

## Spatial and Temporal Variation of Seed Rain in the Canopy and on the Ground of a Tropical Cloud Forest

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### ABSTRACT

Spatial and temporal patterns of seed rain impact plant fitness, genetic and demographic structure of plant populations, and species' interactions. Because plants are sessile, they rely on biotic and abiotic dispersal agents to move their seeds. The relative importance of these dispersal agents may shift throughout the year. In tropical forests, seed dispersal of epiphytes constitutes a major but hitherto unknown portion of seed rain ecology. For the first time, we report on patterns of seed rain for both epiphytic and terrestrial plants across an entire year in a Neotropical montane forest. To examine seed rain, we placed traps in the canopy and on the ground. We analyzed seed dispersal syndrome (bird, mammal, wind) and plant habit (epiphyte, liana, shrub, small tree, large tree) across all seasons of the year (dry, misty, wet). We found that the community of species collected in canopy traps was significantly different from the community in ground traps. Epiphytes were the most common plant habit found in canopy traps, while large trees were most common in ground traps. Species with bird-dispersed seeds dominated all traps. Species richness was significantly higher during the dry season in ground traps, but did not vary across seasons in canopy traps. Our results highlight the distinct seed rain found in the canopy and on the ground and underscore the importance of frugivores for dispersing both arboreal and terrestrial plants in tropical ecosystems.

Abstract in Spanish is available in the online version of this article.

*Key words:* arboreal plants; biodiversity; Costa Rica; epiphytes; montane forest; Monteverde; seed dispersal; tropics.

### INTRODUCTION

SEED DISPERSAL, THE MOVEMENT OF SEEDS AWAY FROM THE PARENT, is a critical stage in the life cycle of plants. Successful dissemination of seeds can lead to escape from pathogens and predators near the parent tree (Janzen 1970, Connell 1971, Terborgh 2012), deposition in sites more favorable for germination (Wenny & Levey 1998), and establishment in new areas (Howe & Smallwood 1982). If seeds are deposited in locations not conducive to germination and growth, then the investment of energy and nutrients in those propagules is lost. Thus, seed dispersal can increase germination of seeds, survival and recruitment of seedlings, and ultimately, plant fitness.

Plants rely on both biotic (*e.g.*, birds, mammals) and abiotic (*e.g.*, wind, gravity, water) vectors to disperse their seeds. The relative importance of these vectors for seed dispersal can vary across space (Moles *et al.* 2007) and time (Culot *et al.* 2011). In tropical forests, the majority of plants rely on animals to disperse seeds (Jordano 2000), whereas in temperate forests, most plants rely on wind (Moles *et al.* 2007). The relative importance of seed vectors for dispersal can also shift seasonally because changes in the diet and breeding behavior of animals can alter their effectiveness as dispersers at different times of the year (Van Schaik *et al.* 1993, Culot *et al.* 2011).

With the exception of mistletoes (Okubamichael *et al.* 2011) and figs (Laman 1996), most research on seed dispersal in forests has

focused on plants that germinate and establish on the forest floor (*e.g.*, Loiselle *et al.* 1996, Wenny & Levey 1998, Clark *et al.* 2005). Yet, unique communities of plants—vascular and non-vascular epiphytes and vines—complete part or all of their life cycle in the forest canopy (Hirata *et al.* 2009), and these communities reach their greatest diversity in tropical cloud forests (Nadkarni *et al.* 2001).

In addition to their remarkably high biodiversity, plants in tropical canopies play important functional roles in the forest ecosystem. They intercept and retain atmospherically delivered water (Clark *et al.* 1998) and nutrients (Diaz *et al.* 2010), provide specialized habitat for arboreal and terrestrial fauna (Ozanne *et al.* 2003), and increase primary productivity and carbon sequestration of the forest (Diaz *et al.* 2010). Thus, a complete understanding of tropical forest dynamics must include both terrestrial and arboreal plants.

Importantly, the communities of seeds landing in the canopy and on the ground may be distinct. True epiphytes germinate and survive only in the forest canopy, while ground-rooted, terrestrial plants germinate and establish only on the forest floor. As a result, we might expect selection on epiphytic and terrestrial plants for seeds that are dispersed to sites where they can establish, the canopy and the forest floor, respectively. Yet, field studies documenting seed rain for entire communities of plants, especially in tropical forests, are few due to the difficulty of identifying seeds (Laman 1996, Clark *et al.* 2005). To our knowledge, no study has ever documented seed rain deposited in both the canopy and on the ground for any ecosystem.

Here, we report patterns of seed rain in the canopy and on the forest floor of a tropical montane cloud forest across an

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entire year. Our aim was to compare seed rain patterns in canopy and ground traps, and to describe these patterns in relation to seed dispersal syndrome, season and plant characteristics. We use the term 'arboreal' to refer to obligate epiphytic plants and vines, and 'terrestrial' to discuss plants that first root in the ground (Nadkarni & Haber 2009). We examined how species richness, seed number, and plant traits (seed dispersal syndrome, plant type, and plant habit) varied across space (canopy vs. ground) and time (season).

## METHODS

**STUDY SITE.**—Monteverde cloud forest preserve (MCFP) is a protected area on the Pacific slope of the Cordillera de Tilarán in the Republic of Costa Rica ( $\sim 10^{\circ}20' \text{ N}$ ,  $84^{\circ}45' \text{ W}$ ). Our field site was located in undisturbed primary forest ranging in elevation from 1450 to 1480 m asl. The area has three seasons: (1) the wet season (May–October) has clear skies in the morning, rainfall during the afternoon, and mean monthly precipitation  $>250$  mm, (2) the transition, or misty-windy season (November–January), has strong winds with mist occurring during the day and night, and (3) the dry season (February–April) has moderate winds and mean monthly precipitation  $<50$  mm (Clark *et al.* 1998).

Fruit production of large trees in Monteverde is highest from September to January and lowest from June to August, although at least 30–40 tree species are fruiting each month of the year (Haber 2000). Shrubs and small trees are less seasonal in their fruiting patterns, although the majority produce fruit in a similar pattern to large trees in Monteverde (Koptur *et al.* 1988). The most common frugivorous mammals in Monteverde include bats, monkeys, coatis, and many species of rodent (*e.g.*, agoutis, squirrels, mice) (see Timm & LaVal 2000). An extensive list of bird frugivores and their food plants from the area is given in Wheelwright *et al.* (1983).

**SEED RAIN SAMPLING.**—We set seed traps on both the forest floor ('ground traps') and in the branches of mature trees ('canopy traps'). Traps consisted of  $50 \times 50 \times 5$  cm black plastic trays with holes in the bottom to allow drainage. The trays were lined with a square piece of nylon fabric. At the end of each trapping period, we lifted the fabric lining and seeds from the tray and placed them in a plastic bag for later sorting in the laboratory. We then placed a clean fabric lining into the tray to capture new seeds.

For the placement of canopy traps, we chose eight mature trees of *Ocotea tonduzii* (Lauraceae) on the basis of their size (diameter at breast height [dbh] of 60–120 cm), height (23–24 m), and our ability to safely climb into the canopy. *Ocotea tonduzii* is a dominant species in the study site, covering more than 30 percent of the basal area of trees with a dbh  $\geq 2$  cm (Ingram & Nadkarni 1993). The eight trees we chose occurred within a 4-ha study plot and trees were separated by at least 15 m from the next nearest sample tree. We used the same tree species for all canopy traps to avoid confounding effects of tree species on visitation of seed dispersers. In each tree, we set between two and

four traps ( $N = 28$ ), with each trap placed on a different branch within 0–3 m of the tree trunk and 19–23 m above the forest floor, which placed them in the mid-canopy of the supporting tree. *Ocotea tonduzii* produce fruit from April–August with the peak in May–July (Wheelwright 1986), and 18 species of birds have been observed feeding on their fruit (Wheelwright *et al.* 1983).

We located up to four positions under each of our sample trees to place ground level seed traps ( $N = 27$ ). Within the crown projection (drip line) of each tree, we generated random cardinal directions and distances from the trunk (3–7 m) to place our traps. If the sample point was under a fallen trunk or large branch, we moved it to the closest, cleared site on the forest floor. Ground traps were of the same dimensions as those of canopy traps, and were suspended on wire frames to hang ca. 20 cm above the forest floor to exclude seed predators.

We collected seeds from traps at the end of each month for an entire year (August 1997–July 1998). We brought seeds back to the laboratory, air-dried them, sorted them by species, and counted the total number. To identify seeds, we drew upon previous work on seed bank composition in Monteverde in which researchers germinated seeds in a greenhouse to identify plants and create a voucher seed collection (Harvey 2000). We assigned seeds to plant type (arboreal or terrestrial), seed dispersal syndrome (bird-, mammal-, or wind-dispersed), and plant growth habit (epiphyte, liana, shrub, small tree [ $<10$  m] or large tree [ $\geq 10$  m]), using the updated Monteverde plant list (Haber 2000, updated 2008) and the Tropicos Project data base from the Missouri Botanical Garden (<http://www.tropicos.org/>). Hemi-epiphytes, plants that germinate in the canopy and then grow roots down to the ground (*e.g.*, *Ficus*), were classified as arboreal rather than terrestrial because they begin their lives in the canopy (Putz & Holbrook 1986). When plant species had more than one type of dispersal syndrome ( $\sim 6\%$  of plants), we used the primary disperser (*i.e.*, the most commonly observed as listed in Haber 2000) for classification (Nadkarni & Haber 2009). For growth habit, we combined both large- and medium-sized trees into the category 'large trees' because their branches were located above the canopy traps. Thus, their fruits and seeds could land in the canopy traps due to passive dispersal (*e.g.*, gravity). In contrast, the upper branches of small trees were lower than the canopy traps and thus, fruits of small trees could only land in the canopy traps via upward movement into the traps (*e.g.*, bird-dispersed). For seeds contained within fruits ( $<3\%$  of trap contents), we counted the fruit, not the seeds within the fruit. Following Nadkarni and Haber (2009), we combined herbs and shrubs for data analysis.

Our count of species did not include plants with extremely small seeds, or 'dust seeds' (length  $<0.2$  mm; Martin 1946). Dust seeds, which are typically wind-dispersed, are common in some arboreal plant families (*e.g.*, Orchidaceae), but are notoriously difficult to detect and track (Rasmussen & Whigham 1993). Although present in our study system, we were unable to detect and include dust seeds in our counts, so wind dispersal is underestimated in this study.

**DATA ANALYSIS.**—One of our goals was to examine the relationship between dispersal syndrome and the number of species and seeds deposited in our traps. Thus, we excluded from our analyses seeds whose dispersal syndromes are unknown because either we do not know enough about the natural history of the plant to classify dispersal syndrome or we could not identify the plant. We combined data from traps within each individual tree to avoid pseudoreplication as a disperser could remain in a tree and contribute seeds to more than one trap during a single visit. Thus, each tree was considered a replicate ( $N = 8$ ) and we averaged the number of seeds and species each month across all traps in each tree. After the numbers of seeds and species in traps of each tree were averaged, we assigned  $N = 8$  unique trap numbers (*i.e.*, one trap number for each of the four pooled and averaged traps associated with each of our eight focal trees) that could be used as blocking factors (random effect) in data analysis.

We separated data into three seasons following Clark *et al.* (1998); dry, misty, or wet. Because some seasons encompass more months than others, we analyzed species and seed number as monthly averages for each season.

We analyzed the factors that best predicted species richness for both trap types combined (canopy and ground) as well as within each trap type (canopy or ground). For the analysis of both trap types combined, we examined if species richness was best explained by dispersal syndrome, season, trap type or an interaction of these factors using linear mixed-effects (LME) models in R (R v. 2.11.1, R Development Core Team 2010). We included seed dispersal syndrome (bird, mammal, or wind), season (dry, misty or wet), and trap type (ground or canopy) as fixed effects and trap number as a random effect to account for the non-independence of traps.

For the analysis within each trap type, we included the fixed effects of seed dispersal syndrome, season and their interaction, and the random effect of trap number to examine the factors that best explained species richness. All models included a Poisson error distribution, as we did not detect overdispersion in the data, and were fit using maximum likelihood estimation. We used Akaike information criterion (AIC) values to choose the best-fit model (Burnham & Anderson 2004) and the difference in AIC values between the null model and the best-fit model to indicate the strength of the relationship ( $\Delta$ AIC). We performed model simplification using likelihood ratio tests between models to test relative fit ( $p$ ) (Crawley 2007). When two models were not significantly different, we chose the best-fit model based on parsimony (*i.e.*, fewest parameters).

Next, we tested whether the contribution of plant species to canopy and ground traps was significantly different among dispersal syndromes and among seasons. Using multiple comparisons (R, multcomp package for simultaneous inference), we tested for significant differences in species richness in canopy and ground traps based separately on season and dispersal syndrome.

Finally, to assess differences in the plant communities represented by seeds in canopy and ground traps, we used non-metric multidimensional scaling (NMS) ordination with a Bray-Curtis (Sørensen) dissimilarity metric in R (package: vegan). We used

presence/absence data for species in the traps, and differences between species in canopy and ground traps were determined with multiresponse permutation procedures (MRPP). MRPP provides a test for assessing if there is a significant difference between groups of sampling units (Mielke 1991).

## RESULTS

We collected a total of 80,040 seeds from 136 species in 47 families. Of the species we identified, 44 (32%) were arboreal species and 92 (68%) were terrestrial species. The total seed count included 21,591 seeds (27%) from arboreal plants and 58,449 seeds (73%) from terrestrial plants. Because we removed seeds from species with unknown dispersal syndromes, we had 78,494 seeds from 116 species and 43 families for our data analysis. Of the species included in the analysis, 35 (30%) were arboreal species and 81 (70%) were terrestrial. The most speciose plant families were Asteraceae (11 species), Solanaceae (10 species), Rubiaceae (9 species) Ericaceae (8 species), Araceae (7 species), and Melastomataceae and Piperaceae (6 species each). The wind-dispersed species *Weinmannia wercklei* (Cunoniaceae) contributed the greatest number of seeds to the traps with a total of 27,636 seeds (35% of the total).

The majority of species captured in both ground (66%) and canopy (83%) traps were bird-dispersed (Fig. 1). The growth habit of species differed between canopy and ground traps (Fig. 2); epiphytes were the most common habit of plants collected in canopy traps (39%), whereas large trees were the most common in ground traps (38%). Twenty-three animal-dispersed species of shrubs and small trees were moved upward into canopy traps.

Seed counts showed similar patterns to species counts, with seeds of epiphytes most abundant in canopy traps and seeds of large trees most abundant in ground traps (Fig. S1). The greatest number of wind-dispersed seeds collected in ground traps was during the misty season; however, bird-dispersed seeds dominated both canopy and ground traps during all other seasons (Fig. S2).

We examined the factors that best predict species richness for both trap types combined (canopy and ground) as well as within each trap type (canopy or ground). For the combined analysis, the most parsimonious model that explained species richness included trap type, dispersal syndrome, season, and the interaction of dispersal syndrome and season (Table S1;  $P = 0.32$ ). Within canopy traps, species richness did not vary across seasons (Fig. 3; Table S2;  $P \geq 0.1$ ); thus, the most parsimonious model that best predicted species richness included only dispersal syndrome of the seed (Fig. 1; Table S3;  $P = 0.47$ ). Within ground traps, species richness was significantly higher during the dry season compared with the misty season (Fig. 3; Table S2;  $P = 0.03$ ) and was best explained by dispersal syndrome, season, and the interaction of dispersal syndrome with season (Table S4;  $P < 0.001$ ).

Based on NMS ordination, community composition of species collected in canopy and ground traps was significantly different (Fig. 4;  $A = 0.08$ ;  $P < 0.0001$  based on 999 permutations).

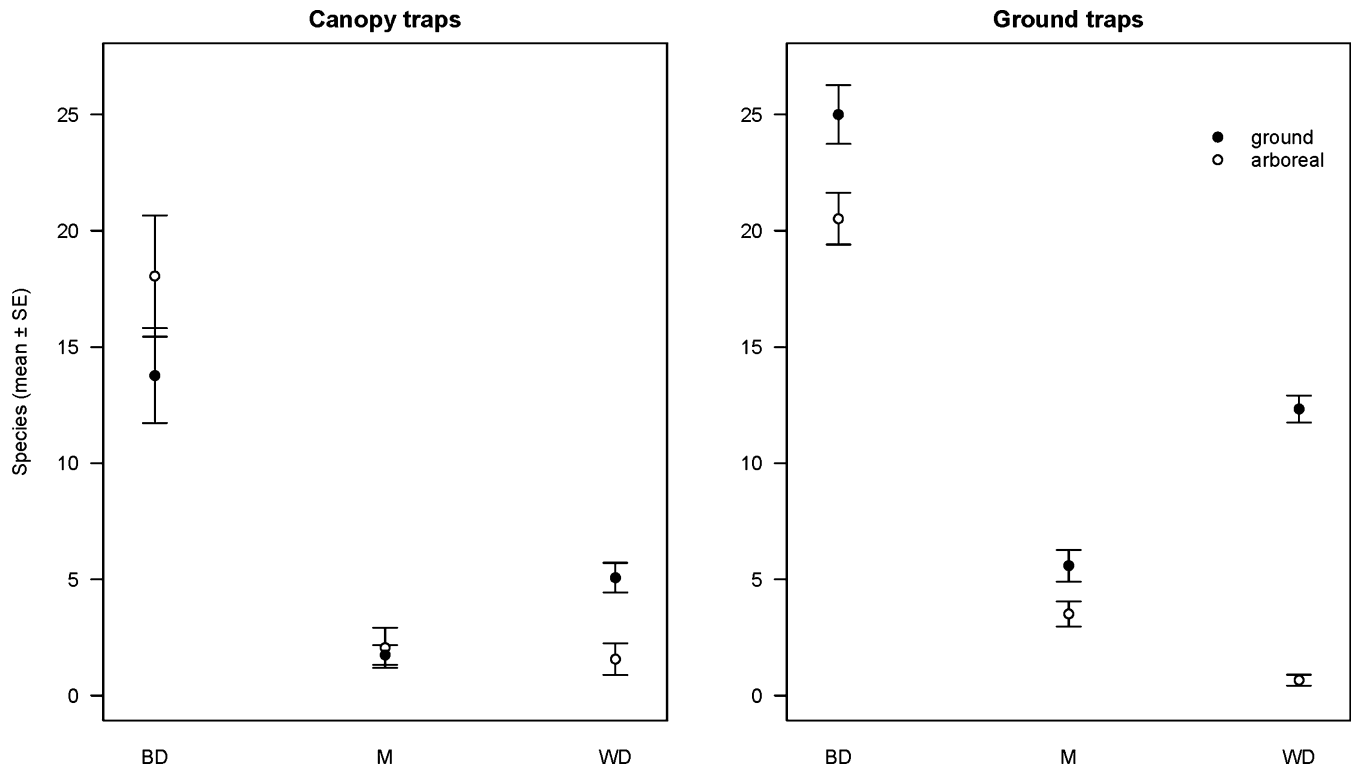


FIGURE 1. Number of species (mean ± SE) of bird- (BD), mammal- (M) and wind- (WD) dispersed plants in canopy and ground traps. Black circles represent terrestrial plants and white circles represent arboreal plants.

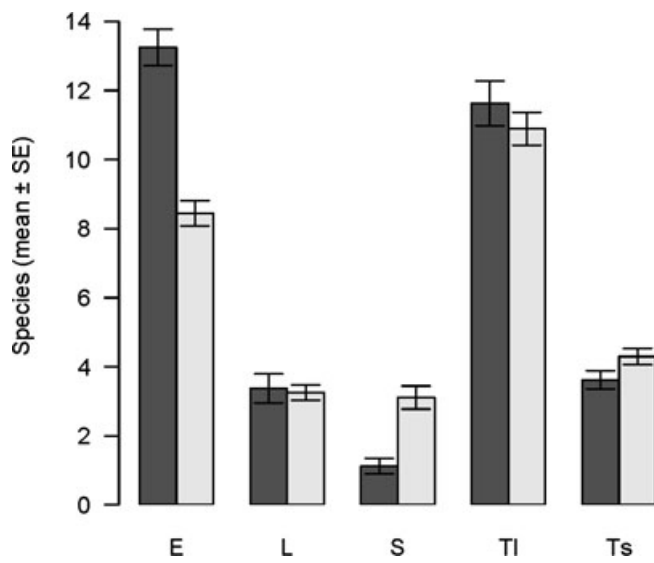


FIGURE 2. Number of species (mean ± SE) in canopy (dark gray) and ground (light gray) traps by growth habit. Growth habits include epiphytes (E), lianas (L), shrubs (S), large trees (TI) and small trees (Ts).

Although many species were found in both canopy and ground traps (47%), more than half of the species were found only in ground traps (43%) or canopy traps (10%) (Table S5). Thus, while the importance of birds as dispersal agents is similar

between trap types, the species composition collected in traps was unique.

## DISCUSSION

The timing and location of seed deposition are critical for seed germination, seedling survival and, ultimately, plant fitness (McConkey *et al.* 2011). In wet tropical forests, seed germination occurs not only in ground soils, but also in canopy soils, which support a diverse community of arboreal plants. Our study is the first to examine seed rain in both the canopy and on the ground for any ecosystem. The ordination revealed that the community composition of species collected in canopy traps was significantly different from that collected in ground traps (Fig. 4). Based on our data, epiphytes were the most common species in canopy traps and occurred in canopy traps in significantly greater numbers than in ground traps (Fig. 2), suggesting that dispersal agents are effectively moving epiphyte seeds to locations where they can establish. Dispersal syndrome of seeds was a significant predictor of species richness in both canopy and ground traps. We also found an interaction between dispersal syndrome and time of year for species richness in ground traps. More bird-dispersed species occurred in ground traps in the dry and wet seasons compared with the misty season. Mammal-dispersed species were the least common of all dispersal syndromes found in traps during the dry and misty seasons, but more common than wind-dispersed species during the wet season. This suggests that the

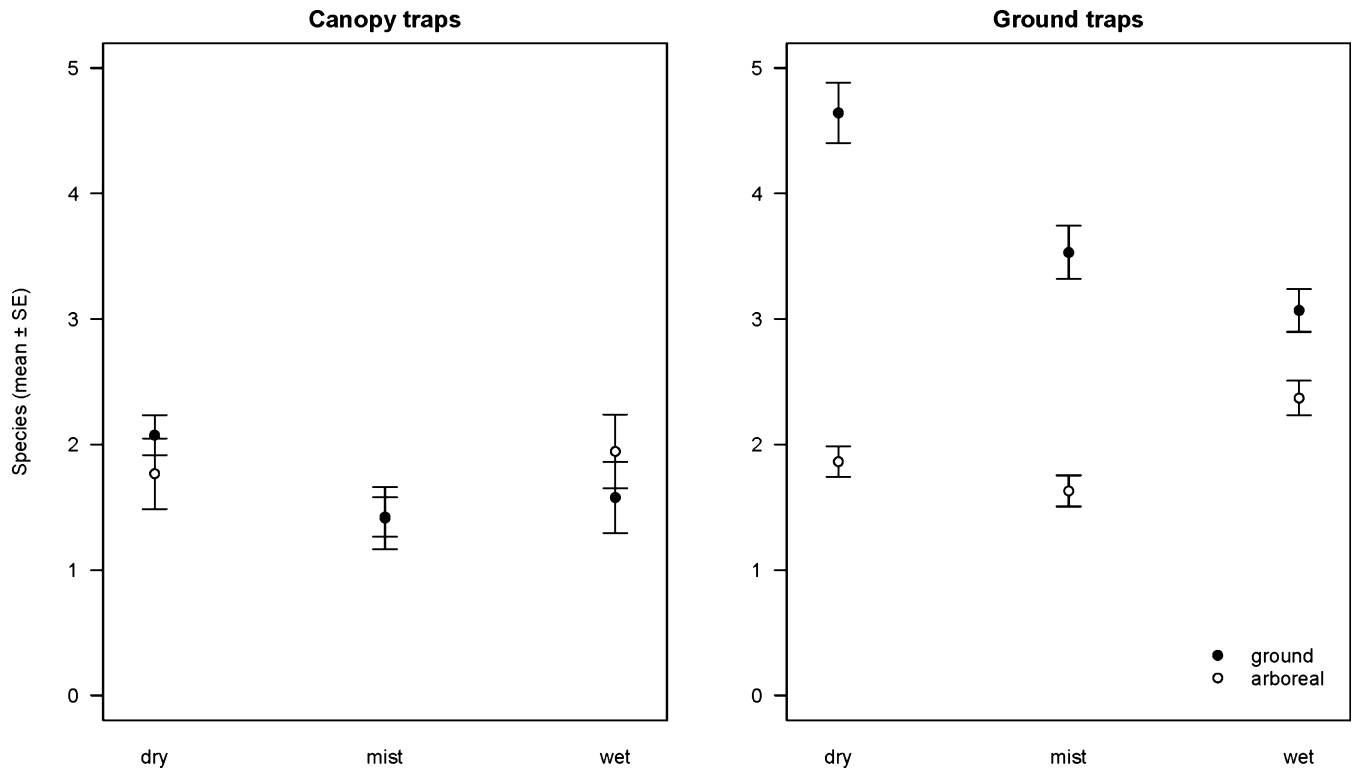


FIGURE 3. Number of species (mean  $\pm$  SE) in canopy and ground traps by season. Black circles represent ground plants and white circles represent arboreal plants. For each trap, species number was averaged across months within a season.

importance of dispersers may shift with seasons in one component of the forest (*i.e.*, ground), but not another (*i.e.*, canopy).

From a plant's perspective, all dispersers are not created equal: some dispersers deposit seeds in non-random locations that are particularly favorable for survival (Wenny & Levey 1998). Known as 'directed dispersal' (Howe & Smallwood 1982, Briggs *et al.* 2009), movement to favorable locations can increase seed germination, seedling survival, and plant fitness (Wenny & Levey 1998). Our data on seed rain suggest that directed dispersal of arboreal plants may occur for two reasons. First, the community of species in canopy traps was significantly different from the community in ground traps (Fig. 4). If seeds were deposited in random locations, we might expect greater overlap in these communities. Second, epiphytes, most of them bird-dispersed, accounted for the majority of species and seeds dispersed into canopy traps, whereas large trees accounted for the majority dispersed into ground traps (Figs. 2 and S1). This suggests that seeds of arboreal and terrestrial plants are actively dispersed rather than passively falling into traps as they might be just as likely to fall into either type of trap.

Although our data provide evidence that directed dispersal may occur in the canopy, arboreal seeds could land in canopy traps simply as a product of proximity—canopy traps are positioned closer than ground traps to arboreal plants. In addition, canopy traps might intercept arboreal seeds before they can land in ground traps. Yet, in tropical forests, we might expect strong

selection for directed dispersal for two reasons. First, following dispersal, seeds of some tropical rain forest plants do not remain viable for long periods of time (Vázquez -Yanes & Orozco-Segovia 1993, Baskin & Baskin 1998). Even the seeds of pioneer species can have relatively short periods of dormancy (Alvarez-Buylla & Martínez-Ramos 1990). Seeds that do have a period of dormancy could fall victim to attack by predators and pathogens that are active year-round (Dalling *et al.* 1998). Thus, the lack of long-term viability for some seeds and the abundance of seed predators and pathogens suggest that arrival in a location where a seed can germinate quickly is critical for seedling establishment of many tropical plants (Vázquez -Yanes & Orozco-Segovia 1993).

Second, in tropical forests, the community of arboreal plants shows little overlap in species composition compared with the community of terrestrial plants (Nadkarni *et al.* 2001). Despite this lack of overlap, seeds of terrestrial plants are found in canopy soils (Nadkarni & Haber 2009) and *vice versa*. Thus, differences in species composition between canopy and ground communities may not be due to a limitation on seed deposition, but may be due to a limitation on germination and survival when terrestrial and arboreal seeds fail to land on the ground or in the canopy, respectively. Given the lack of overlap in species composition of terrestrial and arboreal plant communities, we might expect selection for directed dispersal in tropical plants.



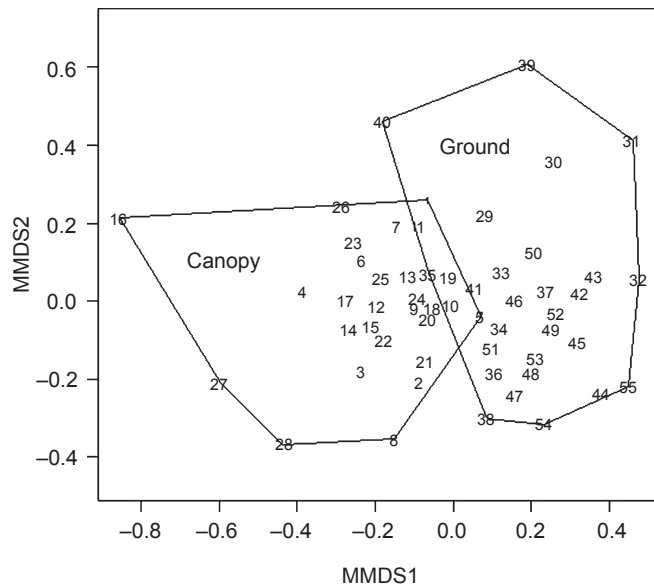


FIGURE 4. Non-metric multidimensional scaling (NMS) ordination based on species collected in canopy and ground traps. The NMS figure is derived from a Bray-Curtis dissimilarity matrix clustered at 80 percent similarity. Numbers represent traps from the canopy and ground.

Even with extensive, year-round sampling, our study had several limitations. First, sampling across only one year in this system may not be representative of long-term patterns, given that many plants have high annual variation in seed production, sometimes fruiting at 2-year intervals (Wheelwright 1986, Wright *et al.* 2005). Second, our methods did not allow us to adequately sample dust seeds, thereby underestimating the relative importance of wind dispersal in this system. We collected wind-dispersed seeds from four arboreal species compared with twelve terrestrial species. Yet, dust seeds are common in the plant family Orchidaceae, a speciose group whose members are primarily arboreal (Martin 1946, Benzing & Atwood 1984). Thus, documenting the role of wind-dispersed seeds remains an opportunity ripe for future research. Third, when a plant had more than one type of disperser (*e.g.*, bird- and bat-dispersed), we classified the dispersal syndrome using the most commonly observed disperser (following Haber 2000). Although multiple dispersers occurred in only six percent of our plants, this could inflate the number of bird-dispersed seeds as avian studies of fruit dispersal are more common than other vertebrate studies. Finally, our methods were not able to capture secondary seed dispersal or seed predation, both of which could alter patterns of plant regeneration and community structure (*e.g.*, Youngsteadt *et al.* 2009, Culot *et al.* 2011) and could alter the patterns we observed in our traps.

Our study design could have biased our results toward bird-dispersed seeds for two reasons. First, seeds dispersed by terrestrial mammals, such as pacas and agoutis, could not arrive in our traps, potentially biasing our results to favor seeds dispersed by birds. Second, we set canopy traps in only a single

species of tree, *O. tonduzii*. Because birds disperse the fruits of *O. tonduzii*, the trees may have attracted more frugivorous birds than a random set of tree species, potentially increasing the abundance and diversity of bird-dispersed seeds arriving in traps. We cannot rule out this possibility because, based on our results, the time of fruit availability of *O. tonduzii* coincides with the time when the greatest number of bird-dispersed seeds arrived in our traps.

Despite these limitations, our study provides valuable insights into seed rain that might aid in tropical forest conservation. Previous research has shown animal-dispersed species are less vulnerable to forest loss compared with wind-dispersed species (Montoya *et al.* 2008). Because the majority of plant species in the tropics are animal-dispersed, tropical forests may be resilient to perturbations if appropriate animal dispersers are present. In tropical ecosystems, birds are one of the most important seed dispersers (Loiselle *et al.* 1996, Jordano 2000). Birds are also one of the most threatened groups on the planet, with more than 2000 species facing extinction by the year 2100 (Sekercioglu *et al.* 2008). Extinctions due to land conversion (Jetz *et al.* 2007) and climate warming (Sheldon *et al.* 2011, Urban *et al.* 2012) are expected to be particularly high in the tropics. The loss of frugivorous birds could disturb seed dispersal mutualisms, decreasing regeneration and altering community structure of plants (Wotton & Kelly 2011).

Given the number of animal-dispersed seeds in traps, the patterns we have identified underscore the importance of maintaining viable populations of vertebrate dispersers for arboreal and terrestrial plant species. More extensive sampling is needed to elucidate the processes and mechanisms leading to differences in species composition in the ground and canopy. Our experimental design did not factor in the spatial arrangement of plants surrounding each trap. This information would be particularly useful in parsing out the proportion of seeds in traps that were due to active versus passive dispersal. Future studies would also benefit from multi-year comparisons of seed rain under varying tree species, and an examination of the importance of secondary seed dispersal and seed predation in similar systems. Aside from mistletoe, directed dispersal has not been demonstrated in arboreal plants. Thus, research on the prevalence of directed dispersal in the canopy would be an important step toward understanding the consequences of dispersal patterns for plant regeneration and community dynamics in tropical forests.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. Results from linear mixed-effects models for factors that best predict species richness in both trap types.

TABLE S2. Multiple comparisons of species richness in canopy and ground traps for season and dispersal syndrome of seeds.

TABLE S3. Results from linear mixed-effects models for factors that best predict species richness in canopy traps.

TABLE S4. Results from linear mixed-effects models for factors that best predict species richness in ground traps.

TABLE S5. List of plant species collected in traps.

FIGURE S1. Number of seeds in canopy and ground traps by growth habit.

FIGURE S2. Seed number by disperser and season for canopy and ground traps.

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