, the most likely removal agents were the rodents *Proechimys semispinosus* (Tomes 1860) (Central American spiny rat) and *Sciurus granatensis* (Humboldt 1811) (red-tailed squirrel) (Flagel *et al.* 2009). *Proechimys semispinosus* is nearly exclusively terrestrial (Lambert and Adler 2000), with adults captured on Pipeline Road weighing between 220 and 620 g (mean = 428 g for males and 360 g for females) (Adler *et al.* 1998). *Sciurus granatensis* is arboreal/scansorial and ranges in weight from 212-520 g (Emmons & Feer 1997). A single trap was placed at each of three heights: ground, understory (1 - 3 meters above ground), and canopy (5 - 10 m above ground) (see Flagel *et al.* 2009; Lambert *et al.* 2005a). Each station was placed in an appropriate location for the canopy set and at least 100 m from the center of the road.

We attached industrial sewing bobbins to the intact fruits of two species of large-seed palms (*Astrocaryum standleyanum* (L.H. Bailey) and *Attalea butyracea* (Mutis ex L.f.) Wess. Boer)), which allowed us to track the fate of removed seeds. *Astrocaryum standleyanum* fruits range in length between 2.5 - 6 cm and 3 - 4.5 cm in diameter, whereas *A. butyracea* fruits are at least 4.5 - 8.5 cm long and 3 - 4.5 cm in diameter (Henderson *et al.* 1995). Bobbins were attached by drilling a small hole in one end of the seed, passing a short piece of 0.22 gauge wire through the seed and attaching the other end to the bobbin. Bobbins contained ca. 200 m of tightly-wound thread that unraveled as the seed was moved, thereby allowing us to view the path of removed seeds in three

dimensions. We divided our sampling into two 30-day sessions (18 May to 18 June 2008 for *A. standleyanum* and 18 June to 18 July 2008 for *A. butyracea*), during which time five locally-collected seeds with intact ripe fruits were placed in each enclosure. Enclosures were examined daily, and any overly-ripe, moldy, or removed fruit was replaced. For each removed fruit or seed, we recorded the distance, direction, height above ground of the seed's path, the seed's final location, and the seed's fate (fruit eaten *in situ* and seed intact, fruit eaten and seed cached in the ground, fruit eaten and seed dropped to the ground, and seed eaten). Seeds that were either cached or dropped were further monitored for tertiary dispersal or predation events.

A series of microhabitat variables was measured at (1) each station, (2) each location a seed was cached or dropped, and (3) a random point that was equidistant to the corresponding cached or dropped seed along a randomly determined compass bearing from the station. For these measurements, at each station a center point was established directly below the canopy enclosure or where the seed fell, and four 5 m transects were laid out at 90 angles to each other from that point. Tree size and liana load were determined by measuring the diameter at breast height (dbh) of the closest tree in each of the four cardinal compass directions from the center point and by counting the number of lianas that contacted that tree. Sapling abundance was quantified by counting the number of saplings > 1 m tall and less than 5 cm in diameter within a 3 m radius of the center point. Leaf litter depth was measured at two points along each transect (2.5 m and 5 m), for a total of eight points per location. The number of woody (all woody stems < 1 m tall) and herbaceous stems that directly contacted the transect were counted. All logs that lay directly below the transect line were counted. Using a densiometer, canopy openness was quantified in each of the four cardinal directions at five points (the center point and at the end of each of the transect lines) for a total of 20 densiometer measurements per station.

Data analysis had 2 specific objectives: (1) determine whether locations where seeds were deposited differed in habitat structure from either random points or the stations, (2) evaluate habitat features associated with seed removal. We began by calculating mean values for tree size, liana load, sapling abundance, litter depth, woody stems, herbaceous stems, woody/herbaceous stem ratio, and canopy openness for each station. Because of

the low number of logs encountered, total number of logs was used rather than the mean. Additionally, because the number of seed-handling events was low, we pooled data from *A. standleyanum* and *A. butyracea* in these analyses. We first used canonical discriminant analysis to determine if our habitat variables could differentiate among the 3 locations: stations, random points, and seed locations (dropped or cached). Those habitat variables that were significant in the discriminant analysis were then further examined using ANOVA and a Tukey's multiple comparisons test to determine how the locations differed. To determine if certain habitat features correlated with higher seed removal/seed handling, we used multiple linear regression with stepwise selection (selection for entry = 0.1, selection to stay = 0.05); we examined two dependent variables: (1) total number of seeds moved from a station, and (2) total number of seeds or fruits eaten (without the seed being moved).

## Results

Over the course of the study, 50 fruits or seeds were used by small mammals (15 for *A. standleyanum* and 35 for *A. butyracea*). More seeds were handled in the ground exclosures (39) than in the understory (11) or canopy (0) exclosures. In the majority of cases (48 out of 50), only the fruit was utilized, and the seed was discarded (Table 1). Removed seeds were moved a mean linear distance of 7.8 m (N = 24, S.D. = 7.5) and a maximum of 35 m. Mean removal distance was 15.9 m (N = 7, S.D. = 10.8) for *A. standleyanum* and 4.9 m (N = 17, S.D. = 3.0) for *A. butyracea*. Seeds removed from ground exclosures were moved a mean of 9 m (N = 18, S.D. = 8.2), whereas seeds removed from understory exclosures were moved a mean of 3.5 m (N = 6, S.D. = 1.8). Of the 18 seeds removed from ground exclosures, five were taken into the canopy to a mean height of 5.5 m.

The canonical discriminant analysis separated the three locations in multivariate space (Wilk's Lambda = 0.17,  $p < 0.0001$ ), with two raw variables (mean number of lianas,  $F = 7.58$ ,  $p = 0.0003$ ; and canopy openness,  $F = 22.47$ ,  $p < 0.0001$ ) making significant contributions to this separation. The ANOVA's revealed that locations differed significantly in terms of canopy openness ( $F = 31.10$ ,  $p < 0.0001$ ), with stations having significantly more open canopies than either seed locations or random points (Tukey's HSD,  $p < 0.05$ ). Mean number of lianas also differed among locations ( $F = 11.52$ ,  $p < 0.0001$ ), with seed locations having significantly

more lianas than either stations or random points (Tukey's HSD,  $p < 0.05$ ). Mean number of vines was the only variable retained by stepwise selection in the models for both number of seeds moved ( $F = 60.17$ ,  $p < 0.0001$ ) and the number of fruits eaten in place ( $F = 8.77$ ,  $p = 0.018$ ).

**Table 1.** Fates of handled *Astrocaryum standleyanum* and *Attalea butyracea* fruits and seeds in exclosures placed at 3 heights (ground, understory and canopy) in central Panamá.

Seed Fate	<i>Astrocaryum standleyanum</i>	<i>Attalea butyracea</i>
Fruit eaten <i>in situ</i> , seed intact	7	17
Fruit eaten, seed cached in ground	1	0
Fruit eaten, seed removed and dropped	6	18
Seed Eaten	1	0

## Discussion

While preliminary in nature, our results revealed three important trends. First, arboreal rodents played an important role in seed fate even after those seeds had dropped to the ground (i.e., those seeds in the ground exclosures). Thus, within this younger forest, arboreal rodents frequently descended to the ground to remove seeds and carried those seeds into the canopy, where they were either eaten or dropped to the ground intact. While the number of seed movements was low (25) compared to the number of seeds presented, these movements are still important to the reproductive success of the palms because seeds beneath parents experience nearly 100 % mortality (Harms & Dalling 2000; Wright 1983). The seed movements we observed did place the seeds away from conspecifics, which could decrease their exposure to species-specific pathogens, potentially increasing their chance of survival. However, caching a seed in the ground greatly increases its survival probability; thus, removal by arboreal rodents did not necessarily constitute effective dispersal.

Second, liana abundance had a strong positive influence on handling of fruits and seeds by mammals. Arboreal mammals frequently use lianas as conduits for moving not only within the canopy but also from the canopy to the ground. Indeed, not only did removal rates increase with increasing liana density, but cache and drop locations also had more lianas than did random points. These results indicate that rodent activity

might center on liana-rich locations. Liana abundance increases as the result of the creation of edges through activities such as fragmentation and logging (Lambert *et al.* 2005b; Lovejoy *et al.* 1986), and lianas are suspected of increasing as the result of climate change (Phillips *et al.* 2002; Schnitzer 2005; Wright *et al.* 2004). Our results suggest that liana abundance plays a key role in seed fate. Thus, changes in liana abundance may ultimately lead to further changes in forest structure, as mediated by mammalian influences on forest regeneration.

The associations between seed removal and drop locations and lianas and the near absence of any other microhabitat associations are surprising given that the variables that we selected are known to be important to both terrestrial and arboreal small mammals (Lambert *et al.* 2005b). No other habitat variables were retained in the regressions, and canopy openness was the only other significant variable in the discriminant analysis. Because our study was conducted entirely within younger forest, it is possible that sufficient variation did not exist to manifest relationships between seed-handling activity and the other microhabitat variables. Although we recorded no removal from canopy exclosures in this study, such removals have been found in the study area using similar methods (Flagel *et al.* 2009). Based on known habitat use by arboreal small mammals (Lambert *et al.* 2005b), it is likely that canopy removals would have shown habitat relationships similar to those that we documented for ground and subcanopy removals.

The extent to which changes in liana abundance ultimately affect forest regeneration, forest structure, and the maintenance of biodiversity would be largely determined by the fates of the removed seeds. Our data indicate that of the 50 times rodents fed on the palm fruit, they generally ignored the seed, and only 25 times did they move the seed in the process. Seeds sometimes were moved considerable distances, but of the removed seeds, only one was actually cached, an event thought necessary to prevent future predation and assure regeneration. Otherwise, seeds generally were discarded on the ground, where they would be susceptible to further predation. However, these seeds were moved away from conspecifics, and left available for tertiary dispersal; clearly, the fate of these seeds is not determined solely by these first movements. Nevertheless, our results suggest that despite the removal activity and near absence of seed predation, seed fate was likely not positively

influenced by rodent activity during our study.

Third, our results indicate that our current understanding of the roles of small rodents in seed predation and dispersal is inadequate, as many previous studies have used simple removal rates as indicators of seed predation or dispersal and found much higher removal rates (Adler & Kestell 1998; Flagel *et al.* 2009; Hoch & Adler 1997; Lambert *et al.* 2005b; Terborgh *et al.* 2001). Our data show that even seeds that are moved substantial distances may be ineffectively dispersed, and therefore simple removal is likely not an adequate measure of rodent-mediated seed fate (Carvajal & Adler 2008). Furthermore, studies that have tracked removed seeds found higher predation and caching rates than we did (e.g., Carvajal & Adler 2008). These conflicting results may be reconciled by considering each such study as a snapshot of a brief period of time in one location and by recognizing that rodent abundances, food availability, and consequent seed-handling activity vary temporally and spatially. Of paramount importance is seed fate in relation to per capita fruit availability. Our study was conducted during a period of unusually high fruit abundance and low rodent abundance (GHA & TDL personal observations), while other studies were conducted during periods of higher rodent abundance. Therefore, it is possible that during this resource-rich period, rodents discarded seeds that they normally would have eaten or cached. Our results further indicate that removal alone does not indicate predation or successful dispersal because often when seeds were moved, only the fruit was consumed and the seed was simply discarded and neither cached nor eaten. We were able to document one tertiary dispersal event, indicating that a seed's movements are not always finished after its first displacement. Perhaps as resources become scarcer, interest in both collected and discarded seeds would increase, thereby leading to higher predation and caching rates.

Despite the small size of our data set and the short duration of our study, we were able to document associations between small mammal seed and fruit utilization and liana abundance, indicating that liana-rich microhabitats could greatly influence seed fate and therefore forest regeneration and ultimately the maintenance of tropical biodiversity. Further studies are urgently needed to examine the influence of both arboreal and terrestrial small mammals on seed fates. Such studies should not only quantify removal rates but also track seed fate in a variety of

microhabitats in relation to per capita fruit availability. Particularly interesting would be continual monitoring of discarded seeds to determine how secondary and tertiary predation and caching affect the survival of seeds.

### Acknowledgments

We thank Scott Mangan for providing housing; the Smithsonian Tropical Research Institute for logistical support; Jeremy Wojdak and two anonymous reviewers for their helpful comments; the Government of the Republic of Panamá for the research permit; and the University of Virginia's College at Wise, Amelia Harris, and Eleanore Sturgill for funding the study through the FINS program and Study Abroad scholarship.

### References

- Adler, G.H. & D.W. Kestell. 1998. Fates of Neotropical tree seeds influenced by spiny rats (*Proechimys semispinosus*). *Biotropica* **30**: 677-681.
- Adler, G.H., D.C. Tomblin & T.D. Lambert. 1998. Ecology of two species of echimyid rodents (*Hoplomys gymnurus* and *Proechimys semispinosus*) in central Panamá. *Journal of Tropical Ecology* **14**: 711-717.
- Asquith, N.M., S.J. Wright & M.J. Clauss. 1997. Does mammal community composition control recruitment in Neotropical forests? Evidence from Panamá. *Ecology* **78**: 941-946.
- Carvajal, A. & G.H. Adler. 2008. Seed dispersal and predation by *Proechimys semispinosus* and *Sciurus granatensis* in central Panamá. *Journal of Tropical Ecology* **24**: 1-8.
- Connell, J.H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. pp. 298-312. *In*: P.J. den Boer & G.R. Gradwell (eds.) *Dynamics of Populations*. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Emmons, L.H. & F. Feer. 1997. *Neotropical Rainforest Mammals, A Field Guide*, 2<sup>nd</sup> ed. University of Chicago Press, Chicago, IL, USA.
- Flagel, D., G.H. Adler & T.D. Lambert. 2009. Influence of seed height on removal rates by rodents in central Panamá. *Mammalia* **73**: 76-77.
- Harms, K.E. & J.W. Dalling. 2000. A bruchid beetle and a viable seedling from a single diaspore of *Attalea butyracea*. *Journal of Tropical Ecology* **16**: 319-325.
- Henderson, A., G. Galeano & R. Bernal. 1995. *Field guide to the palms of the Americas*. Princeton Univ. Press, Princeton, NJ.
- Hoch, G.A. & G.H. Adler. 1997. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). *Journal of Tropical Ecology* **13**: 51-58.
- Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**: 501-528.
- Karr, J.R. 1990. The avifauna of Barro Colorado and the Pipeline Road. pp. 183-198. *In*: A.H. Gentry (ed.) *Four neotropical forests*. Yale University Press, New Haven, CT, USA.
- Lambert, T.D. & G.H. Adler. 2000. Microhabitat use by a tropical forest rodent, *Proechimys semispinosus*, in central Panamá. *Journal of Mammalogy* **81**: 70-76.
- Lambert, T.D., J.R. Malcolm & B.L. Zimmerman. 2005a. Variation in small mammal richness by trap height and trap type at a southeastern Amazonian site, with notes on a new method of canopy trapping. *Journal of Mammalogy* **86**: 982-990.
- Lambert, T.D., J.R. Malcolm & B.L. Zimmerman. 2005b. Effects of mahogany (*Swietenia marcophylla*) logging on small mammal communities, habitat structure, and seed predation in the southeastern Amazon basin, with implications for conservation. *Forest Ecology & Management* **206**: 381-398.
- Lambert, T.D., J.R. Malcolm & B.L. Zimmerman. 2006. Amazonian small mammal abundances in relation to habitat structure and resource abundance. *Journal of Mammalogy* **87**: 766-776.
- Leigh, E.G. Jr. & I. Rubinoff. 2005. Understanding and Conserving Tropical Diversity: Perspectives from Barro Colorado Island. pp. 223-250. *In*: E. Bermingham, C.W. Dick & C. Moritz (eds.) *Tropical rainforests: past, present and future*. University of Chicago Press, Chicago, IL, USA.
- Lovejoy, T.E., R.O. Bierregaard, A.B. Rylands, J.R. Malcolm, C.E. Quintela, I.H. Harper, K.S. Brown, A.H. Powell, G.V.N. Powell, H.O.R. Schubart & M.B. Hay. 1986. Edge and Other Effects of Isolation on Amazon Forest Fragments. pp. 257-285. *In*: M.E. Soule (ed.) *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, MA, USA.
- Malcolm, J.R. 1995. Forest structure and the abundance and diversity of neotropical small mammals. pp. 179-197. *In*: M.D. Lowman & N.M. Nadkarni (eds.) *Forest canopies*. Academic Press, San Diego, CA, USA.
- Mangan, S.A. & G.H. Adler. 1999. Consumption of arbuscular mycorrhizal fungi by spiny rats (*Proechimys semispinosus*) in eight isolated populations. *Journal of Tropical Ecology* **15**: 779-790.
- Phillips, O.L., R.V. Martinez, L. Arroyo, T.R. Baker, T. Killeen, S.L. Lewis, Y. Malhi, A.M. Mendoza, D.

- Neill, P.N. Vargas, M. Alexiades, C. Ceron, A. DiFiore, T. Erwin, A. Jardim, W. Palacios, M. Saldias & B. Vinceti. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* **418**: 770-774.
- Schnitzer, S.A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* **166**: 262-276.
- Struhsaker, T.T. 1997. *Ecology of an African rain forest: logging in Kabale and the conflict between conservation and exploitation*. University of Florida Press, Gainesville, FL, USA.
- Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G.H. Adler, T.D. Lambert & L. Balbas. 2001. Ecological melt-down in predator - free forest fragments. *Science* **294**: 1923-1926.
- Voss, R.S. & L.H. Emmons. 1996. Mammalian diversity in neotropical lowland rainforests: a preliminary assessment. *Bulletin of the American Museum of Natural History* **230**: 1-115.
- Windsor, D.M. 1990. *Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panamá*. Smithsonian Institution Press, Washington, DC, USA.
- Wright, S.J. 1983. The dispersion of eggs by a bruchid beetle among Scheelea palm seeds and the effect of distance to the parent palm. *Ecology* **64**: 1016-1021.
- Wright, S.J., O. Calderon, A. Hernandez & S. Paton. 2004. Are lianas increasing in importance in tropical forests? A 17 - year record from Barro Colorado Island, Panamá. *Ecology* **85**: 484-489.